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Changing subsistence practices in pre-European populations of South Vanuatu

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ABSTRACT

Differences in dietary patterns between the islands of South Vanuatu are expected due to differences in ecological and cultural characteristics of the islands and their complex histories of settlement, adaptation and interaction. This paper examines the human dietary practices of 32 individuals from three of the five islands in the region: Aniwa, Futuna and Tanna, between 2000 BP and the 20th century, using for the first time carbon and nitrogen isotope data measured in bone collagen. Our analysis includes an expanded baseline of local faunal and plant resources, with taxonomic identification of local faunal remains enhanced by proteomic determinations (Zooarchaeology by Mass Spectrometry; ZooMS). Human collagen $\delta^{13}\text{C}$ values ranged from -19.7 to -16.2 ‰, and $\delta^{15}\text{N}$ values from 6.3 to 9.7 ‰, with a large inter-individual variability. Based on our improved baseline, we suggested that the individuals with the highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values would have consumed marine coral reef fish along with C3 plants. An individual with the lowest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values could have consumed mainly resources from mangrove. Four patterns were identified that may reflect the geographical characteristics of the islands, the normalisation of diet over time, the nutritional stress of individuals in relation to environmental and climatic factors, and social differentiation in food acquisition and/or consumption, illustrating issues of equifinality in bioarchaeological data interpretation.

1. Introduction

Scholarship in the Southwest Pacific focusing on the archaeology of death and bioarchaeology more broadly remains uneven across the region, primarily privileging the earliest colonising groups associated with the Lapita culture. In South Vanuatu, unlike in the Central and North parts of the archipelago (e.g. Bedford et al., 2011; Bentley et al., 2007; Buckley et al., 2008, 2014; Foster et al., 2018; Kinaston et al., 2014a and b; Skoglund et al., 2016; Valentin et al., 2010, 2014, 2016), the lifestyles of pre-European populations are almost unknown. Current research is limited to an 800 year-old burial discovered in Tanna (Flexner and Willie 2015), and skeletal remains excavated in rock shelters in Tanna

and Futuna, and open sites on Aneityum that previously lacked a defined chronological framework or formal analysis of skeletal remains (Shutler and Shutler, 1966; Spriggs, 1997; Valentin et al., 2011; Weets, 1996). Our team conducted fieldwork between 2016 and 2019 on three: Futuna, Aniwa and Tanna, out of the five islands that make up South Vanuatu (Fig. 1) and made steps towards building a comprehensive landscape archaeology and bioarchaeological record for the region, including expanding the pool of currently known burials and associated evidence for past mortuary behaviour as well as contributing to a suite of laboratory analyses on skeletal material (e.g. Flexner et al., 2018, 2019; Posth et al., 2018; Valentin et al., 2022; Zinger, 2021; Zinger et al., 2024).

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This paper focuses on past dietary practices on these three islands, based on an analysis of carbon and nitrogen isotope data measured in bone collagen from individuals from Aniwa, Tanna and Futuna. We analyse these in relation to the ecological and cultural characteristics of the islands, and discuss their variation in relation to the islands' complex history of settlement, adaptation, and interaction within the South Vanuatu region and beyond. We also emphasise the need for/importance of establishing a local baseline as a general framework for interpreting human data, an issue generally raised in isotopic analysis of South West Pacific, but whose limitations are rarely considered. Finally, we highlight the different ways in which human data can be interpreted, a classic problem of equifinality in bioarchaeology (Cheung and Szpak, 2021; Vaiglova et al., 2023), which complicates the discussion of factors shaping human dietary patterns or trends.

2. Isotopic dietary reconstruction in Southwest Pacific

Bioarchaeological analyses of burials and skeletal remains provide direct evidence for assessing past dietary practices, particularly through analyses of the biogeochemical composition of bone collagen, which is directly correlated with the protein fraction of the diet (Katzenberg, 2008; Schoeninger, 2010). Since the 1990s, isotopic studies have investigated the respective contributions of marine and terrestrial foods to the diets of various pre-European groups of the South–West Pacific region (25 listed in Appendix A) and provide a general framework for discussion. The results to date tend to confirm the view of the gradual development and adoption of a diet focused on plant foods, particularly the suite of Oceanic domesticates such as yams and taro, documented in early ethnographic writings in the South–West Pacific region (e.g. Barrau, 1958; Humphreys, 1926; Pollock, 1986). This shift apparently occurred at different paces and times, ranging from an early transition in Vanuatu (Kinaston et al., 2014a; Valentin et al., 2014) to a later transition in Fiji and Tonga (Fenner et al., 2021; Herrscher et al., 2024).

Information on local back-ground isotopic values are crucial for such dietary reconstructions (Allen and Craig, 2009). It is now well known that the single use of the trophic fraction between food and consumer tissue as a means to extrapolate the resources consumed by human

(Jarman et al., 2017) is insufficient/inadequate because local environmental and cultural conditions (aridity, vegetation cover, temperatures, manuring, irrigation etc.) modify the stable isotope ratios of food resources at the base of the food chain, which consequently have repercussions up to human tissues (Drucker and Henry-Gambier, 2005; Herrscher and Le Bras-Goude, 2010). Describing the isotopic characteristics of resources as closely as possible to the environment in which the studied human groups lived is therefore critical to guarantee the reliability of proposed dietary interpretations. However, in the case of the Pacific islands including Vanuatu, animal and plant remains are not always well preserved and well represented, which prompted scholars to establish a baseline based on contemporary plant and animal resources (Kinaston et al., 2014b). In addition, and to exemplify the isotopic variability of terrestrial and marine animal food resources in South Vanuatu, we sampled animal bones recovered from a historical (19th century) site on Aniwa Island. As morphological taxonomic determination is often difficult to achieve on fragmentary bone elements, which was the case for the Aniwa remains, we undertook proteomic identifications (Zooarchaeology by Mass Spectrometry; ZooMS) on these animal samples to improve the resolution of the determination (e.g. Bray et al., 2023; Harvey et al., 2022) and therefore the range of the available baseline.

3. Aniwa, Futuna and Tanna cultural and ecological contexts

The cultural history of South Vanuatu follows a trajectory similar to that of the rest of Vanuatu archipelago (Bedford and Spriggs, 2014) and the broader Melanesian region (Kirch, 2017: 55–149; Spriggs, 1997). South Vanuatu's archaeological record begins with settlement around 3000 years ago and post-Lapita regional developments, followed by an early intensification and Polynesian contacts from around 1000 years ago, and European contacts nearly 250 years ago leading to globalisation (Bedford, 2006; Bedford et al., 2016; Spriggs, 1986; Zinger et al., 2020; Flexner et al., 2022). Tanna, Aniwa and Futuna populations are interconnected through local and regional exchange networks to Erromango and Aneityum in South Vanuatu and more widely to the Loyalty Islands, New Caledonia, and Western Polynesia. These interactions, particularly

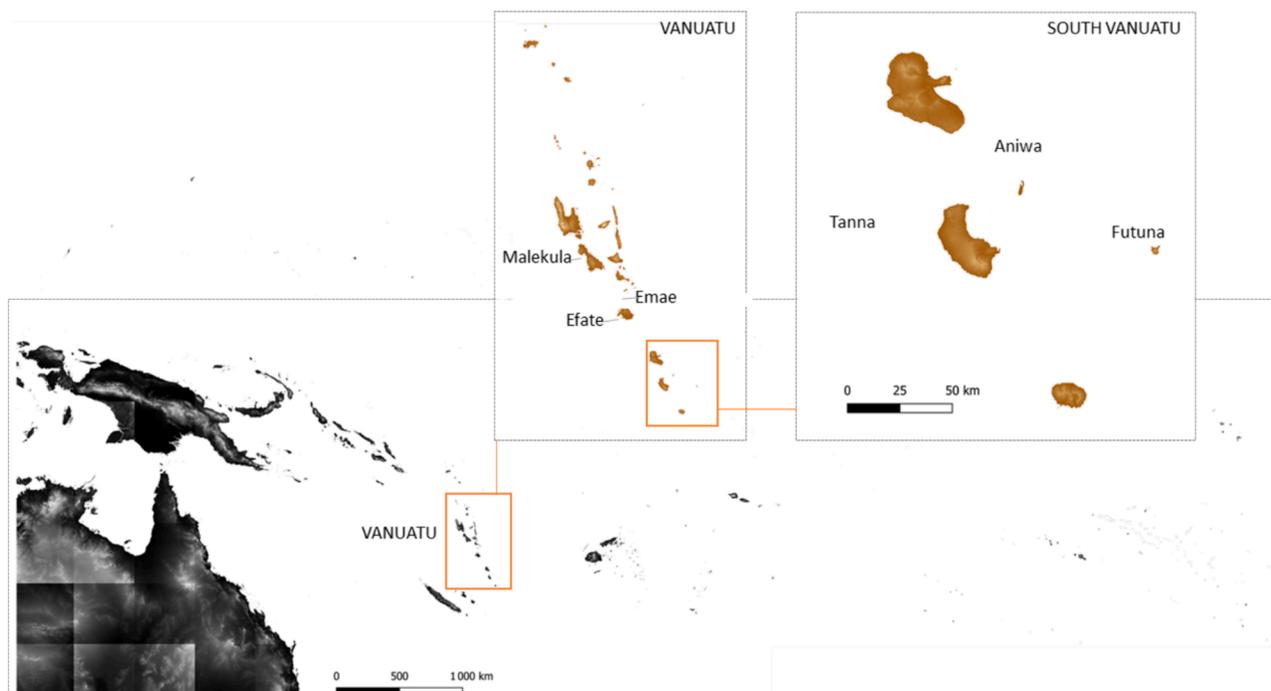


Fig. 1. Geographical map showing location of Vanuatu at north of Loyalty Islands and New Caledonia and South Vanuatu Islands. Map created from Shuttle Radar Topographic Mission coordinates available on CIAT-CSI SRTM <https://srtm.csi.cgiar.org>.

with Western Polynesia, have significantly influenced their genetics, culture and language (Arauna et al., 2022; Lipson et al., 2020; Lynch, 1996; Pawley, 1967; Spriggs, 1997), to the point that Aniwa and Futuna are now recognised as “Polynesian outliers” (Flexner et al. (2019a)). Polynesian outliers are defined as island communities living outside the Polynesian Triangle that have Polynesian languages and other Polynesian cultural traits including some that may be related to cooking and foodways, albeit expressed to varying degrees (Carson, 2012; Feinberg and Scaglione, 2012; Zinger et al., 2020). Differences in foodways and mortuary rituals patterns between islands can be expected, though similarities in resource introduction, production/exploitation and treatment are described across the five southern islands of Vanuatu. Notably there is a clear distinction between food production and consumption, with much of the acquired food reserved for ceremonial exchange (Flexner et al., 2019b; 2022; 2024).

Together with Erromango and Aneityum, the islands of Tanna, Aniwa and Futuna are located in the Southern Province of Vanuatu (TAFEA) (Fig. 1). These five islands are mutually visible, with a distance of about 50 km between Tanna and Aniwa, and about 100 km between Tanna and Futuna. They feature similar endemic fauna and flora. Volcanism is an important component on each island, defining soils and geology, although Tanna has the only active volcanism. Futuna and Aniwa are the smallest islands of the region, and generally lack perennial streams. Adapting to these specific geographical and ecological contexts over the past 3000 years, islanders have developed complex ways of managing terrestrial and marine resources to meet their subsistence and exchange needs (Flexner et al., 2024). Plant microfossil analysis of sediment samples from excavations on Aniwa, Futuna, and Tanna reveal pollen, phytoliths and starch of both introduced domesticates and endemic plants (Horrocks, 2020). Food crops represented include *Musa* sp. (banana), *Colocasia esculenta* (taro), *Dioscorea nummularia* (spiny yam), cf. *Dioscorea bulbifera* (bitter yam), and cf. *Dioscorea pentaphylla* (five-fingered yam), all C3 photosynthetic pathway plants. Analysis of micro particles preserved in human dental calculus of recent individuals from Futuna island indicates the presence of starch granules attributable to several root and tree crops including Polynesian *Tacca leontopetaloides* (arrow root) and *Zea mays* (corn) (Velsko et al., 2024). Islanders have also raised domestic chicken and pigs, hunted wild fauna, and exploited surrounding marine resources (Flexner et al. 2019b; Garabedian, 2018; Sarvanu, 2019). While there is evidence that the introduction of rats was, at least in some cases, ‘semi-intentional’ and that the animals were a regular, albeit minor, part of some Oceanic diets (see Kirch and Jones, 2003; Swift et al. 2018), there is limited direct evidence on whether or not people in southern Vanuatu ate rats. Our excavations at the rockshelter Punanga ruru in Aniwa island recovered thousands of rat bones along with the bones of small birds and lizards that had been preyed upon by the native owl species. However, an oral tradition from Tanna (recorded by JLF in 2013) included the detail that before the culture hero Mwatiktiki arrived, people “ate rats and drank wild kava.” Mwatiktiki, the avatar of Polynesian encounters in southern Vanuatu, is then credited with bringing “real kava” and pigs to the island (Lynch 1996; Flexner 2022; Flexner et al. 2019a: 414–415).

The islands of Aniwa, Futuna and Tanna have contrasting landforms and environments, suggesting differentiated daily production and/or use of food resources. Futuna (11 km²) is an uplifted volcanic cone with a highest point of 666 m, surrounded by seven successive raised limestone terraces. Archaeological surveys have revealed a large number of horticultural terraces for wet and dry cultivation of crops, with indication of an agricultural intensification during the last millennium, while marine resources are limited due to a lack of lagoon and mangrove formations (Flexner et al., 2018; 2022). In contrast, Aniwa (8 km²) is a small coral atoll, with a maximum elevation of 42 m above sea level, and a large lagoon at its northern tip. While several crops can be cultivated on atolls such as coconut, banana, breadfruit and taro, the main focus of subsistence is clearly on marine environments (Cramb and Thompson, 2022). The ancient population of Aniwa may have used the

reef, mangrove and lagoon, and exchanged fish and shellfish with the nearby island of Tanna (Flexner et al., 2019a; 2022). Tanna (550 km²) is a much larger island, with a variety of landforms and geological and ecological contexts that implies uneven constraints, from coastal areas to dry plateaus and hills of about 500 m high in the north and west, an active volcano (Iasur) in the southeast, and high summits of about 1000 m high in the south and east (Siméoni, 2009; Quantin, 1992). While pre-European resource management practices on Tanna are difficult to evaluate due to the quasi-absence of archaeological research (except a few in the south and in the northwest region, Flexner, 2016; Flexner et al., 2022; authors’ data), historical accounts suggest a primarily land-based economy at the time of European contact (Bonnemaison, 1997). Multicrop gardens were organised according to a core periphery pattern, with large earthen mounds built at the centre for the cultivation of socially-valued (prestigious) yams (Bonnemaison, 1991). In the past, mixed subsistence practices would have probably coexisted on the island, with the use of garden produce and raising of pig and chicken, and some use of the shore resources at least by the populations established on the littoral.

4. Material: Burials in Aniwa, Tanna and Futuna

4.1. The burials

The burials we uncovered on Aniwa, Futuna and Tanna were excavated and described using the methodology of *anthropologie de terrain* (field anthropology) (Duday, 2009; Duday et al., 1990; Valentin et al., 2022). During our excavations, skeletal remains were generally not removed in their entirety. Instead, burial contexts were documented in situ, and reburied. In agreement with the local communities, limited artefacts and bone samples were recovered for subsequent analysis, including isotopic studies and radiocarbon dating. We also sampled skeletal remains excavated by the Shutlers during the 1960s (Shutler and Shutler, 1966), which provide less detailed contextual evidence. Skeletal remains have been stored since 1987 at the Vanuatu Cultural Center in Port Vila, Vanuatu, with the Shutler Archives and other archaeological material produced and assembled by Mary E. Shutler and Richard Shutler Jr. Futuna skeletal remains were re-buried on the island of Futuna in 2020.

Twelve burials from Aniwa, Futuna, and Tanna have been directly radiocarbon dated (Valentin et al., 2022). The ages cover a period of about 1200 years, with conventional ages ranging from 1377 ± 20 BP to 228 ± 20 BP. However, when other archaeological and stratigraphic parameters are taken into account, the number of burials with chronological information increases, resulting in a wider age range varying from 2000 BP to the 20th century. The earliest burials were discovered on Aniwa and Tanna, dating between 2000 and 1000 years ago. These are single burials found in open sites. Burial practice is fairly uniform, with male and female bodies lying extended on the back with the upper limbs in various positions, possibly wrapped in a flexible perishable container like a mat, interred in a pit following various orientations. Associated ornaments included large rings made of *Tridacna* sp. or *Strombus* sp. shells. Coral stones were placed on the body or near the head and in Aniwa a fire structure lit by the feet seem to be part of mortuary rituals.

In Futuna, the oldest burials, dating from c. 1270–970 cal BP, show a different way of treating bodies. Males, females, and children were buried in subsurface burials in the sediments of rock shelters. They share three main characteristics: cairn-like features covering the body, the body in a flexed position, and long protocols, at least for some individuals whose skulls were removed after decomposition (Fig. 2). Associated ornaments include necklaces of small shell beads and pendants made of shell, pearlshell or stone, small shell rings, and turtle shell rings (Shutler and Shutler, 1966; Shutler et al., 2002; Valentin et al., 2022). The later burials in Futuna, dating from c. 300 to 0 cal BP, again illustrate a different way of caring for the dead. They correspond to the



Fig. 2. Examples of subsurface burials from Futuna, excavated in 1964 at FURS12 and in 2017 at FURS15. Note the presence of piled stones on the left picture and removal of skull after decomposition on the right picture.

deposition of the body on the floor of rock shelters and in crevices. In such an environment, where human bones are generally scattered under the influence of various taphonomic and anthropic processes, no complete burial and mortuary pattern can be discerned. Associated ornaments comprise a small flat *Conus* ring, *Conus* bracelet, and a pig tooth bead (Shutler and Shutler, 1966; Shutler et al., 2002), the latter being not present in the earlier assemblage. Although males, females, and children are represented in these assemblages, we found an uneven distribution between the sexes. Some sites show an over-representation of females, identified by their coxal bone (Zinger, 2021). We observed that the surface individuals are represented by eight females, accounting for 80 % of the individuals whose morphological sex could be identified, suggesting that females were often buried in these surface burial contexts.

4.2. Bioarchaeological elements

An analysis of the age at death distribution of the Futuna burials suggests anomalies in the representativeness of the subadults. The Futuna subsurface burials show mortality quotient for the age category [5–9] years that is higher than expected from our model of natural mortality, based on pre-industrial populations (Fig. 3). While a bias related to small sample sizes cannot be ruled out, it is interesting to note that higher mortality ratios are observed in the [5–9], [10–14] and [15–19] years age groups in the case of catastrophic mortality, such as that caused by famine or epidemic outbreaks due to plague (eg Castex and Kacki, 2016; de Lépinau et al., 2021).

Subadult skeletal remains from the Futuna subsurface mortuary contexts show a discrepancy between bone growth and developmental indicators; endocranial lesions were observed in one child, and 9 % of adult long bones show new bone formation, suggesting that individuals may have experienced physiological stress due to malnutrition, infection and/or growth deficiencies, that hindered their normal development (Zinger, 2021). Other indicators of physiological stress, such as linear enamel hypoplasia and *cribra orbitalia* (Buckley, 2016; Walker et al., 2009; Hillson, 1996; 2019) have not been assessed due to the poor preservation of orbital fragments and high levels of dental attrition in adults, although at least one case of linear enamel hypoplasia has been identified in a subadult.

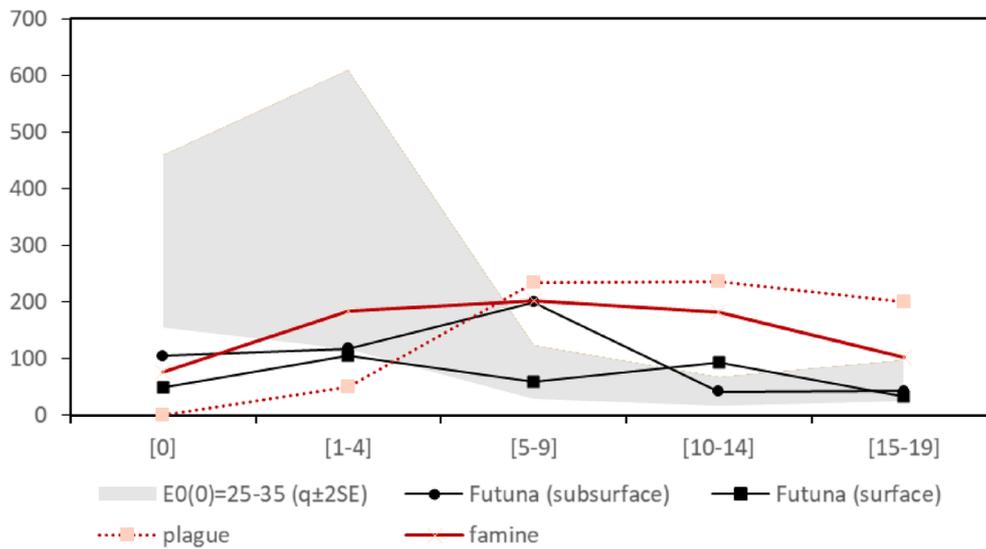
Dental health assessments also reveal different patterns between individuals from subsurface and surface mortuary contexts. Subsurface individuals have a higher frequency of advanced tooth wear: 45 % of these individuals show significant wear, that exposes the pulp chamber. In contrast, only 15,3 % of individuals from surface mortuary contexts display an advanced level of dental wear. The occurrence of caries is slightly higher in subsurface individuals (10 %) than in surface individuals (7 %) (Zinger, 2021). Different dietary practices may have occurred over the time, with a dietary regime involving a more abrasive food, and/or a specific activity involving the mouth and teeth for the individuals buried in subsurface burials. For instance, advanced dental wear observed in individuals from Sigatoka (Fiji) of the middle first millennium CE has been associated with the practice of chewing kava (Visser, 1994; Pietruszewsky et al., 2017).

Finally, a pilot paleoparasitological study of a Futuna rock shelter subsurface burial (FURS15) and an open site burial from Aniwa (Burial 2 at Nakmaroro) was undertaken to assess whether individuals suffered from parasitic diseases. Parasitic infections may have affected the general health of individuals from South Vanuatu, as it has been suggested for individuals from other Pacific islands (Nelson et al., 2016). No evidence of egg worm remains was found in the sediment sampled from under the stomach and pelvis in either of the present cases, though animal parasite eggs were found in other sediment samples from Futuna and Aniwa (Horrocks et al., 2024).

Thirty-two individuals from South Vanuatu mortuary contexts were selected for dietary isotope analysis purposes. Five individuals are from Aniwa, four from Tanna and 23 from Futuna, including 13 from the subsurface (c. 1000 BP) and 8 from the surface (c. 300 BP) burial contexts. Their provenance and chronological attribution are given in Table 1.

5. Method: reconstructing human diet with isotopic data

The diet was assessed using carbon and nitrogen stable isotope ratios measured on the organic part of archaeological skeletal remains (Table 1). The analysis is based on the principle that the isotopic characteristics of the food are recorded in the tissues of consumers with an enrichment in heavy isotopes from food to consumer. Carbon isotope ratios allow terrestrial resources to be distinguished from marine



Futuna (subsurface)	N	S'(x)	quotient	e°0=25, q+	e°0=35, q-
[0]	4	38	105	460	156
[1-4]	4	34	118	608	117
[5-9]	6	30	200	124	30
[10-14]	1	24	42	68	18
[15-19]	1	23	43	97	25
adulte	22				
Total	38				

Futuna (surface)	N	S'(x)	quotient	e°0=25, q+	e°0=35, q-
[0]	2	40	50	460	156
[1-4]	4	38	105	608	117
[5-9]	2	34	59	124	30
[10-14]	3	32	94	68	18
[15-19]	1	29	34	97	25
adulte	28				
Total	40				

Fig. 3. Raw data and mortality profile for individuals of Futuna subsurface and surface mortuary contexts compared to the Ledermann (1969) life tables (life expectancy at birth 25–35 years old) and to mortality profiles associated with plague and famine (eg Castex and Kacki, 2016; de Lépinau et al., 2021).

resources and nitrogen isotope ratios allow the proportion of high trophic level resources (meat) and low trophic level resources (plants) to be quantified (Bocherens and Drucker, 2003; Fernandes et al., 2014; Schoeninger and DeNiro, 1984; O’Connell and Hedges, 1999). Sample pretreatments and isotopes analysis protocols are described in Appendix B.

As the interpretation of human values requires a knowledge of the local foodweb in which the individuals studied lived (Herrscher et al., 2010), their isotopic variability was characterised using a baseline comprising measurements on contemporary and archaeological animal and plant remains. The most probable resources consumed by humans were identified based on the expected isotopic fractionation between food and human bone collagen (trophic enrichment of +5 ‰ for ¹³C, and +3–5 ‰ for ¹⁵N) (Bocherens and Drucker, 2003; Ambrose and Norr, 1993). For this study, we have assembled an animal and plant baseline consisting of historical (n = 24) and contemporary (n = 10) data (Table 2). Contemporary samples were collected on Aniwa, and Emae

islands during fieldwork carried out in 2018 and 2019, representing animal and vegetal samples such as *Gallus Gallus*, *Sus domesticus* and *Canarium indicum*; the latter being represented by its edible nut. As that of chicken and pig, the introduction of *Canarium indicum* in Vanuatu is ancient, confirmed by the significant number of varieties and associated vernacular names throughout Melanesia (Wheatley, 1992: 61–63; Walter and Sam, 1999: 128–130). Historic animal samples are associated with the European contact and later contexts and were uncovered during excavations (2017, 2018, 2019) on Aniwa, in three areas (Mission House, Second Church, Orphanage) of the first Presbyterian Mission established by the Reverend Paton in 1866 (Flexner et al., 2020; Shaw et al., 2022).

Initial morphological identifications of bone were made by Iona Claringbold (Australian National University – ANU) and Pierre Magniez (Aix Marseille University – AMU). The morphological identifications were supplemented by proteomic identifications (ZooMS) to improve the identification of 21 non-discriminating mammals, fish and bird

Table 1Carbon and nitrogen isotopic ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of humans from Aniwa, Futuna and Tanna islands in Southern Vanuatu.

c	Island	Site	Archaeological information	Chronology	Time attribution	Skeletal element	Yield (mg.g ⁻¹)	%C	%N	C: Na	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
PACH111	Aniwa	Gogone	Individual 1	circa 1000 BP	Earlier	R Ulna	19,9	35,1	12,9	3,2	-17,9	8,6
PACH137	Aniwa	Iarisao	TP A	post-contact European	PCE	Fibula	49,2	40,4	14,6	3,2	-19,0	6,3
PACH123	Aniwa	Nakmaroro	Burial 2	circa 1000 BP	Earlier	L radius	22,0	39,9	14,8	3,1	-18,3	7,6
PACH112	Aniwa	Nakmaroro	Burial 1	circa 1000 BP	Earlier	L Fibula	8,4	37,2	13,1	3,3	-16,2	8,3
PACH136	Aniwa	Nakmaroro	Burial 3 (TP19)	between 1000–2000 BP	Earlier	R ulna	32,0	35,2	13,0	3,1	-17,2	8,5
PACH101	Futuna	FURS1A	FURS 1A, Room 2, Burial 1	before circa 1000 BP	Earlier	1rst skull, parietal	31,5	37,6	12,8	3,4	-18,3	9,7
PACH102	Futuna	FURS1A	FURS 1A, Room 2, Burial 1	before circa 1000 BP	Earlier	2nd skull, parietal	48,3	28,8	9,7	3,4	-19,7	8,8
PACH103	Futuna	FURS2	FURS 2 Trench 1	undetermined	–	Radius	7,2	–	–	–	–	–
PACH104	Futuna	FURS3	FURS 3	circa 300 BP?	Later	L ulna	150,1	42,5	15,1	3,3	-18,2	8,2
PACH105	Futuna	FURS5	FURS 5, Room 2, Burial 1	Post 1950 BP	PCE	Fibula	63,8	33,9	11,8	3,3	-18,0	8,7
PACH138	Futuna	FURS 9	FURS9	circa 300 BP	Later	L radius	216,0	42,9	15,9	3,1	-18,6	8,7
PACH100	Futuna	FURS1	FURS 1	circa 300 BP?	Later	R fibula	206,0	44,3	16,4	3,1	-19,3	8,1
PACH107	Futuna	FURS 10	FURS10, ulna 2	circa 300 BP	Later	R ulna	205,5	43,5	16,2	3,1	-18,9	7,6
PACH106	Futuna	FURS10	FURS10, ulna 1,	circa 300 BP	Later	R ulna	186,8	44,0	15,7	3,2	-19,2	8,0
PACH139	Futuna	FURS11	FURS11	circa 300 BP	Later	R humerus	192,6	43,8	16,2	3,1	-19,0	8,3
PACH126	Futuna	FURS12	FURS 12 Burial 1	before circa 1000 BP	Earlier	L ulna	0,0	–	–	–	–	–
PACH127	Futuna	FURS12	FURS 12 Burial 2	before circa 1000 BP	Earlier	Scapula	44,6	40,6	15,0	3,1	-18,9	8,8
PACH128	Futuna	FURS12	FURS 12 Burial 4	before circa 1000 BP	Earlier	L ulna	102,2	42,4	15,5	3,2	-18,3	9,7
PACH129	Futuna	FURS12	FURS 12 Burial 5	before circa 1000 BP	Earlier	L radius	5,0	–	–	–	–	–
PACH130	Futuna	FURS12	FURS 12 Burial 6	before circa 1000 BP	Earlier	R femur	114,1	42,5	15,8	3,1	-18,8	8,1
PACH131	Futuna	FURS12	FURS 12 Burial 8–9	before circa 1000 BP	Earlier	Ulna	59,2	42,6	15,7	3,1	-18,8	8,1
PACH132	Futuna	FURS12	FURS 12 Burial 12	before circa 1000 BP	Earlier	R scapula	94,5	42,6	15,7	3,1	-18,9	8,6
PACH133	Futuna	FURS12	FURS 12 Burial 13	before circa 1000 BP	Earlier	L radius	136,3	45,2	16,6	3,2	-16,9	8,4
PACH108*	Futuna	FURS15	FURS 15, burial 1	before circa 1000 BP	Earlier	L Humerus	5,6	41,8	15,0	3,2	-19,0	8,6
PACH205	Futuna	FURS15	FURS15, mx 1	before circa 1100 BP	Earlier	L Maxillar	135,0	39,8	14,8	3,1	-18,6	8,2
PACH206	Futuna	FURS15	FURS15, mx 2	before circa 1100 BP	Earlier	R Maxillar	104,5	40,8	15,2	3,1	-19,4	8,3
PACH124	Futuna	Manumai	scattered bone	before circa 300 BP	Late	Fibula	3,3	–	–	–	–	–
PACH125	Futuna	Punanga Tu	Unit A L8, spit 2	between 500–3000 BP?	–	Ulna	8,0	–	–	–	–	–
PACH134	Tanna	Enarpap	Burial 1	between 1000–1500 BP	Earlier	R humerus	11,7	21,7	7,6	3,3	-17,7	7,3
PACH135	Tanna	Kolapikin	Burial 1	post-contact European	PCE	R humerus	29,8	27,1	9,8	3,2	-19,1	7,5
PACH113	Tanna	TARS1	Pit 10, Burial 1	pre-contact European	Later	Tibia	12,8	2,3	0,3	9,7	–	–
PACH114	Tanna	TARS3	Burial 1	European contact circa 300 BP	Later	L clavicle	63,5	38,4	13,9	3,2	-18,6	7,8

PCE: Post European Contact.

remains using the same bone sample as for the isotopic analysis. The protocols used for this study are detailed in Appendix C. The mass spectrometry proteomics data were deposited on the ProteomeXchange Consortium (<https://proteomecentral.proteomexchange.org>) via the PRIDE partner repository with the data set identifier PXD047340 (Perez-Riverol et al., 2022) and in S1. The new isotopic data were combined with the 98 contemporary data (plant (n = 68) and animal (n = 30) data) available for central and northern Vanuatu (Efate n = 37 and Malekula n = 61) (Kinaston et al., 2014b, Table 3) to obtain a baseline comprising a total of 132 isotopic signatures.

Isotopic data were explored with statistical tests performed using R version 3.6.1 with RStudio (R Core Team, 2018) with the package Rmisc and onewaytests for descriptive and statistical analysis. The test of Brown-Forsythe based on the homogeneity of variances was used, a 0.05 probability ($p < 0.05$) is considered significant. Data are visualized using ©Excel and the package ggplot2 and ggpubr in RStudio.

6. Results

6.1. Proteomics

The proteomic analysis of the 21 samples allowed us to obtain the taxonomic assignment of 5 of them and to confirm or clarify the taxa for the other samples (Table 2, Supplement S1). Four samples

morphologically identified as canids (PACH_F200, F201, F202, F203, F2024) turned out to be a goat, a pig and individuals of the family Phasianidae (chicken) respectively, and one sample initially identified as a pig turned out to be a fish of the family Scaridae. Proteomic analysis was also used to confirm the attribution of 5 chicken samples and to clarify the family attribution of 11 samples of fish bone fragments, divided into 6 Scaridae, 4 Lutjanidae and 1 Serranidae. Given the local context, the samples attributed to the Phasianidae family are chickens.

6.2. Collagen preservation

Collagen of 29 historic and contemporary animal bones meet all the preservation criteria used in this study (Appendix B, Table 1 and 2). Five seeds of *Canarium* sp. have carbon and nitrogen weight content and C:N ratio in similar ranges to contemporary seeds from similar insular contexts (Kinaston et al., 2014b). Twenty-six out of 32 human collagen extracts were considered well enough preserved to interpret their isotopic data in a dietary perspective. Five samples with collagen extraction yields below 10 mg.g⁻¹ (PACH103, PACH124, PACH125, PACH126, PACH129), and one with a C:N ratio of 9,7, outside the accepted range (PACH113), were discarded (Table 1).

Table 2
Southern Vanuatu isotopic baseline: New data on historic and contemporary samples.

Labcode	Island	Archaeological data	ID	Morphological attribution		Proteomic attribution	Family/ Genus	Element	Yield (mg. g-1)	%C	%N	C: Na	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
				#1	#2									
HISTORIC SAMPLES														
PACH_F200	Aniwa	Area C- "Loose Fill in Cellar"	NA	dog	dog	Capra	<i>Capra hircus</i>	rib	187,4	43,9	15,1	3,4	-18,0	6,0
PACH_F201	Aniwa	Area C- "Loose Fill in Cellar"	NA	dog	dog	Sus	<i>Sus domesticus</i>	rib	126,5	41,2	15,1	3,2	-19,6	5,7
PACH_F202	Aniwa	Area C- "Loose Fill in Cellar"	NA	dog	dog	Phasianidae	<i>Gallus gallus</i>	metatarsal	145,4	42,8	15,6	3,2	-19,4	6,7
PACH_F203	Aniwa	Area C- "Loose Fill in Cellar"	NA	dog	dog	Phasianidae	<i>Gallus gallus</i>	vertebra	198,6	42,8	15,5	3,2	-19,4	6,1
PACH_F204	Aniwa	Area C- "Loose Fill in Cellar"	NA	chicken	chicken	Phasianidae	<i>Gallus gallus</i>	femur	120,0	42,8	15,7	3,2	-15,7	7,6
PACH_F205	Aniwa	Area C- "Loose Fill in Cellar"	NA	chicken	chicken	Phasianidae	<i>Gallus gallus</i>	tibia?	110,1	42,6	15,9	3,1	-16,8	7,9
PACH_F206	Aniwa	Area C- "Loose Fill in Cellar"	NA	chicken	chicken	Phasianidae	<i>Gallus gallus</i>	femur	113,6	42,8	16,0	3,1	-16,6	7,9
PACH_F207	Aniwa	Area C- "Loose Fill in Cellar"	NA	chicken	chicken	Phasianidae	<i>Gallus gallus</i>	coracoide	210,2	42,2	15,7	3,1	-19,7	7,4
PACH_F208	Aniwa	Area C- "Loose Fill in Cellar"	NA	fish	fish	Scaridae	Scaridae	mandibula	121,8	43,4	15,9	3,2	-7,2	7,9
PACH_F209	Aniwa	Area C- "Loose Fill in Cellar"	NA	fish	fish	Serranidae	Serranidae	skull	176,1	40,8	15,5	3,1	-10,7	7,6
PACH_F211	Aniwa	Area A-Trench 1-Spit 2	18.113-57	turtle	pig	-	<i>Sus domesticus</i>	pelvis	35,3	31,2	11,5	3,2	-18,0	7,3
PACH_F212	Aniwa	Area A-Trench 1-Spit 2	18.113-56	pig	pig	-	<i>Sus domesticus</i>	pelvis	20,9	28,7	10,5	3,2	-19,2	6,0
PACH_F213	Aniwa	Area A-Trench 1-Spit 2	18.113-51 & 52	fish	fish	Lutjanidae	Lutjanidae	vertebra	93,7	40,5	15,2	3,1	-10,2	8,3
PACH_F215	Aniwa	Area A-Trench 1-Spit 2	18.113-43	pig	pig	-	<i>Sus domesticus</i>	mandible	33,5	31,5	11,6	3,1	-17,9	7,3
PACH_F216*	Aniwa	Area A-Trench 1-Spit 6	18.134-90	fish	fish	Scaridae	Scaridae	vertebra	61,8	41,9	15,0	3,2	-3,6	6,8
PACH_F217	Aniwa	Area A-Trench 1-Spit 6	18.134-91	fish	fish	Lutjanidae	Lutjanidae	vertebra	86,0	27,4	9,6	3,3	-10,2	10,4
PACH_F218*	Aniwa	Area A-Trench 1-Spit 6	18.134-92	fish	fish	Scaridae	Scaridae	vertebra	70,6	40,7	14,7	3,2	-3,4	6,8
PACH_F219*	Aniwa	Area A-Trench 1-Spit 6	18.134-93	fish	fish	Scaridae	Scaridae	vertebra	69,2	39,8	14,2	3,3	-3,8	6,8
PACH_F220	Aniwa	Area A-TP 1- "Oven Firescoop Z"	18.140-71	fish	fish	Lutjanidae	Lutjanidae	vertebra	31,9	36,4	12,7	3,3	-12,4	10,5
PACH_F222	Aniwa	Area A-TP 1- "Oven Firescoop Z"	18.140-73	fish	fish	Scaridae	Scaridae	rib	72,5	42,5	15,7	3,1	-7,9	7,4
PACH_F223	Aniwa	Area A-TP 1- "Oven Firescoop Z"	18.140-74	pig	fish	Scaridae	Scaridae	rib	80,7	42,5	15,8	3,1	-7,7	7,5
PACH_F224	Aniwa	Area A-Trench 1- "Possible Grave"	18.553-68	fish	fish	Lutjanidae	Lutjanidae	vertebra	76,8	38,3	14,0	3,2	-10,6	8,3
PACH_F225	Aniwa	Area A-Trench 1- "Possible Grave"	18.553-69	fish	fish	Scaridae	Scaridae	rib	117,0	43,0	15,9	3,1	-7,2	8,3
PACH_F226	Aniwa	W Extern-TP 1-L 1 + 2	19.185-9	chicken	chicken	Phasianidae	<i>Gallus gallus</i>	metacarpal	193,4	42,8	16,0	3,1	-17,8	7,3
COMTEMPORARY SAMPLES														
PAC_F106	Emae	-	-	pig	-	-	<i>Sus domesticus</i>	mandible	141,2	40,3	14,8	3,2	-21,2	8,2
PAC_F105	Emae	-	-	pig	-	-	<i>Sus domesticus</i>	mandible	168,3	42,1	15,4	3,2	-20,1	8,0
PAC_F101	Aniwa	-	-	pig	-	-	<i>Sus domesticus</i>	talus	222,7	47,0	17,1	3,2	-20,6	8,0
PAC_F102	Aniwa	-	-	chicken	-	-	<i>Gallus gallus</i>	metatarsal	170,6	43,6	16,0	3,2	-19,0	9,3
PAC_F103	Aniwa	-	-	chicken	-	-	<i>Gallus gallus</i>	phalanx	155,9	40,8	14,1	3,4	-19,7	8,1
PAC_V100	Emae	-	-	nangai	-	-	<i>Canarium indicum</i>	seed	-	86,7	3,7	27,3	-28,7	5,2
PAC_V101	Emae	-	-	nangai	-	-	<i>Canarium indicum</i>	seed	-	69,8	2,4	33,6	-27,3	5,1
PAC_V102	Emae	-	-	nangai	-	-	<i>Canarium indicum</i>	seed	-	68,1	3,0	26,1	-28,1	4,5
PAC_V103	Emae	-	-	nangai	-	-	<i>Canarium indicum</i>	seed	-	69,6	2,2	36,8	-27,6	6,0

(continued on next page)

Table 2 (continued)

Labcode	Island	Archaeological data	ID	Morphological attribution		Proteomic attribution	Family/ Genus	Element	Yield (mg. g ⁻¹)	%C	%N	C: Na	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
				#1	#2									
PAC_V104	Emae	-	-	nangai		-	<i>Canarium indicum</i>	seed	-	70,6	2,1	38,9	-27,2	7,1

* could be the same animal?; Morphological attribution: #1: ANU, #2: AMU. In bold: discordant morphological determination.

Table 3

Descriptive statistics of modern resources isotopic data from Malekula and Efate islands (data in Kinaston et al., 2014b).

	n-samples	$\delta^{13}\text{C}$ -med [Q1–Q3] (in ‰)	$\delta^{15}\text{N}$ -med [Q1–Q3] (in ‰)
Tuber	20	-25,5[-26,4/-24,2]	2,9[2,2/4,2]
Fruit	14	-23,8[-27,1/-22,9]	3,4[2,8/4,6]
Nut	18	-22,9[-23,7/-22,2]	4,6[3,4/6,0]
Nut- <i>Canarium</i>	7	-25,4[-26,0/-24,6]	5,3[3,5/7,5]
Cabbage*	2	-29,4	9,8
		-29,1	5,1
Sugar cane*	3	-12,5	3,4
		-12,7	5,0
		-12,5	3,2
Flying fox**	1	-21,7	7,1
Coastal products	16	-8,3[-13,8/-5,8]	5,9[2,3/7,1]
Coral reef fish	7	-11,5[-13/-11,4]	5,8[5,8/6,9]
Non reef fish*	2	-13,0	7,5
		-12,9	7,1
Mangrove	8	-23,4[-24,5/-19,7]	2,3[0,9/3,3]

*Individual data.

** Bone tissue.

6.3. Baseline

Corrected for pollution, modern terrestrial animals (pig and chicken) have similar $\delta^{13}\text{C}$ values, ranging from -19,7 to -17,5 ‰, to historical animals, ranging from -19,7 to -15,7 ‰ (Fig. 4). Modern terrestrial animals have higher $\delta^{15}\text{N}$ values (8,0 and 9,3 ‰) than historical animals, including chicken, goat and pig (5,7–7,9 ‰), probably due to changes in animal feed. *Canarium* nuts' $\delta^{13}\text{C}$ values range from -27,2 to -25,7 ‰ and $\delta^{15}\text{N}$ values from 4,5 to 7,1 ‰. Historical coral reef fish collagens show a wide range of $\delta^{13}\text{C}$ values, from -12,4 to -3,4 ‰ while $\delta^{15}\text{N}$ values range from 6,8 to 10,5 ‰. Fish $\delta^{13}\text{C}$ values of show a trend according to taxa, with Serranidae and Lutjanidae having lower values (in average around -10,8 ‰) than Scaridae (around -5,8 ‰), a variation consistent with their habitat and or feeding habits.

Overall, our new data for *Canarium* nuts, terrestrial animal, and marine animal resources overlap with the distribution of isotopic data previously published by Kinaston et al. (2014b), despite slight differences (Fig. 4). The Vanuatu resources baseline, as a whole, shows a distribution of the different food resources consistent with three clusters. One, with lower $\delta^{13}\text{C}$ values, overlaps a C3-foodweb for plants as fruit, tuber, nut, and mangrove environment comprising shellfish and crustaceans (-28,1 to -21,1 ‰). A second cluster corresponds to animals, mainly chickens and pigs (-20,2 to -15,7 ‰) and a third, with higher $\delta^{13}\text{C}$ values, corresponds to a C4-plant and marine foodweb (-13,4 to -3,4 ‰). Interestingly, mangrove resources and coastal products have lower $\delta^{15}\text{N}$ values in their respective cluster making it possible to decipher their contribution to the human diet.

6.4. Human diet

Twenty-six human collagen $\delta^{13}\text{C}$ values range from -19,7 to -16,2 ‰, and $\delta^{15}\text{N}$ values from 6,3 to 9,7 ‰ (Tables 1 and 4). We propose here a human diet modelling using an expected trophic enrichment between diet and consumer tissues as described above (Fig. 5). The overall

distribution of the South Vanuatu human isotopic values is closer to a C3-foodweb than a C4-foodweb, suggesting a preferential contribution of terrestrial over marine or C4 pathway resources. The signatures of C4 resources, such as maize, whose starch has been identified in dental calculus (Velsko et al., 2024), may not have been incorporated into the collagen of consumers because they were consumed too close to the time of death of the individuals. Incorporation of isotopic characteristics of a given food takes several years (Hedges et al., 2007). The general isotopic modelling shows an overlap between humans and mangrove and vegetarian diets. Their dietary consumption is focused on foods characterised by low carbon and nitrogen isotopic ratios such as fruits, tubers, nuts and shellfish and crustaceans, and the $\delta^{15}\text{N}$ values indicate a preferential intake of low trophic resources. There is also an isotopic dispersion of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, of more than 3,4 ‰, supporting the hypothesis of a number of different individual diets (O'Connell et al., 2001) (Fig. 5). Considering our Vanuatu baseline, it can be suggested that the individuals with the highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values would have a marine coral reef fish diet in addition to the C3-plant and mangrove intake. One individual, with the lowest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, could have consumed resources from mangroves only.

6.5. Spatial and temporal distributions

Three main observations derive from the analysis of the isotopic values from Aniwa, Tanna and Futuna (Fig. 6). First, the individuals tend to group by island of origin. The observed pattern suggests preferential access to terrestrial resources for the Futuna individuals, including foods with a higher animal protein content for some of them. The same terrestrial input is observed in Tanna individuals (PACH 114: TARS3 Burial 1, PACH 135: Kolapikin), although low nitrogen isotope ratios and high carbon isotope ratios would suggest a contribution from marine shellfish or algae in one individual (PACH 134: Enarpap). Marine protein ingestion dominates in Aniwa individuals, with two showing a probable consumption of marine resources (PACH 112 and PACH 136: burials 1 and 2 from Nakmaroro), and one (PACH 137: Iariso site) with a unique pattern ($\delta^{13}\text{C} = -19,0$ ‰; $\delta^{15}\text{N} = 6,3$ ‰) suggesting contribution of low trophic level foods, which could be focused exclusively on mangrove resources.

Second, the temporal comparison, shown in Fig. 7, highlights two main trends consisting of a wider dispersion of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the earlier individuals (n = 17), ranging from -19,7 to -16,2 ‰ and 7,3 to 9,7 ‰ respectively, than for the later individuals (n = 7), ranging from -19,3 to -18,2 ‰ and 7,6 to 8,7 ‰ respectively, with a significant difference for $\delta^{15}\text{N}$ values (Table 4, Fig. 5). This pattern could be interpreted as a reduction in the dietary breadth over time, characterised by a greater marine protein intake for the earlier individuals and a more vegetarian and mangrove diet for the more recent individuals.

Third, a specific focus on the Futuna individuals (n = 17) shows a difference of $\delta^{15}\text{N}$ variances between earlier and later individuals while $\delta^{13}\text{C}$ values overlap (Fig. 7C, Test Brown-Forsythe: p-value = 0.040). Earlier individuals have higher $\delta^{15}\text{N}$ values, ranging from 8,1 to 9,7 ‰ and later individuals have lower $\delta^{15}\text{N}$ values, ranging from 7,6 to 8,7 ‰. This pattern appears to be primarily related to a temporal change in diet composition and breadth at the island level. The diets of the earlier individuals, uncovered from subsurface mortuary contexts, appear to be more heterogeneous and diversified, than the diets of the later individuals. With a narrower range of diets included in that of the former,

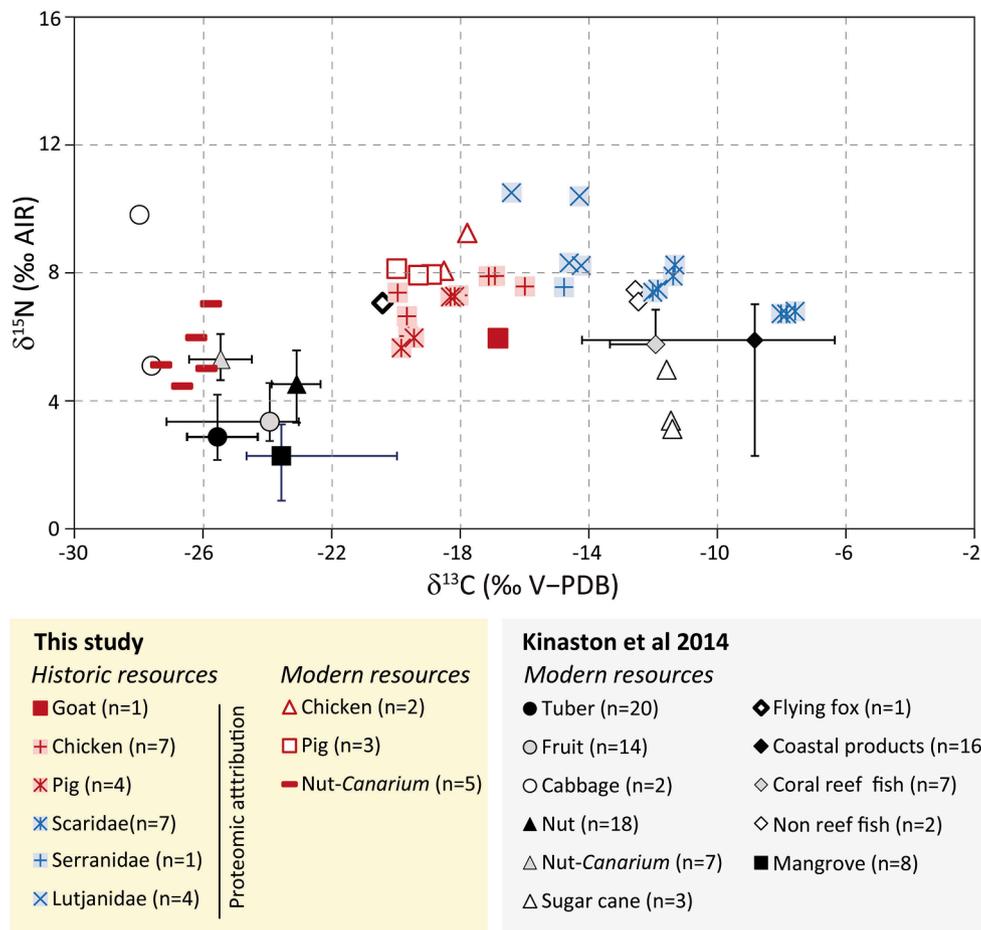


Fig. 4. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of baseline from South Vanuatu. Contemporary and historic isotopic baseline from Aniwa and Emae (this study) and from Malekula and Efate (Kinaston et al., 2014b). Modern $\delta^{13}\text{C}$ values are pollution corrected by adding + 1.5 ‰/+0.86 ‰ for terrestrial and marine resources respectively; animal bone collagen $\delta^{13}\text{C}$ values are converted to flesh by subtracting -3.7 ‰ as recommended by Keegan and DeNiro (1988).

Table 4
Descriptive statistics of isotopic data of human individuals from Southern Vanuatu, from Aniwa, Futuna and Tanna islands.

	n	$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)			
		min	max	Moy \pm 1SD	Med [IQ1–IQ3]	min	max	Moy \pm 1SD	Med [IQ1–IQ3]
Total	26	-19,7	-16,2	-18,5 \pm 0,8	-18,7[-19/-18,2]	6,3	9,7	8,3 \pm 0,7	8,3[8/8,6]
Aniwa	5	-19,0	-16,2	-17,7 \pm 1,1	-17,9[-18,3/-17,2]	6,3	8,6	7,9 \pm 0,9	8,3[7,6/8,5]
Futuna	18	-19,7	-16,9	-18,7 \pm 0,6	-18,8[-19/-18,4]	7,6	9,7	8,5 \pm 0,5	8,4[8,1/8,7]
Tanna	3	-19,1	-17,7	-18,5 \pm 0,7	-18,6[-18,9/-18,2]	7,3	7,8	7,5 \pm 0,3	7,5[7,4/7,7]
Earlier	16	-19,7	-16,2	-18,3 \pm 0,9	-18,5[-18,9/-17,8]	7,3	9,7	8,5 \pm 0,6	8,4[8,2/8,7]
Later	7	-19,3	-18,2	-18,8 \pm 0,4	-18,9[-19,1/-18,6]	7,6	8,7	8,1 \pm 0,3	8,1[7,9/8,3]
Post-European contact	3	-19,1	-18,0	-18,7 \pm 0,6	-19[-19,1/-18,5]	6,3	8,7	7,5 \pm 1,2	7,5[6,9/8,1]
Earlier-Futuna	11	-19,7	-16,9	-18,7 \pm 0,7	-18,8[-18,9/-18,4]	8,1	9,7	8,7 \pm 0,6	8,6[8,2/8,8]
Later-Futuna	6	-19,3	-18,2	-18,9 \pm 0,4	-18,9[-19,1/-18,7]	7,6	8,7	8,1 \pm 0,4	8,1[8/8,3]

Mean \pm 1 SD if n \geq 10; Med = median: Med [IQ1–IQ3] if n \geq 5.

the later individuals indicate a homogenisation of the resources consumed, with an emphasis on low trophic level foods. In parallel with this collagen isotopic composition variation, the Futuna individuals show a change through time in occurrences of advanced occlusal dental wear and caries, with the later individuals being less affected than the earlier individuals, a pattern suggesting a change in food types and/or preparation techniques (Zinger, 2021). An increased use of vegetable food cooked in earth oven may explain such a trend in dental wear, which is consistent with the isotopic results. Archaeological evidence for terraced agriculture and earth ovens from Futuna date to within the last 1000 years (Flexner et al., 2018, 2019a).

7. Discussion

Four patterns in our results illustrate issues of equifinality in bio-archaeological data interpretation, particularly regarding the representativeness of the series of individuals studied and the conditions or circumstances of burial (Pradier and Valentin, 2023). Our isotopic results, obtained from skeletal remains of 26 individuals from Futuna, Aniwa and Tanna, three islands of the South Vanuatu region, may reflect: 1) the geographical characteristics of the islands, 2) the normalisation of diet over time, 3) the nutritional stress on the individuals in relation to environmental and climatic factors, and 4) social differentiation or inequality in food acquisition and/or consumption.

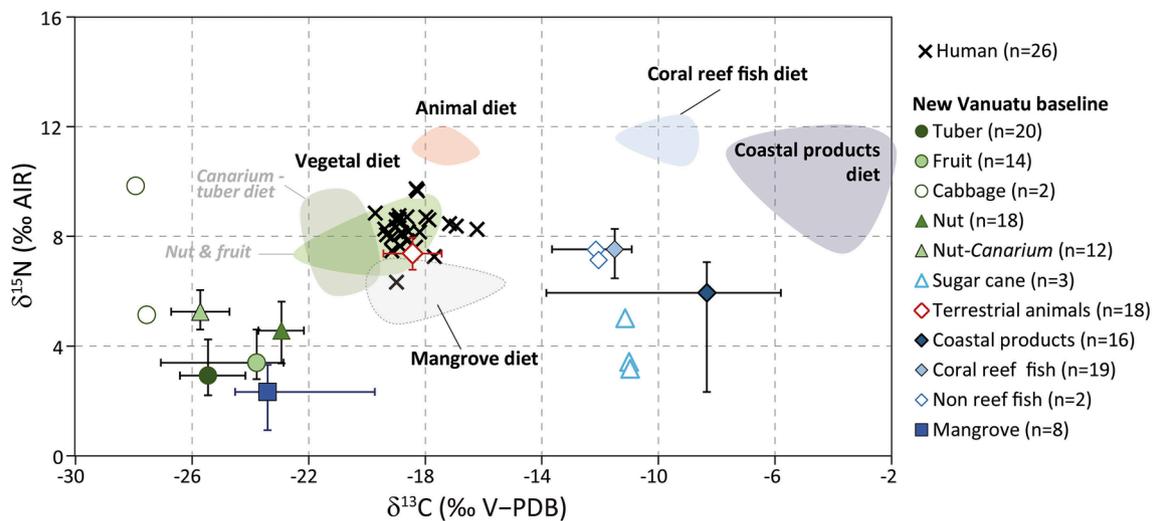


Fig. 5. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of baseline and humans from South Vanuatu. Human isotopic values from Aniwa, Futuna and Tanna with dietary modeling based on the new baseline with a trophic enrichment between diet-consumer of +5 ‰ and +1 ‰ in ^{13}C , (respectively from flesh and collagen), and +3–5 ‰ in ^{15}N . (See Fig. 4 for isotopic correction for pollution and for flesh tissues).

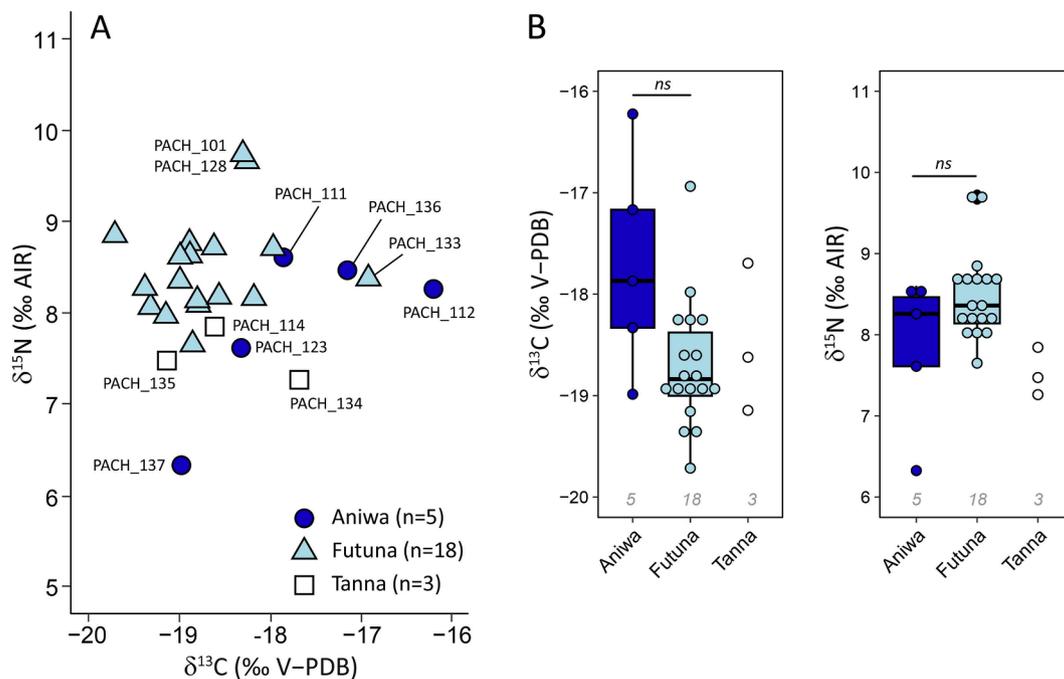


Fig. 6. Distribution of human $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for Aniwa, Futuna and Tanna islands (A); p-value of Brown-Forsythe test (B).

7.1. Geographical characteristics of islands

The pattern of individuals grouped by island initially appears consistent with the highly contrasting biogeographic potential of the islands and their own development towards specific sustainable subsistence lifestyles as evidenced in the archaeological record (Flexner et al., 2022; 2024). Without excluding a vegetal contribution, the diet of early Aniwa individuals (between 2000 and 1100 BP), with isotope ratios between $-19,0$ and $-16,2$ ‰ and $7,6$ and $8,6$ ‰ for carbon and nitrogen respectively, appears to have been directed mainly towards exploiting the highly productive marine environments of the island. This pattern aligns with the relatively limited agricultural potential of the island and the abundance of fish, shellfish and crustaceans sheltered by the northern lagoon. Our archaeological record highlights the use of coastal fishing camp sites with concentrations of shellfish remains and

cooking combustion features, over the last 1000 years (Flexner et al., 2018; 2024).

Conversely, while showing a large variability of diet (ranging from $-19,7$ to $-16,9$ ‰, and $7,6$ to $9,7$ ‰ respectively), the Futuna individuals have developed a significant dietary focus on the terrestrial resources consistent with their subsistence practices. Taking advantage of the successive natural terraces, they have established dry agriculture in the north and west sides of the island and irrigated taro pond-fields in its south and east sides. By 700 BP, steeper areas were being exploited, and by about 400 BP the entire island was covered by terraced gardens (Flexner et al., 2024). The reliance of Tanna individuals on mixed diets, characterised by isotope ratios ranging from $-19,1$ and $-17,7$ ‰ for carbon and $7,3$ and $7,8$ ‰ for nitrogen, is consistent with a more diversified environment, enriched and fertilised by rich volcanic ash (Quantin, 1992). This trend of isotopic variation, paralleling the human

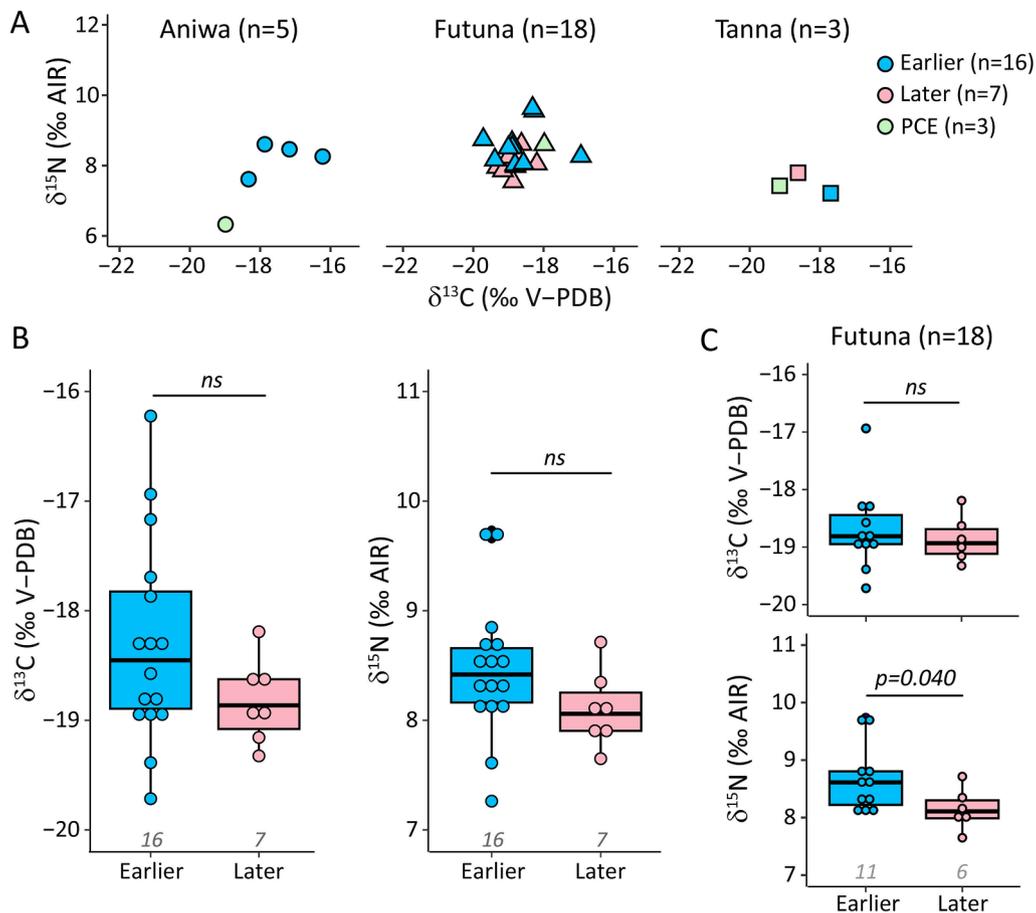


Fig. 7. Human $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values according to time and islands (A). Boxplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value according to earlier and later chronological attributions (B). Boxplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value according to time for Futuna individuals (C). (p-value of Brown-Forsythe test).

response and adaptation to the physical characteristics of the island where people lived, is not uncommon in the South-West Pacific; for example it has been observed in the Fijian archipelago (Field et al., 2009; Jones and Quinn, 2009). Individuals from small islands of the Yasawa and Lau groups show the maintenance of a higher contribution of foods of higher trophic levels and a marine based diet compared to individuals from inland zones of larger islands such as Vitu Levu, which show the persistence of a more terrestrial based diet (Appendix A).

7.2. Normalisation of diet over time

However, factors beyond geographic and territorial influences may have intertwined. We note that 1) the earlier individuals from South Vanuatu, when considered collectively, show a broader diversity of diet than the later individuals and 2) the later individuals from South Vanuatu, also considered collectively, clearly relied on terrestrial proteins of low trophic level. Given these results, we could hypothesise a normalisation of dietary practices over time in the three islands, with a preference for vegetarian resources, and somehow a dependence on a limited number of resources in recent times, although items from the mangrove, like crustaceans, mollusks and/or fish, may have contributed to the diet in Aniwa. This pattern clearly recalls the descriptions of the diet and subsistence strategy reported in early ethnographic records of the region (Humphreys, 1926; Speiser, 1996).

A hypothesis of a dietary transition to a more vegetarian regime has already been formulated to explain changes in isotope ratios observed in several skeletal series from South West Pacific islands (Fenner et al., 2021; Kinaston et al., 2014a; Valentin et al., 2014). The trend towards a more vegetarian subsistence economy observed between the first

settler's communities (c. 3000 BP) and the established agricultural post-Lapita communities (c. 2500 BP) of Central and North Vanuatu is preferentially interpreted as an adaptive response of populations to the conditions of their newly settled local environment (Kinaston et al., 2014a; Valentin et al., 2014). On the other hand, the trend towards a more terrestrial diet, which may have occurred around 700 BP in Tonga, Western Polynesia, is understood in socio-political terms and associated with the formation of the Tongan State formation and the establishment of a new agricultural regime and land management (Fenner et al., 2021). Interestingly, this change in subsistence economy in Tonga may have coincided with the introduction of new crops from East Polynesia (Ussher, 2015, p. 226 but see Yen, 1973).

Regarding South Vanuatu, the incursion of Polynesians groups in the region during the last millennium co-occurs with an intensification of agriculture on Futuna (Flexner et al., 2024) and potentially regional exchanges of cultivated crops and food preparation techniques, although the presence of Polynesian plant species in South Vanuatu has not been archaeobotanically confirmed so far. The introduction of a banana variety known as *kiamu* (*Musa discolor*, Iholena morphotype, Kagy et al., 2016) traced from South Vanuatu to New Caledonia through oral histories would mark the arrival of a group (the Xetriwaan) in the Loyalty Islands from the island of Aneityum (Sand, 1995 p. 210; Spriggs, 1997 p.219–222), and possibly from further east (Sand, 1995). Polynesian loanwords in South Vanuatu include words associated with the preparation and preservation of food and drink: fermented food, kava preparation, and pig (Clark, 1994; Lynch, 1996; see also Barrau, 1958; Yen, 1973). Other plant introductions have also occurred during initial European Contact, such as early examples of *Zea mays* found in missionary contexts in Tanna from the 1800s (Flexner et al., 2019b).

Associated interactions between newcomers and local host communities may also have contributed to the isotopically observed dietary changes in South Vanuatu populations. However, this interpretation of our South Vanuatu isotopic data could be challenged. Other factors, such as nutritional stress or social differentiation, may have interfered.

The focus on the Futuna Island series illustrates the challenge of equifinality that arises in interpreting isotopic data in relation to the nature of the archaeological sample and its representativeness. The Futuna series shows significant difference in diet between ancient (c. 1270–970 cal BP) and more recent individuals (c. 300–0 cal BP), with the diet of the later individuals being significantly less variable than diet of the earlier. The observed pattern may represent two distinct situations, considering the time-gap between the earlier and later isotopic variations. These situations include social specific dietary behaviours (Flexner et al., 2019b, Valentin et al., 2006), or dietary stress related to natural disasters and climate change, which are known to have periodically affected South Melanesia, including Vanuatu, in the deep past as well as in more recent period (Siméoni, 2009).

7.3. Nutritional stress and environmental and climatic factors

Higher nitrogen isotope values in the earlier individuals from Futuna could suggest either consumption of a diet enriched in animal protein or a response to physiological stress. Enrichment in ^{15}N in tissues can occur in contexts of nutritional stress, including water stress and undernutrition (Beaumont and Montgomery, 2016; Mekota et al., 2006; Walter et al., 2020). Dry conditions can also induce an increase in the $\delta^{15}\text{N}$ values of plant cover, which can be transmitted along the local trophic chain and recorded in consumer tissues (Ambrose, 1991; Schwarcz et al., 1999). The first hypothesis of ingestion of a high quantity of animal protein is unlikely because terrestrial animal and fresh water food resources are limited on Futuna, with pig more visible in the archaeological record after Polynesian migration of 1000 BP, but generally reserved for ceremonial purposes (Flexner et al., 2022; 2024). The second hypothesis of physiological stress is more plausible, consistent with the skeletal analysis of the Futuna individuals. Zinger (2021) points to a number of anomalies in the subsurface individuals dated to c. 1270–970 cal BP: mortality quotient of age category [5–9] years slightly higher than expected for natural mortality, discordance between age indicators in subadults, endocranial lesions with new bone formation in one of them and subperiosteal new bone formation on adult long bones (9 % of subsurface individuals). All may account for abnormal mortality, abnormal growth and development and nutritional deficiencies, although non-specific (Geber, 2014; Lewis, 2004; Pietrusewsky et al., 2020; Vlok et al., 2023). Possible cases of malnutrition have been diagnosed in other contexts of transition to agriculture in tropical environments, including Vanuatu where scurvy caused by episodes of resource stress at the time of the archipelago's first colonisation, c. 3000 BP, may have affected perinatals and adults at Teouma (Buckley et al., 2014; Halcrow et al., 2014; Vlok et al., 2023). Interestingly, in the case of Futuna, climatic data document a drier phase around 1100–500 cal BP, possibly associated with cooling and change in marine productivity in South Melanesia and West Polynesia (Sear et al., 2020; Maloney et al., 2022), suggesting the possibility of food shortage episodes and dietary re-orientations in South Vanuatu.

7.4. Social differentiation in food acquisition and/or consumption

The isotopic signatures of the later Futuna individuals, dated to c. 300–0 cal BP, could well reflect on individual identity and socially differentiated patterns of food consumption. Isotopic studies of past populations in the South-West Pacific have reported dietary differences between adults and subadults in Bourewa (Fiji) or between elites and commoners in Atele (Tonga) and Namu (Solomon Islands) (e.g. Fenner et al., 2015; Kinaston et al., 2013; Stantis et al., 2015; 2016; Valentin et al., 2006;). For example, the study of the Namu burials, a Polynesian

outlier community on Taumako island, showed that “richer” individuals consumed different and more valued foods from higher trophic levels than “poorer” individuals (Kinaston et al., 2013), with “grave wealth” determined by the questionable criteria of quantity and quality of artefacts associated to the dead. Regarding the diet of the later individuals from Futuna, we note that they all have low carbon isotope ratios, consistent with ingestion of low trophic level terrestrial proteins derived from tubers, nuts, and/or fruits. This pattern would indicate that individuals whose bodies were deposited on the surface of the rock-shelters, mainly c. 300–200 years ago, had a more vegetarian diet. This variation could tentatively be interpreted as related to the particular dietary behaviour among a specific segment of the Futuna community at that time. Analysis of the skeletal remains exposed in these surface contexts suggests a possible gender-based social differentiation in funerary behaviour and highlights a preferential use of certain rock-shelters for deposition of female individuals (Zinger, 2021).

Gender differences in dietary patterns are not unexpected in past Pacific societies (e.g. Jones, 2009). Several isotopic studies of South-West Pacific human skeletal remains have highlighted significant differences between the sexes, with a consistent trend of female exhibiting lower trophic level dietary regimes compared to males (Kinaston et al., 2014b; 2013; Stantis et al., 2015). Observed in Polynesian or Polynesian-related series dated to c. 500 – 150 BP, such a male–female differential pattern appears to be of second order, generally combined and even partly masked by other social differentiations. Kinaston et al. (2013), for example, noted that “the stable isotope results indicate that “wealthy” individuals and males [from Namu] were eating more foods from higher trophic levels”. Authors generally interpret this sexual differentiation as a consequence of sex-specific practices in food allocation and specialisation in daily labour (Stantis et al., 2015; Kinaston et al., 2013), or the preferential distribution of more socially-valued (prestigious) foods to men (Kinaston et al., 2014b). In the case of Futuna, we suggest that a sex-based difference in diet may also be related, at least in part, to cultural factors and differential female mobility. Anthropometric methodologies applied to Futuna individuals suggest the presence of females with phenotypic characteristics closely associated with modern Polynesian individuals for both periods. Similar Polynesian morphological features are not observed in individuals identified as males. Dispersals and migrations from Polynesia to Futuna may have been gender-specific, suggesting that women from different, potentially distant, islands – including those from Polynesian regions – may have been driven by practices of exogamy, as hinted by oral stories (Zinger et al., 2024). Futuna oral records, indeed, emphasise the theme of a gendered mobility, narrating the arrivals of « winged » females originating from outside Futuna, probably from Tonga in West Polynesia, interacting with local males (Keller and Kuaotonga, 2007, p. 146–165).

8. Conclusion

Our investigation of the human dietary practices of 32 individuals from three islands of South Vanuatu: Aniwa, Futuna and Tanna, dated between 2000 BP and the 20th century, using carbon and nitrogen isotope data obtained from bone collagen, revealed that $\delta^{13}\text{C}$ values ranged from -19.7 to -16.2 ‰, and $\delta^{15}\text{N}$ values from 6.3 to 9.7 ‰ with a large inter-individual variability. Using an expanded baseline of local faunal and plant resources, with taxonomic identification of local faunal remains based on proteomic determinations (Zooarchaeology by Mass Spectrometry; ZooMS), we suggested that the individuals with the highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values would have consumed marine coral reef fish along with C3 plants, and that an individual with the lowest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values may have consumed mainly mangrove resources. However, several challenges persist in comprehending the changes in dietary practices over time in South Vanuatu, starting with the nature of the sample studied, not only because of its size but also because it is culturally defined. Whether the differences in funerary choice of burial place in South Vanuatu were related to sampling issues, the islands'

geographical form and the need to conserve land for cultivation, cultural differences related to the arrival of migrants from Polynesia around 1000 BP, or diseases brought to the region by European voyagers remain open questions. Similarly, a potential transition in subsistence and economic strategies, from exploitation to production and dependence on a narrower range of resources, is not readily isotopically demonstrable in the case of South Vanuatu, in relation to equifinality issues. Dietary variation over time may be linked to locally developed strategies shaped by ecological conditions and/or climate change, although the isotopically observed effect could also be influenced by cultural selection biasing the mortuary assemblages and in turn emphasising specific dietary behaviours of particular social groups sampled within a wider community.

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CRedit authorship contribution statement

Frédérique Valentin: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Estelle Herscher:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Investigation, Funding

acquisition, Formal analysis, Data curation. **Wanda Zinger:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation. **Julien Ponchelet:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation. **Guy André:** Writing – review & editing, Writing – original draft, Validation, Supervision, Investigation, Formal analysis. **Fabrice Bray:** Writing – review & editing, Writing – original draft, Validation, Investigation, Funding acquisition, Formal analysis, Data curation. **James Flexner:** Writing – review & editing, Writing – original draft, Validation, Project administration, Funding acquisition. **Stuart Bedford:** Writing – review & editing, Writing – original draft, Funding acquisition. **Takaronga Kuautonga:** Writing – review & editing, Writing – original draft, Supervision, Project administration. **Edson Willie:** Writing – review & editing, Writing – original draft, Supervision, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Summary Table of isotopic analyses on Southwest Pacific archaeological skeletal series (J. Ponchelet).

Site	n	Dates	Dietary trend	References
PNG				
Watom (New Britain)	8	c. 2800–2350 BP [a]	Mixed, marine resources of low and high trophic levels and terrestrial resources of low trophic level	Kinaston et al. 2015
Nebira ACJ (South Coast)	28	800–300 cal. BP [b]	Terrestrial, terrestrial resources low and high trophic levels	Kinaston et al. 2013a
Site AAK (Motupore)	14	c. 500–400 BP [c]	Marine, marine resources of low trophic level	Leach et al. 2001
SALOMON				
Namu (Taumako)	96	440–150 cal. BP [d]	Mixed, terrestrial resources of low and high trophic level and marine resources low trophic level	Kinaston et al. 2013b
VANUATU				
Teouma (Efate)	49	2940–2880 cal. BP [e]	Marine to mixed, marine resources of low and high trophic levels and contribution of terrestrial resources of low and high trophic levels	Valentin et al. 2010, Kinaston et al. 2014b
Teouma (Efate)	6	2770–2710 cal. BP [f]	Terrestrial, terrestrial resources of low trophic level	Valentin et al. 2014
Vao (Vao)	2	before 2600 BP	Marine to mixed, marine resources of low trophic level and contribution of terrestrial resources of low trophic level	Kinaston et al. 2016
Vao (Vao)	2	c. 2300 – 1900 BP	Terrestrial, terrestrial resources of low and high trophic levels	Kinaston et al. 2016
Uripiv (Uripiv)	6	c. 2800–2600 BP	Marine to mixed, marine resources of low trophic level and contribution of terrestrial resources of low trophic level	Kinaston et al. 2014b
Uripiv (Uripiv)	3	c. 2600–2500 BP	Mixed, marine and terrestrial resources of low trophic level	Kinaston et al. 2014a
Uripiv (Uripiv)	14	c. 2500–2000 BP	Mixed, marine and terrestrial resources of low trophic level	Kinaston et al. 2014a
Uripiv (Uripiv)	4	c. 300–150 BP	Terrestrial, terrestrial resources of low trophic level	Kinaston et al. 2014a
NEW CALEDONIA				
Koné (WKO013B)(Grande terre)	1	2500–2350 cal. BP	Mixed, marine resources of low trophic level and terrestrial resources of high trophic level	Pietruszewsky et al. 1998
Koné (WKO013C)(Grande terre)		2100–1990 cal. BP	Mixed, marine resources of low trophic level and terrestrial resources of high trophic level	Petchey et al. 2011
Tina (Grande terre)	2	c. 850 BP	Marine, marine resources of low trophic level	Leach et al. 2001

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Site	n	Dates	Dietary trend	References
Naitabale (Moturiki)	1	2740–2739 cal. BP	Marine to mixed, marine resources of low trophic level and contribution of terrestrial resources of high trophic level	Nunn et al. 2007
Olo (Waya)	12	2758–2503 cal. BP	Marine to mixed, marine resources of low trophic level and contribution of terrestrial resources of high trophic level	Field et al. 2009
Na Masimasi (Nayau)	3	2760–2700 cal. BP	Terrestrial to mixed, terrestrial resources of low and high trophic levels and contribution of marine resources of low trophic level	Jones et Quinn 2009
Dau Rockshelter (Aiwai Lailai)	1	2460–1310 cal. BP	Mixed, terrestrial resources of low and high trophic levels and marine resources of low trophic level	Jones et Quinn 2009
Naselala (Cikobia)	1	c. 1730 cal. BP	Terrestrial to mixed, terrestrial resources of low trophic level and contribution of marine resources of high trophic level	Valentin et al. 2008
Sigatoka Sand Dune (Viti Levu)	23	1888—1272 cal. BP[h]	Terrestrial to mixed, terrestrial resources of low trophic level and contribution of marine resources of low trophic level	Phaff et al. 2016
Nokonoko (Viti Levu)	1	1300–1174 cal. BP	Terrestrial, terrestrial resources of low and high trophic levels	Field et al. 2009
Qaranicagi (Waya)	2[i]	760–250 cal. BP	Mixed, terrestrial resources of low trophic level and marine resources of low trophic level	Field et al. 2009
Bourewa (Viti Levu)	37	750–150 cal. BP	Marine to mixed, marine resources of low trophic level and contribution of terrestrial resources of low trophic level	Stantis et al. 2016
Lau Group [j]	5	710–0 cal. BP	Mixed, terrestrial resources of low trophic level and marine resources of low trophic level	Jones et Quinn 2009
Wakea (Lakeba)	1	530–450 cal. BP [k]	Marine, marine resources of low trophic level	Leach et al. 2001
Bukusia (Viti Levu)	1	427–4 cal. BP	Terrestrial, terrestrial resources low and high trophic levels	Field et al. 2009
Korotuku (Cikobia)	9	European Contact	Terrestrial to mixed, terrestrial resources of low trophic level and contribution of marine resources of high trophic level	Valentin et al. 2006
TONGA				
Talasiu (Tongatapu)	16	2700–2600 cal. BP	Marine, marine resources of low and high trophic levels	Herrscher et al. 2018
Tongatapu [l]	2	c. 1458–965 BP	Mixed, terrestrial resources of low and high trophic levels and marine resources of low and high trophic levels	Fenner et al. 2021
Tongatapu [m]	91	759–0 cal. BP	Mixed, terrestrial resources of low and high trophic levels and marine resources of low and high trophic levels	Fenner et al., 2021
Atele (Tongatapu)	41	c. 570–145 BP	Mixed, terrestrial resources of low and high trophic levels and marine resources of low and high trophic levels	Stantis et al. 2015
SAMOA				
Fatu-ma-Futi (Tutuila)	7	c. 1000 BP	Terrestrial to mixed, terrestrial resources of low trophic level and contribution of marine resources of low trophic level	Valentin et al. 2011
Lauli'i (Tutuila)	6	c. 500 BP	Terrestrial to mixed, terrestrial resources of low trophic level and contribution of marine resources of low trophic level	Valentin et al. 2011
Tutuila [n]	5	280–0 cal BP	Terrestrial to mixed, terrestrial resources of low trophic level and contribution of marine resources of low trophic level	Eerkens et al. 2019
PALAU				
Chelechol ra Orrak (Orrak)	19	3000–1800 cal. BP	Marine to mixed, marine resources of low trophic level and contribution of terrestrial resources of low and high trophic levels	Stone et al. 2019
Koror Quarry (Koror)	3	2500–1250 cal. BP	Marine to mixed, marine resources of low trophic level and contribution of terrestrial resources of low and high trophic levels	Stone et al. 2019
Peleliu (Peleliu)	1	No date?	Mixed, terrestrial resources of low trophic level and marine resources of low trophic level marine resources	Stone et al. 2019
MICRONESIA				
Putau KA3 (Kapingamarangi)	2	c. 700 BP	Marine, marine resources high trophic level	Leach et al. 2001

[a] Dates in Petchey et al. 2011.

[b] Authors data.

[c] Dates in Allen, J. (2017).

[d] Dates in Kramer et al. (2021)

[e] and [f] Dates in Petchey et al. (2014, 2015).

[g] and [i] Number of skeletal specimens, in Field et al. (2009)

[h] Authors data.

[j] Sites: Nukutubu Rockshelter 2, Nayau (n = 1, 540–420 cal. BP); Qara ni lulu, Nayau (n = 1, 710–620 cal. BP); Ulunikoro, Nayau (n = 1, Mid-Late prehistoric); Korovatu Rockshelter 2 (n = 1, Mid-Late prehistoric); Coastal Rockshelter, Aiwai Levu (n = 1, Late prehistoric), in Jones et Quinn (2009).

[k] Calibrated dates from Petchey et al. (2011).

[l] Sites: To-Pe-1-Ak (n = 1, c. 1458 BP); JO9 (n = 1, c. 965 BP), in Fenner et al. (2021).

[m] Sites: To-Pi-15 (n = 2, after 800 BP); To-Fa-4 (n = 4, c. 750 BP); J28 Aponima (n = 15, c. 500 BP); To-At-36 (n = 27, c. 410–240 BP), Talasiu Sk8 (n = 1, c. 237 BP), Atele (n = 42, c. 570–145 BP) in Fenner et al. (2021).

[n] Sites: Ili'iili, Tutuila (n = 1, 260 cal. BP); Pavai'a, Tutuila (n = 3, 280–0 cal. BP); Auto, Tutuila (n = 1, 250–0 cal. BP) in Eerkens et al. (2011)..

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Appendix B. Isotopic analysis (E. Herrscher)

Bone collagen extraction was performed, between 2018 and 2022, at the *Laboratoire Méditerranéen de Préhistoire Europe-Afrique*, Aix Marseille University. After a cleaning of a piece of bone (250 mg) with MiliQ water, each bone sample was ground into a powder (>700 µm for collagen). Extraction protocol was performed according to the classical ABA protocol as described in [Herrscher et al \(2018\)](#). A preliminary step was carried out on the modern animal bones to delipidify them, involving several successive baths in methanol and chloroform solutions. The seeds were ultrasonically cleaned in MiliQ water, dried and then ground to a powder before being directly encapsulated. Quality of the collagen is assessed using conventional criteria: collagen extraction yield > 10 mg.g⁻¹, %C between 15.3 % and 47 %, %N between 5.5 and 17.3 %, atomic C/N ratio between 2.9 and 3.6 (DeNiro, 1985; Ambrose, 1990; van Klinken, 1999). Only samples with elemental compositions within these ranges are accepted for further analysis.

Pre-weighted bone collagen samples were measured with a Europa Scientific™ elemental analyzer, coupled to a mass spectrometer at Isoanalytical (Crewshire, UK). Stable isotopes were measured relative to standards (V-PDB for carbon, AIR for nitrogen) and expressed in parts per mil (‰). The reference material for collagen is IA-R068 (soy protein, δ¹³C_{V-PDB} = -25.22 ± 0.02 ‰, δ¹⁵N_{AIR} = 0.99 ± 0.07 ‰), and for seed, IA-R001 (wheat flour, δ¹³C_{V-PDB} = -26.43 ± 0.02 ‰, δ¹⁵N_{AIR} = 2.55 ± 0.02 ‰). For collagen samples, measurements uncertainty was monitored using check samples with

well characterized isotopic compositions: IA-R038 (L-alanine, $\delta^{13}\text{C}_{\text{V-PDB}} = -24.99 \pm 0.06 \text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = -0.65 \pm 0.04 \text{‰}$), IA-R069 (tuna protein, $\delta^{13}\text{C}_{\text{V-PDB}} = -18.88 \pm 0.05 \text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = 11.60 \pm 0.09 \text{‰}$) and a mixture of ammonium sulfate and IA-R046/IAEA-C7 (oxalic acid, $\delta^{13}\text{C}_{\text{V-PDB}} = -14.48 \pm 0.21 \text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = 22.04 \pm 0.06 \text{‰}$). Quality control check samples are calibrated and traceable to the international standards IAEA-CH-6 and IAEA-N-1. Measurements uncertainty for seeds was monitored using check samples with well characterized isotopic compositions: IA-R045/IA-R005 (mixture of ammonium sulfate and beet sugar, $\delta^{13}\text{C}_{\text{V-PDB}} = -26.03 \pm 0.11 \text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = -4.71 \pm 0.07 \text{‰}$), IA-R046/IA-R006 (mixture of ammonium sulfate and cane sugar, $\delta^{13}\text{C}_{\text{V-PDB}} = -11.64 \pm 0.03 \text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = 22.04 \pm 0.06 \text{‰}$). Quality control check samples are calibrated and traceable to the international standard IAEA-CH-6 and IAEA-N-1.

Using calculation provided by Szpak et al. (2017) based on repeated measurements of calibration standards, check standards and sample replicates, precision ($u(R_w)$) is of $\pm 0.03 \text{‰}$ and $\pm 0.08 \text{‰}$, respectively for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for bone collagen, and of $\pm 0.03 \text{‰}$ and $\pm 0.17 \text{‰}$, for seeds. The total analytical uncertainty is estimated, for collagen, to be $\pm 0.16 \text{‰}$ and $\pm 0.18 \text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and for seed, to be $\pm 0.10 \text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.29 \text{‰}$ for $\delta^{15}\text{N}$.

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Appendix C.: Proteomic identifications (F. Bray)

Digestion of bones

The protocol of digestion of bones is described in Bray et al (2023) (1). The used bone powder comes from the Laboratoire Méditerranéen de Préhistoire Europe-Afrique, Aix Marseille University. Proteomics analyses were performed at the laboratory Miniaturization for Synthesis, Analysis and Proteomics (MSAP UAR3290 CNRS), university of Lille, in 2023. Briefly, 1–5 mg of bone powder were deposited in 96 wells plate MultiScreenHTS-IP, 0.45 μm (MSIPS4510, Millipore, Billerica, MA, USA). Bone powder was demineralized, washed, gelatinized and digested in the 96 wells plate MultiScreenHTS-IP. The demineralization solution was digested in classical 96 well plates. The peptides from bones and demineralized solution were purified on C18 96 well plates (Affinisep, Petit-Couronne, France).

Purification of peptides

Briefly, the plate was washed once with 500 μL of acetonitrile (ACN) followed by a washing step with 80 % ACN, H_2O 0.5 % acetic acid repeated 3 times and a second washing repeated 3 times with H_2O alone 0.5 % acetic acid. Tryptic peptides from bone powder were resuspended in 200 μL of a H_2O , 0.5 % acetic acid solution. Tryptic peptides from both solutions were transferred to C18 96-well plate and eluted with a vacuum manifold. The plate was washed 3 times with 200 μL of H_2O , 0.5 % acetic acid. Peptides were recovered in a V-bottom well collecting plate using 100 μL of a 80 % ACN, 0.1 % acetic acid solution followed by 100 μL of ACN. The plate was evaporated on TurboVap 96 Evaporator (Caliper LifeScience, Hopkinton, USA). For mass spectrometry analysis, the sample was dissolved again in 10 μL of H_2O 0.1 % formic acid.

Mass spectrometry analysis.

Desalted peptides (1 μL) were deposited on 384 massive MALDI plates (Bruker Daltonics, Bremen, Germany), then 1 μL of HCCA matrix at 10 mg/mL in ACN/ H_2O 70:30 v/v 0.1 % TFA was added for each sample. The spots were dried at room temperature. MALDI FTICR experiments were carried out on a Bruker 9.4 Tesla Solarix XR FTICR mass spectrometer (Bruker Daltonics, Bremen, Germany). The frequency of laser was set to 1,000 Hz using the “Minimum” predefined shot pattern. MALDI FTICR spectra were generated in the m/z range from 693.01 to 5,000 by accumulating 10 scans. 2 M data points were used per spectrum which corresponds to a transient duration of 5.0332 s. The transfer time to the ICR cell was set to 1.2 ms and the quadrupole mass filter set at m/z 600 was operated in RF-only mode.

Bioinformatics

MS raw data from MALDI FTICR were processed using DataAnalysis 5.0. The identification is supported by all peptide markers presented in previous reports (2 à 12). The mass spectrometry proteomics data have been deposited on the ProteomeXchange Consortium (<https://proteomecentral.proteomexchange.org>) via the PRIDE partner repository with the data set identifier PXD047340 (Perez-Riverol et al. (2022)) (13).

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Appendix D. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jasrep.2024.104756>.

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