JOURNAL OF
Pacific
Archaeology

– ARTICLE –

Minding the Gaps –

15 more years of rethinking Polynesian origins

Elizabeth Matisoo-Smith[1*], Brooke L. Whitelaw[2], Catherine J. Collins[3] and Anna L. Gosling[4*]

[1]Dept of Anatomy, Faculty of Biomedical Sciences, University of Otago; ORCID 0000-0002-3500-8307
[2]Dept of Anatomy, Faculty of Biomedical Sciences, University of Otago; ORCID 0000-0002-5555-4612
[3]Dept of Anatomy, Faculty of Biomedical Sciences, University of Otago; ORCID 0000-0002-2811-1496
[4]Dept of Anatomy, Faculty of Biomedical Sciences, University of Otago; ORCID 0000-0003-3151-3346

*Corresponding authors: lisa.matisoo-smith@otago.ac.nz; anna.gosling@otago.ac.nz

Abstract

Addison and Matisoo-Smith (2010) challenged the widely accepted model regarding the settlement history of Polynesia, specifically the Lapita only origin of East Polynesia, and identified possible drivers for the resumption of the eastward expansion of Pacific peoples around 1500 BP. In the last 15 years, there have been some significant advances in our understanding of the events that have led to the biological, cultural and linguistic variation we currently see in the Pacific. Here we will review the evidence, particularly the genetic and genomic evidence, related to Pacific settlement history that has accumulated since the publication of Addison and Matisoo-Smith. We then fully investigate these genomic data to see if we are any closer to understanding and reconstructing Pacific settlement history, and to identify any gaps that still exist.

Keywords: Lapita; Triple-I model; mitogenomes; ancestry; genetic variation

To cite this article:
Matisoo-Smith, E., Whitelaw, B.L., Collins, C.J., and Gosling, A.L. 2026. Minding the Gaps – 15 more years of rethinking Polynesian origins. Journal of Pacific Archaeology, 16(2): Article 3:1-22. DOI: https://doi.org/10.70460/jpa.v16i2.396

Submitted: 03/12/2025, Accepted 05/02/2026, First online 25/03/2026

The Journal of Pacific Archaeology is a peer-reviewed open access journal published by the New Zealand Archaeological Association

1. Introduction

In 2010 Addison and Matisoo-Smith published a paper entitled "Rethinking Polynesians Origins: a West-Polynesia Triple-I model". The premise of this paper was that what was, and to some degree still is, the consensus view regarding the origins of Ancestral Polynesian Society (APS), did not adequately explain the archaeological and biological data that existed for Polynesia as a whole. Specifically, the paper challenged the "Lapita only" model for Polynesian origins – or the idea that Polynesian peoples, languages and cultures were solely derived from the Lapita peoples who settled Samoa and Tonga nearly 3000 years ago. The authors proposed that there were new and significant influences from elsewhere, that were introduced and then amalgamated with the Lapita-derived components already present in West Polynesia. This new Polynesian culture/biology was then carried out into the rest of Polynesia when eastward expansions began again, which we now believe to have been around AD 900 (Sear et al., 2020). This process, they suggested, might be very similar to that described by Roger Green (1991) in his Triple-I model for Lapita origins, namely that the Lapita Cultural Complex was the result of *intrusion* of new biological, cultural and linguistic components from Island Southeast Asia, *integration* of these with indigenous components already present in the Bismarck Archipelago, and *innovation* of new unique components that were then transferred to descendant communities in Near and Remote Oceania. Similarities between cultural and biological components seen in Micronesia and East Polynesia led to the suggestion that "intrusive" post-Lapita migration(s) through the atoll arc into Polynesia might help explain the patterns observed.

The assessment of the genetic data at the time of writing was a significant part of Addison and Matisoo-Smith's critique of the Lapita only model for Polynesian origins. But things have changed dramatically in the last fifteen years with the development of next generation sequencing (NGS) (Millar et al., 2008). The price of whole genome sequencing has reduced substantially with the ability to process large numbers of samples simultaneously. Data generated by large international genome diversity projects such as the 1000 Genomes Project (https://www.internationalgenome.org/) and the Simons Genome Diversity Project (Mallick et al., 2016) has meant that there are now large databases of single nucleotide polymorphisms (SNPs) identified from worldwide populations. This has allowed for the development of a number of commercially available (and some non-commercially available) SNP arrays (tools for genome wide screening of samples) to quickly assess the presence of ancestry informative SNPs in a population. Unfortunately, however, few Pacific samples have been included in the databases that were used to establish these SNP arrays and therefore we do not know that we are capturing all of the important variation that exists in the Pacific. Furthermore, genomic studies that only include small sample sizes (possibly not representative of the entire population) or apply simplistic settlement models that do not take into consideration archaeological or other historic or cultural data that we know could be affecting the populations can result in interpretations that don't align with the likely history of that population. Such studies will continue to be problematic regardless of how good the genomic data might be and thus we have argued elsewhere for strong interdisciplinary approaches with specific hypothesis testing and generation of appropriate data with full community engagement and consent (Matisoo-Smith & Gosling, 2018, 2025).

This NGS technology has also been transformational for ancient DNA studies particularly when combined with developments in ancient DNA sampling and extraction (Hofreiter et al., 2015; Pinhasi et al., 2015). A huge advantage is that contamination, which was a major issue for ancient DNA studies prior to the development of NGS, can now be identified and the reliability of ancient DNA can be assessed through indicators of typical damage that occurs (Gilbert et al., 2007). Another major development in aDNA studies is the targeted sampling of the petrous portion (inner ear) of crania, which has been shown to be particularly good for DNA preservation (Pinhasi et al., 2015). As a result of these relatively recent developments, the amount of genomic data that are now available for Pacific populations had increased significantly and is contributing to debates regarding Pacific origins and population histories. These new genomic data, linked to particular points in time and often to specific cultural contexts, provide the chronological control to assess genetic change through time and help us to interpret the genomic variation we see in modern Pacific populations. It is therefore, perhaps, a good time to reassess our models of Pacific settlement in general and the West Polynesian Triple I model in particular and identify any gaps that still exist in our understanding of Pacific settlement.

2. Lapita and the origins of Polynesians

While there was a strong consensus for the Lapita only model of Polynesian origins and the associated notion of East Polynesian origins lying in Samoa, Addison and Matisoo-Smith were not the only ones who identified elements that did not fit with such a model. Anita Smith, in her monograph on the archaeology of West Polynesia, also argued that there was no evidence of socio-cultural change in West Polynesia (the development of APS) prior to 1000 BP and that the archaeological evidence did not support the direct link between East Polynesian material culture and a Lapita derived West Polynesian source. (Smith, 2002). McLean (McLean, 2008) suggested that the music and musical instruments of East Polynesia were significantly different from those of West Polynesia as to indicate an alternative origin and noted similarities with Micronesia. Similarly, Wilson (1985) initially challenged the notion that East Polynesian languages were derived from Samoan, but instead he highlighted similarities between the Central Northern Outlier (CNO) languages of Takuu and Luangiua (Ontong Java), located off the north coast of the Solomon Islands, with those of East Polynesia (EPN). In further analyses (Wilson, 2012, 2014, 2018, 2021), Wilson strengthened his argument claiming these CNO languages and those of East Polynesia form a subgroup, and proposed a hypothesis where the settlement of East Polynesia occurred from the Central Northern Outliers (Nukuria, Takuu, Nukumanu and Ontong Java), through the Phoenix and Line Islands (Kiribati) into the Marquesas and from there into the rest of Polynesia. He further claimed "(t)he shared innovations of PCNO-EPN stand in stark contrast to the lack of comparable linguistic data supporting the commonly assumed settlement of East Polynesia along a southern pathway originating in Samoa or in Western Polynesian archipelagos relatively close to Samoa such as Tokelau or Tuvalu" (Wilson, 2012:355).

3. Genomic studies of modern Polynesians

Wilson's linguistic proposal for East Polynesian origins has recently received support from the genomic perspective. Hudjashov and colleagues (2018) undertook a study of genome wide data of modern people from the Leeward Society Islands (including Bora Bora, Taha'a, and Ra'iātea), in which they compared their data with a large publicly available dataset that included data from Polynesian Outlier communities (collected by Delfin *et al*. (2012) for mtDNA and Y chromosome studies) with genomic analyses of samples from Rennell, Bellona, Tikopia and Ontong Java (Qin & Stoneking, 2015). They argued that their results supported a model of rapid and relatively recent settlement of the Society Islands (a short chronology) where their Society Island ancestry signatures were more likely to be derived from the Northern Outliers than from Samoa (Hudjashov et al., 2018). Analyses of the frequencies of mitochondrial DNA lineages belonging to haplogroup B4a1a, which make up 96% of the maternal lineages in the Leeward Society Islands, placed the Society Islands closest to Ontong Java. These and the other East Polynesian samples included in the analyses (Hawaii, Cooks and NZ Māori) were all quite different to the frequencies seen in Samoa and other West Polynesian populations (Hudjashov et al., 2018: Figure S8). Genomic studies focused on genetic variants associated with gout and metabolic disease also show significant variation between East and West Polynesian populations, which does not fit well with the traditional out of Samoa origins for East Polynesians (Hollis-Moffatt et al., 2011; Phipps-Green et al., 2010).

In 2020, Harris and colleagues published results of a large, whole genome study of over 1000 Samoans in which they investigated the demographic history of Samoa (Harris et al., 2020). The authors combined their Samoan data with other publicly available data for Oceania and found that the Samoans clustered most closely with Tongans and populations from the Polynesian Outliers. They identified that Papuan ancestry contributed to just under 25% of the Samoan genome and was universally distributed, which they suggest indicates that the admixture occurred before the ancestors reached Samoa. This was less than the 35% of Papuan ancestry seen in the Tongan and Polynesian Outlier genomes. Harris and colleagues also identified evidence of a massive population bottleneck that occurred about 10 generations (300 years) ago, which correlates closely with the arrival of Europeans and the introduction of European diseases. None of these results were particularly surprising, however, they also indicated that modern Samoans likely descended from a population arrival that was more recent than that of the Lapita colonists. Their demographic reconstruction indicated that the population grew very slowly from the arrival of the Lapita peoples nearly 3000 years ago through until about 30-35 generations (~1000 years) ago, at which point they saw evidence of a period of rapid population growth. They suggest this “significant demographic event” was due to the likely arrival of a new group of people in Samoa just prior to this growth period, who were also already admixed 25% Papuan and 75% Austronesian, and who potentially replaced the descendants of the initial Lapita founding population. Harris and colleagues note that their dramatic increase in effective population size in Samoa fits with the suggested arrival of new people in Polynesia proposed by Addison and Matisoo-Smith (2010). The authors remarked that ancient DNA from Samoa would be required to really assess this interpretation. Unfortunately, despite the significant increase in ancient DNA data from the Pacific, we currently have no ancient DNA from Samoa.

4. Recent Developments in Ancient DNA in the Pacific

In the final discussion section of their paper, Addison and Matisoo-Smith noted that “Ancient DNA analyses of the increasing number of Lapita skeletal populations and comparison with ancient DNA obtained from later, post Lapita skeletal populations from across the Pacific will allow us to fully understand the processes leading to the biological diversity seen in the Pacific today” (Addison and Matisoo-Smith 2010:9). As noted previously, in the 15 years since publication, the methods for sampling and sequencing ancient DNA have improved dramatically and as a result, several genomic studies of ancient Pacific populations have provided data that help us to better understand the biological diversity seen in the Pacific at a particular point in time and can help us better understand the processes that led to the genetic landscape that we see in the Pacific today.

4.1. Ancient DNA of Lapita peoples

Perhaps one of the most surprising results in decades of Pacific research were those published in 2016 describing the first genome wide data obtained from Lapita remains – recovered from three crania that were buried in the Teouma site in Vanuatu, and one from Talasiu, Tonga (Skoglund et al., 2016). Prior to this result, it was generally assumed, based on Green's Triple I model, that the Lapita people who settled Remote Oceania would have been a population of mixed Island Southeast Asian (Austronesian) and Bismarck Archipelago (Papuan) ancestry (Kayser, 2010; Kayser et al., 2008; Wollstein et al., 2010). But what Skoglund *et al*. (2016:510) reported was that all four Lapita-associated samples had DNA signatures that indicated "little to no Papuan ancestry".

Three follow-up papers (Lipson et al., 2018; Lipson et al., 2020; Posth et al., 2018) not only confirmed the results of Skoglund *et al*., but provided further data from later Lapita and post-Lapita samples from Vanuatu, which showed a near complete "population turnover" in Vanuatu within a few hundred years of the first Lapita settlement. Ancient samples dating from ~2500 BP from Efate and Malakula showed little evidence of Austronesian ancestry and were most closely related to the Papuan-speaking Baining people living on New Britain today. Interestingly, Posth *et al*. (2018) also included an additional two samples from the Lapita associated Talasiu site (TON 001, 002, dated to between 2690 and 2320 BP) and a later sample from Tonga (LHA 001, dated to 780-550 BP) in their aDNA analyses, along with three individuals recovered from the Taputapuātea site in Ra'iātea, Society Islands, and dated to the 18th century. They found that the Papuan ancestry identified in these Polynesian samples was different that that seen in the Vanuatu samples (likely of New Britain origin) and was a best fit with a Solomon Island origin. The more recent Tongan and Ra'iātea samples, however, did not cluster with the Talasiu and Teouma Lapita samples in their PCA, but were closer to modern samples from the Polynesian Outlier populations from Tikopia and Ontong Java (Posth et al., 2018:Fig 1a). Interestingly, though, Lipson *et al* (2020) found that they could model Polynesian ancestry as the result of the same New Britain source population as seen in the late and post-Lapita Vanuatu samples.

4.2. Ancient and modern genomic studies in Micronesia

Addison and Matisoo-Smith (2010), like many before them (Buck, 1938; Sullivan, 1921), highlighted the similarities between Micronesia and Polynesia in terms of biology and cultural components and raised the possibility of these being related to migration routes. Unfortunately, published archaeological and biological research has generally been less focused on Micronesia than it has on Polynesia and Lapita origins, but recently, this data gap has been addressed by a large genomic study of both ancient and modern populations in Micronesia (Y.-C. Liu et al., 2022). In their study of 166 ancient individuals from Guam, Saipan and Pohnpei dated from 2800-200 BP, and 112 modern individuals from Guam, Palau, Chuuk and Pohnpei, combined with previously published genome-wide data from ancient and modern populations in Island Southeast Asia (ISEA) and the Pacific, Liu and colleagues identified five distinct streams of migration into Micronesia. The first migration (M1), which occurred before 2800 BP, was direct from ISEA to the Mariana Islands. A second migration (M2) occurred from ISEA to Palau slightly later than M1 and from a different source population at some point before 2400 BP. People with this M2 ancestry moved north from Palau to the Marianas and contributed about 15% to the genetic ancestry of the Latte period (by 700 BP) populations there. The third group to contribute to the genetic ancestry of Micronesians (M3) came from the Lapita derived populations from the south (carrying DNA related to the Lapita associated crania recovered from Teouma and Talasiu), and resulted in the settlement of Central Micronesia at some point prior to 2100 BP. Interestingly, these people did not introduce Papuan genomic markers associated with either New Britain or the Solomon Islands – making it unlikely that this Lapita associated migration was from Vanuatu or the Solomon Islands. All of the "Papuan" DNA identified in Micronesians according to Liu *et al*. comes from another PNG source, and is likely related to the fourth migration (M4), which involved the movement of people from the Admiralty Islands of PNG up into Palau and into Central Micronesia sometime before 1800 BP. The fifth and final Pacific migration into Micronesia (M5) involved the settlement of the Polynesian outliers in the Caroline Islands sometime after 1000 BP who, not surprisingly, came from a Polynesian source. Interestingly, almost all of the Papuan ancestry found in Micronesia they argue traced back to Papuan males, indicating sex specific migration from New Guinea to Micronesia (Y.-C. Liu et al., 2022).

Another two recent genomic studies focused on the genetic origins of the population currently living on Kiritimati Island, in the Line Islands, now part of Kiribati (Larena et al., 2025; Palencia-Madrid et al., 2022). While Kiritimati was unoccupied when Capt. James Cook "discovered" the atoll in 1777, archaeological evidence indicates at least intermittent if not continuous occupation of the island from AD 1200 to 1600 (Anderson et al., 2000; Di Piazza & Pearthree, 2001a). The house sites and ceremonial structures that were present on the island were said to resemble those of central East Polynesia, which led Anderson and colleagues (2000) to suggest continuous settlement, likely from the Northern Cook Islands, the Tuamotus or the Society Islands, but possibly Hawai'i. Di Piazza and Pearthree (2001b) suggest that the island was regularly visited but intermittently occupied by Polynesians for collecting turtles and birds, and that it was a part of a major inter-archipelago basalt exchange network involving Samoa, the Marquesas, and possibly the Southern Cook Islands from the mid-12th to the mid-14th centuries. The island was resettled in the 1920s when workers were brought from the Gilbert Islands to work in coconut plantations planted on the island, and in the late 1950s and 60s the island was a site for British and American nuclear testing. Since Kiribati independence in 1979, more I Kiribati have moved to Kiritimati, with the 2020 census listing the population at 7369. The first study (Palencia-Madrid et al., 2022) describes the mtDNA and Y chromosome analyses of 163 unrelated men from Kiritimati. Genealogical data collected confirmed I Kiribati origins for at least three generations on both the maternal and paternal sides. Both the mitochondrial DNA (control region sequences only) and Y chromosome haplogroups present indicated that there was a large degree of haplotype sharing, suggesting a recent "migration" to Kiribati from West Polynesia after the initial "Austronesian" settlement. They dated this migration event to between 363 and 548 years ago. Interestingly, unlike Polynesia, which tends to have a high percentage (~66%) of Near Oceanic Y chromosomes (e.g. C2a-M208) (Kayser et al., 2006), the Kiritimati sample consisted of 84% haplogroup O, which is an Austronesian/ISEA lineage.

The study by Palencia-Madrid *et al*. (2022) was followed up by a second publication from the group (Larena et al., 2025) which selected 19 of the original 163 samples from Kiritimati Island and generated a dataset of autosomal SNPs, which they merged with several other datasets of world-wide and Pacific focused ancient and modern populations, including the large Micronesian dataset of Liu *et al*. (2022). Their results indicated that the Kiritimati samples were most likely derived from, but were equidistant from, the Lapita associated crania from Teouma and Tonga, and they were more distant from the ancient samples from Guam and the Marianas. When compared to modern data, the Kiritimati samples clustered with samples from Chuuk and Pohnpei, with a Society Islands group as the immediate outgroup to the central-eastern Micronesians (Larena et al., 2025).

Given the dramatic increase in both the sampling of Pacific populations and the large amount of genomic data that are now available for both ancient and modern populations, we can step back and investigate the questions and the possible explanatory model presented by Addison and Matisoo-Smith to determine if we are any closer to understanding the settlement processes of the Pacific generally and of Polynesia more specifically.

5. Materials and methods

To provide an overview of the accumulated genomic data and a visual display of the relationships we undertook both a PCA analysis of several compatible genome-wide SNP datasets generated since 2010 and an assessment of all of the complete mitochondrial genome data publicly available for modern and ancient Pacific populations.

5.1. Genome Wide Data and analysis

Modern Samoan, Tokelau, Tuvalu, and Cook Island samples, along with a few Tongan samples were collected in Aotearoa New Zealand as part of a project entitled "The Longest Journey—From Africa to Aotearoa", approved by the Otago Human Ethics Committee (reference number H13/009). DNA was extracted from cheek-swabs using MagMaxTM extraction kits following the manufacturer's protocols. SNP data were generated using the Geno 2.0 SNP array, which targets over 130,000 autosomal and X chromosome SNPs targeting assessment of worldwide genetic ancestry (Elhaik et al., 2013). The previously published and publicly available SNP data used in our analyses are shown in Supplementary Table 1.

Array and capture-based genotype data were obtained either through direct request from data custodians or from publicly available repositories. Genotype data were converted to EIGENSOFT format using convertf and subsequently merged across datasets using mergeit, both part of the EIGENSOFT package (Patterson *et al*., 2006; Price *et al*., 2006). Principal component analysis (PCA) was performed on the merged dataset using smartpca (Patterson *et al*., 2006). Ancient samples were projected onto the PCA space to avoid distortion of the underlying variance structure, and the resulting PCA was visualized in R using ggplot2. The same merged dataset was used to assess admixture, using ADMIXTURE to infer values of k from 2 to 12 (Alexander et al., 2009) and visualized in R using ggplot2.

The same merged dataset was used to assess admixture, using ADMIXTURE (Alexander et al., 2009) and visualized in R.

5.2. Mitochondrial Genome Analyses

FASTA files for published complete mitochondrial genomes from throughout the Pacific, Island Southeast Asia and Australia were downloaded from Genbank, and run through Haplogrep3 using the Phylotree build 17.2 for haplogroup assignments. These updated haplogroup calls were then examined for their distribution across the geographic region.

6. Results

6.1. Genome-wide SNP analyses

Figure 1 shows the PCA of all published Pacific data we could combine together with some key comparative data from ISEA (Taiwan and the Philippines). Previously unpublished data generated by our lab group for individuals of self-identified West Polynesian and Cook Island ancestry living in New Zealand were incorporated to provide additional West and East Polynesian genome-wide SNP data. When all data included in Table S1 were collated 56,303 SNPs were analysed. This number is sufficient for studying ancestry, however when combined with the fact that the selected SNPs are unlikely the most appropriate for assessing variation and ancestry in the Pacific one should be aware that there are potentials for biases in this dataset.

The unsupervised ADMIXTURE analysis identified K=7 as the best supported number of inferred ancestral clusters and is presented in Figure 2.

6.2. Complete mitochondrial genomes

All shared haplogroups were identified by island/archipelago location and are shown in Supplementary Table 2. Note that the haplogroup calls that were made in the original source articles may be different from those presented in Supplementary Table 2 due to the regular updating of Phylotree.

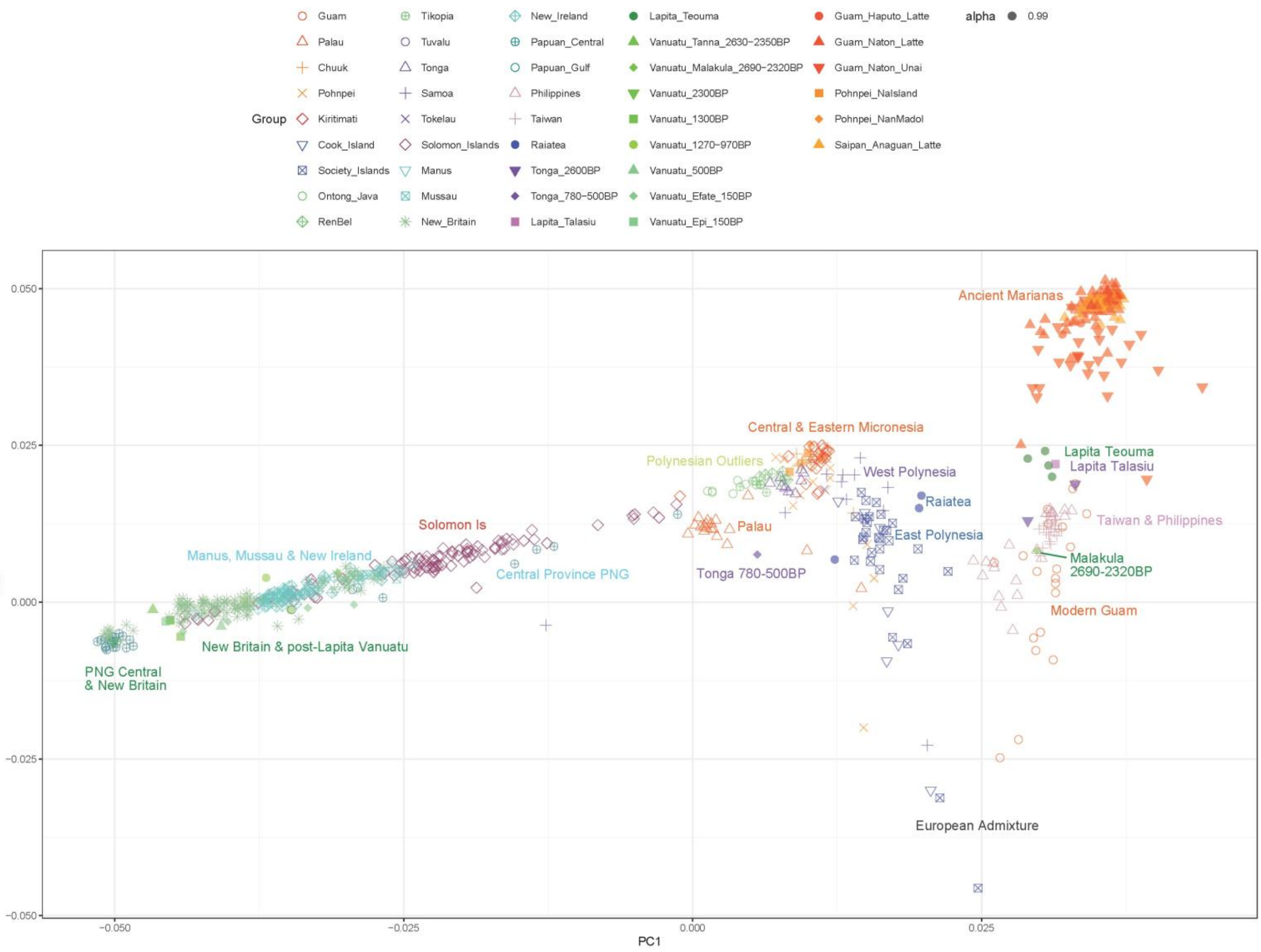

Figure 1: Principle Component Analysis (PCA) of ancient and modern genome-wide data for Pacific populations. Axes were determined based on modern DNA data (unfilled shapes) with ancient DNA samples (solid shapes) projected. Each symbol represents a single individual.

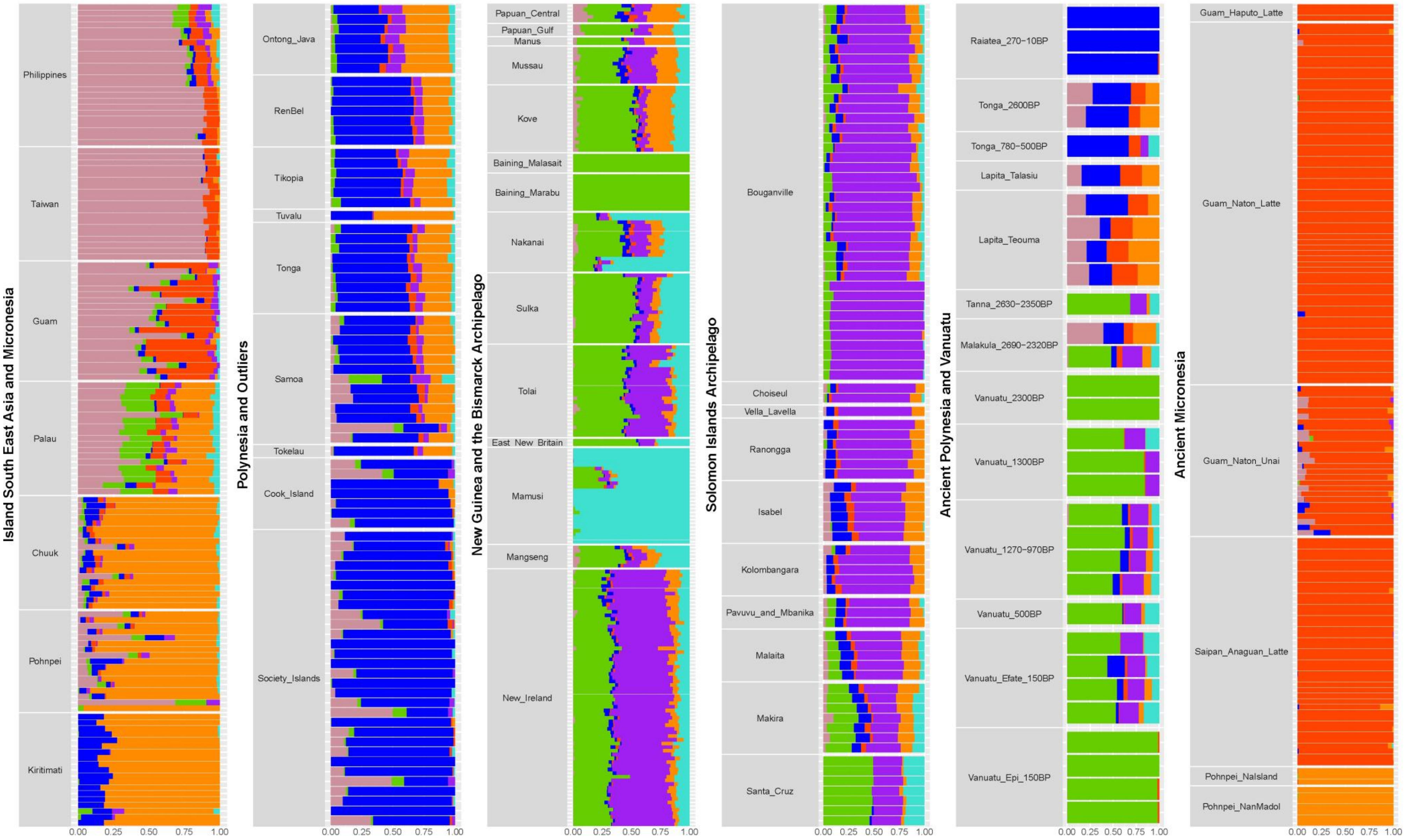

Figure 2: Unsupervised ADMIXTURE plot (K = 7 clusters). Note that each bar represents the admixture signature of a single individual, and each of the inferred ancestral clusters (K) is represented by a different colour. See Supplementary Table 1 for sample details.

7. Discussion

As noted by the authors of most of the genomic studies that have investigated Pacific peoples, and as can be seen in Figure 1, the genomic data generated from Pacific populations over the last decade have indicated that there is likely much more complexity to the settlement history than was often described in classic models. We expect that it comes as no surprise to those who study the Pacific, that the standard definitions of Melanesia, Polynesia and Micronesia clearly make no biological sense, but the clustering of genomic variation in the Pacific is patterned and in some way relates to the history of the region, whether it is deep ancestry or more recent, historic European or Asian admixture. For example, we can see in Figure 1 that the ancient Mariana samples differ markedly from other Pacific populations, including the Palauans. We also see the impact of European admixture in several modern Pacific populations, as those samples are skewed to the positive on the PC1 axis and into the negative space along the PC2 axis, ending up towards the bottom right of the PCA.

The ability to quickly and affordably sequence complete mitochondrial genomes has also dramatically improved our understanding of genomic variation in Pacific populations. Unfortunately, however, since genome-wide array data have become more commonly generated, people have paid less attention to mitogenome data, or more specifically, complete mitogenome sequencing, which we believe still shows some very important historical relationships that may not be easily observed in genome-wide SNP data. Mitochondrial haplotypes show direct and very distinct ancient relationships of maternal ancestry, where the genome-wide data can become diluted over multiple generations due to recombination. When we see links between islands or island groups based on shared mtDNA haplotypes, it means that women carrying that lineage had to have left female offspring in the location. Analyses of the distributions of rare mitochondrial haplotypes in particular, which may not be identified in array data, can also provide some valuable evidence of links between closely related populations.

Prior to the development of next-generation sequencing, most mitochondrial DNA studies only focused on the Hypervariable Region (HVR) variation and some well-known coding-region mutations, such as the 9bp deletion that was one of the defining mutations for the B4a1a1a haplogroup, often referred to as the Polynesian motif. While HVR sequencing suggested that the B4a1a1 and B4a1a1a haplogroups reached over 90% frequency in Polynesia (Kayser, 2010), complete mitogenome sequencing has now shown that there is a significant amount of variation within the B4a1a1a lineages found in the Pacific (Almeida et al., 2025), including variation within East Polynesia (Knapp et al., 2012). While B4a1a1 and B4a1a1a mitogenome frequencies are still very high across the Pacific, the distributions of shared “rare” sub-lineages are proving to be more informative for tracking the movement of women across the Pacific. These may only be identified through complete mitogenome sequencing.

Despite the increase in genomic research in the Pacific, we still have pretty poor sampling across the Pacific region. One area that has been particularly well sampled for complete mitochondrial sequencing is the Solomon Islands. The high level of diversity of sequences, particularly in the B4a1a1a sub-lineages that are, to date, only found in the Solomon Islands can be seen in Supplementary Table 2. More in-depth sequencing elsewhere in the Pacific is likely to identify more new lineages and shared rare lineages that will help us to further tease apart the various historic relationships in the region. With the genome-wide SNP data combined (Figure 1) and the complete mitogenome haplotype distributions (Supplementary Table 2), we can also begin to test some of the predictions and hypotheses that were described by Addison and Matisoo-Smith (2010).

7.1. Lapita only ancestry for Polynesia?

Several unresolved aspects of the Lapita-only model were highlighted by Addison and Matisoo-Smith (2010). At the time, they noted that "the anthropometric data favour a Slow-Boat or Triple-I model for Polynesian origins" because the Lapita-associated remains did not demonstrate the robust phenotypic characteristics of Polynesians (2010:4). In their proposed West Polynesian Triple I model, they took it as given (based on the Lapita skeletal morphology and the modern genetic data at the time) that the original Lapita colonists in West Polynesia would have looked genetically and phenotypically like the indigenous populations we see in Vanuatu, New Caledonia and Western Fiji today, in other words, they would have been carrying a significant amount of Near Oceanic admixture.

While we have little to no genome-wide data to date from New Caledonia or Fiji to include in our analyses, we can say that the ancient genome data from the Lapita samples from Teouma and Talasiu would contradict this assumption of a "Slow-boat" model for Lapita biological origins, as it appears that there is little evidence of admixture from Near Oceania in the genomes of the founding Lapita peoples. From the Admixture plot shown in Figure 2, we can see that the Lapita samples from Teouma and Talasiu carry a combination of blue, pink and orange (light and dark) components that are from ISEA (seen in the Philippines and Taiwan). They do not carry any green, teal or purple components that we see in the ancient post-Lapita samples from Vanuatu, which are the likely "Papuan" contributions to their genomes.

The representativeness of the early Lapita skeletal aDNA, given the unusual context of the crania from which the results were recovered, has been questioned (see comments by Matisoo-Smith in Bedford et al., 2018), but as additional early Remote Oceanic samples have been studied (e.g. the additional ancient Tongan and Vanuatu samples), we are continuing to see a similar pattern of limited Near Oceanic admixture in the earliest samples. It is still possible, however, given that post-mortem removal of skulls from burials was the norm in Teouma and also common in early Talasiu, the rare crania that are present in Lapita burial sites (and from which all of the aDNA results are obtained) are somehow not representative of the population as a whole, or might be those of revered ancestors. Until we can obtain DNA from the early, Lapita-associated post-cranial remains, we have to assess the aDNA data that exist, and, thus, it appears that the first Lapita peoples in Vanuatu and Tonga were a non- or minimally-admixed group from ISEA.

7.2. Post-Lapita Intrusions into West Polynesia ~1500 BP?

The position of the Lapita Teouma, Lapita Talasiu and other early Tongan samples (Tonga 2600BP, which are also from the Talasiu site but sequenced later), as can be seen in the Figure 1, are quite distinct from the later ancient samples from Polynesia (Raiatea and Tonga) and from all modern Polynesian samples. Interestingly, these additional Talasiu samples and the Malakula sample dated to a similar time period, sit closer in the PCA to samples from Taiwan and the Philippines than do the first four Lapita samples sequenced from Teouma and Talasiu. This is a strong indicator that modern and post-Lapita Polynesians are not solely derived from the Lapita ancestors who arrived in West Polynesia 2850 BP, and that there must be additional genetic contributions to Polynesia at some point after 2350 BP (minimum age for the Talasiu samples). This may be suggested in cultural changes seen in the in burial patterns observed in later Tongan burial sites that suggest "…in addition to *in situ* cultural development, the arrival of new migrants after the development of Ancestral Polynesian Society [2650-2350 BP] probably contributed to a re-shaping of funerary practices" (Valentin et al., 2020:1011). Hudjashov *et al*. (2018:6) suggest that their modern data from the Leeward Society Islands indicate Papuan-Austronesian admixture between ~1200 and 1,700 BP, and the whole genome results of Harris *et al.* (2020), indicate evidence of a massive population increase into Samoa around 1000 BP, which they suggest could represent the arrival of new migrants. With multiple biological and cultural signals of the arrival of new peoples in Polynesia, which would represent an intrusion component of the West Polynesian Triple I model, the obvious question is, where did those new migrants come from?

If, as the ancient Lapita data suggest, the first Lapita peoples did not carry substantial amounts of Near Oceanic ancestry, then the indicators of Papuan ancestry in Polynesian genomes (seen as green, teal and purple components in Figure 2) would have had to have been introduced after Lapita settlement of West Polynesia. As is clear from the analyses of the late and post-Lapita Vanuatu samples, Near Oceanic peoples from New Britain arrived in Vanuatu within a few hundred years of Lapita settlement, resulting in a swamping of the ISEA signature there. There is some debate regarding the Near Oceanic ancestry component of Polynesian genomes (both ancient and modern), with both New Britain and Solomon Island ancestry being suggested. We do not think the current data are sufficient to identify specific Near Oceanic source populations for this component in Polynesian genomes. There is little evidence to indicate direct interaction between these populations and Polynesians. It could be that the Papuan components came into Polynesia indirectly via Fiji either before or as a result of the Tongan Maritime Interaction Sphere that linked West Polynesia and Fiji through trade and elite marriages from around 1000 BP (Kaeppler & D'Arcy, 2008), but we do not currently have any appropriate Fijian genomic data to specifically address this possibility.

It is interesting that Liu *et al*. (2022:78) suggest that the majority of Papuan ancestry seen in Micronesia is the result of the arrival of males, with different Papuan genomic signatures contributing to the genomes of people from Palau, Central Micronesia, and post-Lapita and Polynesian ancestries. Where the Papuan ancestry of late-Lapita populations appears to be from New Britain, Liu *et al*. suggested that the migration of the Lapita-derived populations into Western and Central Micronesia likely came from the Admiralty Islands or north coast PNG (not New Britain) rather than the southeast Solomons or northern Vanuatu as archaeological and linguistic evidence has suggested (Kirch, 2017). It could be argued from the data presented in Figure 2 that the green component (found at 100% in Baining) has a significant contribution to the genomes from Palau, but we do not think the data are robust enough to identify any specific group, as there has been significant mobility in the Pacific in the last three thousand years.

7.3. Influx of people from Micronesia?

A combination of genome-wide studies and the commensal mtDNA data reviewed by Addison and Matisoo-Smith (2010) suggested links between Polynesia and Micronesia, which they thought might indicate the arrival of new peoples from ISEA via the low islands of Micronesia that emerged after the last drop in sea level ~2000 BP. We do see Micronesian-Polynesian connections in the PCA (Fig 1) – particularly the overlap between Central Micronesia and West Polynesia. There is also a mixture of Samoan and Pohnpei and even a Palauan sample within the East Polynesian cluster, which could be what we would see in an admixed West Polynesian/Central Micronesian source population for East Polynesia. If this were the case, we might expect to see rare mitochondrial lineages shared between Micronesians and Polynesians. The light orange component in Figure 2 dominates the Central and Eastern Micronesian genomes, particularly the ancient samples from Nan Madol. That same component is also seen in the Lapita samples and modern Samoans, but it is not a major component in the East Polynesian samples and is non-existent in the ancient samples from Raʻiātea.

We can see from the shared mtDNA haplogroup data recorded in Supplementary Table 2 that there is some, but not strong, evidence of shared mtDNA lineages between Micronesia and West Polynesia, except with Tuvalu and early Tokelau. The distribution of haplogroup B4a1a1x shows links between the islands in the atoll arc, and is found in Guam, Chuuk, Kapingamarangi, the Marshall Islands Tuvalu, and Tokelau. But, to date, it is not recorded elsewhere. Haplogroup B4b1a2i, which originates in ISEA is recorded in Java and the Maluku Islands, on Guadalcanal in the Solomons, and in Central and Eastern Micronesia, Nauru and Tuvalu, and in the oldest of the ancient samples recovered from Tokelau (Gosling et al., 2023). It is also found in the ancient samples from Pohnpei (Nan Madol), which are dated to about 500 BP (Liu *et al*. 2020). It has not been recorded in Western Micronesia, or elsewhere in Polynesia, nor have any other ancestral B4b lineages. It is possible that with improved mitogenome sampling in Polynesia, we may find a wider distribution of these rare Pacific lineages that will help us better understand the interactions between Micronesia and Polynesia.

7.4. Settlement of East Polynesia from the Polynesian Outliers?

Hudjashov *et al*. (2018) suggested that the origins of the East Polynesians were in the Northern Outliers, rather than Samoa – in support of the hypothesis put forward by Wilson based on linguistic evidence (Wilson, 2012, 2018, 2021). The relationships presented in Figure 1 do not really support such a scenario. While we do see a slight separation between East Polynesia and Samoa, the Polynesian Outliers merge into the West Polynesian samples (Tikopia and Rennell/Bellona with Tonga in particular) but also overlap and form a fairly tight cluster with the central Micronesians, including ancient and modern samples from Pohnpei. They are more distant from both the ancient and modern East Polynesian samples, which also have some interesting overlap with central Micronesian samples from Pohnpei. The complexity of the Polynesian Outlier genomes is visible in Figure 2, but they do look fairly similar to the modern Samoans and Tongans.

From the mitochondrial perspective, we see several rare haplogroups (B4a1a1a8 and a9 and B4a1a1m1) that link the Polynesian outliers broadly with Polynesia, as would be expected if they originated in West Polynesia and were taken both east to East Polynesia and West to the Outliers. But there are few haplogroups that are, to date, only reported in the Polynesian Outliers and East Polynesia. Haplogoup B4a1a1h is found in the Outliers (Rennell, Bellona, and Ontong Java) and in Hawaii and Haplogroup B4a1a1a11b is found in Bellona, Futuna, Tuvalu and the Cook Islands – but not to date in Samoa or Tonga. There are also haplogroups, such as B4a1a1a16, which is found in Tikopia, Samoa and Tonga, but not in East Polynesia, and B4a1a1o, reported only in Tikopia and Tokelau. It is also possible that there were multiple pathways of introduction of new derived genetic markers being introduced into Polynesia at different points in time – Pacific population mobility and interaction is increasingly evident in the genomic and archaeological data that have been generated in the last 15 years (Allen, 2025; Clark et al., 2014; Cochrane & Rieth, 2016; Nagaoka et al., 2022; Weisler et al., 2016).

7.5. Innovations – unique components within Polynesia

A number of haplotypes found in Polynesia are not recorded in ISEA or even in the Western Pacific, and thus likely emerged within Polynesia. Haplotype B4a1a1m, which is defined by two downstream mutations from the B4a1a1 sequence, is recorded only in Fiji, Tonga, and Samoa. The B4a1a1m1 lineage, a descendant lineage, is found throughout Polynesia, but at much higher frequencies in East Polynesia and in the Polynesian Outliers (Rennell, Bellona and Ontong Java). It has not been recorded in Micronesia, Melanesia, or in Island Southeast Asia. Haplogroup B4a1a1c is also unique to Polynesia (though not recorded in Tokelau or Tuvalu) and is relatively common in East Polynesia but rare in West Polynesia. Both of these distributions could be the result of genetic drift during the settlement of East Polynesia from West Polynesia or, alternatively, the B4a1a1m1 and B4a1a1c lineages may have arisen in East Polynesia (or the Outliers) and spread to West Polynesia as a result of post-settlement interactions. Further analyses of both mitogenome variation and, ideally, whole genome sequencing within Polynesia might be able to tease apart the fine-grained population structure within the region and between Polynesia and other Pacific populations.

8. Conclusion

In the fifteen years since the publication of the West Polynesian Triple-I model, our understanding of the settlement of the Pacific has changed greatly. We have now filled in some of the major gaps that existed in our knowledge – with both increased Pacific sampling and as a result of the technological developments that have allowed us to obtain genome-wide data from archaeological remains.

We now have growing evidence that the Lapita peoples who settled in Vanuatu and Tonga carried very little Near Oceanic ancestry, but that post-Lapita interactions between Near and Remote Oceania were substantial, and likely from a number of different Near Oceanic populations. It therefore does appear that there were later, post-Lapita arrivals of people in West Polynesia, some of whom carried Papuan ancestry, but we cannot conclusively identify any specific source populations or routes of introduction, though there is growing evidence of interactions between Polynesia and Micronesia.

The generation of genomic data from Micronesia, both ancient and modern, has been a huge step in filling that geographic gap, but we still require more data from more populations across the Pacific. We still do not have sufficient genomic data from Polynesia that can be used in ancestry studies, and Central and Eastern Micronesia is still not well sampled. Fiji is an obvious gap that needs to be filled if we are to understand how the Papuan ancestry was introduced into Polynesia. There has also been an increasing number of both ancient and modern genomic studies in Papua New Guinea that are also contributing to our understanding of population origins and mobility in the Pacific (D. Liu et al., 2022; Nägele et al., 2025), which could have impacts on how we interpret the settlement histories elsewhere in the Pacific.

While the amount of genomic data being generated for Pacific populations has improved dramatically, unfortunately, different research groups use different SNP arrays to generate their data, which means they are looking at different SNPs. When combining the data from a wide range of studies, we lose a large number of non-overlapping variants. The PCA generated in Figure 1 was based on only 56,303 SNPs that were shared across the various studies. The use of arrays is significantly cheaper than undertaking whole-genome sequencing, and are often used to specifically avoid SNPs that are of medical interest due to ethical considerations, but sadly the use of arrays make data comparison difficult. Some researchers even use SNP arrays on genetic samples from the Pacific that were designed for assessing variation in specific populations, such Latin American focused arrays (Ioannidis et al., 2021), which is even more limiting.

The whole genome sequencing study by Harris *et al*. (2020) showed that rare variants are extremely important for reconstructing the population structure in Samoa. Unfortunately, because of the consents given in the collection of those samples, they are not publicly available for further ancestry analyses. To date, the genomic SNP arrays that are typically used to generate ancestry data, such as those used to generate the PCA shown in Figure 1, would not include variants that are considered to be rare worldwide, but some of these variants may be less rare within the Pacific. Such Pacific-specific variants are likely to be what is needed to untangle the ancestral relationships within the Pacific, and therefore, we would suggest that future studies engage in whole-genome sequencing whenever possible.

There is an increasing awareness of the importance and value of community engagement and capacity building in Pacific research – this is common in archaeological research, but typically has been less so in genomic research. We argue strongly for full community consultation and collaboration in genomic studies in the Pacific. As real collaborative relationships are established and more Indigenous Pacific researchers are being trained and are contributing to genomic research through projects like the Summer internships for INdigenous peoples in Genomics (SING) that are now involving several Pacific communities (e.g. see https://www.singaotearoa.nz/ and https://www.uog.edu/singmicro), we are confident that more genetic studies in the Pacific will happen with full community consent and decision making over use of the data. Both sampling and the interpretation of results will benefit from community engagement and the incorporation of Indigenous knowledge of historic interactions, which will help us tease out the various threads that make up the complex tapestry of Pacific pasts. Pacific peoples are interested in their history but perhaps they are even more interested in how their past, including their genetic makeup may be impacting their health and their futures.

Supplementary Materials

The supporting information can be downloaded at https://doi.org/10.70460/jpa.v16i2.396 S1: Sample and location details for all samples utilised in PCA and Admixture analyses. S2: Mitochondrial haplogroup distributions

Funding

Funding for the collection and generation of the Geno Chip data was provided to E.M-S. by National Geographic and from the Royal Society Te Apārangi for the project entitled “The Longest Journey—From Africa to Aotearoa”, approved by the Otago Human Ethics Committee (reference number H13/009).

Partnerships

This research did not use any primary data from Indigenous contexts.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

Conceptualization, E.M-S. and A.L.G; formal analysis, A.L.G, B.L.W., C.J.C.; data curation, A.L.G., B.L.W., C.J.C; writing—original draft preparation, E.M-S., A.L.G; writing—review and editing, E.M-S., A.L.G, B.L.W., C.J.C.; All authors have read and agreed to the published version of the manuscript.

Acknowledgements

We would like to thank Seth Quintus and Alex Morrison who organized the SAA conference session in honour of Melinda Allen and invited us to participate and to contribute this paper. We would also like to acknowledge all of the Pacific people who contributed their DNA to the various projects mentioned in this paper.

References

Addison, D. J., & Matisoo-Smith, E., 2010. Rethinking Polynesian Origins: A West-Polynesian Triple-I Model. *Archaeology in Oceania*, *45*, 1–12.

Alexander, D. H., Novembre, J., & Lange, K., 2009. Fast model-based estimation of ancestry in unrelated individuals. *Genome Research*, *19*(9), 1655–1664. https://doi.org/10.1101/gr.094052.109

Allen, M. S., 2025. Reciprocity, Risk, and Rivalry: Variability in Central East Polynesian Exchange Networks. *Journal of World Prehistory*, *38*(1), 1. https://doi.org/10.1007/s10963-025-09189-1

Almeida, M., Gandini, F., Rito, T., Foody, M. G., Brandão, A., Oliveira, M., Olivieri, A., Fichera, A., Oteo-Garcia, G., Zainuddin, Z., Eng, K. K., Pomat, W., Bryk, J., Pereira, L., Farr, H., Pala, M., Oppenheimer, S. J., Richards, M. B., & Soares, P., 2025. Leveraging known Pacific colonisation times to test models for the ancestry of Southeast Asians. *Scientific Reports*, *15*(1), 37044. https://doi.org/10.1038/s41598-025-20856-3

Anderson, A., Wallin, P., Martinsson-Wallin, H., Fankhauser, B., & Hope, G., 2000. Towards a first prehistory of Kiritimati (Christmas) Island, Republic of Kiribati. *The Journal of the Polynesian Society*, *109*(3), 273–293.

Bedford, S., Blust, R., Burley, D. V., Cox, M., Kirch, P. V., Matisoo-Smith, E., NÆSs, Å., Pawley, A., Sand, C., & Sheppard, P., 2018. Ancient DNA and its contribution to understanding the human history of the Pacific Islands. *Archaeology in Oceania*. https://doi.org/10.1002/arco.5165

Buck, P. H., 1938. *Vikings of the Sunrise.* Lippencott.

Clark, G. R., Reepmeyer, C., Melekiola, N., Woodhead, J., Dickinson, W. R., & Martinsson-Wallin, H., 2014. Stone tools from the ancient Tongan state reveal prehistoric interaction centers in the Central Pacific. *Proc Natl Acad Sci U S A*, *111*(29), 10491–10496. https://doi.org/10.1073/pnas.1406165111

Cochrane, E. E., & Rieth, T. M., 2016. Sāmoan artefact provenance reveals limited artefact transfer within and beyond the archipelago. *Archaeology in Oceania*, *51*(2), 150–157. https://doi.org/10.1002/arco.5090

Delfin, F., Myles, S., Choi, Y., Hughes, D., Illek, R., van Oven, M., Pakendorf, B., Kayser, M., & Stoneking, M., 2012. Bridging Near and Remote Oceania: mtDNA and NRY variation in the Solomon Islands. *Mol Biol Evol*, *29*(2), 545–564. https://doi.org/10.1093/molbev/msr186

Di Piazza, A., & Pearthree, E., 2001a. An island for gardens, an island for birds and voyaging: A settlement pattern for Kiritimati and Tabuaeran, two "mystery islands" in the Northern Lines, Republic of Kiribati. *The Journal of the Polynesian Society*, *110*(2), 149–170.

Di Piazza, A., & Pearthree, E., 2001b. Voyaging and Basalt Exchange in the Phoenix and Line Archipelagoes: The Viewpoint from Three Mystery Islands. *Archaeology in Oceania*, *36*(3), 146–152.

Elhaik, E., Greenspan, E., Staats, S., Krahn, T., Tyler-Smith, C., Xue, Y., Tofanelli, S., Francalacci, P., Cucca, F., Pagani, L., Jin, L., Li, H., Schurr, T. G., Greenspan, B., Spencer Wells, R., & Genographic, C., 2013. The GenoChip: a new tool for genetic anthropology. *Genome biology and evolution*, *5*(5), 1021–1031. https://doi.org/10.1093/gbe/evt066

Gilbert, M. T. P., Binladen, J., Miller, W., Wiuf, C., Willerslev, E., Poinar, H., Carlson, J. E., Leebens-Mack, J. H., & Schuster, S. C., 2007. Recharacterization of ancient DNA miscoding lesions: insights in the era of sequencing-by-synthesis. *Nucleic Acids Research*, *35*(1), 1–10. https://doi.org/Doi 10.1093/Nar/Gkl483

Gosling, A. L., Lord, E., Boocock, J., Cameron-Christie, S., Horsburgh, K. A., Kardailsky, O., Prost, S., Wilcox, S., Addison, D., Thompson, A., Kalolo, J., Clarke, A. C., & Matisoo-Smith, E. A., 2023. A population history of Tokelau – genetic variation and change in atoll populations. *The Journal of Island and Coastal Archaeology*, *18*(1), 100–117. https://doi.org/10.1080/15564894.2021.1901805

Green, R. C., 1991. The Lapita cultural complex: Current evidence and proposed models. *Bulletin of the Indo-Pacific Prehistory Association*, *11*, 295–305.

Harris, D. N., Kessler, M. D., Shetty, A. C., Weeks, D. E., Minster, R. L., Browning, S., Cochrane, E. E., Deka, R., Hawley, N. L., Reupena, M. a. S., Naseri, T., McGarvey, S. T., & O'Connor, T. D., 2020. Evolutionary history of modern Samoans. *Proceedings of the National Academy of Sciences*, 201913157. https://doi.org/10.1073/pnas.1913157117

Hofreiter, M., Paijmans, J. L., Goodchild, H., Speller, C. F., Barlow, A., Fortes, G. G., Thomas, J. A., Ludwig, A., & Collins, M. J., 2015. The future of ancient DNA: Technical advances and conceptual shifts. *Bioessays*, *37*(3), 284–293. https://doi.org/10.1002/bies.201400160

Hollis-Moffatt, J. E., Gow, P. J., Harrison, A. A., Highton, J., Jones, P. B. B., Stamp, L. K., Dalbeth, N., & Merriman, T. R., 2011. The SLC2A9 nonsynonymous Arg265His variant and gout: evidence for a population-specific effect on severity. *Arthritis Research & Therapy*, *13*(3). https://doi.org/R8510.1186/ar3356

Hudjashov, G., Endicott, P., Post, H., Nagle, N., Ho, S. Y. W., Lawson, D. J., Reidla, M., Karmin, M., Rootsi, S., Metspalu, E., Saag, L., Villems, R., Cox, M. P., Mitchell, R. J., Garcia-Bertrand, R. L., Metspalu, M., & Herrera, R. J., 2018. Investigating the origins of eastern Polynesians using genome-wide data from the Leeward Society Isles. *Scientific Reports*, *8*(1), 1823. https://doi.org/10.1038/s41598-018-20026-8

Ioannidis, A. G., Blanco-Portillo, J., Sandoval, K., Hagelberg, E., Barberena-Jonas, C., Hill, A. V. S., Rodríguez-Rodríguez, J. E., Fox, K., Robson, K., Haoa-Cardinali, S., Quinto-Cortés, C. D., Miquel-Poblete, J. F., Auckland, K., Parks, T., Sofro, A. S. M., Ávila-Arcos, M. C., Sockell, A., Homburger, J. R., Eng, C.,…Moreno-Estrada, A., 2021. Paths and timings of the peopling of Polynesia inferred from genomic networks. *Nature*, *597*(7877), 522–526. https://doi.org/10.1038/s41586-021-03902-8

Kaeppler, A. L., & D'Arcy, P., 2008. Exchange Patterns in Goods and Spouses: Fiji Tonga and Samoa. In (1 ed., Vol. 3, pp. 253–259). Routledge. https://doi.org/10.4324/9781315247175-14

Kayser, M., 2010. The human genetic history of Oceania: near and remote views of dispersal. *Curr Biol*, *20*(4), R194–201. https://doi.org/10.1016/j.cub.2009.12.004

Kayser, M., Brauer, S., Cordaux, R., Casto, A., Lao, O., Zhivotovsky, L. A., Moyse-Faurie, C., Rutledge, R. B., Schiefenhoevel, W., Gil, D., Lin, A. A., Underhill, P. A., Oefner, P. J., Trent, R. J., & Stoneking, M., 2006. Melanesian and Asian origins of Polynesians: mtDNA and Y chromosome gradients across the Pacific. *Molecular Biology and Evolution*, *23*(11), 2234–2244. https://doi.org/DOI 10.1093/molbev/msl093

Kayser, M., Choi, Y., van Oven, M., Mona, S., Brauer, S., Trent, R. J., Suarkia, D., Schiefenhovel, W., & Stoneking, M., 2008. The impact of the Austronesian expansion: Evidence from mtDNA and Y chromosome diversity in the Admiralty Islands of Melanesia. *Molecular Biology and Evolution*, *25*(7), 1362–1374. https://doi.org/10.1093/molbev/msn078

Kirch, P. V., 2017. *On the Road of the Winds: An Archaeological History of the Pacific Islands before European Contact* (2 ed.). University of California Press.

Knapp, M., Horsburgh, K. A., Prost, S., Stanton, J.-A., Buckley, H. R., Walter, R. K., & Matisoo-Smith, E. A., 2012. Complete mitochondrial DNA genome sequences from the first New Zealanders. *Proceedings of the National Academy of Sciences*, *109*(45), 18350–18354. https://doi.org/10.1073/pnas.1209896109

Larena, M., Chowdhury, A. E., Kels, M. J. T., Tätte, K., Metspalu, M., Schlebusch, C. M., Garcia-Bertrand, R., & Herrera, R. J., 2025. Genetic Origins of the Kiritimati Population from Central-Eastern Micronesia. *Genome Biology and Evolution*, *17*(3). https://doi.org/10.1093/gbe/evaf046

Lipson, M., Skoglund, P., Spriggs, M., Valentin, F., Bedford, S., Shing, R., Buckley, H., Phillip, I., Ward, G. K., Mallick, S., Rohland, N., Broomandkhoshbacht, N., Cheronet, O., Ferry, M., Harper, T. K., Michel, M., Oppenheimer, J., Sirak, K., Stewardson, K.,…Reich, D., 2018. Population Turnover in Remote Oceania Shortly after Initial Settlement. *Current Biology*. https://doi.org/10.1016/j.cub.2018.02.051

Lipson, M., Spriggs, M., Valentin, F., Bedford, S., Shing, R., Zinger, W., Buckley, H., Petchey, F., Matanik, R., Cheronet, O., Rohland, N., Pinhasi, R., & Reich, D., 2020. Three Phases of Ancient Migration Shaped the Ancestry of Human Populations in Vanuatu. *Current Biology*. https://doi.org/10.1016/j.cub.2020.09.035

Liu, D., Peter, B. M., Schiefenhövel, W., Kayser, M., & Stoneking, M., 2022. Assessing Human Genome-wide Variation in the Massim Region of Papua New Guinea and Implications for the Kula Trading Tradition. *Molecular Biology and Evolution*, *39*(8). https://doi.org/10.1093/molbev/msac165

Liu, Y.-C., Hunter-Anderson, R., Cheronet, O., Eakin, J., Camacho, F., Pietrusewsky, M., Rohland, N., Ioannidis, A., Athens, J. S., Douglas, M. T., Ikehara-Quebral, R. M., Bernardos, R., Culleton, B. J., Mah, M., Adamski, N., Broomandkhoshbacht, N., Callan, K., Lawson, A. M., Mandl, K.,…Reich, D., 2022. Ancient DNA reveals five streams of migration into Micronesia and matrilocality in early Pacific seafarers. *Science*, *377*(6601), 72–79. https://doi.org/doi:10.1126/science.abm6536

Mallick, S., Li, H., Lipson, M., Mathieson, I., Gymrek, M., Racimo, F., Zhao, M., Chennagiri, N., Nordenfelt, S., Tandon, A., Skoglund, P., Lazaridis, I., Sankararaman, S., Fu, Q., Rohland, N., Renaud, G., Erlich, Y., Willems, T., Gallo, C.,…Reich, D., 2016. The Simons Genome Diversity Project: 300 genomes from 142 diverse populations. *Nature*, *538*(7624), 201–206. https://doi.org/10.1038/nature18964

http://www.nature.com/nature/journal/v538/n7624/abs/nature18964.html#supplementary-information

Matisoo-Smith, E., & Gosling, A. L., 2018. Walking backwards into the future: the need for a holistic evolutionary approach in Pacific health research. *Annals of Human Biology*, *45*(3), 175–187. https://doi.org/10.1080/03014460.2018.1448889

Matisoo-Smith, E., & Gosling, A. L., 2025. Understanding the human settlement of the Pacific – Are we there yet? *Journal of Archaeological Science*, *180*, 106307. https://doi.org/https://doi.org/10.1016/j.jas.2025.106307

McLean, M., 2008. *Were Lapita Potters Ancestral to Polynesia?* (Vol. 7). Archive of Maori and Pacific Music, University of Auckland.

Millar, C. D., Huynen, L., Subramanian, S., Mohandesan, E., & Lambert, D. M., 2008. New developments in ancient genomics. *Trends in Ecology & Evolution*, *23*(7), 386–393. https://doi.org/DOI 10.1016/j.tree.2008.04.002

Nagaoka, T., Sheppard, P. J., Ross-Sheppard, C., & Kononenko, N., 2022. Obsidian point discovered on Kapingamarangi Atoll, Micronesia: Implications for post-settlement regional interactions. *Journal of the Polynesian Society*, *131*(4), 389–426. https://doi.org/10.15286/jps.131.4.389-426

Nägele, K., Kinaston, R., Gaffney, D., Walworth, M., Rohrlach, A. B., Carlhoff, S., Huang, Y., Ringbauer, H., Bertolini, E., Tromp, M., Radzeviciute, R., Petchey, F., Anson, D., Petchey, P., Stirling, C., Reid, M., Barr, D., Shaw, B., Summerhayes, G.,…Krause, J.., 2025. The impact of human dispersals and local interactions on the genetic diversity of coastal Papua New Guinea over the past 2,500 years. *Nature Ecology & Evolution*, *9*(6), 908–923. https://doi.org/10.1038/s41559-025-02710-x

Palencia-Madrid, L., Baeta, M., Kleinbielen, T., Toro-Delgado, N., Villaescusa, P., Sanchez-Bustamante, E., de Pancorbo, M. M., Luis, J. R., Ware, K. E., Somarelli, J. A., Garcia-Bertrand, R., & Herrera, R. J., 2022. Post-Austronesian migrational wave of West Polynesians to Micronesia. *Gene*, *823*, 146357. https://doi.org/https://doi.org/10.1016/j.gene.2022.146357

Phipps-Green, A. J., Hollis-Moffatt, J. E., Dalbeth, N., Merriman, M. E., Topless, R., Gow, P. J., Harrison, A. A., Highton, J., Jones, P. B. B., Stamp, L. K., & Merriman, T. R., 2010. A strong role for the ABCG2 gene in susceptibility to gout in New Zealand Pacific Island and Caucasian, but not Māori, case and control sample sets. *Human Molecular Genetics*, *19*(24), 4813–4819. https://doi.org/10.1093/hmg/ddq412

Pinhasi, R., Fernandes, D., Sirak, K., Novak, M., Connell, S., Alpaslan-Roodenberg, S., Gerritsen, F., Moiseyev, V., Gromov, A., Raczky, P., Anders, A., Pietrusewsky, M., Rollefson, G., Jovanovic, M., Trinhhoang, H., Bar-Oz, G., Oxenham, M., Matsumura, H., & Hofreiter, M., 2015. Optimal Ancient DNA Yields from the Inner Ear Part of the Human Petrous Bone. *PLOS ONE*, *10*(6), e0129102. https://doi.org/10.1371/journal.pone.0129102

Posth, C., Nagele, K., Colleran, H., Valentin, F., Bedford, S., Kami, K. W., Shing, R., Buckley, H., Kinaston, R., Walworth, M., Clark, G. R., Reepmeyer, C., Flexner, J., Maric, T., Moser, J., Gresky, J., Kiko, L., Robson, K. J., Auckland, K.,…Powell, A., 2018. Language continuity despite population replacement in Remote Oceania. *Nat Ecol Evol*, *2*(4), 731–740. https://doi.org/10.1038/s41559-018-0498-2

Qin, P., & Stoneking, M., 2015. Denisovan Ancestry in East Eurasian and Native American Populations. *Molecular Biology and Evolution*, *32*(10), 2665–2674. https://doi.org/10.1093/molbev/msv141

Sear, D. A., Allen, M. S., Hassall, J. D., Maloney, A. E., Langdon, P. G., Morrison, A. E., Henderson, A. C. G., Mackay, H., Croudace, I. W., Clarke, C., Sachs, J. P., Macdonald, G., Chiverrell, R. C., Leng, M. J., Cisneros-Dozal, L. M., & Fonville, T., 2020. Human settlement of East Polynesia earlier, incremental, and coincident with prolonged South Pacific drought. *Proceedings of the National Academy of Sciences*, 201920975. https://doi.org/10.1073/pnas.1920975117

Skoglund, P., Posth, C., Sirak, K., Spriggs, M., Valentin, F., Bedford, S., Clark, G. R., Reepmeyer, C., Petchey, F., Fernandes, D., Fu, Q., Harney, E., Lipson, M., Mallick, S., Novak, M., Rohland, N., Stewardson, K., Abdullah, S., Cox, M. P.,…Reich, D., 2016. Genomic insights into the peopling of the Southwest Pacific [Letter]. *Nature*, *538*, 510–513. https://doi.org/10.1038/nature19844 http://www.nature.com/nature/journal/vaop/ncurrent/abs/nature19844.html#supplementary-information

Smith, A., 2002. *An archaeology of West Polynesian prehistory*. Pandanus Books.

Sullivan, L. R., 1921. The status of Physical Anthropology in Polynesia. In *Proceedings of the First Pan-Pacific Science Conference (Honolulu) 1920, Part 1* (Vol. 7, pp. 63–69). B.P. Bishop Museum.

Valentin, F., Clark, G., Parton, P., & Reepmeyer, C., 2020. Mortuary practices of the first Polynesians: formative ethnogenesis in the Kingdom of Tonga. *Antiquity*, *94*(376), 999–1014. https://doi.org/10.15184/aqy.2020.89

Weisler, M. I., Bolhar, R., Ma, J., St Pierre, E., Sheppard, P., Walter, R. K., Feng, Y., Zhao, J.-x., & Kirch, P. V., 2016. Cook Island artifact geochemistry demonstrates spatial and temporal extent of pre-European interarchipelago voyaging in East Polynesia. *Proceedings of the National Academy of Sciences*. https://doi.org/10.1073/pnas.1608130113

Wilson, W. H., 1985. Evidence for an Outlier Source for the Proto Eastern Polynesian Pronominal System. *Oceanic Linguistics*, *24*(1/2), 85–133. https://doi.org/10.2307/3623064

Wilson, W. H., 2012. Whence the East Polynesians? Further Linguistic Evidence for a Northern Outlier Source. *Oceanic Linguistics*, *51*(2), 289–359.

Wilson, W. H., 2014. Pukapukan and the NO-EPn Hypothesis: Extensive Late Borrowing by Pukapukan. *Oceanic Linguistics*, *53*(2), 392–442. https://doi.org/10.1353/ol.2014.0013

Wilson, W. H., 2018. The Northern Outliers-East Polynesian Hypothesis expanded. *Journal of the Polynesian Society*, *127*(4), 389–432.

Wilson, W. H., 2021. East Polynesian Subgrouping and Homeland Implications Within the Northern Outlier–East Polynesian Hypothesis. *Oceanic linguistics*, *60*(1), 36–71. https://doi.org/10.1353/ol.2021.0001

Wollstein, A., Lao, O., Becker, C., Brauer, S., Trent, R. J., Nurnberg, P., Stoneking, M., & Kayser, M., 201. Demographic History of Oceania Inferred from Genome-wide Data. *Current Biology*, *20*(22), 1983–1992. https://doi.org/10.1016/j.cub.2010.10.040