



Early tropical crop production in marginal subtropical and temperate Polynesia

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Polynesians introduced the tropical crop taro (*Colocasia esculenta*) to temperate New Zealand after 1280 CE, but evidence for its cultivation is limited. This contrasts with the abundant evidence for big game hunting, raising longstanding questions of the initial economic and ecological importance of crop production. Here we compare fossil data from wetland sedimentary deposits indicative of taro and leaf vegetable (including *Sonchus* and *Rorippa* spp.) cultivation from Ahuahu, a northern New Zealand offshore island, with Raivavae and Rapa, both subtropical islands in French Polynesia. Preservation of taro pollen on all islands between 1300 CE and 1550 CE indicates perennial cultivation over multiple growing seasons, as plants rarely flower when frequently harvested. The pollen cooccurs with previously undetected fossil remains of extinct trees, as well as many weeds and commensal invertebrates common to tropical Polynesian gardens. Sedimentary charcoal and charred plant remains show that fire use rapidly reduced forest cover, particularly on Ahuahu. Fires were less frequent by 1500 CE on all islands as forest cover diminished, and short-lived plants increased, indicating higher-intensity production. The northern offshore islands of New Zealand were likely preferred sites for early gardens where taro production was briefly attempted, before being supplanted by sweet potato (*Ipomoea batatas*), a more temperate climate-adapted crop, which was later established in large-scale cultivation systems on the mainland after 1500 CE.

Polynesia | crop husbandry | commensal species | fire | extinction

Evidence for early crop production in areas outside the optimal conditions for growth is essential for understanding the early transformation of Neolithic societies and ecosystems (1–3). The transfer and production of tropical crops during the Polynesian initial colonization period (ICP; 1200–1500 CE; *SI Appendix, Table S1*) (4) of the subtropical and temperate islands of the South Pacific, including New Zealand (southern Polynesia, Fig. 1), provide striking examples of this process, yet are poorly understood. The cooler climate and contrasting forest ecosystems encountered in southern Polynesia are thought to have initially constrained tropical crop production, particularly taro (*Colocasia esculenta*), a staple crop of much of tropical Polynesia (5, 6). Sweet potato (*Ipomoea batatas*, here termed kūmara) was introduced to Polynesia from South America and is more adaptable to cooler climates and marginal soils (7, 8). It was favored on some islands, but evidence for kūmara production is more apparent after the ICP. Although fossil taro and kūmara starch granules have been tentatively identified from some ICP sites (9–11), wild food resources dominate these assemblages, most notably extinct moa (Aves: Dinornithidae) in New Zealand (12–15). This supports a long-held hypothesis that foraging and hunting were the primary food procurement strategies (16, 17). Some of the subtropical islands were only briefly occupied, and

then abandoned before European contact, proposed as a response to the decline of formerly abundant wild resources (12, 13) (Fig. 1).

Fossil pollen and sedimentary charcoal from wetland deposits show that, before Polynesian arrival, forests of varying canopy height, woodiness, and flammability covered the islands of southern Polynesia. Fire rapidly reduced the dominant low-stature woody and monocotyledon trees (mostly extirpated palms) of the subtropical island lowlands (18, 19). In northern New Zealand, the timing and pattern of forest fires suggest that climate variability influenced the scale of clearance, but this was dependent upon the distribution of fire-prone nonforest vegetation and fire-resistant forests composed primarily of tall conifer and broadleaf trees (20). Widespread forest clearance appears to be associated with expanded crop production after 1400–1500 CE (20, 21), but this process is poorly defined.

By the 18th century, the occupied islands of southern Polynesia, including Raivavae, Rapa, Rapa Nui, and New Zealand, had variable indigenous forest cover and contrasting crop production systems. Raivavae and Rapa retained some indigenous montane cloud forest, with modified nonforest vegetation and

Significance

Fossil evidence shows that Polynesians introduced the tropical crop taro (*Colocasia esculenta*) during initial colonization of the subtropical South Pacific islands and temperate New Zealand after 1200 CE, establishing garden ecosystems with similar commensal plants and invertebrates. Sedimentary charcoal and fossil remains indicate how frequent burning and perennial cultivation overcame the ecological constraints for taro production, particularly the temperate forest cover of New Zealand. An increase in short-lived plants, indicating a transition toward higher-intensity production, followed rapid woody forest decline and species extinctions on all islands. The relatively recent fossil records from the subtropical and temperate islands of Polynesia provide unique insights into the ecological processes behind the spread of Neolithic crops into areas marginal for production.

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Data have been deposited in the Neotoma Paleocology Database, <https://www.neotomadb.org/> (datasets 41503–41523 and 41528–41535).

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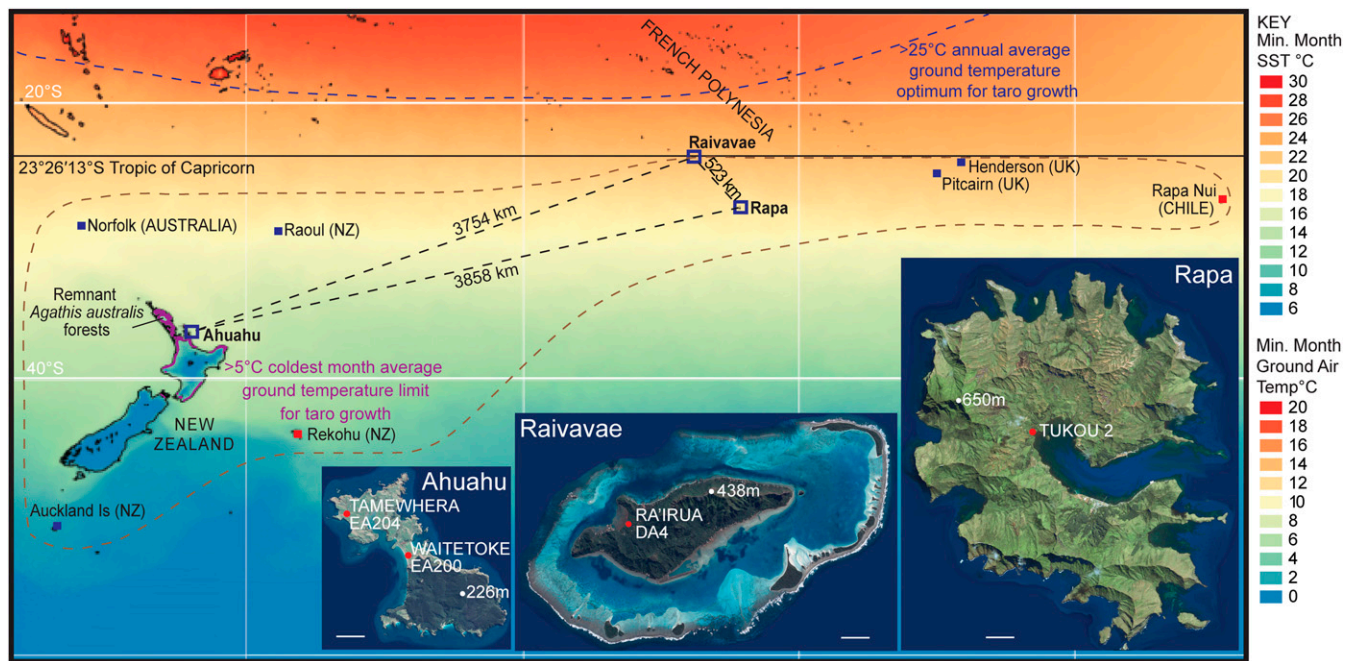


Fig. 1. Map of South Pacific Ocean showing the southern Polynesian islands (brown dashed line) examined in this study (blue boxes), and other islands mentioned in text. Islands marked by blue squares were occupied during the ICP, but abandoned before European contact. Rapa Nui and Rekohu (red squares) were continually occupied. The average sea surface temperatures (SST) and average ground air temperature of the coldest month (GAT) derived from the MARSPEC dataset (74) and WorldClim2 dataset (75), respectively, are presented. Purple areas marked in northern New Zealand (excluding the Waipoua, Waima, and Mataraua *A. australis* conifer-dominant forest remnants in Northland) denote the inland and southern limits for taro cultivation, which are areas where ground frosts are mostly absent and the average minimum GATs of the coldest month are $>5^{\circ}\text{C}$ (*SI Appendix, Table S2*). Insets show the study islands, including sediment core locations and high elevation points. (Scale bars, 1 km.)

extensive taro gardens in the lowlands (22). The gardens included pond fields and raised beds within reticulated irrigation or drainage networks, typical of the tropical Polynesian high islands. Rapa Nui, by contrast, was almost treeless (23), whereas New Zealand retained substantial forest cover, but much of the northern coastal lowlands and the drier eastern areas were cleared, even where crop production was minimal (20). Kūmara was extensively grown as the staple crop, with taro a subsidiary, on these islands, but mainly in the warmer and less seasonal northern areas of New Zealand (24–26). The former importance of taro cultivation during the ICP in New Zealand has not yet been defined.

We assess the influence on tropical crop production of island forest cover over time, by comparing multiple fossil proxies from wetland sediment deposits from Raivavae and Rapa with Ahuahu, a northern New Zealand offshore island (Fig. 1). Abundant plant and invertebrate macrofossils indicate localized ecological changes before and after Polynesian colonization. We also examine the life history traits of fossil plant taxa, particularly weedy species, to assess the changing intensity of cultivation over time. Sedimentary charcoal, wood charcoal, and charred seeds indicate the island-wide and localized role of fire in clearing woody forests for crop production.

We focus on the fossil evidence for taro as one of the oldest and most widely distributed Neolithic crops. Molecular studies indicate that only tropical taro cultivars reached tropical Polynesia at 1000 BCE–1200 CE, where taro became the staple crop of most islands (5, 8, 27, 28). Accordingly, there was a strong cultural impetus to maintain taro as a staple crop in southern Polynesia, even though tropical cultivars were poorly adapted to the marginal climate conditions (Fig. 1 and *SI Appendix, Table S2*) (8, 27, 28). By comparing fossil evidence for taro production from widely separated subtropical and temperate Polynesian islands, we examine the processes of Neolithic crop adaptation to areas marginal for production.

Study Islands

Raivavae and Rapa are subtropical islands positioned *ca.* 4,000 km northeast of warm temperate Ahuahu off the northeast coast of northern New Zealand (Fig. 1). These islands are similar in size and maximum elevation, but have greatly contrasting climates (*SI Appendix, Table S1*) (Fig. 1). Ahuahu currently retains the least indigenous forest cover of all of the study islands. The current lowland vegetation of Raivavae and Rapa is highly modified, with indigenous montane cloud forest remnants found in the steep valleys above 300 m above sea level (asl) to 400 m asl (29).

Raivavae lacks ^{14}C dated stratified archaeological sites, but the close proximity to Tubuai and Rapa (Fig. 1), where the earliest ^{14}C dates fall at 1215–1350 CE (*SI Appendix, Table S2*), as well as the shared oral traditions and material culture, suggests a similar colonization time (30, 31). The earliest archaeological sites on Ahuahu provide ages comparable to the earliest ICP sites identified on mainland New Zealand at 1280–1350 CE (*SI Appendix, Table S3*) (17, 32). Studies of an abandoned irrigated taro pond field and raised-bed garden complex on Rapa shows that taro production commenced in the ICP (22), and is expanded here. The presence of abundant surface garden features such as stone walls, storage pits, or ceremonial sites (ahu or marae) and fortifications (pā or pāre) on each island may relate to increasing population pressure and investment in crop production systems (30, 32). However, complex stratigraphy and site formation processes, with most deposits dated to after 1500 CE (*SI Appendix, Table S3*), limit the accurate dating of these features.

European contact began in the late 18th century (*SI Appendix, Table S2*), and, following disease introduction, the Polynesian populations of Raivavae and Rapa dropped during the mid-19th century, resulting in the abandonment of many crop production systems (33, 34). There are no accounts of gardens on Ahuahu at European contact, and, by 1841 CE, the island was reported to be uninhabited (35).

Paleoecological Contexts

Marshes at Ra'irua (Raivavae) and Tukou (Rapa) are of a similar size (ca. 4 ha) and elevation (0 m asl to 3 m asl), and are both located within catchments of >100 ha in area. Both marshes hold organic-rich terrestrial sediments that overlie deeper mid-Holocene estuarine sediments (Fig. 1). Waitetoke (Ahuahu) is a small (<0.2 ha) mire within a small catchment (<2 ha, at 10 m asl) that holds organic-rich sediments that accumulated when the surrounding dunes were mobilized. This initially occurred during the mid-Holocene sea level highstand at 3500–2500 BCE, then after human arrival (Fig. 1). A series of mires located at Tamewhera (Fig. 1), including a small mire (<0.2 ha, at 20 m asl) examined here, are fed by a perennial stream draining a catchment of <40 ha in area, holding organic-rich sediments overlying compacted alluvial sands.

Active, fallow, and abandoned raised-bed taro gardens are found across Ra'irua Marsh, and, along the inland periphery of the wetland, several stone monuments (ahu and marae) are interspersed between modern dwellings (33). Remnant stone-walled garden terraces and house platforms are similarly found along the periphery and immediately above Tukou Marsh (22). Similar features as well as stone alignments and hollows of modified soil are found on the hillslopes above the Tamewhera and Waitetoke mires on Ahuahu. Domestic animals and invasive plants have modified all of these wetlands since their introduction.

Prehuman Holocene Forests

Raivavae. From 500 CE to 1200 CE, the fossil record indicates a diverse, coastal, swamp forest composed of low-stature nonwoody monocot/palm trees (*Pandanus tectorius*, and extirpated *Pritchardia* and extinct *Incertae sedis*-type palms), common woody subtropical trees (e.g., *Macaranga raivavaensis* and *Pipturus australium*), and now extirpated tropical angiosperm trees (e.g., *Charpentiera australis* and *Rhus taiensis*) and tree ferns (*Cyathea* cf. *societarum*). The presence of *Cocos nucifera* places Raivavae as the most southeastern island for prehuman coconut dispersal in the Pacific Islands, but wild coconuts are no longer found in French Polynesia and were probably rapidly displaced by domesticated varieties (18). The invertebrate sequence is dominated by terrestrial Coleoptera, including numerous carabid and zopherid beetles, and curculionid weevils representing several subfamilies (SI Appendix, Figs. S9 and S15). Most of these taxa are now restricted to remnant forests, but, from the fossil evidence, also occupied prehuman lowland forests. Oribatid and other mites are the most abundant arthropods found through all stratigraphic zones, and sedimentary records of the study islands, presumably because they occupy diverse soil habitats.

Rapa. A similar swamp forest sequence is recorded on Rapa at 7000 BCE–1200 CE which also includes an extinct *Incertae sedis* palm, but less tropical and more subtropical/mesic woody angiosperm trees (e.g., *Metrosideros collina* and *Sophora* spp.). Abundant seeds of the warm-temperate woody tree *Eurya nitida*, currently restricted to higher-elevation areas of the island, dominate the prehuman zone after 3000 BCE. Fewer invertebrate remains were recovered from Rapa than Raivavae, due to limited sediment recovery, but the fossil assemblages are similar. There are fewer species of fossil carabid beetles and more curculionid weevils, and this may reflect the greater diversity and adaptive radiation of weevils on Rapa (36).

Ahuahu. Prehuman sediments were not recorded from the Tamewhera mire. The prehuman mid-Holocene record from Waitetoke reveals a similar dominance of monocot trees (*Cordyline* spp., and the extirpated palm *Rhopalostylis sapida*) along with the subtropical angiosperm trees *Metrosideros* (mostly *Metrosideros excelsa*, also identified from fossil wood) and *Vitex lucens*. Fossil pollen of the tall conifer *Dacrydium cupressinum* is >15% of total palynomorphs (or >35% of dryland sum). Although this pollen can be dispersed long distances by wind, in these proportions, it was likely locally abundant on Ahuahu. Prehuman forests of similar

composition occurred on other offshore islands in northern New Zealand (37–39), with the pollen abundance of other conifers too low to detect local presence (40). Some invertebrate remains were recovered from prehuman sediments on Ahuahu at Waitetoke, and mostly comprised oribatid mites, curculionid weevils, and carabid beetles.

Fossil Taro Pollen

At each of the sites, we identified fossil taro pollen dated to the ICP within what we define as early garden sediments (Fig. 2). Taro pollen has a specific surface ultrastructure, identifiable using compound microscopy (41), and, unlike the pollen of other Polynesian crops including kumara, it has been retrieved from stratified sediments across tropical and subtropical Polynesia (42, 43), and now in New Zealand (this study; Fig. 2). Fossil taro pollen provides direct evidence for the flowering of plants growing at the deposit location. It is also a proxy for perennial cultivation in which plants were left in the soil over multiple growing seasons to obtain greater corm volume and yield, thereby increasing the chance of flowering (27). Taro rarely produces pollen when harvested annually or subannually. It is not dependent on fertilization for reproduction and is replanted using vegetative ramets, not seeds. Within its natural range, pollination occurs through specialist insects and, more rarely, through self-pollination. In the absence of pollinators, most of the pollen will remain in the inflorescence until it withers and falls to the ground. Long-term perennial cultivation, with an increased incidence of plants that flower before harvest, including feral plants outside of cultivation contexts (SI Appendix), would be more likely to lead to pollen deposition than in permanently tended plots.

Early Gardens (1200–1500 CE)

The fossil assemblages from the early garden sediments are similar across all sites and show that most forest taxa declined rapidly from 1200 CE to 1425 CE (Fig. 2). Sedimentary charcoal data show that fire had a minimal role in forest decline on Raivavae compared with Rapa, and especially Ahuahu where localized fires were most pronounced (Fig. 2). Seral taxa including fire-adapted ground ferns on the subtropical islands (e.g., *Dicranopteris linearis*) and New Zealand (e.g., *Pteridium esculentum*), together with grasses and some shrubs, rapidly increase in the early garden records. From 1350 CE to 1420 CE, taro pollen entered each record as forest declined, and this correlates with the influx of macrophytes (*Eleocharis geniculata* and *Schoenoplectus litoralis* subsp. *thermalis* on Raivavae and Rapa, respectively, and *Eleocharis sphacelata* and *Typha orientalis* on Ahuahu) indicative of nutrient enrichment and sediment accumulation within open wetland habitats (SI Appendix, Figs. S8, S12, and S18).

Raivavae and Rapa. The RAIDA4 record from Raivavae begins at 1325–1400 CE with the rapid decline or extirpation of low-stature monocotyledon (*P. tectorius* and *Pritchardia* palms) and woody trees (including *P. australium* and *C. australis*), and the estuarine fern *Acrostichum aureum*. Forest decline begins earlier on Rapa, at 1200 CE, possibly due to limited chronological controls (22), but also resulted in the extirpation of low-stature monocotyledon (*Incertae sedis*-type palm) and woody trees (e.g., *P. australium*). *E. nitida* declines rapidly, further reflecting the impact of crop production on lowland woody trees (SI Appendix, Fig. S11). The lowland swamp forests on these islands were rapidly transformed into freshwater sedge-dominant wetland comprising the cosmopolitan sedges *Cyperus polystachyos* (now extirpated on both islands) and *Cyperus cyperinus*, and the previously mentioned macrophytes, with aquatic beetles further indicating open wetland conditions (SI Appendix, Figs. S8, S12, and S18).

Ahuahu. Across northern New Zealand, the Kaharoa tephra forms a chronostratigraphic marker in sedimentary deposits for 1314 CE (21, 38, 39), but this has only been tentatively identified in sedimentary deposits from Ahuahu. Nevertheless, we suggest that the entire fossil sequence at Tamewhera and the post-1400

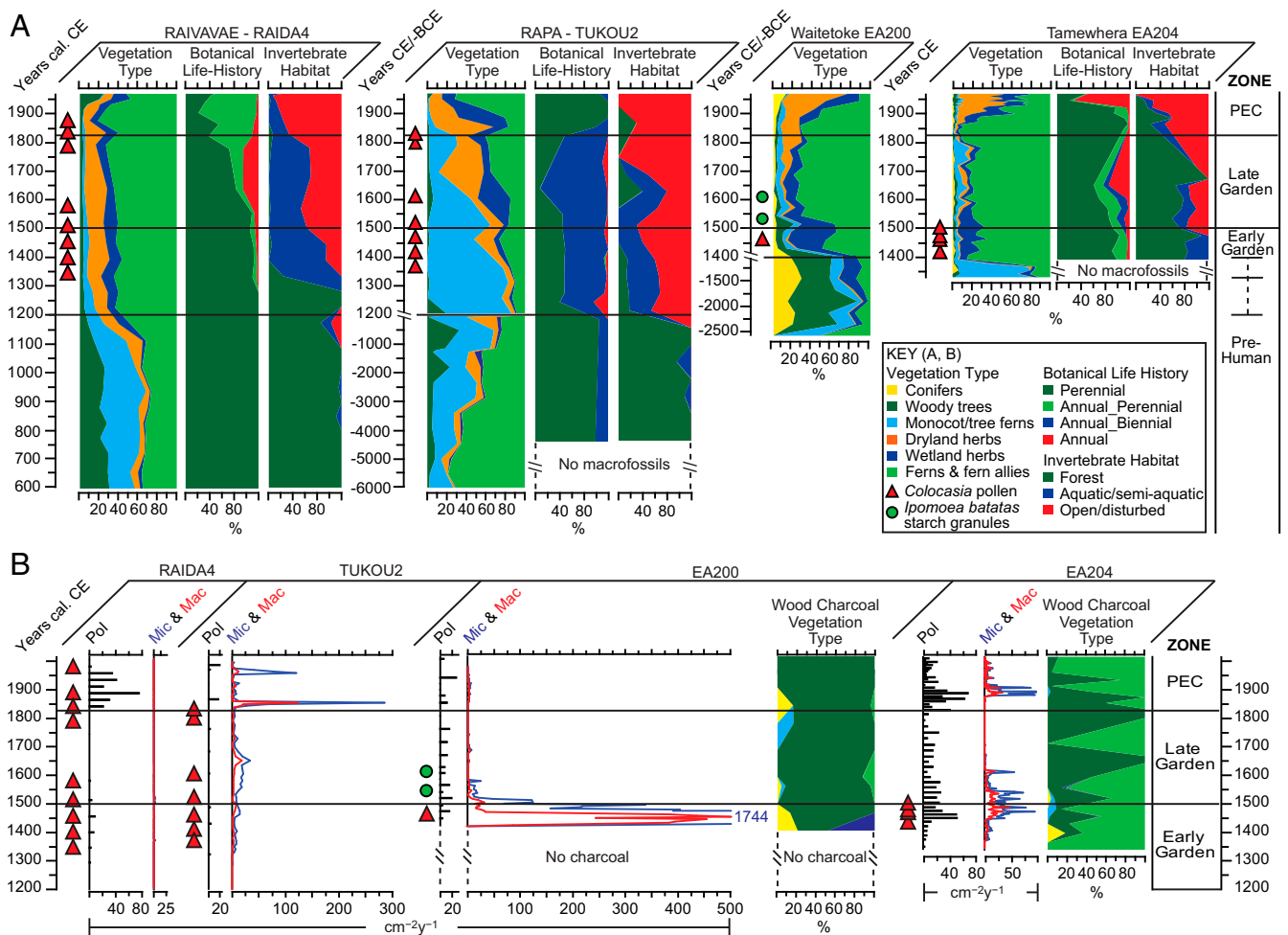


Fig. 2. (A) Stratigraphic diagram of palynomorph-based vegetation types (percent), macrobotanical-based life history (percent), and macroinvertebrate based habitat reconstructions (percent) for the four fossil records. Data are arranged according to the ^{14}C chronology [years CE or (negative sign) BCE] and are divided into four stratigraphic zones, based on the main vegetation changes. The presence of *C. esculenta* pollen (red triangles) and *I. batatas* starch granules (green circles) is indicated to the left of each vegetation type column. Sections of minimal or low sediment accumulation and poor fossil preservation are indicated by the symbol $-/-$. The Tamewhera sequence recorded no prehuman fossil material. (B) Stratigraphic diagrams for post-Polynesian colonization charred plant remains from the four fossil records. Contiguous charcoal accumulation rates (per square centimeter per year, *Methods*) for polCHAR ($\times 1,000$ particles), micCHAR (red) and macCHAR (blue), and wood charcoal-based vegetation types (percent) are arranged stratigraphically as for A. The presence of *Colocasia* pollen and *I. batatas* starch granules is indicated to the left of each PolCHAR column, as in A. No contiguous CHAR was recorded in the prehuman zone from any site. Extremely high macCHARs in the early garden sediments of Waitetoke are associated with a buried hearth feature (32). Modified with permission from ref. 32.

CE sequence at Waitetoke were formed as a result of wetland modification after the Kaharoa eruption. At Tamewhera between 1325 CE and 1425 CE, *Cyathea* tree ferns and sedges dominate the fossil record, indicating a rapidly infilling alluvial sedimentary environment (Fig. 2). Limited island-wide and localized burning occurred during the initial formation of the wetland. The conifer *D. cupressinum* (extirpated on Ahuahu, but recently replanted) dominated the prehuman mid-Holocene sequence at Waitetoke (Fig. 2 and *SI Appendix*, Fig. S22), with only fossil wood charcoal, not pollen, identified from the early garden zone at Waitetoke and, to a lesser extent, at Tamewhera (Fig. 2 and *SI Appendix*, Fig. S24). This shows that residual dead wood of a number of conifer species remained in the landscape and was used for fuel (44). Curculionid weevils and carabid beetles are the dominant indigenous invertebrates in the early garden sediments at Tamewhera, representing the retention of some indigenous trees. Local and island-wide fires and *P. esculentum* become more common after 1425 CE, as taro pollen enters both records.

Late Gardens (1500–1825 CE)

A rapid change in wetland hydrology at each site, with the exception of Waitetoke, is recorded in the late garden sediments with increases in macrophytes, indicating nutrient enrichment, and aquatic beetles indicating pond conditions, perhaps in response to bund terrace construction. Taro pollen is not recorded on Ahuahu after 1500 CE, and is periodically absent on Raivavae and Rapa, particularly from 1500 CE to 1775 CE. This may indicate either shorter growing periods leading to less flowering and a shift from perennial to annual production or the absence of taro, and, on Ahuahu, indicates the abandonment of wetland taro cultivation.

Raivavae and Rapa. The macrophytes, *E. geniculata* and *S. litoralis* subsp. *thermalis* increase in abundance as other sedges decline (*SI Appendix*, Figs. S8 and S12). These cosmopolitan taxa are short-lived perennials, and commonly grow on the margins of watercourses and pools, and currently occupy fallow or abandoned wetland taro gardens, as they do on many other Pacific Island wetlands. Aquatic invertebrates remain abundant, with an increase in veldid water striders indicating pond conditions (*SI Appendix*, Figs. S9 and S15).

Dryland herbs, mainly grasses, increase in the late garden sediments, indicating widespread vegetation clearance (Fig. 2).

Ahuahu. Wetland conditions and fires are recorded at both Waitetoke and Tamewera up until 1600 CE, and this corresponds to an increase in the fire-adapted ground fern *P. esculentum* (Fig. 2 and *SI Appendix*, Figs. S19 and S23). The summer-green, semideciduous macrophytes, *Bolboschoenus fluviatilis* and, to a lesser degree, *T. orientalis*, increase in abundance in the late garden sediments of Tamewera and may reflect pond conditions (*SI Appendix*, Fig. S18). The leaves of these plants die down during winter, reducing shade to cultivated taro plants, and may have escaped weeding, or were favored for other purposes, including for edible rhizomes. These changes are coincident with a shift toward dryland production, represented at Waitetoke by kumara starch granules and the reduction in wetland herbs (Fig. 2 and *SI Appendix*, Fig. S22).

After 1600–1650 CE, poor macrofossil preservation is observed along with high proportions of ferns and continued island-wide burning, but the cessation of local burning (Fig. 2). A rapid shift occurs from aquatic to terrestrial detritivores (e.g., Zopheridae and other beetles) at Tamewera. These changes may relate to the infilling of the wetland with coarse-grained sediments resulting from further vegetation clearance and associated hillslope erosion. This evidence, combined with the absence of taro pollen, indicates that the wetland gardens were likely abandoned at this time.

Post-European Colonization

The lack of indigenous plants and the increase in abundance of exotic species characterizes the post-European colonization (PEC) sediments across all study sites.

Raivavae and Rapa. Dryland herbs and ground ferns increase as more island-wide fires are recorded, but, on Raivavae, localized fires were infrequent (Fig. 2). On Rapa, island-wide and localized fires increase to the highest levels recorded at 1800–1825 CE. Taro pollen is more consistently recorded in the PEC sediments, which may indicate that gardens were only intermittently tended, probably in response to population decline. The rapid influx of introduced and invasive wetland plants, including the sedge, *Cyperus brevifolius*, and the primrose, *Ludwigia octovalvis*, also indicate the reduced production of taro (*SI Appendix*, Figs. S8 and S20). Commensal invertebrates including exotic ants (Formicidae) dominate the fossil assemblage, especially in the 20th century (see Fig. 4 and *SI Appendix*, Figs. S9 and S15).

Ahuahu. From 1820 CE to 1890 CE, island-wide fires are recorded in conjunction with an increase in ground ferns including *P. esculentum* as *Coriaria arborea* and indigenous sedges (e.g., *Carex* and *Cyperus* spp.) colonize the wetland, consistent with taro garden abandonment. From 1890 CE to 1920 CE, localized fires increase with a rapid influx of grasses and fewer ground ferns, indicative of the rapid conversion to pastoral farming across the island. Exotic PEC species including *C. brevifolius* and *Juncus ensifolius* replace the wetland vegetation (*SI Appendix*, Fig. S18).

Extinction

The last fossil appearances of extirpated or extinct palm trees, which were abundant in the prehuman sediments across all study sites, are all recorded during the period of human occupation (18). Several small forest trees were extirpated, including tree ferns (*Cyathea* sp.) on Raivavae. The extinction and extirpation of palms and small forest trees have been recorded elsewhere in southern Polynesia, including Rapa Nui (11, 18, 23). These trees were easily burnt and occupied habitats and soils readily modified for crop cultivation. Closely related trees were extirpated, presumably for their similar ecology, including two Piperaceae species on Raivavae (*Macropiper puberulum* and *M. latifolium*) and one on Ahuahu (*Piper melchior*). Wood charcoal recorded from Ahuahu (Fig. 2) suggests that some conifers may have been present during the early garden period, but this charcoal may

derive from driftwood transported from the coast (44). Pollen evidence indicates that only *D. cupressinum* survived on Ahuahu until extirpation during the PEC period, as has been found on other northern offshore islands (39). The loss of seed dispersers and pollinators, as well as the introduction of predators (e.g., rats), likely compounded the loss of plant species resulting from crop production practices. A number of trees were likely extirpated more recently, especially in New Zealand, from the overlay of European land use practices including from fire and the introduction of invasive mammals (e.g., goats and ship rats). For example, fossil pollen of the tree *Aristotelia serrata* was last recorded during the PEC period from Ahuahu (*SI Appendix*, Fig. S17) and Raoul (18). Living trees were last observed on the Ruamāhua islands 40 km southeast of Ahuahu between 1951 and 1952 (45). In addition, many of the cosmopolitan weedy plants identified in the fossil record from Ahuahu are currently rare in New Zealand, and were mostly extirpated before European contact, and now survive on coastal cliffs or small offshore islands with seabird colonies (46).

The invertebrate record includes abundant evidence of island extirpation (and likely extinction) of a wide range of taxa, mainly beetles. Prehuman parts of all records are dominated by taxa of closed forest habitats (e.g., Cryptorhynchinae and Cossoninae weevils, a range of genera of Zopheridae and Carabidae beetles) which are rarely recorded in early garden or late garden sediments. The records from both Raivavae and Rapa include many species that have never been recorded in historical times. A similar but less diverse assemblage of extinct invertebrates, particularly Cossoninae weevils, has also been identified in prehuman sediments from Rapa Nui (23).

Fire and Hillslope Erosion

The early evidence for taro cultivation in New Zealand from Ahuahu suggests that it may have been confined to the northern offshore islands. These islands contained forest ecosystems dominated by a greater proportion of low-growing monocotyledon trees, compared with the dense and tall conifer-dominant forests of mainland New Zealand. Smaller trees, including palms and tree ferns, familiar to Polynesians from their tropical island homelands, are soft-barked, easier to cut down and burn, and produce abundant leaf litter that, in wetlands, produces organic rich soils suitable for immediate taro production. On islands where the proportion of woody taxa in the prehuman vegetation was low, especially on Raivavae, fire was not as important for garden expansion as on the other islands. This may have also been the case on Rapa Nui, where the proportion of woody taxa and the accumulation of sedimentary charcoal in lake and swamp caldera sediments is low (11, 23). A correlation between woody representation and greater fire use for forest conversion (Fig. 2) is pronounced in areas of mainland New Zealand, where an even greater amount of burning was required to clear the biomass of tall conifer and broadleaf forests, and this likely contributed to a delay in garden expansion in those areas (21). We note that the largest forest remnants of the largest conifer tree *Agathis australis* (kauri), including the Waipoua forest in Northland, lie outside the climatic area most suitable for taro cultivation (Fig. 1). Furthermore, paleoclimate data indicate that El Niño–Southern Oscillation, and strengthening midlatitude westerlies along with stable temperatures after 1400 CE (47), established ideal conditions for forest fires, from which Māori took advantage for expanding gardens (21).

In addition to removing forests, fire also enriched soils with charcoal and exposed hillslope sediments that could be driven and held in small catchments for rapid garden construction. On Ahuahu, and, to a lesser degree, on Rapa, we show that the ICP garden sequence begins with hillslope erosion along with frequent and intense fires. The improvement of conditions for crop production using hillslope sediments operated on many tropical Pacific Islands (48). Highly specific ecosystem selection of forests with workable soils on islands marginal for

crop production is also demonstrated in other parts of Polynesia, including the Hawaiian Islands (6).

Commensal Species

Southern Polynesia and most of the remote Polynesian islands, including the Hawaiian Islands, did not receive the full complement of domesticated and commensal species common to tropical Polynesia (49, 50). Along with taro and kūmara, several crop plants were introduced to southern Polynesia before European contact, including *Dioscorea* spp. (yams or uwhi), *Broussonetia papyrifera* (paper mulberry or aute) (50, 51), and *Cordyline fruticosa* (ti) (52). The nut tree *Aleurites moluccana* (candlenut or tuitui/kukui) and domesticated coconut varieties were only introduced to some of the subtropical islands (12) (this study). Less clear is the status of many herbaceous plants that have a present-day cosmopolitan distribution. These are often regarded as commensal weeds, but most also have economic uses, and have been recorded historically in tropical Pacific Island gardens (53, 54). In southern Polynesia, these plants are predominantly from five plant families (Brassicaceae, Polygonaceae, Oxalidaceae, Solanaceae, and Asteraceae). They are mostly absent from prehuman fossil records, and first appear in the early garden sediments (Fig. 3).

Fossil evidence indicates that some of these commensal plants may have been dispersed naturally, perhaps by seabirds, and by Polynesians. *Sigesbeckia orientalis*, for example, is found in a 40,000-y-old fossil deposit from Tahiti, Society Islands, French Polynesia, indicating that this and other commensal plants may have a prehuman Pacific Island distribution, but this does not discount human-mediated introductions (55). On Rapa, *S. orientalis* and *Oxalis corniculata* appear earlier than the initial appearance of taro pollen. These annual plants may be indigenous to Rapa, as for Tahiti, and either formed part of the pre-cultivation seral vegetation or indicate early cultivation. Given that other cosmopolitan weedy taxa common to taro gardens are not represented in the fossil record until 1350 CE, including *Solanum americanum*, the watercress *Rorippa sarmentosa*, and the daisies *Adenostemma viscosum* and *Sonchus asper*, all consumed as leaf vegetables or regarded as famine foods, we suspect that these plants reflect precultivation disturbance during initial forest clearance.

Many of the weedy taxa were important to Polynesians as well as Māori and were likely tended in gardens, or thrived in these modified ecological conditions. As on the subtropical islands, some were most likely utilized by Māori as leaf vegetables or were consumed during famines (56), including the closely related watercresses *Rorippa divaricata* and *Rorippa palustris*, and *Sonchus kirkii* (Fig. 3). Small tuberous plants are also recorded from Ahuahu, including the polymorphic herbs *Geranium retrorsum* group (57) and *Cardamine* spp. (*C. corymbosa*, *C. dolichostyla*, or *C. forsteri*) (58) (Fig. 3). The cosmopolitan weedy plants recorded in the early garden sediments, including those with economic potential, especially *Rorippa* spp. and *S. kirkii*, were rapidly replaced during the PEC period by more-invasive and productive introduced relatives including the watercresses *Nasturtium officinale* syn. *Rorippa nasturtium-aquaticum*, and the annual sow thistle *Sonchus oleraceus*.

From the evidence presented here, Polynesians introduced a wide range of commensal invertebrates to southern Polynesia, but also established the conditions for disturbance-adapted indigenous or endemic species to thrive in newly constructed garden ecosystems. Of the commensal invertebrates, the most consistently recorded species is the beetle, *Cryptamorpha desjardinsi* (Silvanidae) (Fig. 4). This detritivore is commonly found feeding on molds and mildews on the surface of monocotyledon leaves, but has also been found in sheep carcasses, bird nests, and human habitations, including compost heaps (59). These beetles were formerly thought to be recently introduced to New Zealand and most Pacific Islands, but, like *S. orientalis*, *C. desjardinsi* may also be indigenous, and thrived in garden ecosystems in southern Polynesia. However, because it has never been found in

prehuman sediments anywhere in Polynesia, we regard this as a Polynesian introduction. Other common commensal invertebrates that were likely Polynesian introductions include the detritivorous beetles *Saprosites pygmaeus* (Scarabaeidae), *Dactylosternum abdominale* (Hydrophilidae), the earwig, *Euborellia annulipes* (Anisolabididae), and a range of exotic ants (Formicidae), all consistently identified in the early garden sediments after 1350 CE (Fig. 4). These taxa are common to highly modified habitats throughout much of the tropics, but only *C. desjardinsi* is identified in the fossil record of Ahuahu (Fig. 4 and *SI Appendix*, Fig. S21).

A number of close relatives were identified from Ahuahu, including the indigenous or endemic *Saprosites* cf. *communis* and the Aphodiinae dung beetle *Ataenius* cf. *picipinus* (60), as well as the *Dactylosternum* cf. *marginale* (61). Also recorded at Ahuahu are other detritivorous invertebrates that commonly occupy disturbed habitats, including scirtid marsh beetles that live around stagnant water bodies (62), and the beetles Aleocharinae and *Carpelimus* (Staphylinidae), that usually feed in decaying leaf litter and dung (63). We suggest that, on Ahuahu, these invertebrates were attracted to decaying organic matter associated with gardens. No exotic ants were recovered in the early garden sediments of Ahuahu, but they entered the record in high proportions during the PEC initial pastoral farming period, reaching maximum abundance in the last 40 y.

Crop Production Intensity

A transition from low- (perennial) to high-intensity (annual) cultivation after 1500 CE is evident from the increase in short-lived taxa across all sites and the absence of taro pollen on Ahuahu, and its reduced presence on the subtropical islands, indicative of frequent tilling, harvesting, or other soil disturbance (Fig. 3). On Ahuahu, the absence of taro pollen may indicate higher-intensity production or a shift to kūmara production evident from the presence of starch granules at Waitetoke. Southern Polynesian floras hold few indigenous annual herbs compared with the flora of other regions (64, 65). The most common annuals present in the fossil records include the cosmopolitan daisies *S. orientalis* and *Sonchus* spp. On Ahuahu, six annuals are recorded, including *Montia fontana* and *Ranunculus* cf. *sessiliflorus*, both absent today. Several perennial and polymorphic herbs have the capacity to form annuals in fertile soils, including *Wahlenbergia gracilis* complex (66) and *Cardamine* spp. (58), enhancing their survival in disturbed garden soils. These plants are not known for their present-day weedy capacity, as they were rapidly displaced by exotic herbs, particularly annual pastoral grasses during the PEC period (46).

Along with nutrient enrichment and sediment accumulation, the marked increase after 1500 CE in macrophytes, some of which are summer-green or deciduous (*B. fluviatilis* and *T. orientalis* on Ahuahu), or annuals under certain hydrological conditions (e.g., *E. geniculata* on Rapa and *S. litoralis* on Raivavae), may also reflect high-intensity cultivation (*SI Appendix*, Figs. S8, S12, and S18). Furthermore, the clonal life history of these plants may indicate ditch construction, tillage, and hand-weeding activity at each site, as the separated rhizomes buried in turned soil will quickly regenerate each season.

Conclusions

The fossil records presented here document early tropical crop adaptation in southern Polynesia, placing these islands within the continuous traditions of crop production by Polynesians and their Austronesian ancestors. Traditions of crop introduction and production on Raivavae and Rapa are closely tied to the tropical Society Islands (31), where the importance of taro cultivation since initial colonization is demonstrated from fossil evidence (42, 55). Our findings suggest that southern Polynesian societies initially adapted food production systems in ways that were ecologically dynamic and closely reflect these ancestral connections. While New Zealand Māori retain cultural affinities with the Society Islands, traditions of crop production associate

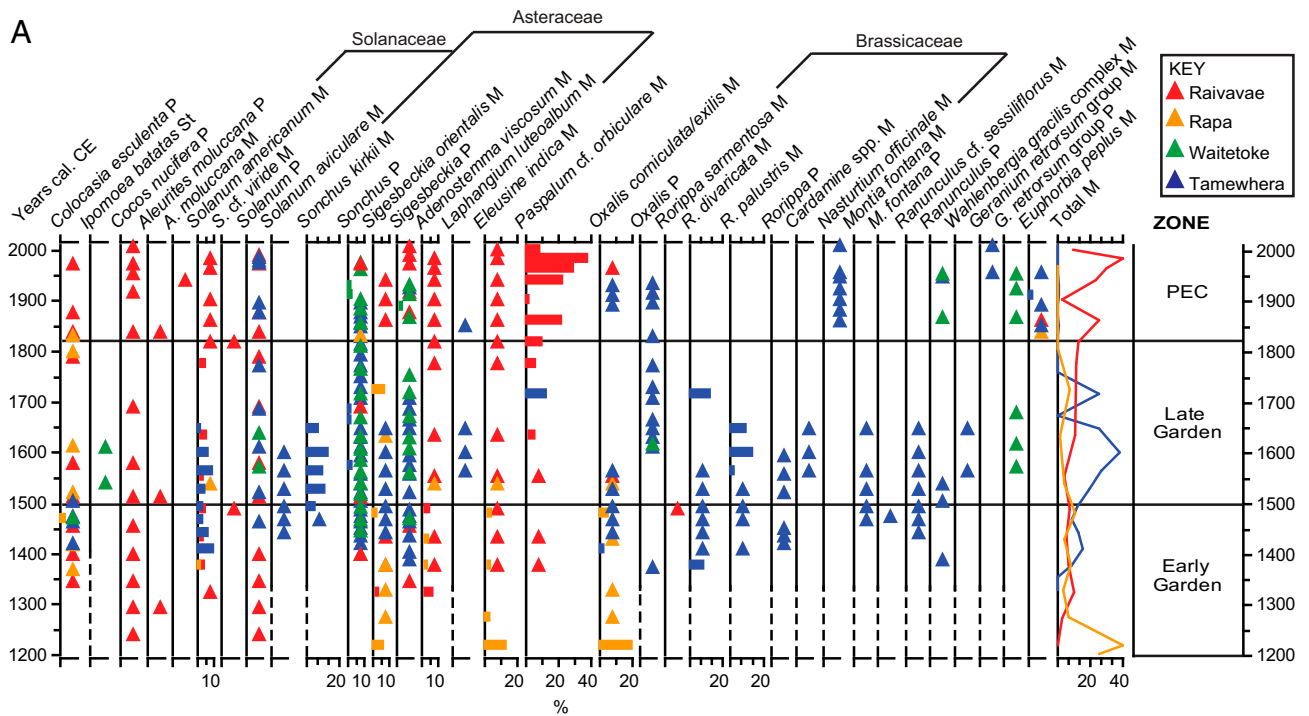


Fig. 3. (A) Stratigraphic diagram for the post-Polynesian colonization proportions of economic or seral plant taxa, identified from the palynomorphs (P), starch granules (St), and macrobotanical (M) remains from the four fossil records. Triangles represent taxa with <5% of the total fossil sum. Bars indicate taxa with >5% of the total fossil sum. Taxa are stratigraphically arranged as for Fig. 2A. Apart from *C. nucifera* pollen on Raivavae, none of these taxa are recorded in the prehuman zone. (B) Photomicrographs (A1, A2, B) and scanning electron micrographs (C–L) of fossils of crops and weedy plant species from Ahuahu are also presented. Photomicrographs B, A1 and B, A2 (pollen, EA204, 225 cm to 226 cm, early garden) are *C. esculenta*; B, B (starch, EA200, 75 cm to 76 cm, late garden) is *I. batatas*. (Scale bar, 10 μ m.) B, C–L are as follows: B, C (seed, EA204, 210 cm to 220 cm) is *R. divaricata*; B, D (seed, EA204, 180 cm to 190 cm, late garden) is *R. palustris*; B, E (seed, EA204, 180 cm to 190 cm, late garden) is *Cardamine* sp.; B, F (seed, EA204, 210 cm to 220 cm, early garden) is *S. americanum*; B, G (achene, EA204, 190 cm to 200 cm, late garden) is *S. kirkii*; B, H (seed, EA204, 80 cm to 90 cm, PEC) is *E. pepplus*; B, I (seed, EA204, 180 cm to 190 cm, late garden) is *Solanum aviculare*; B, J (achene, EA204, 180 cm to 190 cm, late garden) is *S. orientale*; B, K (fruit, EA204, 90 cm to 100 cm, PEC) is *Haloragis erecta*; and B, L (seed, EA204, 210 cm to 220 cm, early garden) is *O. corniculata*. (Scale bar, 100 μ m.)

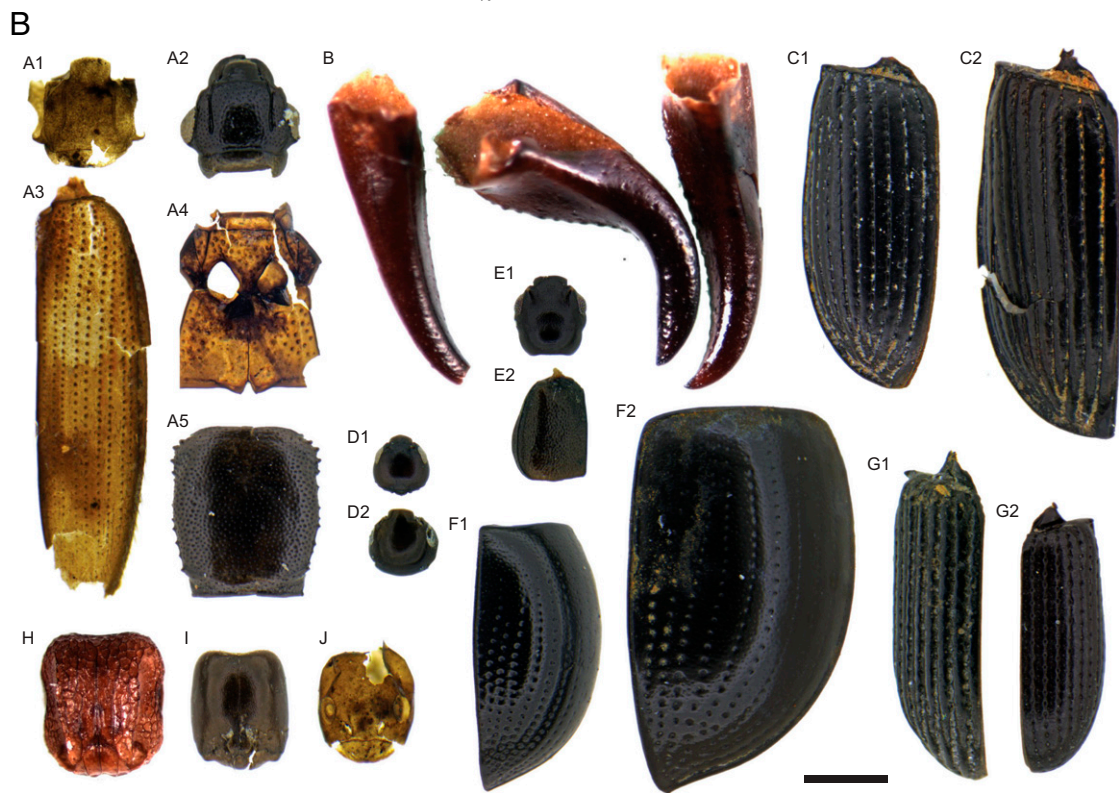
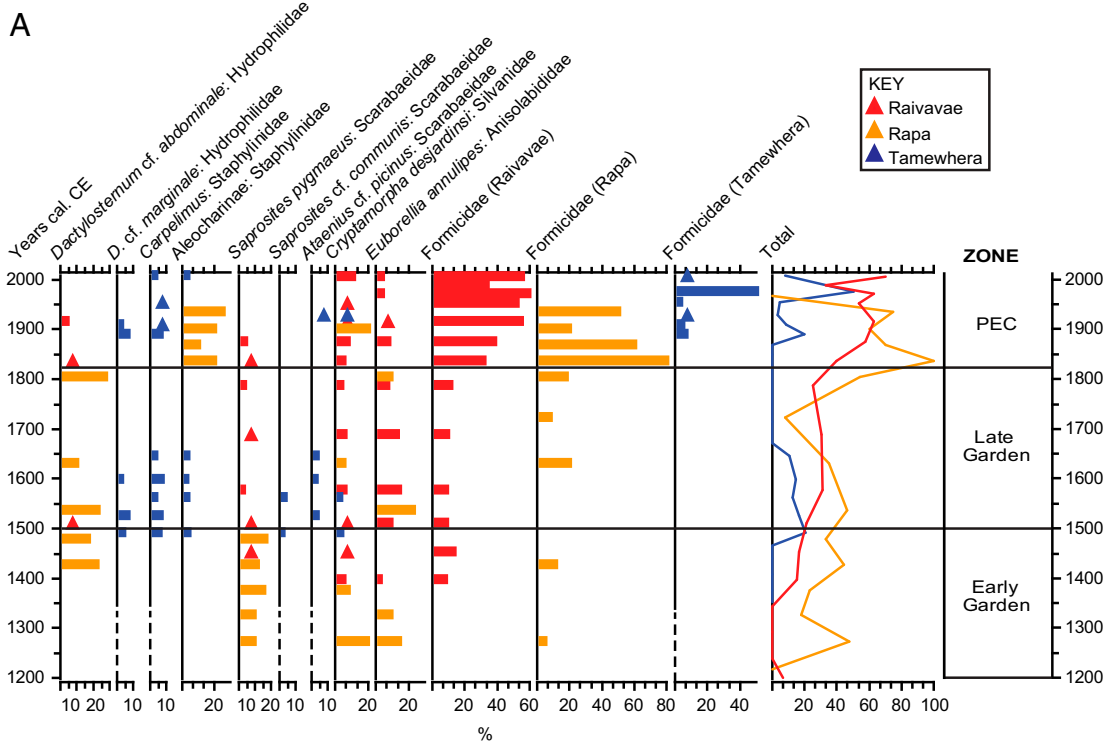


Fig. 4. (A) Stratigraphic diagram for the post-Polynesian colonization proportions of commensal invertebrate taxa identified from macroinvertebrate remains from the four fossil records. Taxa are arranged stratigraphically as for Fig. 3A. (B) Photomicrographs of the invertebrate fossil taxa. B, A1 (head, EA204, 210 cm to 220 cm, early garden), B, A2 (head, RAIDA4, 90 cm to 95 cm, late garden), B, A3 (elytron, EA204, 210 cm to 220 cm, early garden), B, A4 (thorax, EA204, 210 cm to 220 cm, early garden), and B, A5 (prothorax, EA204, 210 cm to 220 cm, early garden) are *C. desjardinsi*; B, B (forceps, TUKOU2, 58 cm to 60 cm, late garden) is *E. annulipes*; B, C1 and C2 (elytra, EA204, 170 cm to 180 cm, late garden) are *Ataenius cf. picinus*; B, D1 and D2 (heads, EA204, 170 cm to 180 cm, late garden) are Aleocharinae spp.; B, E1 (head, EA204, 190 cm to 200 cm, early garden) and B, E2 (pronotum, EA204, 190 cm to 200 cm, early garden) are *Carpelimus* sp.; B, F1 (elytron, EA204, 80 cm to 90 cm, PEC) is *Dactylosternum cf. marginale*; B, F2 (elytron, RAIDA4, 100 cm to 105 cm, late garden) is *D. abdominale*; B, G1 (elytron, EA204, 190 cm to 200 cm, early garden) is *Saproscites* sp.; B, G2 (elytron, RAIDA4, 50 cm to 55 cm, PEC) is *S. pygmaeus*; B, H (head, TUKOU2, 74 cm to 76 cm, late garden) is *Tetramorium pacificum* (Formicidae); B, I (head, EA204, 90 cm to 100 cm PEC) is *Hypoponera cf. punctatissima* (Formicidae); and B, J (head, RAIDA4, 95 cm to 100 cm, late garden) is *Nylanderia* sp. (Formicidae). (Scale bar, 0.5 mm.)

Ahuahu with the initial cultivation of kūmara, not taro (67). Kūmara is of similar importance on Rapa Nui, which, aside from the perennial lakes and swamps of the calderas, lacked wetland habitats and perennial water sources, but did contain extensive palm-dominant forests that occupied workable soils for Polynesian crop production, unlike many of the abandoned southern Polynesian islands (Fig. 1) (18, 24, 25). The fossil evidence from Ahuahu, instead, points to the importance of early wetland taro cultivation that required more crop maintenance in the marginal climate conditions, but does not preclude the role of dryland kūmara or other crops in early cultivation systems. In addition, the diversity of arable weeds and other commensal species recorded in both the early and late garden sediments on Ahuahu were undoubtedly familiar to the founding Polynesian population of the island (e.g., *Sonchus* spp.), and were also commonly recorded in 19th century Māori kūmara gardens across northern New Zealand (56).

The ecological parallels between the fossil records and the geomorphic and biotic characteristics of the three study islands indicate that niche selection and construction was focused on crop cultivation (2, 3, 48). It is likely that wetland deposits from New Zealand that document these preexisting ecosystems are rare and largely restricted to the offshore islands and parts of the northern North Island, where PEC farming practices including wetland drainage were less destructive. The evidence from Ahuahu contrasts with prevailing hypotheses of a strict initial reliance on wild foods in New Zealand. Evidence for the local construction of features like hillslope stone alignments after 1600 CE is most likely associated with the expansion of dryland kūmara cultivation. This formed part of a transition that played out across northern New Zealand, but is apparent and early on Ahuahu, due to the preferable ecological and climatic conditions for crop production. The island may therefore have functioned as a nursery or experimental garden before the expansion of crop production to other areas across New Zealand.

Our study highlights the value of recent sedimentary deposits (centuries rather than millennia in age) which are widely found across Polynesia. These preserve abundant fossil remains of previously unidentified commensal species, and evidence of the spatial and temporal complexity of crop production systems. The abundance of woody vegetation appears to have posed a pronounced ecological limit on taro production in temperate New Zealand. By contrast, this appears not to be case on the subtropical Polynesian islands, where rapid conversion to cultivation of prehuman forests occurred, then dominated by now-extinct, easily cleared monocotyledon tree and tree fern forests. The niche selection and construction of ecosystems for early crop production outlined here for southern Polynesia informs how Neolithic crops may have initially spread into other areas marginal for production.

Methods

Sediment Cores. Cores were retrieved using a 50-mm-diameter, 0.5-m-length D-section corer. At Ra'irua, one of the fallow gardens, 200 m inland from the lagoon shoreline, was cored to a depth of 2.7 m below the marsh surface (RAIDA4). At Tukou, the center of the marsh, 60 m from the lagoon edge, was cored to a depth of 4 m below the surface (TUKOU2). At Waitetoke, a 2-m core (EA200) was retrieved before reaching compacted clay and sand, but this site was also excavated to that same depth in a 1 × 1 m pit, recovering archaeological fire-cracked stones, obsidian flakes, and wood charcoal at a depth of 90 cm to 100 cm (32). At Tamewhera, an open sedge- and grass-covered section of the mire, was cored until a compacted sand layer was reached at a depth of 2.94 m below the surface (EA204). Sedimentation patterns were examined using magnetic susceptibility and incoherent/coherent scattering values using Itrax core scanning (Cox Analytical Systems, coxsyst.se) as measures of organic matter content diagrams (*SI Appendix*, Fig. S6).

Palynomorphs. Core samples for palynomorph analyses (including pollen and spores) were taken at regular intervals to determine baseline vegetation changes. Each 1-cm³ sample was processed using standard procedures (10% HCl, hot 10% KOH, and acetolysis) (68). Samples were spiked with exotic

Lycopodium clavatum L. tablets to allow the palynomorph and charcoal concentrations to be calculated. Counts continued until reaching a sum of at least 100 terrestrial palynomorphs. Reference palynomorphs held in the Australasian Pollen and Spore Atlas (apsa.anu.edu.au/) assisted with identification, along with regional reference keys (69, 70). All names refer to the family or genus of extant plants and their nearest modern affinity. Nomenclature is based on Plant List Version 1.1 (www.theplantlist.org/; *SI Appendix*). Palynomorph percentage and total accumulation data (in square centimeters per year) were placed into stratigraphic diagrams (*SI Appendix*, Figs. S7–S23). Summary diagrams (Fig. 2) show four stratigraphic zones based on the main vegetation changes: (i) prehuman Late Holocene to 1280 CE, (ii) early garden 1280–1500 CE, (iii) late garden 1500–1825 CE, and (iv) PEC 1825 to present. Although samples were not processed with starch as a target, some granules of known cultigens (taro and kūmara) were observed and identified from the palynomorph preparations using a Nikon cross-polarized light microscope.

Sedimentary Charcoal. Charcoal particle accumulation rates (<125 μm of polCHAR per cm²·y⁻¹) were calculated as part of palynomorph counting from the same samples (counted in proportion to the exotic *Lycopodium* spores), as a proxy for island-wide fire activity (Fig. 2). Each core was sampled every 1 cm for charcoal particles (micro > 125 μm < 250 μm and macro > 250 μm size fractions), with the accumulation rates (micCHAR and macCHAR per cm²·y⁻¹) used to reconstruct localized fire activity.

Macrofossils. Additional D-section cores were collected for macrobotanical (including wood charcoal) and macroinvertebrate analyses, extending the taxonomic resolution of the analyses. Potential contaminants were removed in the field, with cores cut into 10-cm-long bulk sediment samples. Sample volume averaged 150 mL, with the exception of Rapa (20-mL samples). From Waitetoke, additional sediment was retrieved from an excavation pit (32). In the laboratory, samples were gently washed through a series of nested sieves (>250 μm to >2 mm) for sorting. All diagnostic remains separated under stereomicroscopy were counted as minimum number of individuals. All data are summarized in stratigraphic diagrams, along with the associated palynomorph data (Fig. 2 and *SI Appendix*, Figs. S7–S24). Macrobotanical remains, mostly seeds, were identified by comparison with reference materials accessioned at the Australian National Herbarium, Allan Herbarium, the Musée de Tahiti et des Îles, an Asia/Pacific regional reference collection held at the Australian National University, and other sources (e.g., www.ars.usda.gov/; refs. 46, 64, and 71). Wood charcoal identification was undertaken on pieces >5 mm in diameter sieved from Tamewhera and Waitetoke under incident light microscopy. Most New Zealand woods have a distinctive cell anatomy that allows for the identification of species, genus, or family based on comparative collections held at the University of Auckland (44). Life history characteristics of the taxa represented in each macrobotanical record allowed inferences about garden modification for low-intensity (perennial) or higher-intensity (annual) production. This includes the proportion of perennial and annual plants, and other subcategories, identified from floral compendia (64, 65) (Fig. 2). Remains of macroinvertebrates, including all arthropods, were identified by comparison with reference collections from French Polynesia held at Deakin University and at the Bishop Museum, Honolulu, and, for New Zealand, from Landcare Research, Lincoln, and online sources.

Chronology. Accelerator mass spectrometry ¹⁴C measurements primarily on macrobotanical remains from each core (*SI Appendix*, Table S4) were placed within Poisson-process depositional models in OXCAL version 4.3 to build calibrated Bayesian age models using SHCal13 calibration data (72, 73). Exotic plant remains in the upper sections of each core provide relative dates of events that occurred during the PEC period. For example, we used the seeds of the milkweed *Euphorbia peplus* as a stratigraphic fossil marker, found on all of the study islands (46, 64) (Fig. 3). We use the calendar year 1825 ± 5 CE for exotic plant introduction to Raivavae and Rapa, and herbarium records to date plant introductions to New Zealand.

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