ria to produce H_2S, which reacts with Fe to form pyrite (38). Observations suggest that in settings of "normal marine" deposition, the burial of pyrite and organic C are positively related, because organic matter is the major substrate used by sulfate-reducing bacteria (38). Thus, a possible explanation for the lower pyrite burial as suggested by the S isotope curve between 120 and 105 Ma could be low organic matter availability for sulfate reducers during this time interval. The geological record, however, shows that the mid-Cretaceous is characterized by ocean-wide high organic matter burial (18–21). This high organic matter burial is also supported by the higher C isotope ratios of dissolved carbonate in seawater at that time (39, 40); thus, limitation of sulfate reduction by organic matter availability is unlikely to be the reason for a lower pyrite burial rate. Alternatively, pyrite formation may have been limited by high pyrite availability. In addition, the variability in response time of organic matter burial may have taken place in continental settings where pyrite formation is limited by sulfate availability (38).

It is interesting to compare the S isotope curve to a compiled C isotope curve of seawater carbonates for the Cretaceous (39, 40) (Fig. 1B). This comparison must be regarded only as a first-order observation because the records are not composed of well-documented oceanic burial a considerable amount of organic matter burial may have taken place in continental settings where pyrite formation is limited by sulfate availability (38).

Before European contact, Hawaii supported large populations in complex societies that were based on multiple pathways of intensive agriculture. We show that soils within a long-abandoned 60-square-kilometer dryland agricultural complex are substantially richer in bases and phosphorus than are those just outside it, and that this enrichment preceded the establishment of intensive agriculture. Climate and soil fertility combined to constrain large dryland agricultural systems and the societies they supported to well-defined portions of just the younger islands within the Hawaiian archipelago; societies on the older islands were based on irrigated wetland agriculture. Similar processes may have influenced the dynamics of agricultural intensification across the tropics.

What determined the distribution and dynamics of intensive agriculture in tropical forest environments, before European contact? The question is controversial; some argue that the soils of most tropical forests are suited only for long-fallow shifting cultivation (1), whereas others contend that many rain forests have been shaped by a long history of intensive cultivation (2, 3). Analyses of Polynesian agriculture are relevant to this question, because Polynesians used a variety of intensive agricultural practices in a broad range of tropical environments. Here we evaluate how climate and soil fertility defined the distribution of large rain-fed dryland systems in the Hawaiian Islands, on both local and archipelago-wide scales.

About 3000 years ago, the progenitors of the Polynesians brought a suite of crops, domestic animals, and agricultural strategies into the central Pacific, where they developed a distinctive culture that in the first millennium A.D. radiated to the margins of Eastern Polynesia (4). By the time of significant European contact in the late 18th century, many Polynesian economies were highly intensive, with short-fallow or irrigated agricultural systems supporting dense populations in societies with substantial social hierarchy and cultural complexity (5, 6).

Soils, Agriculture, and Society in Precontact Hawaii

P. M. Vitousek1*, T. N. Ladehoff,2 P. V. Kirch,3 A. S. Hartshorn,4 M. W. Graves,5 S. C. Hotchkiss,6 S. Tuljapurkar,1 O. A. Chadwick4

Before European contact, Hawaii supported large human populations in complex societies that were based on multiple pathways of intensive agriculture. We show that soils within a long-abandoned 60-square-kilometer dryland agricultural complex are substantially richer in bases and phosphorus than are those just outside it, and that this enrichment preceded the establishment of intensive agriculture. Climate and soil fertility combined to constrain large dryland agricultural systems and the societies they supported to well-defined portions of just the younger islands within the Hawaiian archipelago; societies on the older islands were based on irrigated wetland agriculture. Similar processes may have influenced the dynamics of agricultural intensification across the tropics.

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References and Notes

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Within the range of cultural variability evident in Polynesia, both agricultural intensification and sociopolitical complexity reached their peak in the Hawaiian Islands. The first Polynesians reached Hawai‘i no later than 800 A.D, bringing with them at least 40 species of plants (7) and 4 species of animals. Over the ensuing millennium, largely in isolation even from the rest of Polynesia, the Hawaiians used these plants and animals to develop several highly capital- and/or labor-intensive agricultural systems, including large areas of irrigated taro pondfields and of short-fallow dryland field systems. Many wetland taro systems survived the precipitous drop in Hawaiian population that followed the introduction of continental diseases after 1778 A.D, and a few persist into the present (8, 9). However, the dryland systems largely were abandoned within a few decades, and only the archaeological remains of their field wall and trail systems mark their former extent.

Societies based on irrigated wetland versus rain-fed dryland agriculture differ in their labor requirements, in their capacity to produce a surplus, in their vulnerability to perturbation, and in their economic and sociopolitical structure and dynamics (10). They represent different classes of agricultural intensification: “landesque capital” intensification in the case of pondfield irrigation and “cropping cycle” intensification in the dryland field systems (10–14). Comparative analysis of cultural sequences on several Polynesian islands suggests that the rise of aggressive chiefdoms late in prehistory was closely linked to labor-demanding cropping-cycle intensification in dryland zones (3, 10).

Wetland versus dryland systems have an uneven distribution across the Hawaiian Islands (Fig. 1), reflecting the archipelago’s enormous environmental heterogeneity. The Hawaiian Islands are the product of a hot-spot in Earth’s mantle that now lies under the southeastern edge of the chain, forming the island of Hawai‘i (15). There are few surface streams on young Hawaiian volcanoes, but the older islands support well-developed drainage networks. Not surprisingly, irrigated wetland agricultural systems are found primarily on older islands, and in the few alluvial valleys on younger islands. Less obviously, archaeological evidence indicates that large dryland agricultural systems were confined to discrete areas of the younger volcanoes (Fig. 1).

What factor(s) confined large dryland agricultural systems to the younger Hawaiian islands? Many such systems have a lower rainfall boundary near 500 mm/year, below which sweet potato, the principal staple crop of Hawaiian dryland agriculture, does not flourish (16, 17); they have an upper elevational boundary near 900 m, above which low temperatures delay crop maturation (18, 19). However, there are extensive areas of both the old and the young islands that fall within these climatic bounds, but where the Hawaiians did not develop large dryland field systems (20).

We evaluated climatic and biogeochemical factors that could have controlled the distribution of intensive dryland field systems in the Hawaiian Islands before European contact; we focused on the leeward Kohala field system on the northern end of the Island of Hawai‘i (21). Kohala contains a vast field system (covering at least 60 km2) that has been the focus of several previous archaeological investigations (22–24); the pattern and timing of human use of the area are known reasonably well (22, 23, 25). Human settlement and farming in the region began ~1200 to 1300 A.D, and the most intensive farming probably took place in 1400 to 1800 A.D. The system itself was highly developed, with an extensive network of field walls and stone-lined trails, and a large proportion of the system is well preserved (fig. S1).

Kohala Mountain was constructed by eruptions of tholeiitic basalt from 400,000 to 600,000 years ago; later eruptions from 150,000 to 200,000 years ago covered much of the area with a layer of alkalic basalt (26). Surfaces of both the younger Hawi and the older Pololu formations are present within the field system. Rainfall varies with elevation and exposure to the prevailing northeast trade winds, and the leeward southwest flank of Kohala experiences what may be the most spectacular rainfall gradient on Earth, along which annual precipitation falls from ~4500 to <180 mm/year in a distance of <15 km (27) (Fig. 2). This rainfall gradient has been the focus of a long-term study of climate-soil interactions (28, 29) centered on a transect just outside the Kohala field system (30). This research reveals a striking threshold in soil properties near an annual rainfall of ~1800 mm, below which Ca and other cations are abundant, and evidence from Sr isotopes suggests that most cations derive from atmospheric deposition of marine aerosols, reflecting the long-term weathering and loss of minerals in basalt.

The Kohala agricultural system was embedded in this leeward rainfall gradient, reaching from the coast on the north diagonally up into the rain shadow southwest of the summit of Kohala Mountain (Fig. 2). Its lower elevational boundary followed the 750-mm rainfall isohyet, reaching up to ~600-m elevation on the southern margin of the system; the upper boundary was near the 1600-mm isohyet, but was not so closely tied to rainfall (17).

We synthesized information from archaeology, soils, and biogeochemistry to determine what made the Kohala field system suitable for agricultural intensification and, conversely, to determine what set its boundaries. The approximate correspondence between the upper boundary of the field system and the sharp transition in soil fertility observed by Chadwick et al. (29) suggests that low soil fertility could inhibit the development of intensive dryland agriculture in wetter sites, and we test that suggestion here. We evaluated the mechanisms controlling soil fertility within and outside the Kohala field system, and built on these results to evaluate the distribution of intensive dryland agricultural systems across the Hawaiian Islands.

We focused our analyses of soils on base saturation and phosphorus (21, 32). Base saturation is defined as the percentage of cation exchange sites occupied by Ca, Mg, K, and Na; it is influenced by the concentrations of these cations and by soil acidity, and so represents an integrated measure of the availability of nutritional cations. Base saturation across the Kohala field system declines from dry into wetter sites (Fig. 3A), generally following the pattern observed on the Kohala climate transect (29), although with a distinct increase from dry sites just below the field system into the lower edge of the system itself. The younger Hawi sub-
strate supports significantly greater base saturation than the older Pololu substrates at comparable rainfall (table S1). The upper (wetter) boundary of the Hawaiian field system occurs at the same level of base saturation on both substrates, but this base saturation occurs at lower rainfall on the older Pololu substrate (Fig. 3A).

Phosphorus availability often limits the productivity of agricultural and natural systems in tropical regions (33), and concentrations of resin-extractable P in soils (a measure of biologically available P) are markedly elevated within the field system relative to both wetter and drier sites (Fig. 3B). Also, P is significantly more available on the young Hawi substrate than on the older Pololu substrate (table S1).

These patterns in P availability could reflect variation in the total quantity of P in soils, in the fraction of total P that is resin-extractable, or in both. In fact, both of these components contribute to the pattern. The fraction of total P that is resin-extractable peaks within the field system (Fig. S2A); P availability is reduced by adsorption/precipitation with carbonates in dry soils below and with Fe and Al in acid soils above the system (29). The increased quantity of total P within the field system (Fig. S2B) is more surprising; P is relatively immobile in soils, and greater adsorption/precipitation of available P in soils outside the field system should further reduce its mobility compared to soils within the system.

To understand this pattern, we calculated the net gain or loss (relative to basaltic parent material) of total P from soils within and outside the field system, using Nb as an immobile index element (21, 34). Overall, we found a net gain of P (relative to basalt) in soils within the field system on the young Hawi substrate, and a relatively small net loss on the old Pololu substrate. In contrast, there was a net loss of P from both wetter and drier sites on both substrates, with greater losses from the older substrate (Fig. 3C, table S1). Losses of nutritional cations (Ca, Mg, K) were greater than those of P, but followed the same patterns.

Two processes that could enrich P and cations in soils within the Kohala field system, and so make them a "sweet spot" of high soil fertility and agricultural productivity, are mulching by Hawaiian cultivators and biological transport of P from the subsoil. Organic material brought in from outside the field system would add P and other plant nutrients—but not Nb—to soils. Mulching was an integral part of Polynesian dryland agriculture (35)—although a 60-km² area would be difficult to mulch so intensively. Alternatively, many millennia of nutrient cycling through the native forests that occupied the area before Polynesian cultivation could have transferred P (but not Nb) from deep in the soil and so enriched surface soils (36). Drier sites below the field system might be so unproductive as to lack this enrichment, or any enriched surface layer might have been lost through wind erosion; wetter sites above the field system should lose both P and cations through leaching.

We tested the importance of these alternatives by comparing our results for P gains and losses within the field system with results from along the Kohala climate transect, which incorporates sites with a similar range of rainfall but no history of intensive cultivation (29) (Fig. 2), and from surface soils that had been buried under the walls of the field system itself (21). We assumed that these under-wall soils were isolated from P inputs through mulching at the time agricultural production was intensified.

Both comparisons suggest that enriched surface soils within the field system predated agricultural intensification (Fig. 4). In sites within the rainfall range of the field system, there is a net gain of P within surface soils of the Kohala climate transect (Fig. 4A), and deeper soil horizons there are depleted in P (Fig. S3). Buried surface soils from under the cultivators’ walls are more enriched in P (relative to basalt) than are surface soils (Fig. 4B). The cumulative effect of forests pumping nutrients from subsoil—and not mulching—led to the relatively P-rich environment in which Hawaiians created this intensive agricultural system (37). Indeed, the richness of soils from below field walls suggests that agriculture (and/or subsequent ranching) may have depleted P in surface soils near the upper edge of the field system (Fig. 4B); if so, this depletion eventually could have constrained agricultural productivity.

Our analyses suggest that climate and soil fertility constrained the distribution of dryland agricultural field systems in the Hawaiian Islands, both locally and across the

Fig. 2. Rainfall in leeward Kohala, and the location of the Kohala field system and the Kohala climate transect. Solid black lines represent 100-m elevation contours, and red lines represent rainfall isohyets. The field system (shaded area) reaches uphill from the coast on the north into the rain shadow of Kohala Mountain, with its lower boundary corresponding to a median annual precipitation near 750 mm. The red points represent soil samples collected along multiple transects across the field system, and the blue points represent the Kohala climate transect (29) to the south of the field system.

Fig. 3. Soil properties along two transects across the leeward Kohala field system, Hawai‘i. One transect lies on 150,000-year-old Hawi substrate (●) and the other lies on 400,000-year-old Pololu substrate (○). Dashed and solid vertical lines represent the boundaries of the field system on the Hawi and Pololu substrates, respectively. (A) Base saturation. (B) Resin-extractable P. (C) Total P as a percentage of the P in basaltic parent material, calculated as described in (21). Results from all of the sample points in Fig. 1 are summarized in table S1.
The sequence of intensification within leeward Kohala (23, 25) is one of the best documented cases in the tropics, and our results link this sequence to a set of specific biogeochemical parameters that helped to shape and constrain its development. On the lower boundary, the walls and trails of the field system are well developed where rainfall exceeds 750 mm, and absent in drier sites. On the upper boundary, the field system occurs where base saturation exceeds 20% and resin-P is ≥40 mg/kg; it is absent in less fertile sites (38). These thresholds in soil fertility are reached at lower rainfall on the older, less fertile Pololu substrate than on the younger Hawi substrate (Fig. 3).

We suspect that the wetter margin of the field system was particularly valuable to Hawaiian cultivators, because the combination of fertile soils and higher rainfall would have made crop yields more reliable (18). However, this upper margin is near the climatic threshold at which nutrient supply from rock weathering is exhausted (29), and so any increase in nutrient losses associated with agriculture could have pushed it over the edge into infertility. The greater P that we observed in soils buried under field walls (Fig. 4B) is consistent with this possibility.

Expanding our analysis to the Hawaiian archipelago, the decline in soil fertility from the younger Hawi to the older Pololu substrates (Fig. 3) is consistent with observations of declining nutrient supply in progressively older sites within native forests in Hawai‘i (39, 40), and with the boundaries of a less intensive dryland agricultural system on Haleakala, Maui (41). In addition to the climate gradients on Hawi and Pololu substrates reported here, we evaluated base saturation in soils along a rainfall gradient on 4.1-million-year-old substrate on the island of Kaua‘i (42). Along that much older gradient, even a site receiving ~500 mm/ year of precipitation has very low base saturation (fig. S4); the “sweet spot” of fertile soils and adequate rainfall that we observe on Kohala Mountain is absent on Kaua‘i.

We conclude that low soil fertility precluded the development of large-scale intensive dryland agricultural systems on stable upland surfaces on the older islands of the Hawaiian archipelago (Fig. 1) (20). The resulting contrast in the agricultural bases of societies on the younger versus older islands (rain-fed dryland versus irrigated wetland) influenced the archipelago-wide pattern of sociopolitical complexity that emerged late in Hawaiian prehistory. In comparison to irrigated wetlands, dryland agricultural systems are more labor-intensive, yield smaller surpluses, and are more vulnerable to climatic perturbations—features that probably contributed to the development of the aggressive and expansive chiefdoms that arose on the younger islands (5, 6, 9, 10).

We believe that the implications of these results extend well beyond the Hawaiian Islands. Although the particular thresholds of rainfall and substrate age here are specific to the basaltic bedrock of Hawai‘i, the underlying processes that shape soil fertility (and so the potential for agricultural intensification) are general ones. Just as in Hawai‘i, sustained rain-fed agriculture developed first and most intensively in tropical dry forests as opposed to rain forests on continents; consequently, few of these drier forests escaped clearing and cultivation (43, 44). Many tropical rain forests have a history of shifting cultivation that influences their modern composition (45). However, except for irrigated systems or areas with relatively fertile young soils and/or lower rainfall, few rain forests have experienced large-scale intensive agriculture.

Fig. 4. Causes of P enrichment within the Kohala field system. (A) The percentage of P remaining in soils along the Kohala climate transect, outside the agricultural field system to the south (see Fig. 2). (B) The percentage of P remaining in surface soils within the agricultural system (lines connecting symbols) versus that in surface soils that were buried below field walls (unconnected symbols), along the upper portions of transects on the younger Hawi substrate (C) and on older Pololu substrate (D).

Fig 3

References and Notes


3. Shifting cultivation involves clearing and burning an area, cropping it for a short period, abandoning cropping for a several- to many-year fallow period (during which the success of useful species may be favored), and then repeating the cycle. Agricultural intensification uses inputs (of labor or other factors) to sustain cropping and increase overall yield.


14. Landscapes capital intensification alters physical features of the land in ways that favor agricultural production—as with irrigation works, pondfield systems, and terraces. Cropping cycle intensification uses continuing inputs of labor and other factors to enhance productivity and shorten or eliminate fallow periods. The extensive earth and stone walls of the Kohala field system (fig. S1) suggest that it exhibits elements of both cropping cycle and landscape capital intensification.


20. We focus on large, intensive dryland systems here. Smaller-scale dryland agriculture was practiced more widely across the archipelago, in environments ranging from heavily mulched settlement gardens to terraces at the base of colluvial slopes.

21. Materials and methods are available as supporting online material on Science Online.


30. We believe that this area was not included in the Kohala field system because its surface topography is rugged and because sites with suitable rainfall and soil fertility are at higher elevation and farther from the coast than is most of the field system.


32. Nitrogen also limits plant productivity in many areas, especially intensive agricultural systems. The greater mobility of N compared to P makes it difficult to retain sufficient levels of N availability to past levels, and we know little of how Hawaiian cultivators managed N in dryland systems. However, spatial variation in the current ratio of C to N here suggests that N cycling slows and N availability declines above the upper boundary of the field system (fig. S5).


35. E. S. Handy, E. C. Handy, Native Planters in Old
A Dual Role for Hox Genes in Limb Anterior-Posterior Asymmetry

József Zákány, Marie Kmita, Denis Duboule*

Anterior-to-posterior patterning, the process whereby our digits are differently shaped, is a key aspect of limb development. It depends on the localized expression in posterior limb bud of Sonic hedgehog (Shh) and the morphogenetic potential of its diffusing product. By using an inversion of and a large deficiency in the mouse HoxD cluster, we found that a perturbation in the early collinear expression of Hoxd11, Hoxd12, and Hoxd13 in limb buds led to a loss of asymmetry. Ectopic Hox gene expression triggered abnormal Shh transcription, which in turn induced symmetrical expression of Hox genes in digits, thereby generating double posterior limbs. We conclude that early posterior restriction of Hox gene products sets up an anterior-posterior prepattern, which determines the localized activation of Shh. This signal is subsequently translated into digit morphological asymmetry by promoting the late expression of Hoxd genes, two collinear processes relying on opposite genomic topographies, upstream and downstream Shh signaling.

Shh expression in posterior limb bud cells have been proposed whereby the antagonism between the Gli3 and dHand transcription factors would initially divide the bud into anterior and posterior domains (15). Although this model is supported by genetics and experimental data (11, 12, 16–18), it falls short in explaining the spatial restriction of Shh expression.

A similar limb bud posterior specificity was observed for both Hoxa and Hoxd genes in their earliest phases of expression (19–21). Hoxd genes are activated in a collinear fashion, with Hoxd1 and Hoxd3 expressed throughout the early bud, whereas Hoxd12 and Hoxd13 are expressed posteriorly (Fig. 1A) in a domain containing future SHH-positive cells. This restriction occurs before Shh expression (5, 6, 9, 22), which suggested a role for Hox genes in AP polarity (19). In addition, ectopic expression of Hoxb8 and Hoxd12 revealed the potential of some HOX products to trigger Shh expression (23–25). Here, we use two novel genomic rearrangements to show that posterior Hoxd genes are key determinants in the early organization of limb AP asymmetry.

We engineered a loxP/Cre-dependent inversion of the HoxD cluster (Fig. 1A) and asked whether gene expression would be con-

References

42. O. A. Chadwick, unpublished data.
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Supporting Online Material

www.sciencemag.org/cgi/content/full/304/5677/1665/DC1

Materials and Methods Figs. S1 to S5 Table S1

Abbreviations

AP, anterior-posterior; Cre, recombinase; E9, embryonic day 9; ELCR, expressionally lated Cre recombinase; ELR, expressionally lated recombinase; E9.5, embryonic day 9.5; HoxD, Hox cluster, D for digital.

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Supporting Online Material

Materials and Methods

Field Sampling

We established multiple transects reaching from wetter areas above the field system, across the system itself, and into drier areas below it (Fig. 2). Current land use across all of these transects is cattle ranching. On each transect, we sampled points approximately 200 m apart, selecting sampling locations on the basis of distance but avoiding large rock outcrops and remnant field walls and trails. Where these were encountered we sampled in the closest feasible location. Global Positioning System (GPS) coordinates were obtained at each point. Soils were collected as integrated samples to a depth of 30 cm; comparisons with much deeper profiles sampled on the nearby Kohala climate transect (S1) showed that the 30 cm samples captured most between-site variation. Five complete transect lines were sampled – 2 on the younger Hawi substrate in the southern portion of the field system, and 3 on older Pololu substrate to the north (Fig. 2); the uphill portion of one of the Pololu transects was deflected in order to remain on that substrate type. In all, 183 of the 30 cm depth-integrated samples were collected – 56 above the field system (in wetter sites), 103 within the field system, and 24 below it. Rainfall at each of the sample points was calculated using a Geographic Information System (GIS) data layer from http://www.state.hi.us/dbedt/gis/index.html, based on (S2).

We compared results from these transects with soils sampled by Chadwick et al. (S1) along rainfall gradients outside the field system, and from soils that we collected within the system from beneath field walls. The under-wall samples were used as an
indicator of low-mobility components of soil fertility (particularly total soil P) at the time that Hawaiians intensified their use of the agricultural system. For these samples, we identified the old soil surface (which often contained charcoal), and collected depth-integrated 30 cm samples below that point.

Soil Chemical Analyses

All soil samples were sieved and divided into three subsamples. One subsample was analyzed for resin-extractable P and for total C and N at Stanford University. Resin P was determined following the method of Kuo (S3), with the addition of cation exchange resin to reduce cation concentrations in solution. Total C and N were analyzed on a Carlo Erba CN analyzer.

A second subsample was analyzed for pH (1:1 water) as well as exchangeable cations and cation exchange capacity (CEC) at the University of California, Santa Barbara, using a modification of the NH₄OAc method at pH 7.0 (S4). The third subsample was shipped to ALS Chemex (Sparks, Nevada) and analyzed for 15 elements (Si, Al, Fe, Ca, Mg, Na, K, Cr, Ti, Mn, P, Sr, Ba, Nb, Zr) by x-ray fluorescence spectrometry.

Data Analysis

We determined the net loss or gain of elements from soils with reference to concentrations of an immobile index element (S5, S6); we use Nb here, because (with Ta) it is the least mobile of the many elements that have been evaluated in Hawaiian soils (S7). Soil concentrations of Nb decrease from the driest sites into the middle of the field system, reflecting increasing hydration and the addition of soil organic matter as rainfall increases from low to intermediate levels; Nb concentrations then
increase into the wettest sites, reflecting the cumulative loss of much of the soil matrix (Table S1). The percentage of an element that remained in a soil sample (relative to basaltic parent material) was calculated as:

\[ L_{i,j} = 100 \times \left( \frac{C_{i,j}}{C_{Nb,j}} \times \left( \frac{C_{i,pm}}{C_{Nb,pm}} \right) \right) \]  

(1)

where \( L_{i,j} \) is the percentage of element \( i \) remaining in soil sample \( j \), \( C_{i,j} \) and \( C_{Nb,j} \) are the concentrations of element \( i \) and of Nb in sample \( j \), and \( C_{i,pm} \) and \( C_{Nb,pm} \) are element concentrations in basaltic parent material (which generally differ for the young Hawi and old Pololu substrates).

Results for the surface soils were analyzed in two ways – by transect and by climate/land use history. For transect analyses, we calculated 3-point moving averages for the soil properties of interest, and plotted these against GIS-derived rainfall. For climate/land use history, we stratified the samples into old Pololu versus young Hawi substrates, and into areas that fell within the field system, above the system (and so wetter than it), and below it (and so drier). These classes were then analyzed by ANOVA, after log-transforming the data where appropriate. Results for underwall samples were compared with those from surface samples along the same transects.
Supporting Online Figures

Fig. S1. A portion of the remains of the leeward Kohala field system; densely spaced field walls run parallel to contours over an area of at least 60 km². Photograph by Terry Hunt, reproduced with permission.
Fig. S2. Soil P along two of the transects across the leeward Kohala field system, Hawai‘i - one on 150,000 yr old Hawi substrate (hollow symbols) and other on 400,000 yr old Pololu substrate (solid symbols). Dashed and solid vertical lines represent the boundaries of the field system on the Hawi and Pololu substrates respectively.  A. Total soil P. B. The fraction of total P that is resin extractable (%).
Fig. S3. Depth profiles of P remaining relative to basaltic parent material (%), for soils in three sites along the Kohala climate transect (outside the field system). A. Site C, which is drier than sites that were cultivated within the field system. B. Site I, within the rainfall zone where agriculture was intensified. C. Site M, wetter than sites that were cultivated. P is enriched in surface soil in the intermediate site, and depleted deeper in the soil. P is depleted in both the wetter and drier sites, reflecting losses via leaching in the wetter site and possibly via wind erosion of an enriched surface layer in the dry site (S1).
Fig. S4. Base saturation for soils collected across 3 precipitation gradients within the Hawaiian Islands, on substrates that are 150,000 (Hawi - hollow circles and dotted line), 400,000 (Pololu – solid circles and line), and 4,100,000 yrs old (island of Kaua‘i – solid squares and dashed line) (S8). The transition from base-rich to infertile base-poor soils occurs at a progressively lower rainfall on older substrates, to the point that even sites that are too dry to support rain-fed intensive agriculture on oldest island also have infertile soils.
Fig. S5. Soil C and N along transects in the Kohala field system, Hawai‘i; lines and symbols as in Fig. S2. A. Soil organic C increases from dry to wet sites across the field system. B. The ratio of C to N is constant across the field system, but increases in wetter sites above it. This pattern suggests that N cycles more slowly and is relatively less available in the wetter sites above the upper boundary of the field system,
Table S1. Properties of surface soils within and adjacent to the leeward Kohala field system on the younger Hawi and older Pololu substrates, island of Hawai‘i,. Values are means, with standard errors in parentheses. P, Ca, Mg, and K remaining represent the % of these elements remaining in soil, relative to the amount in basaltic parent material. Significance levels are based on ANOVA, on log-transformed data for resin P and total Nb; S represents the effect of substrate (Hawi versus Pololu), while P represents position relative to the Hawaiian system (below, within, or above the intensively cultivated area). * = P<.05, ** = P<.01, and ***=P<.001.

<table>
<thead>
<tr>
<th>Property</th>
<th>Hawi – 150ky</th>
<th>Pololu – 400ky</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Base Saturation (%)</td>
<td>45(3) 54(2) 17(2)</td>
<td>44(4) 46(2) 17(2)</td>
<td>P***</td>
</tr>
<tr>
<td>Resin P (mg/Kg)</td>
<td>132(25) 242(28) 27(6)</td>
<td>23(4) 116(13) 17(4)</td>
<td>S***, P***</td>
</tr>
<tr>
<td>Total Nb (mg/Kg)</td>
<td>54(3) 44(2) 84(7)</td>
<td>51(3) 51(1) 63(3)</td>
<td>S*, P***, SxP***</td>
</tr>
<tr>
<td>P Remaining (%)</td>
<td>84(19) 122(11) 57(6)</td>
<td>35(7) 77(7) 55(6)</td>
<td>S***, P***, SxP*</td>
</tr>
<tr>
<td>Ca Remaining (%)</td>
<td>27(5) 55(6) 8(2)</td>
<td>1(.2) 3(.2) 1(.1)</td>
<td>S***, P***, SxP***</td>
</tr>
<tr>
<td>Mg Remaining (%)</td>
<td>54(5) 60(3) 16(2)</td>
<td>4(.4) 4(.1) 3(.2)</td>
<td>S***, P***, SxP***</td>
</tr>
<tr>
<td>K Remaining (%)</td>
<td>41(7) 68(4) 37(3)</td>
<td>54(5) 71(2) 51(2)</td>
<td>S***, P***, SxP*</td>
</tr>
</tbody>
</table>
Supporting References


S8. O. A. Chadwick et al., unpublished data.