ORIGINAL ARTICLE

Abrupt late Pleistocene ecological and climate change on Tahiti (French Polynesia)

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ABSTRACT

Aim To reconstruct ecological changes from the fossil record of a unique wetland on the tropical oceanic island of Tahiti, between 44.5 and 38 cal. kyr BP.

Location Vaifanaura'amo'ora, Tamanu Plateau, Punaru'u Valley, Tahiti, Society Islands, French Polynesia (17°38′S, 149°32′50″E).

Methods Fossil pollen, spores, seeds, diatoms and invertebrates were examined from a 3.7 m core consisting of Pleistocene-aged algal sediment overlain by late Holocene peat.

Results Between 44.5 and 41.5 cal. kyr BP, *Ficus* trees, sub-shrubs including *Sigesbeckia orientalis* L., the C_4 grass species *Paspalum vaginatum* Sw., and extinct *Pritchardia* palms dominated the Vaifanaura'amo'ora wetland. This vegetation association is no longer present in the tropical oceanic Pacific islands. After 41.5 cal. kyr BP, the climate rapidly became drier and cooler with grasses, sedges and ferns dominating the vegetation. Algal sediment accumulation ceased after 38 cal. kyr BP due to prolonged dry climate conditions recorded across the Pacific Ocean. Sediment accumulation recommenced in the late Holocene.

Main conclusions The ecological responses identified from Tahiti provide evidence counter to the prevailing view that the tropical oceans buffered the ecological effects of abrupt climate changes during the last glacial period.

Keywords

climate change, multiproxy analyses, Pacific Ocean, Pleistocene, precession-forcing, tropical oceanic islands, vegetation change

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INTRODUCTION

The relatively young geological age and high endemic biodiversity of tropical oceanic islands make them important for understanding evolutionary processes (Gillespie *et al.*, 2008). Endemism on these islands is often thought to have accumulated under stable climate conditions, with some authors suggesting, for example, that the thermal mass of the oceans buffered any climatic extremes during glacial periods (Jansson, 2003). The ecological responses of island biota to the last glacial period (here referring to Marine Isotope Stage 3, MIS 3 between 60 and 27 ka, van Meerbeeck *et al.*, 2009), however, are poorly understood, yet this period is perhaps typical of climate conditions experienced since island emergence (Whittaker & Fernández-Palacios, 2007). Most of the tropical oceanic islands in the Pacific Ocean currently lie within the Inter-tropical Convergence Zone (ITCZ) and the South Pacific Convergence Zone (SPCZ), which influence regional rainfall patterns more than temperature changes (Leduc *et al.*, 2009). While geochemical evidence has shown rapid shifts in these globally important climate systems during MIS 3, evidence for ecological responses is limited (Clement & Peterson, 2008).

Most existing MIS 3 records from the tropics are continental and have revealed highly variable ecological responses to obliquity or precession-forcing. These records may also have been influenced by internalized continental climate processes or human activity. In western South America, high-elevation sites near the ITCZ reveal changes in tree lines and/or low-latitude glacier advances or retreats that respond to obliquity forcing. Precession-forcing, however, may be more important in adjusting the expanse of forest at

low-elevation sites (<1000 m a.s.l., e.g. Bogotá-A *et al.*, 2011). In north-eastern Australia, pollen records from Lynch's Crater at ~700 m a.s.l. indicate substantial vegetation change that may signal responses to precession-forcing or human-induced burning between ~45 and 40 ka (Kershaw *et al.*, 2007; Rule *et al.*, 2012). By contrast, in subtropical Taiwan, at Toushe Basin (~650 m a.s.l., Fig. 1), wet and temperate deciduous forest (in the apparent absence of human activity) prevailed throughout MIS 3 with increased wet periods between ~42 and 37 cal. kyr BP (Liew *et al.*, 2006).

In order to address the role of MIS 3 climates in shaping the terrestrial ecosystems of the tropical oceanic Pacific islands, unaffected by human activity, we present a rare 'snapshot' of ecological changes on Tahiti. A unique wetland, 4 ha in size, at 580 m a.s.l., was cored to a depth of 3.7 m revealing MIS 3 and late Holocene-aged sediments. Using multiple fossil proxies, we compare Tahiti with other oceanic islands in the region and continental sites at similar latitude. We also compare this MIS 3 record to the late Holocene, represented in the upper 85 cm of the core, but also with a lake core from Vaihiria (Parkes *et al.*, 1992), in order to better understand the response of key taxa to climate change.

MATERIALS AND METHODS

Study site

Tahiti is 1045 km^2 in area and the largest high island in the Society Islands, French Polynesia (Fig. 1). The island emerged from a geological hot spot located near the island of Mehetia, 110 km east of Tahiti by 870 ka (Devey & Haase, 2004; Hildenbrand *et al.*, 2008). Tahiti has since undergone extensive erosion leading to deep and broad valleys separating sharply ridged mountains that rise to above 2200 m a.s.l. The ~400 ha surface of the Tamanu Plateau, in the Punaru'u Valley (Fig. 2) is mostly composed of mid-Pleistocene breccia deposits formed from the remnant flanks of the two main Tahiti-Nui calderas (Hildenbrand *et al.*, 2008). In situ cementation processes probably smoothed the relief which may explain why the plateau, that is no older than 450–500 ka, has a flat surface with a rounded shape in aerial view (Hildenbrand pers. comm. 2013, Fig. 2).

The climate of Tahiti, particularly precipitation, is strongly linked to the inter-annual variability of the SPCZ and the El Niño Southern Oscillation (ENSO). Annual rainfall on the western leeward coast is ~1500 mm, but averages more than 8 m on the sharp relief of the windward montane valleys,
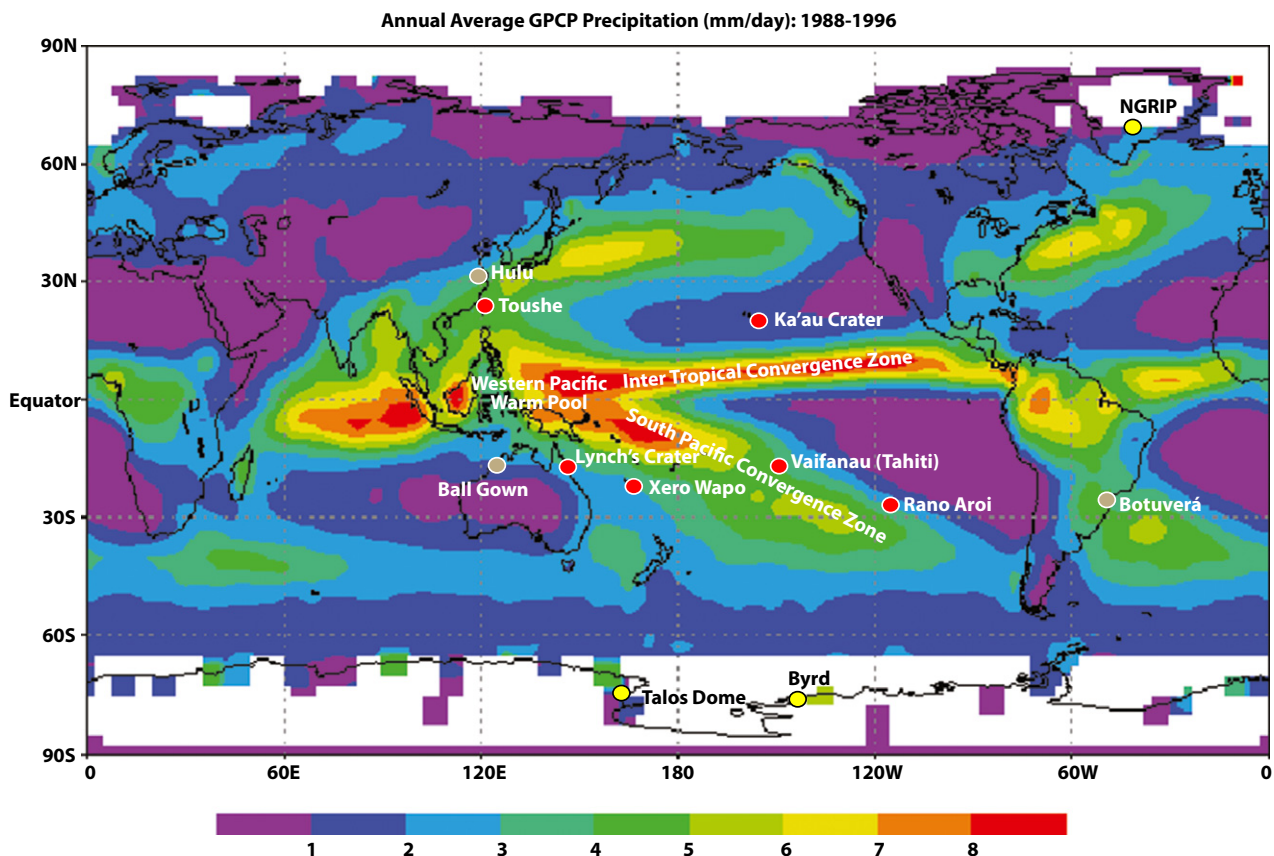

Figure 1 Map of Pacific showing the precipitation data from the Global Precipitation Climatology Project (GPCP, http://precip.gsfc.nasa.gov/). Highlighted are the positions of the main climate systems, the key palaeoecological sites (red circles), speleothem records (grey circles) and ice cores (yellow circles) mentioned in the text.
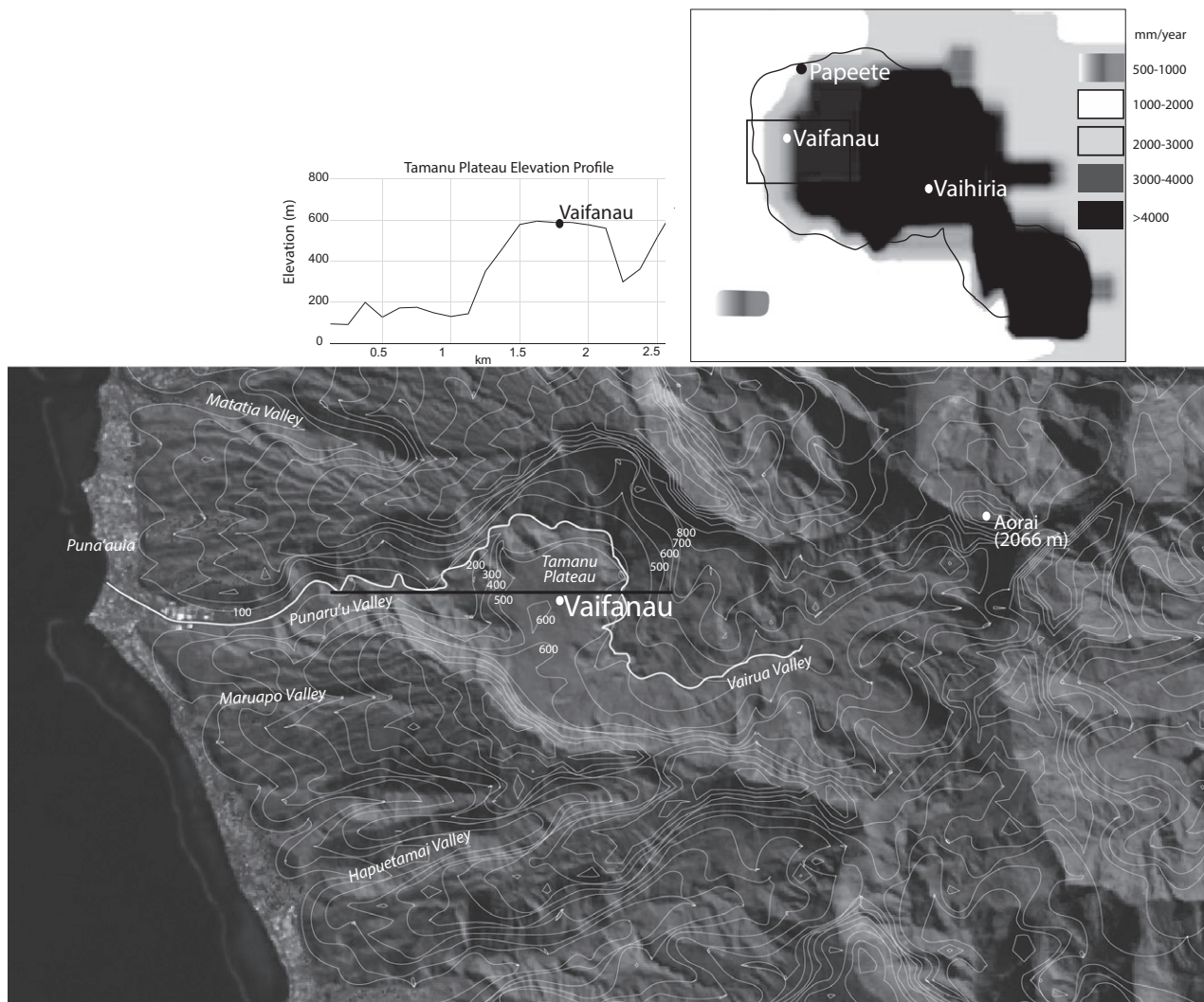
Figure 2 Map of location of the Vaifanau mire and Vaihiria lake on Tahiti (top-right) with precipitation data taken from the TRMM 234B radar series (http://trmm.gsfc.nasa.gov/). The bottom map shows the location and topography of the Punaru'u Valley and west-east elevation profile of the Tamanu Plateau (black line, data presented in top-left graph). Both the digital elevation model derived contours and hillslope shading, and the elevation profile are generated from the NASA SRTM global 1 arc second dem (v3.0) dataset (http://www2.jpl.nasa.gov/srtm/) using the Google Earth Engine API interface (https://earthengine.google.org/).

and has reached 11 m during extreme years due to strong orographic precipitation (Wotling *et al.*, 2000; Fig. 2). The Tamanu Plateau and Vaifanaura'amo'ora (here abbreviated to Vaifanau), a perennial ombrotrophic mire, is in a more leeward location, and receives an average annual rainfall of ~3835 mm (TRMM 234B 1998–2012, http://trmm.gsfc.nasa.gov/, Fig. 2).

Most indigenous and endemic flora and fauna on Tahiti (see Hembry & Balukjian, 2016; Meyer, 2010) are generally located at high elevation in montane cloud-forests and on subalpine ridges (see Table S1.1, Appendix S1 for a description of the main vegetation zones), with the remaining endemics persisting in marginal littoral/para-littoral zones that have escaped the impact of human activities and invasive species (Meyer, 2004). The Vaifanau mire lies at the interface between the paralittoral, xeric/mesic and montane cloud-

forest vegetation, making it an ideal place to explore climate−vegetation relationships. Introduced herbaceous weeds, including *Ludwigia octovalvis* (Jacq.) P.H.Raven, *Commelina diffusa* Burm.f. and *Persicaria glabra* (Willd.) M.Gómez., have infested the mire over the last 30 years, forming root-bound material which has in-filled a small pond (N. Tutavae-Estall pers. comm. 2011).

Sampling and analyses

Sediment cores were obtained from the approximate centre of the mire in 2011 using a 50 mm diameter Russian D-Section corer. Coring continued until an impenetrable mineral layer (not bedrock) was reached at 3.7 m in depth. A single core (RWMP1211-01) was collected for palynomorph analyses to determine the baseline vegetation changes, and

was sampled at 5 cm intervals. Each 1 cm³ sample was processed using standard procedures (10% HCl, hot 10% KOH − where necessary, and acetolysis for all samples) described by Moore *et al.* (1991). All samples were spiked with exotic *Lycopodium clavatum* L. tablets (20,848 spores) to calculate the palynomorph concentrations. The concentrations of microscopic charcoal particles (<80 μm), were also counted from the same palynomorph samples (in proportion to the *L. clavatum* spike), as a proxy for regional fire activity (Whitlock & Larsen, 2002). The core was also sampled every 1 cm³ for macrocharcoal particles (>250 and >125 μm in size) following Whitlock & Larsen (2002), to reconstruct local fire activity.

Palynomorph (pollen, pteridophyte and bryophyte spores) identification was assisted by the examination of reference material held at the Australian National University (ANU) and in the Australasian Pollen and Spore Atlas (www.apsa.anu.edu.au). All palynomorph names refer to the family or genus of an extant taxa and their nearest modern affinity (see Table S1.2, Appendix S1). The percentages of palynomorphs, microcharcoal and total palynomorph concentration data were placed into stratigraphic diagrams (Figs 3 & 5a; Figs S3.1 & S3.3, Appendix S3), as for all fossil data, using the program C2 DATA ANALYSIS (Juggins, 2005). Zonation of the MIS 3 stratigraphic diagrams for all proxies is based on the main changes in the palynomorph assemblages assessed using CONNISS (Grimm, 1987).

In order to determine the hydrological stability of the site, diatoms (Fig. 3; Fig. S3.2, Appendix S3) were processed from 1 cm³ samples from the same core and sampling depths as the palynomorph analyses using standard processing procedures (e.g. hot 10% HCl, hot 30% H_2O_2, Battarbee *et al.*, 2002). The taxonomic and ecological affinities were assessed using tropical Pacific Ocean diatom publications (e.g. Foged, 1987), and by consultation with K. Wolowski (pers. comm., 2013). The nomenclature is based on http://www.algaebase.org.

Three additional D-Section cores were collected in parallel with the main Vaifanau core (RWMP1211-02, 03, 04) in order to derive enough material for macrobotanical and macroinvertebrate analyses. These analyses contribute information on the localized ecological responses and additional data on biodiversity changes. The cores were scraped back in the field, to remove any potential contaminants, and cut into 10 cm long bulk-sediment samples for macrofossil analyses. The volume of each sample varied but averaged at ~150 mL. In the laboratory, samples were gently washed through a series of nested sieves (between > 250 μm and > 2 mm) for sorting. All diagnostic macrofossil remains of both invertebrates and plants were separated under stereomicroscopy and counted as minimum number of individuals (MNI). Macroinvertebrate remains (Figs 4 & 5b), including all arthropods, were identified by comparison with a reference collection from French Polynesia held at Deakin University, and images of material from the Bernice P. Bishop Museum, Honolulu. The concentrations of Diptera mandibles found in the palynomorph preparations were calculated, as for other palynomorphs, and used as an additional marker of hydrological stability.

Plant macrofossils (Figs 3 & 5b; Fig S3.1, Appendix S3), comprised mostly of seeds, were identified by comparison to specimens accessioned at the Allan Herbarium (CHR), Lincoln, New Zealand; the Musée de Tahiti et des Iles (PAP), Tahiti; and an Asia/Pacific regional reference collection held at the ANU. Most seeds are within the families Asteraceae and Cyperaceae and were compared with reference material from the Australian National Herbarium (ANH); references on New Zealand plants (e.g. Webb & Simpson, 2001).

The chronology for the Vaifanau sequence was established using nine accelerator mass spectrometry (AMS) radiocarbon measurements based on plant macrofossils (Table 2; see Fig. S2.1, Appendix S2). The calibrated ages were calculated using the program OXCAL 4.3 (Ramsey, 2009) with IntCal13 calibration data (Reimer, 2013). The sediment does not contain carbonates, and the water at the mire surface is slightly acidic. All except two of the nine radiocarbon samples were from *Sigesbeckia orientalis* L. (Asteraceae) achenes retrieved from the bulk-sediment samples. We used the Poisson-process depositional model in OXCAL 4.3 to build a Bayesian age model for the core (Ramsey, 2008).

Magnetic susceptibility, bulk organic δ¹³C and δ¹⁵N isotopic measurements were also completed as additional measures of environmental changes (see Fig. S2.2, Appendix S2). A multivariate analysis comparing late Holocene (including Vaihiria, Parkes *et al.*, 1992) with MIS 3 assemblages was also applied to the palynomorph data, in order to approximate Pleistocene climate conditions on Tahiti (see Fig. S3.4, Appendix S3).

RESULTS AND INTERPRETATION

Stratigraphy and chronology

The core consists of fine brown algal gyttja from 350 to 85 cm with no evidence of coarse grain mineral sedimentation, but some compacted clay is present at the base from 370–350 cm. Organic matter is very high as no hydrofluoric acid treatment was required to remove mineral content during palynomorph processing. No carbonate or manganese content was observed in any of the sediments suggesting that there is limited potential for old carbon effects on radiocarbon dating. Above the algal gyttja sequence, the sediment is characterized by a sharp transition to dark-brown/black peaty sediments at ~85 cm in depth, which grades to root-bound material from 40 cm to the mire surface (see Fig. S2.3, Appendix S2).

Macrofossils, particularly seeds, were prevalent in the core dated below 85 cm, and we focused on the abundant achenes of *Sigesbeckia* due to their assumed reliability for radiocarbon dating (Figs 3 & 7). In parts of the core, in which fewer achenes were available, bark or twig material (not identified to taxa) was dated. One date is beyond radiocarbon calibration (> 45 cal. kyr BP, Reimer, 2013), and the basal date is
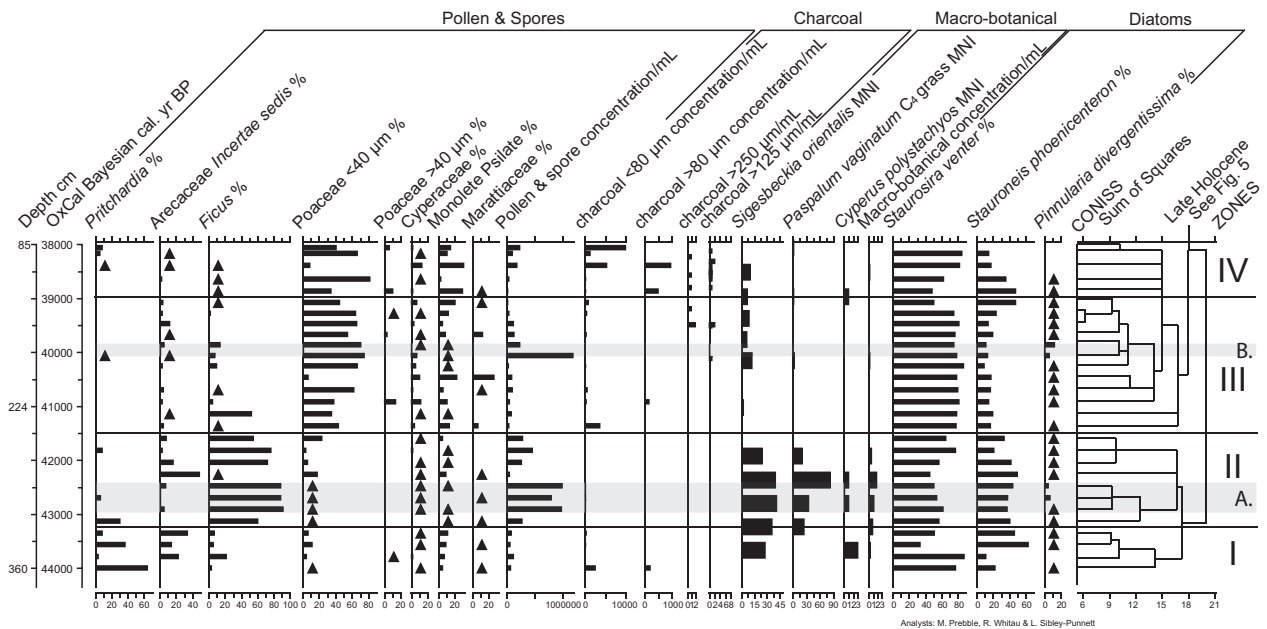
Figure 3 Stratigraphic diagram for the main palynomorphs, macrobotanical remains (MNI = (minimum number of individuals) and diatoms recorded in the MIS 3 record of the Vaifanau core (RWMP1211-01). The remaining MIS 3 botanical data are presented in Fig. S3.1, Appendix S3. Taxa are arranged according to depth and radiocarbon chronology (left column) and first appearance using the sort function in C2 DATA ANALYSIS. The triangles represent data points with < 2% of the total sum. Concentration data, including charcoal particles (from palynological preparations) and macrocharcoal, are also presented. Two sections (A & B) indicating different preservation conditions are highlighted and discussed in the text. The four zones (right column) are based on the palynomorph changes revealed in the CONISS analysis.
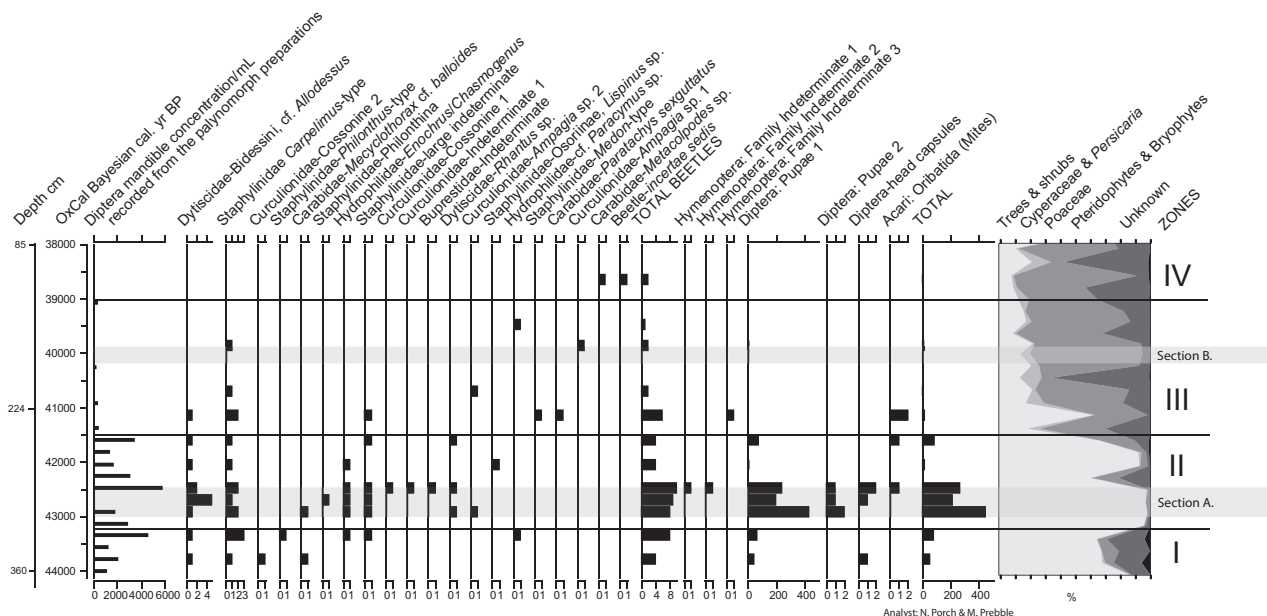

Figure 4 Stratigraphic diagram of the macroinvertebrate data (MNI) from the MIS 3 record of the Vaifanau core. Taxa are arranged as for Fig. 3. Also included in the diagram are the concentration data for Diptera mandibles (identified in the palynomorph preparations; left), further indicators of wet conditions, counted from the palynomorph preparations, and a summary of the palynomorph percentage data (right) for comparison with the main vegetation changes.

inverted, thus we excluded these resulting ages from subsequent analyses (Table 2; Fig. S2.1, Appendix S2). The sediment stratigraphy of the core changed from compacted clay and algal sediments at the base to algal gyttja sediments, and

this may have produced an age inversion as the pond began to infill. Other Pacific Island sites (e.g. New Caledonia and Easter Island) have frequent age inversions that may have resulted from similar sedimentation patterns, but also
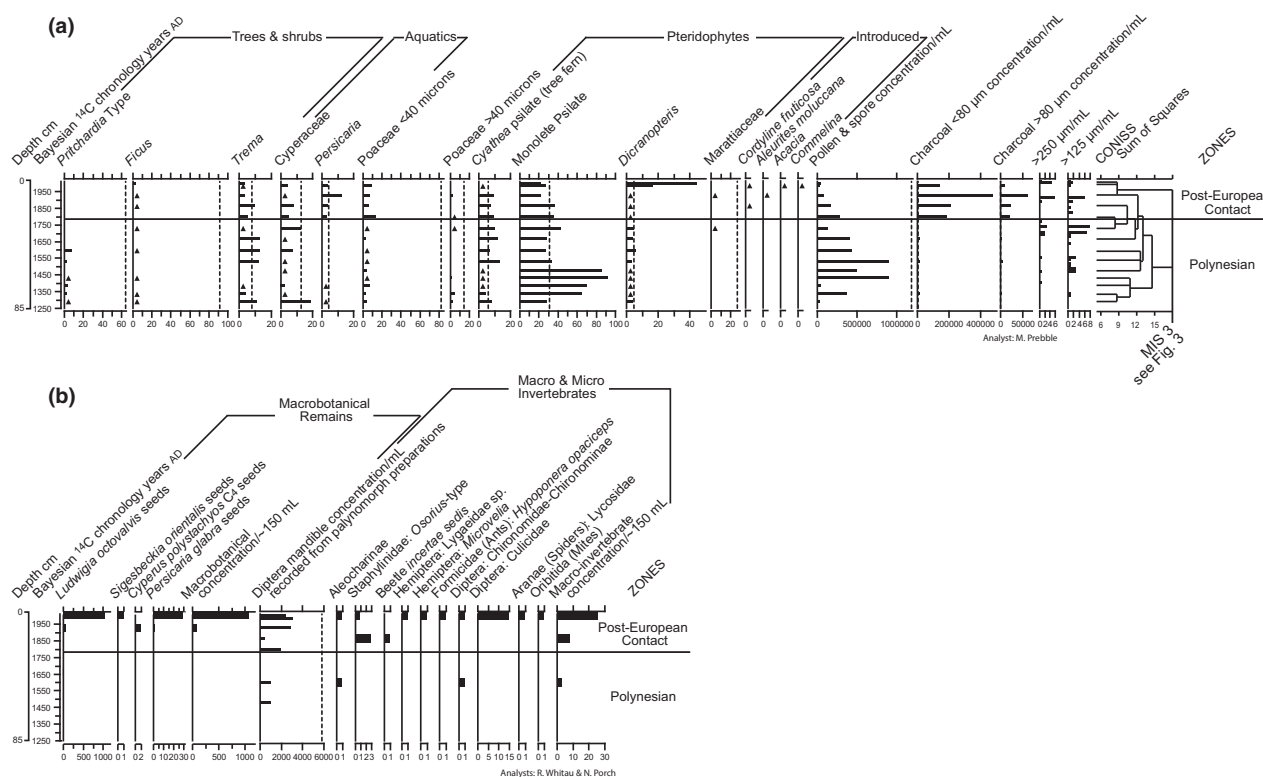
Figure 5 Stratigraphic diagram for the main palynomorphs and macrofossil remains (plant and invertebrate as MNI) recorded in the late Holocene record of the Vaifanau core (RWMP1211-01). The remaining Holocene botanical data are presented in Fig. S3.3, Appendix S3. Taxa are arranged as for Fig. 3. The CONISS analysis of the entire Vaifanau dataset is also presented (right of diagram). The two zones (right column) are based the Bayesian radiocarbon chronology, with European contact beginning before AD 1800. Dashed vertical lines represent the maximum percentages of these taxa recorded in MIS 3.

problems with radiocarbon dating bulk organic sediments or pollen concentrates (Stevenson *et al.*, 2010; Margalef *et al.*, 2013). The coverage of radiocarbon dates obtained for the Vaifanau core was sufficient to discount any major disruption in sediment accumulation.

The depositional model provided a basal age for the record of ~44.5 cal. kyr BP (Fig. S2.1, Appendix S2). The core chronology overlaps with the Laschamp geomagnetic excursion at ~41.65–39.77 cal. kyr BP which has been associated with a ^{10}Be–^{36}Cl peak and concomitant peak in $\Delta^{14}C$ recorded in polar ice cores (e.g. Muscheler *et al.*, 2005). Two AMS dates at ~40 cal. kyr BP suggest that any $\Delta^{14}C$ fluctuations are not reflected in the sedimentation pattern.

The age of the sharp transition from algal to peaty sediments at ~85 cm in the Vaifanau core is poorly constrained. A depositional model, based on a single AMS date at 55.5–56.5 cm, and fossil markers of known introduced and anthropogenic taxa, (Fig. 5a; Fig. S2.1, Appendix S2), provides an age of ~1200 cal. AD at ~85 cm (Table 1).

MIS 3 pollen, spores, plant macrofossils and charcoal particles

Four palynomorph-based zones are described for the MIS 3 period between 44.5 and –38 cal. kyr BP at Vaifanau (Fig. 3,

see summary in Tables 2 & 3; Fig. S3.1, Appendix S3). The record is characterized by a transition from a palm (primarily *Pritchardia*) and *Ficus* forest with a *Sigesbeckia orientalis* and C4 *Paspalum vaginatum* Sw. understorey (Zones I & II), to grassland (Zones III & IV) occurring between ~42 and 41 cal. kyr BP. Two sections (A & B) with high palynomorph concentrations but lower diversity between ~43 and –42 cal. kyr BP and at ~40 cal. kyr BP indicate different preservation conditions. Ferns increase after ~39.4 cal. kyr BP. A number of abrupt shifts in vegetation composition occur throughout the record, including at ~40.5 cal. kyr BP when ferns briefly increase in abundance. A total of 40 palynomorph taxa were recorded in the MIS 3 period, with the lowest diversity recorded in the basal *Pritchardia* palm dominant zone (I), and the highest diversity occurring in the Poaceae dominant zone (III). Zone IV is distinct in being dominated by Poaceae pollen and pteridophyte spores, and is the only zone with consistent charcoal particles of all size fractions.

MIS 3 diatoms and macroinvertebrates

Only seven diatom taxa were identified throughout the MIS 3 record at Vaifanau (almost no diatoms were recorded in the late Holocene), suggesting limited hydrological changes (Table 2; Fig. S3.2, Appendix S3). *Staurosira*

Table 1 Radiocarbon dates focused on *Sigesbeckia orientalis* achenes for the Vaifanaura'a mo'ora core (RWMP1211-01). Other materials are from unidentified taxa.

Lab Code S-ANU#	Sample	Material	%Modern Carbon	Error±2α	Δ14C	Error±	^{14}C age	Error±	Depth cm
37035	VFM10	charcoal	93.75	0.50	−62.5	5.0	520	45	55.5–56.5
33728	VFM08	*Sigesbeckia*	1.94	0.11	−980.6	1.1	31690	450	90–100
33727	VFM07	*Sigesbeckia*	1.00	0.11	−990.0	1.1	37000	850	100–110
33726	VFM06	*Sigesbeckia*	0.96	0.11	−990.4	1.1	37330	890	120–130
33725	VFM05	*Sigesbeckia*	1.56	0.11	−984.4	1.1	33400	550	180–190
33116	VFM04	*Sigesbeckia*	1.33	0.10	−986.7	1.0	34690	640	190–200
33113	VFM02	twig	0.78	0.11	−992.2	1.1	38970	1090	260–270
*33114	VFM03	*Sigesbeckia*	0.41	0.10	−995.9	1.0	44120	2040	260–270
33112	VFM01	bark	0.81	0.10	−991.9	1.0	38710	1040	325–326

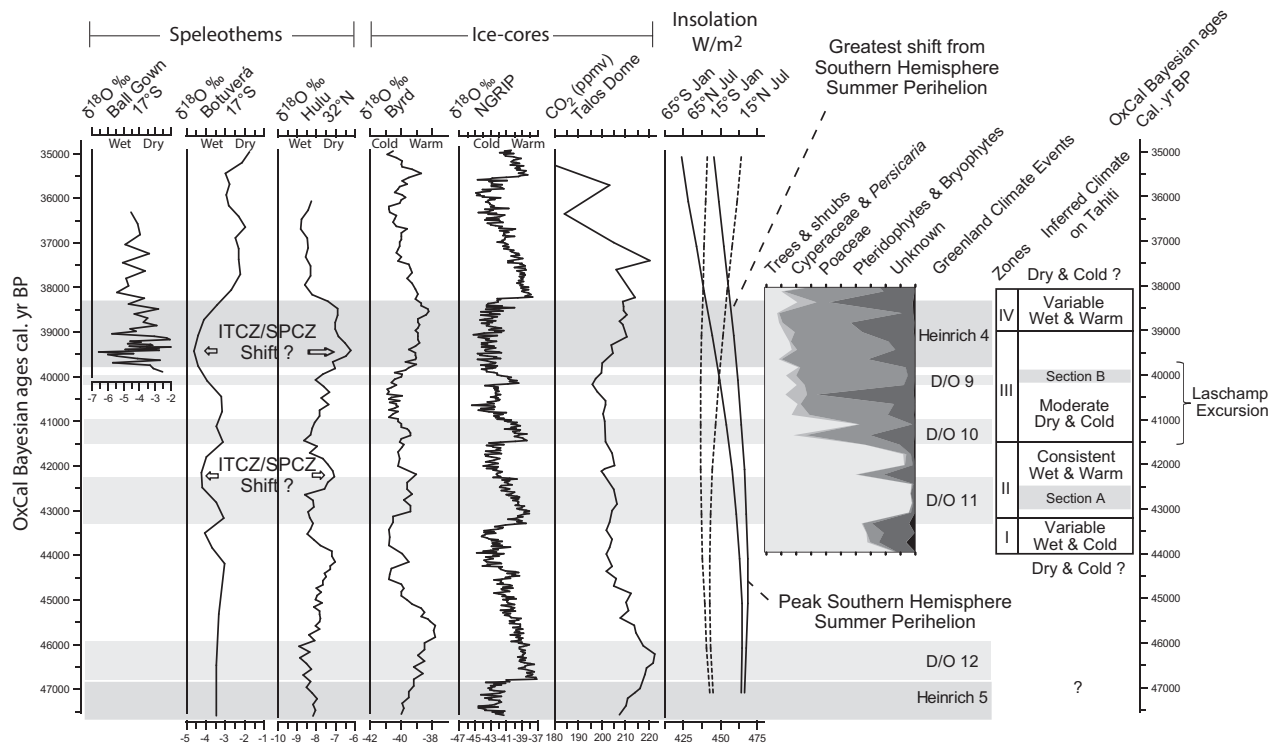*Excluded from the Bayesian analysis as exceeds the IntCal13 radiocarbon calibration curve (Reimer, 2013).

Figure 6 Diagram comparing the key MIS 3 (48–35 ka) geochemical profiles (mainly δ^{18}O), from polar ice core and tropical speleothem records including: Ball Gown (Denniston *et al.*, 2013), Botuverá (Wang *et al.*, 2007), Hulu (Wang *et al.*, 2001), Byrd (Blunier & Brook, 2001), NGRIP (Svensson *et al.*, 2008), Talos Dome (atmospheric CO$_2$ data, after Buiron *et al.*, 2011), encompassing two Heinrich events and four Dansgaard-Oeschger events derived from Greenland ice core data. Possible shifts in the SPCZ, possibly related to shifts in the ITCZ, are indicated by wet−dry oscillations between Hulu and Botuverá. Insolation data for four different latitudes are also presented (Berger & Loutre, 1991), and these link key points of precessional forcing. A percentage summary and zonation of the palynomorph record is presented to compare the key ecological changes on Tahiti. The main climate inferences for each palynomorph zone, and the Laschamp excursion, are also indicated. The two sections (A & B) are also highlighted given the chronological relationship to D/O 11 and 9, as discussed in the text.

venter (Fig. 7) and *Stauroneis phoenicenteron* dominate with both taxa considered benthic, but capable of becoming planktonic, and indicate a permanent water body. *Stauroneis phoenicenteron* is also considered periphytic and its abundance may reflect either an increase in aquatic plants growing at the site or a reduction in pond depth (Foged, 1987). *Pinnularia divergentissima*, an epipelic species, is

found in relatively high proportions in sections A and B and may indicate highly seasonal conditions, particularly pronounced dry seasons.

We note that Vaifanau has the only macroinvertebrate data, for the period recorded, from the tropical Pacific islands (Table 2, Fig. 4). Macroinvertebrates have been identified from late MIS 3 sediments (31–26 ka) from

Table 2 Summary of the Vaifanaura'a mo'ora core (RWMP1211-01) MIS 3 fossil record.

Zone; Depth (cm); Calibrated age range	Pollen & spores (Fig. 3 & S3.1, Appendix S3, see Table S1.2, Appendix 1 for the botanical status of the taxa outlined.	Macro-botanical (Fig. 3 & S3.1, Appendix S3, also see Table S1.2, Appendix 1 for botanical status data) / Macro-invertebrates (Fig. 4)	Diatoms (Figs 3; Fig. S3.2, Appendix S3)
I; 370–325 cm; 44,000–43,200 cal. yr BP	High percentages of Arecaceae including *Pritchardia* and an *insertae sedis* type, *Ficus*, pteridophytes and Poaceae.	Dominated by *Sigesbeckia orientalis*, *Paspalum vaginatum* (C_4) with some *Cyperus polystachyos* (C_4)/ Invertebrates are dominated by beetles and dipteran mouth-parts. *Mecyclothorax* cf. *balloides* is only recorded in this zone.	*Staurosira venter* and *Stauroneis phoenicenteron* dominate the entire MIS 3 diatom record indicating consistent pond conditions. An increase in *S. phoenicenteron* towards the top of the zone may indicate decreased water levels on the pond.
II; 325–246 cm; 43,200–41,500 cal. yr BP	*Ficus* dominates the zone with lower proportions of *Pritchardia*. The highest palynomorph concentrations are recorded in **section A** (43,000–42,400 cal. yr BP), higher than recorded in Holocene-aged sediments, indicating different preservation conditions. Arecaceae type *incertae sedis* increases to its highest proportion at ~42, 250 cal. yr BP, as *Ficus* temporarily decreases. The lowest number of taxa are recorded in this zone.	*Sigesbeckia orientalis* and *Paspalum vaginatum* increase, as *Cyperus polystachyos* declines. Macro-botanical remains decline in concentration towards the top of the zone. Macro-fossils, like palynomorphs, are recorded in the highest concentrations for the record in **section A**. / A number of Curcullonid weevils and the Staphylind beetles *Lispinus* and *Philonthina* are only recorded in this zone.	*S. phoenicenteron* is represented in consistently high percentages. *Pinnularia divergentissima* (an epipelic species) is recorded in high percentages in **section A**, further indicating differing preservation conditions. nutrient conditions.
III; 246–126 cm; 41,500–39,000 cal. yr BP	Aside from one sample at around 41,000 cal. yr BP, *Ficus* is replaced by Poaceae as the dominant taxa. Arecaceae pollen is almost absent in this zone. Tree and shrub abundance and diversity decrease as Cyperaceae, Poaceae and pteridophytes increase, indicating more open vegetation. At ~40,500 Poaceae declines as Marattiaceae ferns increase to the highest levels in the record. In **section B** (~40,000 cal. yr BP), a peak in palynomorph concentration indicates differing preservation conditions. The highest number of taxa are recorded in this zone.	Macro-botanical remains are rare in this zone. Apart from a few *Paspalum vaginatum* caryopses the C_4 plants drop out of the record. *Sigesbeckia orientalis* achenes increase towards the top of the zone / Invertebrate preservation is very poor in this zone. The staphylinid beetle, *Medori*-type, the carabid *Paratachys sexuttatus* and the weevil *Ampagia* are only recorded in this zone. These may point to a range of ecological conditions at the site.	A spike in *Pseudoschizaea* spores recorded in the pollen count at the base of this zone may indicate exposed soil or highly seasonal conditions. *S. phoenicenteron* is found in percentages below 20% throughout this zone. A peak in *Pinnularia divergentissima* percentages in **section B**, may again indicate different preservation conditions. An increased in chrysophyte cysts indicates reduced
IV; 126–85 cm; 39,000–38,000	Poaceae fluctuates in abundance but are generally high in this zone. Pteridophyte percentages increase. Spikes in charcoal particles are consistently recorded in this zone. Dry forest taxa including *Macaranga*, *Trema* and *Celtis* increase towards the top of this zone.	Apart from *Sigesbeckia orientalis* achenes, almost no macro-botanical remains were recovered from this zone / Invertebrate preservation is also very poor. A single carabid, *Metacolpodes*, an indeterminate beetle, and some *Dasyhelea* (Ceratopogonidae) mouth-parts (see Fig. 7), are the only invertebrates recorded in this zone.	*S. phoenicenteron* is found in higher percentages in this zone indicating drier conditions. Chrysophyte cysts reach the highest levels found in the record in this zone, and indicate poor nutrient levels. Spikes in *Pseudoschizaea* spores at the base of this zone again may indicate exposed soil or highly seasonal conditions.

subtropical Easter Island in similarly low concentrations and with an assemblage dominated by Oribatid mites and weevils (Cañellas-Boltà *et al.*, 2012). Around twenty beetle (Coleoptera) and three wasp (Hymenoptera) taxa, along with flies (Diptera), and mite remains, were recorded in the Vaifanau core between 44.5 and 38 cal. kyr BP. Oribatid mites were most abundant at Vaifanau between 42 and 41 cal. kyr BP. Like the palynomorphs, invertebrate preservation was best in Zone II, especially in section A (Fig. 4). Although small, the fauna contains components that occur on the mire surface (e.g. *Rhantus* sp. and bidessine Dytiscidae, hydrophilids, ceratopogonid midges, the tachyine ground beetle *Paratachys sexguttatus* (Fairmaire, 1849), and a small assemblage of species (*Mecyclothorax* and *Metacolpodes* carabids, *Ampagia* and cossonine weevils, and a range of Staphylinidae) that are present today in the

Table 3 Ecological and climate inferences from the Vaifanaura'a mo'ora MIS 3 and late Holocene records.

Zone; Depth (cm); Calibrated age range	Ecological inference	Climate inference from polar ice core and tropical speleothem geochemistry / from Vaifanau proxies
I; 370–325 cm; 44,000–43,200 cal. yr BP	The dominance of aquatic invertebrates and consistency of diatom taxa suggests that a pond environment may have remained stable throughout this zone. The pond was surrounded by palms and *Ficus* with an understorey of ferns and grasses.	Variable wet and cool climate under higher atmospheric CO_2 / Arecaceae, C_4 plant and aquatic invertebrate dominance indicative of cool and drier climate conditions.
II; 325–246 cm; 43,200–41,500 cal. yr BP	Continued stable pond conditions, but with *Ficus* dominant forest. There is a higher diversity of taxa recorded which may indicate distinct or improved ecological conditions.	Wetter and warmer climate under lower CO_2 / *Ficus* and C_4 plant dominance indicating low light conditions under the canopy, with a warm and dry climate conditions. **Section A** (43,000–42,400 cal. yr BP) corresponds to D/O 11, which may explain the different preservation conditions (see Fig. 6).
III; 246–126 cm; 41,500–39,000 cal. yr BP	The pond water level may have fluctuated seasonally in this zone. Grass dominant ecosystem with lower numbers of taxa. Invertebrates with a wider range of ecological tolerances suggest more variable environmental conditions, but it unclear whether any of these taxa prefer grassland ecosystems.	Moderately dry and cold conditions / The abundance of Poaceae (presumably C_3) in this zone also indicate drier conditions. Due to the poor preservation, it is probable that the invertebrate assemblages represent drier and or cooler climate conditions. **Section B** (~40,000 cal. yr BP) corresponds to D/O 9, which may explain the different preservation conditions (see Fig. 6).
IV; 126–85 cm; 39,000–38,000	Grass and fern dominant vegetation surrounding a shallow pond. Infrequent and low intensity fire events are recorded.	Variable wet and warm conditions / Pteridophyte spores and Ceratopogonidae aquatic midges may indicate wetter conditions, but the abundance of Poaceae probably indicates drier climate conditions.

montane vegetation zone; some of which, like Osoriinae, are associated with dead wood/bark.

Late Holocene

We suggest that the late Holocene record began to accumulate at Vaifanau as a consequence of human arrival, through forest clearance, produced hillslope erosion that impounded the drainage of the plateau. From this record, we describe two zones: 'Polynesian' and 'Post-European Contact' (PEC, post ~AD 1770). The 'Polynesian' zone (see Table 4, Fig. 5a & b; Fig. S3.3, Appendix S3 which also includes a summary of the archaeology of the Punaru'u Valley) is poorly defined due to the lack of anthropogenic markers commonly found in other East Polynesian island pollen records (e.g. Rapa, Prebble *et al.*, 2013). Macrofossils were poorly preserved in this zone. Arecaceae (*Pritchardia* and Arecaceae Type *incertae sedis*) pollen initially declines then is extirpated after ~AD 1700, a similar trend recorded elsewhere in East Polynesia (Prebble & Dowe, 2008). An aleocharine staphylinid beetle, that may be a pre-European introduction, is first recorded at this time.

The PEC zone on Tahiti is marked by the presence of introduced plants and invertebrates, but also unprecedented concentrations of charcoal particles. Three specimens of *Osorius*-type (Staphylinidae) beetles were recorded at the base of this zone, and may represent early European introductions. Pollen of *Commelina,* an introduced herb, and the abundant seeds of *Ludwigia octovalvis* (Jacq.) P.H. Raven, were recorded in the upper part of the zone along with spiders (Lycosidae), Oribatid mites, and a single specimen of the ant

Hypoponera opaciceps (Mayr, 1887). All of these taxa, with the possible exception of the spiders and mites, which have yet to be identified to species, were most likely introduced to Tahiti in the twentieth century, and are used here as additional chronological markers in the depositional model (see Fig. S2.2, Appendix S2).

The multivariate analysis of all fossil palynomorph data from Tahiti (see Fig. S3.4, Appendix S3) shows that with the exception of two samples at ~38.4 and ~40.5 cal. kyr BP, which had a strong affinity with late Holocene Vaifanau samples dominated by ground-fern spores (e.g. *Microsorum* and *Pteris*), the Pleistocene assemblages are quantitatively distinct from the late Holocene assemblages.

DISCUSSION

To assess whether the oceanic climate of Tahiti in some way buffered the effect of abrupt climate changes during MIS 3, we initially discuss the likely impacts of globally recognized climate episodes. Secondly, we examine the ecological imprint of regional climate processes recorded from similar archives found across the Pacific Islands (Table 5). Finally, we discuss the main taxa specific indicators of climate-driven ecological changes recorded at Vaifanau and their implications for understanding evolutionary processes on tropical oceanic islands.

Global MIS 3 geochemical signatures

In Fig. 6, we compare the key geochemical profiles from polar ice cores and tropical speleothems from 48–35 ka

Table 4 Summary of the Vaifanaura'a mo'ora late Holocene record.

Zone; Depth (cm); Calibrated age ranges	Pollen & spores (Fig. 5a & Fig S3.2, Appendix S3). See Table S1.2, Appendix 1 for the botanical status of the taxa outlined.	Macro-botanical / macro-invertebrates (Fig. 5b, also see Table S1.2, Appendix 1 for botanical status data) / diatoms (not presented).	Ecological and climate inference
Polynesian; 84–36 cm; ~AD 1250–1790	Monolete ferns dominate the assemblage along with *Cyathea* spores with Cyperaceae and *Trema*. *Trema*, a dry/warm forest taxa, is recorded in higher percentages than in the MIS 3 sequence. *Pritchardia* pollen is represented in the base of the zone up until ~AD 1600 at which time *Trema* increases. Charcoal particle counts are low throughout this zone. Grass pollen is found in low percentages (<10%), well below levels recorded in the MIS 3 sequence.	None preserved/ Invertebrate preservation is poor in this zone. A few dipteran, probably Ceratopogonidae mouth-parts, are recorded along with a single rove beetle Aleocharinae sp., commonly found in terrestrial habitats. / Only a few *Achnanthes inflata* diatoms, an epiphytic freshwater species, were preserved at 60 cm (~AD 1475 +/− 100). No other diatoms were preserved within the late Holocene record.	Dominance of xeric and mesic forest taxa and ground ferns with some evidence for human disturbance with low intensity fire events. Indicative of warm and wet climate conditions.
Post-European Contact; 36–0 cm; ~AD 1790–present	A marked rise in charcoal particle concentrations (>all size fractions) characterises the beginning of this zone. Poaceae pollen is recorded in slightly higher percentages than in the Polynesian zone. *Persicaria* (*P. glabra* an indigenous species) pollen is relatively abundant in this zone. The Polynesian introductions *Cordyline* (*C. fruticosa*) and *Aleurites* (*A. moluccana*) are recorded for the first time in this zone (see Table S1.2, Appendix S1). In the upper part of the zone, pollen from cf. *Acacia* and *Commelina*, known to have been introduced in the twentieth century, are recorded. *Dicranopteris* spores show increase at this time, probably in response to shift in vegetation cover identified in the macro-botanical record.	*Cyperus polystachyos* and *Sigesbeckia orientalis* achenes are recorded in the top of the zone, but their lack of presence in the modern vegetation cover of the mire suggests that they were brought up from basal MIS 3 sediments during the coring process. *Ludwigia octovalvis* (introduced in the twentieth century and *Persicaria glabra* (an indigenous taxa, as interpreted from this record) seeds are recorded in large numbers in the uppermost sample of this zone representing a distinct shift in vegetation cover of the mire/ Invertebrate preservation increases in this zone, especially towards the top of the record. Most of taxa recorded are probably introduced species.	Modern mire dominated by introduced species, with frequent and high intensity fire events.

Table 5 MIS 3 pollen records from similar latitudes to the Vaifanaura'a mo'ora record.

Site	Latitude	Longitude	Elevation (m)	Annual rainfall (mm)	Approximate MIS 3 abrupt climate & ecological changes	References
Vaifanaura'amo'ora, Tahiti, French Polynesia	17° 38′S	149° 32′W	580	~3825	43 ka: C_4 to C_3?41.5 ka: *Ficus*/Arecaceae forest to poaceae grassland, increased charcoal38 ka end of record	This paper
Lynch's Crater, Atherton Tablelands, Queensland Australia	17° 21′S	145° 41′E	770	500–1000	41 ka: Araucariaceae to sclerophyll forest, increased charcoal	(Kershaw *et al.*, 2007; Rule *et al.*, 2012)
Xere Wapo, Grande Terre, New Caledonia	22° 17′S	166° 59′E	235	~2000	45 ka: Araucariaceae decline38 ka: sedimentary hiatus?	(Stevenson & Hope, 2005)
Rano Aroi, Easter Island, Chile	27° 5′S	109° 22′W	430	1000	45 ka: C_4 to C_3?40 ka: Arecaceae forest to grassland39 ka: sedimentary hiatus?	(Flenley *et al.*, 1991; Margalef *et al.*, 2013, 2014)

(see Fig. 1), allowing the examination of possible lead-in and lead-out climatic conditions that may have initiated and terminated the Vaifanau sequence. The period from 48 to 35 ka encompasses two Heinrich Events (HE: recurrent catastrophic episodes of enhanced ice rafting), and four Dansgaard-Oeschger events (D/O: millennial-scale climate

transitions from cold stadials to warmer interstadials). These events, which are defined from Greenland ice core records, may have had global climate impacts from their influence on ocean-circulation patterns (van Meerbeeck *et al.*, 2009).

From between 48 and 44 ka, prior to the initiation of the Vaifanau record, polar ice core records are characterized by high atmospheric CO_2 particularly during HE 5 (~48–47 ka) followed by D/O event 12 (~46.7–46 ka). Antarctic $\delta^{18}O$ records reveal warmer conditions in the Southern Hemisphere at ~46 ka followed by a cool phase between 45 and 44 ka coupled with high atmospheric CO_2. Speleothem records of $\delta^{18}O$ show that conditions were drier between 48 and 44 ka and became wetter in the Southern Hemisphere tropics after 44 ka. From these comparisons, we suggest that the Vaifanau sequence was initiated at ~44 ka during a variable, wet and cold climate.

Speleothem records from Hulu Cave in the Northern Hemisphere (Wang *et al.*, 2001) show the opposite pattern to Botuverá in the Southern Hemisphere subtropics after 44 ka (Wang *et al.*, 2007). Wang *et al.* (2007) suggest that these records provide strong evidence for pronounced southern shifts in the ITCZ between 42.5 and 41.5 ka (Zone II) and between 40 and 38 ka (Zone IV). This same coupling effect on climate may have also re-oriented the SPCZ, bringing more precipitation to Tahiti.

The climate systems of both hemispheres may be more closely coupled during the Southern Hemisphere summer perihelion (Wang *et al.*, 2007; Clement & Peterson, 2008). Orbital eccentricity values ebb whereas obliquity values reach their peak at ~45 ka, as summers in both hemispheres receive more insolation, and winters receive less. High insolation values favour greater sea-water evaporation, potentially creating a larger tropical moisture source (Severinghaus *et al.*, 2009). Conversely, when obliquity decreases, summers receive less insolation, and winters more. This occurs at ~41.5 cal. kyr BP, when the Vaifanau sequence records the largest ecological transition from *Ficus* forest to grassland (Zone II to III). This abrupt change from wet and warm to cool and dry conditions, may be driven by precessional forcing and a complex, albeit poorly understood, atmosphere-ocean feedback process (Clement & Peterson, 2008). As the precession shifts further away from a summer perihelion, the impact of HEs may become more pronounced, and it is likely that the dry HE 4 (Zone IV) resulted in the eventual termination of the Vaifanau sequence at ~38 cal. kyr BP. Major shifts in the ITCZ and SPCZ, along with a marked decline in global sea levels at this time, may have also reduced precipitation on Tahiti as it did in other parts of the tropical Pacific, and transformed ocean-circulation patterns (Chappell, 2002).

We also note that preservation conditions improved within sections A and B at Vaifanau, highlighted in Fig. 6, and these correspond to D/O events 11 and 9, respectively. There is no obvious explanation why these and not other D/O events may have influenced fossil preservation, but our data suggest that more seasonal precipitation may have played a role.

Regional MIS 3 pollen records

Of the MIS 3 records located at similar latitudes to Vaifanau (Table 5, Fig. 1), the mire within the volcanic caldera of Rano Aroi on Easter Island reveals the most comparable record of vegetation change. Margalef *et al.* (2014) suggest that an early and late MIS 3 phase can be distinguished at Rano Aroi. The early phase between 60 and 42 ka is characterized by short and abrupt events of higher sediment delivery, presumably produced by high precipitation. Palynomorph and $\delta_{13}C$ data, show an initial dominance of grasses (presumably C_4 species) which were later replaced by a combination of Asteraceae, *Coprosma*, Poaceae and ferns between 51 and 48 ka. Overlaid with the abrupt high precipitation events, the Rano Aroi deposit records a shift in C_4 to C_3 plant representation after 48 ka (Flenley *et al.*, 1991; Margalef *et al.*, 2014). In addition, at ~45 ka, the oldest preserved rhizomes of the large C_3 sedge *Schoenoplectus californicus* (C.A.Mey.) Soják (Cyperaceae) from the island were identified (Margalef *et al.*, 2013). The transition from C_4 to C_3 may also be associated with a drop in atmospheric CO_2 and more consistent precipitation patterns (Fig. 6). A comparable transition from C_4 to C_3 occurs within the Vaifanau record on Tahiti between ~44 and 42 cal. kyr BP demonstrated by the decline in C_4 *Paspalum* caryopses ($\delta_{13}C$ data on bulk organic samples from Vaifanau does not reveal this transition; see Fig. S2.2, Appendix S2). It is plausible that a combination of an abrupt climate transition as well as the colonization of more competitive C_3 plants, like that of *S. californicus* for Easter Island (Margalef *et al.*, 2014), may have led to the reduction in C_4 plants at Vaifanau. Alternatively, *S. californicus* may have survived in small populations before C_4 plants declined.

The late MIS 3 phase at Rano Aroi is characterized by geochemical evidence for peat oxidation occurring between ~42 and 31 ka. Palynomorph and macrobotanical data indicate that conditions were dry and relatively cold on Easter Island during that time. Very low sediment accumulation rates and Poaceae dominance between 31 and 28 ka may have been due to low temperatures that altered mire growth. As at Rano Aroi, the Vaifanau record changes abruptly at ~41.5 cal. kyr BP in response to a drier climate.

Lynch's Crater, in north-east Australia, provides one of the most well-studied pollen records covering MIS 3 (e.g. Kershaw *et al.*, 2007). An abrupt transition from *Araucaria* rain forest to sclerophyll vegetation, observed at ~45–40 ka, has invoked considerable debate about the relative contributions of climate-forcing and human activity (Rule *et al.*, 2012). The Xero Wapo pollen record from New Caledonia has been directly compared with Lynch's Crater (Stevenson & Hope, 2005) although reliable dating of MIS 3 records from this and other proximate sites remains elusive (Stevenson *et al.*, 2010). Prior to ~45–40 ka, the vegetation

alternated between rain forest and maquis with fire, an important disturbance factor, despite the absence of human colonization. The most compelling aspect of these records is the matching *Araucaria* decline at ~45–40 ka. On New Caledonia, this was accompanied by a transition from *Araucaria* to Podocarpaceae forest, but also a reduction in natural fires. We draw on this comparison to suggest that the abrupt wet−dry transition at ~41 cal. kyr BP found at Vaifanau, again in the absence of human activity, but also with fire as an important disturbance factor, corresponds to the same ~45–40 ka transition exhibited at Lynch's Crater and Xero Wapo. We suggest that Lynch's Crater may have responded to climate–forcing differently, not only due to ongoing influence of human activity particularly on fire regimes (Rule et al., 2012), but also due to the steep altitudinal and seasonal rainfall gradients exhibited in the Atherton Tablelands of north-east Australia.

Ecological change and taxon responses

Arecaceae – Pritchardia

Pritchardia is a palm genus comprised of 27 species, primarily single-island endemics from the Hawaiian Islands (Bacon et al., 2012). The Hawaiian *Pritchardia* are found from sea level up to 2000 m a.s.l. in areas with average annual rainfall between 1500 and 2000 mm, but they also favour islands or leeward areas with lower precipitation. Fossil pollen from Ka'au Crater, O'ahu (463 m a.s.l.; Fig. 1), shows that *Pritchardia* was locally abundant at ~35 ka, but declined during the Last Glacial Maximum (Hotchkiss & Juvik, 1999). *Pritchardia* also declined during wet phases of the Holocene, perhaps due to competition from other species, and following human colonization, as has been found on other islands in the archipelago (Hotchkiss & Juvik, 1999; Prebble & Dowe, 2008). We suggest that *Pritchardia* on Tahiti probably responded similarly to climate-forcing and species competition.

Only three extant species occur outside of the Hawaiian Islands including *P. mitiaroana* J.Dransf. & Y.Ehrh, found on the raised atolls of Makatea and Niau in the Tuamotu Archipelago, north-east of Tahiti. Late Holocene pollen records, including from Vaifanau, show that *Pritchardia* extinctions occurred on several Pacific Islands following human arrival (Prebble & Dowe, 2008). The current survival of *Pritchardia* and low species diversity on a few Pacific Islands may also be due to its 'habitat specialization', being adapted to low lying islands, and areas with low annual rainfall, or from competition with other forest species not present in the Hawaiian Islands (e.g. *Ficus*).

Moraceae – Ficus

Many *Ficus* spp. are adapted to rapid island colonization, as found on the Krakatau islands (Indonesia), and because of their small fleshy synconia, are preferentially eaten, and dispersed by frugivorous birds, and bats (Whittaker et al., 1989).

Ficus prolixa G.Forst. is indigenous to the tropical Pacific islands, found across the main archipelagos, but is absent in the Hawaiian Islands and the subtropical islands, and is now rare on some islands (Larrue & Meyer, 2013). It has a wide distribution on Tahiti from near sea level in xeric forests to montane forest up to 1000 m a.s.l. (Florence, 1997). *Ficus prolixa* can also grow as an epiphyte on other trees and on rocky substrates, thus can be regarded a 'habitat generalist'. We associate the abrupt transition in the Vaifanau pollen record from a palm (with some *Ficus*) to *Ficus* dominant forest at ~42–41 cal. kyr BP with a shift from variable to stable, wetter and warmer conditions. The competitive characteristics of *F. prolixa* under these climatic conditions may have prevented *Pritchardia* from radiating on Tahiti as it did in the Hawaiian Islands where *Ficus* is absent. We suggest the low number of *Pritchardia* spp. found outside of the Hawaiian Islands may be due to niche pre-emption (Silvertown, 2004) on Tahiti by *Ficus* and other tree species that out-competed palms under wetter, and maybe warmer climates.

Poaceae – Paspalum

Of the Panicoideae species found in the flora of Tahiti (all C$_4$), *Paspalum vaginatum* Sw. caryopses hold a close morphological affinity with the fossils from Vaifanau (Fig. 7; others include: *Cenchrus caliculatus* Cav., *Garnotia stricta* Brongn. and *Microstegium glabratum* (Brongn.) A.Camus), but this does not exclude other Panicoideae that may have been present on the island during MIS 3. The endemic Hawaiian *Paspalum*, for example, have similar caryopsis morphologies. *Paspalum vaginatum* is a perennial stoloniferous grass currently restricted to coastal habitats on Tahiti and is tolerant of a wide range of environmental conditions. It is regarded as an invasive species on most Pacific Islands and in many parts of the tropics, but its origin is uncertain (Liu et al., 1994). The fossil association of *P. vaginatum* with palm and *Ficus* forest between 44 and 42 cal. kyr BP at Vaifanau, shows that this grass occupied very different and more variable habitats from its present-day coastal setting.

Despite the abundance of *Paspalum* caryopses between 44 and 42 cal. kyr BP, Poaceae pollen is rare in the Vaifanau record until after ~41 cal. kyr BP. Poaceae pollen, where abundant in fossil records, is often used as a palaeoclimatic indicator of cool and dry conditions. However, the representation of Poaceae pollen is influenced by a number of factors, such as the proportion of other plants represented in the pollen flora that are anemophilous (wind dispersed), and the size of local wetlands (Bush, 2002). Tropical floras, presumably including Tahiti, are dominated by entomophilous plants (including *Ficus* by a wasp mutualism), thus pollen records from the island are likely to contain an over-representation of Poaceae (Bush, 2002). According to Bush (2002), very high (50–90%) abundances of Poaceae pollen provide a strong indicator of grasslands conditions, especially when combined with other non-forested habitat indicators. Both conditions are satisfied at Vaifanau during MIS 3 with
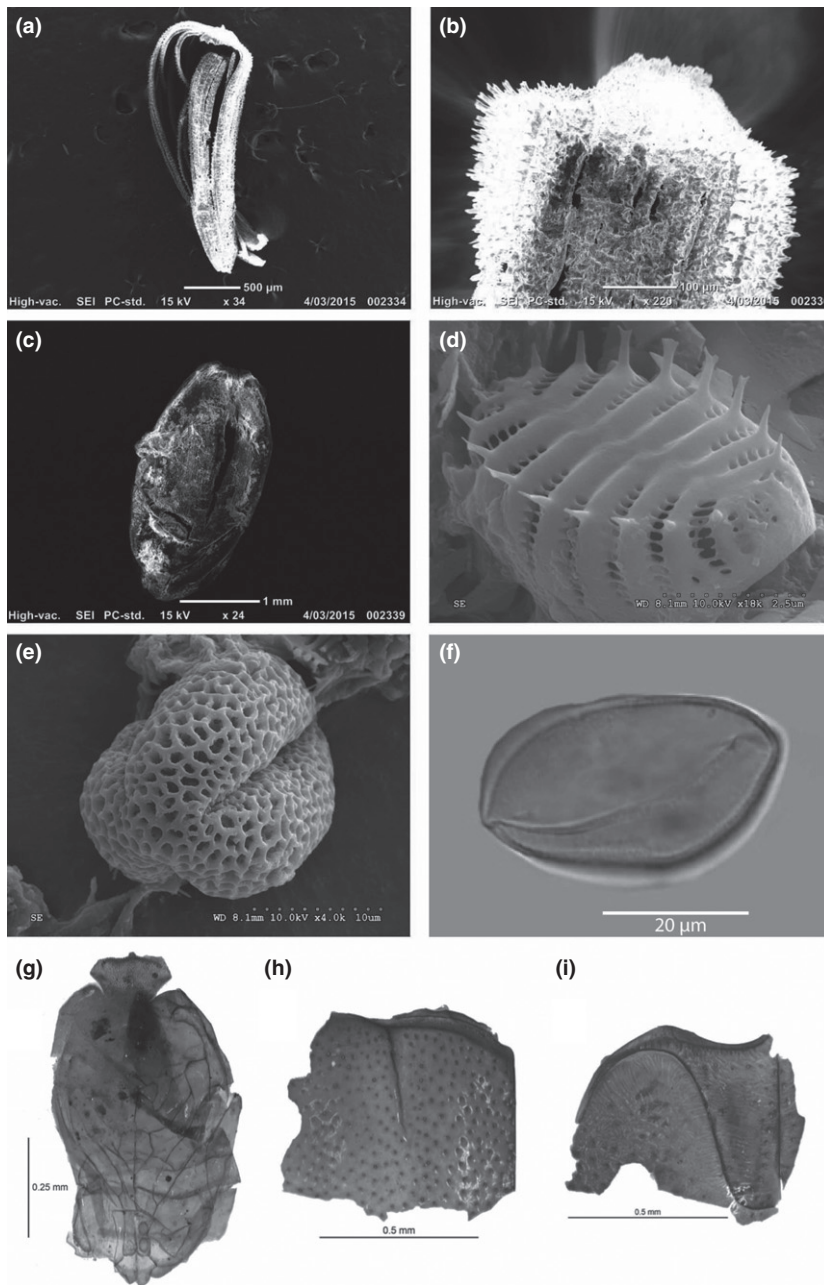
Figure 7 Vaifanau fossils: a-e. Scanning electron micrographs: (a, b) fossil *Sigesbeckia orientalis* achene in longitudinal view; 310–300 cm (a), base of achene in oblique view (b). (c) cf. *Paspalum vaginatum* caryopsis in longitudinal view; 310–300 cm). (d) *Staurosira venter* diatom; 295 cm). (e) SEM of a fossil *Zanthoxyllum* pollen grain, 250 cm). (f–i) Optical micrographs: (f) *Pritchardia* pollen grain; 330 cm. (g) *Dasyhelea* (Diptera: Ceratopogonidae) pupal case; 290–280 cm. (h, i) cf. *Allodessus* (Coleoptera: Dytiscidae: Hydroporinae: Bidessini) elytral fragment; 290–280 cm (h), metacoxal plate fragment 230–220 cm (i).

high Poaceae pollen percentages, but particularly after ~41 cal. kyr BP. In addition, the charcoal records from Vaifanau indicate both increased local and regional fires after ~40 cal. kyr BP, which provide a further indicator of the expanse of grasslands, that we assume are more flammable (Whitlock & Larsen, 2002).

Asteraceae – Sigesbeckia orientalis L.

The achenes of the annual Asteraceae sub-shrub *Sigesbeckia orientalis* were found throughout the MIS 3 record at Vaifanau (Fig. 7), but are most abundant before ~41.5 cal. kyr BP. The abundance of achenes between 44 and 41.5 cal. kyr BP suggests that it prefers consistently wet climate conditions.

Due to its capacity for long-distance seed dispersal, *S. orientalis* is regarded as an invasive weed on many of the Pacific Islands, and is thought to have originated in either Africa or Asia. As the Vaifanau record confirms that *S. orientalis* is indigenous to Tahiti and abundant during MIS 3, we suggest it may have been indigenous across the Pacific Islands. Although achenes are preserved throughout the sequence, we identified no Asteraceae type pollen. Differential preservation of Asteraceae pollen and achenes may occur due to dispersal constraints. Vaifanau was a small shallow pond during MIS 3, and we suggest that winds probably dispersed pollen further distances from the pond than the achenes. *Sigesbeckia* pollen are highly echinate and adapted for anemophily, whereas their achenes are presumably adapted for zoochory.

Invertebrates

Although the fossil invertebrate record from Vaifanau and our understanding of the modern ecology of most invertebrates from Tahiti are limited, the presence of montane taxa such as *Mecyclothorax* in the palm and *Ficus* dominant parts of the record, between 44 and 41.5 cal. kyr BP, is intriguing. There are 101 *Mecyclothorax* species recorded from present-day Tahiti, all from above ~1000 m a.s.l. (Liebherr, 2013), but this genus also inhabited Vaifanau at 580 m a.s.l. during MIS 3. Modern invertebrate distributions are clearly biased by substantial human impact in the lowlands (Meyer, 2004), but isolation of different *Mecyclothorax* populations between the steep valleys of Tahiti during the dry, grass dominant phases of MIS 3 may have provided a pivotal evolutionary driver for this striking endemic radiation.

CONCLUSIONS

The Vaifanau record from Tahiti provides a powerful basis for interpreting the ecological responses to changing MIS 3 climates between 44.5 and 38 cal. kyr BP. None of the fossil proxy evidence we have compiled provides an accurate gauge of temperature fluctuations, so comparisons with geochemical proxies, particularly from ocean drill cores are difficult to reconcile. These data could also not distinguish any major influence of sea-level change, which only minimally altered the bathymetry of the island's coastline during MIS 3. An increasing number of geochemical records, however, particularly from speleothems, are revealing highly variable tropical climates during the Pleistocene, with palaeoecological evidence revealing synchronous and abrupt forest to grassland transitions, like at Vaifanau. Precipitation changes combined with sea-level changes (see Fernández-Palacios et al., 2015), and other atmospheric changes associated with precessional cycles are critical in explaining these transitions.

The Vaifanau record conclusively shows that climate stability, buffered by the thermal mass of oceans, should no longer be used as a base assumption for explaining species radiations and terrestrial ecological responses on tropical oceanic islands. Species radiations, by definition, involve ecological diversification, but some of the proposed mechanisms rely on the progression rule, treating younger islands as static platforms, ready-made with vacant niches for older island species to colonize. However, the combined analysis of molecular and fossil data has shown that back colonization, within-island differentiation, adaptation and extinction, among other events, can confound the progression rule (Silvertown, 2004).

Molecular evidence for within-island phylogeographical barriers, suggests the isolation of the two main volcanoes on Tahiti, with their associated peaks and massifs, may have promoted species diversification (Hembry & Balukjian, 2016). We suggest that the Vaifanau fossil record provides strong evidence that MIS 3 climates accentuated this within-island phylogeographic pattern. The greater integration of palaeoecological and palaeoclimate records with molecular evidence will be essential to provide better explanations for the striking endemism found on tropical oceanic islands.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Vegetation zones, botanical taxon status, affinity and fossil representation.
Appendix S2 ^{14}C chronology, magnetic susceptibility, stable isotope data and core images.
Appendix S3 Remaining MIS 3 and late Holocene fossil data, multivariate analysis and summary of archaeology of the Tamanu Plateau.

DATA ACCESSIBILITY

All fossil and geochemistry data from this study have been deposited on the NEOTOMA (http://www.neotomadb.org/) database.

BIOSKETCH

Matthew Prebble is a researcher in palaeoecology, ecology, archaeology and island biogeography at the Australian National University. His research interests are focused on human–environment interactions and the biogeography of the Pacific Islands.

Author contributions: M.P. conducted the palynological analyses, analysed all biological and palaeoclimate data, and wrote the manuscript with contributions from the co-authors. R.W. conducted the macrobotanical and charcoal particle analyses; L.S-P. completed the diatom analyses; J-Y.M. selected the study site and analysed the available botanical data; S.F. conducted the radiocarbon, carbon and nitrogen isotope analyses; N.P. analysed the invertebrate remains.

Editor: José María Fernández-Palacios