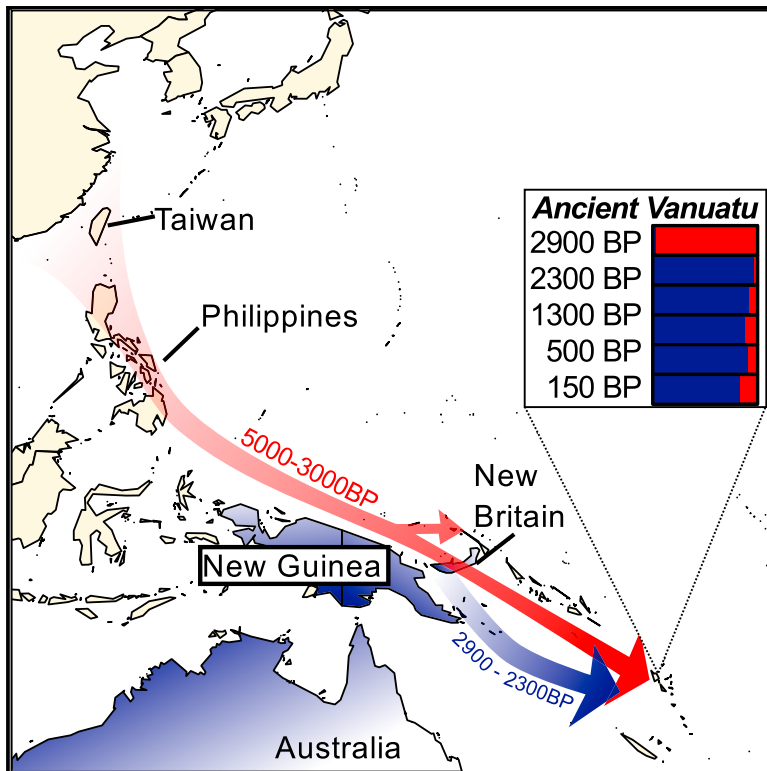# Current Biology

Population Turnover in Remote Oceania Shortly after Initial Settlement

Graphical Abstract

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In Brief

Lipson, Skoglund, et al. analyze ancient
DNA from the Pacific island chain of
Vanuatu over its entire span of
occupation. After humans first arrived
around 3,000 years ago, there was a
nearly complete replacement of the
original inhabitants by 2,300 years ago,
and this second wave forms the primary
ancestry of people in Vanuatu today.

Highlights

- The population of Vanuatu in the Pacific was largely replaced 2,900–2,300 years ago

- This second wave of migrants came from New Britain, east of New Guinea

- A third wave spread different ancestry to the far-flung islands of Polynesia

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Population Turnover in Remote Oceania Shortly after Initial Settlement

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SUMMARY

Ancient DNA from Vanuatu and Tonga dating to about 2,900–2,600 years ago (before present, BP) has revealed that the "First Remote Oceanians" associated with the Lapita archaeological culture were directly descended from the population that, beginning around 5000 BP, spread Austronesian languages from Taiwan to the Philippines, western Melanesia, and eventually Remote Oceania. Thus, ancestors of the First Remote Oceanians must have passed by the Papuan-ancestry populations they encountered in New Guinea, the Bismarck Archipelago, and the Solomon Islands with minimal admixture [1]. However, all present-day populations in Near and Remote Oceania harbor >25% Papuan ancestry, implying that additional eastward migration must have occurred. We generated genome-wide data for 14 ancient individuals from Efate and Epi Islands in Vanuatu from 2900–150 BP, as well as 185 present-day individuals from 18 islands. We find that people of almost entirely Papuan ancestry arrived in Vanuatu by around 2300 BP, most likely reflecting migrations a few hundred years earlier at the end of the Lapita period, when there is also evidence of changes in skeletal morphology and cessation of long-distance trade between Near and Remote Oceania [2, 3]. Papuan ancestry was subsequently diluted through admixture but remains at least 80%–90% in most islands. Through a fine-grained analysis of ancestry profiles, we show that the Papuan ancestry in Vanuatu derives from the Bismarck Archipelago rather than the geographically closer Solomon Islands. However, the Papuan ancestry in Polynesia—the most remote Pacific islands—derives from different sources, documenting a third stream of migration from Near to Remote Oceania.

RESULTS AND DISCUSSION

We generated genome-wide data for 14 ancient individuals from central Vanuatu, including 11 newly reported individuals and higher-quality data for three previously reported individuals [1]

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(Table 1; Data S1). We identified and selected cochlear bone sections of petrous bones and processed them into powder in dedicated clean rooms at University College Dublin [4]. We shipped the powder to Harvard Medical School, where in a second set of clean rooms we extracted DNA [5, 6] and created individually barcoded Illumina sequencing libraries, some of which we treated with the enzyme uracil-DNA glycosylase (UDG) to greatly reduce the characteristic errors associated with ancient DNA [7, 8]. We screened these libraries for evidence of authentic ancient DNA by enriching for DNA overlapping the mitochondrial genome [9], sequencing on an Illumina NextSeq500 instrument, and measuring the rates of cytosine-to-thymine damage in the terminal nucleotide and consistency with the consensus mitochondrial genome (STAR Methods) [10]. For libraries that were promising after screening, we enriched for regions targeting approximately 1.24 million single-nucleotide polymorphisms (SNPs) and sequenced the enriched products (STAR Methods). We determined sex by examining the ratio of sequences overlapping the X and Y chromosomes, and for males, we estimated nuclear contamination based on the rate of apparent polymorphism on the X chromosome (present in only one copy in males) (STAR Methods; Data S1). The data for the 14 individuals passing quality control were derived from 46 Illumina libraries (one to eight per individual; Data S1). We assembled direct accelerator mass spectrometry radiocarbon dates for all 14 individuals, including ten newly reported dates (STAR Methods; Data S1). Finally, we generated genome-wide SNP genotype data on the Affymetrix Human Origins array for 185 present-day individuals from Vanuatu who gave informed consent for studies of genetic variation (STAR Methods; Data S1).

Genome-wide Clustering Analyses

We performed automated clustering analysis with the ADMIXTURE software [11], using a dataset consisting of the ancient and present-day Vanuatu samples together with other Oceanian, East Asian, and worldwide populations genotyped on the Human Origins array [1]. At K = 8 clusters, four ancestry components were inferred to be widespread in Oceania (Figure 1A; Figure S1). Three correlate (predominantly) to Papuan ancestry and are maximized in New Guinea (black in the plot), Mamusi and Baining from New Britain (blue), and Nasioi from Bougainville in the Solomon Islands (red). The fourth component (green), correlating to First Remote Oceanian ancestry, is maximized in the ~2900–2600 BP (before present) individuals from Vanuatu and Tonga. Other Oceanian populations display variable combinations of these components, forming gradients of ancestry between New Guinea, New Britain and New Ireland in the Bismarck Archipelago, and the Solomon Islands. The great majority of present-day and ancient groups from Vanuatu show similar ratios of the three Papuan ancestry components (although their First Remote Oceanian proportions vary), showing that they are consistent with largely deriving their Papuan ancestry from the same source. Among populations in Near Oceania, the most similar to Vanuatu in terms of the Papuan ancestry component ratio (black:blue:red) are groups from New Britain in the Bismarck Archipelago, with a majority of the blue component and smaller contributions of black and red, suggesting that the Papuan ancestry in Vanuatu derives from populations in the Bismarck Archipelago (rather than the geographically

closer Solomon Islands). A similar pattern was previously inferred for the Papuan ancestry in Santa Cruz, to the immediate north of Vanuatu [12], a result that we replicate here.

We also carried out a principal-component analysis (PCA; Figure S2), which corroborated the findings from ADMIXTURE, with the primary feature being a U-shaped cline from (1) western New Britain in the Bismarck archipelago to (2) eastern New Britain, (3) most of Vanuatu, (4) the atypical Vanuatu island of Tutuba along with the Tolai of New Britain, (5) New Ireland in the Bismarck archipelago, and finally (6) Bougainville in the Solomon Islands. This cline closely correlates to the gradient of decreasing blue and increasing red components in ADMIXTURE (Figure 1A; Figure S1). The position of the Vanuatu samples in the PCA again supports the hypothesis that the inhabitants of the region after the initial Lapita settlement derived ultimately not from populations closely related to those in the closer Solomon Islands but instead from populations related to those from the island of New Britain in the Bismarck Archipelago. We also replicated this result via the statistic f_4(Australian, Vanuatu; Solomon Islands, Bismarck Archipelago), which is significantly positive for each choice of populations in the PCA ($Z > 2$ for all 160 comparisons; median $Z > 6$; STAR Methods), implying that Vanuatu populations share more alleles with groups from the Bismarck Archipelago than the Solomon Islands.

Papuan and First Remote Oceanian Ancestry Proportions

It has been shown that the strongest driver of genetic variation in Oceania today is the widespread but highly variable admixture between Papuan and First Remote Oceanian ancestry sources, the former representing original inhabitants of Near Oceania and the latter descendants of an expansion from East and Southeast Asia [1]. From our clustering results, a dramatic turnover is apparent in Vanuatu after around 2,900 and before around 2,300 years ago, with First Remote Oceanian populations being joined or possibly completely replaced by individuals of (almost) entirely Papuan ancestry. To provide precise estimates of mixture proportions, we used f_4-ratio statistics [13], with East Asian reference populations Atayal (aboriginal Taiwanese related to the source population of the Austronesian expansion) and Kankanaey (an Austronesian-speaking population from the Philippines—on the migratory path from Taiwan to Remote Oceania—that has been shown to be descended from the same genetic sources as the First Remote Oceanians) [1] (Figure 1; Table 1; Data S1; STAR Methods). Taking advantage of our increased coverage compared to the first study of Lapita samples, we find that the ~2900 BP Lapita individuals had a nonzero proportion of Papuan-related ancestry (2.4% ± 0.9%), although it remains striking that the initial First Remote Oceanian migrants were only minimally admixed. Given the small proportion, we did not have sufficient statistical power to determine whether this Papuan-related ancestry is derived from the region surrounding New Guinea or could perhaps have been acquired elsewhere, such as in the Philippines or eastern Indonesia. Notably, the first post-Lapita sample (2300 BP from the site of Mele-Taplins) had almost entirely Papuan ancestry, but with a small fraction derived from First Remote Oceanians (4.2% ± 1.1%). The more recent ancient individuals are similar in their proportions to present-day populations: 8%–26% First Remote

Table 1. Details of Ancient Vanuatu Samples Analyzed in This Study

Sample	Code	Radiocarbon Dates	Population Label	Location	Sex	mtDNA Haplogroup	Y Haplogroup	SNPs	Papuan Ancestry (%)
I1370	B17.P3	3080–2780 calBP (3083 ± 26 BP, Wk-21026)	Vanuatu_2900BP	Teouma, Efate	F	B4a1a1	–	237,405	−0.2 ± 1.4
I1369	B10B.P3	3020–2750 calBP (3045 ± 30 BP, Poz-81126)	Vanuatu_2900BP	Teouma, Efate	F	B4a1a1	–	271,048	3.0 ± 1.4
I1368	B30A.P3	2990–2750 calBP (2983 ± 32 BP, Wk-22657)	Vanuatu_2900BP	Teouma, Efate	F	B4a1a1	–	185,282	1.6 ± 1.4
I5951	TeoQE	2920–2720 calBP (2955 ± 20 BP, PSUAMS-2411)	Vanuatu_2900BP	Teouma Quarry Edge	M	B4a1a1	CT	23,107	3.9 ± 3.5
I4451	TAP1	2360–2160 calBP (2348 ± 32 BP, Wk-20390)	Vanuatu_2300BP	Mele-Taplins, Efate	M	M28a7	K2b1	340,152	95.8 ± 1.1
I4096	BURU5B	1380–1240 calBP (1380–1270 calBP [1490 ± 15 BP, PSUAMS-2460], 1350–1180 calBP [1464 ± 30 BP, Wk-25769])	Vanuatu_1300BP	Burumba, Epi Island	M	B4a1a1k	K2b1	888,003	92.2 ± 1.2
I3921	BURU5D	1340–1180 calBP (1410–1280 calBP [1530 ± 20 BP, PSUAMS-1841], 1300–1170 calBP [1395 ± 15 BP, PSUAMS-2428])	Vanuatu_1300BP	Burumba, Epi Island	M	P1d1	K2b1	855,305	91.6 ± 1.1
I5259	Mang1	630–330 calBP (559 ± 30 BP, Wk-20030)	Vanuatu_500BP	Mangaliliu, Efate	F	P1f	–	799,098	88.4 ± 1.2
I4105	WAMB1	300–0 calBP (255 ± 20 BP, PSUAMS-1922)	Vanuatu_Epi_150BP	Wambi Bay, Epi Island	M	M28a+204	O1a2	1,012,081	92.6 ± 1.2
I4106	WAMB2	280–0 calBP (225 ± 20 BP, PSUAMS-1923)	Vanuatu_Epi_150BP	Wambi Bay, Epi Island	M	B4a1a1a11	O1a2	1,020,436	90.6 ± 1.1
I4450	SEPU1	430–0 calBP (305 ± 15 BP, UCIAMS-188793)	Vanuatu_Efate_150BP	Pangpang, Efate	F	P1d2	–	735,460	90.8 ± 1.2
I4425	EF3_2_E	270–0 calBP (200 ± 20 BP, UCIAMS-188795)	Vanuatu_Efate_150BP	Ifira, Efate	F	P2	–	700,783	73.6 ± 1.4
I4424	EF_Pango1	280–0 calBP (190 ± 15 BP, UCIAMS-188794)	Vanuatu_Efate_150BP	Pango Village, Efate	M	B4a1a1	M1b	780,469	78.6 ± 1.4
I4419	BB1	260–20 calBP (135 ± 15 BP, UCIAMS-188792)	Vanuatu_Efate_150BP	Banana Bay, Efate	M	B4a1a1	K2b1	763,556	86.2 ± 1.2

The first three samples listed are previously published individuals [1] but with new libraries now added to increase coverage; the other 11 are newly published individuals. Radiocarbon date calibrations are given as 95% confidence intervals, after applying a correction for marine reservoir effect (STAR Methods; Data S1). Mitochondrial DNA haplogroups were called after merging data from all libraries. For the mtDNA and Y chromosome columns, underlining indicates typical East Asian (First Remote Oceanian) haplogroups, whereas lack of underlining indicates typical Australo-Papuan haplogroups (the italicized Y haplogroup *CT* is unclassified). BP, before present; calBP, calibrated years BP. See also Data S1.
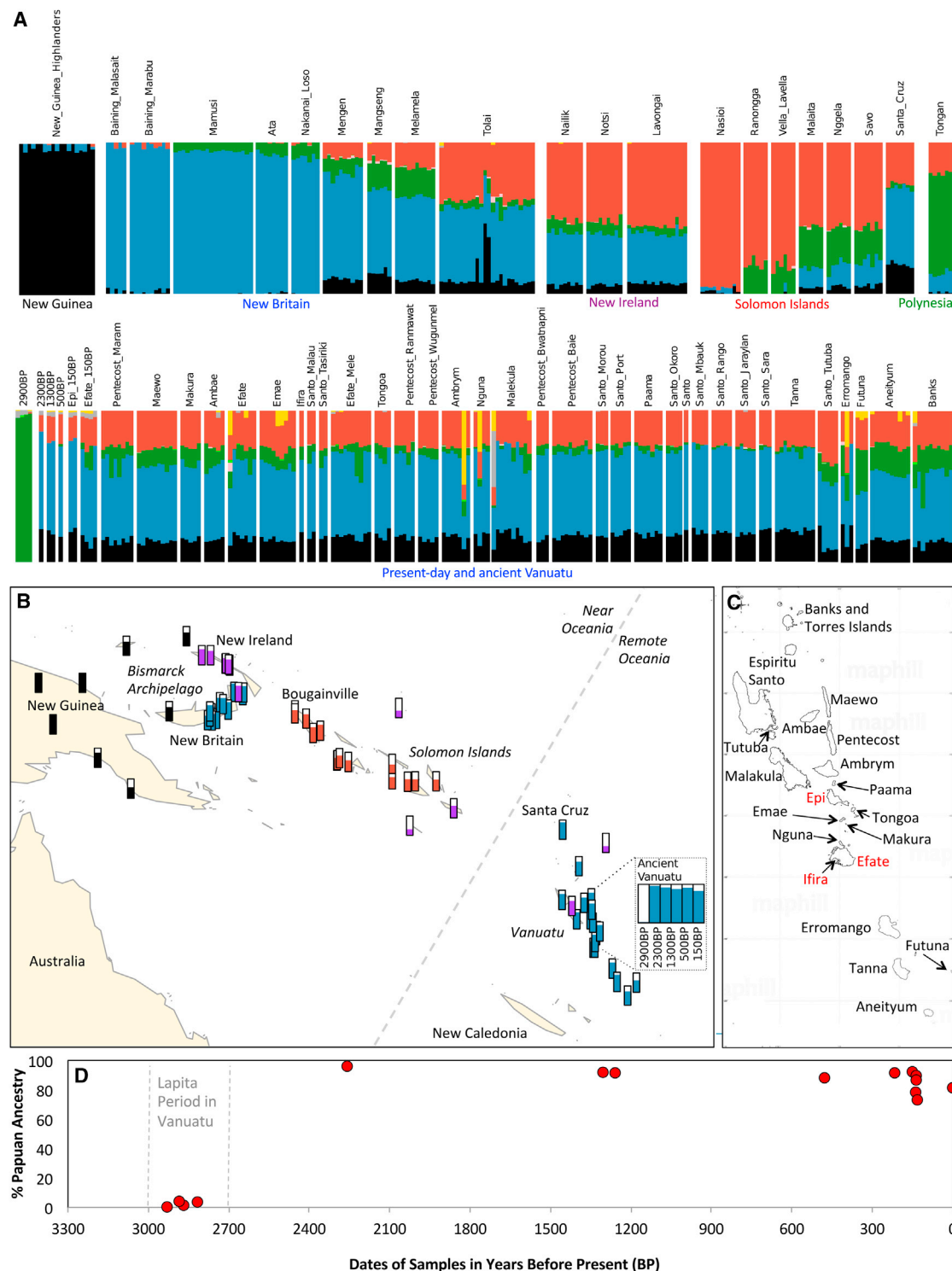
Figure 1. Locations and Broad-Scale Genetic Structure of Analyzed Populations

(A) ADMIXTURE results with K = 8 clusters for selected populations (full results are in Figure S1). The analysis suggests three primary Papuan components (black, maximized in New Guinea; blue, maximized in New Britain in the Bismarck Archipelago; red, maximized in the Solomon Islands) and a component maximized in First Remote Oceanians (green).

(B) Population locations with colored clusters assigned based on the ratio of Papuan ancestry components in ADMIXTURE. We loosely adopt the color scheme from ADMIXTURE, with black indicating a New Guinea-like profile, blue a New Britain-like profile, red a Solomon Islands-like profile, and purple a profile mixed

(legend continued on next page)
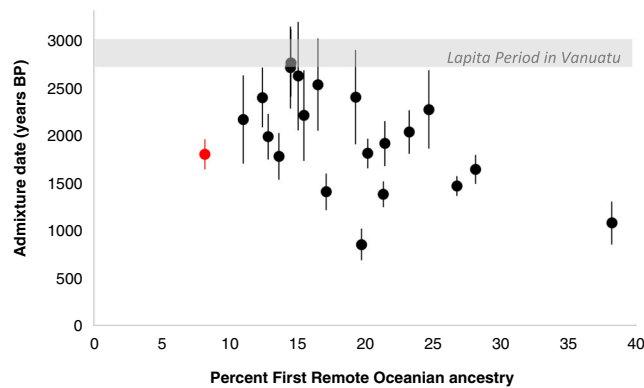
Figure 2. Ancestry Proportions and Dates of Admixture in Vanuatu

Black points represent the 20 present-day populations with the most confident admixture date estimates from ALDER (as measured by *Z* score for difference from zero), assuming 28 years per generation and showing 1 SE in each direction. The red point represents a pair of ancient individuals with a mean calibrated date of 1283 BP (18 ± 6 generations, or 1,800 ± 160 years BP). Gray shading indicates the Lapita period in Vanuatu (∼3000–2700 BP). See also Data S1.

Oceanian ancestry, as compared to a range of 9%–38% today (mostly 12%–20%, and highest on the island of Futuna, which harbors a "Polynesian Outlier" population, that is, one that speaks a Polynesian language, potentially due to east-to-west back migration from Polynesia [14]). For time points with multiple samples, the individuals' mixture proportions are statistically indistinguishable, except for 150 BP Efate (point estimates of 9%, 14%, 21%, and 26% First Remote Oceanian). The post-Lapita ancestry turnover is also evident in uniparental markers, as the majority of mtDNA and Y chromosome haplogroups observed from 2300–150 BP are typical of Papuan populations, albeit with the presence of some East Asian-derived haplogroups in both mtDNA and Y, showing that members of both sexes in both ancestral populations participated in the post-2300 BP Vanuatu admixture process (Table 1).

Dates of Admixture

We estimated dates of admixture based on weighted admixture linkage disequilibrium (LD) [15] using ALDER [16], with Ami (aboriginal Taiwanese) and New Guinea Highlanders as references (Figure 2; Data S1). We obtain significant evidence for admixture LD in almost all present-day populations and three ancient population groupings (noting that power is highly dependent on sample size). The date estimates are mostly 40–100 generations before present, or 1,100–2,800 years ago assuming 28 years per generation [17], consistent with admixture having occurred soon after the early settlement of Vanuatu and continuing through time (in cases of multiple pulses of admixture, ALDER produces a single average date). We observe a significant

negative correlation between admixture date and First Remote Oceanian ancestry proportion (R^2 = 0.33 at p < 0.01 for populations in Figure 2; R^2 = 0.21 at p < 0.01 for all present-day populations; STAR Methods), as expected if a subset of populations (e.g., Efate, Emae, Futuna, and Makura) received more recent pulses of gene flow from groups with high proportions of First Remote Oceanian ancestry. This scenario is plausible in light of Polynesian (Samoan) cultural influences and language replacement and the establishment of Polynesian Outlier populations on islands such as Ifira and Emae in central Vanuatu and Futuna in southern Vanuatu within the last several hundred years [14, 18].

We also obtain a direct ALDER date of 18 ± 6 generations in the past (500 ± 160 years) for a pair of ancient samples from Vanuatu radiocarbon dated to ∼1,300 years ago, coinciding with the typical range of admixture dates in present-day groups (Figure 2). Together with the present-day results, this observation is relevant to the ongoing debate about the timing of admixture between people of East Asian and Papuan ancestry in Remote Oceania. Methods based on wavelet transformations have suggested mixing at a date older than 3000 BP, prior to the Lapita expansion to Remote Oceania [12, 19], whereas methods based on admixture LD have suggested more recent dates, implying that mixture occurred after later streams of gene flow [20]. It has been argued that the differences may reflect systematic biases of the methods for dates older than a couple of thousand years [12]. Thus, our finding of a definitively post-Lapita date in samples that are closer in time to the admixture provides compelling evidence for the hypothesis of more recent mixture. A plausible scenario is that the initial migration of Papuan populations occurred during the late Lapita period (before ∼2700 BP), at which time archaeological evidence such as the transport of New Britain obsidian to Vanuatu documents links between the New Britain region and Remote Oceania (Santa Cruz and Vanuatu) bypassing much of the Solomon Islands [3], a pattern very similar to the population affinities seen in the genetic data. The near-complete population turnover attested to by genetic data may thus correspond to the evidence of transformation at the end of the Lapita period to more localized cultures, initiating a period of hundreds of years when inter-archipelago contacts appear to have nearly ceased [3].

Phylogeny of First Remote Oceanian Ancestry

To test whether the First Remote Oceanian ancestry in ancient and present-day groups is more closely related to Lapita samples from Tonga or Vanuatu, we compared the values of the statistics f_4(*Test*, Han; Atayal, Tonga_2600BP) and f_4(*Test*, Han; Atayal, Vanuatu_2900BP) for Oceanian populations as *Test* (STAR Methods). We found a trend toward greater allele sharing with Tonga, with significant results in Polynesian and to a lesser degree Polynesian Outlier populations (Data S1). These results show that the First Remote Oceanian ancestry in Polynesians today is derived from a source that was closer to the sampled

between New Britain and the Solomon Islands. The level of fill in the bars indicates Papuan ancestry proportion. The map was plotted in R using the "maps" package with data from http://www.naturalearthdata.com/.

(C) Close-up view of Vanuatu labeling islands for which new data are reported. Islands with ancient samples are indicated in red (for Efate and Ifira, both present-day and ancient individuals). The map was downloaded from http://www.maphill.com/vanuatu/simple-maps/blank-map/no-labels/.

(D) Papuan ancestry proportions for ancient samples over time; Efate Island is used to represent the present.

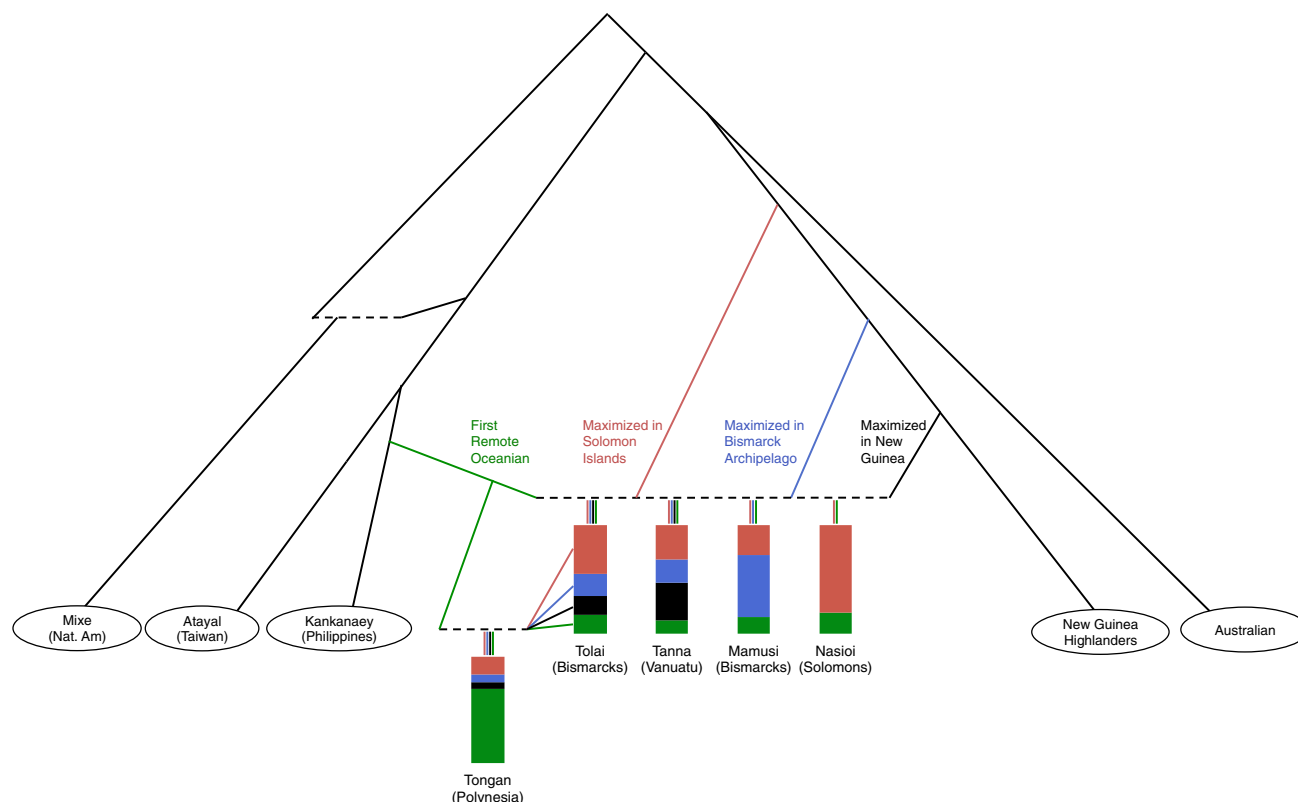See also Figure S2 and Data S1.

Figure 3. Inferred Admixture Graph Model with Diverse Present-Day Oceanian Populations

Dotted lines denote admixture events. For five populations, the proportions of four fitted ancestry sources maximized in First Remote Oceanians (green), the Solomon Islands (red), the Bismarck Archipelago (blue), and New Guinea (black) are shown. Papuan ancestry is inferred to be highly similar in the Tolai and in the Tongan population, allowing Tongan to be fit as a mixture of a group with ancestry similar to Tolai and additional ancestry from First Remote Oceanians. Colors were chosen to be correlated to the components inferred from ADMIXTURE (Figure S1), but the ADMIXTURE components represent combinations of the sources given here, and hence the ratios differ between the methods. Full model parameters for the admixture graph are shown in Figure S3.

Lapita-period population from Tonga than to the Vanuatu Lapita population. For post-Lapita populations (ancient and present-day) from Vanuatu, however, we do not have sufficient statistical power to determine which potential First Remote Oceanian source is closer.

Phylogeny of Papuan Ancestry

We built admixture graphs to explore in more detail the different streams of Papuan ancestry present in Oceania. We used as reference populations Australia, Kankanaey, Atayal, and Mixe together with representatives of major poles of Papuan genetic variation inferred from the ADMIXTURE analysis: Vanuatu_Tanna, Mamusi (New Britain), Nasioi (Solomon Islands), New Guinea Highlanders, and Tolai (New Britain and/or New Ireland). To avoid overfitting, we adopted a restricted framework in which the ancestry in each population was modeled as a combination of the same set of source lineages, with the exception of the unadmixed New Guinea Highlander population. We found that three Papuan source lineages were necessary in order to obtain a good fit for the model—one maximized in Mamusi, one maximized in Nasioi, and one closest to New Guinea Highlanders—showing that the implied ancestry components from ADMIXTURE (Figure 1A; Figure S1) are all well supported in formal models based on allele-sharing statistics. Additionally,

the admixture graph analysis suggests that the blue (Bismarck Archipelago majority) and red (Solomon Islands majority) ADMIXTURE components represent admixed ancestry. In particular, both include First Remote Oceanian ancestry ($\sim$20% for red and $\sim$5% for blue), and the two are additionally admixed with each other, as we could not fit a Solomon Islands population (e.g., Nasioi) and a Bismarck Archipelago population (e.g., Mamusi or Baining) simultaneously without admixture from one to the other. In our model, we included Solomon Islands-type ancestry in Mamusi (inferred as approximately one-third of its total Papuan ancestry), although we were unable to distinguish the direction(s) of gene flow. Vanuatu was confidently inferred to have ancestry from all three Papuan sources ($|Z| > 8$ for omitting any source).

We next asked whether we could add Polynesians (Tongan) as a mixture of a component related to one of the other Oceanian populations along with additional First Remote Oceanian ancestry. Such a model was successful only in one configuration, with Tongan as a mixture of a population related to the Tolai of New Britain plus additional First Remote Oceanian ancestry (all f statistics fit to within 2.0 SEs of their observed values except for one residual, f_4(Kankanaey, Tongan; Australian, Vanuatu_Tanna), at Z = 2.7; Figure 3; Figure S3). Our choice to include Tolai in the model was guided by the ADMIXTURE analysis, in

which the Papuan ancestry profile in Polynesians appears to match that in Tolai (and Tutuba, from near Santo island in Vanuatu) more closely than other populations. The Tolai are known to be descended from relatively recent mixture between groups from New Ireland and New Britain (resulting from displacement caused by the eruption of the Rabaul caldera ~1400 BP [18]), so their ancestors cannot represent the true source population of the Papuan ancestry in Polynesians. However, the similarity of Tolai Papuan ancestry to Polynesians suggests that the Papuan component in Polynesians could similarly be from a mixture of multiple Near Oceanian sources. Given that Tolai are genetically intermediate between populations from New Britain and New Ireland (the latter with higher Solomon Islands-related ancestry), Polynesians could plausibly have acquired New Britain-related ancestry from Vanuatu or Santa Cruz, along with ancestry more closely related to that in New Ireland or the Solomon Islands via a distinct stream of migration.

As suggested by similar mixtures of components in ADMIXTURE, the ancient Vanuatu individuals are broadly consistent with descent from the same common ancestral population as present-day groups from Vanuatu. In the admixture graphs, we could fit most of the ancient sample groups as sister populations to Vanuatu_Tanna, albeit with different proportions of First Remote Oceanian ancestry. The one exception was the 150 BP grouping of individuals from Efate (with ~18% First Remote Oceanian ancestry), which showed significant un-modeled allele sharing with Tongan (maximum residual $Z = 3.7$, after accounting for excess First Remote Oceanian ancestry). Some present-day Vanuatu populations, such as Efate, Makura, and Polynesian Outliers, show a similar pattern when tested in the model, most likely reflecting migration of Polynesians to Vanuatu in the last thousand years or less.

Conclusions

By analyzing a time transect of central Vanuatu from initial settlement through the present, combined with dense geographical sampling of present-day populations from 18 islands in Vanuatu and dozens of populations outside Vanuatu, we document a series of dramatic genetic shifts associated with consistently high human mobility through a total of at least four distinct streams of migration and admixture. First, the initial human migration to central Vanuatu involved First Remote Oceanians associated with the Lapita culture. Second, by ~2300 BP, these groups were almost completely displaced by Papuan-ancestry populations originally from the Bismarck Archipelago, who remain the source for most of the ancestry of people in Vanuatu today. Third, in Polynesia, we find evidence for a different Papuan ancestry type that reflects a distinct migration. Finally, these streams of ancestry reconnected in parts of Vanuatu, influenced by back migration from Polynesia. These results highlight a history of multiple episodes of migration and mixture in shaping the human diversity of Oceania.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information includes three figures and one data file and can be found with this article online at https://doi.org/10.1016/j.cub.2018.02.051.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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