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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 iron availability despite high sulfate reduction rates (41), or in addition to the 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).

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 using the same cores, which may result in age offsets. In addition, the variability in response time of C and S as a result of the different residence times of these elements in the ocean is not considered here (17). It has been suggested that a general negative correlation between $\delta^{34}S_{SO_4}$ and $\delta^{13}C_{CaCO_3}$ exists (42, 43). Indeed, the broad low $\delta^{34}S$ between 120 and 105 Ma is mirrored by high $\delta^{13}C$ between 120 and ~100 Ma. However, as previously seen for the Cenozoic, over shorter time scales (one million to several million years), the isotopic records are not negatively correlated (13, 44), which suggests that the deposition of organic C and pyrite S has not been compensatory, resulting in fluctuations in atmospheric oxygen (44). Such changes in atmospheric oxygen have important implications for the evolution and dispersal of organisms (16). Alternatively, these data may imply that another process, such as changes in the cycles of Fe or P (2, 7, 10–12), operated to consume/produce oxygen to balance the system.

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Materials and Methods

Fig. S1

Table S1

References

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Soils, Agriculture, and Society in Precontact Hawai'i

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Before European contact, Hawai'i 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 predated 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).

Within the range of cultural variability evident in Polynesia, both agricultural intensity 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 (5, 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 bound 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 weathering of basalt (29, 31). At higher rainfall, cations are less abundant and mostly derived 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-

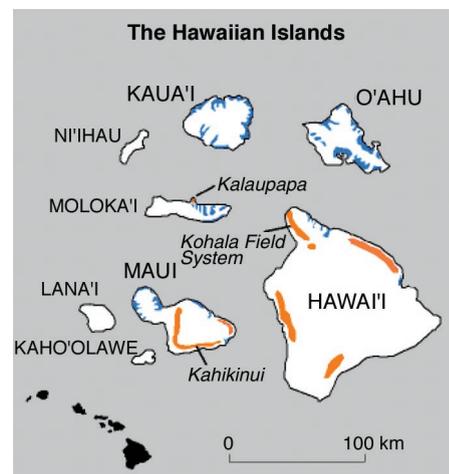


Fig. 1. The distribution of large, intensive, rain-fed dryland agricultural systems (orange shading) and irrigated wetland systems (blue shading) across the Hawaiian archipelago [updated from (10)]. Large dryland systems mostly were confined to the younger volcanoes on the islands of Maui and Hawai'i.

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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.

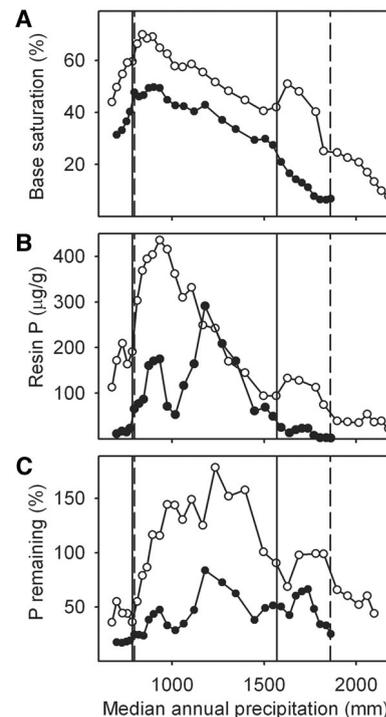
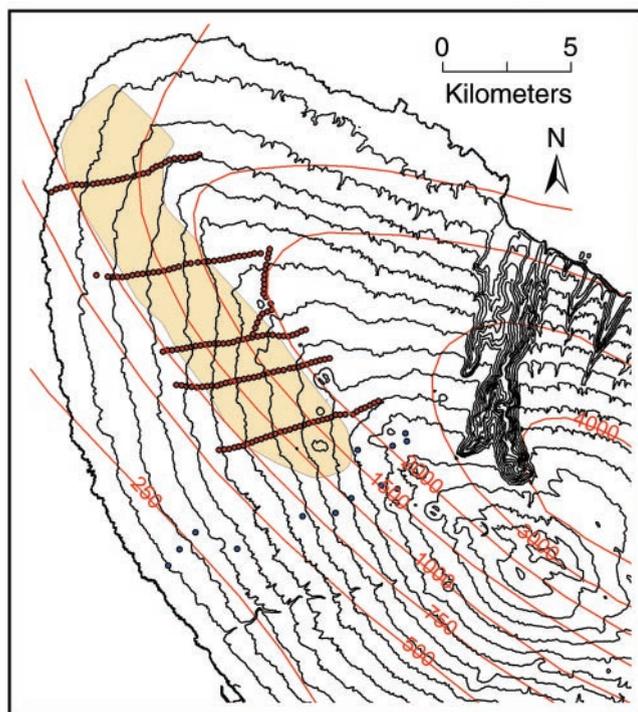


Fig. 3. Soil properties along two transects across the leeward Kohala field system, Hawai'i. One transect lies on 150,000-year-old Hawi substrate (○) and the other lies on 400,000-year-old Pololu substrate (●). Dashed and solid vertical lines represent the boundaries of the field system on the Hawi and 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.

archipelago. 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 de-

clining 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.

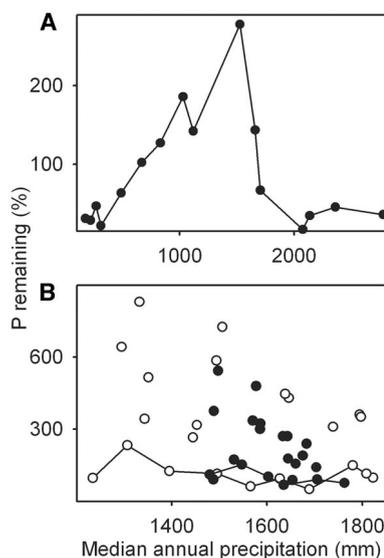


Fig. 4. Causes of P enrichment within the Kohala field system. (A) The percentage of P remaining in soils along the Kohala climate transect, outside the agricultural field system to the south (see Fig. 2). (B) The percentage of P remaining in surface soils within the agricultural system (lines connecting 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 (○) and on older Pololu substrate (●).

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14. Landesque 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 landesque capital intensification.
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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.
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37. While mulching by Polynesian cultivators was not responsible for the presence of enriched soils within the field system, it could have contributed to the sharpness of the transition in soil properties from within the field system to just outside it (Fig. 3).
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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

References

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A Dual Role for *Hox* Genes in Limb Anterior-Posterior Asymmetry

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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.

Anterior-posterior (AP) asymmetry in tetrapod limbs is reflected by the anatomy of lower arms and hands. In humans, the thumb is shorter and more mobile than other digits. These differences result from the presence in the developing posterior limb bud of a zone of polarizing activity (ZPA) (1), defined by its potential both to induce supernumerary digits and to modify digit identity when transplanted anteriorly. Cells within the ZPA express the *Shh* gene (2), whose product propagates posterior identity in the growing bud, likely through a graded, long-range intercellular signaling mechanism (3, 4).

The effects of *Shh* signaling in limbs are mediated, at least in part, by posterior *Hoxd* genes (2, 5–9) because of the potential of SHH to prevent the production of the repressor form of GLI3 protein, which negatively regulates *Hox* gene transcription (10–12), likely through a global digit enhancer located near the *HoxD* cluster (13, 14). Models for the restriction of

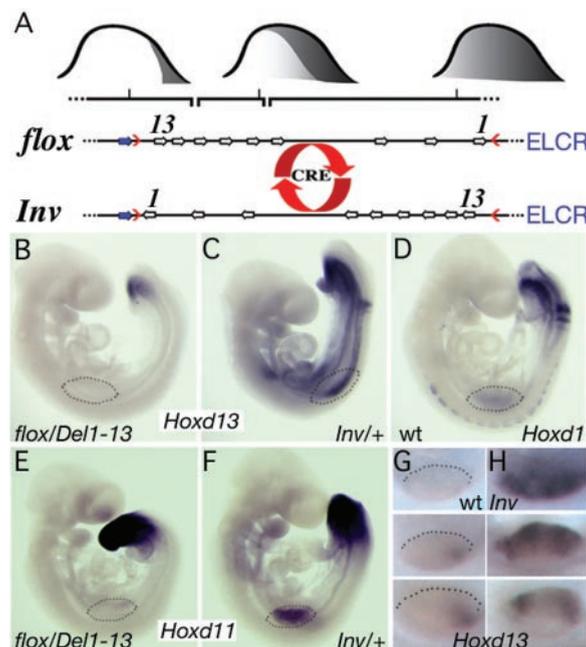
Shh expression in posterior limb bud cells have been proposed whereby the antagonism between the *Gli3* and *dHand* transcription factors

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-

Fig. 1. Targeted inversion of the *HoxD* cluster. (A) Collinear expression patterns (in gray) of *Hoxd* genes in limb bud. The *HoxD* cluster is shown with blue arrows for a *Hoxd11lac* reporter gene (27) and white block arrows for *Hoxd* genes. Red arrowheads are *loxP* sites. The presence of an ELCR is shown in blue. The *loxP*/Cre conditional inversion allele is also shown. Exposure to the Cre recombinase in vitro (red arrows) generated both *flox* and *Inv* alleles. (B) Control *Hoxd13* expression (one copy) in an E9.5 embryo. (C) *Hoxd13* expression in a de novo isolated (28) (Materials and Methods) *Inv*^{+/+} embryo, showing an anterior shift in expression including the forelimb field (dotted lines), similar to *Hoxd1* (D). *Hoxd11* expression in E9 embryo with one copy (E) or *Inv*^{+/+} embryo (F). *Hoxd13* staining in forelimb buds of normal (G) and *Inv* chimeric (H) embryos. The expected posterior pattern is seen in the larger two specimens [(G), bottom], whereas chimeras show premature expression in the entire bud (H).



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