Changing sources of nutrients during four million years of ecosystem development

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As soils develop in humid environments, rock-derived elements are gradually lost, and under constant conditions it seems that ecosystems should reach a state of profound and irreversible nutrient depletion. We show here that inputs of elements from the atmosphere can sustain the productivity of Hawaiian rainforests on highly weathered soils. Cations are supplied in marine aerosols and phosphorus is deposited in dust from central Asia, which is over 6,000 km away.

Terrestrial biogeochemists traditionally distinguish atmospherically derived from rock-derived elements[1,2]. Atmospherically derived elements such as carbon and nitrogen have an important gas phase; they enter terrestrial ecosystems either through biological processes such as photosynthesis and biological N_2 fixation, or through deposition from the atmosphere (for example, dissolved in precipitation or by dry deposition of particles and gases). Rock-derived elements such as calcium, magnesium, potassium and phosphorus are important constituents of minerals; they enter terrestrial ecosystems through partial or complete dissolution of these minerals (chemical weathering). A central conceptual model for the development of soils and ecosystems is built around this distinction[3]; new substrates that are laid down by volcanic eruptions, glacial recessions, or other processes that initiate the formation of wholly new soils and ecosystems, generally lack atmospherically derived elements, particularly nitrogen and carbon, but they are rich in minerals that can supply rock-derived elements. Consequently, rates of plant production and other ecosystem processes are often constrained by the supply of nitrogen in young developing ecosystems, or such systems are dominated by plants with well developed N_2-fixing symbioses, such as alder and various legumes[4–6].

This model assumes that, over time, the stock of weatherable minerals in soil is depleted and rock-derived elements are lost without replacement, whereas atmospherically derived elements can be replenished continuously. Eventually, in the absence of disturbance of the substrate, ecosystems can reach a terminal steady state of profound and irreversible depletion of rock-derived elements. Phosphorus in particular is commonly implicated as the master regulator of ecosystems in the long term[3,7], although other rock-derived elements (Ca, Mg, K) are more mobile than phosphorus and should be depleted more rapidly.

Several lines of evidence suggest that the sharpness of the dichotomy between rock- and atmospherically derived elements has been overstated, with significant consequences for our understanding of biogeochemistry. These include: (1) studies of the mass balance of elements in watersheds show that the quantities of putatively rock-derived elements dissolved in precipitation can be a substantial fraction of the weathering sources of those elements[8,9]; (2) large quantities of dust are entrained in the atmosphere in arid regions, and transported globally[10–14]; and (3) atmospheric deposition of all elements may be understated by standard measurements. The dry deposition of particles and gases to vegetation surfaces can be substantial[15,16], and where cloudwater is deposited in forests it is likely to be a particularly important source of elements[17,18].

We evaluated sources of biologically significant elements and their implications for ecosystem functioning across a developmental sequence of sites in the Hawaiian islands. Although recent analyses of ecosystem dynamics have focused on climate and climate change, in Hawaii as elsewhere[19–21], the quantity and availability of nutrient elements in the soil also control plant productivity and other aspects of ecosystem functioning[22]. Moreover, terrestrial ecosystems are altered by anthropogenic changes in nutrient supply[23,24] and by interactions between climate change and nutrient availability[25] at least as much as by climate change itself.

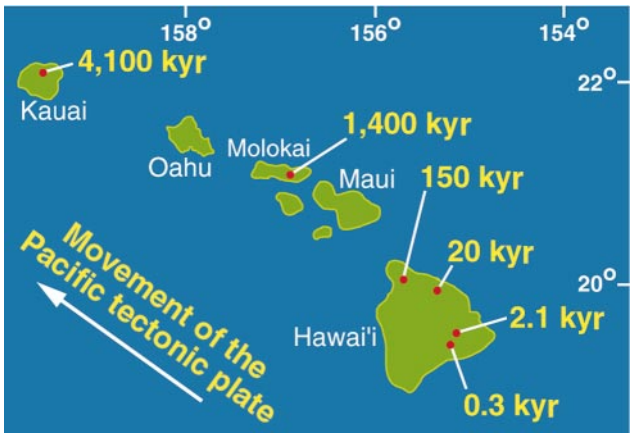

Figure 1 Location of the study sites. The youngest two sites are on the still-active Kilauea volcano; the 20,000-yr-old site is on Mauna Kea, the 150,000-yr-old site is on Kohala, the 1,400,000-yr-old site is on East Molokai, and the 4,100,000-yr-old site on Kauai.

Hawaii is a model ecosystem

The Hawaiian islands are formed by a stationary convective plume (hot spot) that taps lava from the upper mantle. The volcanoes grow for about 600,000 yr, drifting to the northwest on the Pacific lithospheric plate[26]. Each island (and each volcano within an island) is progressively older along a transect from active volcanoes in the southeast to the oldest islands in the northwest[27]. Along the island chain, we located six sites that differ markedly in the age of their underlying substrate, from 300 through to 2,100, 20,000, 150,000, and 1,400,000 to 4,100,000 years old (Fig. 1). The sites are similar in their current climate, with a mean annual temperature of 16 °C, and about 2,500 mm of precipitation annually. The substrate is basaltic rock admixed with tephra and pumice, with an initial chemistry that varies relatively little in space or time[28]. Over time, the topography evolves from classical shield volcanoes with gentle slopes, to deeply dissected landforms[29]; however, we were able to

locate residual shield surfaces on even the oldest sites. None of the sites has been cleared or systematically altered by people.

Finally, the Hawaiian islands form the most remote archipelago on Earth. Relatively few species reached Hawaii naturally (blown there in storms or attached to migrating birds) in the tens of millions of years before human discovery[30]. Some of these species then radiated to occupy a range of environments far broader than do continental species, resulting in an astonishing degree of biological similarity among sites. Overall, this near constancy in geology, topography, climate and biota, coupled with a very wide and well characterized range in substrate age, makes the Hawaiian islands an extraordinary resource for studies of soil and ecosystem development.

We cannot analyse soil and ecosystem development by following a single site through time; these processses are too slow for that. Rather, we are comparing sites with substrates of different ages: in so doing, we implicitly assume that this substitution of space for time[31,32] will provide an insight into factors that control ecosystem development on geological timescales. We do not assume that all sites have been influenced by identical conditions throughout their history; older sites have been subjected to greater climatic variation[33–35] and isostatically and thermally driven subsidence[26,36]. Nevertheless, along the transect the constant substrate has been exposed to the effects of environmental and biological forcing for substantially different lengths of time.

Ecological changes and substrate age

We evaluated patterns in soils, nutrient availability, forest composition and structure, net primary production (NPP), and nutrient limitation to NPP across the developmental sequence. The soils of the two youngest sites are little weathered; their properties are strongly influenced by the properties of the coarse-textured pumice-rich parent material. The two intermediate-aged sites have highly weathered andisols that contain high levels of chemically active non-crystalline minerals that readily complex organic matter and adsorb phosphorus, whereas the soil at the 1.4-million-year-old (Myr) site is an ultisol in which most of the chemically reactive non-crystalline minerals have transformed to less-active clays, with loss of much of the nutrient-holding capacity of the younger soils. Finally, the soil at the oldest site is an oxisol that has lost most of its active minerals to weathering and leaching; most of the remaining soil is made up of inert iron and aluminium minerals typical of highly weathered tropical soils, with no capacity to supply nutrients and little ability to retain recycled or added nutrients[37].

The biological availability of essential plant nutrients also varies systematically along the sequence; the young sites have high concentrations of available cations (Ca, Mg, K) and little available nitrogen and phosphorus; the intermediate-aged sites have fewer available cations and more nitrogen and phosphorus; and the oldest site has low phosphorus and cation availability and high nitrogen availability (Fig. 2a, b)[38,39]. Low nitrogen availability in the young sites reflects a lack of nitrogen in the substrate and the time required to accumulate nitrogen from the atmosphere[40]. The mechanisms that control patterns in available cations and phosphorus are discussed below.

The species composition of the forest vegetation is remarkably consistent across the sites, despite the wide range in soils and available nutrients. The native tree *Metrosideros polymorpha* makes up 80–88 per cent of each forest's basal area, and several other species are found in all of the sites[41]. We analysed element concentrations in leaves of *Metrosideros* and other species across the sequence to provide an assessment of nutrient availability as it is experienced by vegetation[42]. The leaves reflect soil nutrient availability quite closely, with peak cation concentrations in young sites and peak concentrations of nitrogen and phosphorus in the intermediate-aged sites (Fig. 2c, d); the main difference between soil and

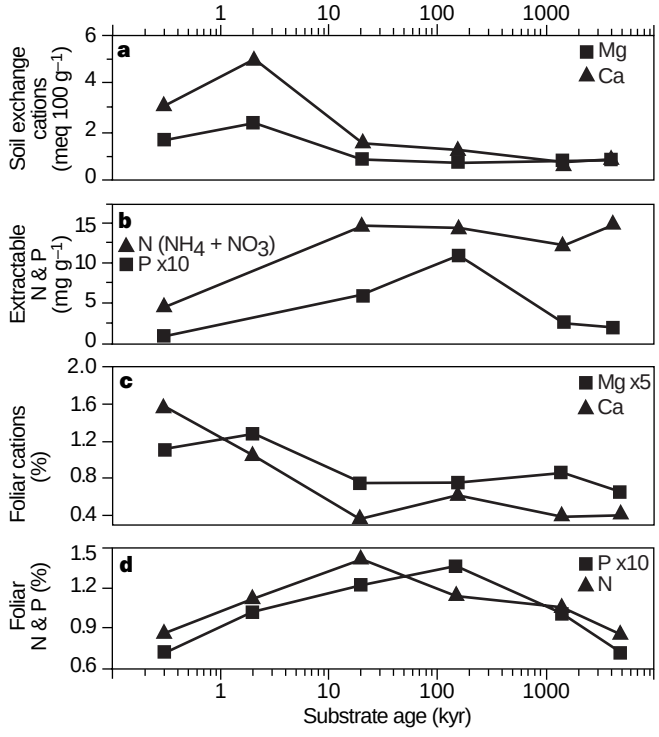

Figure 2 Plant-available nutrients in soil and nutrients in leaves. **a**, Ca and Mg exchangeably bound to soil colloids[36]. **b**, Phosphate-P and ammonium-N plus nitrate-N in soil solution or exchangeably bound to colloids, forms that are readily available for plant uptake[39] (P. A. Matson, unpublished data). **c**, Ca and Mg in *Metrosideros* leaves[42]. **d**, P and N in *Metrosideros* leaves[42].

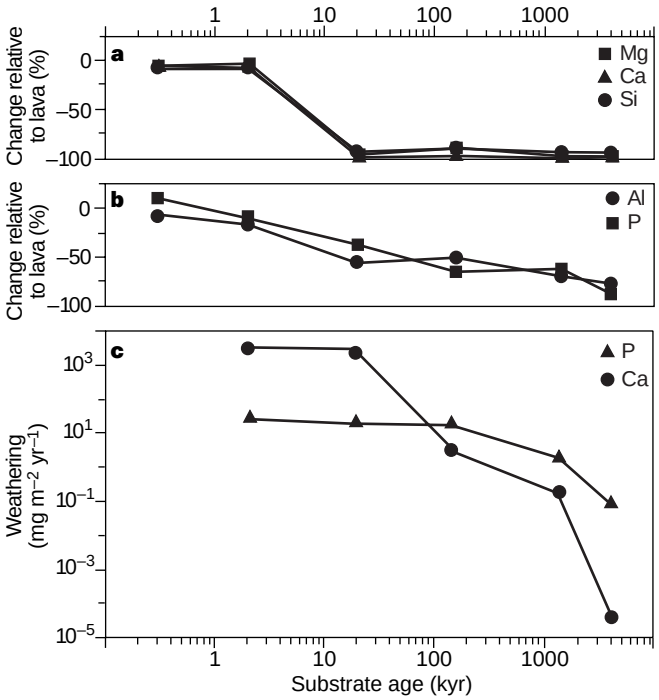

Figure 3 Change in soil element content integrated over the top metre of soil, compared with element contents in the lava parent material[38]. Measured element concentrations (**a**, Mg, Ca, Si; **b**, Al, P) were corrected for changes in density and loss of mass during soil formation[71]. In **c**, the rates of loss of P and Ca are calculated using the mass of an element lost between two sites and the corresponding difference in age.

plant measurements is that the nitrogen concentration in leaves declines (together with phosphorus) in the oldest site, whereas soil availability of nitrogen remains high. When the leaves rich in nitrogen and phosphorus in the intermediate-aged sites senesce and fall, they decompose and release nutrients much more rapidly than do decomposing leaves in either young or old sites—providing a positive feedback to high nitrogen and phosphorus availability in the intermediate-aged sites[39].

The net primary production of the forests follows a pattern similar to that of nitrogen and phosphorus availability, peaking in the relatively fertile intermediate-aged sites[38,43]. We evaluated nutrient limitation to forest growth/NPP in three sites on the sequence using factorial fertilization experiments, and found that nitrogen (and no other element) limits forest growth in the youngest site, whereas phosphorus (and no other element) does so in the oldest site[43–45]. Adding nitrogen and phosphorus together (but not for either alone) stimulated growth in the 20,000-yr-old intermediate-aged site[40]. Additions of other important rock-derived cations (Ca, Mg, K) and micronutrients (Cu, Fe, Mn, Mo, Zn) had no significant effect on plant production in any of the sites.

Sources of nutrients

Overall, patterns in soil and ecosystem properties along the Hawaiian sequence are consistent with the model that young ecosystems are characterized by low concentrations of atmospherically derived nutrients, whereas old ones are characterized by low concentrations of rock-derived nutrients[3]. Moreover, the fertilization experiments provide the first clear experimental test of the model's applicability to nutrient limitation in unmanaged ecosystems[40]. However, these results also raise a number of questions—most notably, why does low phosphorus availability limit NPP in ecosystems on old substrates, when the rock-derived cations are much more readily leached from ecosystems than phosphorous is?

We answered this question by measuring both weathering and atmospheric sources of elements along the Hawaiian sequence. The constancy of these sites in climate, geology, topography and species composition provides a consistent background against which the sources of elements can be determined; the range in the age of the sites allows a direct calculation of weathering inputs. We determined the rock-derived elements remaining in primary mineral forms and those retained within the soil as a whole, in each of the sites along the sequence. Initially, rock-derived elements are weathered rapidly, followed by declines to very low weathering rates in the oldest sites. The loss of elements to leaching leads to soil collapse. In the older sites, most of the mass of rock present at the initiation of ecosystem development has been lost; a metre of highly altered soil is all that remains of more than 10 m of rock[38].

Most of the calcium, magnesium and silicon weathered from primary minerals was lost rapidly; in contrast, phosphorus and aluminium were retained within the soil for much longer after their release (Fig. 3a, b). The mobility of these elements differs because calcium and magnesium are large divalent ions that are relatively weakly sorbed to soil colloids, and silicon in the undissociated form of $Si(OH)_4$ is not strongly attracted to soil colloids. In contrast, hydrated aluminium and phosphorus compounds form dissociated weak acids that are highly reactive with mineral and organic surfaces and hence are much less susceptible to leaching. Consequently, weathering-derived calcium is more available to plants early but leaches much more rapidly than phosphorus (Fig. 3c). Still, despite its mobility and the lack of a weathering source of calcium in the older sites, the fertilizer experiments show that calcium does not limit ecosystem productivity anywhere[40]. These observations suggest

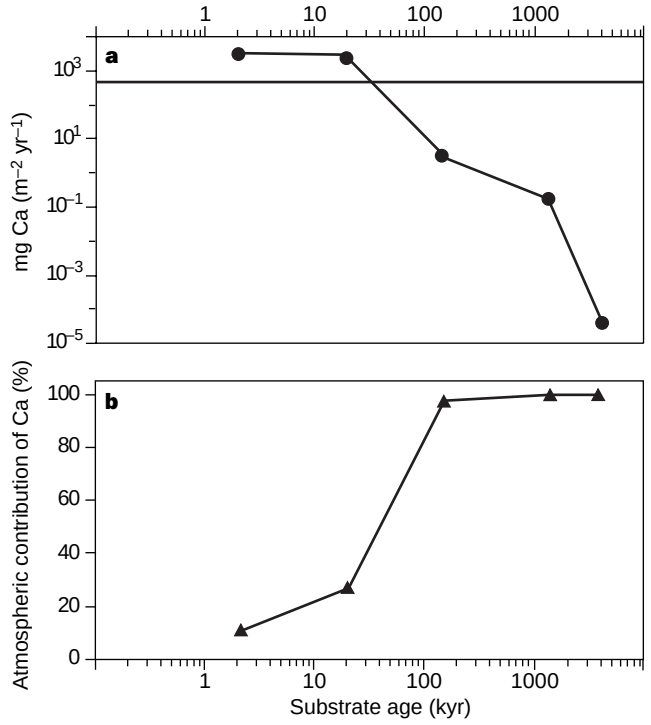

Figure 4 Comparison of Ca inputs from substrate and the atmosphere. **a**, Rate of Ca loss from substrate (Fig. 3c) plotted with the present addition of Ca in rain water and cloud water. **b**, The per cent of total Ca inputs that are derived from the atmosphere, calculated by dividing the atmospheric contribution by the sum of atmospheric and weathering (actually loss from substrate) contribution.

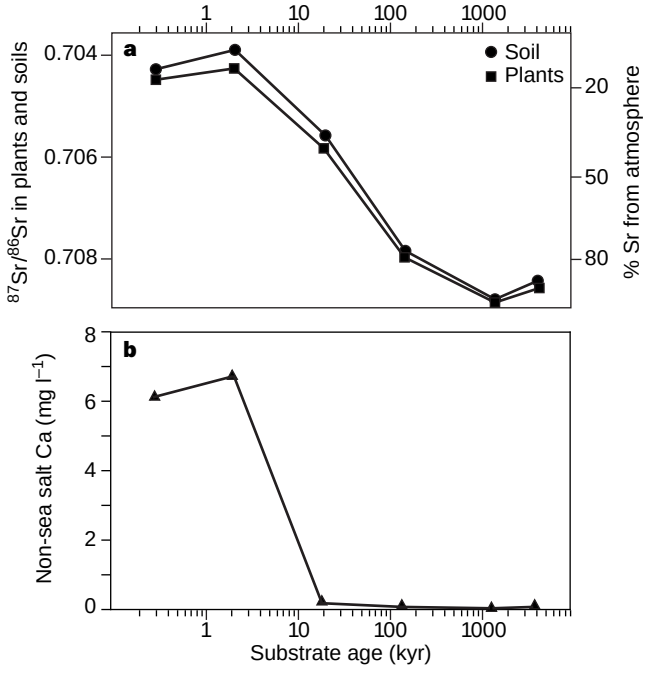

Figure 5 Indicators of the sources of Sr and Ca measured for each site. **a**, The $^{87}Sr/^{86}Sr$ ratio of Sr extracted from soil exchange sites and from *Metrosideros* leaves. The isotope ratio is primarily constrained by the value for Hawaiian lava of 0.7035 and a value for sea water (and hence rainfall in Hawaii) of 0.7092 (ref. 48). **b**, The concentration of Ca in soil solution collected by lysimeters inserted below the primary rooting zone in the soils. The measured values have been normalized using a standard sea-salt ratio to reflect Ca released to soil solution by mineral weathering only.

that there must be an atmospheric source of calcium that maintains calcium pools and plant productivity in the older sites.

Atmospheric inputs of calcium were measured directly in the 300-yr-old site by independent analysis of the quantity and chemistry of rainfall, dry deposition, and cloudwater interception[18]. We found that the rate of input of calcium, mostly from marine aerosols, is 600 ± 400 mg Ca m^{-2} yr^{-1}. These atmospheric inputs are low relative to inputs from rock weathering in sites of less than 20,000 yr old, but as weathering inputs decline the atmosphere becomes the dominant source of calcium in sites older than 20,000 yr (Fig. 4a, b).

We tested the magnitude and implications of atmospheric additions of calcium by using strontium isotopes. The $^{87}Sr/^{86}Sr$ ratio of a sample and its isotopically distinct sources has been used to evaluate atmospheric compared with rock sources of strontium, and by implication, of its fellow alkaline earth elements calcium and magnesium[46]. However, differential weathering rates of minerals in rocks often leads to long-term fractionation of weathering sources and their isotopic values, and inhomogeneities in atmospheric sources have also made such calculations difficult to constrain[47,48]. Fortunately, Hawaiian lavas and their minerals have a relatively homogeneous chemical and isotope composition which is distinct from that of continental crust and sea water. We demonstrated that strontium in plants and soils shifts from being over 90 per cent rock-derived at the 300- and 2,100-yr sites, to a mixture of rock and atmospheric sources at the 20,000-yr site, to over 80 per cent atmospherically derived by 150,000 yr and thereafter (Fig. 5a)[48]. These results can be extended more or less directly to calcium and magnesium; potassium is even more mobile than the alkaline earth elements in this system, and it should become dominated by atmospheric sources sooner. As an independent check on the importance of atmospheric sources, we measured the concentrations of the principal non-seasalt-derived (that is, rock-derived) cations in soil solution below the rooting zone of the sites. Rock-derived calcium contributes substantially to solution chemistry in young sites, but it disappears entirely by the 150,000-yr-old site (Fig. 5b). Overall, it is clear that the atmosphere becomes the dominant source of most putatively rock-derived elements in older sites. The dilute contribution of sea-salt cations in rainfall and intercepted cloudwater is enough to maintain ecosystem productivity after the rock sources are depleted.

The dynamics of phosphorus differ from those of the other rock-derived elements in that, even after its release by weathering from primary minerals, its low mobility through soil means that the rock-derived element remains important into much older sites. However, most phosphorus has been lost from the oldest sites (Fig. 3b), and that remaining is largely in forms that are unavailable or only slowly available to plants[39]. Over time, plant production becomes constrained by the low biological availability of phosphorus.

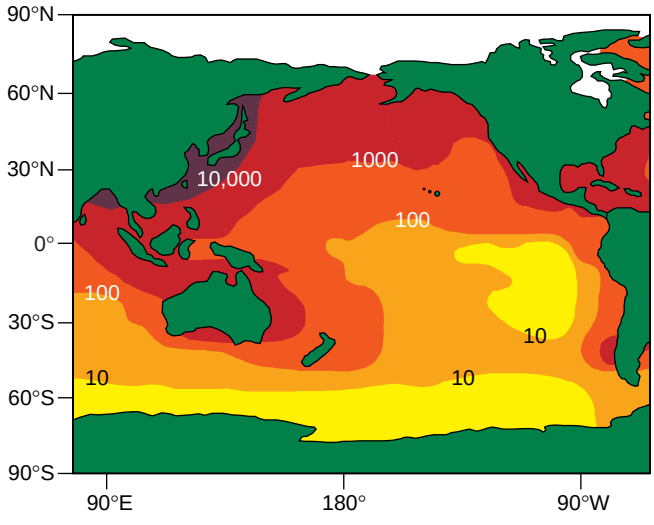

Figure 6 Map showing estimates of the long-term (integrated glacial plus interglacial) rate of dust deposition to the Pacific Ocean (from ref. 58). The isopachs (mg m^{-2} yr^{-1}) are based on models of atmospheric dust transport[58] and are in general agreement with data collected from numerous ocean cores[52].

Could the atmosphere make any significant contribution to phosphorus supply in these older systems[49]? The seawater contribution of phosphorus to marine aerosols is vanishingly small, because uptake by marine organisms maintains very small amounts of phosphorus in surface waters[50]. The largest source of atmospheric phosphorous must be transported by dust through the troposphere on the prevailing westerly winds from central Asia (Fig. 6)[51–54]. Rates of dust deposition are now relatively small but were several-fold greater during the last glacial period when Asia was less vegetated and overall wind speeds were faster[52].

The presence of exotic minerals deposited by aeolian processes in Hawaiian soils is well established[55,56]. Even averaged over time, Asian dust could make only a small contribution to inputs of Ca, Mg or K in comparison to marine sources, but its relative contribution could be substantially greater for phosphorus[48]. Over the past 2–3 Myr, the rate of dust deposition in the Pacific ocean near Hawaii is estimated at 250–500 mg m^{-2} yr^{-1} (ref. 52). If dust delivers an average crustal phosphorus concentration of 700 p.p.m. (ref. 57), then about 0.17–0.35 mg P m^{-2} yr^{-1} would be added to the soil. However, dust can be scavenged by rainfall and probably cloudwater, and, owing to orographic processes, the sites receive much more rainfall than the open ocean. Can we estimate phosphorus inputs from the dust deposition to our sites?

Just as the isotope composition of strontium can be used to distinguish the source of alkaline earth elements, refractory trace elements and isotopes of neodymium, a rare earth element, may be useful for resolving the contribution of phosphorus from continental dust. Phosphate minerals such as apatite also carry relatively high concentrations of many refractory trace elements, including rare earths and thorium, making these elements useful tracers of phosphorus. Differences between the $^{143}Nd/^{144}Nd$ ratios (or other tracers) of Asian dust and Hawaiian rock can be used as endmembers to calculate the amount of exogenous material that has been added to the soil as dust. If we then know the P/Nd ratio of the endmembers, we can calculate the amount of phosphorus contributed from the atmospheric source. Hawaii is an ideal site to use geochemical tracers in this manner because there is a strong contrast between the chemical properties of continental dust and Hawaiian basalts[58–61]. We applied this approach using $^{143}Nd/^{144}Nd$, Eu/Eu* and Hf/Th as tracers (see Box 1) and calculate an input value of 0.9 ± 0.3 mg P m^{-2} yr^{-1} added by dust, which is significantly more than the phosphorus contributed to the open ocean.

In contrast to calcium, which is lost from these ecosystems shortly after being weathered from primary minerals, rock-derived phosphorus continues to contribute to ecosystems for more than 1 million years (Fig. 8a). However, losses eventually accumulate to the point where most lava-derived phosphorus has been leached. By the oldest site on the sequence, phosphorus provided by Asian dust is a substantially larger source than is the parent rock (Fig. 8a, b). Plant production in this old site now is limited by phosphorus. However, the limitation would probably be far more severe were it not for phosphorus transported more than 6,000 km from central Asia, most of it over 10,000 years ago.

Broad implications of the Hawaiian model

We can draw several conclusions from our research on the sources of nutrients to Hawaiian ecosystems. First, the distinction between rock-derived and atmospherically derived elements is not sharp; on this sequence of sites, the atmosphere becomes the dominant source of all major biological nutrients apart from phosphorus in less than 100,000 years. It is input from the atmosphere that sustains

Box 1 Geochemical tracers of atmospheric inputs to soils and ecosystems.

To quantify the deposition of the phosphorus by dust, we use the fact that soils accumulate relatively immobile trace elements[67,68]. Differences in the isotopic and trace-element composition of Asian dust compared with Hawaiian basalt and its weathering products allow us to define endmembers for contributions from dust relative to basalt[59–61]. We use quantities and mixing ratios of these elements to estimate inputs from dust relative to basalt in the 150,000-yr soil profile, and then extend the analysis to determine phosphorus deposition by dust.

The chemical characteristics of Hawaiian lavas differ substantially from those of average continental crust, and allow us to define unique and useful endmembers on the basis of isotopic and trace element data, including the rare earth elements (REE). Two useful measures of REE sources that are not greatly affected by soil processes are the Eu anomaly, defined as $Eu/Eu^* = [Eu]/([Sm] + [Gd])$ (the ratio between the 'expected' Eu concentration as interpolated between Sm and Gd, and the observed value), and the $^{143}Nd/^{144}Nd$ ratio, expressed as ϵ_{Nd} (ref. 69). Fresh Hawaiian basalts at our sites have a slight positive Eu anomaly (Eu/Eu^* is 1.0–1.1), and $\epsilon_{Nd} = +7$, whereas eolian sediments from the Pacific Ocean near Hawaii have a pronounced negative Eu anomaly typical of continental materials ($Eu/Eu^* = 0.6$), and $\epsilon_{Nd} = -10$ (ref. 58) (Table 1). REE patterns in soils from our study sites show a range of patterns that are intermediate between these endmembers. Using mixing equations, we can calculate the contribution from each source.

Similarly, ratios of refractory trace elements can also be used to distinguish continental and basalt sources. In particular, Th and Hf exhibit low mobility in the soil environment. Th/Hf ratios in Hawaiian basalts are near 0.25, whereas those in continental crust are near 1.8 (Table 1). Data from Hawaiian soils suggest that Th/Hf is not significantly changed by weathering processes, providing another tracer for determining the contribution of continental dust to Hawaiian soils.

The fraction of the Nd in a soil sample that is derived from dust can be calculated from the isotopic mass balance (a similar calculation can be used for Eu/Eu* or Th/Hf):

$$f^{Nd}_{dust} = \left(\frac{\epsilon^{soil}_{Nd} - \epsilon^{basalt}_{Nd}}{\epsilon^{dust}_{Nd} - \epsilon^{basalt}_{Nd}}\right)$$

Individual soil horizons in Hawaii have $Eu/Eu^* = 0.63$ and ϵ_{Nd} as low as –7, and Th/Hf as high as 1.5, indicating that >80% of the Nd, Eu or Th can be derived from Asian sources (Fig. 7).

We integrate the dust Nd (or Eu or Th/Hf) contribution to the soil profile using the soil Nd concentration [Nd], the mass fraction of Nd derived from dust sources (f^{Nd}_{dust}) and the dry bulk density (ρ) as functions of depth (z) to obtain the integrated flux of Nd that the soil has received over time:

$$Nd^{tot}_{dust} = \int_0^z [Nd]_z f^{Nd}_{dust}(z)\rho(z)dz$$

To obtain an aerosol phosphorus deposition rate, we multiply the integrated Nd flux by the P/Nd ratio of dust sources[50] and divide by the duration of soil development:

$$P_{dust} = Nd^{tot}_{dust} \times (P/Nd)_{dust} \times \Delta t^{-1}$$

This analysis using $^{143}Nd/^{144}Nd$, Eu/Eu^* and Th/Hf yields estimates of long-term aerosol phosphorus fluxes ranging from 0.6 to 1.2 mg P m^{-2} yr^{-1} to the 150,000-yr-old site (Table 1). We cannot be certain that any given trace element is immobile during weathering, but the similarity among independent estimates of dust flux suggests that we have chosen reliable tracers of dust input. Th and Hf are less mobile than the REE during weathering, yield the highest calculated dust inputs, and may provide the best time-integrated estimate of dust flux. The range of estimates is higher than that calculated using a long-term rate derived from the deep sea record of eolian deposition to the north central Pacific (0.17–0.35 mg P m^{-2} yr^{-1})[52]. It is lower than an estimate of modern phosphorus fluxes (2.5 mg P m^{-2} yr^{-1}) based on direct measurements of mineral aerosol deposition rates in Hawaii and Samoa[70]. The modern numbers have large uncertainties, but they may reflect enhanced atmospheric dust loading due to human activity in Asia.

biological activity in the long run. Second, phosphorus acts as a master regulator of biological activity in the oldest sites on this sequence, in agreement with existing conceptual models for terrestrial biogeochemistry[3]. It does so not only because the weathering source of phosphorus is depleted, but also because atmospheric inputs of phosphorus are very low in comparison with those of calcium and potassium and other putatively rock-derived elements. And third, even for phosphorus, dust from arid central Asia becomes the dominant source of inputs on a million-year timescale.

We cannot be sure that we have identified all the important sources of element inputs, especially for phosphorus. In particular, locally generated dust from exposed sea cliffs and beaches, and from semi-arid areas within Hawaii might contribute elements to our wet forest sites under some conditions—particularly during the glacial periods when sea level was lower and climates were probably drier[35]. Also, nesting seabirds could have brought marine phosphorus into

Table 1 Typical endmember values for geochemical tracers

Tracer	Basalt	Dust	Amount of P (mg m^{-2}) delivered in dust
ϵ_{Nd}	+7	−10	0.56
Eu/Eu*	1.06	0.61	1.04
Th/Hf	0.25	1.84	1.22

The Hawaiian basalt values were measured in the geochemistry laboratory at Cornell (L.A.D. and W. M. White, unpublished results). The estimates of the dust end members are from ref. 57. The final column contains estimates of the flux of P delivered to the 150,000-yr-old site.

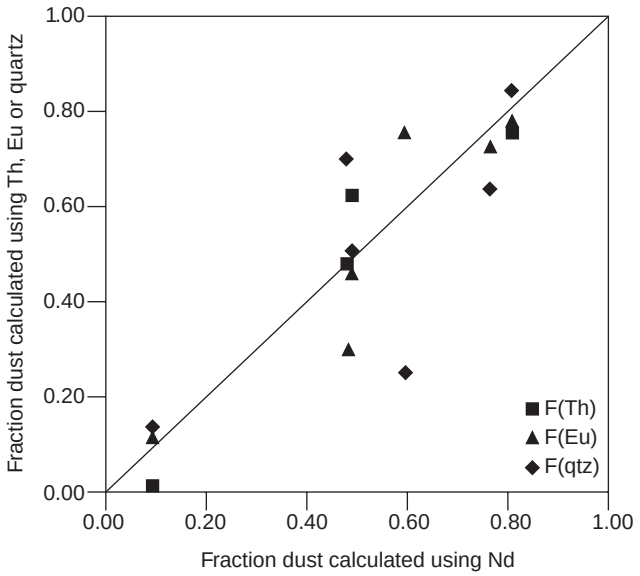

Figure 7 The mass fraction of dust-derived soil component based on Th/Hf ratios, Eu anomalies, and quartz content plotted against the dust mass fraction derived from Nd isotopes for the 150,000-year-old site. General agreement between independent geochemical indicators of dust input suggests that trace element and isotopic ratios can constrain dust inputs even when mineralogical indicators such as quartz content have been lost to dissolution.

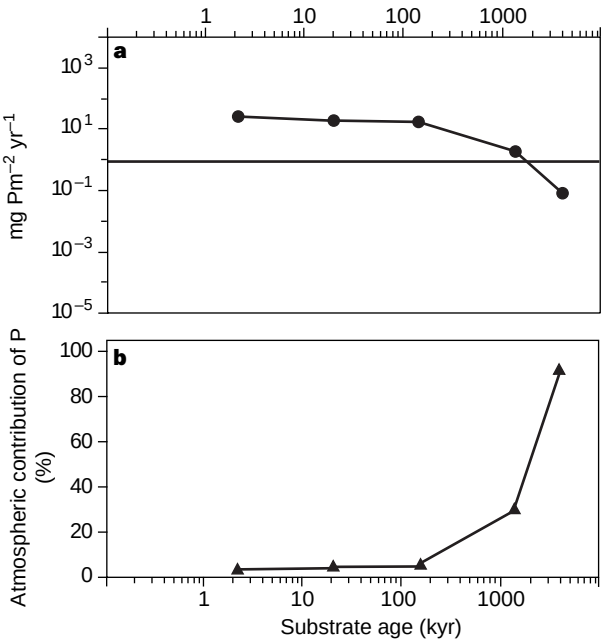

Figure 8 Comparison of phosphorus inputs from substrate and the atmosphere. **a**, Rate of P loss from the soil as a whole (Fig. 3c) plotted with the long-term average addition of P in mineral aerosol. **b**, The per cent atmospheric contribution for each site calculated by dividing the atmospheric contribution by the sum of the atmospheric inputs and contribution from soil phosphorus release.

terrestrial ecosystems, before they were largely extirpated by humans and introduced mammals. These pathways are worth further investigation—but, in any case, it is clear that lava sources decline in importance as a source of elements during the course of ecosystem development, even for phosphorus.

We cannot extrapolate the Hawaiian measurements directly to most continental settings, because both weathering and atmospheric contributions to ecosystems differ in Hawaii compared to most other places. The basaltic substrate is rapidly weathered, making the contribution of weathering to young sites greater in Hawaii than elsewhere, and the contribution to old sites less. More importantly, glaciation resets soil and ecosystem development at relatively frequent intervals over much of the temperate zone, maintaining it at young developmental stages in which weathering is a substantial source of most elements[62]. Tectonically induced erosion can similarly reset soil and ecosystem development anywhere on earth[63,64].

For atmospheric inputs, marine aerosol is a less important source of elements in the interior of continents than in Hawaii, and dust is a more important source. For example, Hawaii receives 10–1,000-fold less dust than much of the continental United States[65], and the rainwater concentrations of Ca, Sr, K and P are larger in continental interiors than over the ocean[66]. On very old, highly weathered substrates in the humid interior of continents (such as the Amazon basin), the combination of less marine aerosol and greater long-distance dust inputs could cause a shift in the limitation of biological processes from phosphorus to the more mobile cations.

Despite these differences, we can use Hawaii to identify some of the general patterns and characterize fundamental mechanisms underlying soil and ecosystem development. Most important, the dependence of biological processes in Hawaii on conditions in, and transport mechanisms from, central Asia demonstrates that the dynamics of long-term soil and ecosystem development cannot be evaluated as a local phenomenon in isolation: nowhere on Earth is that isolated. □

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