PALEOECOLOGY OF EASTER ISLAND: NATURAL AND ANTHROPOGENIC DRIVERS OF ECOLOGICAL CHANGE

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PALEOECOLOGY OF EASTER ISLAND: NATURAL AND ANTHROPOGENIC DRIVERS OF ECOLOGICAL CHANGE

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Sunset at Ahu Tahai, near Hanga Roa
Photo: Valentí Rull

After more than three decades of paleoecological research, the potential role of climatic and anthropogenic drivers on Easter Island's ecological and cultural change is still under discussion. This eBook aims to provide a synthetic view of the topic using evidence from different research fields such as paleoecology, archaeology, history and molecular phylogenetics. A holistic approach is provided to combine the results of these research fields into a comprehensive framework able to account for most of the available multidisciplinary evidence.

This eBook is dedicated to the memory of John R. Flenley, the pioneer of paleoecological study of Easter Island, who passed away on June 22, 2018.

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EDITORIAL
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Editorial: Palaeoecology of Easter Island: Natural and Anthropogenic Drivers of Ecological Change

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Keywords: Easter Island, Rapa Nui, deforestation, cultural change, climate change, ecological collapse, cultural collapse, last millennia

The Editorial on the Research Topic

Palaeoecology of Easter Island: Natural and Anthropogenic Drivers of Ecological Change

Easter Island (Rapa Nui), the most remote inhabited place on Earth, lies in an intermediate position between Polynesia and South America, which has led to contrasting hypotheses regarding their human colonization and the ensuing ecological impacts (Heyerdahl, 1989; Flenley and Bahn, 2003; Hunt and Lipo, 2006; Thorsby, 2012). The small size, the isolation and the possibility of past climatic and ecological reconstructions before and after human settlement make the island a natural laboratory to disentangle climatic and anthropogenic causes of past ecological change, which is useful to develop predictive models of ecological responses to future climate changes. The first palaeoecological studies (Flenley and King, 1984; Flenley et al., 1991) suggested the occurrence of an ecological catastrophe—as indicated by an abrupt island-wide deforestation-during the last millennium, followed by a cultural collapse of the ancient Rapanui civilization that built the emblematic megalithic statues called *moais*. Such socio-ecological demise was considered an ecocide, as a result of over-exploitation of natural resources by the first settlers, a view that became paradigmatic and was taken as a microcosmic model for the whole planet (Diamond, 2005). Further archeological studies challenged this vision and proposed an alternative genocidal hypothesis, according to which the cultural collapse was caused by the introduction of unknown epidemic diseases and slave trading after the European contact in AD 1722 (Hunt, 2007). Under this view, deforestation took place well before the cultural collapse, and the Rapanui society was resilient to forest removal, remaining as a healthy society until the European arrival (Hunt and Lipo, 2011; Stevenson et al., 2015).

Until recently, human activities were considered to be the main drivers of ecological change and the potential influence of climatic changes was explicitly dismissed (Flenley and Bahn, 2003). However, further palaeoecological studies suggested that climate changes have been more relevant than usually thought. Since the onset of the twenty-first century, lake and peat coring intensification has refined our view of the main palaeoclimatic trends since the last glaciation, and their potential relationships with landscape and ecological changes, have been investigated more intensively (Sáez et al., 2009; Rull et al., 2013; Rull, 2016). This has opened a new era in the study of Easter Island's climatic and ecological histories, which has questioned former paradigms. An update of the new findings obtained seems pertinent to summarize the state-of-the-art and to realize where future research should be focused. This is the main purpose of our Research Topic, which is also an opportunity for sharing knowledge among the different disciplines and points of view on Easter Island's palaeoecology. The Research Topic was open to all researchers and research teams working in palaeoecological issues or in other fields of research with palaeoecological implications, including present-day ecological, cultural, and climatic aspects.

The first paper (Rull et al.) introduces the topic from a multidisciplinary perspective. The recently found palaeoecological evidence of climatic change during the last millennia is placed

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in a chronological and cultural context to disentangle the role of natural and anthropogenic drivers of socio-ecological change. It is concluded that a transdisciplinary synthetic approach including every type of available evidence is needed to resolve the ecological and cultural history of Easter Island since its human settlement. In order to facilitate this task, the second paper summarizes all the chronological information obtained to date (1984–2015) using radiocarbon dating of lake and peat sediments from the three coring sites available on the island (Rano Aroi, Rano Kao, and Rano Raraku). This database, called EIRA (Easter Island Radiocarbon Ages), is useful to develop new and customized age-depth models, as well as to plan further coring campaigns.

The second part of the Research Topic consists of two papers focused on human settlement using DNA phylogenies to unravel the timing of colonization and the origin of the first settlers. West et al. base their colonization model on the human-transported Pacific rat (*Rattus exulans*) as a proxy for human migrations across Oceania. Using mitochondrial DNA, these authors find support for a Polynesian origin of the first settlers and propose a novel migration route. In the second paper, Thorsby reviews the available genetic evidence (human DNA) on an eventual early contribution of Amerindians to the island's culture. The author concludes that, although the first settlers could have been arrived from Polynesia by AD 1200–1253, there is firm evidence for native Americans to have reached Easter Island by AD 1280–1495.

The third section deals with human demographic trends in relation to the available natural resources. In the first paper, Merico reviews the topic with emphasis on economic and ecological aspects, and discusses the models considered to date for the cultural collapse as a result of over-exploitation. The author recommends the use of Agent-Based Models (ABM), still unexplored on Easter Island, as a useful tool to address human-resource interactions. The second paper (Puleston et al.) models the agricultural potential of the island before the European contact on the basis of climatic and soil nutrient parameters. The authors conclude that the limiting factor is nitrogen availability and estimate that pre-European conditions would have supported population sizes of 17,500 or even higher. Lipo et al. comment on this paper and seriously question Puleston et al. demographic figures, based on purported modeling flaws. The points of Lipo et al. are answered in a second commentary by Puleston et al.

The concluding paper of this Research Topic (Rull et al.) is an attempt to merge the evidence from various disciplines -mainly palaeoeclimatology, palaeoecology, archeology, and historical records—into a holistic framework called CLAFS (Climate-Landscape-Anthropogenic Feedbacks and Synergies), to address the deforestation timing of the island and its potential causes, and the cultural shift that determined the disappearance of the *moai* culture. Several working hypotheses are postulated and the better suited testing methods are proposed, based on the use of new palaeoecological proxies (biomarkers) and the combination of multiple fields of research. We hope that this Research Topic will contribute to increase our understanding of Easter Island and to stimulate transdisciplinary collaboration.

AUTHOR CONTRIBUTIONS

VR wrote the paper and SG edited the manuscript and approved submission.

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OPINION
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Three Millennia of Climatic, Ecological, and Cultural Change on Easter Island: An Integrative Overview

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Eastern Island (Rapa Nui) is famous for the legacy of an extinct civilization symbolized by the megalithic statues called *moai*. Several enigmas regarding the colonization of the island its deforestation and a presumed cultural collapse of the ancient civilization still remain elusive. According to the prevailing view, the first settlers arrived between AD 800 and AD 1200 from east Polynesia and overexploited the island's natural resources causing an ecological catastrophe leading to a cultural collapse (Flenley and Bahn, 2003). The main evidence for this theory was the abrupt replacement of palm pollen by grass pollen in the sediments of the island's lakes and mires (Raraku, Kao, and Aroi), which was interpreted in terms of a thorough deforestation between approximately AD 1200 and AD 1400/1600 (Flenley and King, 1984; Flenley et al., 1991; Mann et al., 2008). This ecocidal view is widely accepted not only by the scientific community but also by society, thanks to its popularization by the mass media. Under this perspective, Easter Island has been considered a microcosmic model showing how human selfishness can eventually cause our own destruction (Diamond, 2005). Another view is that Polynesian colonizers arrived slightly later, between AD 1200 and AD 1300 (Wilmshurst et al., 2011), and the deforestation—which was not completed until AD 1650—was the result of massive palm fruit consumption by rats carried to the island by the first settlers (Hunt, 2006, 2007). According to this view, the cultural collapse did not occur until the European arrival (AD 1722) and was a genocide caused by the introduction of previously unknown illnesses and slave trading (Lipo et al., 2016).

During the last decade, the study of Easter Island has benefited by the proliferation of lake and peat coring and the introduction of new analytical methods. Former paleoecological analyses were based on sediments that contained frequent age inversions and extensive sedimentary gaps hiding the paleoecological trends of a significant part of the last millennia (Rull et al., 2010, 2013). A recent improvement has been the finding of new paleoecological sequences with continuous sedimentation during the last 3000 years, which has provided new insights on paleoecological trends with potential climatic and cultural implications (e.g., Cañellas-Boltà et al., 2013; Rull et al., 2015). Other progress has included the development of multiproxy studies including independent evidence for either ecological or climatic changes. Former paleoecological studies were based mostly on pollen analysis alone and attempted to derive climate changes from biological evidence, which is inadequate to evaluate the ecological responses to climatic changes. Recent studies include detailed lithostratigraphic, sedimentological, geochemical, and biological proxies, which allow separation of ontogenetic factors from external environmental drivers of ecological change, notably climatic changes and human activities (Sáez et al., 2009; Cañellas-Boltà et al., 2012, 2016; Margalef et al., 2013, 2014). The introduction of new analytical techniques to identify remains of cultigens, as for example phytoliths and starch, has been useful to locate human fingerprints in sedimentary sequences (Horrocks et al., 2012a,b, 2013, 2015; Bowdery, 2014). New developments based on DNA analysis of modern humans and food remains from ancient skeletons have shed new light on the origin of settlers (Thorsby, 2012; Thromp and Dudgeon, 2015). In addition, some new analyses and meta-analyses on radiocarbon dates associated with archeological remains have provided relevant information on human activities, land use and demography (Mulrooney, 2013; Stevenson et al., 2015). We believe that the incorporation of these new findings into a coherent history needs the development of a novel synthesis of the historical and recent evidence into a holistic framework, where the different interpretations are viewed as complementary, rather than incompatible, contributions. This paper is a first proposal for such an integrated approach.

Concerning human settlement, archeological and anthropological evidence is consistent with the Polynesian origin of the ancient civilization represented by the *moai* (Flenley and Bahn, 2003). Using this evidence, the former hypothesis of Heyerdahl (1968) that Amerindian settlers would have arrived several centuries before the Polynesian colonizers was dismissed. However, new findings have revitalized Heyerdahl's proposal (albeit not his cultural interpretation). Indeed, recent palynological analyses revealed that the first deforestation event recorded so far occurred at 450 BC and was associated with the initiation of fires and the first appearance of *Verbena litoralis*, a human-dispersed weed of American origin (Cañellas-Boltà et al., 2013; **Figure 1**). In addition, Thromp and Dudgeon (2015) found starch remains of *Ipomoea batatas* (sweet potato), also of American origin, in the dental calculus of human skeletons as old as AD 1330 and concluded that this plant was important in the diet of the ancient islanders four centuries before the European contact. Thorsby (2012) analyzed the gene pool of modern Polynesian descendants and found evidence of Amerindian contact before, at least, two centuries prior to the European arrival (**Figure 1**). Therefore, the presence of Amerindian settlers before and/or during the development of the ancient *moai* culture is strongly supported from varied and independent sources of evidence.

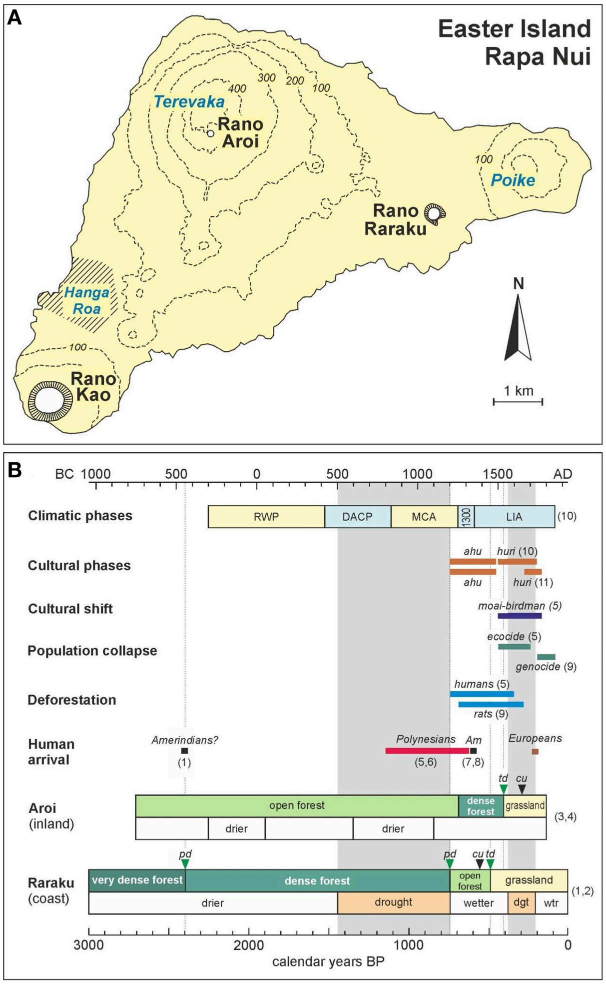

FIGURE 1 | (A) Sketch map of Easter Island indicating the localities mentioned in the text. **(B)** Summary of the climatic, ecological, and cultural trends of Easter Island over the last three millennia. The uppermost climatic phases summarize the current northern hemisphere and Pacific climatic phases according to Nunn (2007). Drought phases recorded at Raraku are shaded and deforestation pulses are highlighted by dotted lines. RWP, Roman Warm Period; DACP, Dark Ages Cold Period; MCA, Medieval Climate Anomaly; 1300, "1300 event;" LIA, Little Ice Age; Am, Americans; cu, first evidence of local cultivation; dgt, drought; pd, partial deforestation; td, total deforestation; wtr, wetter. References: 1, (Cañellas-Boltà et al., 2013); 2, (Horrocks et al., 2012a); 3, (Rull et al., 2015); 4, (Horrocks et al., 2015); 5, (Flenley and Bahn, 2003); 6, (Wilmshurst et al., 2011); 7, (Thorsby, 2012); 8, (Thromp and Dudgeon, 2015); 9, (Hunt, 2007); 10, (Nunn, 2007); 11, (McLaughlin, 2007).

Recent palynological results on peat and lake cores with nearly continuous sedimentation during the last three millennia suggest that forest clearing did not occur at the same time over the whole island and proceeded at different rates according to the site analyzed. For example, in Lake Raraku, situated in the coastal lowlands, the deforestation was a long and gradual process that took place in three pulses at 450 BC, AD 1200 and AD 1500 (Cañellas-Boltà et al., 2013; **Figure 1**). The first signs of cultivation in this catchment were recorded slightly before AD 1400 (Horrocks et al., 2012a). Contrastingly, in the Aroi mire, located inland at higher elevations, a densification of the former open palm forests occurred at AD 1250 and the resulting dense forests were removed abruptly, between AD 1520 and AD 1620, using fire (Rull et al., 2015). Cultivation inside the Aroi catchment did not start until AD 1640 (Horrocks et al., 2015). These results are compatible with a heterogeneous pattern of land use and occupation prior to the European contact (Stevenson et al., 2015), with a conspicuous pattern of coastal abandonment toward inland/upland settlements, which was characteristic of many eastern Pacific archipelagos during the same times (Nunn, 2003, 2007).

Recent multiproxy surveys have suggested a relationship between climate variability and landscape shifts, some of them of potential cultural significance. Mann et al. (2008) favored the occurrence of Late Holocene droughts and Sáez et al. (2009) suggested their potential role in deforestation. This view was not shared by Junk and Claussen (2011) who believe that, during the last millennium, climate changes alone might have been too small to explain strong vegetation changes that have occurred on the island. Further analyses on nearly continuous cores from Lake Raraku and Aroi mire have provided additional insights. In Raraku, the first deforestation event (450 BC) took place under climates drier than at present, when the present lake did not exist and the basin was occupied by a marsh (Cañellas-Boltà et al., 2013). Arid conditions intensified between AD 500 and AD 1200, leading to a drought phase coeval with the Classic Maya Collapse of Central America (∼AD 900), attributed to the increased frequency of prolonged droughts (Haug et al., 2003). In the Pacific islands, this time interval was characterized by climatic stability, sea levels higher than today and increasing food production thanks to the development of irrigation practices and terracing. These conditions favored long-distance navigation and new settlements, especially in eastern Polynesia (Nunn, 2007). According to the prevailing theory, the Polynesian colonization of Easter Island occurred during this phase (**Figure 1**). However, Goodwin et al. (2014) suggested that, during the Medieval Climate Anomaly (MCA), navigation to and from Easter Island was possible in both eastward and westward directions.

A significant shift to wetter climates and higher lake levels occurred at AD 1200 (**Figure 1**), roughly coinciding with the onset of a regional Pacific phase called the "1300 event," which represented the transition between the MCA and the Little Ice Age (LIA). The 1300 event was characterized by cool and wet climates, increased storminess due to ENSO intensification and a sea level drop below its present position (Nunn, 2007). During this wet period, which, at Easter Island, lasted until AD 1570, the Aroi and Raraku catchments exhibited disparate landscape trends. In Aroi, open palm forests underwent a densification that transformed them into relatively dense palm forests likely as a consequence of increased moisture availability (Rull et al., 2015). In Raraku, on the contrary, the second fire-driven, likely anthropogenic, deforestation pulse occurred and the reverse shift, from dense forest to open forest, took place (Cañellas-Boltà et al., 2013). Under the ecocidal view, this second pulse coincided with the beginning of the total deforestation of the island, whereas for the defenders of the rats as deforestation agents, the clearing began some 50 years later (**Figure 1**). This wetter phase coincided also with the phase known as *ahu moai* (roughly AD 1200–1500), during which these megalithic statues were built and venerated, which was also the time of maximum prosperity and expansion of the ancient Polynesian culture on the island (Nunn, 2007). A direct cause-effect relationship between climate and cultural traits cannot be established with the available evidence; however, it could be argued that increased water availability would have favored cultural flourishment.

Palm forests were almost totally removed from Raraku and Aroi in AD 1570 and AD 1620, respectively, before the end of the wet phase (**Figure 1**). Again, the sharp increase in charcoal, at both sites, strongly suggests anthropogenic burning. This was the "coup de grace" of the deforestation of these basins and, likely, of the whole island (Rull et al., 2015). A second drought between AD 1570 and AD 1720 occurred when the island was mostly (according to the rat theory) or totally (according to the ecocidal theory) deforested and grass meadows dominated the landscape. The population collapse of the ecocidal theory—which is attributed by its defenders to resource exhaustion and internal wars—occurred during this drought, which suggests that this cultural demise would have not been fully ecocidal but the result of a synergistic effect of climate severity and anthropogenic landscape degradation. Some authors (e.g., Nunn, 2007) consider that the phase of *huri moai*—characterized by the abandonment of the *moai* cult and the toppling of these statues, and the initiation of the birdman cult (**Figure 1**)—began at AD 1500, in which case this cultural shift would have paralleled the demographic collapse. Others believe that the *huri moai* phase started at AD 1680 (e.g., McLaughlin, 2007), in which case, there is no indication of climatic forcing in the paleoecological body of evidence available so far. Wetter climates returned by AD 1720, close to the European arrival, which marked the onset of a genocidal cultural collapse that has been well documented historically (Hunt and Lipo, 2011). The landscape did not experience any significant changes and grasslands dominated the scene.

This preliminary synthesis needs further refinement and could be considered a first approach to a synthetic framework toward a holistic Easter Island history combining climatic, ecological and cultural evidence. An important message is that environmental and human drivers of change can either have separate effects, or can act synergistically, coupled in positive feedbacks (Vegas-Vilarrúbia et al., 2011; Zahid et al., 2015). Under a synthetic framework, it is hoped that hypotheses that are usually presented as incompatible—e.g., environmental vs. cultural determinism, ecocide vs. genocide, or human vs. rat deforestation, among others—may be analyzed under a more complementary perspective. For example, Brandt and Merico (2015) developed a demographic model in which elements of both ecocidal and genocidal hypotheses concur to produce a long and slow population decline between ca. AD 1300 and 1800. The desired synthesis should also benefit from the incorporation of new analytical techniques available in paleoecology, as for example DNA and fecal lipid analysis of sediments, to enhance the possibilities of detection of human fingerprint (Rull et al., 2013). Also, new coring campaigns are necessary to deal with problematic sites, mainly in terms of dating, as for example Rano Kao.

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VR conceived the idea and wrote the paper. NC, OM, SP, AS, and SG provided new ideas and participated in discussions and writing.

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The EIRA Database: Glacial to Holocene Radiocarbon Ages from Easter Island's Sedimentary Records

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Keywords: Easter Island, Rapa Nui, lake sediments, mires, chronology, radiocarbon dating, Late Pleistocene, Holocene

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INTRODUCTION

The archaeological and anthropological relevance of Easter Island (Rapa Nui) for human history in a regional Pacific context has been highlighted since the early twentieth century (Routledge, 1919). At first, the interest was focused on the giant stone statues called *moai*, which had been carved on the island's volcanic rocks by an enigmatic ancient civilization. The interest on the island received a boost several decades ago, after the expedition leaded by Thor Heyedahl (Heyerdahl and Ferdon, 1961) and the first palynological studies suggesting a recent ecological catastrophe, led by an abrupt island-wide deforestation likely due to the over-exploitation of natural resources, and an ensuing cultural collapse (Flenley and King, 1984; Flenley et al., 1991). This "ecocidal" theory became paradigmatic and the case of Easter Island was considered a microcosmic model for the whole planet and a warning against the uncontrolled use and of natural resources (Flenley and Bahn, 2003; Diamond, 2005). Further, archaeological and palaeoecological studies have challenged this ecocidal theory (Hunt and Lipo, 2006, 2011; Hunt, 2007; Lipo and Hunt, 2016), which has revitalized the debate on the recent cultural history of Easter Island (reviews in Rull et al., 2010, 2013).

In comparison to the concern for human developments and their influence on the island's environment, the palaeoclimatic history of Easter Island and its potential paleoecological consequences has received little attention until the last decade. Earlier palaeoecological studies emphasized the influence of human activities on vegetation and landscape shifts and undervalued the potential action of climatic changes as ecological drivers. This view was based on the continuity of forests, as reconstructed from pollen analysis, during the last ∼37,000 years and their sudden disappearance and replacement by treeless meadows coinciding with the arrival of the first Polynesian settlers (Flenley and King, 1984; Flenley et al., 1991). The main argument was that the ecological effect of a global climatic shift as intense as for example the Last Glacial Maximum (LGM) was negligible as compared to the ecological changes induced by anthropogenic activities during the last millennium. Propositions suggesting a potential influence of climatic shifts such as the Little Ice Age (LIA) or the ENSO variability on Easter Island's ecological and cultural history (Hunter-Anderson, 1998; McCall, 1993; Nunn, 2000, 2007; Nunn and Britton, 2001; Nunn et al., 2007; Stenseth and Voje, 2009) were dismissed as they were mostly based on theoretical assumptions without empirical support. Recent palaeoecological studies are changing this view by documenting significant climatic shifts and their influence on ecological patterns and processes during the last ∼70,000 years (e.g., Mann et al., 2008; Sáez et al., 2009; Cañellas-Boltà et al., 2012, 2013; Margalef et al., 2013, 2014).

Since the beginning, the paleoclimatic and palaeoecological study of Easter Island has faced a persistent drawback caused by the occurrence of dating inconsistencies, mainly extensive chronostratigraphic gaps and frequent age inversions (Butler et al., 2004; Rull et al., 2013). These inconsistencies have prevented the development of reliable age-depth models in many cases, especially in Holocene intervals including the last millennia, thus preventing researchers to disentangle climatic and anthropogenic causes of ecological change, which is essential for incorporating palaeoecological and palaeoclimatic trends into predictive models. In the past, age-depth models were relatively simple and consisted mainly of interpolations and extrapolations assuming linear sedimentation rates between adjacent dating points. Dates that significantly deviated from this trend were usually rejected and not included in the model. Further improvements consisted of curve fitting using linear, exponential, logarithmic, or polynomial models, among others, which enable the calculation of statistical errors for the estimated ages. Recently, new approaches using a variety of methods, including Bayesian analysis, have been developed (e.g., Blaauw, 2010; Blaauw and Christen, 2011). In Easter Island, these new methods have been applied to the new cores obtained in the last years but historical dates and age-depth models have not been reconsidered in light of these new statistical developments.

Statistical re-analyses of the existing radiocarbon dates may provide new insights on Easter Island's chronostratigraphy useful to strengthen paleoclimatic and paleoecological inferences. In order to facilitate this type of investigation, a dataset called EIRA (Easter Island Radiocarbon Ages) has been assembled with all the radiocarbon dates published to date (1984–2015). The EIRA database provides paleoecologists and paleoclimatologists with a thorough chronological dataset to be analyzed statistically as a whole or by parts (by sites, by age intervals, etc.), aimed at contributing to the development of new age-depth models, reconsider the existing ones, or plan new studies and coring campaigns. It would be especially interesting to test whether it is possible to derive site-specific or island-wide coherent chronostratigraphic patterns by multi-core age-depth modeling. Also, further analyses of the EIRA database in comparison with recent compilations of radiocarbon ages from archaeological materials (e.g., Vargas et al., 2006; Wilmshurst et al., 2011; Mulrooney, 2013; Stevenson et al., 2015; Lipo and Hunt, 2016), could contribute to improve correlations among climatic, ecological, and cultural trends toward a holistic framework for Easter Island's history (Rull et al., 2016).

METHODS

Study Area and Coring Sites

Easter Island is a volcanic island located in the southeastern Pacific Ocean, at 27° 07′ 16″ Lat N and 109° 21′ 59″ Long W (**Figure 1**), at >3500 km of the American continent and ∼2100 km of the nearest inhabited Polynesian island (Pitcairn). The island (164 km^2) defines a small triangle originated by the fusion of three volcanic cones (Terevaka, Poike, and Kao). The highest point of the island is the summit of the Maunga Terevaka, situated at 511 m elevation. Easter Island's volcanic rocks are highly porous and precipitation infiltrates easily through them thus preventing the formation of surface stream flow. The only permanent sources of freshwater are two lakes (Rano Kao and Rano Raraku) and a mire (Rano Aroi), which contain the sediments where all palaeoecological studies conducted so far have been developed.

Rano Aroi is a mire of ∼150 m diameter situated at 430 m elevation within a crater near the highest summit of the island (**Figure 1**). Water level is controlled by groundwater inputs subjected to the influence of seasonal variations in precipitation and human extraction (Herrera and Custodio, 2008). The aquatic vegetation is dominated by *Scirpus californicus*, *Polygonum acuminatum,* and ferns of the genera *Asplenium*, *Vittaria,* and *Cyclosorus*, whereas the surrounding area is covered by grasslands and a small *Eucalyptus* forest planted during the 1960s (Zizka, 1991). The mire infilling is predominantly peat and is at least 16 m deep in the center, which represents an age of approximately 70,000 cal y BP (Margalef et al., 2013, 2014). Flenley et al. (1991) described this organic accumulation as a mixture of coarse detritus and finer material intermingled with layers of spongy monocotyledonous peat and brown clay. Peteet et al. (2003) reported the occurrence of several types of peats and organic clays with fibrous material. A similar composition was described by Horrocks et al. (2015). Margalef et al. (2013, 2014) did a detailed lithological study and distinguished four main organic facies: (A) reddish peat of sedges and *Polygonum*; (B) granulated muddy peat of coarse organic fragments, mainly roots, with low terrigenous content; (C) organic mud or dark-brown to black peat; and (D) dark-brown fine-grained peat. Facies B is the more common throughout the sequence. This mire has been cored several times between 1977 and 2009, and five of the cores obtained have been radiocarbon dated (**Figure 1**). An additional core was retrieved and dated in a nearby small depression, Rano Aroi Iti, in 2009. The original data and methodological details are in Flenley (1979), Flenley and King (1984), Flenley et al. (1991), Peteet et al. (2003), Margalef (2014), Margalef et al. (2013, 2014), Rull et al. (2015), Horrocks et al. (2015).

Rano Kao contains the largest lake of the island, with ∼1250 m diameter, situated at 110 m elevation (**Figure 1**). This lake is very peculiar as its surface is a mosaic of water and aquatic vegetation in the form of floating mats up to 3 m deep overlying the water column, which is up to 10 m deep. The oldest ages recorded so far in the floating mat are around 700–900 cal yr BP (Gossen, 2007; Horrocks et al., 2013). Therefore, during roughly the last millennium past ecological and environmental evidence has been accumulating in both the floating peats and the upper layer of lake sediments. It has been suggested that these two archives would have been partially mixed by immersion of mat fragments thus causing chronological anomalies, typically age inversions, in the sedimentary sequence (Butler et al., 2004). The floating mats are dominated by the characteristic aquatic species of the island, *S. californicus* and *P. acuminatum*, together with another sedge, *Pychreus polystachius* (Zizka, 1991). A significant number of archaeological sites have been found around Rano Kao, notably the ancient village of Orongo, which is one of the more important and well preserved archaeological

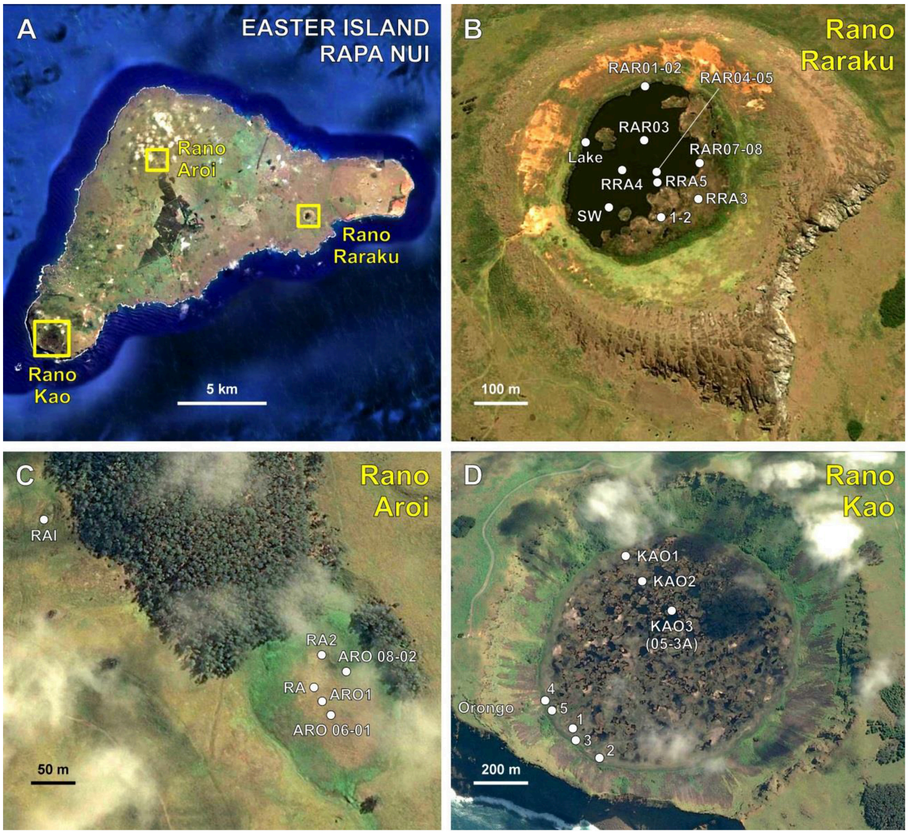

FIGURE 1 | Google Earth images of the lakes and mire studied, indicating the location of the cores from which radiocarbon ages originate. (A) Location of the lakes/mires, **(B)** Lake Raraku, **(C)** Aroi mire, **(D)** Lake Kao.

complexes of the island. The maximum depth of lake sediments recorded thus far is ∼21 m and the maximum age measured is ∼34,000 cal yr BP (Gossen, 2007, 2011; Horrocks et al., 2013). The Kao lake sediments have been described as coarse organic detritus derived from aquatic and catchment vegetation, with a basal layer of coarse detritus and clay (Flenley and King, 1984; Flenley et al., 1991; Horrocks et al., 2013). This lake was cored between 1977 and 2005. Eight of the cores retrieved were radiocarbon dated and are included in this compilation. The following references contain the original data and methodological details: Flenley (1996), Butler and Flenley (2001, 2010), Butler et al. (2004), Gossen (2007, 2011), Horrocks et al. (2012b, 2013).

Rano Raraku contains a lake of intermediate size (∼300 m diameter), situated at 80 m elevation (**Figure 1**). Hydrologically, the lake is closed, with no surface outlet, and is used by humans as a freshwater source for consumption and irrigation. The main water inputs are rainfall and catchment runoff (Herrera and Custodio, 2008). The maximum water depth recorded in modern times is ∼3 m (Sáez et al., 2009). The aquatic vegetation is dominated by *S. californicus*, which forms a more or less continuous floating belt in the east margin of the lake. Rano Raraku is one of the more emblematic sites of the island as it was the quarry where the *moai* were sculptured. The sedimentary infilling is at least 14 m deep in the center of the lake, which corresponds to an age of 34,000 cal yr BP (Sáez et al., 2009). These sediments have been described as a mixture of coarse and fine detritus originating from lake and catchment vegetation, intermingled with layers of gyttja, clay, and mud and, occasionally, volcanic ashes (Flenley et al., 1991; Horrocks et al., 2012a). A more detailed sedimentological study reported that the Raraku sediments were dominated by organic matter with variable amounts of terrigenous mineral particles from the catchment rocks. The organic matter was a mixture of plant remains from the catchment and, in lower proportion, autochthonous organic matter derived from lake production (Sáez et al., 2009). The same study distinguished four sedimentary facies: (1) laminated, dark gray-reddish organic-rich silts and mud; (2) laminated and massive brownish organic mud; (3) brown-reddish massive or banded peaty sediment, composed mainly of plant (sedge) remains; and (4) peat and silty clay. These sediments have been cored between 1977 and 2009, with 14 cores having radiocarbon dates (**Figure 1**). The raw palaeoecological and palaeoclimatic information from these cores is in Flenley (1979), Flenley and King (1984), Flenley et al. (1991), Dumont et al. (1998), Azizi and Flenley (2008), Sáez et al. (2009), Horrocks et al. (2012a), Cañellas-Boltà (2014), and Cañellas-Boltà et al. (2012, 2013, 2014).

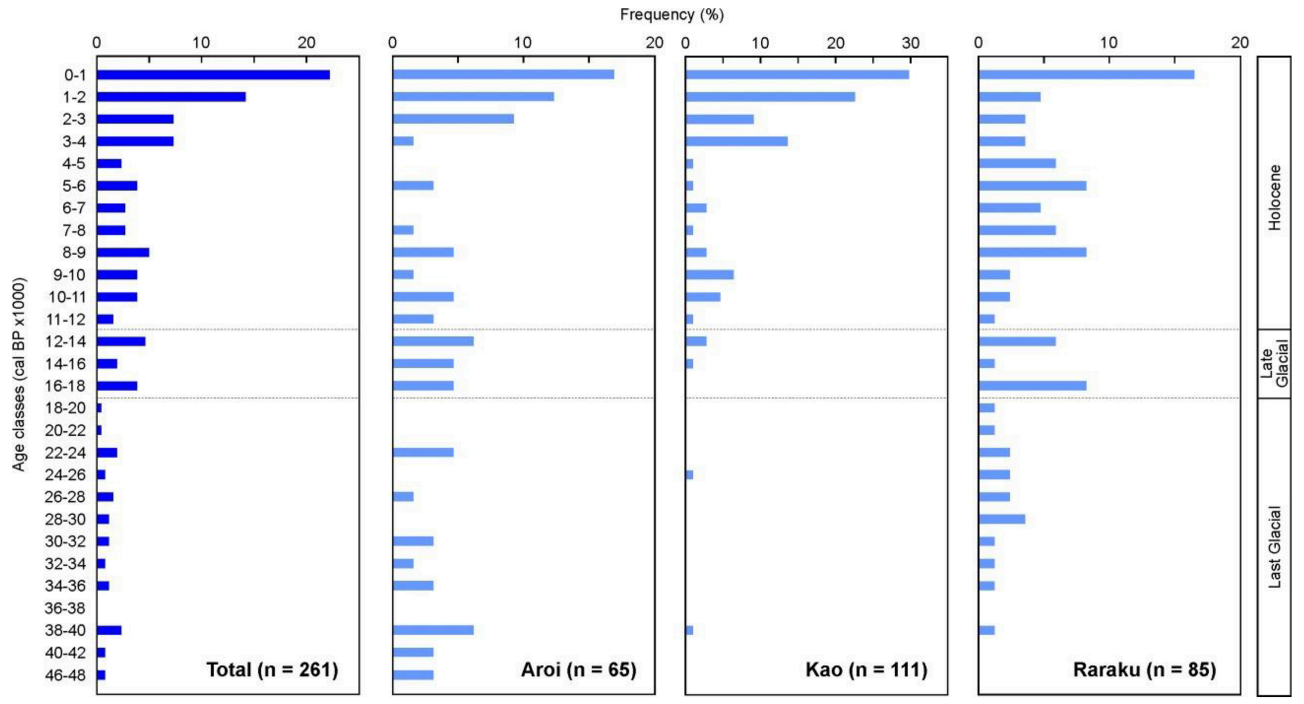

FIGURE 2 | Histogram with the distribution of radiocarbon ages by time intervals. Only calibrated ages (median probability) have been considered. Raw data in the Supplementary Material.

The Dataset

The EIRA database contains all the radiocarbon ages from Aroi, Kao, and Raraku sediments published to date (1984–2015). In order to preserve objectivity, all radiocarbon dates from all the cores dated by this method have been included in this compilation, regardless of whether the original authors have considered them in their age-depth models or not. The raw ^{14}C data are exactly as they appear in the original references, except for post-bomb ages, which are given as negative ^{14}C ages for homogeneity. Whenever, possible—i.e., when all the necessary data were available and the dates are within the age range for radiocarbon dating- the original radiocarbon ages have been calibrated or re-calibrated with CALIB 7.1 (http://calib.qub.ac.uk/calib/) using the SHCal13 curve (Hogg et al., 2013). Post-bomb (negative) ^{14}C ages were calibrated with clam 2.2 (Blaauw, 2010; http://chrono.qub.ac.uk/blaauw/clam.html), using the curve SH zone 1-2 (Hua et al., 2013). The database is provided in the Supplementary Material as an Excel file (EIRAdb 2.5), which is also freely available at the NOAA International Climatic Data Center, section Paleoclimate, under the accession number 19805 (https://www.ncdc.noaa.gov/paleo/study/19805).

The Excel file consists of four sheets named cores, data, lab codes, and references, respectively. The core sheet contains the cores from which dated samples proceed, with the following information arranged in columns: site name (lake/bog), site coordinates (at the center of each site), elevation, core name, core coordinates, water depth at the coring site, core length, date retrieved, coring system, and references from where these data were obtained. The data sheet displays the radiocarbon dates organized in the following columns: site, core, references, sample code assigned by the corresponding radiocarbon laboratory, sample depth (top, base, and average), material dated, ^{14}C date, dating error, calibrated dates at 95% probability ranges (maximum and minimum), median probability and observations. In some cases, only calibrated age ranges are provided because they appear in this form in the original references. ND means "No Data." The third sheet, lab codes, provides the identification of each radiocarbon laboratory according to their acronyms and the fourth sheet contains the references cited in sheets one (cores) and two (data). The current version (2.5) of this file was validated March 31, 2016 and will be updated and uploaded to the NOAA repository each year.

The total number of radiocarbon ages is 279, corresponding to 28 cores, ranging from ca. 48,000 to the present. The number of calibrated dates is 261, distributed as follows: Aroi, 65 dates; Kao, 111 dates, and Raraku, 85 dates. Overall, most dates correspond to the Holocene, especially to the last two millennia, which is the period most intensively studied due to its cultural relevance (**Figure 2**). In contrast, the period between 4000 and 8000 cal yr BP is the least represented. This is true for Aroi and Kao but not for Raraku, where this early-middle Holocene interval is well represented. In general, Late Glacial ages are intermediate in frequency but they are also irregularly distributed among sites, as they are fairly well represented in Aroi and Raraku but not in Kao. Last Glacial dates are the least represented, especially in the interval corresponding to the LGM (18,000–22,000 cal yr BP), which is represented only in Raraku. Noteworthy, Pleistocene ages are almost absent in Kao. Whether the paucity of specific age intervals is due to the scarcity of sediments of these ages, which may help identifying eventual sedimentary gaps, or to differential sampling effort, is worth to be analyzed for its potential significance in terms of local and island-wide sedimentation patterns.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fevo.2016.00044

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The Pacific Rat Race to Easter Island: Tracking the Prehistoric Dispersal of *Rattus exulans* Using Ancient Mitochondrial Genomes

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The location of the immediate eastern Polynesian origin for the settlement of Easter Island (Rapa Nui), remains unclear with conflicting archeological and linguistic evidence. Previous genetic commensal research using the Pacific rat, *Rattus exulans*; a species transported by humans across Remote Oceania and throughout the Polynesian Triangle, has identified broad interaction spheres across the region. However, there has been limited success in distinguishing finer-scale movements between Remote Oceanic islands as the same mitochondrial control region haplotype has been identified in the majority of ancient rat specimens. To improve molecular resolution and identify a pattern of prehistoric dispersal to Easter Island, we sequenced complete mitochondrial genomes from ancient Pacific rat specimens obtained from early archeological contexts across West and East Polynesia. Ancient Polynesian rat haplotypes are closely related and reflect the widely supported scenario of a central East Polynesian homeland region from which eastern expansion occurred. An Easter Island and Tubuai (Austral Islands) grouping of related haplotypes suggests that both islands were established by the same colonization wave, proposed to have originated in the central homeland region before dispersing through the south-eastern corridor of East Polynesia.

Keywords: ancient DNA, mitochondrial haplotypes, prehistoric dispersal, Polynesia, Easter Island, *Rattus exulans*

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INTRODUCTION

The expansion of modern humans into the wider Pacific, culminating with the colonization of eastern Polynesia within the last 1,000 years, represents one of the last major migrations in human history (Duggan et al., 2014; Matisoo-Smith, 2015). Aided by the development of new watercraft technologies and navigational abilities, the appearance of the Lapita peoples in the Bismarck Archipelago between 3,400 and 3,200 B.P. (Green et al., 2008; Summerhayes et al., 2010) and successful movement of humans beyond the Solomon Islands instigated a phase of long-distance voyaging and settlement across Remote Oceania (see **Figure 1**; Irwin, 2008). Eastward expansion led to the colonization of Vanuatu and Fiji by 3,100 and 3,000 B.P. respectively (Denham et al., 2012), Tonga by 2,850 B.P. (Burley et al., 2015) and Samoa by 2,750 B.P. (Petchey, 2001; Clark et al., 2016).

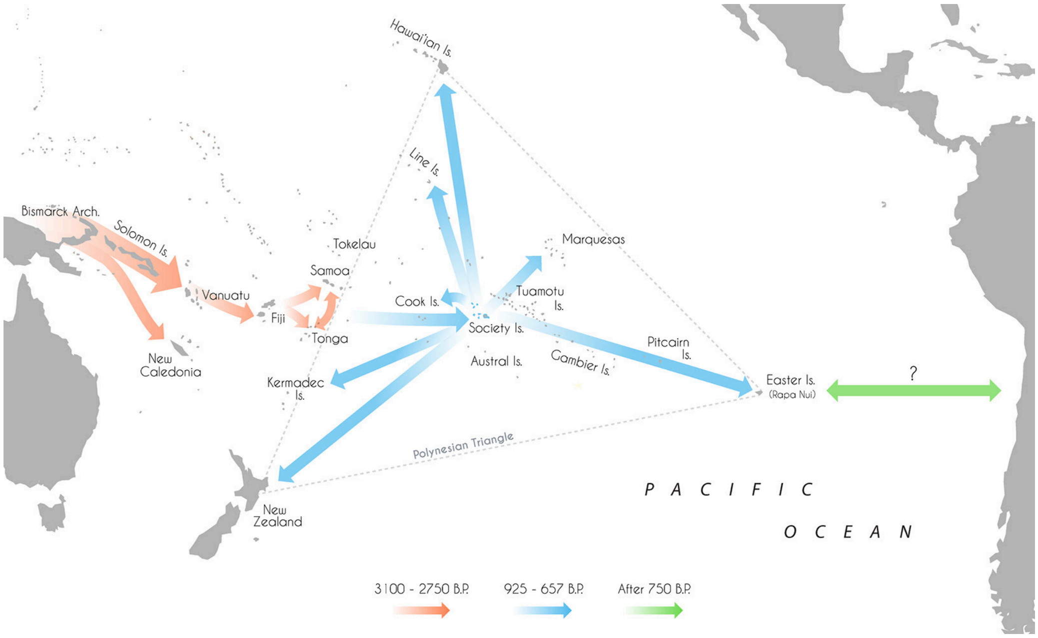

FIGURE 1 | Map of the Pacific islands with Lapita/Polynesian dispersal trajectories and associated dates.

After some period of time, the descendants of these migrants proceeded to move further east into what is now denoted "The Polynesian Triangle;" a 20 million sq. km stretch of ocean comprised of over 500 islands scattered between Hawai'i, Easter Island (Rapa Nui) and New Zealand (Matisoo-Smith, 2015). Nearly every habitable island in this region was colonized, some subsequently used for permanent settlements and others abandoned (Kirch, 2000). The timing and sequence of settlement across many of the major archipelagos of central East Polynesia however remain largely unresolved, with conflicting estimates of initial colonization varying by more than 1,000 years (Wilmshurst et al., 2008, 2011). Recent research has generally supported a short and rapid colonization of eastern Polynesia in the early second millennium A.D (after 950 B.P.; Hunt and Lipo, 2006; Petchey et al., 2010; Molle and Conte, 2011; Rieth et al., 2011; Wilmshurst et al., 2011; Kahn, 2012; Mulrooney, 2013; Commendador et al., 2014; Kahn et al., 2015; Kahn and Sinoto, 2017). A two-phase sequence of settlement has been proposed—establishment in the Society Islands ∼925–830 B.P. before a widespread radiation toward the Marquesas, ∼750–673 B.P.; Easter Island, ∼750–697 B.P.; Hawai'i, ∼731–684 B.P.; New Zealand, ∼720–668 B.P.; Southern Cooks, ∼700–669 B.P.; and the Line Islands, ∼675–657 B.P. (Wilmshurst et al., 2011). However, there are still irreconcilable differences in the chronological boundaries of some island groups, with some researchers advocating for an earlier settlement of the Cook Islands, the Marquesas, Hawai'i and Mangareva (Gambier Islands; Kirch et al., 2010; Allen and McAlister, 2013; Athens et al., 2014; Conte and Molle, 2014; Weisler et al., 2015).

The settlement of Easter Island, in the eastern-most corner of the Polynesian Triangle, has long held a fascination in prehistoric Pacific studies and popular literature. Paleoenvironmental evidence of severe deforestation and a proposed societal collapse (Mieth et al., 2002; Diamond, 2005; Butler and Flenley, 2010; Delhon and Orliac, 2010), have prompted many questions in relation to the immediate origin and timing of initial settlement, the potential of multiple colonization and/or interactions, and the long-term isolation of the Rapanui people. Faunal remains of the Pacific rat (*Rattus exulans*), a commensal species transported by ancient Polynesians, uncovered in the earliest archeological layers of human occupation, provide support for an initial Polynesian colonization of Easter Island (Martinsson-Wallin and Wallin, 2000; Barnes et al., 2006). Material remains, such as one-piece fish hooks and harpoon heads, are also distinctly Polynesian in origin (Weisler, 1996; Green, 1998). Based on material assemblages, potential migration routes through the Marquesas-Tuamotu-Mangareva area, the Mangareva-Pitcairn-Henderson area or directly via the Marquesas have been suggested (Green, 1998; Martinsson-Wallin and Crockford, 2001). However, Irwin (1992) and Green (1998) have noted potential difficulties in directly sailing from the Marquesas to Easter Island.

There is also increasing evidence for an Amerindian connection to Easter Island and wider Polynesia, particularly with regards to the presence of the kumara, or sweet potato, a South American tuber which was distributed throughout East Polynesia prior to European arrival in the region. Whether this reflects a post-settlement arrival of Amerindians to Easter Island and/or an eastern Polynesian return voyage to South America, remains unclear. Human ancient DNA studies have attested to the Rapanui people being of Polynesian descent (Hagelberg et al., 1994), yet recent research has identified

Native American admixture—attributed to pre-European Native American contact (Moreno-Mayar et al., 2014; Thorsby, 2016). Technical and cultural concerns toward the sequencing, storage and interpretation of indigenous human DNA in the Pacific however, has limited access to human genetic material in this region, leaving such questions unresolved for the time being.

Subsequently, the commensal approach, using the genomes of transported (usually domesticated) plant and animal species as a proxy for human migration, has been increasingly applied to investigate human dispersal and interaction patterns across the Pacific (see Matisoo-Smith, 2015). The Pacific rat was the first commensal species studied in relation to human migration in Oceania (Matisoo-Smith, 1994). Proposed to have originated in Flores, Indonesia (Thomson V. et al., 2014), Pacific rats were transported by ancestral Polynesians and are now widely distributed across the region, including Hawai'i, New Zealand and Easter Island. Initial research investigating genetic variation in 400 bp (base pairs) of the hypervariable mitochondrial control region in modern Pacific rats, identified a central East Polynesian interaction sphere comprised of the southern Cook and Society Islands (Matisoo-Smith et al., 1998). This broad interaction sphere was central to a northern (i.e., the Marquesas and Hawai'i), and a southern Polynesian sphere (i.e., Kermadec Islands and New Zealand). The authors suggested that this likely reflects a central homeland region from which major East Polynesian islands were colonized.

A later phylogeographic analysis targeting ∼200 bp of the mitochondrial control region in both ancient and modern Pacific rats across the Pacific (see **Figure 2**), found three major control region haplogroups; the first, an isolated group within Southeast Asia; the second, a dispersed group from Southeast Asia to Near Oceania; and the third, a primarily Remote Oceanic group (Matisoo-Smith et al., 2004). Haplogroup III is associated with the Lapita/Polynesian movement through Remote Oceania; its distribution extending from Vanuatu across to Central and East Polynesia, to Hawai'i, New Zealand and Easter Island, and from likely back migrations, into the Caroline and Marshall Islands. Haplogroup III is further divided into subgroups IIIA and IIIB, the latter derived from IIIA. These subgroups overlap in West Polynesia, however only subgroup IIIB has been found in East Polynesia (Matisoo-Smith et al., 2004). Samples from the haplogroup IIIB either belong to or are derived from the haplotype R9, which has been found across central East Polynesia. Unfortunately, given that most East Polynesian ancient rat specimens adhere to the R9 haplotype, there has been limited success in distinguishing finer-scale movements between the islands within the Polynesian Triangle. This was evident in a control region study on ancient Pacific rat skeletal remains from Anakena, Easter Island (Barnes et al., 2006). All samples presented the R9 control region haplotype and therefore it was not possible to distinguish the immediate origin of the Easter Island population from within eastern Polynesia.

Recent advances in second-generation sequencing technologies and bioinformatics processing however, have made it viable to recover complete ancient mitochondrial genomes from preserved archaological and paleontological samples (Knapp and Hofreiter, 2010). Recent applications of complete mitochondrial sequencing in the Pacific have documented an increase in molecular resolution that can be utilized for fine-scale phylogenetic analyses (Miao et al., 2013; Duggan et al., 2014; Greig et al., 2015). This is of particular importance in Pacific research, as multiple population bottlenecks, the result of successive island migrations, may have severely reduced genetic variation in study species. Here we document complete and partial mitochondrial genome sequences from 13 ancient Pacific rats, sourced from early archeological deposits across West and East Polynesia. It was anticipated that with greater molecular resolution provided by complete mitochondrial genome sequencing, a greater number of Pacific rat lineages would be distinguished and could be used as a proxy to investigate the origins and dispersals of East Polynesian peoples. Our chief objective was to identify a potential immediate origin for the Polynesian settlers who introduced these rats to Easter Island.

MATERIALS AND METHODS

Sample Collection and DNA Extraction

A total of 77 ancient Pacific rat skeletal remains from Easter Island, Tonga, Tokelau, American Samoa, Austral Islands, Cook Islands and the Society Islands were collected for mitochondrial genome extraction and sequencing. These samples were sourced from multiple archeological excavations (see SI Table 1) and were placed within a dark and dry environment for long-term storage. All ancient DNA (aDNA) extractions and library building prior to PCR amplifications were conducted in a purpose-built aDNA laboratory in the Richardson Building at the University of Otago, following recommendations in Knapp et al. (2012a). Access and use of the aDNA laboratory requires adherence to strict protocols in place to minimize contamination risks, particularly from areas where amplified DNA is present, i.e., modern DNA laboratories. Femora were common in the acquired Pacific rat bone assemblage and were targeted for further processing. Prior to DNA extractions, bone samples were soaked in 5% bleach for 10 min, rinsed several times with ultrapure water to remove residual bleach and left to dry overnight. Each bone sample was ground into a fine powder using a sterile mortar and pestle and extracted using a silica based extraction protocol (Rohland and Hofreiter, 2007). Samples were processed in sets of nine in conjunction with one extraction blank.

Library Preparation

Double-stranded barcoded libraries were generated from aDNA extracts and extraction blanks as described in Knapp et al. (2012b), in preparation for hybridization capture and paired end sequencing on an Illumina MiSeq platform. A quantitative PCR (qPCR) was then performed to determine the number of cycles required for the sufficient amplification of each library for immortalization. If libraries presented a significant amount of adapter dimer, a second attempt at library preparation was made or the sample was removed from further processing. Libraries were immortalized by PCR with the following reagent concentrations: 19 μl of adapter ligated library; 1xTaq Buffer; 2.5 mM $MgCl^2$; 1 mM of dNTPs; 3.75 U of AmpliTaq Gold

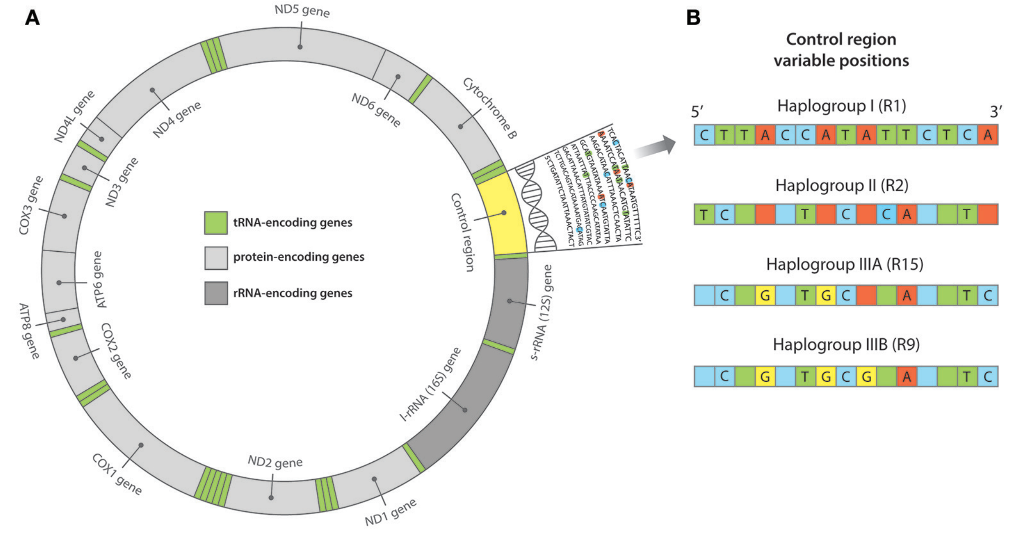

FIGURE 2 | (A) Structure of the mitochondrial genome. At ~16,300 base pairs (bp) in length, the Pacific rat mitochondrial genome is comprised of protein, transfer RNA (tRNA) and ribosomal RNA (rRNA) encoding regions, in addition to the non-coding control region. The control region is often referred to as "hypervariable" as it accumulates mutations at a much higher rate than both the nuclear genome and the remaining regions of the mitochondrial genome. As such, the control region is often targeted for its variation in population genetic studies. **(B)** Pacific rat control region haplogroups as outlined in Matisoo-Smith et al. (2004). Variable positions across ~200 bp of the control region (from position 15,382 to 15,584 bp) have distinguished multiple haplotypes belonging to three major haplogroups—I, II, and III (A & B).

polymerase (ThermoFisher Scientific); 0.2 µM of extension primer, Sol_ext_P5; and 10 µM of a barcoded index primer, Sol_ext_P7. The following immortalization conditions were used: 95°C, 12 min, 22–30 cycles (determined by when the plateau was reached during the previous qPCR) of: 94°C, 30 s; 58°C, 30 s; 72°C, 1 min, followed by a final extension of 72°C for 10 min. Following immortalization, samples were purified with a MinElute PCR Purification Kit (QIAGEN) with the following modification: 2x PE washes. Immortalized libraries were then amplified using a KAPA HiFi PCR Kit (KAPA Biosystems) in preparation for hybridization capture, each 50 µl reaction containing: 1 µl of immortalized library; 1x KAPA HiFi Buffer; 0.3 mM dNTPs; 0.3 mM each of amplification primers, Sol_amp_p5 and Sol_amp_p7; and 1 U of KAPA HiFi DNA Polymerase. The following amplification conditions were used: 94°C, 5 min, 10 cycles of: 94°C, 20 s; 55°C, 55 s; 72°C, 15 s, followed by a final extension of 72°C for 5 min. Following amplification, samples were once again purified.

Bait Production

Bait was produced for hybridization capture using DNA extracted from tissue of a laboratory rat (*Rattus norvegicus*), sourced from the Department of Anatomy, University of Otago, following the protocol described by Maricic et al. (2010). The complete mitochondrial genome of the *R. norvegicus* specimen was targeted using primers designed to amplify two 8–9.5 kb overlapping mitochondrial fragments (see **Table 1**).

Hybridization Capture and Sequencing

Ancient libraries were captured using a modified hybridization protocol, adapted from Maricic et al. (2010). A hybridization mixture containing: 2 µg of barcoded library; 1 µM each of blocking oligonucleotides; 0.6x Agilent blocking agent; and 0.6x Agilent hybridization buffer was prepared for each sample and treated to the following conditions: 95°C, 3 min; 37°C, 30 min. The hybridization mixture was then added to the pre-prepared baited beads and rotated at 12 rpm for 48 h at 65°C. The streptavidin beads were then isolated and washed as described in Maricic et al. (2010), re-suspended in 15 µl of 1x TE solution and heated at 95°C, 3 min, denaturing the captured libraries from the beads. Captured libraries were re-amplified using a KAPA HiFi PCR Kit (KAPA Biosystems) with each 50 µl reaction containing: 15 µl of post-captured library; 1x KAPA Buffer; 0.3 mM dNTPs; 0.3 mM each of the amplification primers, Sol_amp_p5 and Sol_amp_p7; and 1 U of KAPA HiFi DNA Polymerase. The following amplification conditions were used: 94°C, 5 min, 20 cycles of: 94°C, 20 s; 55°C, 55 s; 72°C, 15 s, followed by a final extension of 72°C for 5 min. Libraries were then purified with a MinElute PCR Purification Kit (QIAGEN), quantified with a Qubit 2.0 Fluorometer (Invitrogen), pooled in equimolar concentrations and sequenced using 2 × 75 base pair-end runs on an Illumina MiSeq sequencing platform, conducted by New Zealand Genomics Limited (NZGL) at Massey University, New Zealand. Libraries prepared from extraction blanks were sequenced separately.

Raw Data Processing

Sequencing reads were initially processed in AdapterRemoval (v.2; Lindgreen, 2012) to remove adapters, merge paired-end fragments (overlapping by at least 11 base pairs), and remove stretches of Ns, bases with low quality scores (<30) and short reads (<25). Reads were then mapped to a reference genome (*R. exulans*, GenBank accession NC_012389)

TABLE 1 | Long-range PCR amplification for bait production.

Region amplified	Primer pairs	Primer sequences (5′–3′)	Amplicon length	Annealing temperature
COI → *Cyt b*	BatL5310 & RCb9H	CCTACTCRGCCATTTTACCTATG TACACCTAGGAGGTCTTTAATTG	9.5 kb	47°C
Cyt b → *COI*	RGlu2L & R6036R	CAGCATTTAACTGTGACTAATGAC ACTTCTGGGTGTCCAAAGAATCA	8.3 kb	49°C

in BWA v.0.7.12 (Li and Durbin, 2009), following recommended settings for ancient DNA, i.e., −n 0.03 (allow for more substitutions), -o 2 (allow more gaps at the beginning) and −l 1,024 (deactivate seed mapping; Schubert et al., 2012). Reads were also mapped to mitochondrial reference genomes from cow (*Bos Taurus*, GenBank accession NC_006853.1), pig (*Sus scrofa*, NC_0012095.1), human (*Homo sapiens*, GenBank NC_012920.1), chicken (*Gallus gallus*, GenBank NC_001323.1) and dog (*Canis lupus familiaris*, GenBank NC_002008.4) to detect any contamination. Unmapped reads were removed using SAMtools (Li et al., 2009; See Supplementary Materials).

PCR duplicates were then removed from unmerged reads using Picard's MarkDuplicates tool and from merged reads using script from PaleoMix (Schubert et al., 2014). Merged and unmerged reads were combined into one BAM file and coverage plots were produced for each sample using SAMtools (Li et al., 2009). The program mapDamage (v.2.0; Jónsson et al., 2013) was then implemented to assess damage patterns and lower the quality score of these damaged sites using the "–rescale" option. Plots to assess characteristic aDNA damage patterns were produced for each sample (see Supplementary Materials). A variant call file was generated and a consensus sequence produced, that was then converted to a FASTA file using GATK's FastaAlternateReferenceMaker (McKenna et al., 2010), masking positions with a read depth of <2. SNPs were visually inspected using the Integrative Genomics Viewer (IGV; Robinson et al., 2011; Thorvaldsdóttir et al., 2013) to ensure consistency with the variant calling criteria. Consensus sequence coverage was evaluated in Geneious (v.8.1.8; http://www.geneious.com, Kearse et al., 2012); sequences with large fragments missing (more than 50% of the reference genome) and/or that exhibit read depth <2 were removed from subsequent phylogenetic analyses.

Phylogenetic Analyses

Ancient mitochondrial sequences were aligned using MUSCLE in Geneious (v.8.1.8). Two phylogenetic analyses were conducted: 1. with near complete sequences (>90% of the reference sequence), and 2. with all near complete and partial sequences (>50% of the reference genome). Sites were masked where any of the sequences provided missing data, using the Mask Alignment tool in Geneious.

A Bayesian inference analysis of phylogeny was conducted using the MrBayes plugin (v.2.2.2: Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) implemented in Geneious (v.8.1.8). This consisted of running four chains with the heated chain temperature set at 0.2 to allow sufficient chain-swapping over 20 million generations, with a burn-in length of 100,000 and sampling every 2,000 generations. The best-fit model for nucleotide substitution was determined using jModeltest2 (https://github.com/ddarriba/jmodeltest2, Guindon and Gascuel, 2003; Darriba et al., 2012) with 11 substitution schemes. Model selection was computed using the Bayesian and Akaike information criteria (BIC and AIC). The HKY85 substitution model (Nst = 2; Hasegawa et al., 1985) with invariable rate variation (rate variation command "propinv") was applied for the ancient sequence analysis. Complete mitochondrial sequences from Thailand, Papua New Guinea and New Zealand (Genbank EU273710.1, EU273709.1, EU273711.1; Robins et al., 2008) were added for the purposes of outgrouping (Thailand) and to assess where they position in relation to the ancient sequence assemblage. The resulting Bayesian consensus trees were visualized and exported from Geneious (v.8.1.8). Convergence was assessed using the Trace tool in Geneious; there were no obvious trend lines to suggest that the MCMC was still converging and there were no large-scale fluctuations that would suggest poor mixing. Effective sample sizes (ESS) for all traces exceeded 100.

Maximum likelihood (ML) analyses (Felsenstein, 1981) were conducted using the PhyML plugin (v.3.0: Guindon et al., 2010) implemented in Geneious (v.8.1.8). Substitution rate categories were set to 4 and bootstrap support was estimated using 1,000 replicates. The HKY85 substitution model (Hasegawa et al., 1985), with software-optimized estimates of the proportion of invariable sites, the gamma shape parameter and the transition/transversion ratio was applied. Convergence was assessed by comparing multiple runs and ensuring that bootstrap support was consistent at a determined level of replicates.

The population structure of the ancient Polynesian rat assemblage was evaluated using a median-joining network analysis, generated in PopArt (v 1.7; Bandelt et al., 1999; Leigh and Bryant, 2015) with default settings. In addition, the control region fragment (15,387–15,590 bp) was extracted from the complete mitochondrial sequences, in order to assign each sample into the three major control region haplogroups—I, II, III (A & B) as described in Matisoo-Smith et al. (2004). This was used to compare the molecular resolution between control region and complete mitochondrial genome analyses.

RESULTS

DNA Preservation and Sequence Recovery

Forty of the 77 samples produced adequately preserved DNA that amplified and was subsequently sequenced. However, 27 samples were removed post-sequencing as a result of missing large fragments and low read depth (<2) when mapped to a Pacific rat mitochondrial reference genome. This resulted in a total of 13 complete and partial sequences to be used in subsequent phylogenetic analyses. Complete mitochondrial genomes were obtained from six samples, with the remaining seven samples providing partial coverage (ranging from 53 to 94%; see **Table 2**). The average read depth for the thirteen samples is 135.6x (ranging between 1.8x and 657.8x; see SI Figure 1). Ignoring missing data across the sequences (designated "N"), the average read depth for the 13 samples is 136.2x (ranging between 2.8x and 657.8x).

DNA preservation and recovery is largely dependent on environmental factors (i.e., temperature, moisture, and acidity of the surrounding environment) and the age of the sample. Pacific preservation varies across tropical to temperate climates, and whether the sample was recovered from a protected, open and/or coastal context (Robins et al., 2001). Specimens recovered from East Polynesia generally provided greater DNA preservation than those from West Polynesia. It is clear from the read fragment distributions (see SI Figure 2), that the Easter Island samples in particular were less fragmented, providing peak read length between 100 and 120 bp. Rat specimens retrieved from Easter Island provided greater DNA preservation than all other surveyed locations in central East Polynesia. This is consistent with previous commensal research that has recovered complete ancient mitochondrial genomes from another temperate location in the Pacific, i.e., New Zealand (Greig et al., 2015).

Sequence Authenticity

To estimate the degree of contamination, reads from each sample were mapped to mitochondrial reference genomes that represent common contaminants i.e., pig, human, cow, chicken, and dog. Only one ancient sample (MS10605) exhibited a small amount of human contamination equating to ~0.03%. A lack of exogenous DNA, particularly from cow, pig, and chicken, indicates that reagents used in this study were free from contamination. It has previously been asserted that laboratory reagents, such as dNTPs, can contain DNA from domestic and laboratory animals that may obscure endogenous DNA amplification (Leonard et al., 2007; Thomson V. A. et al., 2014). No blank processed with any of the modern and ancient samples exhibited contamination, providing no indication of cross-contamination during the processing of samples. The deamination patterns exhibited in the reads from each ancient sample were consistent with expected damage in ancient DNA sequences (see SI Figures 3–6). The observed C to T misincorporation rate of 0.20 for the first nucleotide position of the 5′ end exceeds the maximum rate of 0.05 for samples <117 years old, and is consistent within samples older than 500 years (Sawyer et al., 2012). This indicates that the sequences are endogenous mtDNA of rats obtained from early archeological deposits across Polynesia.

Phylogenetic Analyses

Across the 13 ancient mitochondrial genomes, a total of 88 variable sites were identified. Interestingly, only three sites of variation were identified in the hypervariable (HVR) I region (positions 16,024–16,383 bp) of the control region. This hypervariable region is commonly targeted for population studies as it is considered fast mutating. However, in the ancient *R. exulans* sequences assessed in the current study, a higher degree of variation is observed across the protein-coding regions.

The consensus maximum likelihood (ML) and the Bayesian Inference trees for the complete ancient sequences were congruent and illustrated two major groupings—the first consisting of the Papua New Guinea and Thailand sequences, and the second consisting of the ancient rats sampled from across Remote Oceania (see **Figure 3A**). The Fakaofo (Tokelau; MS10592), Maupiti (Society Islands; MS10502), New Zealand (GenBank EU273711.1) and Easter Island sequences are similar, however there is high bootstrap and Bayesian posterior probability support for a distinct grouping of the

TABLE 2 | Ancient samples used in the phylogenetic analyses.

Location	Site	Sample code	GenBank accession number	Associated layer date
Tonga	Faleloa, Foa	MS20596	KY814713	2,600 ± 50 B.P.
Tokelau	Fakaofo	MS10591	KY814711	1,090 ± 60 B.P.
		MS10592	KY814712	1,090 ± 60 B.P.
Austral Islands	Atiahara, Tubuai	MS10600	KY814714	769–675 B.P.
		MS10601	KY814715	769–675 B.P.
Society Islands	Terre Namotu, Maupiti	MS10502	KY814709	495–320 B.P.
	Haumi archeological site, Mo'orea	MS10523	KY814710	911–652 B.P.
Easter Island	Anakena	MS10602	KY814716	610–560 B.P.
		MS10604	KY814717	610–560 B.P.
		MS10605	KY814718	610–560 B.P.
		MS10606	KY814719	610–560 B.P.
		MS10609	KY814720	610–560 B.P.
		MS10610	KY814721	610–560 B.P.

Associated layer dates are as reported in archeological excavation publications (see SI Table 1).

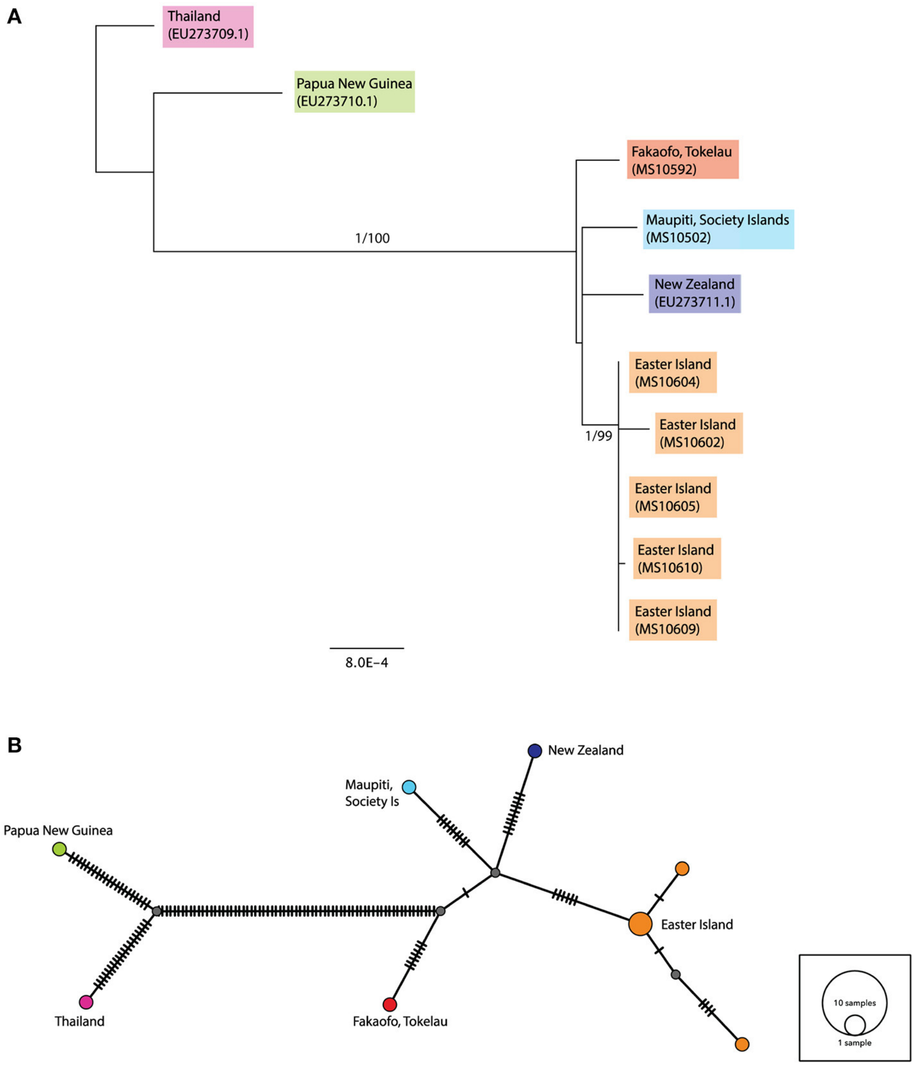

FIGURE 3 | (A) Rooted maximum likelihood (ML) tree inferred from the complete (>90%) mitochondrial sequence dataset. Values above each node represent Bayesian posterior probabilities (obtained using MrBayes) and ML bootstrap values (obtained from PhyML). Only posterior probabilities/bootstrap values, where one or both are above 0.7 and 70, respectively, are included. Individual sample names are included and geographic populations defined by color. Scale bar represents amino acid substitutions per site. Additional *R. exulans* sequences (Thailand, Papua New Guinea (outgroup) and New Zealand; Genbank EU273709.1, EU273710.1, EU273711.1; Robins et al., 2008) were included. **(B)** Median-joining (MJ) network inferred from the complete (>90%) mitochondrial sequence dataset. The diameter of each circle is proportional to the frequency of a specific haplotype. Small gray circles indicate missing haplotypes. Nucleotide substitutions between haplotypes are represented by dashes.

Easter Island samples. In the median-joining (MJ) network, the Remote Oceanic samples radiate off two central nodes within 10 mutational steps (see **Figure 3B**). The Easter Island samples form a distinct cluster, whereby three of the samples (MS10604, 605, and 609) share the same mitochondrial haplotype.

In the ML tree containing both complete and partial ancient mitochondrial sequences (see **Figure 4A**), a sample from Fakaofo (Tokelau; MS10591) occupies a branch outside of the remaining Remote Oceanic sequences. In the corresponding MJ network (**Figure 4B**), MS10591 is clearly distinct, radiating from a central Remote Oceanic node by six mutational steps. Within the remaining Remote Oceanic samples, there is high Bayesian posterior probability support for four distinct groups, the first solely containing the New Zealand sequence; the second containing the Foa, Tonga (MS10596) and the Fakaofo, Tokelau (MS10592) sequences; the third containing the Society Island sequences (MS10523 and MS10502); and the fourth, an Easter Island/Tubuai (Austral Is) group of eight sequences. In the MJ network, these groups are not highly distinct, radiating from the central node by one mutation. However, its needs to be clarified that by including partial sequences in a PopArt network analysis, missing sites may potentially mask phylogenetically informative sites that

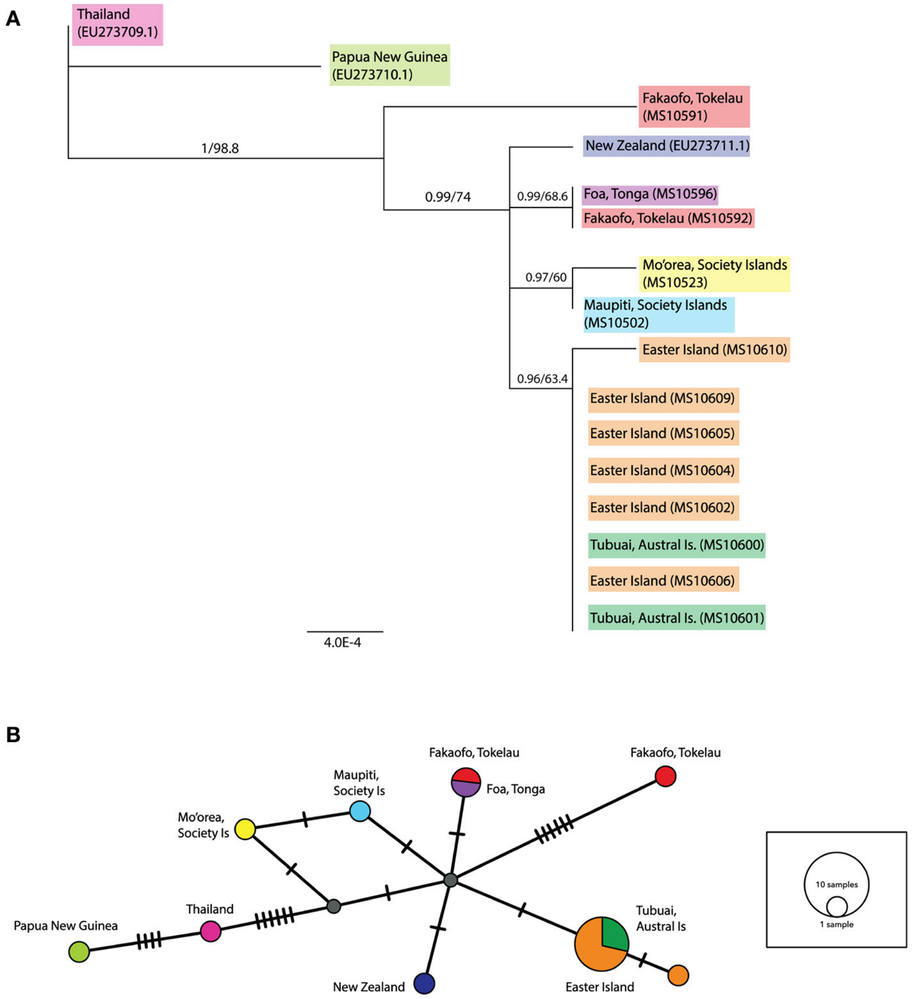

FIGURE 4 | (A) Rooted maximum likelihood (ML) tree inferred from the complete and partial mitochondrial sequence dataset. Values above each node represent Bayesian posterior probabilities (obtained using MrBayes) and ML bootstrap values (obtained from PhyML). Only posterior probabilities/bootstrap values, where one or both are above 0.7 and 70, respectively, are included. Individual sample names are included and geographic populations defined by color. Scale bar represents amino acid substitutions per site. Additional *R. exulans* sequences (Thailand, Papua New Guinea (outgroup) and New Zealand; Genbank EU273709.1, EU273710.1, EU273711.1; Robins et al., 2008) were included. **(B)** Median-joining (MJ) network inferred from the complete and partial mitochondrial sequence dataset. The diameter of each circle is proportional to the frequency of a specific haplotype. Small gray circles indicate missing haplotypes. Nucleotide substitutions between haplotypes are represented by dashes.

were present in the MJ network of complete mitochondrial genomes.

A network analysis of 203 bp of the control region was undertaken to categorize samples into the three major haplogroups—I, II, III as described in Matisoo-Smith et al. (2004). All of the ancient Polynesian samples that were not missing fragments in the control region, clustered within Haplogroup IIIB, in particular adhering to the R9 haplotype (see **Figure 5**). It is clear that there is little nucleotide variation in the control region that can be used to distinguish ancient Pacific rat populations in Remote Oceania. Interestingly, the Thailand sequence (GenBank EU273710.1), clustered outside all three major haplogroups, indicating the existence of potentially another major Pacific rat haplogroup.

DISCUSSION

The Application of Complete Mitochondrial Genome Sequencing

Mitochondrial hypervariable regions accumulate mutations at a faster rate than other mitochondrial regions (Stoneking, 2000), producing a greater amount of population variation that can be utilized for phylogenetic research. As such, the majority of commensal studies in the Pacific, particularly those using archeological specimens, have targeted fragments of 100–600 bp in the mitochondrial control region (e.g., Barnes et al., 2006; Larson et al., 2007; Storey et al., 2007, 2010; Oskarsson et al., 2012). As ancient DNA is highly fragmented, it is practical to target fragments of the mitochondrial control region

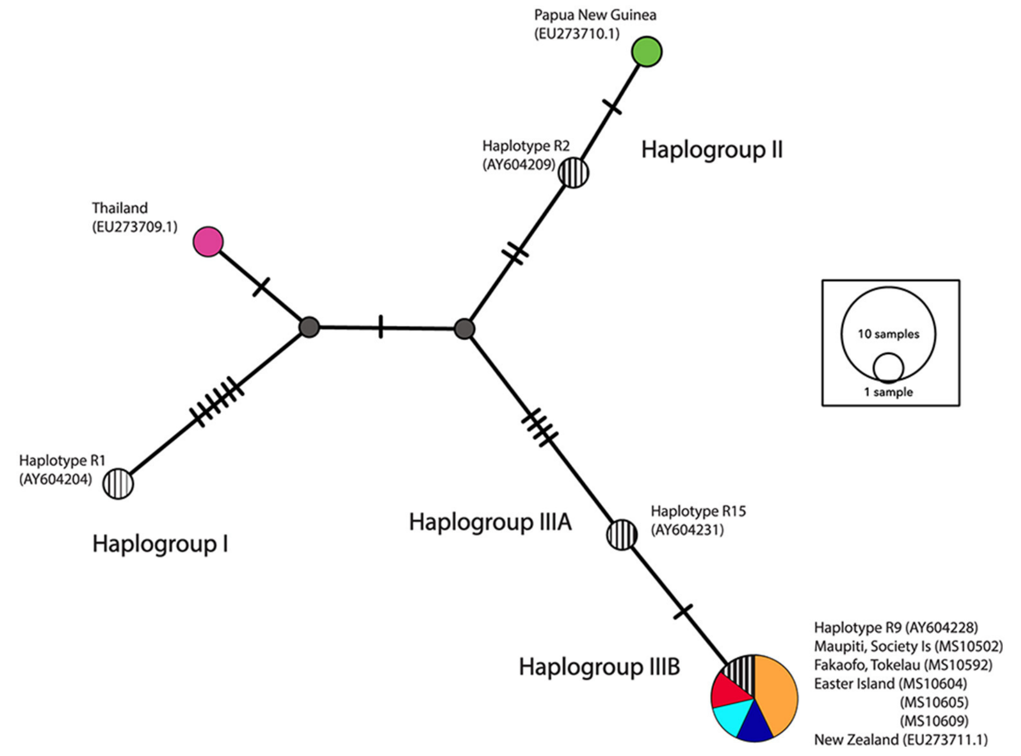

FIGURE 5 | Median-joining (MJ) network of control region haplotypes. Striped circles represent four central haplotypes chosen to represent each haplogroup (I, II, IIIA, and IIIB). The diameter of each circle is proportional to the frequency of a specific haplotype.

that produce the most usable variation. The emergence of second-generation sequencing however has made it viable to generate longer DNA sequences, e.g., complete mitochondrial genomes, from fragmented aDNA (Knapp and Hofreiter, 2010). The use of hybridization capture for target DNA enrichment prior to second-generation sequencing (Ng et al., 2009), is also beginning to supersede the traditional primer-based PCR amplification that can often amplify large amounts of exogenous contaminant DNA (Burbano et al., 2010; Knapp et al., 2012b; Li, 2013; Greig et al., 2015). Recent studies using complete mitochondrial genomes in the Pacific have reported a higher level of molecular resolution that can distinguish phylogenetic groups and individuals with greater accuracy than use of the control region alone (Miao et al., 2013; Duggan et al., 2014; Greig et al., 2015).

The control region analysis conducted in this study showed that all ancient Polynesian samples (that did not contain missing sites in the control region) clustered within Haplogroup IIIB, in particular, possessing the R9 haplotype. The use of this control region fragment alone did not produce enough variation to distinguish island groups or specific lineages. The low variation in the hypervariable regions of the ancient Pacific rat genomes may reflect a number of bottlenecks in the establishment of populations. Pacific rats, carried by migrating humans, would have been established on Pacific islands in a stepping-stone manner. A subset of the population (and therefore haplotypes) would have been carried on each migratory journey, as humans moved eastwards into the far reaches of Polynesia. Furthermore, as populations were established on islands, gene flow would have been heavily restricted and subsequently prolonged low variation. Our study indicates that targeting one region (e.g., HVR I) may not provide enough variation across all samples to sufficiently distinguish populations. In conjunction with previous Pacific commensal research using complete mitochondrial genomes, our results suggest that complete mitochondrial sequencing is necessary to assess all mitochondrial variation and gain the highest molecular resolution for subsequent phylogenetic analyses.

Implications for Pacific Rat and Associated Human Dispersal

Archaeological and linguistic evidence suggests that Tonga and Samoa form the West Polynesian homeland from which East Polynesian populations are derived (Emory, 1946; Green, 1966, 1981; Pawley, 1966; Groube, 1971). The median-joining network analyses conducted in this study illustrate a star-shaped pattern whereby the Remote Oceanic sequences radiate off two shared central nodes. This is consistent with the scenario of an eastern dispersal from West Polynesia into the central East Polynesian archipelagos, before a widespread expansion to the extremes of Easter Island, Hawai'i and New Zealand. In the MJ network containing both complete and partial ancient rat sequences, the Tongan sequence (MS10596) shares the same haplotype as a sequence from Fakaofo, Tokelau (MS10592). Tokelau has previously been described as an intermediary between West and East Polynesia (Burrows, 1939). Whilst it has not yet been established whether key Tokelauan islands were directly settled from the West Polynesian homeland or from a back migration originating from central East Polynesia, re-analyzed radiocarbon determinations suggest that Fakaofo and Atafu were colonized by 750 B.P (Petchey et al., 2010). This coincides with the widespread expansion from central East Polynesia to the outliers of the Polynesian Triangle. Regardless of its immediate origin, the Tokelauan (MS10592) haplotype is present in an early Tongan deposit that predates East Polynesian expansion. Therefore, this shared haplotype is established to have been present in a Tongan population and subsequently carried with either West Polynesian or descendent East Polynesian settlers into Fakaofo, Tokelau. The other ancient Tokelauan haplotype, MS10591, is highly diverged in both the ML and MJ analyses. This haplotype may either represent another form carried by Tongan/Samoan populations—presently unsampled in West Polynesia, or a later evolved haplotype that diverged post-settlement of Tokelau.

The earliest radiocarbon dates associated with human settlement in central East Polynesia are found in the Society Islands (∼925–830 B.P.; Wilmshurst et al., 2011). The Society Islands are often represented as the central East Polynesian homeland from which widespread eastern expansion occurred after 750 B.P. The ancient Society Island sequences obtained from Maupiti and Mo'orea (MS10502 and MS10592) represent two closely related haplotypes that radiate from the same central nodes in the MJ network as the rest of the Remote Oceanic assemblage. These two haplotypes however, are not ancestral to the remaining East Polynesian samples. As no other recovered ancient central East Polynesian haplotypes are derived from the haplotype found on Mo'orea, which given its associated layer date of 911–652 B.P. (Kahn, 2016) would have existed at the time of widespread expansion, or the haplotype from Maupiti, it could be argued that the continued East Polynesian expansion did not originate from these islands. However, given our limited success in recovering complete mitochondrial genomes from the Society Islands, we may have not sampled potential ancestral haplotypes present in archeological deposits in this region. Further sampling of ancient Pacific rats across the Society Islands and nearby Cook Islands is required to assess whether an ancestral haplotype, corresponding to the central nodes in the MJ networks, were established in these central island groups and whether it existed concurrently with derived haplotypes, such as those found in Mo'orea and Maupiti.

The Wilmshurst et al. (2011) re-analysis of East Polynesian radiocarbon determinations from early settlement deposits, suggests that Easter Island was colonized between ∼750 and 650 B.P. The initial colonization is supported to be of Polynesian origin (Weisler, 1996; Green, 1998; Martinsson-Wallin and Wallin, 2000; Barnes et al., 2006), however the immediate origin remains unclear. The grouping of the Tubuai (Austral Is) and Easter Island haplotypes in this study suggests that both island groups were established by the same colonization wave, that would have carried the haplotype that the Easter Island and Tubuai rats share or are derived from. Whilst haplotype networks, such as the median-joining network, do not indicate ancestor-descendent relationships and therefore the direction of migration, it is unlikely that the Tubuai haplotypes are derived from the Easter Island population. Geographically, Easter Island is situated in the eastern-most corner of Polynesia. Migratory voyages are likely to have passed through other island archipelagos in a stepping-stone manner before reaching Easter Island. Therefore, it is highly likely that the Austral Islands were colonized prior to Easter Island. Preliminary radiocarbon dating on Tubuai suggests that it had been occupied earlier than Easter Island (Worthy and Bollt, 2011) and was contemporaneous with sites in the southern Cooks (Walter, 1998). This is the first commensal study to specify a potential immediate origin for the Easter Island population, providing support for the colonization of Easter Island through a south-eastern voyaging corridor, originating from the Austral Islands and potentially moving through the Gambier, Pitcairn and Henderson Island regions. Similar cultural assemblages documented by Weisler (1996), indicate the existence of an interaction sphere between Mangareva (Gambier Islands), Pitcairn and Henderson Island. Further sampling would be required in the Gambier, Pitcairn and Henderson Islands however to establish haplotype continuity in this south-eastern corridor.

The absence of variation in the Barnes et al. (2006) study of Easter Island rats, was attributed to a single or limited introduction of rats, followed by long-term isolation. The early divergence of the Rapanui language from the East Polynesian language group (Trudgill, 2004) is consistent with an early Easter Island colonization followed by extreme isolation from all other East Polynesian groups. The adherence of the ancient Easter Island rats sampled in this project to three haplotypes suggests that there may have been limited variation in the colonizing population of rats, however the sample size is too small to assess population variation. Notably, all Easter Island rat samples in this study were sourced from the earliest occupation layers at Anakena; described in traditional history as the landing place of the initial colonists (Métraux, 1940). Further sampling of ancient Easter Island rats from various time periods and archeological contexts would determine, from the absence or introduction of new haplotypes, whether inter-island contact was prevalent post-colonization.

CONCLUSION

Recent developments in target DNA enrichment and sequencing technologies have improved the cost-effectiveness and viability of recovering complete mitochondrial genomes from ancient fragmented DNA. Complete mitochondrial genome sequencing provides a higher degree of molecular resolution that can be used to distinguish Pacific rat populations across Remote Oceania. Our results indicate that Remote Oceanic rat haplotypes are closely related and are consistent with the scenario of a central East Polynesian homeland from which widespread expansion occurred. We also document the clustering of Tubuai and Easter Island haplotypes, which suggest that Easter Island may have been settled via a south-east voyaging corridor through the Austral Islands, Gambier, Pitcairn and Henderson regions. While the 13 mitogenome sequences presented here provide new details regarding relationships between various Pacific rat populations, further sequencing of ancient *R. exulans* samples and similar analyses of genetic variation of other commensal species in East Polynesia will refine our understanding of human dispersal and interaction across this vast region.

AUTHOR CONTRIBUTIONS

KW and EM conceived the research and wrote the manuscript with contributions from all co-authors; KW, CC, and OK performed the experiments and analyzed data; JK, TH, and DB obtained and provided samples and important site information; all authors reviewed the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fevo.2017.00052/full#supplementary-material

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Genetic Evidence for a Contribution of Native Americans to the Early Settlement of Rapa Nui (Easter Island)

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Available evidence strongly suggests that the first to settle on Rapa Nui were Polynesians arriving from the west around AD 1200–1253. There are, however, also signs of an early contact between Rapa Nui and South America, but genetic evidence of an early contribution of Native Americans to the peopling of Rapa Nui has until recently been lacking. In this review our own genetic studies of blood-derived DNA collected on Rapa Nui since 1971 are summarized. For the first time human molecular genetic data are obtained which strongly suggest that some Native Americans arrived early at Rapa Nui, probably as early as AD 1280–1495. Whether they sailed directly from South America to Rapa Nui on their own rafts or whether they came with Polynesians returning from visits to South America cannot be established by our studies, but the latter possibility may be the most likely given other evidence of early visits by Polynesians to South America. In any case, our data suggest that some Native Americans arrived Rapa Nui not long after its first settlement by Polynesians, but long before the island was discovered by Europeans in 1722. Native Americans may therefore have had an influence on the early human colonization of Rapa Nui and thus on its ecology.

Keywords: Rapa Nui, Easter Island, early settlement, Polynesians, Native Americans, Europeans

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INTRODUCTION

It is now generally accepted that Polynesia was first populated from the west, with peoples who originally came from Southeast Asia, probably around Taiwan. Having reached Samoa and Tonga ∼3000 years before present (BP) (see **Figure 1**), where they apparently stayed for more than 1000 years, some sailed further east in their double canoes and populated most islands in East Polynesia, including Rapa Nui (Friedlander et al., 2008; Kirch, 2010; Wollstein et al., 2010; Wilmshurst et al., 2011). The timing of the first colonization of Rapa Nui has been much debated. Dates ranging from AD 400–800 have previously been given (references in Hunt and Lipo, 2009). Recent studies based on refined calibrated radiocarbon dates from multiple samples strongly suggest, however, that its first settlement occurred as late as AD 1200–1253 (Wilmshurst et al., 2011).

In contrast, Thor Heyerdahl proposed that East Polynesia, including Rapa Nui, was first populated by Native Americans (Amerindians), arriving from South America ∼AD 500 (Heyerdahl, 1952). Among his arguments were the prevailing winds and ocean currents in the area, Polynesian legends, similarities between old fishing gear found in East Polynesia and on the coast of northern Chile, linguistic and other clues, and the presence of some South American plants in East

FIGURE 1 | A very schematic illustration of the colonization of the Polynesian triangle of islands. It is generally accepted that Polynesia was first populated with people who came from Southeast Asia, leaving around Taiwan ~5.500 years before present (BP). They first arrived Samoa and Tonga ~3 000 years BP, from where they sailed further east and arrived at the Society Islands ~AD 1100 (marked with an interrupted red line). From here they populated most of the Polynesian islands. They reached Rapa Nui ~AD 1200 (marked with a red line and 1). An early contribution of Native Americans to Rapa Nui ~AD 1340, as strongly suggested by our investigations summarized in this review, is also indicated, arriving either on their own rafts from South America (marked with a dotted blue line and 2a), or together with some Polynesians returning from visits to South America (marked with a dotted green line and 2b).

Polynesia and on Rapa Nui such as the Andean sweet potato (*Ipomoea batatas*) and the bottle gourd (*Lagenaria siceraria*). He also argued that the giant stone statues, *moai*, and their platforms, *ahu*, on Rapa Nui (and some other East Polynesian islands) are very similar to some pre-Inca stone statues and platforms in South America, particularly at Tiahuanaco in Bolivia. Thus, Heyerdahl suggested that the first *moai* and *ahu* builders on Rapa Nui had brought the exquisite masonry techniques with them from South America. In 1947 he demonstrated by his *Kon-Tiki* expedition that it was possible to reach East Polynesia with a balsa raft from Peru.

His theory received little support, however, and was to a large extent strongly opposed by most other scholars. Among the evidence against his theory were investigations of mitochondrial DNA (mtDNA) and Y chromosome markers, which demonstrated that Polynesians and Southeast Asians share particular genetic polymorphisms; i.e., genetic variants (Friedlander et al., 2008; Kirch, 2010). Furthermore, mtDNA studies of East Polynesians have not been able to reliably demonstrate a contribution by Native Americans (Bonatto et al., 1996), albeit others claimed that these studies were inconclusive (Cann and Lum, 1996). The presence of some Native American Y chromosomes on Rapa, another island in Polynesia, was assumed to be the result of repatriation following the Peruvian slave raids in Polynesia in the 1860s, which resulted in an admixture of Native American and European genes in the area (Hurles et al., 2003).

Previous investigations on Rapa Nui have also given little support to Heyerdahl's theory, namely that Rapa Nui was first populated by Native Americans. Instead strong evidence of an original Polynesian ancestry has been obtained (Hunt and Lipo, 2011). This includes the results of typing of mtDNA markers from 12 ancient skeletal specimens from the island, dating from ~AD 1100–1868, which revealed only typical Polynesian mtDNA markers (Hagelberg et al., 1994). Investigations of Rapanui for 18 Alu genetic insertion polymorphisms demonstrated a high genetic affinity to Southeast Asian populations and failed to show an early contribution of Native Americans (González-Pérez et al., 2006).

EVIDENCE OF A "PRE-HISTORIC" CONTACT BETWEEN POLYNESIA AND SOUTH AMERICA

Notwithstanding this evidence of a Polynesian origin of the initial settlement of East Polynesia, there are, however, also clues of a "pre-historic" (i.e., before Europeans discovered Polynesia) contact between East Polynesia and South America. The strongest of these is the presence of the Andean sweet potato in East Polynesia, which has to have been introduced by man, and has been grown on Rapa Nui long before the island was discovered by Europeans (Wallin et al., 2005; Roullier et al., 2013). Recent studies have also detected starch remains of the sweet potato of American origin in dental calculus of human skeletons from Rapa Nui as old as ∼AD 1330 (Tromp and Dudgeon, 2015). Suggestive evidence that the South American bottle gourd was introduced in pre-historic time has also been presented (Kirch, 2010). A pre-historic contact between South America and Polynesia was recently supported by analyses of the remains of some chickens found in El Arenal in the southern part of Chile. The mtDNA of the chickens was found to be of Polynesian type, and radiocarbon investigations showed that the remains dated back to ∼AD 1321–1407, i.e., before Columbus discovered America (Storey et al., 2007). These results were, however, very recently questioned in similar studies performed by others (Thomson et al., 2014). Suggestive evidence of human skeletal remains of pre-Columbian Polynesian ancestry on Mocha Island in Chile has also been reported (Matisoo-Smith and Ramirez, 2010), as well as other evidence of Polynesian presence in South America in pre-Columbian time (Kirch, 2010; Lawler, 2010). Very recently, genomic Polynesian ancestry, but no Native American ancestry, was detected in two ancient skulls of indigenous Botocudos from Brazil (Malaspinas et al., 2015), but more studies are needed to firmly establish that this is the result of a pre-historic voyaging by some Polynesians to South America.

Thus, while there are several clues of a pre-historic contact between East Polynesia and South America, previous studies have failed to demonstrate genetic evidence of an early contribution of Native Americans to Rapa Nui. Instead it was generally assumed that some Native Americans did not reach Rapa Nui until sometime after the island was discovered by Europeans.

INVESTIGATIONS OF RAPANUI HLA MOLECULES

Human Leucocyte Antigens (HLA) are molecules in our cell membranes which are encoded by some very polymorphic genes at neighboring loci in the HLA genetic complex on chromosome 6 (see **Table 1**). Soon after their discovery in the early 1960s it was found that these molecules exist in several different variants, which differ greatly in frequencies in different populations. Thus, it was suggested early that serological typing for the different variants of HLA molecules might become informative in anthropological studies. Therefore, in 1971 we collected blood samples from 69 Rapanui who had Rapanui ancestors dating back for many generations and where no foreign admixture was known, based on medical and historical records as well as by interviews (Thorsby et al., 1973; Thorsby, 2012). Most of the individuals belonged to a large family, descendant from *Pacomio Maori* (∼1816–1909) and his two wives (see Figure 1 in Thorsby, 2012).

By comparing our results with those obtained by others of typing HLA antigens in other populations in this area, however, we could not convincingly demonstrate an early contribution of Native Americans to Rapa Nui (Thorsby et al., 1973). Typing for some blood groups and other genetic markers also did not reveal reliable genetic traces of Native Americans. Since, however, HLA investigations at that time were based on serological typing and had a very low resolution (very few of the HLA variants which became known later could be serologically typed for at that time; see next paragraph), we stored serum samples in liquid nitrogen for future studies when better methods might become available.

GENOMIC HLA INVESTIGATIONS OF RAPANUI DNA

By 2006 typing of HLA genes by genomic methods had become available and more than 2500 HLA alleles (genetic variants) had been detected which varied in frequency among different populations (Sanchez-Mazas et al., 2011). Thus, we thawed the serum from our 1971 samples and were able to extract DNA from 48 of them.

The results are described in detail elsewhere (Lie et al., 2007; Thorsby, 2012). A total of 11 different HLA haplotypes (the combination of particular HLA alleles carried by the HLA complex on a given chromosome 6) were detected among the investigated individuals. Ten of these haplotypes carried HLA alleles that had previously been observed in Polynesia. Furthermore, *all* individuals carried one or two HLA haplotypes with typical Polynesian HLA alleles. These results further support an initial Polynesian origin of the population on Rapa Nui.

One haplotype also carried some typical European HLA alleles, which are found in high frequency in Southern Europeans (Solberg et al., 2008). The primary source of these HLA alleles may have been a European crewmember on a ship visiting Rapa Nui in the early 1800s (Thorsby, 2012).

The DNA was also typed for mtDNA markers, which revealed in all investigated samples a combination of mtDNA markers typical of Polynesians. Typing for Y chromosome markers also revealed that most men had haplogroups typical of Polynesians, while five of them had a typical European haplogroup. No traces of Native American mtDNA or Y chromosome markers were found.

NATIVE AMERICAN HLA ALLELES FOUND IN SOME RAPANUI

Most interesting of the HLA haplotypes, however, were two (*a* and b, see **Table 1**) that carried the HLA alleles *A*02:12* and *B*39:05*.

TABLE 1 | Two HLA haplotypes (i.e., combinations of particular alleles at the HLA gene loci in the HLA genetic complex on a given chromosome 6) found in some Rapanui.

HLA gene locus	*A*	*C*	*B*	*DRB1*	*DQA1*	*DQB1*
HLA haplotype *a:*	***A*02:12;***	***C*07:02:01;***	***B*39:05;***	***DRB1*08:02:01;***	***DQA1*04:01;***	***DQB1*04:02***
HLA haplotype *b:*	***A*02:12;***	***C*07:02:01;***	***B*39:05****;*	*DRB1*04:03:01;*	*DQA1*03;*	*DQB1*03:02*

HLA alleles which are almost specific for Native Americans are marked in bold letters, while typical Polynesian HLA alleles are marked in normal letters. See Sanchez-Mazas et al. (2011) for a description of the nomenclature used for HLA alleles.

These alleles have previously been found almost only among Native Americans and people of Native American ancestry, and are very rare or absent in Polynesian and other non-Native American populations (Solberg et al., 2008; see Figure 2 in Thorsby, 2012).

Thus the *A*02:12* and *B*39:05* alleles may have been generated in America after the migration of an East Asian population via the Bering Strait ∼12–15.000 years BP (Sanchez-Mazas et al., 2011). The other HLA alleles on haplotype *a* also have their highest frequency in Native Americans, but are also found in some other populations. HLA haplotype *a* is therefore most probably a haplotype of Native American origin. HLA haplotype *b* is identical to haplotype *a* in its A-C-B segment, while the HLA alleles in its DR-DQ segment are much more frequent in Polynesians. Thus, haplotype *b* is most probably the result of a recombination between the A-C-B segment of a Native American HLA haplotype and the DR-DQ segment of a Polynesian HLA haplotype.

The most important question is when these Native American HLA alleles were introduced on Rapa Nui. Since we had the genealogy of the investigated individuals (see Figure 1 in Thorsby, 2012) we could demonstrate that haplotype *a* in all probability was introduced in the investigated family by the second wife of *Pacomio Maori*, who was born on Rapa Nui ∼1846. This is many years before the Peruvian slave trades in the 1860s which resulted in some population mixture in the area. We could not determine how much earlier than in ∼1846 this Native American haplotype was first introduced on the island. Haplotype *b* is most probably the result of a recombination between a Native American and a Polynesian haplotype, and recombinations between the closely linked loci in the HLA complex are rare events (∼1% of meioses). Thus, the presence of this haplotype suggests that the Native American HLA alleles have been present on Rapa Nui for many generations prior to the early 1900s. Together with other data from our genomic HLA investigations (reported in detail in Thorsby, 2012), the combined results of our HLA investigations suggest that some Native Americans reached Rapa Nui before the island was discovered by Europeans in 1722; i.e., in pre-historic time.

ADDITIONAL NATIVE AMERICAN HLA GENES FOUND IN RECENTLY COLLECTED RAPANUI DNA

In 2008 we collected blood samples from 21 additional Rapanui, who at least had some Rapanui ancestors dating back for several generations. Genomic HLA typing revealed that two individuals had an HLA haplotype carrying some other HLA alleles mainly found in Native Americans. One of these haplotypes carried *B*39:09* and *DRB1*08:02,* the other *B*15:07* (Thorsby et al., 2009; Thorsby, 2012). These two haplotypes carrying typical Native American HLA alleles may also be the result of recombinations with other HLA haplotypes on the island, suggesting an early introduction of the Native American HLA alleles. However, from the known genealogy of the two individuals we cannot establish when these Native American HLA alleles may have been introduced.

The results of investigations of mtDNA and Y chromosome markers were similar to that found in the samples collected in 1971; all individuals carried mtDNA markers typical of Polynesians, and Y chromosome testing revealed only Polynesian or European haplogroups.

GENOME-WIDE INVESTIGATIONS OF THE RAPANUI DNA

In order to obtain further evidence of an early Native American contribution to the early settlement on Rapa Nui and better information on how early the Native Americans might have reached the island, we initiated a collaboration with the Centre for GeoGenetics at the National History Museum in Copenhagen. DNA from 27 of the Rapanui from whom we had collected blood samples in 1971 and 2008 was genotyped for >650.000 SNPs (single nucleotide polymorphic markers). SNPs vary in frequencies between populations, and by comparing the Rapanui SNP data set with similar data sets from other relevant populations we found a mostly Polynesian ancestry, but with an average Native American admixture of ∼8% and an average European admixture of ∼16% among the investigated Rapanui (Moreno-Mayar et al., 2014). These results confirm and extend the results from our genomic HLA typing and again demonstrate a predominant Polynesian genetic background of the investigated Rapanui, but with a significant contribution of Native American and European ancestry.

In some other non-Rapanui Polynesians we found a Native American admixture of only 0.08%, which is significantly lower than among the Rapanui. This finding, which may indicate a higher level of Native American admixture among Rapanui than non-Rapanui Polynesians needs confirmation in other studies before it is possible to speculate on the causes.

The most important question is when the Native American admixture may have taken place on Rapa Nui. As time passes by after a population admixture event, the lengths of genetic ancestry segments become smaller because of recombinations in successive generations. By measuring the lengths of SNP ancestry segments of Polynesian, Native American and European origin we found a much higher number of short Native American compared to European ancestry segments, strongly suggesting that Native Americans arrived in pre-historic time. Further, by various methods (see Moreno-Mayar et al., 2014) we could estimate that the Native American admixture took place 19–23 generations ago; i.e., AD 1280–1495, or ∼1340. In contrast, the European admixture was estimated to have taken place 2–3 generations ago; i.e., 1850–1895, or ∼1870. Thus, some Native Americans probably arrived Rapa Nui not long after the first Polynesians arrived in 1200–1253.

COMMENTS AND CONCLUSIONS

This review summarizes our molecular genetic studies so far carried out using blood-derived DNA collected on Rapa Nui. The results further support an initial Polynesian colonization of the island from the west. However, for the first time human genetic evidence of an early contribution of Native Americans was also found, both by genomic HLA typing and genome-wide investigations of SNPs. By analysis of SNP ancestry tracts the Native American admixture was estimated to have taken place AD 1280–1495, or ∼1340.

The results of our genomic HLA and SNP investigations are in contrast to previous and our own investigations of mtDNA and Y chromosome markers of Rapanui. One explanation for these contrasting findings is that Native American HLA alleles may have been subject to different selective forces than Native American mtDNA and Y chromosome markers. HLA molecules are of instrumental importance for immune responses and some Native American HLA alleles may therefore have been selected which encode HLA molecules of importance for immune responses against given pathogens on Rapa Nui. Another not mutually exclusive explanation is genetic drift. At the end of the 1800s only ∼100 Rapanui were left on the island. This may cause a genetic bottleneck and thus a more random genetic transmission of genes from one generation to the next, leading to random genetic changes including loss of genetic variants in the population. Uniparental genetic markers like mtDNA and Y chromosome markers are more sensitive to genetic drift than genes which are inherited from both parents (see also Thorsby, 2012).

Our results need confirmation in studies of ancient DNA from the island. We tried to extract ancient DNA from Rapanui skeletal remains available at the Kon-Tiki museum in Oslo, but the DNA turned out to be of insufficient quality. Many skeletal remains exist on the island, but it has so far been difficult to obtain the necessary permissions from the local community to obtain access to small pieces of bone for studies of ancient DNA.

A tentative summary of available data for the early colonization of Polynesia, including the results of our own investigations, is schematically illustrated in **Figure 1**. The initial colonization from Southeast Asia via Melanesia to Samoa and Tonga and the Society Islands is indicated with a dotted red line, while the later continuation to Rapa Nui ∼AD 1200 is marked with a red line and 1 in the figure. Our finding of a contribution by Native Americans to Rapa Nui ∼AD 1340 is also indicated. How the Native Americans may have reached Rapa Nui is unknown. There are at least two, not mutually exclusive possibilities (see also Thorsby, 2012). One, marked by a dotted blue line and 2a in the figure, is that some Native Americans sailed directly to Rapa Nui on their own *Kon-Tiki* like rafts from South America. This was recently proven possible by the *Kon-Tiki 2* expedition from Callao to Rapa Nui. The other possibility is that some Polynesians sailed further east from central East Polynesia or Rapa Nui, reaching South America, but returned to Rapa Nui taking some Native Americans (and possibly the sweet potato etc.) with them. This possibility is marked by a dotted green line and 2b in the figure. Because of several signs of early visits of Polynesians to South America (mentioned above), the latter possibility may be the most likely. Storey et al. (2007) reported traces of visits by Polynesians to the coast of Chile ∼AD 1321–1407. If this timing is proven correct it fits well with our estimates for the first arrival of Native Americans to Rapa Nui 1280–1495, who may have accompanied some returning Polynesians.

It has been argued that return trips between East Polynesia and South America in ancient boats would be difficult, not only because of the long distance, but also due to difficult wind conditions. Following reconstruction of sea level pressure and wind fields for the South Pacific in the period AD 800–1600, Goodwin et al. (2014) were, however, able to describe several likely climate windows for off-wind sailing from Rapa Nui to South America, including 1260–1290 and 1400–1440, and for off-wind sailing in the opposite direction 1220–1260 and 1440–1460. Thus, in these periods the wind conditions may have been particularly favorable for return trips from East Polynesia or Rapa Nui to South America, which coincide well with our estimates for when some Native Americans first arrived at Rapa Nui.

Since our studies strongly suggest that some Native Americans arrived on Rapa Nui not long after the first settlement by Polynesians from the west, Native Americans may have contributed to the early human colonization on the island. This may have included an influence on the ecology of the island (see Rull et al., 2016), as well as its cultural development such the art of *moai* and *ahu* building.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and approved it for publication.

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Models of Easter Island Human-Resource Dynamics: Advances and Gaps

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Finding solutions to the entangled problems of human population growth, resource exploitation, ecosystem degradation, and biodiversity loss is considered humanity's grand challenge. Small and isolated societies of the past, such as the Rapanui of Easter Island, constitute ideal laboratories for understanding the consequences of human-driven environmental degradation and associated crises. By integrating different processes into a coherent and quantitative framework, mathematical models can be effective tools for investigating the ecological and socioeconomic history of these ancient civilizations. Most models of Easter Island are grounded around the Malthusian theory of population growth and designed as Lotka-Volterra predator-prey systems. Within ranges of plausible parameter values, these dynamic systems models predict a population overshoot and collapse sequence, in line with the ecocidal view about the Rapanui. With new archaeological evidence coming to light, casting doubts on the classical narrative of a human-induced collapse, models have begun to incorporate the new pieces of evidence and started to describe a more complex historical ecology, in line with the view of a resilient society that suffered genocide after the contact with Europeans. Uncertainties affecting the archaeological evidence contribute to the formulation of contradictory narratives. Surprisingly, no agent-based models have been applied to Easter Island. I argue that these tools offer appealing possibilities for overcoming the limits of dynamic systems models and the uncertainties in the available archaeological data.

Keywords: Rapanui, modeling, exploitation, renewable resource, collapse, sustainability

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INTRODUCTION

Only a few years ago, humanity reached a new demographic milestone, the birth of the Earth's seventh-billion resident. Demographers have not been alone in expressing concern that with the population expected to reach 9 billion by the middle of this century, Earth's ability to feed and provide other necessities for human life will soon be surpassed. The collapse of historical societies has attracted the attention of both ecologists and economists in relation to current issues of population growth, environmental degradation, and sustainability. A large body of literature, popularized by Jared Diamond in his bestselling book *Collapse* (Diamond, 2005), argues that ancient civilizations such as the Maya of Mesoamerica, the Anasazi of the southwest United States, the Norse of Greenland, and the Rapanui of Easter Island, collapsed because they degraded the environment or overexploited the ecological resources sustaining them.

This field of research has generated an emerging modeling literature focusing on human-resource interactions. Most of the modeling studies are grounded around the Malthusian theory of population growth (Malthus, 1798) and designed as Lotka-Volterra predator-prey systems, in which the human population is the predator and the resource is the prey. The Malthusian theory postulates that over time population growth tends to outrun food supply locking humans into a trap characterized by environmental degradation and overexploitation and leading to a collapse of the human-resource system. Among all potential cases of historical collapse, Easter Island is probably the most attractive because it constitutes a sort of natural laboratory of the past, due to its small size and isolation (**Figure 1**).

Modeling studies on Easter Island, which started to emerge approximately two decades ago with the pioneering work of Brander and Taylor (1998), are not very numerous and could be covered, at least briefly, by a short review such as the present one. Therefore, my aims are to survey the existing literature on models of Easter Island (comprising some 30 articles), critically review the advances made over the last two decades, point out the existing gaps, and provide an outlook on where we could direct our attention in the future. The rest of this article covers these aspects as follows. The next two sections briefly describe modeling studies focused, respectively, on socioeconomic aspects and on ecological aspects. Although, as we shall see, the line separating these two kind of studies may be a thin one. After these descriptions, I will highlight gaps in our approaches and current knowledge and will suggest possible areas for future research efforts. I will conclude in the final section by summarizing the main points.

STUDIES FOCUSED ON SOCIOECONOMIC ASPECTS

Some years ago, Reuveny (2012) conducted a very insightful analysis of the literature on the collapse of historical civilizations from a resource economics modeling perspective. Considering Easter Island the best example for studying collapse, due to its isolation and its potential for responding with innovations, institutions, and conflict, Reuveny (2012) centred his attention on models applied to the Rapanui society. To avoid unnecessary repetitions here I will present these studies only very briefly and qualitatively (i.e., without describing equations), and I will refer the reader to Reuveny's (2012) review for further details. I will complement the list of articles discussed by Reuveny (2012) with the latest publications in the field.

Reuveny (2012) subdivided the literature into two major types of studies: (1) those assuming a myopic resource extraction (i.e., agents do not maximize utility across multiple time periods but instead focus on the given period) and (2) those based on farsighted decision making. The earliest and most representative modeling study based on a myopic resource extraction assumption (one that satisfies many proponents of the ecocidal view of the ancient Rapanui people, e.g., Flenley and Bahn, 2003; Diamond, 2005) is that of Brander and Taylor (1998). Brander and Taylor (1998) considered a resource stock, represented by a forest-soil complex, increasing logistically and decreasing linearly due to harvest. The economy produced and consumed two goods, the resource harvested and some manufactured good. Labor was the only other factor of production, which was assumed equal to population size. Harvest was simulated with a Schaefer function depending on resource and population levels and manufacturing on population levels only. This model could reproduce a boom and bust cycle in human population, peaking at about 10,000 individuals around 1250 AD and falling to 3,800 by the year 1850, in line with the understanding of the island's history at that time. Given the model assumptions, they concluded that the ancient Rapanui collapsed because they were myopic, lacked understanding of the forest-soil complex, and experienced increase growth with resource consumption. They also argued that resource depletion might have gone unnoticed because the forest disappeared relatively slowly compared to the typical 30-year life span in prehistoric Polynesia, although later studies suggested that about 40 % of the Rapanui lived between 40 and 55 years (Shaw, 2000; Hunt and Lipo, 2001).

The model of Brander and Taylor (1998) has been refined in a number of ways. Anderies (2000) added a minimum resource consumption per capita to capture the end of monument carving at around 1500 AD. Erickson and Gowdy (2000) included a capital stock, accumulating by a full conversion of the extracted resource into manufacturing of tools and boats and depreciating at a constant rate. Also Roman et al. (2017) included a capital stock produced from extracting natural resources but in addition explored the effects of movements of people and goods between two hypothetical societies sharing the characteristics of Easter Island. Matsumoto (2002) considered a discretized version of the time-continuous Brander and Taylor's (1998) model to investigate the sensitivity of the model dynamics to changes in time-dependent parameters. D'Alessandro (2007) considered two resources, forest and land area, and included a threshold in resource level below which exhaustion became inevitable. Taylor (2009) also included a threshold in resource stock. Other models have considered the possibility for social adaptation either through negative changes, for example via conflict (Reuveny and Maxwell, 2001; Maxwell and Reuveny, 2005; Reuveny et al., 2011) or rivalry (de la Croix and Dottori, 2008), or through positive changes, for example by technical progress (Reuveny and Decker, 2000; Decker and Reuveny, 2005; Dalton et al., 2005), by forming resource management institutions (Dalton and Coats, 2000; Erickson and Gowdy, 2000; Pezzey and Anderies, 2003; Taylor, 2009; Chu et al., 2014), or by introducing economic stratification in the form of elites, commoners, and wealth accumulation (Motesharrei et al., 2014). All these modeling studies showed that a collapse was inevitable unless the population growth was sufficiently slow or resource renewal rate was sufficiently fast.

Models based on foresight, (i.e., models simulating a population who cares about its future, a premise consistent with the genocidal view on the fate of the Rapanui, e.g., Peiser, 2005; Hunt, 2007; Hunt and Lipo, 2011), are only a few. Among them, the work of Good and Reuveny (2006) is probably the most prominent and the first applied to Easter Island. They showed that even if the islanders had complete assignment of

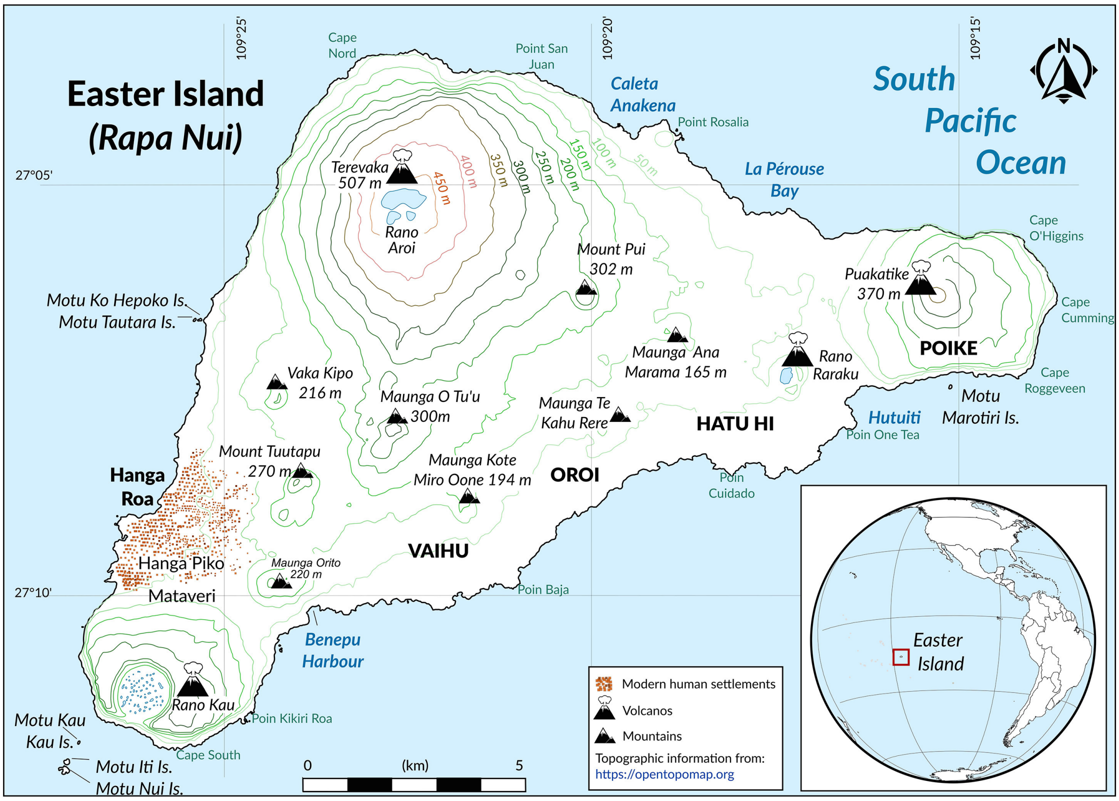

FIGURE 1 | Geography of Easter Island and its location (inset) in the South Pacific. The small size, about 165 km^2, and isolation make the island a natural laboratory for studying past human-resource interactions. Map courtesy of Jailson Fulgencio de Moura.

property rights and implemented optimal resource management with infinite horizon, or equivalently had a social planner that implemented such an optimal plan, a similar boom and bust cycle obtained by Brander and Taylor's (1998) model would have occurred. This work was expanded a few years later by the same authors (Good and Reuveny, 2009) with the inclusion of social welfare functions to confirm that these best-case institutions would have done little to prevent the social collapse of the Rapanui.

STUDIES FOCUSED ON ECOLOGICAL ASPECTS

As for studies focused on ecological aspects, I will consider those based on models that do not entirely follow the orthodox resource economics approach, which typically structures models to capture a small, closed economy represented by a renewable resource and human labor producing different types of goods (e.g., harvested and manufactured goods). I will therefore focus on models in which a population of assumed identical agents harvests from a resource assumed to follow a logistic growth function, without much considerations of economical nature. This distinction may appear minimal, but it can lead to substantial differences in the way these two classes of models can be further developed and applied. A model with such an ecologically-centred flavor is that of Basener and Ross (2005). Much in line with the results of models embedded into resource economics principles, Basener and Ross (2005) found that when the harvest rate was faster relative to the rate at which the resource renewed itself, a boom and bust cycle occurred. Alternatively, population and resource coexisted, when the harvest rate was slower than the resource regeneration rate. In a subsequent study, Basener et al. (2008) further developed their model to include a rat population that ate palm seeds, in accordance with the hypothesis advanced by Hunt (2007) asserting that the rats could have been the primary cause of the forest decline. Their modeling work confirmed Hunt's (2007) hypothesis. Bologna and Flores (2008) developed a model very similar to the one of Basener and Ross (2005) with the difference that the original harvest rate is now called deforestation rate and is defined by the ratio between the capability of exploiting the resource and the capability of the resource to regenerate itself. They thus reproduced the conditions that lead to a collapse. Wolcott and Conrad (2011), developed two models: a two-state variable model of human population and resource, and a three-state variable model of human population, resource, and agriculture. They showed that the three-state model reduced to the two-state model and produced dynamics that were consistent with the history of Easter Island. Basener et al.

(2011) created a spatially-explicit version of their previous model (Basener et al., 2008) by including a reaction-diffusion scheme to capture movements of people and rats within the island. They showed that by increasing the mobility of the rats the model shifted from a stable equilibrium, characterized by the coexistence of people, rats and forest, to an unstable equilibrium, driving the populations to a collapse. Takács et al. (2016) took Basener et al. (2011)'s spatial model, introduced a diffusion parameter for tree, and showed that this had a stabilizing effect on the model system. Finally, Brandt and Merico (2015) developed a modified version of (Basener et al., 2008)'s model and included an epidemic component comprising susceptible, infected, and recovered individuals to capture the effects of the diseases introduced by Europeans. Rather than trying to predict the classical collapse, Brandt and Merico (2015) used the model to test the plausibility of the two main competing hypothesis, collapse (ecocide) and long-term resilience with a fall at the time of the European contacts due to diseases (genocide). In addition, Brandt and Merico (2015) suggested and tested a third scenario, a long and slow demise. While none of the three scenarios could be completely ruled out, the slow demise appeared to be the most plausible when compared to the temporal pattern of deforestation inferred from the latest compilations of radiocarbon dates on charcoal remains (Hunt and Lipo, 2006; Mulrooney, 2013). The model could reproduce the three scenarios fairly easily. This was surprising especially because only a few parameters (seven, excluding those relevant to the epidemic module, which was activated after 1722 AD) needed to be adjusted within reasonably small ranges to reproduce the different scenarios. In a way, this model result mirrors the controversy between scholars and demonstrates how uncertainties in the assumptions (i.e., the parameter values from a modeling perspective) can lead to very conflicting views. With new archaeological evidence coming to light, casting doubts on the classical narrative of a human-induced collapse, some of these models have begun to incorporate the new pieces of evidence and started to describe a more complex historical ecology.

ADVANCES AND GAPS

Notion of Collapse

None of the studies presented provided an operational definition of collapse. The problem seems to be widespread over the broad literature on human-resource interactions (Tainter, 2006). Authors assume probably that the meaning is obvious, without concerns for individual, cultural, or temporal variation (Tainter, 2006). By considering economic reasons an important determinant of the fall of historical societies, Tainter (1988) defined collapse as a phenomenon according to which a society "displays a rapid, significant loss of an established level of socio-political complexity." Diamond (2005), instead, gave priority to the population: "By collapse, I mean a drastic decrease in human population size and/or political/economic/social complexity, over a considerable area, for an extended time." A definition of collapse should be the starting point in a modeling exercise that aims at reproducing such process, if only to avoid equivocal interpretations concerning the nature and characteristics of the event in question.

Observations and Model Assumptions

Most of the models presented have been developed around the premise that Easter Island was first colonized sometime between 400 and 800 AD and that a collapse occurred sometime between 1,200 and 1,500 AD. However, the time of first colonization remains contentious, with more recent studies suggesting 1,200 AD (Hunt and Lipo, 2006; Wilmshurst et al., 2011), and a fierce debate has erupted on the dynamics and consequences of deforestation (Diamond, 2007; Flenley and Bahn, 2007; Hunt and Lipo, 2007, 2009).

Currently, population estimates are based either on indirect evidence (e.g., fossil pollen analysis producing deforestation patterns) or conceptual reconstructions (based on historical demographic arguments) with very contrasting results. But models depend critically on this information. Two contrasting narratives have been developed. That of Flenley and Bahn (2003) and Diamond (2005), contemplating a human population overshoot reaching between 10,000 and 15,000 individuals and followed by a collapse; and that of Hunt (2007), contemplating an initial increase, up to 4,000 individuals, followed by a plateau. Flenley and Bahn (2003) use forest fossil pollen data to reconstruct hypothetical changes in population size assuming a relationship between human population change and forest vegetation/ecosystem change. Later, Cole and Flenley (2008) admitted that this assumed relationship between human population change and forest vegetation was probably overly simplistic because "we still know very little about the way forest vegetation and ecosystems contribute to human population change." Hunt (2007 see Figure 14) use a 3 % human population growth based on qualitative assessments of the population dynamics of hunters and gatherers of the Pleistocene (Birdsell, 1957), but it is not clear what kind of evidence on Easter Island would suggest a plateau at 4,000 individuals.

I am not contesting here the notion of a profound and dramatic ecological transformation of the Island with deforestation and associated extinctions, the evidence in this respect is clear and undisputed. I am rather raising a note of caution about the idea of a collapse on Easter Island as a population *overshoot* followed by an *abrupt* societal and ecological failure because of the unavoidable uncertainties affecting the archaeological method. All these archaeological and modeling studies have contributed tremendously to our understanding of human-resource interactions in general and of Easter Island history in particular. But the ongoing, fervid scientific debate, by highlighting strengths and weaknesses in each narrative, suggests that the available evidence is at least contradictory. Although being critically important for modeling, estimates about the timing of first colonization and about the population dynamics remain among the most controversial aspects. If the hypotheses of a late colonization (Hunt and Lipo, 2006) and of a steady population at around 4,000 individuals (Hunt, 2007) are proved correct, all the modeling applications based on the abrupt collapse narrative will turn out to be spectacularly ill-posed.

Climate Change

Despite the occurrence of droughts and other adverse climatic events have been proposed in the past by various authors (McCall, 1993; Hunter-Anderson, 1998; Nunn, 2000), anthropogenic activities have been traditionally considered the major drivers of ecological change on Easter Island. This tendency has been supported by a study of climate variability focused in the period 800 – 1,750 AD (Junk and Claussen, 2011). An analysis of global climate model results, consisting of 30-year running means of near-surface air temperature, precipitation, and Niño3.4 index (an index used to classify El Niño Southern Oscillation conditions), lead Junk and Claussen (2011) to conclude that the region of Easter Island has not been affected by significant climatic changes during pre-industrial times. A recent study (Rull, 2016), however, brought again the attention on climate. On the base of newest paleoecological data obtained from analysis of peats and lake sediments, Rull (2016) proposed that a major change on Easter Island occurred due to a combination of climatic, ecological, and anthropogenic drivers. The climatic events involved the Rano Raraku catchment (located in the eastern part of the Island, **Figure 1**), which supported intense cultural activities in a forested landscape and a freshwater lake until 1,450 AD. A period of intense drought during the Little Ice Age, Rull (2016) suggested, transformed the basin into a wasteland depleted of freshwater, leading to social and ecological crises and to the cessation of the carving activities. The role of climate and its effects (e.g., reduction of rainfall, drying out of basin catchments, vegetations shifts, etc.) on human-resource interactions appears to be underexplored and could be a valuable avenue of research in future modeling studies of Easter Island.

Myopic versus Farsighted Society

The assumptions of a myopic society and of environmental changes too slow to be noticed are also problematic, especially in the light of a society engaged in sophisticated projects such as carving and moving large statues. To facilitate water permeability, limit evaporation, and create moist conditions, the Rapanui covered lands with scattered lithic mulch. They most likely collected and stored rainwater, built stone dams across streams to divert water to their fields, and expanded land for agriculture (Van Tilburg, 1994; Wozniak, 2001; Stevenson et al., 2006). Unfortunately, only a few modeling studies have been undertaken so far around the notion of foresight. These dynamic systems models showed that the Rapanui could have collapsed even if they were farsighted. However, the level of abstraction typical of these models does not allow to capture the complexity and heterogeneity of people's preferences and production technologies, even in a small world such as Easter Island. In this respect, alternative modeling techniques such as Agent-Based Modeling (ABM) offer intriguing possibilities for overcoming the mentioned limitations.

Alternative Modeling Techniques

Surprisingly, no ABM techniques have been considered so far to analyse the social-ecological history of Easter Island, although this approach has a relatively rich history of applications in human-resource interactions (Bousquet and Le Page, 2004) and was applied to study the growth and collapse of the Anasazi civilization (Axtell et al., 2002). ABMs not only allow hypotheses to be tested, but they can also allow counterfactual scenarios about human-environment interactions to be explored (Perry et al., 2016), which may significantly advance our understanding of the processes that took place on Easter Island. By emulating the behaviors of many heterogeneous agents interacting over and with an historical environment coded on a digitized map, ABM can potentially provide more realistic conditions and hopefully better insights into the complexity of the social-ecological microcosm of the Island. For example, by linking biological responses to heterogeneity and variability in the physical environment, ABMs could help testing the role that climatic events, such as the drying out of the Rano Raraku catchment (Rull, 2016), might have played on the Island. ABM could also be a more effective alternative to the diffusion models of Basener et al. (2011) and Takács et al. (2016), who tried to account for the movements of people, rats, and trees using a reaction-diffusion scheme. For example, ABM can account for a spatially-explicit background of location and intensity of agricultural practice and could thus provide better predictions on the size of a population that agriculture could have sustained. Recent studies such as those of Stevenson et al. (2015) and Louwagie et al. (2006), respectively, on regional land use and on the evaluation of land suitability for agricultural production, provide valuable data for constraining such a modeling application. Some ideas about potential ABM applications have been presented by Edmonds (2015), who proposed that to fully reflect the dynamics and complexity of real ecologies one needs to have a multi-agent model concerning human decision-making and social interaction combined with an individual-based model of an ecology.

CONCLUSIONS

Scholars are divided into two opposing factions. A larger group supporting the notion of a collapse based on the early, classical archaeological and anthropological studies and a smaller group supporting the notion of a steady population size with the involvement of rats in the deforestation process based on most recent archaeological evidence. Modeling studies have been following these two different school of thoughts in a chronological manner. Early modeling applications were embedded into the notion of collapse. As recent studies proposing a later colonization and a resilient response of the Rapanui society to declining resources emerged, models have started to include elements of this new narrative, contributing to the description of a more complex ecological history for the island. Agent-Based Models offer appealing possibilities for overcoming the limits of both dynamic systems models and available archaeological data, for example, through the systematic analyses of alternative scenarios. Experiments with different agents' characteristics, their interactions, and features of the landscape would produce a variety of behavioral responses to social relationships and environmental forcing. Such investigations could provide valuable insights into arguably some the most intriguing and debated events of recent human history.

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The author confirms being the sole contributor of this work and approved it for publication.

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Rain, Sun, Soil, and Sweat: A Consideration of Population Limits on Rapa Nui (Easter Island) before European Contact

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The incongruity between the small and apparently impoverished Rapa Nui population that early European travelers encountered and the magnificence of its numerous and massive stone statues has fed a deep fascination with the island. Ethnographic and archaeological evidence suggest that the indigenous population was previously greater than the estimated 1,500–3,000 individuals observed by visitors in the eighteenth century. Our goal was to determine the maximum population that might have lived on the island by estimating its agricultural productivity in the time before European contact. To determine the agricultural potential of the island we sampled soils and established six weather stations in diverse contexts and recorded data over a 2-year period. We find that the island is wetter on average than previously believed. We also find that rainfall and temperature respond linearly to elevation, but a spatial model of precipitation requires correction for a rain shadow effect. We adapted to Rapa Nui an island-wide spatial model designed to identify agriculturally viable zones elsewhere in Polynesia. Based on functions relating climate and substrate age to measurements of soil base saturation, we identified 3,134 ha that were suitable for traditional dryland sweet potato cultivation, or about 19% of the 164 km^2 island. We used a nutrient-cycling model to estimate yields. Modeled yields are highly sensitive to nitrogen (N) inputs and reliable estimates of these rates are unavailable, requiring us to bracket the rate of N inputs. In the case of low N availability, yields under continuous cultivation were very small, averaging 1.5 t/ha of wet sweet potato tuber. When the N fixation rate was quadrupled sustainable yields increased to 5.1 t/ha. In each N scenario we used a model of food-limited demography to examine the consequences of altering agricultural practices, the labor supply, the ability of the population to control its fertility, and the presence or absence of surplus production to support social inequalities. In the low-N case viable populations average approximately 3,500 individuals across all parameter combinations, vs. 17,500 in the high-N case, although sustainable populations in excess of 25,000 were possible under some assumptions.

Keywords: agricultural potential, nutrient cycling, population dynamics models, Polynesians, density dependence, climate modeling, sweet potato, food-limited demography

INTRODUCTION

The incongruity between the small and isolated Rapa Nui (Easter Island, Chile) population that Europeans first encountered and the magnificence of the massive stone figures that dot the island has led to deep fascination with what transpired there. According to most early accounts, the wind-scoured island was barren of trees and it seemed impossible to many of the early European explorers that the small population that lived on the island was capable of crafting and moving these monuments. It is widely believed that the island and its people went through a process of dramatic change between the time of first colonization by approximately 1,200 A.D. (Hunt and Lipo, 2006, 2008; although the timing of colonization remains in dispute, see Cañellas-Boltà et al., 2013; Mulrooney, 2013; Rull et al., 2013) and the arrival of the earliest European explorers in the eighteenth century. The island initially was densely wooded and archaeological evidence suggests that at its pre-contact peak the island's population was much larger (7,000–9,000, Van Tilburg, 1994, summarizing others) than it was when Europeans first arrived (1,500–3,000, Boersema, 2015, from original records). Diamond (1995) proposed that a maximum population of 20,000 seems reasonable for the ecological context, and later writes that 15,000 seems "unsurprising" (Diamond, 2005). Fischer (2005) estimates a peak of 12,000, while Fagan (2008) estimates 15,000. Using a baseline of 150 persons per km^2 Rallu (2007, p. 22) estimates 25,650. However, echoing the concerns of other researchers, Anderson (2002) wrote of Rapa Nui: "All estimates of the peak size of the prehistoric population are entirely speculative."

In contrast to Admiral Jacob Roggeveen's (1903) description of the island as "exceedingly fruitful" when he made the first recorded European contact in 1722, Capt. James Cook in 1774 concluded after a brief survey by members of his crew that the island was impoverished and land that had formerly been cultivated appeared abandoned (Cook, 1777). There remains ethnographic and archaeological evidence of social inequalities in the pre-contact period (Stevenson and Haoa, 2008), in addition to the apparent specialization of labor required to produce and organize the transport of the stone statues. These practices were lost or much diminished by the time outsiders began to make more careful observations (e.g., Routledge, 1919).

It is possible that internal conflict (Heyerdahl and Ferdon, 1961; Bahn, 1993; Flenley and Bahn, 2003, p. 153) reduced the population from its maximum before European contact, and some have argued that human-mediated environmental degradation led to the loss of agricultural productivity (e.g., Mieth and Bork, 2003; Diamond, 2005; Hunt, 2007), further reducing the island's ability to support human life. The picture of what life was like before Europeans arrived is further clouded by the changes that occurred soon after this contact and before any accurate census was made. The island's population was ravaged by both introduced diseases and by slaving raids from South America.

Several attempts have been made to estimate what Rapa Nui's population might have been at its peak before the Nineteenth century, independently from the observations of early visitors. Most of these evaluations fall into two categories: those that rely on (1) population densities taken from other Polynesian islands, or (2) estimates from surveys of residential features. With regard to the former (e.g., Métraux, 1957; Rallu, 2007), Rapa Nui is unusual in that it receives less sunlight and is cooler than most of the otherwise comparable Polynesian islands, as it lies south of the Tropic of Capricorn. Additionally, most inhabited Polynesian islands were incorporated into trade networks with other islands, even those at considerable distance from their nearest neighbors. Rapa Nui, however, was likely unable to sustain trade networks as a result of its relative isolation. These factors suggest that estimates based on other islands are likely to overestimate Rapa Nui's population.

Archaeological evidence in the form of residential features has been used around the globe to estimate population size, and Rapa Nui is no exception (e.g., McCoy, 1976, 1979; Stevenson, 1984; Stevenson and Cristino, 1986; Stevenson and Haoa, 2008). However, this method is subject to several potential errors. First, it can be difficult or impossible to determine the average number of inhabitants a residential feature might have housed. Second, contemporaneity can be difficult to establish. It is also sometimes difficult to identify and characterize more ephemeral structures.

Here we take a third approach, estimating potential population size from potential agricultural yields. The use of agricultural potential to estimate population has a long history in anthropology, but the results of this method are highly sensitive to the assumptions that go into them, and the heterogeneity of the landscape is often given short shrift. The end product of such analyses is usually a single number, with little analysis of what that number might mean in context. Further, such calculations typically do not account for the potentially important roles of hunger, surplus requirements, competition for access to land, or labor availability as a consequence of the demographic characteristics of the population. In the most thorough consideration of agricultural potential on the island, Louwagie et al. (2006) made a careful analysis of several sites based on climate and soil characteristics, but did not consider key nutrients, alternatives to continuous cultivation or extend their findings to population estimates.

To generate estimates of Rapa Nui's agricultural potential, we assemble climate data from several sources to create a high-resolution map of the island in which each 100 m grid cell is described in terms of its seasonal pattern of temperature and rainfall. We exclude zones of the island that do not meet the minimum criteria for agriculture, using climate and soil fertility data. Over the remaining area we applied a nutrient cycling and productivity model to simulate potential yield of sweet potato (*Ipomoea batatas*), which represents the primary cultigen grown on Rapa Nui. We use these crop yields to derive estimates of maximum population under various assumptions about human behavior using a model of food-limited human demography, in which rates of birth and death at various ages depend on food availability. The estimates of peak population are derived from the resulting population trajectories.

CHARACTERIZING CLIMATE

Rainfall

Of the many characteristics that determine agricultural productivity, climate is among the most important. In non-irrigated systems like those of Rapa Nui, the most important component of climate is often rainfall. Rainfall is also the vector of nutrient inputs by atmospheric deposition, and ultimately their loss via leaching. On the high islands of the Pacific, rainfall can vary dramatically over short distances due to the strong relationship between altitude and precipitation. In the simplest cases this orographic process is linear and is quantified as a precipitation lapse rate. To estimate the lapse rate we used data from six weather stations placed at various points on the island and a long independent series from the Mataveri Airport in the southwest, near the town of Hanga Roa. The new climate data were collected by HOBO U30 weather stations, Version 2.0.0, manufactured by Onset Computer Corporation. The airport data came from two sources: a monthly record of the years 1950–2000 published by Genz and Hunt (2003), and online weather data to capture the period 1999–2011.

The six weather stations provide important information about how climate varies across the island, but these series were very short, less than two years, with some gaps. We used the airport data as a reference series and determined the relationship between it and each of the six newly placed weather stations based on daily rainfall for all days in which we had observations at both sites (see Supplemental Materials, Figure S1 for distributions). Rainfall at the six weather stations was well predicted by linear functions of rainfall at the airport, with r^2-values that average 0.77, including a 0.57 value from a very short series at one of the stations. We eliminated two data points from the comparison because it appeared the airport data were in error, as all the other stations recorded a downpour and the airport series showed little or no rainfall that day.

We used these relationships to generate a long rainfall series for each of the six new stations from the daily airport rainfall data. This helps to correct for some of the sampling bias expected in relatively short samples of temporally correlated and cyclical sources in the new station records. For example, if the data we collected came from an unusually wet period, we expect that would be reflected in the airport data over the same span. We assume that the linear relationship observed in the synchronous observations is constant and that unexplained variation was noise that could be disregarded. We also assume that the relationships would hold on the coarser monthly timescale, which is required by our models. The result is seven synchronized 62-year records of monthly rainfall at various points around the island.

Working from the predicted annual mean rainfall at each station (see Supplemental Materials, Table S1) we find a strong linear relationship with elevation ($r^2 = 0.87$). It is clear, however, that the airport series is an outlier. When we remove the airport from the analysis (see Supplemental Materials, Figure S2) the temporary weather stations describe a much stronger relationship between elevation and mean annual rainfall ($r^2 = 0.98$). An explanation for the difference between the airport and these six weather stations is presented below.

The function that comes from this analysis is *rain* (mm/year) $= 1240 + 1.749 \times$ *elevation* (m). We used this relationship to generate isohyets purely as a function of elevation (**Figure 1**). However, the resulting rain map contained evident anomalies. For example, the area to the west of Rana Aroi (the peak of Teravaka in the northern part of the island) is observably quite dry, containing soils with pedogenic carbonates, despite its elevation.

To address this discrepancy at Rana Aroi we examined data on wind direction from the stations and determined that the speed-weighted origin of the wind was from the east—as expected for the southern hemisphere Trade Winds. Using the relationship between distance from the ridgeline and the decrease in rainfall on the leeward side at the Kohala Peninsula on the Island of Hawai'i (Giambelluca et al., 2013) as a guide, we derived a function to approximate the rain shadow effect of being on the leeward side of a rise. This function requires a calculation of the "shade fraction" of each point or pixel on the map. We used a hillshade image created with the assumption that the artificial light source was 5° above the horizon and due east of the island (**Figure 2**). The red indicates pixels that are "shaded" under these conditions. We used this information to calculate the *shade fraction (f)* of each point on the map by calculating the Euclidean distance to the nearest unshaded point. We then divided by the value of the greatest distance observed on the island, creating a range of shadedness from 0 to 1. The areas of the island deepest in the rain shadow would have $f = 1$ and any unshaded points have $f = 0$, most points being somewhere in between. The shade fraction was used to define a unitless local rainfall multiplier that reduced rainfall in a manner similar to that observed at Kohala, Hawai'i: $M = [0.5 + (\exp(-4.6 \times f))/2]$. The multiplier $M = 1$ if the pixel is unshaded and $M = 0.505$ when $f = 1$. We then adjusted the expected annual rainfall using the function *rain* (mm/year) $= [1240 + 1.749 \times$ *elevation* (m)$] \times M$. The resulting map (**Figure 3**) aligns better with observations than the unmodified one, despite the under-constrained parameterization of the rain shadow function.

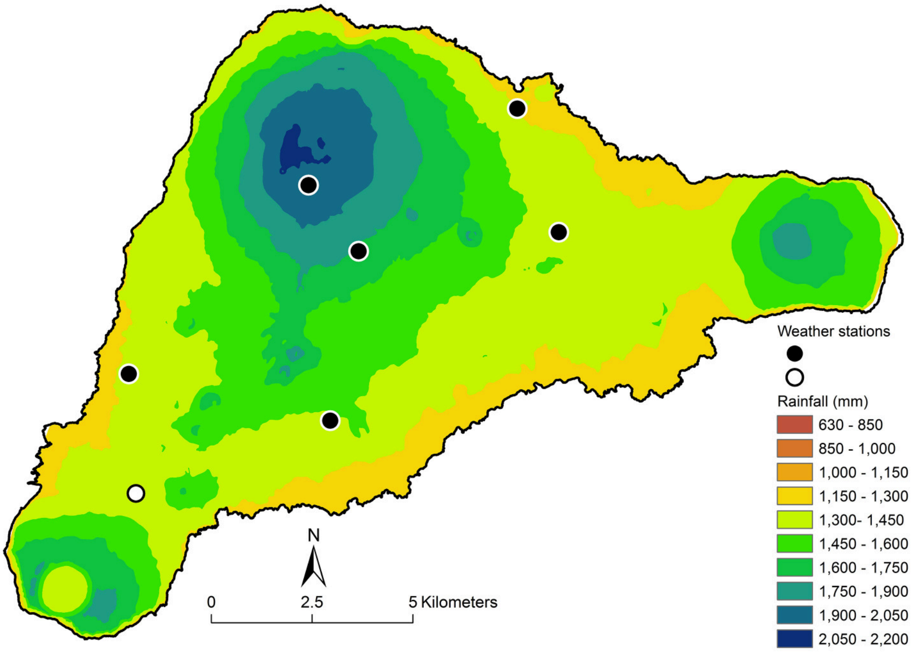

FIGURE 1 | The black dots represent the six new weather stations. The white dot shows the location of Mataveri Airport. The isohyets are derived from the linear relationship *Rain* (mm/year) = 1240.4 + 1.7487 × *elevation* (masl).

In particular, accounting for the rain shadow helps explain sparse vegetation cover to the leeward of both Rana Aroi and the Poike Peninsula to the east.

The modified rain map also suggests why the absolute value of annual rainfall at the airport is less than elevation alone predicts. The location, noted by a large white dot in the southwest region of the island (**Figure 3**), is actually in a moderate rain shadow zone and has an expected rainfall of 1,361 mm based on elevation (69 masl) alone, vs. the 1,097 mm actually observed. This correction and the assumption that rain is more likely to be under-reported by imprecise rain gauges than over-reported may explain the difference between the patterns at the airport and at the new stations. Because the airport has been the only freely available source of rainfall information on Rapa Nui, its status as an outlier has led to the perception that the island is drier than it is (e.g., Genz and Hunt, 2003; Louwagie et al., 2006; Junk and Claussen, 2011, using a function derived by Norero, 1998).

Temperature

Local temperature in Polynesian islands typically changes linearly with elevation, driven by the same orographic process that drives precipitation. Accordingly, we determine the temperature function using similar methods. We appended more recent internet-available airport data to the long series of monthly average temperature calculated from Genz and Hunt (2003). Monthly averages of the daily web data were calculated as the mean of daily averages, which were determined by taking the mean of the daily high and low temperatures. As with rainfall, we determined a function relating the new stations' daily series to the airport data 1999–2011. This function was used to generate a 12-year daily temperature series at each station. We then calculated mean monthly temperatures at each location and used the correlations between the reference airport series and the others to generate monthly mean temperatures over the period 1950–2011. As with precipitation, the assumption is that the relationships observed in the relatively short overlap between the short-term weather stations and the airport series remains constant. We then extrapolate using the airport as a reference series to expand our long-run means over a greater span to include a better sampling of temporal variation, as with the rainfall series (see Supplemental Materials, Table S2).

The monthly series at each location follow a typical sinusoidal pattern through the year, peaking in February and reaching a minimum in August. The annual means are highly linear with respect to elevation, with an r^2 of 0.99 using the relationship *annual mean temp* (°C) = 20.99 − 0.008452×*elevation* (m). We use this function to calculate monthly mean temperatures across the island.

Analysis of the long-term patterns of climate by Junk and Claussen (2011) support the use of modern data to describe the historical pattern. Although it remains a matter of some debate (e.g., Mann et al., 2008; Stenseth and Voje, 2009) there is no overwhelming evidence for a systematic shift in either rainfall or temperature over the time period we are interested in. In the same vein, while it is possible that the presence of the remnants of the ancient forest had the effect of cooling the island and increasing precipitation during the early phases of the island's occupation, the effect on rainfall in particular should be small on a trade-wind island of Rapa Nui's size.

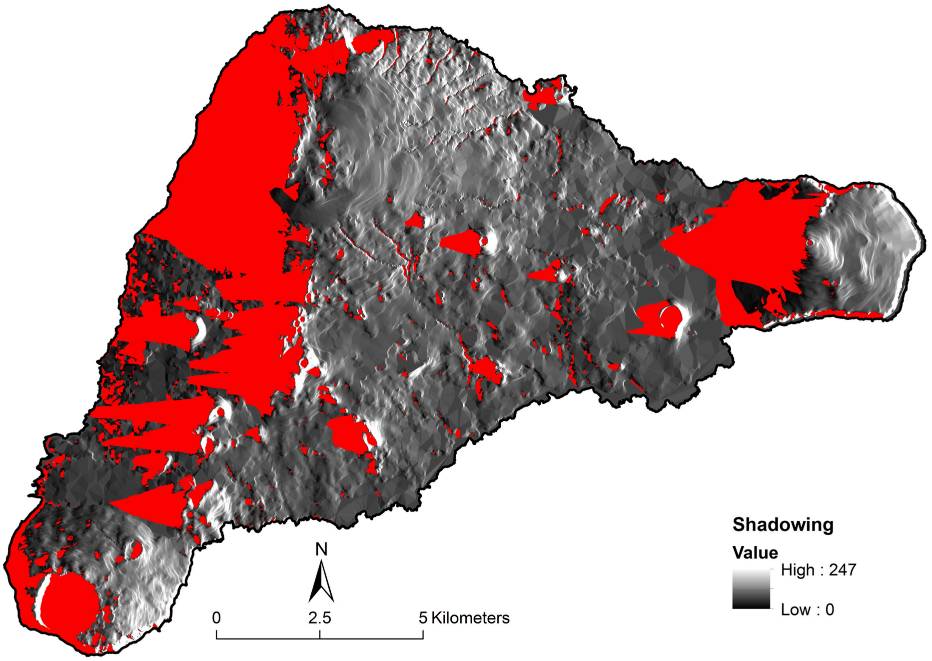

FIGURE 2 | The red areas indicate what parts of the island would be in shade if we imagine an artificial light source coming from due east at 5° above the horizon. We use this information to estimate the effect of the rain shadow caused by topography, given the dominant direction of the wind during rainfall. Areas in red received less rain than the others, according to a formula to estimate the shadow fraction (*f*).

Other Factors

Plant growth is constrained by solar energy. We found no significant relationship between solar radiation recorded at our six weather stations and elevation. The monthly means were well described by the sinusoidal function $R_s = (77.9\times\cos(\pi/6\times(month\text{-}12.25)) + 196.1)\times 0.0864$ in MJ/m^2/day, where *month* is the number of the month from 1 to 12 ($r^2 = 0.95$). Approximately 45% of this light is photosynthetically active radiation (*PAR*) (Jacovides et al., 2004). We followed Ruimy et al. (1999) to determine the potential productivity of sweet potato and fallow grasses as a function of light availability using their function for the fraction of photosynthetically active light that plants intercept, $FPAR = 0.95\times(1-\exp(-K\times LAI))$, where *LAI* is the leaf area index of the plant and *K* is a constant that modifies *LAI* based on the morphology of the plant. We used estimates of *K* for grass (0.35) and crops (0.85) from Monteith and Elston (1983) and maximum values of *LAI* from various sources, including Ramírez García et al. (2012) for grass (2.5 cm^2/cm^2) and crops (3.5 cm^2/cm^2). Finally, we determined potential production—or light-limited carbon assimilation rate per unit area—by multiplying the product $PAR\times FPAR$ by light use efficiency (*LUE*) for grass (0.860 gC/MJ) or crops (1.044 gC/MJ) (Zhao and Running, 2010).

Nitrogen is often the most limiting nutrient in crop productivity. What N is available in Polynesian agricultural systems that lack a symbiotic N fixer comes primarily from two sources: dissolved N in rainfall and from the fixation of nitrogen from the atmosphere by the microbial community as it decomposes sugarcane and other plants (Lincoln and Vitousek, 2016). The deposition rate of dissolved mineral N has been measured in some places and estimated for others across the globe, but the remote Pacific remains under studied in this regard. Based on measurements in remote areas of Hawaii (Heath and Huebert, 1999; Raich et al., 2000), we estimate that deposition of dissolved N could be 0.0014 gN/m^2/cm rain. For N fixation by microbes, we evaluate the lower half of the range of N fixation rates in decomposing sugar cane mulches in Polynesian cropping systems reported by Lincoln and Vitousek (2016), 4.8–20 kgN/ha/year.

ESTIMATING EXTENT OF VIABLE AGRICULTURAL SYSTEMS

We adapted the model presented by Ladefoged et al. (2009), which was used to identify agriculturally productive areas of the Hawaiian Archipelago, to the situation on Rapa Nui (**Figure 4**). The model eliminates areas that are too dry, too cool, too high or too poor in soil nutrients. The temperature and rainfall gradients on Rapa Nui were determined from our analysis of weather station data, described above. The non-nitrogen soil nutrient estimates were based on measurements of plant-available P and Ca (exchangeable cations) in soils sampled along transects of the island (Ladefoged et al., 2005, 2010) and concentrated samplings in and near archeological sites (Vitousek et al., 2014; Stevenson et al., 2015). The lower limit of base saturation, a proxy for the availability of cations, in the dryland agricultural zones of Hawaiʻi was approximately 30% (Ladefoged et al., 2009). On Rapa Nui

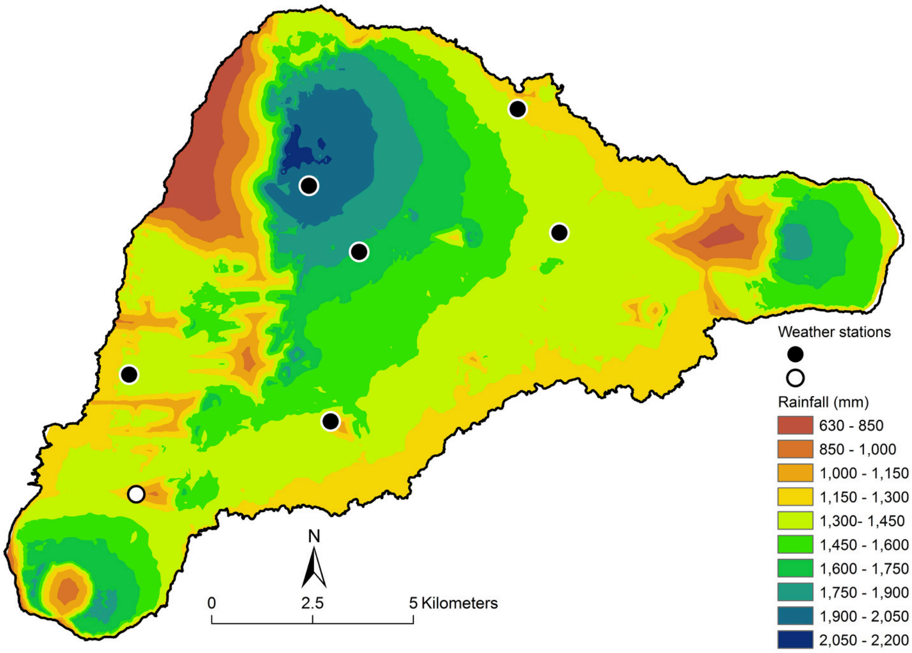

FIGURE 3 | Isohyets after accounting for the rain shadow effect. Note that the area in the NW of the island now appears as quite dry, as does the area immediately west of Poike, the peninsula on the extreme east of the island. Both of these areas are in fact drier than elevation alone predicts. The airport rain gauge (white dot) is also in a moderate rain shadow.

this corresponds to areas with rainfall of 1,300 mm/year or less. Applying the criteria of Ladefoged et al. (2009) to the area at or below 1,300 mm rainfall identifies 2,889 hectares (of the total of 16,425 1-ha cells) as suitable for dryland agriculture. This process eliminates most of the Poike area (the eastern peninsula), much of Rano Aroi (in the north) and its dry western slope, and the steep areas around Rano Kau in the southwest. It is possible that some of these areas were cultivated in the past, but the modern climate and soil data suggest that such efforts would be unsustainable. Further, it has been shown that once depleted, volcanic soils like Rapa Nui's do not rejuvenate their fertility themselves over time (Chadwick and Chorover, 2001; Chadwick et al., 2003), suggesting that modern data should be a reliable picture of the past in this case.

In addition, on Rapa Nui it appears that people were farming patchy areas receiving rainfalls greater than 1,300 mm/year, as many of the agricultural features identified in Ladefoged et al. (2013) lie above that isohyet. Ladefoged et al. (2013) mapped the distribution of these cultivated rock garden areas using supervised classification of WorldView 2 satellite data. They specified three alternative classifications ("maximal," "medial," and "minimal"), and here we took a conservative approach and used their "minimal" classification of areas of rock gardens throughout the island. Their "minimal" classification identifies rock gardens in 5,548 1-ha cells that fulfill the original criteria of Ladefoged et al. (2009) located above the 1,300 mm rainfall isohyet. Within those 5,549 1-ha cells, a total area of 244.9 ha of gardens are identified in Ladefoged et al.'s (2013) "minimal" classification of the WorldView 2 satellite data. Combining both (1) the area below 1,300 mm annual rainfall identified as agriculturally viable by the Ladefoged et al. (2009) criteria, and (2) the area above the 1,300 mm isohyet that otherwise fulfills the Ladefoged et al. (2009) criteria and contains gardens identified by the "minimal" classification of Ladefoged et al. (2013), we estimate there were 3,134 ha suitable for dryland agriculture on Rapa Nui.

MODELING PRODUCTIVITY

To model agricultural productivity we parameterized a version of the Century nutrient cycling model (Parton et al., 1987) for dryland sweet potato production on Rapa Nui, using parameters from elsewhere in Polynesia when necessary (see Supplemental Materials, Table S3). The model tracks plant production on a monthly timescale as a function of the climate and environmental factors described above. We track the stores of carbon and nitrogen in the plants' above- and below-ground parts, the ratios of which are constrained to biologically realistic ranges (Parton et al., 1987; US Department of Agriculture, Agricultural Research Service, and Nutrient Data Laboratory, 2016). Soil N availability is calculated from N inputs from rainfall, biological fixation and the local recycling of dead plant matter, mostly through microbial action. Small amounts of plant-available N are also lost from the system through volatilization and leaching. For simplicity we assume that all grid cells identified as agriculturally viable are identical in their soil structure and water holding characteristics, with the exception of rainfall and temperature, and the effects these have on the site variables.

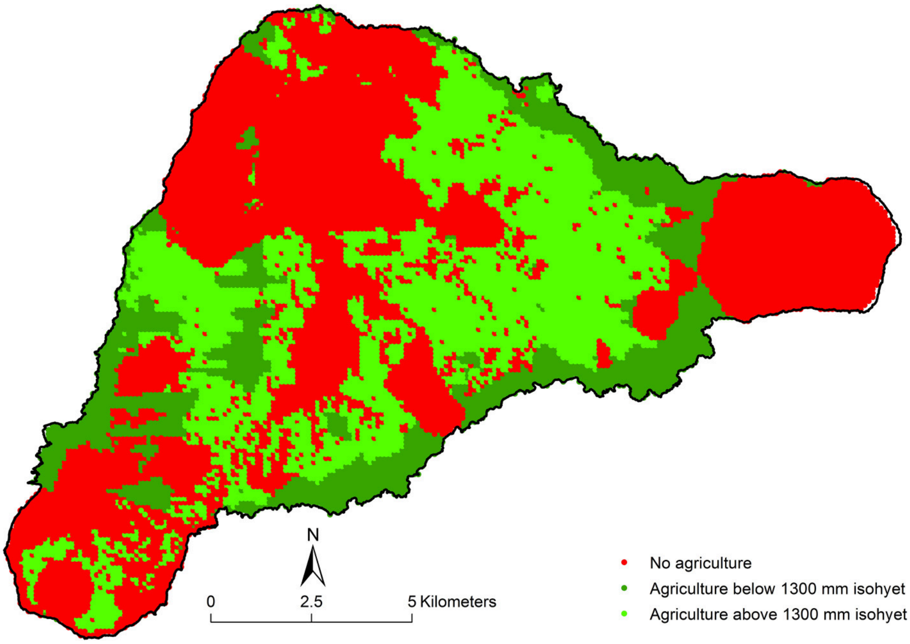

FIGURE 4 | The results of applying the criteria for agricultural viability from Ladefoged et al. (2009) with modifications for Rapa Nui. Soils were generally lower in nutrient availability on Rapa Nui, and we ruled out those areas with more than 1,300 mm rainfall annually unless there was clear evidence of garden activity, according to Ladefoged et al. (2013). The darker green areas are those below 1,300 mm rain that meet the other criteria, totaling 2,889 hectares. Lighter green areas show the 1-ha cells that contain evidence of gardens, although these garden areas are often small and sparse, adding only 245 hectares of agricultural area. The red indicates areas that are ruled out from being agricultural by the model.

We do not model phosphorus explicitly, although we do track the minimum mass of P required to produce the yields of sweet potato the model estimates. The mass of phosphorus removed at harvest is calculated at 1/500 times the mass of carbon removed (US Department of Agriculture, Agricultural Research Service, and Nutrient Data Laboratory, 2016), assuming tubers are 23.5% C by mass.

Earlier versions of the model have been used to examine productivity of Polynesian dryland agriculture (e.g., Lee et al., 2006; Ladefoged et al., 2008; Kirch et al., 2012). In addition to the model changes described in Kirch et al. (2012), we have updated the model to include soil-water dynamics based on the dual crop coefficient method and the FAO Penman-Monteith equation for calculating grass-reference evapotranspiration (Allen et al., 1998). To model the low-productivity environment of Rapa Nui we added a shifting cultivation module that allows us to specify the fallow crop and the length of the fallow and cropping period. The grasses that grow during fallow are burned before planting, resulting in the loss of all above-ground biological carbon and 50% of the above-ground nitrogen and 10% of the phosphorus. The difference remains as ash and is plant-available, representing a simplification of the process described by Ewel et al. (1981) and Palm et al. (1996).

The model runs on a monthly timescale, with the exception of water dynamics, which are tracked on a weekly basis. Rainfall and temperature vary according to the observed seasonal pattern appropriate for the elevation and degree of rain shadow effect. Monthly production in gC/m^2 is limited by the amount of available sunlight striking the canopy, which changes according to the plant's stage of growth. It is further reduced by factors representing the effects of water stress and the crop-specific response to temperature. These factors include losses due to plant respiration. If maximum production exceeds that allowed by the crop-specific maximum C:N ratios, then all plant available N is incorporated and the maximum amount of carbon allowed by the C:N ratios is assimilated by the plant. Otherwise climate is at least co-limiting and mineral N may be left over in the soil, depending on the minimum C:N ratios of the plant.

Nitrogen inputs are limited to N dissolved in rain and biological fixation, and losses are limited to volatilization (through burning and as a function of decomposition) and leaching (through deep percolation), in addition to N removed at harvest. Monthly plant-available N is derived as the balance of these fluxes, plus the N released by decomposition.

The scenarios we examine are divided into two environmental classes: one with a low rate of N fixation (4.8 kgN/ha/year) and one with a high rate of N fixation (20 kgN/ha/year). In each of these we consider three agricultural approaches: continuous cultivation, 5 years of fallow with 5 years of cropping, and 15 years of fallow with 3 years of cropping. In the shifting cultivation scenarios we alternated between grassland fallow and sweet potato cultivation until the pattern had stabilized in all cases, and saved results from the last 200 years. In the case of continuous sweet potato cultivation we used the same time scales to calculate mean yields.

There are several human behavioral, or cultural, factors that might influence population densities and we considered three classes of these. The first regards societal expectations with regard to effort in agricultural labor, the second regards expectations with regard to fertility, and the third regards societal expectations with regard to social stratification, surplus production, and specialization of labor.

We used a model of food-limited demography described in Lee and Tuljapurkar (2008) and Puleston and Tuljapurkar (2008) to examine the response of human population size and structure to the productivity of the environment and our behavioral assumptions. The demographic model has been used to examine the linkages between early agricultural populations and their food supply (e.g., Lee et al., 2009; Puleston et al., 2014; Winterhalder et al., 2015) and has been applied to Polynesian contexts in particular (Puleston and Tuljapurkar, 2008; Kirch et al., 2012). The model requires input of a potential yield, which we identified earlier, and calculates per capita food availability based on the amount of arable land, labor supply and the size and structure of the population. It iterates a population forward in annual steps, adjusting birth and death rates in response to food availability. We extend the model's functionality here to examine the consequences of fertility control and the existence of a non-agricultural elite class, discussed below.

Our default expectation of labor effort in dryland sweet potato production in Polynesia is that a typical adult worker will plant and harvest just under 1 ha of land per year (Kamakau, 1976) and we begin with the assumption that 50% of the working-age population is employed full time in agriculture. This could occur in the case that all men, and only men, are fully employed in agriculture, or that men and women both work, but each for only half of a full work day. This default scenario is identified in the summary of results under the heading "workfrac = 0.5." We also examine the cases where 75% of the working-age population is fully employed in agriculture, in addition to the hypothetical case in which 100% of the working-age population is engaged in farming. These scenarios are labeled "workfrac = 0.75" and "workfrac = 1," respectively.

The second cultural parameter we examine is the responsiveness of fertility to hunger. The equilibrium state of the demographic model is defined by the level of hunger at which fertility and mortality achieve balance: the number of births and the number of deaths are equal. Both age-specific fertility and survival probability have default values that are in effect when food is plentiful. We follow Puleston and Tuljapurkar (2008) and Kirch et al. (2012) in assuming the default total fertility rate of this Polynesian population is 4.9 children per woman, and the expected lifespan of the population in the absence of hunger is 45 years (see Supplemental Materials, Table S4 for more information on demographic parameters). When a population grows to the extent that it outstrips the ability of the land to provide sufficient food, the rates of fertility and survival begin to drop, even as the population continues to grow at a reduced rate. Eventually births and deaths balance and equilibrium is achieved. This describes the default scenario, although alternatives exist. One we consider here is the scenario of "fertility control," in which the population's response to the experience of hunger is to immediately reduce fertility rates as much as is required to achieve equilibrium without a substantial increase in either hunger or mortality. This scenario maintains a high quality of life for the entire population at the expense of much reduced probability of childbearing and the difficulty that effecting and enforcing that requirement might entail.

The third cultural feature we consider is social stratification, surplus production, and occupational specialization. The "egalitarian" scenario refers to the case in which the entire population is made up of agricultural workers and their families. In the "hierarchical" scenario we examine the effects of a stratified society that demands some degree of tribute in both food and labor. This includes the resources necessary to feed a non-agriculturally productive class, or classes, including chiefs and their retinues, and would include moai-producing stone carvers if we assume they did not contribute agricultural labor as well. This scenario assumes 10% of all food is taken as tribute and that 25% of agricultural labor is lost in non-agricultural tribute. We also assume that the non-producing class remains at 1% of the overall population.

RESULTS

Average annual yields increase, as expected, as the fallow period increases in shifting cultivation (**Table 1**). The low-N environment with no fallow yields 1.46 t/ha/year of wet sweet potato tuber, while the 5-year fallow yields an average of 2.38 t/ha/year over 5 years, and the 15-year fallow yields an average 5.61 t/ha/year over 3 years of cultivation. In the high-N environment these values rise to 5.10, 8.00, and 17.60 t/ha/year, respectively. **Figure 5** shows the spatial distribution of these yields.

Using the conversion of 1 t/year of wet sweet potato = 2,809 kcal/day (based on 100 g wet sweet potato providing 102.5 kcal), the low-N environment provides 4,101 kcal/day/ha under continuous cultivation, and 6,685 kcal/day/ha for land in active cultivation in the short-fallow regime. The long-fallow scenario yields 15,758 kcal/day per ha of cultivated land.

Assuming a C:P ratio of 500:1 for sweet potato tubers, in the low-N environment the continuous production scenario

TABLE 1 | Stable sweet potato yields (t/year for each non-fallow ha) and area in cultivation ("effective ha") under two N-fixation scenarios and three patterns of cultivation: continuous, shifting cultivation of 5 years fallow followed by 5 years of cropping, and shifting between 15 fallow years and 3 cropping years.

Frequency	N availability	Tons/ha/year	Effective ha
Continuous	low N fix	1.46	3133.9
Continuous	high N fix	5.09	3133.9
Shift 5/5	low N fix	2.38	1566.9
Shift 5/5	high N fix	8.00	1566.9
Shift 15/3	low N fix	5.61	522.3
Shift 15/3	high N fix	17.60	522.3

The low-N fix scenarios assume a fixation rate of 4.8 kgN/ha/year, while the high-N fix scenarios assume 20 kgN/ha/year.

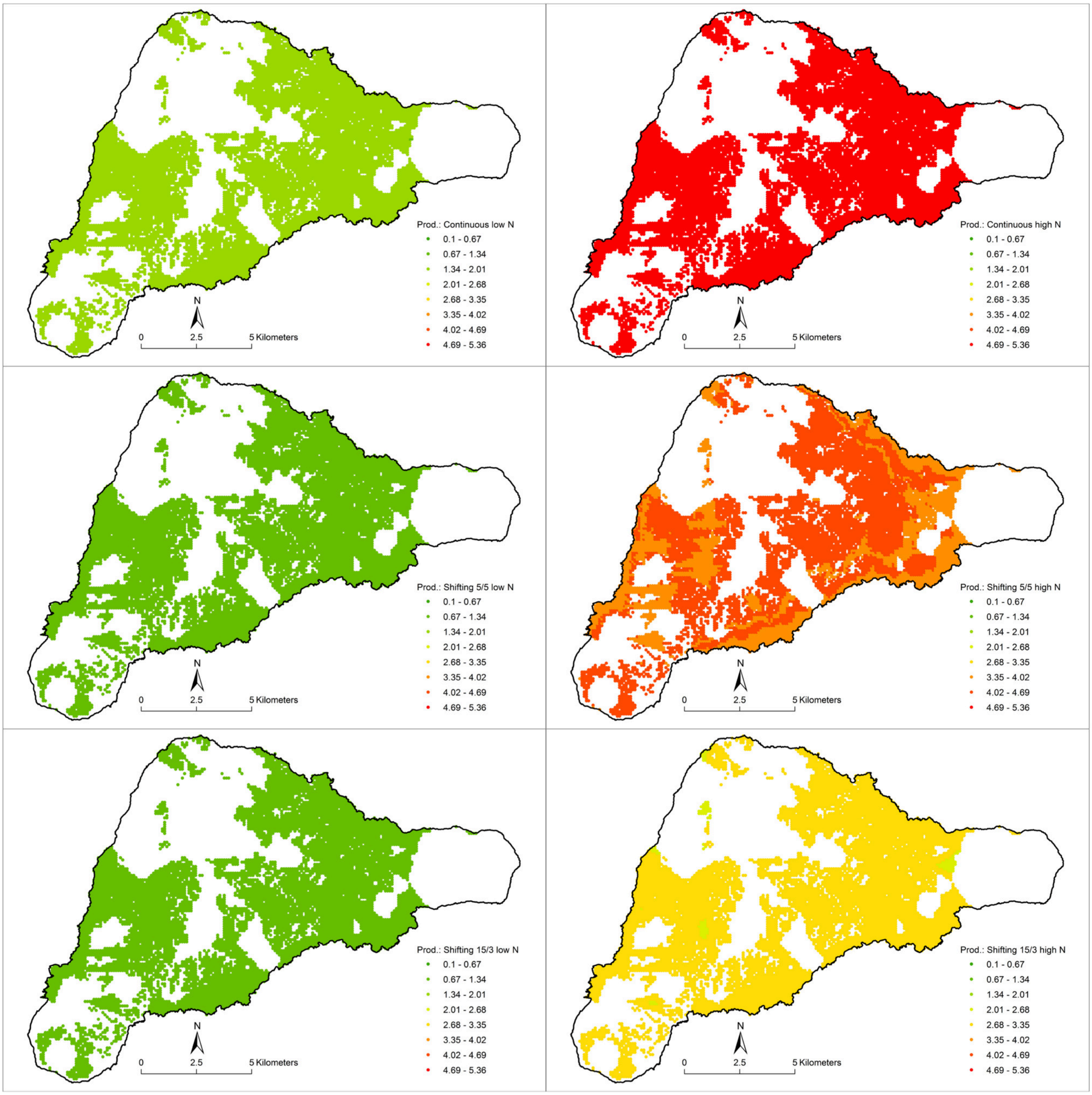

FIGURE 5 | The column of images on the left represent the low-N case and the right column represents the high-N case. The rows represent continuous cultivation, shifting cultivation with 5 years in use and 5 years fallow, and the shifting case with 3 years in use and 15 years fallow, from top to bottom. The legend is the same for each, showing annual yield of sweet potato (t/ha), averaged over fallow and non-fallow years.

removes 0.91 kgP/ha/year. The short-fallow scenario removes 1.47 kgP/ha/year in cultivated areas, in addition to the 10% of above-ground P lost to the burn at the end of the fallow period. For a sustainable yield this short-fallow scenario requires annual inputs of 0.74 kgP for each of the 3,134 arable ha, including fallow. The long-fallow scenario removes 3.55 kgP/ha/year for the three years of cultivation, in addition to the burn losses. The combined losses require inputs of 0.60 kgP/ha/year to all arable ha for the yield to be sustainable. In the high-N environment the average annual losses are 3.10, 2.47, and 1.86 kgP/ha/year for the continuous cultivation, short fallow and long fallow systems, respectively.

The sweet potato yields, after conversion to food calories, are used as an input to an updated version of the food-limited demographic model (Lee and Tuljapurkar, 2008; Puleston and Tuljapurkar, 2008). We find that in several of the low-N scenarios the population is non-viable, meaning that the agricultural population is unable to grow enough food to avoid extinction. This occurs when yield is too low for a family to feed itself on the amount of land its labor can farm. We predict labor shortages in the majority of parameter combinations under continuous cultivation, but such shortages are less likely when a greater fraction of the population is employed in agriculture (**Table 2**). The egalitarian populations with 75 and 100% of the working-age population engaged in agriculture manage equilibrium numbers of 4,023 and 6,176, respectively, when there is no concerted attempt to limit fertility. The only hierarchical population to avoid extinction occurs in the case of 100% worker participation (i.e., workfrac = 1) when no attempt is made to control fertility. The population levels out at 2,633 individuals in this scenario.

The low-N scenario is generally associated with low population estimates, the largest numbers occurring in the short-fallow case with an egalitarian social structure and no fertility control. The maximum low-N population is observed in such a situation with 100% worker participation in agriculture, totaling 6,385 individuals. The costs of adding a hierarchy and fertility control are severe in the low-N case. The greatest population size under these assumptions is 3,075 individuals and occurs in the long-fallow case with the assumption of all working-age individuals being employed in agriculture.

Populations are universally higher in the high-N scenarios. The maximum we observe is 29,120 individuals, occurring in an egalitarian population with no fertility control and 100% labor participation using continuous cultivation. The maximum hierarchical population is 26,132 and occurs when there is no fertility control and 100% participation in continuous cultivation. Fertility control reduces the equilibrium population size by shifting the tradeoff between a larger, hungrier population and a smaller, better-fed population. In the hierarchical case with fertility control the maximum of 16,443 occurs under high-N continuous cultivation with 100% worker participation. The lowest population estimate under the high-N fixation scenario totals 10,059 and occurs in the hierarchical population with fertility control and 50% participation.

DISCUSSION

The goals of this study are twofold: to estimate the maximum sustainable population that could have lived on the agricultural resources available to the early settlers of Rapa Nui, and to understand the importance of the ecological and cultural factors that contribute most to that estimate. From our estimates of agricultural productivity, which inform our model of food-limited demography, we find that the range of possible maximum populations runs from approximately 3,000 individuals on the low end to more than 29,000 individuals at the high end. Given our relatively conservative assumptions, we estimate the maximum population of Rapa Nui before European contact would have been closer to 17,500, the approximate average of the high-N scenarios, than the low-N average of 3,500.

The rate at which new nitrogen is added to the system is the most important of the factors we examined. The importance of the other factors we considered depends on whether the N fixation rate was low or relatively high. In the case of lower soil N existence is marginal. The availability of labor is all-important, and the effect of all the factors can be interpreted through their effects on the labor supply. When yields are too low hunger decreases the growth rate and the agricultural population cannot replace itself in the following generation. Even though land is available in such cases, a worker cannot farm enough of it to avoid starvation. In the case of higher N fixation, we find agricultural yields are more typical of long-inhabited Polynesian islands and the maximum population is less dominated by a single factor. In order of importance the controlling factors are: (1) the extent to which lands were left in fallow, (2) the efforts of the population to control fertility, (3) the imposition of tribute to support a non-agricultural elite, and in extreme contrast to the low-N case, (4) labor participation. We examine these factors in turn.

Our assumptions regarding the rate of N-fixation from the decomposition of sugar cane have an outsized effect on our population estimates. The average population size across all parameter combinations is 2,650 individuals in the low-N environment. We find 9 of 36 parameter combinations are non-viable and another three that number fewer than 150 individuals, far too low to be reasonable. Eliminating these 12 scenarios gives an average of 3,534 individuals across the low-N environment. The scenarios in the high-N environment have a mean population of 17,425. The average population increases by a factor of 6.6 entirely as a result of a 4.2-times increase in the N-fixation rate. At this point we do not have evidence that points clearly to one end of the N-fixation spectrum or the other, although we do know that varieties of sugar cane associated with nitrogen fixation during decomposition were cultivated on Rapa Nui, as in Hawai‘i, where the estimates originated (Lincoln and Vitousek, 2016).

The relationship between food supply and labor supply is especially important when the productivity of the land is low, as in our low-N fixation scenarios. Only under the assumption that low-N land was farmed in long-fallow shifting cultivation do we see the effect of increasing labor supply (via the parameter "workfrac") begin to disappear. Elsewhere throughout the low-N scenarios in **Table 2** population numbers respond sharply to the fraction of the population dedicated to agricultural labor. Low-yield environments have unusual characteristics driven by the non-linear relationships between labor and food supply (Puleston et al., 2014). There are thresholds below which the yield per hectare is too small for a family to support itself, due to limitation by how much land a worker can manage. In marginal locations, when a population can provide enough labor to support itself, it may grow very slowly, suffering the hunger-driven depression of growth rate from early in the population trajectory. We find that in the high-N fixation regime increasing the worker fraction has much less of an effect on population numbers, and its effect is greatest where the yield per cultivated hectare is lowest, i.e., the continuous cultivation scenarios.

The effect of agricultural practice on population is driven by the return on investment to labor and the effect of agricultural choices on soil nutrient dynamics. In continuous cultivation we assume workers cultivate as much of the available land as

TABLE 2 | Maximum sustainable population sizes in the low-N fixation regime (top) and high-N fixation regime (bottom) under different assumptions.

Organization	**Egalitarian**						**Hierarchical**					
Pop control	**No fertility Control**			**Fertility Control**			**No fertility Control**			**Fertility Control**		
Work frac	**0.5**	**0.75**	**1**	**0.5**	**0.75**	**1**	**0.5**	**0.75**	**1**	**0.5**	**0.75**	**1**
LOW-N-FIXATION REGIME												
Continuous	0	4,023	6,176	0	0	1,952	0	0	2,633	0	0	0
ShiftS/5	3,889	5,775	6,385	42	2,655	3,613	11	3,612	4,933	0	138	1,951
ShiftEL5/3	5,165	5,319	5,343	3,103	3,437	3,519	4,241	4,703	4,816	2,070	2,835	3,075
HIGH N-FIXATION REGIME												
Continuous	27,752	28,912	29,120	16,155	18,482	19,094	22,069	25,285	26,132	9,703	14,786	16,443
ShiftEB/5	22,717	22,866	22,878	14,601	15,094	15,175	19,977	20,661	20,774	11,862	13,298	13,660
ShiftE15/3	16,778	16,778	16,778	11,135	11,141	11,142	15,243	15,252	15,253	10,059	10,123	10,128

possible, drawing a maximum yield from the ground year after year. Over time nutrient dynamics stabilize and removals in the form of food are defined by the balance of inputs and losses. Shifting cultivation, on the other hand, removes some fraction of the land from cultivation so that part can accumulate nutrients while it lies fallow. When the time comes to plant a fallow area the cover is burned, resulting in losses of nutrients to volatilization and leaching, but the plant-available nutrients that remain generally provide higher initial yields per year than continuous cultivation would have supplied. The result is greater yields per unit of cultivated land, but over a smaller area.

It is typically assumed that small colonizing populations rely more on shifting cultivation early in their growth trajectories due to the relatively high return on labor. However, as population density increases, the population may be forced to employ shorter fallows, and even begin continuous cultivation to avoid hunger (Boserup, 1965). Kirch (2010, pp. 190–201) examined this process in the Polynesian context. The high-N environment conforms closely to the expectation that population densities are greater under continuous cultivation and longer fallow times are associated with lower population densities. The only place we see that generalization violated in our results is in the case of a labor shortage imposed by a fertility-controlled population with a 50% labor fraction in combination with the imposition of labor tribute.

A population using shifting cultivation might exceed the size of one using continuous cultivation where soil fertility is generally poor due to the increased yields in longer fallowed land and the nonlinearities in the relationship between labor and food supply. In the low-N environment, within worker fraction scenarios, population generally increases as yields per *cultivated* hectare increase at each step from continuous cultivation to short fallow and then long fallow. However, in cases where the labor supply is generally adequate the population responds as Boserup (1965) expected, increasing in size with increasing labor inputs.

It should be noted that our model of agricultural viability of the 1-ha grid cells was based on the assumption of continuous cultivation. It is possible that shifting cultivation was employed to farm more marginal land at higher elevations even if the preference was for continuous cultivation in places that could support it. This would increase the expected population beyond our predictions.

Additionally, there are alternate sources of calories that may have been available to the population that are not included in the model. These include the availability of marine resources, however limited, birds, both wild and domesticated, and less calorie-rich crops that could be grown at higher elevations. It is also possible that the Rapa Nui were more efficient in their use and control of plant resources than we have assumed here. We have not included the practice of transporting mulch from alternate locations to supplement nutrients, or assumed that the Rapa Nui forwent the consumption of sweet potato leaves in favor of the more calorically efficient practice of leaving them in the fields to recycle their nitrogen. Each of these factors would tend to increase population estimates.

Similarly, our decision to limit our scope to sustainable yields likely underestimates productivity in the initial development of agriculture. Founding populations may benefit from a flow of nutrients from the soil organic matter pools left over from when the plant biomass was greater and the nutrient pools larger. These nutrients would be released on decadal and (for P) considerably longer timescales, potentially increasing yields. However, Puleston et al. (2014) estimate that a population like Rapa Nui's would take approximately 400 years to reach its maximum under the assumptions of food-limited demography. Many of the ecological transitions initiated by human occupation of the island would be well under way at that point, including changes to the soil organic matter pools and deforestation. Winterhalder et al. (2015) discuss some of the consequences of a food-limited population's agricultural yield becoming elevated and then returning to a lower level; these consequences include potential famine and social upheaval.

Models of food-limited demography (Lee and Tuljapurkar, 2008; Puleston and Tuljapurkar, 2008; Lee et al., 2009) generally work from the assumption that populations are passive, or at best ineffective, in controlling their own numbers. In the absence of such endogenous control, nature takes its course in Malthusian fashion, driving down rates of fertility and survival as food becomes more and more scarce until the population is driven to zero growth and achieves equilibrium at the maximum level of misery that can be endured. The end result is a relatively large population suffering from significant hunger. Among the alternatives to this fate is fertility control (or high infant mortality). We examine the consequences of perfect fertility control, in which the population reduces births at the first sign of food insufficiency, bringing it to an equilibrium where each person has precisely what they require to feed themselves and mortality is low, and thus life expectancy remains at its maximum.

There is a basic tradeoff between quality and quantity of life at equilibrium. A better-fed, longer-lived population is a smaller population, all else being equal. Our results bear this out. For example, in the high-N environment under continuous cultivation and with 75% worker participation the imposition of fertility control results in a 36.1% decrease in population in the egalitarian scenario and a 41.5% decrease in the hierarchical scenario. We observe similar decreases in the low-N environment, but the comparison is complicated by the non-viability of so many of those populations due to the scarcity of labor. In practice, population control via fertility control or other coordinated approaches may have been difficult to achieve. Also, environmental stochasticity could have played a role in maintaining populations at levels lower than stable equilibria predict, and achieved some of the benefits of fertility control, including average food availability and life expectancy, at the cost of occasional famines (Winterhalder et al., 2015). However, we have limited ourselves in this study to stable seasonal variation, meaning that seasonality is included, but each year is the same as the next. In its effects on productivity and demographic rates the inclusion of environmental stochasticity (i.e., the possibility of periods of drought or above-average rainfall) would be expected to lower population estimates (Lee et al., 2009).

The cost to the agricultural population of maintaining one or more classes of individuals who do not contribute to agricultural production but require feeding and might demand the contribution of labor that would otherwise be spent in farming can be significant. As is the case throughout the indigenous cultures of Polynesia, Rapa Nui's first inhabitants probably arrived with notions of social stratification. The development of the exquisite craftsmanship required to produce the nearly 1,000 moai statues found on the island speaks to a further specialization of labor. Our assumptions in the hierarchical scenario are relatively modest, and the results are similarly modest, except where labor becomes in short supply. The 25% labor tribute has an especially profound effect in the low-N environment. Where four of the 36 parameter combinations are effectively non-viable in the egalitarian scenario, eight of 36 result in populations of less than 150 in the hierarchical scenario. The impact of stratification in the long-fallow cases, where labor is less in demand, becomes similar to the much reduced effect in the high-N regime. The assumption of a more elaborate or demanding social hierarchy should decrease the population estimates.

The importance of labor supply cannot be overstated in a low-yield environment, but in the high-N environment it becomes much less of a factor, even approaching negligibility in the egalitarian shifting cultivation scenarios. In the higher-yield scenarios labor becomes more important as the importance of other factors we modeled is increased. It is not a factor in the egalitarian, non-fertility control, shifting cultivation populations, and becomes more important in the hierarchical, fertility-control, continuous cultivation populations.

Our estimates of population densities center around 21, and 107 persons (p) per km^2 in the low- and high-N environments, respectively. However, when we consider only the area we identify as agriculturally viable these become 112 and 558 p/km^2. Putting these numbers in context, data from Kirch (2010, Table 4.2) estimates the islands of Hawai‘i and Maui had densities of 262 and 389 persons (p) per km^2 of "prime agricultural land," respectively. These two islands relied heavily on dryland sweet potato to support their populations, but also were able to irrigate 2.5 and 14.8% of their agricultural land, respectively, suggesting that they are probably overestimates of the density that could be supported by dryland agriculture alone. Although the size of pre-contact populations on the Hawaiian Archipelago are also uncertain, these densities per unit of agricultural land on Hawai‘i and Maui projected over 31.3 km^2 of agricultural land on Rapa Nui result in population estimates of 8,211 and 12,176, respectively. Without discounting for Hawai‘i's more favorable climate for sweet potato, this range is consistent with our high-N scenario with a hierarchy, fertility control and 50% of the adult agricultural population in full-time work in any of the cultivation methods.

CONCLUSIONS

The purpose of this exercise is to reexamine the relationship between agricultural potential and population on Rapa Nui before the arrival of European explorers. New tools in demography and a better understanding of the limitations on agriculture on the island provide new insight into these complex interactions. We find that maximum population numbers are highly dependent on the rate at which nitrogen accumulates, and that our ability to estimate Rapa Nui's population peak is limited by the relatively poor information we have on N input. However, given rates of nitrogen accumulation that are found in other parts of Polynesia, population sizes of 17,500 and higher were theoretically possible.

AUTHOR CONTRIBUTIONS

CP did modeling and drafted the manuscript. TL provided data and figures, edited and contributed ideas. SH contributed to parameterization of models, contributed ideas and edited. OC, PV, and CS contributed data, ideas and edited.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fevo.2017.00069/full#supplementary-material

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Commentary: Rain, Sun, Soil, and Sweat: A Consideration of Population Limits on Rapa Nui (Easter Island) before European Contact

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A commentary on

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Rapa Nui (Easter Island) has long-presented a challenge to researchers seeking to explain the nearly 1,000 multi-ton statues carved and more than 600 transported across this tiny, remote island where Europeans observed a population just a few thousand in number. The stark contrast between the island's impressive monuments and its marginal resources led to early European speculations of a once larger population under more prosperous conditions, most famously espoused in Diamond's (2005) narrative of "collapse." Recently, Puleston et al. (2017) bring needed attention to the issue of pre-contact population size for Rapa Nui to examine the "collapse" debate. Their work combines demographic and agricultural productivity modeling with parameter estimates from Rapa Nui and other Pacific Islands. While such modeling has many strengths, their conclusion—that the island once supported a population of 17,500—is based on questionable assumptions and contradicts a range of available evidence.

Given early European observations, the conclusion that Rapa Nui once supported a population of 17,500 *requires* a pre-European demographic collapse, in contradiction to archeological and historical evidence, including some of the authors' own work (e.g., Mulrooney et al., 2009, 2010; Stevenson et al., 2015). Predilections for large population estimates follow assumptions, sometimes tacit, that hundreds or even thousands of workers were needed to make and move the multi-ton statues and even more required to produce surplus food in support of these activities. Recent quantitative analyses and experiments demonstrate that relatively small numbers of people could transport the statues (Lipo et al., 2013). Popular notions of "collapse" can be traced to historical misconceptions as some have described (e.g., Lipo and Hunt, 2009; Mulrooney et al., 2009; Hunt and Lipo, 2011). There are currently few *archeological* indications that the population was ever much larger than the ca. 3,000 witnessed at European contact (Hunt and Lipo, 2009) or clear evidence for the precipitous decrease in land-use expected in a massive pre-contact population decline (Mulrooney et al., 2010; Mulrooney, 2013; Stevenson et al., 2015) required if Puleston et al.'s conclusions were valid. In addition, there is little evidence for the level of conflict expected with a dense population of 17,500 on such a small island, including limited lethal skeletal trauma, no systematic production of lethal weapons, nor fortifications

(Lipo and Hunt, 2009; Hunt and Lipo, 2011; Gill and Stefan, 2016; Lipo et al., 2016; Owsley et al., 2016; DiNapoli et al., in press). Moreover, Rapa Nui lacks the kind of dense, nucleated settlement pattern often cited for elsewhere in Polynesia and expected for 17,500 inhabitants on a 164 km^2 island (Kirch, 1984, 2017; Morrison and O'Connor, 2015). Early European population estimates around 3,000 are consistent with an archeologically-documented low-density and dispersed settlement structure (McCoy, 1976; Morrison, 2012).

The population estimate of 17,500 chosen by the authors reflects a fallacy of averaging where the number argued as the "most likely" is arbitrary and apparently little more than subjective preference. In their modeling, maximum population size ranged from 0 to 30,000, but they do not explain how or why the mean is an accurate estimate of the "true" number. Moreover, and as emphasized by the authors, the outcomes are highly dependent on how they chose to parameterize the model, with N values, length of fallow period, amount of labor participation, fertility controls, and degree of surplus used to support "elites" being critical. Yet, the critical soil N values are not well understood, and there are essentially no archeological or ethnographic data available that would allow the authors to estimate these model parameters in a valid way. From a modeling perspective, lacking reasonable parameter values, one must choose outcomes that best fit any empirical evidence. In the authors' "low-N" scenarios, average population sizes are around 3,500, in contrast to their preferred 17,500 in the "high-N" situations. Based on limited evidence for Rapa Nui, the low-N values are just as likely, or more likely, than the high-N values. The results of the low-N scenarios, however, do correspond to the limited empirical demographic evidence we have—the observations of early European visitors. Finally, paleopathological evidence of dietary stress (e.g., enamel hypoplasia, Polet, 2006), suggests that the lower values are consistent with the conditions of food-limited demography for the island.

Importantly, their model neglects annual variance in agricultural productivity. When there is variance in productivity, population growth is limited by minimal productivity and better modeled using the geometric mean rather than the arithmetic mean (Renshaw, 1993; Nations and Boyce, 1997; Freckleton and Watkinson, 1998, p. 113), and populations in variable environments can stabilize at substantially lower levels than under more constant conditions. Rapa Nui has unpredictable annual rainfall and on longer-term timescales, resulting in potentially substantial variability in food productivity (Genz and Hunt, 2003; Morrison, 2012). Consequently, models ignoring temporal variability could, and likely, dramatically overestimate population sizes (Boyce et al., 2006; Lee et al., 2009). As Maynard Smith (1974, p. 13; cited in Boyce et al., 2006, p. 141) points out, "the use of deterministic rather than stochastic models can only be justified by mathematical convenience." The significance of variance in productivity also raises the question whether Hawai'i or other comparisons to Rapa Nui's mean growing productivity are warranted. In the Pacific, Rapa Nui is distinctive in its poor soil fertility, seasonality, pre-contact land-use, settlement patterns, and investments in monument construction, making analogs with other islands potentially misleading.

In addition to the issues raised, this study suffers from problems of irreproducibility. The authors do not provide comprehensive data, adequate description of methods, computer code, or results needed to replicate or verify the outcomes of their model; at odds with current best-practices in science, and in archeology in particular (e.g., Marwick et al., 2017). Studies that include relatively complex computational models, but no code or necessary data needed for model replication, remain essentially unverifiable "black boxes" (Morin et al., 2012).

Ultimately, building an empirically supported and theoretically sound framework for estimating past populations of Rapa Nui is vital to explaining the remarkable archeological record of the island. We need good demographic models with empirically estimated parameters, including longer-term variability in productivity and, critically, whose outcomes can be replicated and evaluated against the archeological record. In the case of Puleston et al. the problems are not necessarily embedded in the model, but in unsound assumptions and a conflation of what might be *possible* with what is *probable*. Successful models depend on dynamic and empirical sufficiency (*sensu* Lewontin, 1974) and are evaluated on the degree to which they are useful. Thus, if the results of a model contradict multiple lines of empirical evidence, then the model is not wrong, but instead not useful for this particular case. Such is the case in this study of pre-contact Rapa Nui.

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Response: Commentary: Rain, Sun, Soil, and Sweat: A Consideration of Population Limits on Rapa Nui (Easter Island) before European Contact

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A recent commentary (Lipo et al., 2018) takes issue with some of the conclusions of our study of population potential on Rapa Nui (Easter Island) before European contact (Puleston et al., 2017). We have no objections to their vision of early Rapa Nui, and we believe it is consistent with our analyses, but we believe that they have misread our analysis substantially.

First, the commentary mistakenly asserts that we concluded "that the island once supported a population of 17,500." We did conclude that "given rates of nitrogen accumulation that are found in other parts of Polynesia, population sizes of 17,500 and higher were theoretically possible" (p. 12). This calculation is both well supported and carefully qualified in our analysis. The purpose of our study was to evaluate the dependence of maximum population on ecological and social factors. We repeatedly emphasized that the estimates of maximum sustainable population were highly conditional on the scenario being tested and not intended to settle once and for all the question of Rapa Nui's pre-contact population size.

Second, Lipo et al. (2018) misread our findings as an argument in favor of the pre-European "collapse" narrative. It is precisely because our estimates of quasi-equilibrium population sizes span such a wide range that we do not uncritically embrace this argument. In fact other recent work by our group demonstrated that prior to European contact, populations declined in some parts of Rapa Nui and not others. We concluded that constraint was a more appropriate framework than collapse for evaluating pre-contact Rapa Nui populations (Stevenson et al., 2015). This paper (Puleston et al., 2017) explores potential constraints quantitatively and, as noted in the abstract, our results varied depending on plausible assumptions of nitrogen availability, clustering around 3,500 individuals in the low-nitrogen case and 17,500 in the high-nitrogen case.

The commentary correctly points out that the fluxes of plant-available nitrogen accumulation on the island are poorly understood. We made this point ourselves; it is why we chose to explore two nitrogen scenarios. One represents the case where nitrogen inputs are limited to the best available estimates of rates of dissolved N deposition in rainwater along with a small amount of biological fixation of N. The high-N case also included N fixation occurring as a byproduct of sugar cane decomposition. Cultivars of sugar cane associated with N-fixation in a study by Lincoln and Vitousek (2016) in Hawaiʻi are found on Rapa Nui and believed to have pre-dated European contact. Thus, we could not ignore the possibility that Rapa Nui cultivators partially overcame a nitrogen constraint through their management practices, as Hawaiian cultivators did.

Third, Lipo et al. (2018) make several perplexing misstatements about our methodology, including their assertion that our scenarios overestimate maximum population because we do not account for annual variability in food yields. Our methods section describes in detail how climate variability observed at six weather stations placed across the island by the research group informs the agricultural model, and how we captured additional rainfall variability by incorporating long-term data from the airport weather station. Perhaps (as we said in our paper) climate, and so food yield, is even more variable than our data-based analysis recognizes, but to say we ignored the influence of stochastic variability is simply wrong.

Lipo et al. (2018) also suggest that our use of arithmetic rather than geometric means is inappropriate. We strongly disagree, but in any case the use of the geometric mean would change our high-N population mean across all treatments to 16,580 individuals, a decrease of about 5%. They also suggest that our results include a hidden assumption that there must have been large numbers of workers because they were required for statue construction and transport. Our methods make clear that we made no such assumptions.

Finally, Lipo et al. (2018) assert that our models are "black boxes." In fact we build upon a version of Century, a nutrient cycling model that has been fully accessible to the research community, widely used, thoroughly documented, and tested since the late 1980s. The food-limited population model we used has been described and analyzed in several publications (e.g., Lee and Tuljapurkar, 2008; Puleston and Tuljapurkar, 2008; Puleston et al., 2014). It is surprising that the authors suggest our modeling was opaque, as we provided them with our population code (and Century is available from Colorado State University) and an offer to help with interpretation of any unclear portions prior to publishing their commentary. They made no request for clarification and so we must assume that our modeling was sufficiently transparent.

We stand by our methods and results, and note that the reason why we use models in human ecology is to approach complicated problems from a new direction, evaluate potential constraints, and generate hypotheses, which may then be examined and tested. Perhaps our low-nitrogen scenario, which agrees with the population estimates preferred by Lipo et al. (2018), is a better representation of pre-contact Rapa Nui than is the high-nitrogen scenario—but if so, we have to ask why cultural practices that enhanced nitrogen input elsewhere in Polynesia were not implemented on Rapa Nui. More generally, we believe that it is sometimes better to determine what might have been possible (and why) than to limit ourselves to what we believe is probable.

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CLAFS, a Holistic Climatic-Ecological-Anthropogenic Hypothesis on Easter Island's Deforestation and Cultural Change: Proposals and Testing Prospects

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This paper reviews the existing hypotheses concerning the cultural shift from the Ancient Cult (AC) to the Birdman Cult (BC) that occurred on Easter Island (Rapa Nui) during the last millennium and introduces a holistic new hypothesis called CLAFS (Climate-Landscape-Anthropogenic Feedbacks and Synergies), which considers a variety of potential drivers of cultural change and their interactions. The CLAFS hypothesis can be tested with future paleoecological studies on new sedimentary sequences such as the new continuous and coherent record encompassing the last millennium from Rano Kao (KAO08-03) using a combination of pollen, non-pollen palynomorphs (NPP), charcoal, and fecal lipid analyses, at decadal to multidecadal resolution. The Kao record should be compared with other continuous records of the last millennium available for the two other freshwater bodies of the island, Rano Aroi and Rano Raraku, to obtain an island-wide perspective of spatio-temporal deforestation patterns in relation to climatic shifts and human activities. The CLAFS hypothesis predicts that the shift from the AC to the BC was associated with the drying out and deforestation of Rano Raraku (the center of the AC) by ∼1,570 CE, followed by human migration to Rano Kao (the social center of the BC), where freshwater and forests were still available. Under the CLAFS scenario, this migration would have occurred by ∼1,600 CE. Findings to the contrary would require modification and refinement, or outright rejection, of the CLAFS hypothesis and the consideration of alternate hypotheses compatible with new paleoecological evidence. Regardless the final results, archeological evidence will be required to link climatic and ecological events with cultural developments.

Keywords: Easter Island, Rapa Nui, radiocarbon dating, age-depth model, last millennium, deforestation, cultural change

INTRODUCTION

Easter Island (Rapa Nui) is a small and remote Pacific island of triangular shape (**Figure 1**) formed by the coalescence of three submarine volcanoes that emerged from the sea ~780 kyrs ago and whose latest major eruption occurred 200–110 kyrs ago (González-Ferrán et al., 2004; Vezzoli and Acocella, 2009). Easter Island has been considered a microcosm to illustrate the potential consequences of the worldwide overexploitation of natural resources (Diamond, 2005). According to the ecocide hypothesis, the original Rapanui society caused their own destruction by resource exhaustion, as manifested in the total removal of forests that had covered the island for millennia before human settlement (Flenley and Bahn, 2003). This hypothesis has dominated the Easter island narrative for decades since its formulation based on pollen analysis of lake sediments, which showed an abrupt change from palm to grass pollen, interpreted as the abrupt replacement of palm-dominated forests by grass meadows similar to those that cover the island today (Flenley and King, 1984; Flenley et al., 1991).

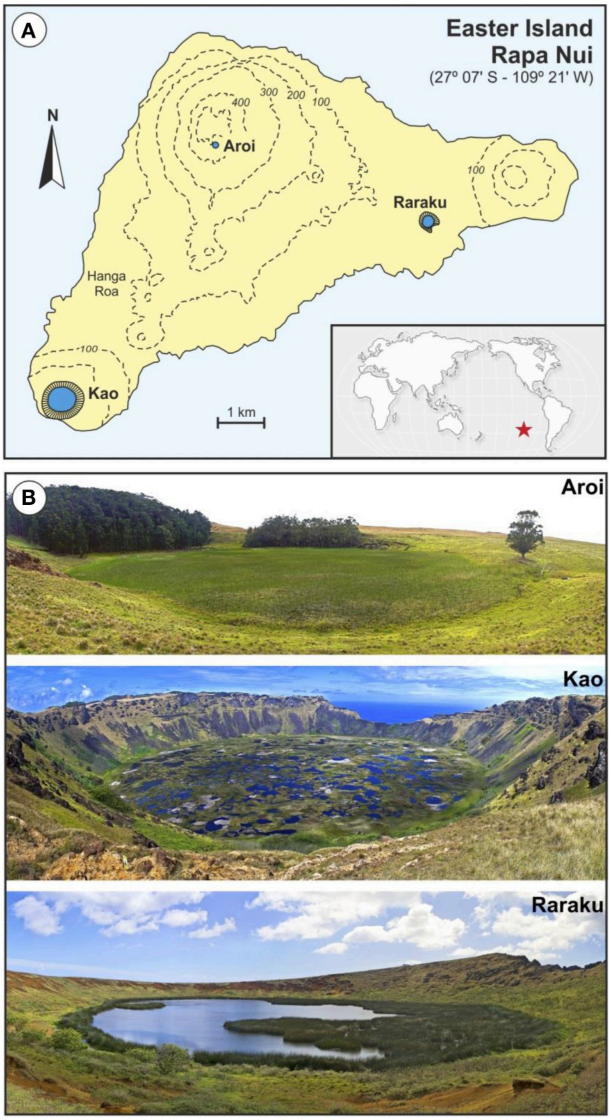

FIGURE 1 | Location map and cored lakes. **(A)** Sketch map of Easter Island showing the location of the three freshwater bodies cored for paleoecological studies (Aroi, Kao and Raraku). The position of the island in the Pacific Ocean is indicated by a red star. **(B)** Permanent freshwater lakes and mires from Easter Island (Photos: V. Rull).

Paleoecological reconstructions (notably palynological analyses to examine vegetation and landscape dynamics and charcoal analyses to document fire history) have been instrumental in the study of ecological and cultural change on Easter Island (Rull et al., 2010). Most paleoecological records have been obtained using sediment cores from the three natural freshwater bodies of the island: a mire (Aroi) and two lakes (Kao and Raraku), all of which are located inside volcanic craters; a combination that is locally called "rano" (Herrera and Custodio, 2008) (**Figure 1**). The sedimentary sequences underlying these water bodies have provided long records extending back to the last glaciation (Flenley and King, 1984; Flenley et al., 1991; Sáez et al., 2009; Margalef et al., 2013). However, detailed records of the last millennia, when the most relevant ecological and cultural shifts seem to have occurred, are rare, which can be attributed to intrinsic sedimentary challenges (Rull, 2016b). Since the earlier studies (Flenley and King, 1984; Flenley et al., 1991), a major obstacle for paleoecological reconstruction has been the difficulty in obtaining continuous and chronologically coherent records, free from sedimentary gaps, and age inversions (Butler et al., 2004). This has been especially problematic for the last millennia, where extensive sedimentary gaps have impeded continuous paleoecological reconstructions (**Figure 2**). The apparent abruptness of the island's deforestation, cited as supporting evidence for the ecocide hypothesis, is considered to be an artifact resulting from a sedimentary hiatus that obscured vegetation shifts occurred between about 4.0–4.2 and 0.8 cal kyr BP (Mann et al., 2008; Sáez et al., 2009) and created the incorrect impression that replacement of palm forests by grass meadows occurred almost instantaneously (Rull et al., 2013).

During the last decade, new coring efforts have provided more complete records for the last millennia. Noteworthy are two nearly continuous and chronologically coherent sequences from Aroi and Raraku embracing roughly the last three millennia, which have allowed the reconstruction of deforestation patterns across the island and revealed significant spatial heterogeneities (Cañellas-Boltà et al., 2013; Rull et al., 2015). Such recent studies have also provided evidence for the potential role of climatic shifts and climate-human synergies on the island's ecological and cultural developments, which has challenged former paradigms (Rull et al., 2013). Similar paleoecological reconstructions are still unavailable for Rano Kao, where the attainment of reliable age-depth models for the last millennia has been hampered primarily by the occurrence of frequent age inversions (Flenley and King, 1984; Flenley et al., 1991; Butler et al., 2004; Butler and Flenley, 2010; Horrocks et al., 2012b, 2013). Gossen (2007, 2011) obtained a coherent sequence for the last millennia but paleoecological analyses similar to those of Aroi and Raraku, useful to unravel deforestation trends, are unavailable.

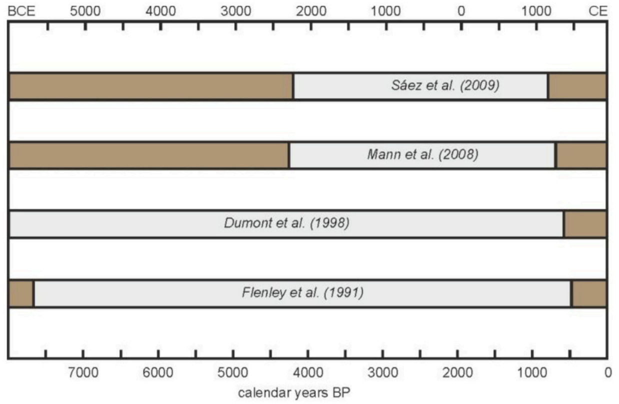

FIGURE 2 | Sedimentary gaps (gray bars) from previous paleoecological analyses on Rano Raraku sediments, from where most paleoecological inferences have been obtained. Redrawn from Rull et al. (2013).

In this paper, we introduce the first continuous and coherent sequence from Rano Kao encompassing the last millennium and discuss the potential significance of its paleoecological analysis, which is in progress, for testing previous and novel hypotheses about deforestation in relation to eventual climate changes and/or cultural developments (Rull, 2016a). This Kao sequence will complement the aforementioned Aroi and Raraku records of the last millennia to provide an island-wide history, capable of resolving spatio-temporal trends and patterns of deforestation, as well as addressing questions concerning human occupation and eventual intra-island migrations. The paper begins with an account of cultural developments of the last millennium in relation to ecological shifts, with an emphasis on the island's deforestation. The next section discusses the potential role of climate and climate-human interactions on ecological and cultural shifts. Then, Rano Kao and its sediments are briefly introduced and the new continuous record from this lake is presented, showing the age-depth model and describing the analyses that are in progress. Finally, the potential significance of this new record is discussed in light of the hypotheses and theories previously debated and others that can emerge from the new sedimentary evidence.

CULTURAL CHANGE AND DEFORESTATION

Current archeological evidence seems to point to a relatively recent human settlement of Easter Island by 1,100–1,300 CE (Hunt and Lipo, 2006; Wilmshurst et al., 2011), although earlier dates ranging from 800 to 1,000 CE have also been proposed (Flenley and Bahn, 2003; Vargas et al., 2006). Regarding the origin of colonizers, the dominant view is that they proceeded from East Polynesia (Flenley and Bahn, 2003) but potential contributions from Amerindian cultures cannot be dismissed (Thorsby, 2016). Therefore, the main cultural developments of Easter Island seem to have occurred in the last millennium, during which two major cultural transformations have been documented. The first was a profound change in lifestyle, social organization and ritual practices within the Rapanui society symbolized by the shift from the so called Ancient Cult to the Birdman Cult (Edwards and Edwards, 2013). The second cultural change was the consequence of the arrival of the first Europeans in 1722. In Easter Island, this date marks the boundary between prehistoric and historical times.

The Prehistoric Cultural Shift

During the Ancient Cult (AC) phase, the standard worship subjects were the *moais*, the iconic megalithic and anthropomorphic statues that have become the most popular symbol of Easter Island. The moais represented deified ancestors and were considered to guarantee land and sea fertility and, hence, social prosperity (Edwards and Edwards, 2013). The socio-political center of the AC was Rano Raraku, the quarry were almost all moais were carved from the relatively soft volcanic tuff that forms this crater using basalt tools (metals were not known) obtained from other craters (Gioncada et al., 2010). During those times, the Rapanui culture flourished and its society attained its population maximum, estimated to be approximately 6,000–8,000 inhabitants (range: 3,000–20,000) (Brandt and Merico, 2015; Puleston et al., 2017). The Rapanui society was organized into clans (**Figure 3**) in a hierarchical pyramidal organization where the maximum authority of the island, the *Ariki Mau*, was invariably the chief of the *Miru* clan, considered to directly descend from the first Polynesian settlers. Rapanui society was organized around the moai industry (carving, transport, and emplacement on their final platforms or *ahu*), and people involved in these tasks, especially sculpture makers, were a privileged class (Flenley and Bahn, 2003). The process of moai building and the related industry has been called *ahu moai*.

The shift to the Birdman Cult (BC) represented a cultural revolution (Robinson and Stevenson, 2017). The cult of the *moais* declined and was eventually abandoned and the religion became monotheistic, with Make Make as the highest deity. The hierarchical dynasty-based political system disappeared and was replaced by a system in which the most powerful people were the clan chiefs and the warrior leaders (*matato'a*). In the BC, the symbols of fertility and prosperity were migratory birds, notably the sooty tern or *manutara* (*Onychoprion fuscatus*) nesting on the surrounding islets, which was considered to be a nexus between the divine and the human worlds (Edwards and Edwards, 2013). The maximum authority (the Birdman or *tangata manu*) or the representative of Make Make on Earth) was renewed yearly following a competition among representatives of all clans. The Birdman of the year was the chief of the clan whose representative (*hopu manu*) was able to swim to the Motu Nui islet, obtain the first sooty-tern egg of the season and carry it back, in intact condition, to the ceremonial village of Orongo, situated on the SW rim of the Kao crater (**Figures 4**, **7**). Therefore, the geographical core of the Rapanui culture shifted from Rano Raraku, the

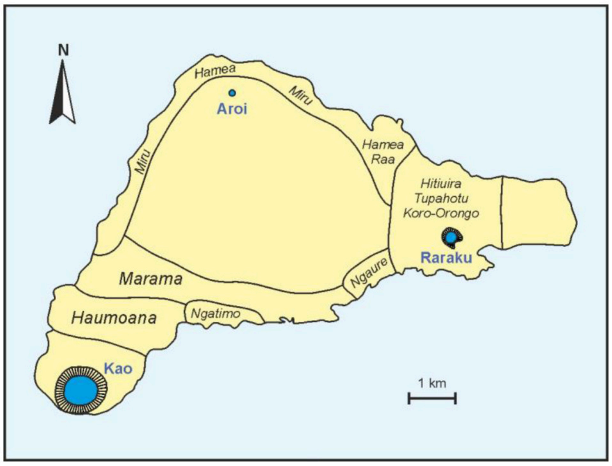

FIGURE 3 | Sketch-map of Easter Island showing the clans of the ancient Rapanui civilization. Redrawn from Routledge (1919).

moai quarry, to Rano Kao, the headquarters of the BC (Kirch, 2000).

The timing of the AC-BC shift has been debated for a long time, mainly on the basis of oral tradition, which may have been subject to historical biases and distortions (Hunt and Lipo, 2011). A minimum age could be provided by the foundation of the ceremonial village of Orongo, the center of the BC (Robinson and Stevenson, 2017) (**Figure 4**). The first excavations, performed by the Norwegian expedition led by Thor Heyerdahl gave radiocarbon ages between 1,540 and 1,576 CE for the beginning of room construction in Orongo (Ferdon, 1961). However, these ages have been considered unreliable due to the lack of accurate sample descriptions (Robinson and Stevenson, 2017) and dubious stratigraphic correlations (Golson, 1965). Robinson and Stevenson (2017) summarized all the reliable chronometric information available from radiocarbon and obsidian hydration dating (Orliac and Orliac, 1996; Stevenson et al., 2013) and concluded that the first petroglyph complexes and stone houses of Orongo are not older than 1,600 CE and the activities on the site experienced an intensification in the very late 18th century (**Figure 5**), well after the European contact (Robinson and Stevenson, 2017).

Additional evidence of human activity in the Kao catchment has been found in the lake shores just beneath Orongo (**Figures 4**, **7**), where pollen, phytolith, and starch analyses of marginal sediment cores have documented relatively intense horticultural activity based on cultigens of Polynesian origin (Horrocks et al., 2012b, 2013, 2016). Unfortunately, sediments had been mixed by human activity, which has prevented the development of a reliable chronological model. Therefore, it is not possible to know whether agricultural activities on lake terraces predated the foundation of Orongo. In summary, the available evidence points toward a minimum age of 1,600 CE for the AC-BC cultural shift. According to Van Tilburg (1996), however, the AC and the BC would have overlapped for some time and the cultural shift would have not been abrupt but transitional (Edwards and Edwards, 2013).

FIGURE 4 | The ceremonial village of Orongo at the SW rim of the Kao crater. See **Figure 7** for the precise location. **(A)** Google Earth view showing the typical ellipsoidal boat-shaped stone houses. **(B)** Close front view of a typical stone house (Photo: N. Cañellas).

The Ecocide Hypothesis

According to the ecocide hypothesis, the AC-BC shift was a direct consequence of the island's deforestation. Based primarily on paleoecological evidence, the proponents of this hypothesis argue that deforestation commenced by 1,200–1,300 CE and was complete by 1,400 CE or, at the latest, by 1,600–1,650 CE (Orliac, 2000; Flenley and Bahn, 2003; Mann et al., 2008; Mieth and Bork, 2010). Mieth and Bork (2010) estimated that, prior to deforestation, ∼16 million palm trees would have dominated the forests that covered ∼70% of the island. The botanical identity of this palm is still a matter of controversy but the dominant view is that the species was endemic to Easter Island and is now extinct (Dransfield et al., 1994). In the ecocide scenario, deforestation would have been part of a general process of natural resource exhaustion by uncontrolled exploitation leading to an ecological crash and a profound crisis of the Rapanui culture (Flenley and Bahn, 2003; Diamond, 2005). Such ecological and cultural collapse would have instigated a general degradation of Rapanui society characterized by dramatic demographic reduction due to starvation, social conflicts and internal warfare, as well as a general and profound reorganization characterized by the shift to the BC. It has also been suggested that the abandonment of the moai cult

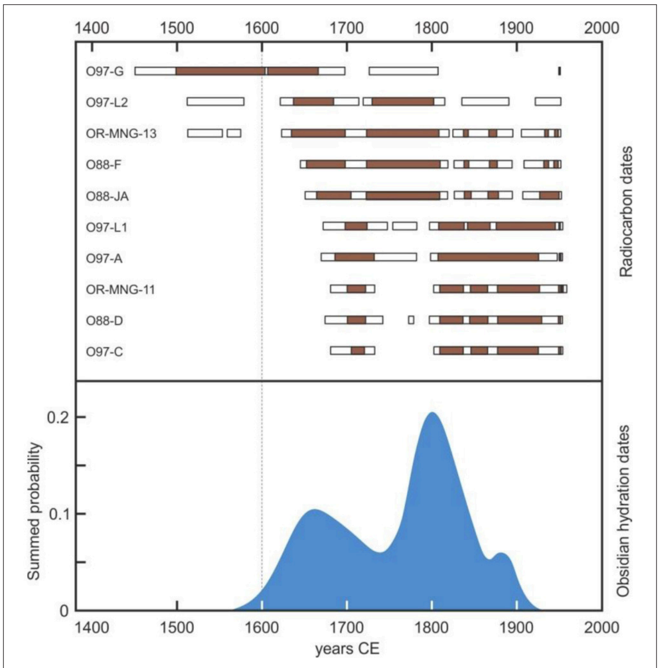

FIGURE 5 | Summary of all reliable radiocarbon and obsydian hydration dates obtained in Orongo. Redrawn from Robinson and Stevenson (2017), after original data from Orliac and Orliac (1996) and Stevenson et al. (2013). Radiocarbon dates are expressed as 1 α (brown bars) and 2 α (white bars) intervals.

included the intentional toppling of these statues, a practice called *huri moai*. According to some model-based estimates, the demographic reduction of Rapanui would have been >80%, from ∼14,000 to ∼2,000 inhabitants (Brandt and Merico, 2015), who lived in precarious conditions, mostly inhabiting lava-tube caves for protection. Some proponents of the ecocide hypothesis interpret the geographical shift of the Rapanui cultural center from Raraku to Kao and the onset of the BC as a manifestation of newly acquired supremacy of western clans over eastern ones (**Figure 3**), which had dominated the scene until then, following internal conflicts (McCall, 1980; Flenley and Bahn, 2003).

Cultural Resilience and the Historical Genocide

An alternative hypothesis is that deforestation was not caused directly by humans but by massive consumption of palm fruits by rats, thus preventing forest regeneration. This idea is based on the frequent occurrence in soils and archeological sites of endocarps of palm fruits with rat gnaw-markings (Hunt, 2006, 2007; Hunt and Lipo, 2011). Rats would have been of Polynesian origin, likely transported by the first settlers (West et al., 2017). In this scenario, the timing of deforestation does not differ considerably from that of the ecocide hypothesis. Regardless of the ultimate cause of deforestation, a number of researchers dismiss the occurrence of social crisis following forest clearing and argue that the Rapanui were resilient to forest removal and remained healthy until European contact (Hunt and Lipo, 2011; Boersema, 2015; Jarman et al., 2017). Analysis of widespread land-use evidence and radiocarbon dates from archeological sites across the island support this hypothesis and suggest that the ancient Rapanui developed sustainable agricultural practices and did not experience a social crisis prior to Europen arrival (Stevenson and Haoa-Cardinali, 2008; Mulrooney, 2013; Stevenson et al., 2015). According to this view, the cultural collapse of Rapanui society was in fact a genocide, which started with the European arrival and was the outcome of direct violence, the introduction of unknown epidemic diseases (smallpox, syphilis, tuberculosis), and slave trading (Hunt and Lipo, 2011). Such post-contact cultural and demographic degradation of the Rapanui society has been confirmed by historical documents (Routledge, 1919; Métraux, 1940) and seems to have been especially intense during the 19th century (McCall, 1980; Fischer, 2005; Boersema, 2015). In this scenario, the AC-BC shift, the deforestation and the collapse of the ancient Rapanui culture are separate events that are not causally linked. A pre-contact population reduction is not dismissed but is attributed to land-use heterogeneities leading to an eventual decline in food production, rather than to a hypothetical island-wide pre-contact collapse, as proposed by the ecocidal theory (Stevenson et al., 2015; Puleston et al., 2017).

Other Hypotheses

Other hypotheses have been proposed to explain cultural changes on the Rapanui during the last millennium. For example, a theory combining elements from both the ecocide and genocide hypotheses was developed by Brandt and Merico (2015), who modeled the demographic evolution of Rapanui society since 1,200 CE and suggested an initial population decline around 1,400 CE, likely linked to deforestation, and a second decline by 1,800 CE, as a consequence of European contact. Others contend that the collapse of Rapanui society would have occurred in a short time period between European contact (1,722 CE) and the visit of Captain Cook (1,774 CE). This is based on the respective navigation logs, the first reporting a healthy society still practicing moai worship and the second documenting a depauperate island with toppled moais. Some speculate that the change must have been due to a catastrophic event between the times of the two visits, such as an internal war (Fischer, 2005; Hunt and Lipo, 2011).

CLIMATIC AND ECOLOGICAL SHIFTS

The hypotheses discussed above attributed ecological and cultural changes on Easter Island to anthropogenic causes and this has become the prevalent narrative. McCall (1993) speculated that climatic changes, especially eventual Little Ice Age (LIA) droughts, should also have had a role. However, this proposal was ignored or explicitly dismissed owing to the lack of empirical support (Flenley and Bahn, 2003). However, the intensification of coring campaigns and paleoecological studies during the past decade have challenged this paradigm (Rull et al., 2013, 2016). For example, Mann et al. (2008) and Sáez et al. (2009) interpreted the sedimentary gap recorded in the

Raraku peaty sediments between about 4.0–4.2 and 0.8 cal kyr BP (**Figure 2**) as evidence for drought and lowered lake levels, which would have caused subaerial exposure and erosion of former wetland sediments. The fairly continuous Raraku and Aroi records obtained later closed the sedimentary gap and allowed for refined paleoecological interpretation, with authors proposing the existence of two episodes of drought at about 880–1,170 CE and 1,570–1,720 CE, respectively (Cañellas-Boltà et al., 2013). The first encompassed most of the Medieval Climate Anomaly (MCA) and the second occurred during the LIA (Rull et al., 2016), supporting the initial proposal of McCall (1993), that there is a connection between climatic severity and Rapanui societal changes. However, the link between environmental and cultural shifts remained unclear (Rull, 2016a). Palynological analysis of the Raraku and Aroi continuous sequences provided more information in this regard.

In the Raraku catchment, a significant forest reduction coinciding with the continuous presence of charcoal was recorded shortly after the MCA drought (880–1,170 CE) (**Figure 6**) and was interpreted as anthropogenic forest clearing using fire (Cañellas-Boltà et al., 2013). The timing is consistent with early deforestation hypotheses and the evidence for burning points toward clearance by humans, rather than deforestation by rats. However, forest removal was not complete and open palm woodlands remained around the lake. It is possible that drought would have increased vegetation flammability by increasing the accumulation of dead biomass or by decreasing the moisture content of live biomass (Bond and Keane, 2017), thus facilitating burning practices. The anthropogenic hypothesis is reinforced by the fact that climatic dryness did not affect the open palm woodlands that covered Rano Aroi area, which was likely inhabited by those times (Horrocks et al., 2015; Rull et al., 2015).

A subsequent humid phase, between about 1,200 and 1,550 CE, coincided with a significant increase of palm forests in Rano Aroi but not in Rano Raraku (**Figure 6**), perhaps due to the continued human pressure (Rull et al., 2016). Indeed, fires persisted in Raraku and the first signs of cultivation appeared around 1,400 CE (Horrocks et al., 2012a). A second deforestation event, linked to an increase in evidence for burning, took place in Raraku by 1,450 CE and palm forests disappeared from the catchment by 1,500 CE (Cañellas-Boltà et al., 2013). In Aroi, wet climatic conditions and the absence of human settlements, would have favored palm forest expansion and/or densification.

During the LIA drought (1,570–1,720 CE), the Raraku catchment was likely devoid of forests and freshwater due to the combination of former human deforestation practices and the drought-induced desiccation of the lake (Cañellas-Boltà et al., 2013). The Aroi forests still remained but were totally removed by 1,620 CE, also with the aid of fire, roughly a century after the deforestation around Raraku (Rull et al., 2015) (**Figure 6**). During this dry phase, by 1,640 CE, Rano Aroi started to be cultivated (Horrocks et al., 2015), which suggests the presence of humans and enough freshwater availability for agriculture. A subsequent humid phase did not change the situation in Raraku, where forests did not recover likely due to the continued fires. A similar situation was recorded in Aroi, where fires peaked at about 1,720 CE and strongly receded later (**Figure 6**).

In addition to climate change, other natural hazards such as regional volcanic eruptions or tsunamis have been considered potential drivers for ecological and cultural change across the

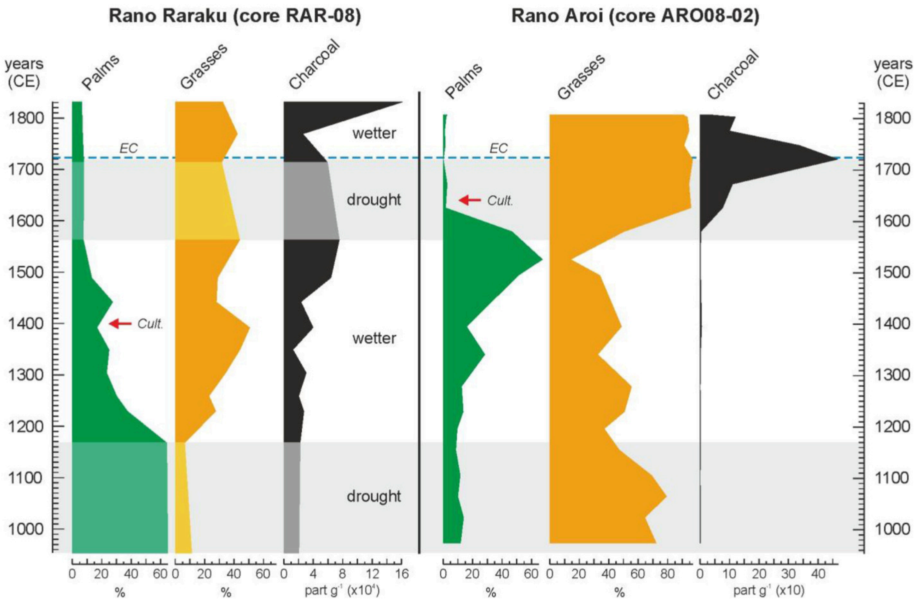

FIGURE 6 | Summary pollen diagrams of Raraku and Aroi continuous sequences for the last millennia. Redrawn from Cañellas-Boltà et al. (2013) and Rull et al. (2015). In Raraku, light-colored areas indicate the sedimentary gaps with no pollen data. Red arrows indicate the first evidence of cultivation according to Horrocks et al. (2012a, 2015). The European contact (EC) is indicated by a dotted blue line.

Pacific archipelagos, including Easter Island (Margalef et al., in press). Evidence for the influence of these environmental shifts on Easter Island is still to be identified in sedimentary records but the interest on verifying this possibility is increasing due to geomorphological and documentary evidence for the impact of historical tsunamis on some coastal moai complexes (Cortez et al., 2009).

AN ALTERNATIVE SCENARIO

The combination of the available paleoecological evidence and the known cultural developments of the ancient Rapanui society described above may provide a new holistic scenario that considers climatic changes and human activities, as well as their corresponding feedbacks and synergies, as the main drivers of Easter Island's ecological and cultural change. This proposal should be considered an integrative hypothesis to be tested with future studies from the different disciplines involved. The overall framework for this integrative hypothesis, tentatively called CLAFS (Climate-Landscape-Anthropogenic Feedbacks and Synergies), is provided hereafter.

The MCA drought (880–1,170 CE) roughly coincided with the time range proposed for initial human settlement. If settlement was early (i.e., between 800 and 1,000 CE), then significant deforestation began 200 to 400 years after Polynesian arrival. This may suggest that resource exploitation had a low impact on vegetation until 1,200 CE when land-use practices became unsustainable (Orliac, 2000; Mann et al., 2008; Mieth and Bork, 2010). If, on the contrary, Polynesian settlement took place later, between 1,100 and 1,300 CE, deforestation practices would have started almost immediately in Rano Raraku. The humid phase between the MCA and the LIA (1,200–1,550 CE) coincided with the *ahu moai* practices characteristic of the AC and the florescence of the ancient Rapanui society. It is possible that favorable weather conditions promoted human population growth thus increasing the demand for food and raw materials, which would have led to the above-mentioned unsustainable land-use practices and exacerbated deforestation likely due to positive feedbacks.

The transition from Ancient Cult to Birdman Cult occurred shortly after the onset of the LIA drought (1,570–1,720 CE), suggesting a novel hypothesis for the cultural change and the corresponding geographical displacement of the Rapanui cultural core (Rull, 2016a). During this drought, Rano Raraku was a very inhospitable place devoid of forests and freshwater due to the synergistic action of climatic drought and unsustainable human practices. As a consequence, lifestyles and cultural developments characteristic of the ancient Rapanui society that practiced the AC would have become unworkable. The Rapanuis might have been forced to abandon the catchment in the search for freshwater and other natural resources. It is likely that part of the Rapanui population migrated to Rano Aroi by 1,500–1,600 CE, where forests and freshwater were still available, but the small size of this catchment would have led to quick resource exhaustion after 1,620 CE. The other option for relocation was Rano Kao, which contained a large and permanent lake that could provide freshwater and possibly more extensive forests to exploit. According to the available chronological evidence, Orongo, the center of the BC, was founded by 1,600 CE (Robinson and Stevenson, 2017), shortly after the beginning of the LIA drought, which is consistent with the idea that the Rapanui migrated in search of more favorable living conditions. It is also possible that the environmental deterioration of Rano Raraku contributed to an eventual superiority of western clans (**Figure 3**) due to their permanent freshwater supply from Lake Kao.

The walls of the Rano Kao vent are made of basalt, which is too hard for moai carving with the rocks available on the island (the Rapanui was a Neolithic society that did not know metals). Indeed, stone tools used during the *ahu moai* phase of statue carving were obtained in Rano Kao and other quarries, where basalt was hard enough to sculpt the softer Raraku tuff (Gioncada et al., 2010; Simpson and Dussubieux, 2018). This could explain, in part, why the relocation of the Rapanui cultural center to Rano Kao coincided with the decline of moai carving and the shift to different ritual practices. The shift to a radically different lifestyle and social organization requires a more complex explanation. As we mentioned before, the flourishing of the Rapanui civilization occurred during a phase of wet climate and the oncoming LIA drought, along with the deforestation of the craters containing freshwater, would have been unfavorable for population growth. In this context, it has been speculated that a more flexible socio-political organization would have increased human adaptability to less predictable environmental and probably unprecedented conditions. The shift from the AC rigid, hierarchical and dynasty-based political system to the more dynamic BC system, based on the continuous political renovation has been interpreted in terms of cultural adaptation to more unpredictable environmental conditions (Rull, 2016a).

Some archeological evidence for intra-island cultivation shifts is consistent with this CLAFS view. Stevenson et al. (2015) suggest that the AC-BC cultural transition was associated with reductions in land-use intensity in the drier sectors of the island and in infertile soils from upland areas, which increased land pressure in other parts of the island. Similar intra-island migrations, notably from coastal to inland sites, have been reported for many other Pacific islands by the same LIA times (Nunn, 2003, 2007; Nunn et al., 2007). From a paleoecological perspective, a continuous and coherent Kao record similar to those of Raraku and Aroi is essential to resolve deforestation trends and patterns over time and across space, in relation to cultural developments.

LAKE KAO AND THE NEW RECORD

The Lake and Its Sediments

Rano Kao is the largest freshwater body of Easter Island with about 1,250 m diameter and >10 m of maximum water depth (**Figure 7**). A notable feature of this lake is the presence of a discontinuous floating mat typically up to ∼3 m depth that forms a mosaic with open water spots all around the lake surface. The floating mat is dominated by *Scirpus californicus* (Cyperaceae) and *Polygonum acuminatum* (Polygonaceae) a common association in the island's freshwater bodies (Zizka, 1991). According to the available information, this floating mat formed during the last 900–1,000 years by progressive accumulation of plant remains; therefore, during roughly the last millennium, sediments (and therefore proxies for ecological change) have been accumulating on both the floating mat (developing a peat-like deposit) and at the lake bottom (as lacustrine sediments) (Rull, 2016b). It has been suggested that these two archives have been partially mixed by the eventual sinking of mat fragments to the lake bottom, causing the observed chronological anomalies in the Kao sedimentary sequence (Butler et al., 2004). This idea is supported by the morphological patterns of the floating mat mosaic, where the mostly sharp and straight edges of vegetation patches (**Figure 7**) suggest disaggregation and sinking of mat fragments. Therefore, it seems reasonable to assume that best likelihood for a continuous and coherent paleoecological record of the last millennium would be found within the floating mat, rather than in the lake-bottom sediments.

Eight coring localities within the lake basin have been documented: six near the lake shores, one close to the lake center, and another in an intermediate position (**Figure 7**). The more marginal sites have provided composite sequences where the floating mat overlies the bottom sediments, whereas in more central localities, the floating mat and the bottom sediment records are separated by a water column of variable depth, up to ∼10 m. The longest sequences retrieved from the lake are of ∼10 to 20 m depth, and have maximum ages between ∼15 and ∼34 cal kyr BP, respectively (Gossen, 2011; Horrocks et al., 2013). These cores did not reach the bedrock and the total depth of Kao sediments remains unknown.

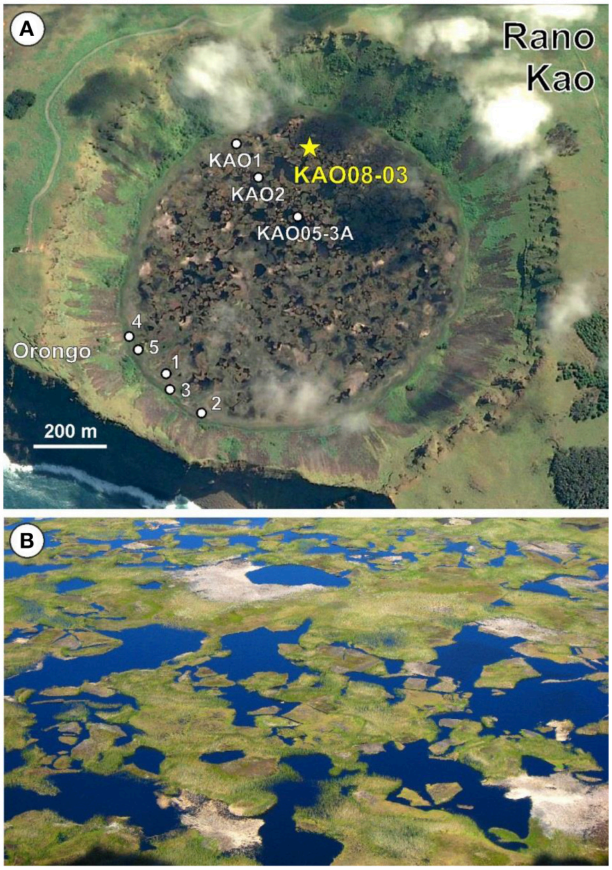

FIGURE 7 | Rano Kao. **(A)** Google Earth view of Rano Kao indicating the coring sites from previous works (white dots) and the locality described in this paper (yellow star). The ceremonial village of Orongo is also indicated. Redrawn from Rull (2016b). **(B)** Close up of the floating mats around the center of Lake Kao. Note the sharp and angular nature of most mat/water contacts (Photo: O. Margalef).

The KAO08-03 Core Record

The new sedimentary record reported in this paper (KAO08-03; 27° 10′ 57.526″ S - 109° 26′ 7.591″ W; 109 m elevation) was taken in October 2008 with a Russian corer, on a floating mat close to the northernmost lake shore (**Figure 8**). The uppermost part of the core was water and the sedimentary record started at 80 cm, extending downward until 300 cm, which was the depth of the floating mat at the coring point. The sediment consisted of fibrous peat, light to dark brown in color. The core (consisting of five drives) was sealed and transported to the Institute of Earth Science Jaume Almera (ICTJA, Spain), where it was preserved in a cool chamber at 4°C.

Nine samples were obtained for radiocarbon dating, which was conducted at the Radiocarbon Laboratory of the Université Laval (Canada). We used pollen extracts obtained by acid/base digestion (KOH, HCl and HF) to remove the rejuvenating effect of eventual incorporation of younger plant material and/or humic acids percolating through the peat profile (Vandergoes, 2003). All samples yielded ages corresponding to the last millennium except one (**Table 1**), which was considered

FIGURE 8 | Coring the Rano Kao floating mat. **(A)** Two members of the 2008 expedition (V. Rull and S. Pla) coring the floating mat of Rano Kao with a Russian corer at site KAO08-03. **(B)** Drive 2 (131-181 cm) of core KAO08-03 showing the fibrous brown peat.

TABLE 1 | Results of radiocarbon dating carried out at the Radiochronology Lab of the Université Laval (Canada).

Core sample	Lab code	Depth (cm)	Material	^{14}C yr BP	Cal yr BP	Range (2σ)	Prob.
KAO3-1-24	ULA-5790	106	Pollen residue	305 ± 15	312	289–327	0.805
KAO3-1-43	ULA-5792	125	Pollen residue	290 ± 15	304	283–323	0.988
KAO3-2-39	ULA-5789	141	Pollen residue	355 ± 20	392	350–452	0.816
KAO3-2-20	ULA-5791	160	Pollen residue	470 ± 20	499	468–516	1.000
KAO3-6-15	ULA-5872	196	Pollen residue	695 ± 15	597	563–658	1.000
KAO3-6-35	ULA-5821	216	Pollen residue	885 ± 20	748	720–791	0.967
KAO3-7-16*	ULA-5874	247	Pollen residue	5060 ± 20	5755	5658–5891	1.000
KAO3-7-40	ULA-5817	271	Pollen residue	1060 ± 20	934	906–962	0.977
KAO3-8-12	ULA-5873	297	Pollen residue	1165 ± 15	1017	968–1059	1.000

Samples are sorted by total depth. The sample with an asterisk was not used in the age-depth model.

anomalous and was excluded from the age-depth model. This type of anomalies have been attributed to an increase of the reservoir effect due to (i) punctual increases of aquatic plants, (ii) reductions in CO_2 exchange with the atmosphere due to increase of depth-to-surface ratio, (iii) incorporation of older oxidized organic matter from former shore-lake lacustrine deposits, and (iv) inflows of CO_2-rich waters due to volcanic degassing or eventual inputs from nearby aquifers (Philippsen, 2013). In our case, the more probable causes were (i) and (iii) but more detailed studies are needed for a sound assessment. Radiocarbon calibration was carried out with CALIB 7.1 (calib.org/calib) using the SHcal13 database for the Southern Hemisphere (Hogg et al., 2013). Age-depth modeling was done using the smooth-spline option (smoothness 0.4) in the Clam.R 2.2 software (Blaauw, 2010). The model obtained shows strong chronological coherence and continuity, indicating that the record can provide a detailed and continuous paleoecological reconstruction for the last millennium, and can provide comparison with the main cultural and ecological events discussed above (**Figure 9**). We also tried the Bayesian age-depth model called Bacon (using R programming) for comparison (Blaauw and Christen, 2011). Results are shown in Figures S1, S2 of the Supplementary Material, where it can be realized that differences in estimated ages are small and non-significant.

A total of 107 samples were collected from the core, 55 for palynological analysis and 52 for lipid analysis, providing an average resolution of <20 years between adjacent samples. Palynological analysis is in progress at the Laboratory of Paleoecology of the (ICTJA), and consists of analysis of pollen, spores, microcharcoal and non-pollen palynomorphs (NPP), notably the spores of coprophilous fungi. These proxies will provide information on deforestation, fires, and the eventual presence of introduced plants and domestic animals (Bennett and Willis, 2001; Van Geel, 2001; Whitlock and Larsen, 2001). These samples will also be used to conduct macrocharcoal analyses for a better record of local fires and also to try to distinguish fuel types (Aleman et al., 2013), notably palms and grasses. Lipid analysis is being carried out at the Lamont-Doherty Earth Observatory (LDEO) of Columbia University (USA). This analysis is aimed at identifying specific fecal lipids, including 5α-stanols and bile acids, biomarkers for the presence of humans and/or ruminant livestock (Leeming et al., 1996; Bull et al., 2002; D'Anjou et al., 2012). Together, this suite of analyses is expected to provide direct *in situ* evidence for the level of human activity in and around the catchment.

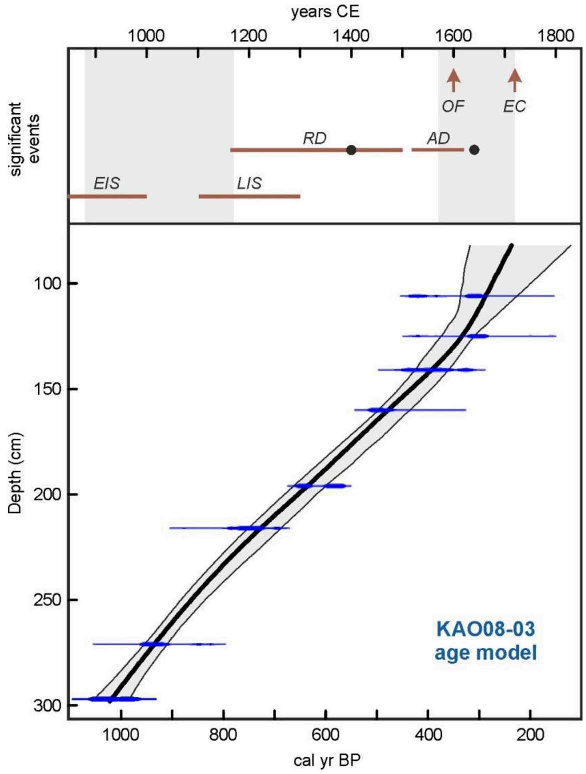

FIGURE 9 | Age-depth model of core KAO08-03 using the smooth-spline option. See text and **Table 1** for more details. The upper part of the figure shows some significant events discussed in the text. Gray bands are the droughts recorded at Rano Raraku (Cañellas-Boltà et al., 2013). EIS, Proposed range for early island settlement (Flenley and Bahn, 2003; Vargas et al., 2006); LIS, proposed range for late island settlement (Hunt and Lipo, 2006; Wilmshurst et al., 2011); RD, Rano Raraku deforestation (Cañellas-Boltà et al., 2013), the black dot indicates the first evidence of cultivation (Horrocks et al., 2012a); AD, Rano Aroi deforestation (Rull et al., 2015), the black dot indicates the first evidence of cultivation) (Horrocks et al., 2015); OF, Foundation of the ceremonial village of Orongo (Robinson and Stevenson, 2017); EC, European contact.

SOME TESTABLE PREDICTIONS

Hypothesis tests that can be conducted with the new Kao record concern the timing of human occupation and deforestation of the Kao catchment, whether these events were simultaneous or not, and the rates at which they occurred. Comparison of the new Kao records with those from Raraku and Aroi could provide the pan-island, continuous, and coherent paleoecological reconstruction of the last millennium. Regardless the results obtained, further archeological evidence will be necessary to examine their cultural implications. Among the predictions of the CLAFS scenario, the following could be highlighted:

The CLAFS hypothesis predicts that evidence for full human occupation of the Kao catchment should be found close to the date of the foundation of Orongo (∼1,600 CE). An earlier occupation cannot be dismissed but, under the CLAFS hypothesis, this would have been minimal with a significant increase ca. 1,600 CE. If the Kao catchment was fully occupied before the LIA drought (1,570–1,720 CE) and there is no evidence supporting a population increase at Kao by 1,600 CE, the CLAFS hypothesis should be reconsidered in favor of alternative hypotheses, such as the ecocide hypothesis. If a population increase is found to have occurred later than 1,600 CE, the migration to Kao, and possibly the onset of the BC, could conceivably have been influenced by European contact (1,722 CE), as has been suggested by some researchers (Robinson and Stevenson, 2017).

Regarding deforestation, the CLAFS scenario is compatible only with spatio-temporal heterogeneities; that is, with different deforestation timing among Aroi, Raraku and Kao. Evidence for this already exists for the first two sites, for which the onset of deforestation appears to have been separated by several centuries (**Figure 6**). The CLAFS hypothesis predicts that deforestation of the Kao catchment coincided with the intensification of human activity at the site ca. 1,600 CE, similar to the timing of forest clearing at Aroi. Again, an earlier deforestation, coeval with that of Raraku, would instead favor ecocide hypothesis, whereas a later forest clearing, after the LIA drought, would support the influence of post-contact events. Under the CLAFS scenario, it is expected that deforestation and fire occurrence, as inferred from sedimentary charcoal counts, are strongly related, as has been observed for Raraku and Aroi (**Figure 6**). However, while the coincidence of proxies for fire, deforestation, and human presence support anthropogenic forest clearing practices, such a co-occurrence cannot distinguish between the CLAFS and ecocide hypotheses.

It is important to note that there are no unique predictions under the CLAFS hypothesis concerning rates of Kao deforestation and human settlement. Possibilities include (1) fast and synchronous events, as inferred for Aroi (**Figure 6**), (2) early settlement and gradual deforestation, as inferred for Raraku, and (3) gradual settlement and abrupt deforestation.

ALTERNATIVE SCENARIOS

There also remains the possibility of obtaining unexpected results. Some of these eventual findings could support the CLAFS hypothesis while others do not, in which case the working hypothesis should be reconsidered or reformulated to become more general. We are not particularly attached to any specific hypothesis, but rather in the explanation that best fits the entire body of available evidence. We use the multiple working hypotheses approach that seeks to explore any reasonable explanation for observed phenomena and develop every testable hypothesis (Chamberlin, 1965). In this framework, the CLAFS model should be viewed as a research tool to be subjected to scrutiny through hypothesis testing, and improvement or rejection, just as any other hypothesis. It is possible that paleoecological analysis of the new Kao record will suggest a different framework for understanding the complexities of the Rapanui, thereby promoting new unexpected ideas, in which case, the results will inspire new opportunities for a better understanding of Easter Island's prehistory.

CONTRIBUTION TO GLOBAL DATABASES

The results obtained in this and future research on core KAO08-03 will be contributed to the EIRA database (https://www.ncdc.noaa.gov/paleo-search/study/19805) (Rull, 2016b) in the case of radiocarbon dates, Global Charcoal Database (http://paleofire.org) for charcoal data and Neotoma (http://neotomadb.org) for pollen counts.

AUTHOR CONTRIBUTIONS

VR: Conceived and wrote the paper; EM: Did the age-depth model; IS and WD: Processed and analyzed samples; VR, NC-B, OM, SP-R, and SG: Obtained the core. All authors contributed to the manuscript with ideas, comments, edits and references, and approved submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00032/full#supplementary-material

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