Language continuity despite population replacement in Remote Oceania

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SUMMARY PARAGRAPH
Recent genomic analyses show that the earliest peoples reaching Remote Oceania – associated with Austronesian-speaking Lapita culture – were almost completely East Asian, without detectable Papuan ancestry. Yet Papuan-related genetic ancestry is found across present-day Pacific populations, indicating that peoples from Near Oceania have played a significant – but largely unknown – ancestral role. Here, new genome-wide data from 19 South Pacific individuals provide direct evidence of a so-far undescribed Papuan expansion into Remote Oceania starting ~2,500 years before present, far earlier than previously estimated and supporting a model from historical linguistics. New genome-wide data from 27 contemporary ni-Vanuatu demonstrate a subsequent and almost complete replacement of Lapita-Austronesian by Near Oceanian ancestry. Despite this massive demographic change, incoming Papuan languages did not replace Austronesian languages. Population replacement with language continuity is extremely rare – if not unprecedented – in human history. Our analyses show that rather than one large-scale event, the process was incremental and complex, with repeated migrations and sex-biased admixture with peoples from the Bismarck Archipelago.

MAIN TEXT
Sahul – the continent comprising present-day Australia, Tasmania and New Guinea – was colonized by modern humans during the Pleistocene as early as 65,000 years before present1 (y BP). Yet it took more than 60,000 years for humans to move east of the Solomon Islands, from Near Oceania out into Remote Oceania2 (Fig. 1B). These seafaring Neolithic peoples, part of the Austronesian Expansion beginning ~5,500y BP, likely in present-day Taiwan and the nearby mainland3,4, carried farming technology and a major branch of the Austronesian language5 into Island Southeast Asia, eventually reaching New Guinea and the Bismarck Archipelago and encountering indigenous Papuans. Here, ~3,300y BP the Lapita cultural complex1 appeared – characterized by distinctive dentate-stamped pottery – and using the out-rigger sailing canoe Lapita peoples expanded east, leap-frogging beyond the Solomon Islands5,6 and transporting their landscapes3 and proto-Oceanic languages out into Remote Oceania. First arriving in the Reef-Santa
Cruz islands, Vanuatu10 and New Caledonia ~3,000y BP11, they rapidly navigated >800km of open ocean to Fiji, reaching western Polynesia by ~2,850y BP12.

Uncovering the extent of interaction between incoming Austronesian-Lapita and indigenous Papuan peoples is critical to understanding all subsequent Pacific prehistory. ‘Papuan’ here refers to both the non-Austronesian languages found across New Guinea and a component of genetic ancestry, likely to have diverged from the ancestors of present-day East Asians at least 27,000y BP13. The linguistic, cultural and genetic diversity in New Guinea is immense, due to complex histories of differentiation since occupation14. While the majority of Near Oceania today speak Papuan languages, Remote Oceania almost exclusively speaks Oceanic languages of the Austronesian family15. Bayesian phylogenetic analyses of 400 of the >1,200 Austronesian languages16 broadly support the Express Train model of the Austronesian Expansion, whereby Austronesian-speaking groups had negligible cultural or genetic interaction with indigenous Papuans in Near Oceania before moving further into the Pacific. However, the genetic composition of the present-day South Pacific indicates a more complex history, comprising major East Asian-Austronesian and minor Papuan components of genome-wide ancestry (~79:21%/6, ~87:13%/7).

Mitochondrial DNA (mtDNA)17 and Y-chromosome18,19 studies show that populations across Polynesia have maternal ancestry largely of Austronesian origin (>96%/20) while the majority of their Y-chromosomes derive from Near Oceania (>60%/20), confirmed in recent X-chromosome analyses12,21. This suggests that Oceanic-speaking populations – prior to or during the formation of the Lapita cultural complex – experienced significantly sex-biased admixture, involving women of Austronesian origin and Papuan men. This model requires that Lapita peoples, while maintaining proto-Oceanic language(s), had admixed ancestry in Near Oceania prior to their eastward expansion into Remote Oceania. However, the first genome-wide ancient data from the region21 demonstrates – consistent with craniofacial analyses22 – that Papuan ancestry is largely absent in individuals from Lapita sites in both Vanuatu and Tonga. The present-day genetic ancestry of Remote Oceania can therefore only be explained by subsequent population expansion, carrying Papuan ancestry into the Pacific.

Vanuatu has been an important hub in the western Pacific23 from Lapita onwards. Uncovering the detailed demographic processes shaping the genetic and linguistic landscape of Vanuatu is thus crucial to understanding those of the wider Pacific. Here we provide the earliest direct evidence of Papuan genetic ancestry in Remote Oceania. Our results reveal that peoples from Near Oceania began arriving just a few centuries after the first Lapita settlements in Vanuatu. This was followed by an almost complete – yet incremental – replacement of Lapita-Austronesian by Bismarck Archipelago-like genetic ancestry.

RESULTS

Ancient and modern genome-wide data. We recovered genome-wide and mitochondrial aDNA data from the bones or teeth of 19 individuals from archaeological sites 14C-dated to ~2,600-200y BP across Vanuatu (n=12), Tonga (n=3), French Polynesia (n=3) and the Solomon Islands (n=1) (Table 1, Supplementary table 1, Supplementary table 2, Methods). DNA was extracted24 and converted into double stranded genetic libraries25,26 in dedicated cleanroom facilities. Hybridization capture targeted the complete mitochondrial genome and ~1.24 million single nucleotide polymorphisms (SNPs) (1240K),27 followed by next generation sequencing. The isolated aDNA was authenticated based on the presence of typical degradation patterns, low levels of mtDNA contamination, X-chromosome contamination in males, and analyses were restricted, if necessary, to the likely endogenous deaminated sequences29 (Supplementary table 3, Supplementary table 4, Supplementary figure 1, Methods). The genome-wide aDNA was co-analyzed with four published Lapita samples25, 781 present-day Oceanian and East Asian samples genotyped for ~600K SNPs on the Affymetrix Human Origins (HO) Array27,28 and 308 high coverage genomes31. We also genotyped 27 ni-Vanuatu samples from the islands of Malakula and Efate (Methods, Supplementary figure 2) on the HO Array, with eight also shotgun sequenced (SG) at low coverage (0.6-3 fold) (Supplementary table 5). All newly generated data were analyzed alongside published genome-wide Illumina HumanOmni-24 data from 754 individuals across Remote Oceania, including 610 from Vanuatu32 (Supplementary table 6).

Demographic history of Vanuatu. While early Lapita people in Vanuatu had largely East Asian-Austronesian ancestry2, principal component analysis (PCA) shows that – though diverse – the ~27 present-day individuals fall instead within the Near Oceanic cline, in close proximity to Santa Cruz and New Britain populations (Fig. 1a,b), demonstrating an almost complete population turnover since initial settlement. Previous ALDER2 analysis estimated the time of Papuan admixture into Remote Oceania at 1,927-1,239y BP for Polynesian populations23, and our analyses on regional populations give similar estimates of ~2,000-1,500y BP (see below). Yet the 14C dates for the ancient samples demonstrate that Papuan ancestry was already in Vanuatu up to 1,000 years earlier, from ~2,500y BP. Both the earliest (T-AN002) and latest (T-AN009f) ancient samples from Tanna (Supplementary figure 2) lay inside the distribution of the new
present-day HO samples, but it is striking that ancient samples from Malakula and Futuna within this
timeframe do not (Fig. 1a). The Malakula time-transect bridges much of the massive genetic distance
between initial Lapita inhabitants and contemporary ni-Vanuatu. ADMIXTURE analyses on ancient and
modern Vanuatu SN data support a complex population replacement. With K=3 ancestral components –
allowing the distinction between Asian-Austronesian (blue) and Near Oceanian-Papuan (green) – Vanuatu
demonstrates a general but heterogeneous trend of increasing Papuan ancestry through time (Fig. 2a), from
largely Austronesian Lapita (ref. 21, and M-AL006) to predominantly Papuan ni-Vanuatu ancestry.

A newly sequenced ancient Tongan female sample (TON002)34 from the Talasai site in Tonga21, confirmed the ir genetic similarity to early peoples in Vanuatu (Fig. 1a), indicating that present-day ni-Vanuatu may
carry an additional genetic component not found in ancient populations. In Vanuatu, a population associated with
ancestry within Malakula (Supplementary table 8). In particular, MAL006– a male with typical Papuan Y-
chromosome haplogroup M16 – carries as much as ~50% Austronesian maternal excess (and Polynesian
mtDNA haplogroup B4a1a1), providing the first direct snapshot of this sex-biased admixture in progress35.64. The latest ancient sample, TAN001, shows similar autosomal admixture proportions to
temporary ni-Vanuatu, and carries a Papuan mtDNA haplogroup and Polynesian Y-chromosome
haplogroup (P1d and O2a26, respectively).64

To identify potential source populations of post-Lapita ancestry we calculated D-statistics on the new
ancient Vanuatu data, down-sampled to the more geographically extensive HO dataset (Supplementary
table 9). Using the model D(Near Oceanian, New Guinea; Vanuatu ancient, Mbuti), where Near Oceanian is
drawn from all potential sources reported in ref. 21, we identified Baining Marabu and Baining Malasait in
New Britain, Bismarck Archipelago (Fig. 1b) as the closest present-day proxy sources of Near Oceanian
ancestry in the ancient Vanuatu individuals (Z=0). One possible confounding factor is the significant
difference in the levels of Austronesian ancestry in Baining populations compared to New Guinea Papuans
shown by D(Baining Marabu or Baining Malasait, New Guinea; Ami, Mbuti): Z=3.7 or 4.2. However, TAN002
does not show such an attraction to Ami, confirming that its affinity to Baining relative to Papuans is not
explained by shared Austronesian ancestry (Supplementary table 9). Furthermore, although Denisovan
admixture levels are observed to decline with increased Austronesian ancestry proportion64, the best-
supported source populations have values consistent with New Guinea Papuans (D(Baining Marabu or
Baining Malasait, New Guinea; Denisenow, Mbuti): Z=-0.8 or -1.9). Thus, D-statistics confirm the close
relationship observed in PCA between Baining populations and the earliest Vanuatu individual carrying
Near Oceanian ancestry (TAN002), despite the immense geographical distance (Fig. 1a,b).

Analyses of two new Lapita individuals (TON001, TON002) from the Talasai site in Tonga21, confirmed their genetic similarity to early peoples in Vanuatu (Fig. 1a). Notably, TON002 is a male carrying Y-chromosome haplogroup O1a1a1, providing direct evidence that
this clade – like the "Papuan mtDNA mt" haplogroup B4a1a1 – was associated with the Austronesian
expansion35. Post-Lapita, the populations of Vanuatu and Tonga appear to follow a considerably different
generic trajectory; PCA analyses indicate that present-day Tongans fall between the East Asian and Near
Oceanian clines (Fig. 1a, Supplementary figure 5), more specifically between Lapita individuals and
Solomon Islanders. A newly sequenced ancient Tongan female sample (JH-0001), from 780-530y BP, lay
relatively close in PCA to modern Tongans, but its lower affinity to Solomon Islanders suggests that
modern Tongan ancestry was not yet completely in place by this time (D(JH-0001, Tongan; Samo, Mbuti); Z=3).
We obtained genome-wide data from three individuals unearthed at the monumental site Taputapuātea (TAP002, TAP003, TAP004) on the island of Raʻiāea, French Polynesia dated to the time of European contact in the 18th century AD39. ADMIXTURE34 analyses (Fig. 2a) show these individuals have major Austronesian (blue) and Polynesian (green) ancestry components, and both carry typical Polynesian mtDNA haplogroups (Table 1). In PCA space they fall in close proximity to LH1-1001 – slightly more towards the East Asian cline – suggesting that the population expansion to East Polynesia ~900-800y BP40 may have originated in western Polynesia. ADMIXTURE analyses (K=4) on a subset of HO data – including 454 present-day and 13 ancient Near and Remote Oceanian individuals (Supplementary figure S) – show that present-day ni-Vanuatu carry a heterogeneous proportion of three major components that are maximized in Near Oceanian populations (Papuan, Baining and Bougainville), with a minor Lapita-related component (Supplementary figure S). Conversely, present-day Tongans have substantial Lapita ancestry, with a minor component of Near Oceanian admixture (with different proportions of Papuan, Baining and Bougainville) (Supplementary figure S). qtl-adm analyses further support modelling modern Tongans as a two-way admixture between ancestral Austronesians and a population ancestral to some present-day Solomon Island groups – such as Malaita and Makira – or represented by the ~500y BP Malaita individual (MAL002), even when Papuan and Bismarck are included as an additional outgroup (Supplementary table 10). Thus, Solomon Islanders alone can explain the Near Oceanian ancestry found in Tongans, without contribution from New Guinea Papuans. This higher affinity to Solomon Islanders provides evidence that, post-Lapita, Tonga likely received its Near Oceanian ancestry from a different source than did Vanuatu.

Genetic cline in present-day Vanuatu. We analyzed the new ancient and modern data alongside a dataset from Remote Oceania32, which includes 754 individuals from New Caledonia, Vanuatu, Fiji and Tonga (Supplementary table 6), genotyped on the HumanCore-24 BeadChip, with ~160K and ~50K SNP overlap with the 2420K and HO data, respectively. After removing individuals with genetic evidence of non-autosomal ancestry, PCA (Supplementary figure 6) demonstrated high genetic diversity in ni-Vanuatu from the islands of Santo and Maewo (north of Malakula, Supplementary figure 2), with these individuals laying on acline running from close to New Britain, through Vanuatu, New Caledonia and Fiji, towards present-day Tonga. The new Vanuatu HO data from the islands of Malakula and Efate (Supplementary figure 7), lay overwhelmingly towards the New Britain end of this cline. Down-sampled to ~50K SNPs, the different trajectories for post-Lapita Vanuatu and Tonga populations identified in the HO analyses are less distinguishable. We used D-statistics to test whether this cline describes a separate demographic process to that which brought Bismarck-like ancestry to Vanuatu (Methods) but – at the resolution of currently available genotyping data – we are unable to distinguish between the two clines with confidence (Supplementary figure 7), suggesting that a Tongan-like ancestry may have played some role in the formation of present-day genetic diversity in Vanuatu. However, the HO analyses demonstrate that present-day Tongan ancestry, forming one end of this cline, was not fully in place prior to ~780-550y BP (LH1-1001), so this influence may be significantly later than the initial arrival of Bismarck ancestry in Malakula (~2,500y BP).

We have shown that Lapita ancestry in Malakula,Efate and Tanna is largely replaced by that from the Bismarck Archipelago. Indeed, ADMIXTURE analysis of Vanuatu HO alongside the Parks et al.33 data shows that – unlike Maewo and Santo – Malakula is home to people (~8%) carrying negligible amounts of Austronesian ancestry (Supplementary figure 8). The apparent excess Tongan-like affinity in individuals sampled in Maewo and Santo32 could be due to direct descent from heterogeneously admixed populations – similar to ancient Malakula and Futuna – or due to later interaction with people from Tonga, New Caledonia and Fiji. The latter scenario suggests that Tongan-like influence was finely geographically structured within Vanuatu, affecting the northern islands but less so further south. Well-preserved present-day data from southern Vanuatu will be instrumental in testing any geographic structuring explicitly, but the close similarity of TAN001 (1690-1950 AD) in the south to the new HO data (Supplementary figure S) is consistent with such a scenario. Y-chromosome data support this interpretation, with Polynesian-related haplogroup O3 found only in northeasten Vanuatu41.

Austronesian-Papuan admixture date estimation. We performed ALDER35 analyses on both modern and ancient Vanuatu data to gain independent estimates of arrival times for the Papuan ancestry component. We obtain an estimate of 60.7±8.2 generations BP for the 27 HO Vanuatu individuals, which – assuming a 28.1 year generation-time34 – equates to 1,705±232y BP (Fig. 3b, Methods). Interestingly, admixture time estimates similarly obtained for ancient Vanuatu provided 51.2±17 generations for three Futuna individuals (FTU002, FTU006 and FTU007) and 5.6±1.8 generations for three ancient Malakula individuals (MAL002, MAL004 and MAL007). Accounting for ancient sample ages, the admixture date is estimated at 2,560±477y BP for Futuna and 2,451±51y BP for Malakula, coinciding with the latest presence of individuals in the new Vanuatu time-transect with unadmixed Papuan (TAN002) or
Austronesian (M-IL606) ancestry (Fig. 3b). ALDER analyses of the Parks et al. data gave dates ranging from 1,569±79y BP (Fiji) to 1,999±101y BP (Port Olry, Vanuatu), overlapping the interval proposed by Skoglund et al., yet still significantly later than the directly dated admixed ancient individuals in Malakula (Supplementary figure 9).

**Discussion**

The population history of Remote Oceania is relatively short but these early stages appear complex, particularly in Vanuatu. New genome-wide aDNA data directly demonstrates the presence of Papuan peoples in Remote Oceania far earlier than estimated with present-day regional genome-wide data (Supplementary figure 9, and ref. 21), with unadmixed Bismarck-like individuals apparent in Vanuatu as early as ~2,500y BP, possibly contemporaneous with the end of the Lapita horizon. The new HO data from contemporary Malakula and Efate shows that while proto-Oceanic speaking Lapita peoples were genetically replaced by a population closely related to Papuan-speaking Baining people, present-day Ni-Vanuatu continue to speak Oceanic languages. The almost complete replacement of a population's genetic ancestry that leaves the original languages in situ is extremely rare – possibly without precedent – in human history and requires explanation. Alongside linguistic and archaeological evidence, our aDNA analyses provide a plausible and compelling model for this language continuity, namely an extended and incremental process of population replacement by peoples from the Bismarck Archipelago (Fig. 3a), rather than a single massive turnover event that would likely have brought a shift from Oceanic to Papuan languages.

The >120 languages spoken today in Vanuatu – per capita the most linguistically diverse place on Earth – are exclusively Oceanic, yet many aberrant, seemingly Papuan, linguistic features are evident. These include quinary numeral systems, rounded labial phonemes, dual exclusion of p and t phonemes, and serial verb construction. These features are heterogeneous across Vanuatu, extremely rare or absent in other Austronesian languages and are shared almost exclusively with Papuan languages (e.g. Supplementary figure 10). A number of ethnographically attested cultural practices or artifacts also share this near exclusive distribution, including large nasal piercing ornaments, penis sheaths, head-binding and the rearing of full-circle tusker pigs. These shared cultural and linguistic features provide further support for the Baining-Papuan genetic connection we identify. While some linguists argue for a single admixed expansion into Vanuatu from Near Oceania, others propose a 2-wave model, where an initial unadmixed proto-Oceanic-speaking population arrive, followed closely by a separate Papuan-speaking expansion. The latter is supported because the putative Papuan linguistic features found in Vanuatu cannot be reconstructed for proto-Oceanic, and their marked deviation from most other Oceanic languages suggests development within Vanuatu. Some features can be reconstructed for the proto-languages of Vanuatu – rounded labials and the p/c gap for proto-North-Central Vanuatu, and quinary numeral systems for proto-Southern Vanuatu – pointing to their early development and strongly supporting early Papuan influence. An undifferentiated proto-Oceanic speaking *lingua franca* for linguistically diverse Papuan migrant groups could explain the continuity of Oceanic languages in the face of secondary Papuan waves of expansion.

Our aDNA analyses lend direct support to this historical linguistic model. Indeed, some archaeologists have argued that the process by which Papuans made their way into Remote Oceania was strikingly different to the initial arrival of Lapita people, suggesting a continuing process of long-distance interaction rather than a simple dispersal event. One element of this process – namely the sex-biased admixture inferred from present-day South Pacific populations is already becoming clearer, with such genetically admixed ancient individuals (e.g. M-IL606) observed shortly after the very earliest arrival of Near Oceanian peoples in Remote Oceania (Fig. 2b, Supplementary table 8). We show that initially genetically homogeneous Lapita peoples in Vanuatu and Tonga follow strikingly different post-Lapita population trajectories, reflected in the clear cultural separation seen in the archaeological record. As a defined stylistic horizon, Lapita lasted only a few hundred years after settlement – local differentiation in pottery design beginning ~2,700y BP suggests significant fragmentation of the previously well-connected Lapita peoples. In central Vanuatu, the appearance of the incised Mangaasi ceramic complex ~2,500y BP seems to parallel a contemporaneous stylistic shift across island Melanesia, including both New Caledonia and the Bismarck Archipelago. It is an intriguing possibility that the early arrival of Bismarck-like people we now directly observe in Vanuatu may have exacerbated – even triggered – the process of Lapita fragmentation, while the ongoing long-distance interactions we uncover may explain the widespread distribution of Mangaasi-like pottery, rather than it resulting from independent, yet convergent, processes of stylistic simplification.

Our analysis of present-day Remote Oceanian data suggests a possible Tongan-like influence on the genetic diversity of present-day eastern Melanesia, with populations in northern Vanuatu, New Caledonia and Fiji lying on a cline towards modern Tonga (Supplementary figure 6). Given the data resolution, we
were unable to clearly distinguish this from the other cline formed by the post-Lapita population trajectory in Vanuatu (Fig. 1a), but the ancient Tongan individual LHA001 suggests that it formed later. One possibility is that this genetic structure arose with migration(s) from western Polynesia leading to the many Polynesian outlier communities – characterized by retention of various Polynesian linguistic features, cultural practices and genetic ancestry3 – distributed across Micronesia, New Guinea, the Solomon Islands, New Caledonia and Vanuatu. While the timing, scale and impact of this westward Polynesian migration is not yet precisely estimated, it likely coincided with the initial colonization of eastern Polynesia ~900-800y BP40.

In conclusion, our analyses of Vanuatu genome-wide data – both ancient and modern – combined with linguistic and archaeological evidence, strongly support a model of interaction and incremental admixture between Lapita-Austronesian peoples and incoming Bismarck Islanders that lead to an eventual population turnover, but left the pre-existing Oceanic languages in place. This multidisciplinary work has begun to uncover the complex, localized demographic processes that drove the initial colonization of the wider South Pacific and formed the enduring cultural and linguistic spheres that continue to shape the Pacific today.
METHODS

Ancient and modern-day DNA processing.

Ancient DNA sampling. All samples were processed in dedicated laboratories at the Max Planck Institute for the Science of Human History in Jena, Germany. Bone powder for DNA extraction was obtained from the Vanuatu Kaljoral Senta, the institution that regulates all research in the country. Sampling was carried out in 5 communities that are already participating in the linguistic and anthropological project, directed by Prof. Russell Gray and Dr. Heidi Colleran at the Max Planck Institute for the Science of Human History (http://www.shh.mpg.de/456217/vanuatu-languages-lifeways).

Modern DNA sampling. For aDNA authentication and contamination estimates screening DNA libraries were built from 20 µl of DNA extract in the absence of uracil DNA glycosylase (non-UDG libraries), following a double stranded library preparation protocol. After assessing human DNA contamination levels, one or two additional 25µl aliquots of DNA extract were transformed either into non-UDG libraries or into "UDG-half" double-stranded libraries with a protocol that makes use of the UDG enzyme to reduce but not eliminate the amount of deamination induced damage towards the end of aDNA fragments. Negative and positive controls were carried out alongside each experiment. Libraries were quantified using the IS7 and IS8 primers in a quantification assay with DyNAmo SYBP Green qPCR kit (Thermo Fisher Scientific). mtDNA capture was performed on screened libraries that after shotgun sequencing showed the presence of aDNA, highlighted by the typical CtoT and GtoA substitution pattern towards 5' and 3' molecule ends, respectively. Furthermore, samples with a percentage of human DNA in shotgun data around 0.1% or greater were enriched for a list of 1,237,207 targeted SNPs across the human genome (1240K capture).

Sequencing. The enriched DNA product was sequenced on an Illumina HiSeq 4000 instrument with 75 cycles single-end or 50 cycles pair-end runs (for TAN001 and FUT006) using the manufacturer's protocol. The output was de-multiplexed using bcl2fastq v2.17.1.14 and dpbclustering v3.0.0.

Modern DNA extraction and library preparation. Extraction and library preparation were performed in the molecular biology laboratories of the Max Planck Institute for the Science of Human History in Jena, Germany. Modern-day DNA was extracted from the Oragene kit following the manufacturer's protocols with the only modifications that 600µl of sample volume was used accordingly adjusting the following reaction volumes. 10µl of eight modern-day DNA extracts (Supplementary table 5) were used to build double-stranded DNA libraries. They were then indexed in one reaction following the same protocols mentioned above, pooled equimolarly and shotgun sequenced on an Illumina HiSeq 4000 instrument (75 cycles single-end run).

Genotyping of present-day humans. The company Atlas Biosalbs in Berlin, Germany genotyped 27 modern DNA extracts on the Axiom Genome-Wide Human Origins array. After checking DNA quality and quantity on
both a 1% Agarose gel and a NanoDrop, samples were adjusted to 20ng/ul using a Qubit high sensitivity kit (Thermo Fisher Scientific), loaded on the Axiom Genome-Wide Human Origins array (Affymetrix) and genotyped on a GeneTitan. Genotyping was performed using the Affymetrix Genotyping Console, and all individuals had >94% genotyping completeness.

Genomic data processing. Pre-processing of the sequenced reads was performed using EAGER v1.9.2443.

Reads resulting from the sequencing of modern and ancient DNA libraries were clipped to remove residual adaptor sequences using Clip&Merge54 and AdapterRemoval v2.5, respectively. Clipped sequences were then mapped against the human reference genome hg19 using BWA56 turning seeding off and with the –e parameter set to 6.0. Duplicates were removed with DeDup55 that removes reads with identical start and end coordinates. Additionally a mapping quality filter of 30 was applied using samtools57. Alignment files were filtered for reads showing the presence of likely deaminated bases as the result of post-mortem damage (PMD) using pmdtools v0.65.0. Both damage restricted and non-restricted sequences from either non-UDG or UDG-half libraries were trimmed for the first and last three positions in order to reduce the impact of deamination induced miss-incorporations during genotyping. Trimmed reads were genotyped using pileupCaller (https://github.com/stschiff/sequenceTools/tree/master/src-pileupCaller) a tool that randomly draws one allele at each of the 1240K targeted SNPs covered at least once. The generated pseudo-haloid calls for 19 ancient Pacific individuals (Table 1) were merged to a pull-down of the 1240K SNPs from the Simon Genome Diversity Project (SGDP)59, eight shotgun sequenced modern-day individuals from Vanuatu and four previously published 1240K captured individuals associated with the Lapita culture from Vanuatu and Tonga21. Moreover the newly generated capture data for the ancient individuals as well as 27 genotyped modern-day individuals (Supplementary table 5) were merged to the ~600K SNPs of the Human Origins (HO) dataset21,30.

Authentication of ancient DNA. In the field of aDNA several methods have been developed to assess authenticity of the retrieved DNA. First, the typical features of aDNA were inspected with DamageProfiler (https://bintray.com/apeltzer/EAGER/DamageProfiler), e.g. short average fragment length (~40-70bp) and an increased proportion of miscoding lesions due to deamination at the molecule termini (Supplementary table 3). Sex determination was performed by comparing the coverage on the targeted X-chromosome SNPs (~50K positions within the 1240K capture) normalized by the coverage on the targeted autosomal SNPs to the coverage on the Y-chromosome SNPs (~30K), again normalized by the coverage on the autosomal SNPs (Table 1). Individuals falling in an intermediate position between male and female are assigned to undetermined sex and indicate the presence of present-day DNA contamination. For male individuals, ANGSD was run to measure the rate of heterozygosity of polymorphic sites on the X-chromosome after accounting for sequencing errors in the flanking regions60. This provides an estimate of nuclear contamination in males that are expected to have only one allele at each site. For all male samples that exhibit X-chromosome contamination levels below 2% with at least 100 X-chromosome SNPs covered twice, all reads were retained for further analyses (Supplementary table 4). Otherwise only PMD fragments that are likely of endogenous origin were used61 (Table 1). For both male and female individuals mtDNA captured data was used to jointly reconstruct the mtDNA consensus sequence and estimate contamination levels with schmutzy42 (Supplementary table 11). For specimens where a relatively low proportion of mtDNA molecules compared to nuclear DNA (mt/nuclear DNA ratio) was observed (Supplementary table 11), mtDNA contamination estimate can be used as reliable predictor for nuclear contamination58. Population genetic analyses on samples presenting mtDNA levels of contamination above 4% were restricted to PMD fragments. Moreover, for each individual the positioning in PCA space was compared to the data after restriction to deaminated sequences50. Samples that were substantially displaced in PCA space (Supplementary figure 1) were restricted to PMD fragments for population genetic analyses.

Population genetic analyses. PCA were computed with present-day populations from the HO dataset composed of 781 Oceanians and East Asians21 and 27 modern-day Vanuatu individuals newly genotyped here, for a total of 808 individuals. Ancient individuals were projected onto the two first components using smartpca (v13050)54 with the options “-makegrid: YES” and “-numoutlieriter: 0” (Fig. 1 and Supplementary figure 1). Another PCA was computed on the ~50K SNPs overlapping the HO dataset and a recently published Illumina HumanCore-24 dataset typed on ~240K SNPs in total (Supplementary figure 6). The same 808 modern-day Oceanians and East Asians were used to build the principal components on which 669 individuals across Remote Oceania (Supplementary table 6) and 15 ancient Pacific individuals with more than 6K SNPs were projected. The software ADMIXTURE v1.3.048 was run in unsupervised mode on high coverage genomes of 308 modern-day worldwide individuals, eight shotgun sequenced present-day Vanuatu individuals and all 23 ancient Pacific individuals. Only transversions sites of the 1240K SNPs (~220K positions) were considered in order to reduce the impact on the clustering algorithm of residual damage still present in non-UDG treated libraries. An additional regional ADMIXTURE analysis was carried out also on the...
transversions subset of the HO data (~110K SNPs) including 13 ancient individuals from Vanuatu and Tonga (more than 15K SNPs) and 454 modern-day Oceanian individuals (Supplementary figure 5). Finally, ADMIXTURE was run on the overlapping SNPs between HO and Parks et al.36 datasets for the 27 newly genotyped present-day individuals from Malakula and Efate in Vanuatu (Supplementary table 5) in addition to 754 present-day individuals from New Caledonia, Vanuatu, Fiji and Tonga (Supplementary figure 8). From the latter dataset 85 individuals harboring more than 2% of non-local ancestry at K=5 were removed for a total of 609 individuals retained (Supplementary table 6). In the following analyses all SNPs were investigated for individuals with UDG-half libraries whereas only transversion SNPs were used for individuals with non-UDG libraries to avoid spurious results originating from leftover aDNA damage.

D-statistics were calculated with qpDatata r v711 program from the AdmixTOOL suite (https://github.com/DReichLab) in the form DI(Pop1, Pop2; Pop3, Outgroup). A negative value implies that either Pop1 and Outgroup, or Pop2 and Pop3 share more alleles than expected under the null hypothesis of a symmetrical relationship between Pop1 and Pop2 (Supplementary table 9). To jointly observe the affinity of modern-day Fiji, Tonga, New Caledonia and Vanuatu individuals from Parks et al.32 and HO datasets as well as ancient Vanuatu individuals towards Ami and Tonga populations, we calculated two sets of D-statistics in the form A: DI(Baining, Xi; Ami, Mbuti) and B: DI(Baining, Xi; modern Tongan, Mbuti), where X is drawn from Fiji, Tonga, Malaita (Vanuatu), Port Vila (Vanuatu), Saint (Vanuatu) and New Caledonia from Parks et al.32, as well as the Vanuatu HO and ancient Malakula, Futuna, Tanna samples. Plotting A against B (Supplementary figure 7) shows that we cannot see a clear deviation between modern and ancient individuals, as all values do not appreciably differ from the straight line expected for no differential ancestry.

$qbF_{ev} r v400^9$ was implemented on the HO dataset in order to test if the ancient individuals are consistent with two sources of ancestry represented by modern-day Ami (as the best proxy for ancestral Austronesian) and Papuan individuals, with respect to a set of outgroups (Mbuti, Denisovan, Sandinian, English, Yabat, Cakchel, Mala, Japana, Jau, Jau-North, Miao, Osage, Yenou). This is obtained when rank $n-1$ cannot be rejected (p>0.05) as shown for all our ancient Vanuatu individuals, as well as modern Vanuatu HO individuals despite a much lower p-value (Supplementary table 7). The same populations for both HO and 1240K datasets were then used in $qg-Adm v610^3$ to estimate admixture proportions for ancient and modern-day Vanuatu individuals (Supplementary figure 3, Fig. 2b and Supplementary table 8). $qg-Adm$ models each individual as a mixture of Ami and Papuan by fitting admixture proportions that match the observed matrix of $f4$-statistics and computing standard errors with a block jackknife. To evaluate potential sex bias admixture, $qg-Adm$ analysis, as described above, was run only on X-chromosome SNPs (option “chrom=23”) of the 1240K dataset. Differences in admixture proportions between autosomal and X-chromosome SNPs provide an indication of sex-biased admixture (Supplementary table 8).

Modern-day Tongans were modeled in $qg-Adm$ as resulting from a two-way admixture between Ami (as the best proxy for ancestral Austronesian) and ancient (MAB002) or modern-day Solomon Islanders from the island of Makira, Malaita and Bougainville (Naisoi and Choineul populations). When selecting the 12 outgroups listed above, Tongans can successfully be modeled with p>0.05, using a block jackknife to calculate standard errors as indicated previously. $qg-Adm$ was re-run expanding the outgroup population list with Papuan and Baining Marabu. For present-day individuals from Makira, Malaita and the ancient individual from Malaita (MAB002) rank $n-1$ can still not be rejected, indicating that additional Papuan New Guinean or Bismarck ancestry is not necessary to model modern-day Tongans (Supplementary table 10).

Admixture dates were estimated based on linkage disequilibrium using ALDER33 on the ~160K overlapping SNPs between 1240K capture and Parks et al.32 datasets. As source populations, 20 Asian (Ami, Atayal, Igorot, Kinh, Dai, She, Lahu, Han) and 16 Papuan individuals were chosen. The estimated dates of admixture were converted into years assuming a generation time of 28.1 years12,14 for the 27 Vanuatu HO individuals (Fig. 3b) and for modern-day New Caledonia, Vanuatu, Fiji and Tonga populations13 (Supplementary figure 9). Admixture dates were also estimated for SNPs overlapping to the 1240K capture for three ancient Futuna individuals (FU0062, FU0060, FU0007) with average age set to 1,123y BP and three ancient Malakula individuals (MAL002, MAL004, MAL008) with average age set to 2,293y BP (Fig. 3b).

Admixture graphs on the HO dataset were fitted with qpGraph r521130 that matches a matrix of f-statistics testing the relationships between all analyzed populations at the same time. An initial backbone graph modern-day populations without signs of admixture were built into the tree (Mbuti, Ami, New Guinea). The differential proportion of Denisovan ancestry between Mbuti-Ami and New Guinea populations32 was not modeled here since this is accommodated in the graph by shifting the splitting point of the African Mbuti population. Baining Marabu was then incorporated as admixed between an Ami-related and a New Guinea-related lineage, as suggested from D-statistics analyses (Supplementary table 9). Ancient UDG-half individuals from Vanuatu (three Futuna individuals grouped, three Malakula individuals grouped and two Tanna individuals separately) were added chronologically one-by-one at each possible position of the graph reporting every time the highest D-statistic between the observed and fitted model and calculating the Z-score with a block jackknife. The graph reported in Fig. 3a is built with a total of
38,789 SNPs and fits the allele frequency relationships between modern-day and ancient individuals with all empirical f-statistics within the 3 standard error interval and only one significant D-statistic (Z = 2.6). The modern-day Vanuatu HO population can be fitted as admixed between modern-day Baining Mariba and Ami-related populations but this relatively simple model with only four populations has already the worst Z-score, equal to 2.3 (Supplementary figure 4a). Moreover, we were unable to fit a modern-day HO Vanuatu population in the graph once ancient individuals are included, neither by replacing the ~200y BP T-an009 individual (Supplementary figure 4b) nor modeling Vanuatu HO as deriving part of its ancestry from the ~1,100y BP Futuna population (Supplementary figure 4c) with the worst Z-score of 6 and 5.2, respectively.

Haplogroup assignment for uniparental markers.

After enrichment of the libraries for the mitochondrial genome (mtDNA capture) reads were pre-processed in EAGER r1.92.55 as described above and aligned to the mitochondrial reference genome (rCRS) using CircularMapper, a program that takes into account the circularity of the mtDNA. Contamination was estimated while assembling the mitochondrial genome using schmutz2 with the parameters “–nonsepsread–uselength”. Present-day human contamination estimates were performed using a comparative database of 197 modern-day worldwide mtDNAs provided with the software package. For the resulting sequences we filtered positions with likelihood above 20 or 30 (Supplementary table 11) and used HaploGrep2 to assign the corresponding mtDNA haplogroup. For the FUT007 individual the mtDNA consensus sequence was reconstructed from the mtDNA off-target reads in the combined non-UDG and UDG-half 1240K capture data (Table 1 and Supplementary table 11). Sequenced reads overlapping the Y-chromosome SNPs present in the ISOGG database r11.349 (http://www.isogg.org/tree) were investigated to assign Y-chromosome haplogroups. ANG2ID90 was used to count ancestral and derived allele occurrence and perform a majority call for positions covered at least once. For this analysis UDG-half and no-UDG data were combined for each sample (Supplementary table 3). To avoid miss-assignments due to DNA damage, CsnT and GcoA mutations required a minimum of two consistent nucleotides to be called. Haplogroup assignment was based on the most downstream SNP retrieved after evaluating the presence of upstream mutations along the related haplogroup phylogeny90.

DATA AVAILABILITY

All newly reported ancient DNA data including nuclear DNA alignment files and mtDNA sequences are archived at the European Nucleotide Archive database (accession number PRJEB24810). Newly reported SNP genotyping and shotgun sequence data will be made available on request to H.C. and A.P (powell@shh.mpg.de). SNP genotyping was performed at the Human Protein Reference Center (Heidelberg, Germany) and shotgun sequence data was retrieved after evaluating the presence of upstream mutations along the related haplogroup phylogeny.

REFERENCES

AUTHOR CONTRIBUTIONS

We would like to thank the communities in Malakula and Efate in Vanuatu who participated in this study, and particularly all sample donors. We are grateful to Mark Stoneking, Irina Pugach and Chau-Chao Wang for comments, and to Guido Brandt, Raffaella Bianco and technicians at the Max Planck Institute for the Science of Human History for laboratory support. Archaeological investigations on Malakula, Vanuatu were funded by the Sasakawa Pacific Island Nations Fund, the Marsden Fund of the Royal Society of New Zealand (Fast-Start 9011/5602128; 04-U00-007), a National Geographic Scientific Research Grant (7738-04) and an Australian Research Council Discovery-Project Grant (DP0880789). A.P. is funded by an Australian Research Council DECRA Grant (DE150100600). K.N. is funded by a European Research Council Starting Grant (ERC758967). We would like to thank the communities in Malakula and Efate in Vanuatu who participated in this study, and particularly all sample donors. We are grateful to Mark Stoneking, Irina Pugach and Chau-Chao Wang for comments, and to Guido Brandt, Raffaella Bianco and technicians at the Max Planck Institute for the Science of Human History for laboratory support. Archaeological investigations on Malakula, Vanuatu were funded by the Sasakawa Pacific Island Nations Fund, the Marsden Fund of the Royal Society of New Zealand (Fast-Start 9011/5602128; 04-U00-007), a National Geographic Scientific Research Grant (7738-04) and an Australian Research Council Discovery-Project Grant (DP0880789). A.P. is funded by an Australian Research Council DECRA Grant (DE150100600). K.N. is funded by a European Research Council Starting Grant (ERC758967).

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The study was conceived and coordinated by C.P., K.N., H.C., R.G., J.K. & A.P.

**Competing Interests**

The authors declare no competing financial interests.
Fig. 1: Spatial and genetic distribution of ancient and present-day individuals. (a) Principal component analysis of modern-day East Asian and Near and Remote Oceanian populations genotyped on the Affymetrix Human Origins Array, with 23 ancient individuals projected. Ancient samples are indicated by filled symbols – the new data from this study have a black border – and present-day samples are indicated by open symbols. (b) Regional map, showing locations of Near and Remote Oceanian sample populations and ancient individuals.
Fig. 2: Admixture proportions of Papuan- vs. Lapita-related ancestry in ancient and present-day populations using 1240K genome-wide data. (a) Unsupervised ADMIXTURE analyses of present-day global populations and ancient Pacific individuals, with 5 ancestral components. (b) Austronesian ancestry proportion (modeled by indigenous Taiwanese population Ami) in ancient and present-day Vanuatu individuals estimated through qpAdm analyses. Symbol legend is given in Fig. 1, and standard errors are indicated by black lines if larger than the symbol (see also Supplementary table 8).
Fig. 3: Demographic history of ancient Vanuatu individuals. (a) qpGraph model that fits observed allele frequency patterns with branch lengths representing drift in $F_{ST}$ units and edge percentages indicating admixture proportions. Ancient samples or groups are indicated with a red border. (b) ALDER analyses estimating the date of Papuan and East Asian admixture, converted into years with a generation time of 28.1 years. Standard error bars are shown for date estimates, while sample ages for the two ancient groups (Futuna and Malakula) are averaged radiocarbon dating confidence interval (CI) midpoints. As the earliest ancient Vanuatu individual with unadmixed Near Oceanian ancestry, TAN002 is included for age comparison, with error bar indicating the 95.4% radiocarbon dating CI.
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