QUATERNARY ECOLOGICAL AND ENTOMOLOGICAL CHANGE OF `OPUNOHU VALLEY, MO`OREA (FRENCH POLYNESIA)

JOANNA L. NISHIMURA

Earth and Planetary Science, University of California, Berkeley, California 94720 USA

Abstract. Research in recent decades has revealed that Polynesians greatly altered previously pristine Pacific island ecosystems. This paper assesses Quaternary ecological and entomological change in `Opunohu Valley on Mo'orea, French Polynesia. Stratigraphic, sedimentary, paleobotanical, and entomological data are used to reconstruct past environmental and entomological changes, with an emphasis on changes that occurred during the initial human colonization of Mo'orea. My results indicate that fluctuations in sea level resulted in the flooding of `Opunohu Valley and the preservation of large deposits of organic matter in anaerobic settings. Changes in local vegetation and a sharp increase in charcoal flecking provide a relative time estimate in the sedimentary record for human colonization. Ant subfossils collected from post-Polynesian colonization sediments suggest that at least 3 ant genera were introduced by the Polynesians. The lack of ant subfossils from pre- Polynesian colonization sediments implies that there were no ant species on Mo'orea prior to human colonization. These results greatly contribute to knowledge of current distributions of ant species in Polynesia and serve to revise the current theory of ant dispersal in Polynesia.

Key words: Mo'orea, French Polynesia; ants; paleoecology; paleoentomology; fossil

INTRODUCTION

Continental species are experiencing unprecedented levels of habitat fragmentation because of human development, road building, and habitat conversion (Ewers *et al*. 2005). Fragments of suitable habitats become increasingly more isolated in a "matrix" of disturbed land (Ewers *et al*. 2005). Residual populations of organisms remaining in these habitat fragments are subject to limited resources and little genetic diversity, contributing to their vulnerability to slight fluctuations in climate, natural resources, and competition (Ewers *et al*. 2005). Pacific islands serve as proxies for habitat fragments because of their limited natural resources, unique flora and fauna, well- defined boundaries, and isolation (Vitousek 2002, MacArthur and Wilson 1967). Understanding the effects of humans on habitat fragments is paramount as pristine continental habitats are being disturbed with increasing alacrity (MacArthur and Wilson 1967).

Given the relatively recent human colonization of the Pacific archipelagos during the Holocene epoch, significant amounts of archeological and ecological data is preserved from pre- and post-human colonization environments; this provides invaluable information regarding types and rates of human induced environmental change (Vitousek 2002). Previous research has identified signals associated with the initial Polynesian colonization of Pacific islands. Palynological studies conducted by Ellis (1994) on Mangaia island (Cook Islands) identified two distinct zones of pollen assemblages associated with pre- and post-Polynesian colonization (Ellis 1994). Pre-colonization assemblages are dominated by pollen from trees like *Pandanus tectorius, Ficus* sp., Palmae, Malvaceae, and *Cocos nucifera* and spores from forest ferns (Ellis 1994). A dramatic decrease in tree pollen coupled with a rise in *Dicranopteris linearis*, a plant taxon associated with disturbance, characterizes post- colonization sediment (Ellis 1994). There is also a simultaneous increase in exotic plant taxa pollen that were either accidentally introduced or intentionally introduced for agriculture like *Colocasia* taro, bananas, gourds, breadfruits, and legumes (Lal and Fortune 2000). In order to clear land for agriculture, Polynesians extensively used fire for deforestation, which resulted in increased charcoal grains/cm^3, rate of sedimentation, and increased clay deposition (Ellis 1994).

Environmental change from Polynesian colonization on Mo'orea island (French Polynesia) is consistent with that observed on other Pacific islands. Currently, the earliest evidence of Polynesian colonization on Mo'orea is from anaerobically preserved coconuts identified as an early hybrid of wild and domesticated varieties (Lepofsky *et al.* 1992). The coconuts were radiocarbon dated to ca. A. D. 650; however, the inference that these coconuts were introduced by colonizing humans is disputed because of the ease of self-dispersal of these seeds (Lepofsky *et al.* 1992).

Prior to colonization, palynological studies show an abundance of tree pollen from *Pandanus tectorius*, *Macaranga tahitensis, Neonauclea forsteri, Ficus tinctoria, Tream orientalis*, and *Cocos nucifera* (Parkes and Flenley 1985). Around the proposed time of colonization, there was a dramatic increase in the rate of sedimentation, which is attributed to either deforestation and subsequent agriculture or a deliberate attempt to accumulate fertile topsoil in the lower valley slopes (Parkes and Flenley 1985). Post- colonization sediments are characterized by an abundance of pollen derived from domesticated food crops and *Dicranopteris linearis* (Parkes and Flenley 1985).

While research regarding major botanical changes in pre- and post-colonization Mo'orea has been performed, relatively little is known about the effects of Polynesian- colonization on insect communities. Preliminary studies on Kauai (Hawai'i), suggest that a number of insect species were unintentionally introduced by Polynesians and at least 2 genera of beetles went extinct shortly after human-colonization (Porch 2007 in Elias 2010). Of the indigenous insect taxa, the large, ground- dwelling, and flightless genera were the most vulnerable to extinction via predation by the Polynesian- introduced Pacific rat (*Rattus exulans)* (Elias 2010). Ants, cockroaches, and beetles were likely among first accidental Polynesian introductions, as reflected in the fossil record (Elias 2010).

Changes in lithology, preserved plant material, and basic stratigraphy will be used to assess changes in the paleoenvironment of `Opunohu Valley during Polynesian colonization. Additionally, insect subfossils extracted from sediment samples will be used to assess changes in ant communities before and after Polynesian colonization.

METHODS

Location

`Opunohu Valley (Fig. 1), located on the north side of Mo'orea island (17°32'21.98"S latitude, 149°49'47.70"W longitude), French Polynesia, is a large amphitheatre type valley that drains an area of 1500 ha, of which 800 ha are characterized as low- lying floodplains (Lepofsky *et al.* 1996). The abundance of fertile soil, large areas with gentle slope, and favorable climate make the valley optimal for agriculture. Previous archeological work in the region suggests that `Opunohu Valley historically was a locus of intense Polynesian agricultural activity, as implied by the presence of paleosols and abundance of charcoal deposits (Lepofsky *et al.* 1996). Around the 7th century, extensive deforestation and intensive agriculture resulted in a drastic increase in sedimentation in the lower valley (Lepofsky 1996). Lepofsky *et al.* (1996) identified 4 distinct stratigraphic layers in

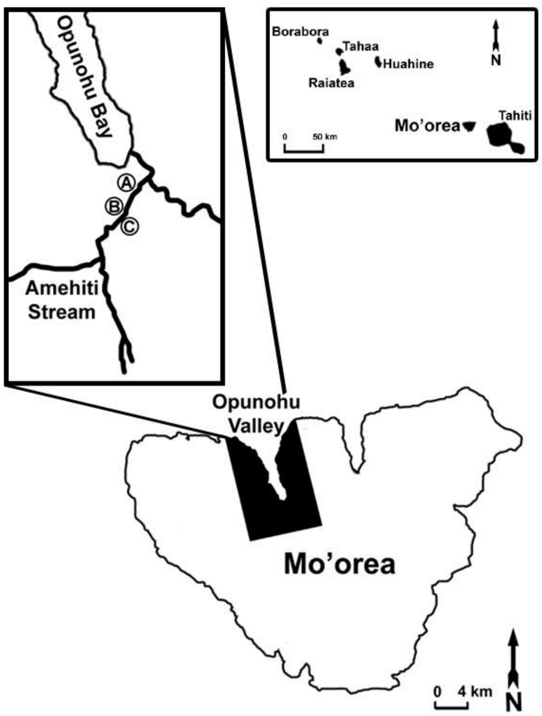

FIG. 1. Maps depicting the study site locations. The map in the upper right hand corner shows the location of Mo'orea, French Polynesia. The inset and lower right hand map depict the location of study sites A, B, and C in 'Opunohu Valley on Mo'orea.

the lower `Opunohu Valley, listed from oldest to youngest: 1) basal deposits, 2) reduced anaerobic deposits, 3) fluvial and colluvial sediment, 4) modern alluvium. The basal deposits are characterized by compact clay layers and mixed colluvium derived from nearby slopes. French Polynesia experienced an increase in sea level by .2- .95m above current level between approximately 5000- 1500 years B. P., which resulted in the flooding of `Opunohu Valley and other coastal inlets (Lepofsky *et al.* 1996, Montaggioni *et al.* 1984). As sea level increased, basal layers of colluvium were covered by thick layers of fine- grained anaerobic mud, typical of low-energy, brackish- water marsh environments (Lepofsky *et al.* 1996). Anaerobically preserved plant matter from this layer is dominated by coastal environment vegetation like *Hibiscus tiliaceus, Barringtonia asatica* (L.) Kurz, and *Cocos nucifera* (Lepofsky *et al.* 1996). The larger grain size of the fluvial and colluvial sediment, found above the anaerobic deposits, indicated a change in paleoenvironment to a drier, higher energy, and stream dominated terrain (Lepofsky *et al.* 1996). The modern sediment has been heavily altered by modern agriculture (Lepofsky *et al.* 1996).

Stratigraphy

Three study sites (A, B, and C), each approximately 2 meters wide (Fig. 1, Table 1) along the Amehiti Stream were cleared of vegetation. The exposed 5 cm of sediment were removed from each section by scraping with a flat- edge trowel to reduce contamination by modern sediment. Each section was then described in terms of color, lithology, stratigraphic features (contacts, bedding, unconformities, etc.), and presence of organic material (including charcoal). Soil colors were characterized using the Munsell color system.

Study Site	Latitude	Longitude
A	17°31'15.46"S	149°50'55.17"W
B	17°31'20.48"S	149°50'59.66"W
C	17°31'20.80"S	149°50'59.66"W

TABLE 1. GPS coordinates of study sites.

Sampling

Two .5- liter of sediment samples were collected every 20 cm, beginning at the top of the water table and ending at the disturbed sediment at site B. Samples at sites A and C were collected only from the anaerobic sediment. Two sediment samples from below the water table were collected at site C. Sediment samples were bagged in liter- size Ziploc bags for further analysis in the lab.

Sediment Analyses

To determine the percentage of organic matter in each sample, a modified loss- on-ignition protocol was used, as outlined in Dean (1974). Samples were dried over low heat for at least 24 hours, weighed, placed in aluminum cups, and heated in a muffle furnace at 450˚F for 4 hours. After baking, samples were weighed to determine the amount of organic matter lost on ignition.

Grain size analysis was used to determine the dominant grain size of each sediment sample. Samples were dried over low heat for 24 hours and then passed through a set of 6 nested Hubbard sieves to determine percentage grain size by weight.

Organic Matter

The tub flotation method, outlined by Struever (1968), was used to separate organic from mineral matter. Samples were immersed in a tub of water and gently agitated to disaggregate clumps. Floating material was skimmed off with a 250 μm sieve and dried for 12 hours before analysis with a dissecting microscope. Charcoal pieces larger than 500 μm, seeds, plant material, and insect parts were removed for counting and further identification. Plant material was either classified as herbaceous (forb material) or woody (bark and branches). Ant parts recovered from sediment samples were identified to genus using the Pacific Invasive Ant Key (PIA) and additional support from Pacific ant specialists.

RESULTS

Stratigraphy

From the Amehiti Stream, 3 distinct stratigraphic facies were identified: 1) reduced layer, 2) fluvial sediment, and 3) modern sediment (Fig. 2).

Anaerobic Sediment

Anaerobic sediment was identified at all 3 study sites on the Amehiti Stream. Anaerobic sediment was characterized by a dark blue- grey gley color. In most locations, the anaerobic layer extended 30- 40 cm above the water table; however, the actual extent of this layer is unknown because its base lies below the water table. Grain size in the reduced layer was medium to fine grained sand and a lens of sub-rounded and rounded pebbles, was observed from sample C/VIb, which was gathered approximately 40 cm below the water table at Site C. Mottling was observed in anaerobic sediments as was an abundance of preserved organic matter. While identification of plant material to species was not conducted, Lepofsky *et al.* (1996) determined that observed plant material was dominated by coconut roots and wood from *Hibiscus tiliaceus* and *Barringtonia asiatica*.

Fluvial Sediment

Fluvial sediment was homogenous in internal structure and consisted of cobble, pebble, gravel, silt, and clay layers. Fluvial sediment was observed immediately overlaying the anaerobic sediment at all three study sites. Three distinct fluvial layers immediately overlaying the reduced sediment were identified at Site B and Site C and 1 layer of fluvial sediments was observed at Site A. Fluvial sediment

Site/ Layer	Interpreted Lithology	Depth (cm)	Charcoal Present	Ants *Strumigenys sp.*	Ants *Pheidole sp.*	Ants *Monomorium sp.*
A/V	Anaerobic	140	X	1	4	
A/VI	Anaerobic	160	X		1	
B/I	Modern	65	X			
B/II	Alluvial	85	X		2	
B/IIIa	Alluvial	105	X		4	
B/IIIb	Alluvial	125	X		1	2
B/IV	Anaerobic	145	X		1	
B/V	Anaerobic	165	X			
B/VIa	Anaerobic	185	X		1	
B/VIb	Anaerobic	205	X			
C/V	Anaerobic	300	X			
C/VIa	Anaerobic	320				
C/VIb	Anaerobic	340				

TABLE 2. Ant head identifications from different stratigraphic layers, correlated with depth sampled and presence of charcoal.

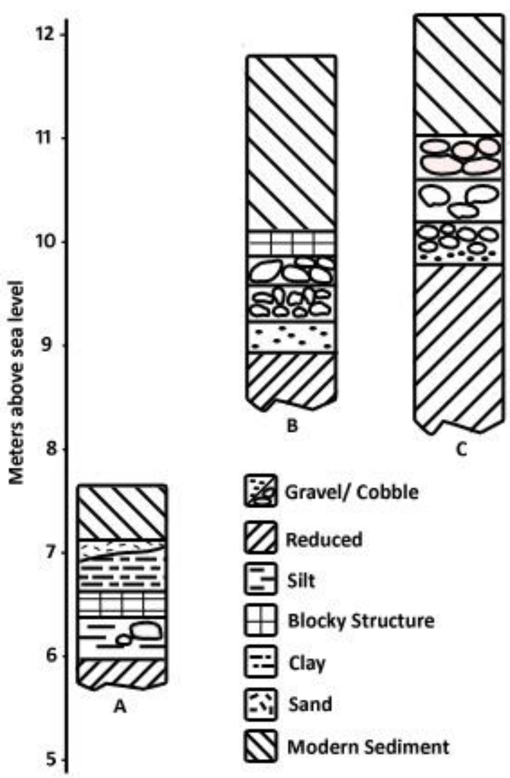

FIG. 2. Stratigraphic columns depicting the correlation of the major sedimentary facies from sites A, B, and C.

coarsened to gravels, pebbles, and small cobbles at the top. Large cobbles were supported in a matrix of fine sand and pebbles. Layer B/II, originally interpreted as a paleosol by Lepofsky *et al.* (1996), is now believed to have been deposited in a low-velocity meandering bend of a stream.

Modern sediment

Modern sediment deposits varied in thickness at the 3 study sites. Pieces of coral were observed in the modern deposits as was evidence of extensive anthropoturbation.

Loss- on- Ignition Protocol and Charcoal Flecking Abundance

The loss- on- ignition protocol revealed fluctuations in concentrations of organic matter across layers (Fig. 3). The concentration of organic matter was the highest in layer B/I (modern and disturbed sediment), decreased in layers B/II through

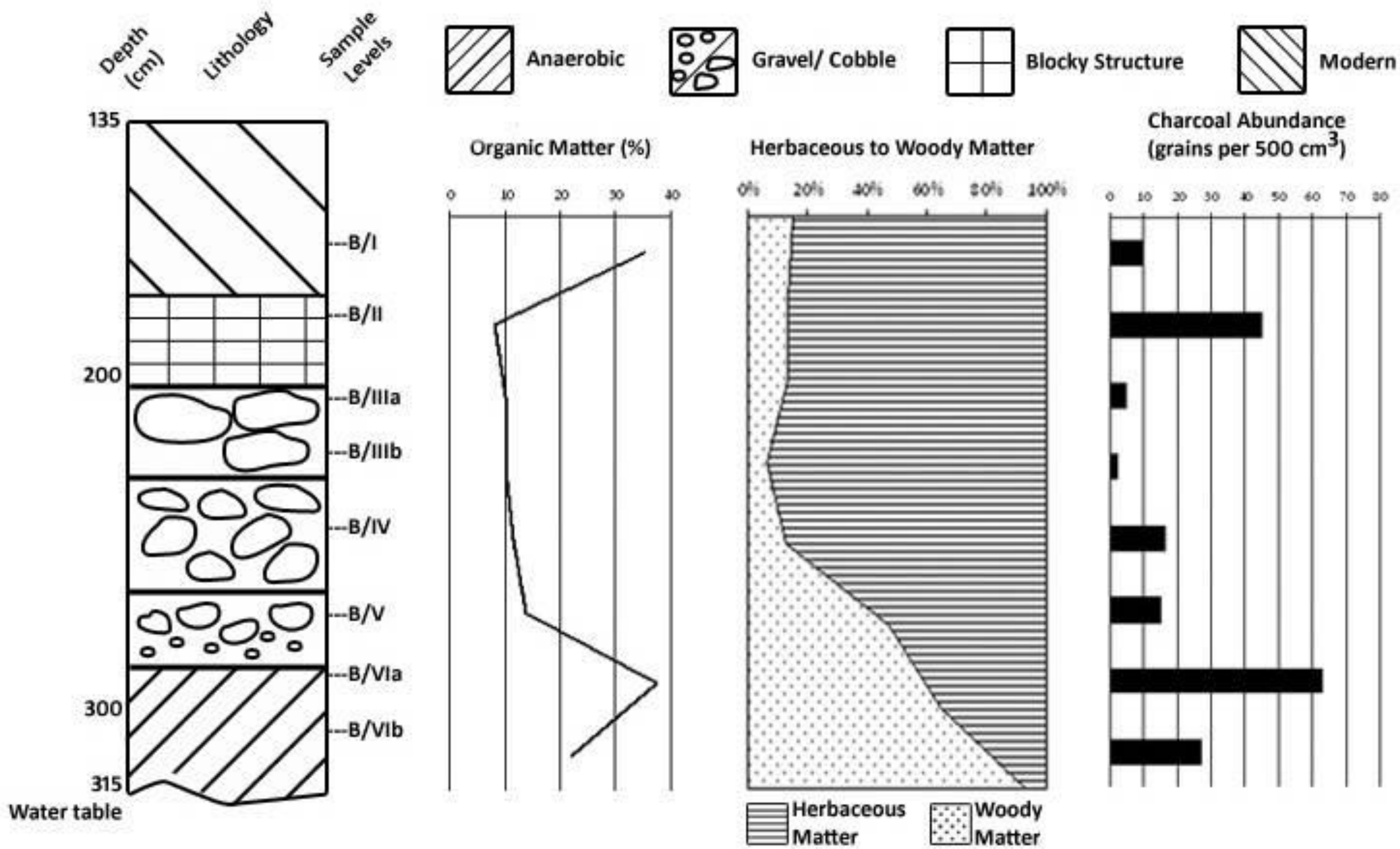

FIG. 3. Correlation between stratigraphy and amount of organic matter, ratio of herbaceous to woody plant material, and abundance of charcoal grains.

B/V(fluvial sediment), increased in layer B/VIa (upper anaerobic sediment), and decreased in B/VIb (lower anaerobic sediment). Abundance of charcoal grains also varied across layers and peaked in the sample B/VIa, at the top of the reduced layer (Fig. 3). Charcoal abundance decreased in layers B/V, B/IV, and B/III, and peaked in sample B/II. Charcoal flecking was absent in samples C/VIa and C/VIb, which were both collected from reduced sediment from below the water table (Table 2). The greatest abundance of charcoal flecking was observed in sample A/VIb.

The ratio of woody to herbaceous was the highest in layer B/I and steadily declined in layers B/II through B/VIb (Fig. 3).

Entomological Remains

Abundance of ant remains varied in different layers and at different sites. Ant remains consisted of 3 distinct genera of ants (Table 2). Ant remains included the pronotum, mesonotum, propodeum, head, and legs from at least 3 ant species. Ant heads were recovered from all sediment samples except B/I, B/V, B/VIB, C/VIa, and C/VIb. A *Pheidole* sp. ant was found in the greatest abundance across different layers.

DISCUSSION AND CONCLUSION

Paleoecological Change

Analysis of the stratigraphy and organic matter from 3 sections of the Amehiti Stream revealed changes in the paleoenvironment and intense past human disturbance and alteration of the local environment.

From about 5000- 1500 years before present, sea level in French Polynesia was roughly 1 meter higher than current sea level, resulting in the flooding of coastal inlets like `Opunohu Valley (Montaggioni *et al* 1984., Lepofsky *et al.* 1996). The fine grained sand and silt of the reduced sediments indicates a low- energy depositional environment. A small lens of sub-rounded pebbles and gravel sized grains, located near the base of the anaerobic sediments, may have been deposited from slight variations in sea level or the presence of an ephemeral stream formed after a major storm event. Coarsening of sand grains was observed in the contact between the underlying reduced and overlying fluvial sediment, which is typical of this paleoenvironment transition.

Changes in lithology of the strata immediately overlaying the anaerobic sediment reflect fluctuations in sea level. Approximately 1500 years ago, sea level in the South Pacific began to decrease and river systems extended further into 'Opunohu Valley, resulting in the deposition of the overlying fluvial sediments. Layer B/II, characterized by a blocky texture and an increase in charcoal flecking may represent a paleosol.

Human Arrival

The correlation between the presence of charcoal flecking in sediment samples and human colonization is well documented on other Pacific islands (Fig. 3) (Kirch 1996, Flenley *et al.* 1991, Ellison 1994). Two major fluctuations in charcoal flecking were observed across the strata. The first spike in charcoal flecking, observed in the top of the anaerobic layer, is most likely attributed to the initial burning of upland forests for agriculture. The decrease in charcoal flecking, observed in the overlaying fluvial sediments, is attributed to the unfavorable depositional and preservational setting created by the fluvial environment. Increased charcoal flecking in the modern sediment is credited to modern burning for agriculture in 'Opunohu Valley.

Changes in the composition of local vegetation are also indicative of human colonization. Previous palynological research on Mo'orea found a decline in primary and secondary plant taxa (*Cocos nucifera*, *Pandanus tectorius*, *Hibiscus tiliaceus*) and an increase in introduced ruderal herbs (Parkes and Flenley 1985). The change in composition of the plant organic matter collected from the strata, reflect the arrival of humans on Mo'orea. Decreasing woody plant matter coupled with an increase in herbaceous plant matter is an observed trend on Polynesian colonized islands as a result of intensive burning and deforestation for agriculture and the subsequent regeneration and regrowth of herbaceous plants (Ellis 1994).

Entomological Changes

No identifiable ant remains were recovered from samples C/VIa and C/VIb, sampled from anaerobic sediment below the water table. Samples C/VIa and C/VIB contained no charcoal, suggesting the absence of ants on Mo'orea prior to human arrival.

The presence of ant subfossils and charcoal in samples B/VIb through B/I suggests the definite presence of ants after initial human arrival. Without more complete ant subfossils, it is difficult to identify the subfossils to species. Additionally, the subfossils have been stained different colors by the preservational material, making identification using body color difficult.

From the anaerobic sediment, the 2 genera of ant subfossils identified have been classified as probably tramp species by Wilson and Taylor (1967). The current theory of ant distribution, posited by Wilson and Taylor (1967) states that few, if any ants were native to Polynesian archipelagoes east of Rotuma, Tonga, and Samoa prior to European arrival. Wilson and Taylor posit that the majority of "tramp" ant species were introduced by Europeans (1967). However, data from this study suggests that at least 2 species of ants from the *Strumigenys* and *Pheidole* genera were introduced and established following Polynesian colonization. The results of this study suggest that there were no ant species on Mo'orea prior to Polynesian arrival. The results of this study are preliminary, and more intensive sampling of pre- Polynesian sediment is needed to confidently state the absence or presence of ants on Mo'orea prior to the arrival of Polynesians.

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