

Genome-wide Ancestry Patterns in Rapanui Suggest Pre-European Admixture with Native Americans

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Summary

Background: Rapa Nui (Easter Island), located in the easternmost corner of the Polynesian Triangle, is one of the most isolated locations on the planet inhabited by humans. Archaeological and genetic evidence suggests that the island was first colonized by Polynesians around AD 1200, during their eastward expansion. Although it remains contentious whether Polynesians reached South America, suggestive evidence has been brought forward supporting the possibility of Native American contact prior to the European “discovery” of the island in AD 1722.

Results: We generated genome-wide data for 27 Rapanui. We found a mostly Polynesian ancestry among Rapanui and detected genome-wide patterns consistent with Native American and European admixture. By considering the distribution of local ancestry tracts of eight unrelated Rapanui, we found statistical support for Native American admixture dating to AD 1280–1495 and European admixture dating to AD 1850–1895.

Conclusions: These genetic results can be explained by one or more pre-European trans-Pacific contacts.

Introduction

Polynesia is often defined as the Pacific islands located within a triangle defined by New Zealand to the south, Hawaii to the north, and Rapa Nui (Easter Island) to the east, i.e., a territory equivalent to the size of the entire North Atlantic. More than 99% of this territory is ocean. Located 2,300 miles (3,700 km) west of South America, 4,300 miles (6,900 km) south of Hawaii, and 3,700 miles (5,950 km) north of the Antarctic, with a surface of only 63 square miles (163 km²), lies Rapa Nui, also known as “the navel of the world” (Te Pito o Te Henua; see e.g. [1]).

Although it has been long debated whether Polynesia (including Rapa Nui) was colonized from the west or from the east, it is now largely accepted that the islands were colonized as a result of an Austronesian expansion into remote Oceania from the west. This expansion is thought to have its origins in the proximities of Taiwan and the Philippines ~5,000 years ago and is characterized by (1) a linguistic identity, (2) a distinct culture and ceramic series called “Lapita,” and (3) shared design in sailing outrigger canoes [2–4]. During their eastbound journey, Austronesian-speaking groups would have admixed with Papuan-speaking groups from Melanesia, as suggested for example by genetic data [5]. It is estimated that the Samoa/Tonga area, lying in the Central Pacific, was colonized by 800 BC [6], and that between AD 1200 and AD 1300, according to recently refined chronologies based on radiocarbon dating, Polynesian settlers had discovered nearly every island (~500 islands) in the Eastern Pacific—including the Cook Islands, the Marquesas, New Zealand, Hawaii, and Rapa Nui. Rapa Nui is thought to have experienced a single colonization occurring around ~AD 1200 [7, 8], by a population of 30–100 men, women, and children distributed over two or more double-hulled canoes [1].

Rapa Nui distinguishes itself not only by its geographical location but also by the scope and extent of the archeological record, even more so when its diminutive size is considered. After settling on this isolated island, inhabitants constructed giant stone platforms (ahu), on which monumental stone statues (moai) still stand to this day. Over 900 statues have been recorded to date on the island [1], along with nearly 150 ahu [9]. These structures have attracted the interest of anthropologists and archaeologists for decades (e.g., [10]), with particular attention being paid to several “mysteries”: namely, how statues weighing up to 82 tons and measuring up to 32 feet in height were transported from the quarries to their platforms, whether the statues were inspired by South American architecture, and whether the islanders committed “ecocide” via widespread deforestation—effectively trapping themselves on this tiny speck of land (see e.g. [11, 12], but see also [1]).

Rapa Nui remained unknown to the Western world until Easter Sunday of AD 1722 [1], when the Dutch commander Jakob Roggeveen arrived with his ships. This contact started a new era in the history of Rapa Nui, including exposure of the islanders to novel pathogens. Arguably the most dreadful period in the history of the island took place during the Peruvian slave raids of the 1860s. Throughout this decade, the population of Rapa Nui, estimated at originally ~4,000 individuals, decreased by ~60% as a result of forced labor recruitment by Peruvian ships [13]. Moreover, in the following decade, the population continued to decline owing to diseases introduced by repatriated individuals, eventually reaching as few as 110 inhabitants ([1], p. 167). An additional consequence of this contact was a changing genetic composition owing to increased gene flow with outside populations [14–17].

Despite this well-known recent history and a general understanding of Polynesian colonization, the precise origin of the first inhabitants of Rapa Nui has remained elusive. Previous genetic studies performed on selected loci (mtDNA, Y

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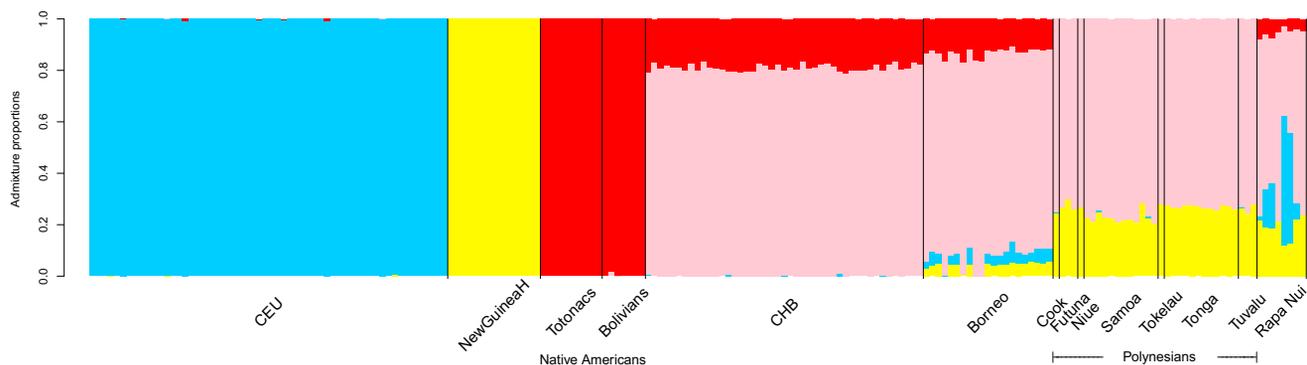


Figure 1. *ADMIXTURE* Analysis for a Merged Data Set Including Europeans, New Guinea Highlanders, Native Americans, Han Chinese, Borneans, Polynesians, and Rapanui for $K = 4$

This analysis was based on 197 individuals genotyped over 654,452 sites from [5, 29, 30]. Each bar represents an individual, and each color represents the admixture proportion from each ancestral component. See Figure S1B for other values of K .

chromosome, and HLA complex) [15, 16, 18] have supported a Polynesian origin of Rapanui. However, a series of archaeological and genetic observations suggest contact between East Polynesians (including Rapanui) and Native Americans prior to the first contact with Europeans. The presence of crops native to the Americas (the Andean sweet potato [19] and the bottle gourd [20]) on the islands long before European contact has been one of the most compelling arguments supporting such contact. For example, carbonized sweet potato remains found on Mangaia Island in Central Polynesia have been dated to as early as AD 988–1155 [21]. Unfortunately, sweet potatoes appear to have been introduced into Polynesia multiple times [22], leading to ambiguity in the interpretation of this example in some cases. In another line of evidence for pre-Columbian contact, chicken remains with a Polynesian genetic signature from the archaeological site of El Arenal, in Chile, have been radiocarbon dated to pre-Columbian times [23]. However, these results remain controversial due to potential contamination and a possible reservoir effect in radiocarbon dating [24–27]. Cultural similarities have also been noted, including similarities in fishing gear and watercraft used by Polynesians and coastal Native Americans ([28], pp. 71–93). Finally, genetic studies of the HLA complex [15–17] have identified alleles in Rapanui that are at high frequencies in Native American populations. Lie et al. [15] presented evidence that these alleles were introduced prior to the slave raids of the 1860s and concluded that their presence in the population may have predated the first European contact in AD 1722, although data were insufficient to establish this unequivocally (see [17] for review). Thus, although these multiple lines of evidence are suggestive of pre-Columbian Polynesian-Native American contact, no unequivocal genetic evidence has been presented to date. Nonetheless, because of its location and the previous cultural and genetic evidence, Rapa Nui is a good candidate among other Polynesian islands for pre-Columbian admixture between Native Americans and Polynesians.

To further investigate this hypothesized admixture event, we generated and analyzed data from >650,000 SNP markers from 27 native Rapanui collected in previous studies [15–17]. We compared these data with a worldwide set of individuals including Europeans, New Guinea Highlanders, Native Americans, Asians, and other Polynesian islanders [5, 29, 30]. Below, we characterize the Native American and European admixture events with Rapanui in terms of both timing and intensity.

Results

Admixture Analysis and Local Ancestry Inference

We analyzed data for 27 Rapanui in total. As described below, all 27 were used for phasing, while only the 8 unrelated individuals were used for admixture analyses (using *ADMIXTURE* [31] and *RFmix* [32]) and for demographic inference (using *tracts* and the method described in [33]). We compiled a data set that includes genotype data from 58 Europeans (CEU), 15 New Guinea Highlanders, 17 Native Americans, 45 Chinese (CHB), 21 Borneans, 33 Polynesians (seven different locations: Futuna, Niue, Samoa, Tokelau, Tonga, Tuvalu, and Cook Islands), and 8 unrelated Rapanui. We explored population structure in our data set using *ADMIXTURE* [31] with different numbers of admixture components (K ; Figure 1; see also Figure S1B available online). Note that we included only unrelated individuals (8 Rapanui out of 27 that passed our quality filters), because the underlying model in *ADMIXTURE* assumes that individuals are unrelated. For $K = 2$ and $K = 3$, there was no obvious difference between Rapanui and other Polynesians, other than a higher European proportion among Rapanui. Similar to other Polynesians, Rapanui share an admixture component with New Guinea Highlanders. At $K = 4$, a Native American component arose, thus separating Native Americans from the remaining populations of Asian descent. For this value of K , Rapanui presented a fraction corresponding to the Native American cluster (between 3.1% and 8.8% for the eight individuals) not observed in the other Polynesian individuals (see also Supplemental Experimental Procedures). At $K = 5$, Polynesians formed their own cluster separate from Asian individuals. Finally, at $K = 6$, Rapanui could be distinguished from the rest of the Polynesians.

To examine the Native American admixture in Rapanui in more detail, we ran *ADMIXTURE* [31] with $K = 3$ on a data set restricted to the 58 Europeans, the 17 Native Americans, the 33 Polynesians, and the 8 unrelated Rapanui (Figure 2). We found that Rapanui have an average Native American admixture proportion of ~6% and an average European admixture proportion of ~16%. Note that non-Native Americans had some degree of inferred Native American admixture. Specifically, we estimated 0.08% and 0.05% Native American admixture in non-Rapanui Polynesians and Europeans, respectively, which we interpret as the background noise levels. The Native American proportion detected in Rapanui was significantly

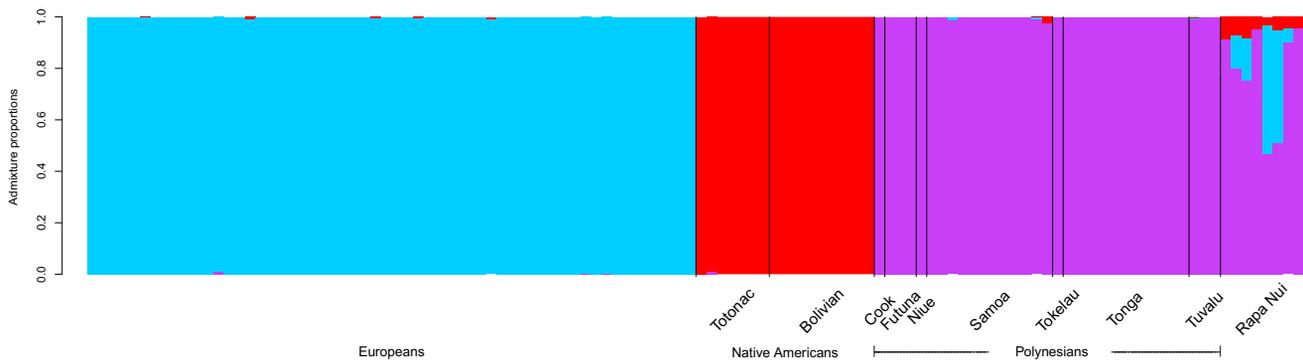


Figure 2. *ADMIXTURE* Analysis for the Data Set Including Europeans, Native Americans, Polynesians, and Rapanui

This analysis was based on 87 individuals genotyped over 654,452 sites. Each bar represents an individual, and each color represents the admixture proportion from each of the K assumed ancestral components.

larger than that detected in other Polynesians and Europeans (Wilcoxon test, $p = 3.3 \times 10^{-8}$ and $p = 5.8 \times 10^{-11}$, respectively).

We also obtained admixture proportions from local ancestry inference using haplotype structure, as implemented in the *RFmix* program [32]. This method identifies ancestry tracts—contiguous segments of DNA in an individual—originating from one of the source populations. In contrast to *ADMIXTURE*, *RFmix* assumes dependence among sites (linkage disequilibrium). To apply the method, we phased the genotype data using all 27 Rapanui samples included in this study, since including related individuals has been shown to improve the phasing effectiveness [34]. For this analysis, we assumed three ancestral populations (Europeans, Native Americans, and Polynesians) and summed over all ancestry tracts from each ancestry for each individual. The results of the *ADMIXTURE* and *RFmix* analyses are similar (Table S2). We found a mean European admixture proportion in Rapanui of 16% and a lower mean Native American admixture proportion of 8%.

The presence of Native American admixture in Rapanui does not in itself show that there was pre-Columbian contact. To establish that the contact was not mediated by Europeans, we need to show (1) that the time of admixture between Native Americans and Rapanui is older than the admixture time with Europeans and (2) that it predates the first contact between Rapanui and Europeans. There are two almost independent lines of evidence that can be used to date an admixture event from genetic data. First, as time passes after an admixture event, the lengths of the ancestry tracts become smaller as they are broken up by recombination in successive generations. The length distribution of ancestry tracts therefore contains information regarding admixture times [35–37]. Additionally, due to sexual reproduction, ancestry tracts being exchanged among individuals leads to a more homogenous distribution of ancestry proportions among individuals as time passes [33, 38].

In the *RFmix* analyses, we found a variance in European admixture proportions 100 times larger than the variance of the Native American proportions. Moreover, we found that the Native American ancestry tract length distribution had a high frequency of short tracts compared to the European distribution (Figure 5). These observations suggest that the Native American admixture time is considerably older than the European time.

Below, we use these two lines of evidence first to estimate Native American and European admixture times and then to

formally test the null hypothesis of equally old first-admixture times for Europeans and Native Americans.

Modeling Demographic Scenarios

To infer the admixture times, we first used a likelihood-based approach implemented in the software *tracts* [36]. *tracts* assumes that the copying process that generates the chromosomes present at a given time t follows a Markovian Wright-Fisher model. In this model, each new chromosome at time t is formed by randomly recombining all chromosomes present at time $t + 1$. Under this model, the recombination events are exponentially distributed along a given chromosome. Additionally, admixture events are modeled as discrete migration pulses; therefore, admixture time estimates should be interpreted as average times over all actual gene flow events. This method uses the observed ancestry tract length distributions in unrelated individuals (eight Rapanui) as summary statistics. We explored the likelihood of the observed tract length distributions for different combinations of Native American (t_{NA}) and European (t_E) admixture times for a model involving a single Native American pulse and a single European pulse of magnitude p_{NA} and p_E , respectively. We found that the likelihood surface has only one optimum (Figures 3 and S5), which corresponds for the Native American pulse to $\hat{t}_{NA} = 22$ generations ago and $\hat{p}_{NA} = 0.09$, and for the European pulse to $\hat{t}_E = 4$ generations ago and $\hat{p}_E = 0.17$. By assuming a human generation time between 25 and 30 years [39, 40] and by setting the “present” time to 1970 (when the first samples were collected [15]), these estimates translate to AD 1310–1420 for \hat{t}_{NA} and AD 1850–1870 for \hat{t}_E .

Second, we used a new complementary method for estimating admixture times based on the variance in admixture proportions among individuals [33]. This method assumes that a “hybrid” population is formed according the “random union of gametes” model and characterizes the admixture proportion distribution (as estimated by *ADMIXTURE*) based on already established linkage disequilibrium results. In this case, and as opposed to *tracts*, the new generation is not formed by randomly recombining all chromosomes. We fitted the expression described in the Supplemental Experimental Procedures to the data and, assuming $N_e = 1,000$, we obtained point estimates of $\hat{t}_{NA} = 13$ generations and $\hat{t}_E = 2$ generations ago. These point estimates are more recent than those obtained using tract-based inferences but have overlapping confidence intervals with those obtained using ancestry tracts

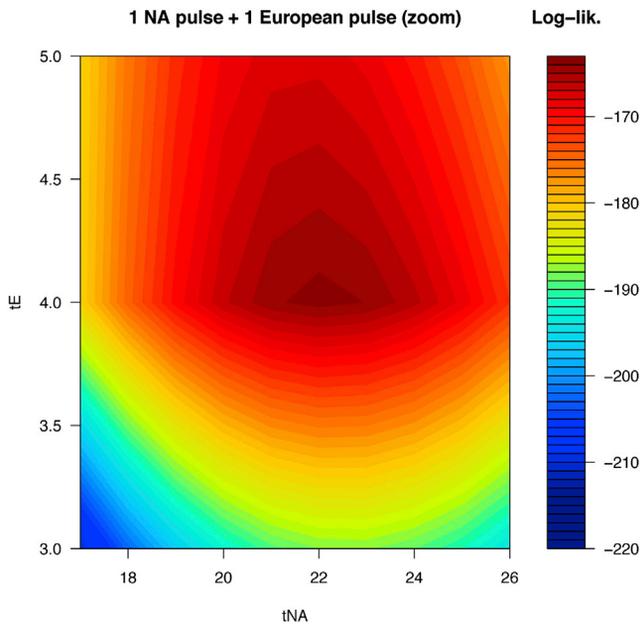


Figure 3. Likelihood Surface Obtained for Different Values of Native American and European Admixture Times
Native American and European admixture times are denoted by t_{NA} and t_E , respectively. See Figure S5 for larger values of t_{NA} and t_E .

(see Supplemental Experimental Procedures). The effective population size has little effect on the estimates. Indeed, we used different values of N_e ranging from 100 to 100,000 and found that \hat{t}_{NA} varied by only one generation and \hat{t}_E remained unchanged. This almost independent information regarding admixture times again demonstrates that the admixture time of Europeans is substantially more recent than that of Native Americans.

To further characterize the admixture pulses and their respective ordering, we considered two competing models compatible with the observed admixture patterns (schematics of the models are shown in Figure 4). For both models, the admixture proportions and admixture times are the parameters being estimated while we applied constraints on the times for each model. The key feature that varies between models is the ordering of the Native American and the European admixture events (M1, “Native American first,” and M2, “European first”). Note that model M2 also includes the case in which both admixture events occur at the same time (Figure 4). Qualitatively, we found that the “Native American first” model produced a better fit to the data (Figure 5). Maximum-likelihood estimates (MLEs) and log-likelihood values are given in Table 1. Below, we proceed to formally test models of admixture using likelihood ratio statistics.

Hypothesis Testing, Maximum-Likelihood Estimates, and Confidence Intervals

Because ancestry tracts are not statistically independent [37], we cannot rely on standard asymptotic results to approximate the distribution of the likelihood ratio statistic under the null hypothesis to test the significance of each competing model. Therefore, we ran coalescent simulations to test the significance of each competing model and used a nonparametric bootstrap approach for the confidence intervals. For the coalescent simulations, we assumed a model with four ancestral

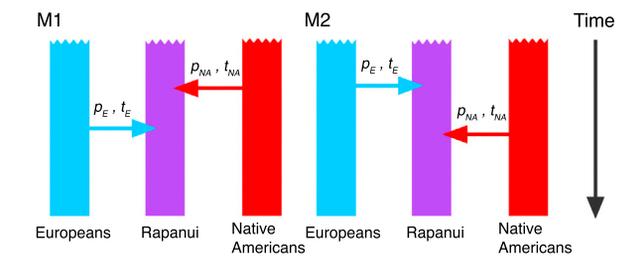


Figure 4. Schematic Representation of the Two Competing Models
Each model is parameterized by p_{NA} and p_E (i.e., the Native American and European admixture proportions, respectively) and t_{NA} and t_E (i.e., the Native American and European admixture times). M1 is a “Native American first” model ($t_{NA} > t_E$), whereas M2 is a “European first” model ($t_{NA} \leq t_E$).

populations (corresponding to Europeans, Native Americans, Polynesians, and Rapanui) with constant population sizes (see Figure 6 for a description of population sizes and split times [5, 41]) and added Native American and European migration pulses that correspond to the MLEs from each of our competing models accordingly (Figure 6). Although *tracts* [36] makes no assumptions about the relationship or split times between the ancestral populations or population sizes, we find that ancestry tract length distributions from simulated data fit well with the observed data and with the distributions expected by *tracts* (Figure 5).

We used the likelihood of the simulated data under each of the competing models to compute the significance of the likelihood ratios for competing models. To test the ordering of the migration pulses, we simulated data under the “European first” model (M2). We then tested the null hypothesis (M2) against the alternative hypothesis of a Native American pulse that predates the European pulse (M1). We were able to reject the null hypothesis (“European first”) at a significance level of 1% ($p < 0.004$). See Figure S6 for the simulated likelihood ratio distribution.

We computed confidence intervals for the parameters estimated for the “Native American first” model (M1). To do so, and since we do not know the demographic history of the populations, we used a nonparametric block bootstrap approach by resampling whole chromosomes. Confidence intervals and the distribution of the parameters after resampling are reported in Figure S2A. For M1, we estimated that the Native American migration into Rapa Nui occurred between AD 1280 and AD 1495 and the European migration occurred between AD 1850 and AD 1895, assuming a human generation time between 25 and 30 years [39, 40] (Figure S2A). We get similarly narrow confidence intervals for a parametric bootstrap approach (Figure S2B). For the admixture proportion-based method, we used a parametric approach, and we estimate that the Native American migration into Rapa Nui occurred between AD 1280 and AD 1745 and the European migration between AD 1850 and AD 1945. The confidence intervals between the two methods overlap (Figure S2C).

We qualitatively tested the robustness of the observed signal to (1) SNP ascertainment in Europeans, (2) departure from a simple constant population size model, (3) a Wright-Fisher model instead of a Markovian Wright-Fisher model, and (4) a second European migration pulse. We found that the simulated ancestry tract length distributions qualitatively remained the same for all cases, suggesting that the ordering of the admixture events is robust to those model

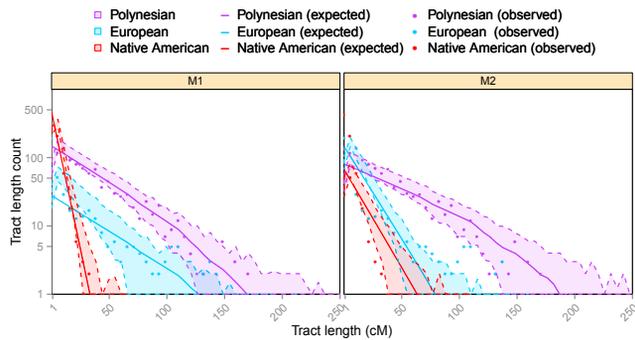


Figure 5. Ancestry Tract Length Distributions for the Eight Unrelated Rapanui after Local Ancestry Inference

Each color corresponds to one of the three ancestral populations used in the *RFmix* analysis (purple, Polynesians; cyan, Europeans; red, Native Americans). Points correspond to the observed data, and solid lines correspond to the expected tract length distributions as predicted by the model implemented in *tracts* for models M1 and M2. Shaded areas correspond to the 95% confidence region (by ancestry) built from all the *fastsimcoal2* runs under each model. For a schematic representation of the models, see Figure 4.

misspecifications (see Supplemental Experimental Procedures for details).

Discussion

Polynesian Origin of Rapanui People

Our results reveal a mostly Polynesian ancestry among Rapanui, in agreement with most anthropological studies that have been published to date (for review, see [3]) as well as genetic results based on selected markers from modern and ancient samples [15–18]. Polynesians have been shown to originate from an admixture event between Southeast Asians (~80%) and Melanesians (~20%), dated to around ~3,000 years ago [5, 42]. We demonstrate that Rapanui bear a similar signal, suggesting genetic continuity between the Polynesians from Futuna, Niue, Samoa, Tokelau, Tonga, Tuvalu, the Cook Islands, and Rapa Nui. Interestingly, from the *ADMIXTURE* run with $K = 6$ (Figure 1), in which Rapanui differentiate from the rest of the Polynesians, the sole Cook Islander that we included in this analysis displays a component from the Rapa Nui cluster. This could be indicative of a west-east genetic differentiation in Polynesians, but more data are needed to test such a hypothesis. It was argued previously by Thor Heyerdahl [11] (in part to explain the exceptional archaeological record) that Native Americans were the first to colonize Rapa Nui. This theory seems quite unlikely with the data at hand. Instead, our data suggest an initial colonization of the island by Polynesians.

European Admixture

Although the samples in this study are from individuals native to Rapa Nui, we detected genome-wide European admixture (~16%) in a largely Polynesian ancestral background. Such admixture had already been documented for Y chromosome and HLA markers for those samples [14–16] and is consistent with the known European history on the island beginning in AD 1722. Indeed, by the start of the slave trade in AD 1862, more than 50 ships from various European nations (Holland, Spain, England, and France) had visited the island. During that period, trafficking in women was reported by visiting ships [43]. More recently, the Peruvian slave raids and the annexation of the

Table 1. Maximum-Likelihood Estimates for the Two Competing Models

Model	$\hat{\rho}_{NA}$	\hat{t}_{NA} (Calendar Date)	$\hat{\rho}_E$	\hat{t}_E (Calendar Date)	Log Likelihood
M1	0.09	21 (AD 1340–1445)	0.15	4 (AD 1850–1870)	–162.7
M2	0.06	8 (AD 1730–1770)	0.15	8 (AD 1730–1770)	–344.5

In order to get an estimate for the time (in generations) of each migration pulse, \hat{t}_{NA} and \hat{t}_E were rounded up to the nearest integer (see Supplemental Experimental Procedures). Numbers in parentheses are time estimates expressed in calendar dates assuming a human generation time between 25 and 30 years [39, 40].

island by Chile in AD 1888 connected the island even further with the outside world [14].

Native American Admixture

We detected approximately 8% Native American admixture in unrelated Rapanui on a genome-wide scale, confirming previous results based on the HLA complex [15, 16]. To our knowledge, Native American admixture has not been reported previously in other Polynesians on a genome-wide basis. This signal could be explained by two non-mutually exclusive scenarios: (1) a post-European admixture event facilitated by the slave trade in the 1860s, as suggested in [44], and/or (2) a pre-European trans-Pacific admixture event.

Evidence for a Pre-European Native American Contact

The possibility of trans-Pacific Polynesian-American contact has been proposed by archaeologists since the early 1900s ([28], p. 1). Although an early contact has been proposed by previous studies [15–17], no unequivocal genetic evidence has been reported to date. Our results suggest that Native American admixture occurred prior to European admixture. Specifically, we detect a lower variance in Native American ancestry components, and smaller ancestry tracts, as compared to Europeans. To characterize the timing of the admixture event in a statistical framework, we infer parameters from specific demographic scenarios, using a maximum-likelihood method that has been validated before in similar human data sets (e.g., [45]), as well as a new method based on the variance in admixture proportions. Using these approaches, we can statistically reject “European first” scenarios. It is noteworthy that models with several pulses are a generalization of single-pulse models and will therefore provide a better fit to the data. In our case, we find that (1) adding a second European pulse does not improve the fit significantly when assuming that the European gene flow postdated the first documented presence of Europeans in the Pacific in AD 1520 [46], and (2) the second pulse was found to be of such low magnitude that the associated admixture time spanned a whole range of times equally well (Figure S5).

Although our data suggest that modern-day Rapanui are the result of a pre-Columbian gene flow event between Native Americans and Polynesians, we cannot, with the data at hand, determine how this gene flow happened. Nevertheless, it is interesting to consider the evidence presented in other fields. There are two main scenarios compatible with the data: Native Americans sailing to Rapa Nui, or Polynesians sailing to the Americas and back. Although “boats on occasion can sail from almost anywhere to anywhere” [47], from a purely seafaring capability perspective, it is probably fair to say that the latter scenario is more likely. Let us consider the geographical situation of Rapa Nui and the feasibility of such a voyage, especially in the context of the Polynesian expansion.

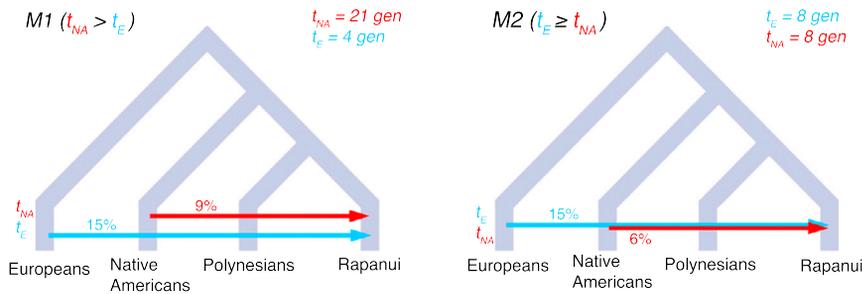


Figure 6. Schematic Representation of the Two Competing Demographic Scenarios that Were Used for Coalescent Simulations

Both models include three population splits that we set at 1,280 generations ago (~32,000 years ago) for the European split, 920 generations ago (~23,000 years ago) for the Native American split, and 32 generations ago (~800 years ago) for the Polynesian Rapa Nui split, and we assumed a population size of $N_e = 10,000$ for Europeans and a population size of $N_e = 1,000$ for each of Native Americans, Polynesians, and Rapanui. The simulations were run with the corresponding MLEs obtained by *tracts* from the observed data for models M1 and M2 (Table 1).

The colonization of the Polynesian islands did not occur as the result of a single trip, but the most prevalent view—supported by the data we generated—suggests that they were colonized during the same expansion. It is believed that this expansion was part of an intentional and systematic exploration of the region ([28], pp. 64–66). An interesting feature of the seascape is that the islands in East Polynesia are farther apart from each other than those located in Central Polynesia [47]. Radiocarbon dates suggest that most of East Polynesia was colonized within one century [8]. Not only did the first colonizers reach islands separated by thousands of miles, they seemingly did so in a rapid upwind fashion, since the most prevalent winds blow east to west at those latitudes. In this regard, one interesting hypothesis is that the islanders could have decided to sail toward the east to facilitate return trips. By the time Polynesians settled on Rapa Nui, the Americas had become a large target at a feasible distance with long-distance sailing technology already in place ([28], p. 249). The feasibility of such a trip was elegantly demonstrated in a sailing simulation study wherein Fitzpatrick and Callaghan [48] showed that all sailing voyages heading intentionally east from Rapa Nui would always reach the Americas with a trip lasting from two weeks to approximately two months. The return trip appears more challenging. Simulations with a starting point in Chile lead to mostly unsuccessful voyages (for any of the Polynesian islands). With a starting point in Ecuador, most sailing canoes bypassed Rapa Nui without foreknowledge. Perhaps a similar point can be made when one considers the relatively late “discovery” of Rapa Nui by Europeans as compared to the other Polynesian islands.

Jones et al. [28] reviewed in 2011 the archaeological, physical anthropological, linguistic, and navigational evidence for pre-Columbian contact. They identified three regions of potential contact, namely Chile, the Gulf of Guayaquil in Ecuador, and the Santa Barbara Channel in California, and constrained the contacts to a period between AD 700 and AD 1350. They argued that the most parsimonious explanation in all cases is a return voyage by Polynesians, but they could not exclude the scenario of a one-way raft trip, as suggested for example in the mid-20th century by Thor Heyerdahl [11]. One of their primary arguments is the lack of Native American influence in Polynesia, particularly in terms of Polynesian architecture ([28], pp. 263–265)—aside, perhaps, from one of the platform sites on Rapa Nui, Ahu Vinapu.

These considerations, taken together, lead to the speculation that a return voyage is perhaps the most likely scenario. If this is indeed true, it is intriguing that, to date, no Polynesian genetic signal has been reported in modern Native American populations (e.g., [49], but see [50]). This observation could

be explained by hypothesizing that (1) only a few Polynesian individuals were involved compared to the size of the Native American populations, (2) the migration was so recent that it would only impact some yet-unsequenced populations in the Americas, and/or (3) cultural differences prevented gene flow.

Although it is important to avoid overinterpreting our results, it is interesting to consider the timing of the admixture in context with evidence reported in other studies. We have inferred the Native American admixture event to have occurred between AD 1280 and AD 1425. These dates should be treated with caution given the simplifying assumptions of the underlying model. For example, generation time in humans is still debated and has a direct impact on the translation into calendar years [39, 40]. Moreover, admixture events are assumed to occur in a discrete fashion in our demographic models. Therefore, our admixture times should be interpreted as average times over all actual gene flow events. Nevertheless, they are in surprisingly good agreement not only with the colonization history of Easter Island, thought to have occurred not later than AD 1200 [7], but also with the observation that at some point in time, Polynesians stopped sailing long distances. It is indeed estimated by Jones et al. ([28], pp. 265–267) that by around AD 1450, the expansion had ceased. By the time Europeans reached the islands, Polynesian boat technology had changed in such a way that long-distance ocean sailing had seemingly come to an end.

Future Work

Future work from combined fields should allow us to (1) address the question of the directionality of the contact, (2) refine the timing of the contact, and (3) establish the cultural impact of such an event on Rapanui. In particular, it will be interesting to determine which Native American populations were involved in the contact and which Polynesian populations exhibit such an admixture signature, given that the evidence from sweet potato studies suggests that such a signal could be found in additional islands. This will require the generation of further genomic data. Whole-genome data from Polynesians and Native Americans will also be valuable in overcoming biases introduced by SNP ascertainment in genotyping platforms. Finally, ancient DNA data would allow for deeper insight into the timing of admixture. Although numerous human skeletons have been found on the island [51] and although the field of ancient DNA has entered the genomics area (e.g., [52]), it remains challenging to gain access to human remains sufficiently well preserved and predating first European contact.

Experimental Procedures

See [Supplemental Experimental Procedures](#) for complete materials and methods.

E.T. collected blood samples in 1971 and 2008 on Rapa Nui. All participants were informed about the purpose of the study with the assistance of an interpreter and gave their informed consent when contributing blood samples, in accordance with the Declaration of Helsinki. Ethical approval for the project was provided by the Regional Ethics Committee in Norway. Genotype data are available for population history research upon request.

Supplemental Information

Supplemental Information includes six figures, six tables, and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.09.057>.

Author Contributions

This project was initiated by E.T. and started as a collaboration between E.W. and E.T. E.W., E.T., and A.-S.M. conceived the project. A.-S.M. designed the project with input from R.N., E.W., and M.R. E.T. provided background information. E.W., A.-S.M., and S.R. supervised the project. E.T. provided the samples. S.T.F. prepared the DNA samples she had extracted for a previous study. A.S.-O. conducted the lab work with input from M.R. J.V.M.-M. and M.L. analyzed the data. J.V.M.-M. and A.-S.M. interpreted the data with input from S.R., M.L., M.R., and R.N. J.V.M.-M. and A.-S.M. wrote the manuscript with input from all authors.

Acknowledgments

We would like to thank Morten E. Allentoft, Omar E. Cornejo, Laurent Excoffier, M. Thomas P. Gilbert, Brenna M. Henn, Jeffrey D. Jensen, Manfred Kayser, Greger Larson, Carl Lipo, Andrés Moreno-Estrada, Molly Przeworski, Mark Stoneking, and Francisco Torres Hochstetter for discussions. We thank Helene Martinsson-Wallin, Paul Wallin, and Grant McCall for helpful information about the colonization of Rapa Nui. We thank AROS Applied Biotechnology for producing the data. We also thank Oscar Lao, Andreas Wollstein, and Jinchuan Xing for providing and helping with the genotype data included in our reference data set. GeoGenetics members were supported by the Lundbeck Foundation and the Danish National Research Foundation (DNRF94). J.V.M.-M. was supported by a scholarship from Consejo Nacional de Ciencia y Tecnología (Mexico). A.-S.M. was supported by a fellowship from the Swiss National Science Foundation (PBSKP3_143529). Collection of blood samples on Rapa Nui and preparation of DNA from these samples were supported by Inven2, the University of Oslo, and Oslo University Hospital.

Received: July 31, 2014

Revised: August 29, 2014

Accepted: September 22, 2014

Published: October 23, 2014

References

- Hunt, T., and Lipo, C. (2011). *The Statues that Walked: Unraveling the Mystery of Easter Island* (New York: Free Press).
- Hurles, M.E., Matisoo-Smith, E., Gray, R.D., and Penny, D. (2003). Untangling Oceanic settlement: the edge of the knowable. *Trends Ecol. Evol.* **18**, 531–540.
- Kirch, P.V. (2010). Peopling of the Pacific: A holistic anthropological perspective. *Annu. Rev. Anthropol.* **39**, 131–148.
- Ko, A.M., Chen, C.Y., Fu, Q., Delfin, F., Li, M., Chiu, H.L., Stoneking, M., and Ko, Y.C. (2014). Early Austronesians: into and out of Taiwan. *Am. J. Hum. Genet.* **94**, 426–436.
- Wollstein, A., Lao, O., Becker, C., Brauer, S., Trent, R.J., Nürnberg, P., Stoneking, M., and Kayser, M. (2010). Demographic history of Oceania inferred from genome-wide data. *Curr. Biol.* **20**, 1983–1992.
- Rieth, T.M., and Hunt, T.L. (2008). A radiocarbon chronology for Samoan prehistory. *J. Archaeol. Sci.* **35**, 1901–1927.
- Hunt, T.L., and Lipo, C.P. (2006). Late colonization of Easter Island. *Science* **311**, 1603–1606.
- Wilmshurst, J.M., Hunt, T.L., Lipo, C.P., and Anderson, A.J. (2011). High-precision radiocarbon dating shows recent and rapid initial human colonization of East Polynesia. *Proc. Natl. Acad. Sci. USA* **108**, 1815–1820.
- Martinsson-Wallin, H. (1994). *Ahu, the Ceremonial Stone Structures of Easter Island: Analyses of Variation and Interpretation of Meanings* (Uppsala: Societas Archaeologica Upsaliensis).
- Bahn, P., and Flenley, J. (1992). *Easter Island, Earth Island* (London: Thames & Hudson).
- Heyerdahl, T. (1952). *American Indians in the Pacific: The Theory Behind the Kon-Tiki Expedition* (London: Allen & Unwin).
- Diamond, J. (2007). Archaeology: Easter Island revisited. *Science* **317**, 1692–1694.
- Maude, H.E. (1981). *Slavers in Paradise: The Peruvian Slave Trade in Polynesia, 1862–1864* (Canberra: Australian National University Press).
- González-Pérez, E., Esteban, E., Via, M., García-Moro, C., Hernández, M., and Moral, P. (2006). Genetic change in the polynesian population of Easter Island: evidence from Alu insertion polymorphisms. *Ann. Hum. Genet.* **70**, 829–840.
- Lie, B.A., Dupuy, B.M., Spurkland, A., Fernández-Viña, M.A., Hagelberg, E., and Thorsby, E. (2007). Molecular genetic studies of natives on Easter Island: evidence of an early European and Amerindian contribution to the Polynesian gene pool. *Tissue Antigens* **69**, 10–18.
- Thorsby, E., Flåm, S.T., Woldseth, B., Dupuy, B.M., Sanchez-Mazas, A., and Fernandez-Vina, M.A. (2009). Further evidence of an Amerindian contribution to the Polynesian gene pool on Easter Island. *Tissue Antigens* **73**, 582–585.
- Thorsby, E. (2012). The Polynesian gene pool: an early contribution by Amerindians to Easter Island. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **367**, 812–819.
- Hagelberg, E., Quevedo, S., Turbon, D., and Clegg, J.B. (1994). DNA from ancient Easter Islanders. *Nature* **369**, 25–26.
- Ballard, C., Brown, P., Bourke, R.M., and Harwood, T. (2005). *The Sweet Potato in Oceania: A Reappraisal* (Oceania Monograph 56/Ethnology Monographs 19) (Sydney: University of Sydney).
- Green, R. (2000). A range of disciplines support a dual origin for the bottle gourd in the Pacific. *J. Polyn. Soc.* **109**, 191–198.
- Hather, J., and Kirch, P.V. (1991). Prehistoric sweet potato (*Ipomea batatas*) from Mangaia Island, Central Polynesia. *Antiquity* **65**, 887–893.
- Roullier, C., Benoit, L., McKey, D.B., and Lebot, V. (2013). Historical collections reveal patterns of diffusion of sweet potato in Oceania obscured by modern plant movements and recombination. *Proc. Natl. Acad. Sci. USA* **110**, 2205–2210.
- Storey, A.A., Ramirez, J.M., Quiroz, D., Burley, D.V., Addison, D.J., Walter, R., Anderson, A.J., Hunt, T.L., Athens, J.S., Huynen, L., and Matisoo-Smith, E.A. (2007). Radiocarbon and DNA evidence for a pre-Columbian introduction of Polynesian chickens to Chile. *Proc. Natl. Acad. Sci. USA* **104**, 10335–10339.
- Gongora, J., Rawlence, N.J., Mobegi, V.A., Jianlin, H., Alcalde, J.A., Matus, J.T., Hanotte, O., Moran, C., Austin, J.J., Ulm, S., et al. (2008). Indo-European and Asian origins for Chilean and Pacific chickens revealed by mtDNA. *Proc. Natl. Acad. Sci. USA* **105**, 10308–10313.
- Gongora, J., Rawlence, N.J., Mobegi, V.A., Jianlin, H., Alcalde, J.A., Matus, J.T., Hanotte, O., Moran, C., Austin, J.J., Ulm, S., et al. (2008). Reply to Storey et al.: More DNA and dating studies needed for ancient El Arenal-1 chickens. *Proc. Natl. Acad. Sci. USA* **105**, E100.
- Storey, A.A., Quiroz, D., Ramirez, J.M., Beavan-Athfield, N., Addison, D.J., Walter, R., Hunt, T., Athens, J.S., Huynen, L., and Matisoo-Smith, E.A. (2008). Pre-Columbian chickens, dates, isotopes, and mtDNA. *Proc. Natl. Acad. Sci. USA* **105**, E99, author reply E100.
- Thomson, V.A., Lebrasseur, O., Austin, J.J., Hunt, T.L., Burney, D.A., Denham, T., Rawlence, N.J., Wood, J.R., Gongora, J., Girdland Flink, L., et al. (2014). Using ancient DNA to study the origins and dispersal of ancestral Polynesian chickens across the Pacific. *Proc. Natl. Acad. Sci. USA* **111**, 4826–4831.
- Jones, T.L., Storey, A.A., Matisoo-Smith, E.A., and Ramirez-Aliaga, J.M. (2011). Polynesians in America: Pre-Columbian Contact with the New World (Lanham: Altamira Press).
- Frazer, K.A., Ballinger, D.G., Cox, D.R., Hinds, D.A., Stuve, L.L., Gibbs, R.A., Belmont, J.W., Boudreau, A., Hardenbol, P., Leal, S.M., et al.; International HapMap Consortium (2007). A second generation human haplotype map of over 3.1 million SNPs. *Nature* **449**, 851–861.
- Xing, J., Watkins, W.S., Shlien, A., Walker, E., Huff, C.D., Witherspoon, D.J., Zhang, Y., Simonson, T.S., Weiss, R.B., Schiffman, J.D., et al. (2010). Toward a more uniform sampling of human genetic diversity: a

- survey of worldwide populations by high-density genotyping. *Genomics* 96, 199–210.
31. Alexander, D.H., Novembre, J., and Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* 19, 1655–1664.
 32. Maples, B.K., Gravel, S., Kenny, E.E., and Bustamante, C.D. (2013). RFMix: a discriminative modeling approach for rapid and robust local-ancestry inference. *Am. J. Hum. Genet.* 93, 278–288.
 33. Liang, M., and Nielsen, R. (2014). Understanding admixture fractions. *bioRxiv*, <http://dx.doi.org/10.1101/008078>. <http://biorxiv.org/content/early/2014/08/16/008078>.
 34. Delaneau, O., Zagury, J.F., and Marchini, J. (2013). Improved whole-chromosome phasing for disease and population genetic studies. *Nat. Methods* 10, 5–6.
 35. Pool, J.E., and Nielsen, R. (2009). Inference of historical changes in migration rate from the lengths of migrant tracts. *Genetics* 181, 711–719.
 36. Gravel, S. (2012). Population genetics models of local ancestry. *Genetics* 191, 607–619.
 37. Liang, M., and Nielsen, R. (2014). The lengths of admixture tracts. *Genetics* 197, 953–967.
 38. Verdu, P., and Rosenberg, N.A. (2011). A general mechanistic model for admixture histories of hybrid populations. *Genetics* 189, 1413–1426.
 39. Tremblay, M., and Vézina, H. (2000). New estimates of intergenerational time intervals for the calculation of age and origins of mutations. *Am. J. Hum. Genet.* 66, 651–658.
 40. Sun, J.X., Helgason, A., Masson, G., Ebenesersdóttir, S.S., Li, H., Mallick, S., Gnerre, S., Patterson, N., Kong, A., Reich, D., and Stefansson, K. (2012). A direct characterization of human mutation based on microsatellites. *Nat. Genet.* 44, 1161–1165.
 41. Rasmussen, M., Guo, X., Wang, Y., Lohmueller, K.E., Rasmussen, S., Albrechtsen, A., Skotte, L., Lindgreen, S., Metspalu, M., Jombart, T., et al. (2011). An Aboriginal Australian genome reveals separate human dispersals into Asia. *Science* 334, 94–98.
 42. Kayser, M., Lao, O., Saar, K., Brauer, S., Wang, X., Nürnberg, P., Trent, R.J., and Stoneking, M. (2008). Genome-wide analysis indicates more Asian than Melanesian ancestry of Polynesians. *Am. J. Hum. Genet.* 82, 194–198.
 43. McCall, G. (1976). European impact on Easter Island: Response, recruitment and the Polynesian experience in Peru. *J. Pac. Hist.* 11, 90–105.
 44. Hurles, M.E., Maund, E., Nicholson, J., Bosch, E., Renfrew, C., Sykes, B.C., and Jobling, M.A. (2003). Native American Y chromosomes in Polynesia: the genetic impact of the Polynesian slave trade. *Am. J. Hum. Genet.* 72, 1282–1287.
 45. Moreno-Estrada, A., Gravel, S., Zakharia, F., McCauley, J.L., Byrnes, J.K., Gignoux, C.R., Ortiz-Tello, P.A., Martínez, R.J., Hedges, D.J., Morris, R.W., et al. (2013). Reconstructing the population genetic history of the Caribbean. *PLoS Genet.* 9, e1003925.
 46. Bardach J.E., Cotter H.C, and Morgan J.R. (2014). Pacific Ocean. *Encyclopaedia Britannica Online*, <http://www.britannica.com/EBchecked/topic/437703/Pacific-Ocean>.
 47. Irwin, G. (2008). Pacific seascapes, canoe performance, and a review of Lapita voyaging with regard to theories of migration. *Asian Perspect.* 47, 12–27.
 48. Fitzpatrick, S.M., and Callaghan, R. (2009). Examining dispersal mechanisms for the translocation of chicken (*Gallus gallus*) from Polynesia to South America. *J. Archaeol. Sci.* 36, 214–223.
 49. Reich, D., Patterson, N., Campbell, D., Tandon, A., Mazieres, S., Ray, N., Parra, M.V., Rojas, W., Duque, C., Mesa, N., et al. (2012). Reconstructing Native American population history. *Nature* 488, 370–374.
 50. Gonçalves, V.F., Stenderup, J., Rodrigues-Carvalho, C., Silva, H.P., Gonçalves-Dornelas, H., Líryo, A., Kivisild, T., Malaspinas, A.S., Campos, P.F., Rasmussen, M., et al. (2013). Identification of Polynesian mtDNA haplogroups in remains of Botocudo Amerindians from Brazil. *Proc. Natl. Acad. Sci. USA* 110, 6465–6469.
 51. Dudgeon, J.V. (2008). The genetic architecture of the late prehistoric and protohistoric Rapa Nui. PhD thesis (Manoa: University of Hawaii at Manoa).
 52. Shapiro, B., and Hofreiter, M. (2014). A paleogenomic perspective on evolution and gene function: new insights from ancient DNA. *Science* 343, 1236573.