

Amplified temperature dependence in ecosystems developing on the lava flows of Mauna Loa, Hawai'i

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Through its effect on individual metabolism, temperature drives biologically controlled fluxes and transformations of energy and materials in ecological systems. Because primary succession involves feedbacks among multiple biological and abiotic processes, we expected it to exhibit complex dynamics and unusual temperature dependence. We present a model based on first principles of chemical kinetics to explain how biologically mediated temperature dependence of "reactant" concentrations can inflate the effective temperature dependence of such processes. We then apply this model to test the hypothesis that the temperature dependence of early primary succession is amplified due to more rapid accumulation of reactants at higher temperatures. Using previously published data from the lava flows of Mauna Loa, HI, we show that rates of vegetation and soil accumulation as well as rates of community compositional change all display amplified temperature dependence (Q_{10} values of ≈ 7 –50, compared with typical Q_{10} values of 1.5–3 for the constituent biological processes). Additionally, in young ecosystems, resource concentrations increase with temperature, resulting in inflated temperature responses of biogeochemical fluxes. Mauna Loa's developing ecosystems exemplify how temperature-driven, biologically mediated gradients in resource availability can alter the effective temperature dependence of ecological processes. This mechanistic theory should contribute to understanding the complex effects of temperature on the structure and dynamics of ecological systems in a world where regional and global temperatures are changing rapidly.

ecosystem development | metabolic theory of ecology | primary succession | Q_{10} | elevation

Biological metabolism—the uptake, transformation, and allocation of energy and materials by living things—shapes ecological phenomena (1). The metabolic theory of ecology has identified body size and temperature as critical variables driving metabolic rates and, thereby, ecological processes such as photosynthesis, respiration, population growth, and secondary succession (1–3). Through such processes, biological metabolism largely controls global cycles of carbon and nitrogen.

Primary succession—the development of ecosystems on new substrates such as lava flows, sand dunes, or land exposed by receding glaciers—is a complex process involving the accumulation of carbon and nutrients in biomass and soil and the concurrent assembly of a diverse biotic community (4, 5). It is driven by multiple interacting processes, including substrate weathering, primary production, soil formation, and colonization and subsequent turnover of plant, animal, fungal, and microbial species. Most of these processes are mediated by organisms whose biological function exhibits clear temperature dependence (1). It is known that temperature affects the rate of primary succession (4, 6–9). Not well understood, however, is how the multiple ecological processes interact to affect the overall rate of ecosystem development and to determine its temperature dependence.

Rates of ecological processes are ultimately consequences of chemical kinetics (1). It is standard to characterize the rate of a chemical reaction as the product of a temperature-dependent rate constant and the concentrations of reactants (10). For a

simple case, where two reactants combine to produce a product, this gives

$$V = v_0 e^{-E_a/kT} [R_1]^{m_1} [R_2]^{m_2}, \quad [1]$$

where V is the reaction rate; v_0 is a normalization constant; and $e^{-E_a/kT}$ is the Arrhenius expression, where T is temperature (Kelvin), k is Boltzmann's constant (8.62×10^{-5} eV·K⁻¹), and E_a (eV) is an activation energy characterizing the magnitude of the temperature dependence. The last two terms, $[R_1]^{m_1}$ and $[R_2]^{m_2}$, are the concentrations of the reactants, R_1 and R_2 , raised to powers m_1 and m_2 (assumed >0), which quantify the effects of their concentrations on V . When reactants are not limiting or where their concentrations do not vary systematically with T , Eq. 1 reduces to $V \propto e^{-E_a/kT}$, the familiar exponential increase in rate with temperature characteristic of both abiotic and metabolic processes (1). This Arrhenius formulation from physical chemistry theory differs from the Q_{10} commonly used in biology in that its somewhat shallower form more accurately characterizes fundamental reaction kinetics (10–13). Our focus is on the strength of the temperature response, here characterized by E_a (higher E_a signifies stronger temperature response).

The inherent kinetics of the constituent processes of primary succession have been described using data from a variety of systems. Rates of abiotic substrate weathering exhibit modest temperature dependence in both field ($E_a \approx 0.4$ –0.5 eV for basalt) (14, 15) and laboratory ($E_a \approx 0.4$ –0.9 eV for a variety of silicate minerals) (16). Most of the other processes involved in ecosystem development are consequences of biological metabolism, and their temperature dependence reflects the kinetics of the underlying reactions (1, 11). Photosynthesis-fueled rates, such as net primary production (2) and biomass accumulation during secondary succession (3), typically have E_a values of ≈ 0.3 eV (equivalent to $Q_{10} \approx 1.5$) over the temperature range 0–30°C, reflecting the temperature dependence of Rubisco-limited C_3 photosynthesis (2). In contrast, respiration-fueled rates, including heterotrophic respiration and growth (11, 17), typically exhibit E_a values of ≈ 0.65 eV (equivalent to $Q_{10} \approx 2.5$), reflecting the average activation energy for enzyme-catalyzed aerobic metabolism (11). Biological nitrogen fixation also is temperature-dependent. *In vitro*, the temperature dependence of the nitrogenase reaction is biphasic ($E_a = 2.18$ eV below 22°C and 0.65 eV above 22°C) (18), but empirical *in vivo* estimates of E_a appear to be intermediate (e.g., $E_a \approx 0.95$ eV for Mauna Loa's lichen *Stereocaulon vulcani*) (19).

The kinetics of primary succession could be vastly different from those of its constituent processes (as described above) if the rates of contributing reactions depend on concentrations of

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Table 1. Multipredictor models for various rates of primary succession on the slopes of Mauna Loa as a function of average annual temperature, precipitation, and lava flow type

Models	n*	Temperature		Precipitation		Flow Type	R ²
		ϵ (SE) [†]	t	Response or α ; β (SE) [‡]	t	'a'a > pāhoehoe, t	
Aboveground biomass accumulation							
Model 1	25	2.6 (0.2)	6.8	wet > dry	8.7	n.s.	84.8
Model 2	25	≥ 1.4 (0.35) [§]	4.0	4.05 (0.56); -0.0011 (0.0003)	7.3; -3.6	n.s.	92.2
Soil accumulation							
Model 1	24 (29)	>2.1 (0.5)	4.1	wet > dry	2.8	-2.6	56.2
Model 2	24 (29)	>1.3 (0.5)	2.3	$\beta = 0.0001$ (0.0002)	4.3	-3.5	64.8
Soil C accumulation							
Model 1	24 (29)	>3.2 (0.7)	4.5	wet > dry	5.2	n.s.	66.5
Model 2	24 (29)	>2.3 (0.8)	3.0	2.8 (1.1); -0.0003 (0.0006)	2.6; -0.4	-2.2	80.0
Soil N accumulation							
Model 1	24 (29)	>3.1 (0.7)	4.6	wet > dry	4.3	n.s.	62.3
Model 2	24 (29)	>2.6 (0.7)	3.5	2.7 (1.1); -0.0004 (0.0006)	2.5; 0.6	-2.0	77.6
Soil P accumulation							
Model 1	24 (29)	>2.6 (0.5)	5.0	wet > dry	1.1	n.s.	54.9
Model 2	24 (29)	2.6 (0.4)	5.8	$\alpha = 0.7$ (0.2)	3.0	-2.8	71.0
Community compositional change							
Colonization	5	1.6 (0.2)	6.7	—	—	—	93.7
Loss	5	2.8 (0.7)	4.2	—	—	—	85.5
Turnover	5	1.8 (0.3)	6.1	—	—	—	92.6
All processes[¶]							
Model 1	136	2.8 (0.3)	10.7	wet > dry	9.4	-3.2	85.2
Model 2	136	1.8 (0.3)	6.0	1.8 (0.5); -0.0001 (0.0003)	3.9; -0.4	-3.9	87.8

Precipitation is analyzed either categorically (wet or dry; Model 1) or quantitatively (mm·yr⁻¹; Model 2) (see Eq. 3). All accumulation rates are in g·m⁻²·yr⁻¹. Community compositional change is measured as species per year. n.s., nonsignificant effects ($P > 0.05$); —, nonapplicable cofactors. Nonsignificant parameters characterizing the effects of temperature and precipitation are reported, along with their t values.

*Numbers in parentheses include zero-values that were excluded from the reported analyses.

[†]> indicates that replacing zero-values with any reasonable value (e.g., lowest measured value, 1/10 lowest measured value) results in a steeper slope (higher ϵ).

[‡]See Eq. 3.

[§]Exclusion of one to three highly influential points gives higher ϵ .

[¶]Process type (i.e., biomass accumulation, soil accumulation, etc.) is included as covariate and is highly significant ($P < 0.0001$).

in wet climates, regardless of whether the effects of precipitation are characterized categorically or quantitatively, and the effects of precipitation are nonlinear (Table 1). Finally, rates tend to be higher on chunky 'a'a than on ropey pāhoehoe lava flows, although lava type is often not a significant contributor when precipitation is characterized categorically (Table 1).

Community compositional change is also strongly temperature dependent; rates of plant species colonization, loss, and turnover (species per year) all increase with temperature ($\epsilon = 1.6$ – 2.6 ; $R^2 = 85.5$ – 93.7). Because peak rates of community change occur later in time in the colder environments at high elevations (25), this analysis underestimates the true degree of temperature dependence. We note, however, that the temperature dependence of rates of community change during succession is highly complex, influenced by factors such as species richness, dispersal, and temporal patterns in succession rate; therefore, this temperature dependence should be viewed not as a mechanistic explanation but as an empirical response variable.

When all of the aforementioned rates are combined into a single statistical model characterizing the overall rate of primary succession (Fig. 2), the integrated model gives $\epsilon = 1.8$, with precipitation analyzed as a continuous variable, and shows that temperature, precipitation, and lava type all have significant effects on the overall rate of primary succession (Table 1).

Resource concentrations increase over the course of ecosystem development, resulting in a gradient in resource availability

along the temperature gradient. As has been previously documented (5, 23, 24), soil N and P (%) are lower in young (<140 yr) than in old (>2,800 yr) ecosystems (both $t > 4.9$; $P \geq 0.0001$) and leaf N (%) is higher in old ecosystems ($t = 6.3$; $P < 0.0001$); however, there is no significant age-related variation in leaf P (%) on this centennial timescale ($P = 0.68$). Correspondingly, when ecosystems of similar ages (109–140 yr) at different elevations are compared, the concentrations of the reactants increase with temperature (Fig. 3). Specifically, leaf biomass (g·m⁻²; $E_{[R]} = 0.47 \pm 0.43$; P not significant) (Fig. 3A), leaf N and P (both $P < 0.03$) (Fig. 3B), and soil N and P (both $P < 0.003$) (Fig. 3C) all increase with temperature, meaning that the $E_{[R]}$ values characterizing their temperature dependence are greater than zero. In the case of leaf and soil nutrients, after significant effects of precipitation are accounted for, $E_{[R]}$ values are $\geq 0.17 \pm 0.04$ for leaf N, $\geq 0.11 \pm 0.04$ for leaf P, 1.31 ± 0.49 for soil N, and 1.12 ± 0.34 for soil P (all $P \leq 0.02$) (see SI Table 4).

Biogeochemical fluxes in Mauna Loa's young ecosystems (110–136 yr) also respond strongly to temperature (Table 2); comparisons of four young wet-side ecosystems reveal high values of ϵ for rates of aboveground net primary production, litterfall, N and P uptake by plants (g·m⁻²·yr⁻¹; $\epsilon = 1.10$ – 1.53), and decomposition (k ; $\epsilon = 0.90$).

Discussion

The strong temperature dependence of the rate of early primary succession, together with observed gradients in resource con-

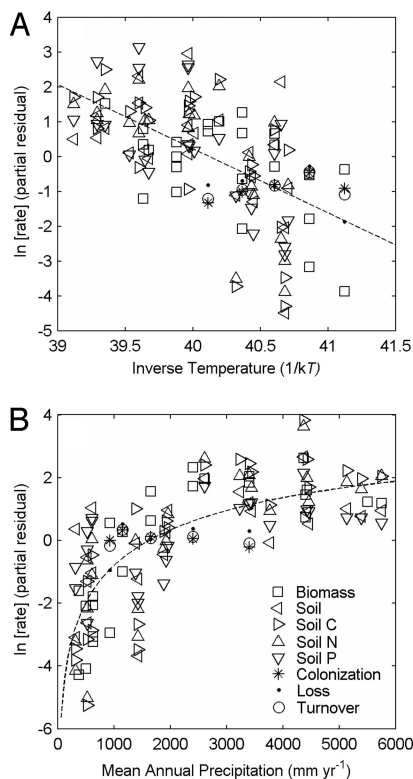


Fig. 2. Effects of mean annual temperature (plotted as inverse temperature, $1/kT$, so that the slope is $-\varepsilon$) (A) and mean annual precipitation (Eq. 3) (B) on rates of primary succession on the lava flows of Mauna Loa. Plotted are partial residuals or the rate corrected for all variables but the one of interest. The full model (Table 1) accounts for process type, temperature, precipitation (Eq. 3) and lava type ('a'a versus pāhoehoe).

centrations and the kinetics of biogeochemical fluxes in young ecosystems, supports the hypothesis that the temperature dependence of early primary succession is amplified through more rapid accumulation of reactants at higher temperatures. First, the overall temperature dependence of ecosystem development

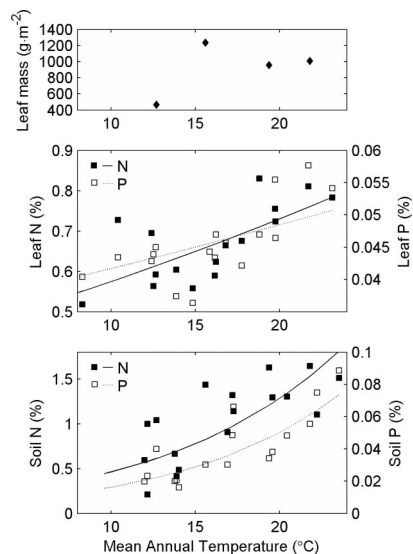


Fig. 3. Concentrations of key reactants (leaf biomass, leaf nutrients, and soil nutrients) in young sites (109–138 yr) spanning a temperature gradient.

Table 2. Estimated temperature dependence of various fluxes on young (i.e. 110–136 yr) flows on Mauna Loa

Fluxes	Temperature response				R^2
	$\varepsilon \pm \text{SE}$	t	p		
ANPP	1.53 ± 0.42	-3.6	0.07	86.9	
Litterfall	1.24 ± 0.24	-5.1	0.04	92.9	
N uptake	1.27 ± 0.19	-6.7	0.02	95.7	
P uptake	1.10 ± 0.12	-8.9	0.01	97.6	
Decomposition	0.90 ± 0.14	-6.3	0.02	95.2	

All fluxes are measured in $\text{g m}^{-2} \text{yr}^{-1}$, except decomposition, which is measured as k . Small sample sizes (all $n = 4$) precluded consideration of the effects of precipitation.

is greater than that inherent to any of its constituent processes ($\varepsilon > E_a$). Accumulation rates of aboveground biomass and soil (Fig. 1) and rates of species compositional changes have effective activation energies, ε , ranging from 1.4 to 2.8 ($Q_{10} \approx 7\text{--}50$) (Table 1), and the overall temperature dependence (estimated from a combination of all rates) is similarly strong ($\varepsilon = 1.8$; $Q_{10} \approx 12$) (Fig. 2). The magnitude of this temperature dependence is much greater than that of the constituent processes of substrate weathering, photosynthesis, and aerobic respiration measured in isolation ($E_a \approx 0.3\text{--}0.7$ eV; $Q_{10} \approx 1.5\text{--}3.0$) (Fig. 4) and is much greater than that of biomass accumulation during secondary succession ($E_a \approx 0.3$ eV; $Q_{10} \approx 1.5$), whose kinetics appear to be driven by photosynthesis (3). Consequently, it is unlikely that the dynamics of primary succession are due to domination of a single temperature-dependent process. The only single process that might account for such high values of ε is nitrogen fixation; it has a very high activation energy ($E_a = 2.18$ eV below 22°C) (18) when measured in isolation in the laboratory. However, observed rates of biological N fixation by Mauna Loa's lichen *S. vulcani* have a smaller (although still substantial) temperature dependence ($E_a \approx 0.95$ eV) (19). In any case, soil N accumulation rates on Mauna Loa are controlled primarily by atmospheric deposition rather than nitrogen fixation (5, 22). Rates of atmospheric deposition of N probably scale with precipitation, which does not vary monotonically with elevation on Mauna Loa. This exceptional temperature response of ecosystem development remains after the removal of a precipitation response (Fig. 2B) that is much stronger than the precipitation effect on global productivity (26), suggesting that effects of precipitation may also be amplified.

Second, age- and temperature-related variation in reactant concentrations supports our prediction that gradients in $[R]$ values should develop in relation to temperature ($E_{[R]} > 0$). Indeed, leaf biomass, N, and P as well as soil N and P all are present at higher concentrations or densities in warmer sites (i.e.,

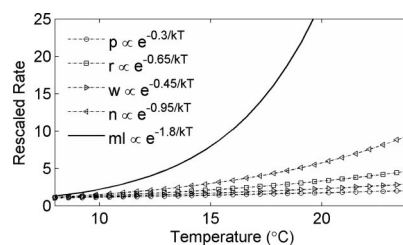


Fig. 4. Comparison of the average temperature dependence of primary succession on Mauna Loa (ml ; $\varepsilon = 1.8$) (Table 1) with the rates typically observed for some of the constituent processes: nitrogen fixation by *S. vulcani* (n ; $E_a \approx 0.95$ eV), basalt weathering (w ; $E_a \approx 0.4\text{--}0.5$ eV), aerobic respiration rates (r ; $E_a \approx 0.65$ eV), and photosynthesis (p ; $E_a \approx 0.3$ eV). For display purposes, values are rescaled to normalize the rates to 1 at 7°C .

$E_{[R]} > 0$) (Fig. 3). The low $E_{[R]}$ values (<0.2) of leaf N and P are not surprising given that plants tend to allocate available nutrients more toward new leaf growth than to increased leaf N (27); however, they do represent a meaningful difference for physiological function (21, 28) and, when multiplied by leaf biomass, for total ecosystem leaf nitrogen ($\text{g}\cdot\text{m}^{-2}$). Although our analysis focuses on leaf and soil N and P, we note that other resources also accumulate fastest at high temperatures (e.g., other soil nutrients, soil organic matter, and the nitrogen-fixing lichen *S. vulcani*) (9, 23, 29), thereby contributing to the temperature dependence in reactant concentration.

Finally, biogeochemical fluxes in young sites—ANPP, litterfall, N and P uptake by plants, and decomposition—have unusually strong temperature responses, which are presumably driven by the temperature dependence of reactant concentrations, such as those described above. The four vegetative processes have ε values ranging from 1.1–1.5 ($Q_{10} \approx 4.8$ –8.3) (Table 2), much stronger than photosynthesis-fueled metabolism ($E_a \approx 0.3$ eV; $Q_{10} \approx 1.5$) (2). Likewise, the rate of litter decomposition increases more steeply with temperature on these young Mauna Loa flows ($\varepsilon = 0.9$; $Q_{10} \approx 3.4$) (Table 2) than in environments where it is controlled straightforwardly by the kinetics of respiration ($E_a \approx 0.65$ eV; $Q_{10} \approx 2.5$) (2). An even stronger temperature dependence of decomposition was previously observed for additional substrates on both young and old lava flows (Q_{10} values of 4–11) and was interpreted as reflecting greater nutrient supply in warmer ecosystems (30), an interpretation that is entirely consistent with our feedback hypothesis. Thus, three lines of mutually consistent evidence support the hypothesis that the temperature dependence of early primary succession on the lava flows of Mauna Loa is amplified through more rapid accumulation of reactants at higher temperatures.

The amplified temperature dependence, together with existing evidence of several major feedbacks, suggests that positive feedbacks govern the dynamics of early ecosystem development on Mauna Loa. As yet, we cannot assess the relative importance of several potentially important feedbacks that could contribute to the observed high ε . First, biotic growth feeds back on itself; for example, growth of leaves allows more photosynthesis and thereby more growth. Second, biological activities (e.g., enhanced acidity at weathering surface and plant rooting) accelerate weathering (31) such that the weathering rate of Hawaiian basalts is at least an order of magnitude greater underneath plants than on nonvegetated surfaces (32, 33). In turn, substrate weathering enhances plant growth through the release of phosphorus and other elements that can limit plant production (34) and biological nitrogen fixation (22, 35–37). Third, plant productivity and nitrogen accumulation are mutually dependent. Nitrogen is the most strongly limiting nutrient in Hawaii's young ecosystems (5, 34, 38), and biota increase the rate of nitrogen accumulation by retaining atmospheric inputs and through limited nitrogen fixation (22). Lastly, accumulation of biota and soil organic matter, both of which are driven by temperature-dependent growth and metabolism, are mutually dependent. Soil organic matter is derived from biomass that decomposes through the action of microorganisms and invertebrates. In turn, organic matter enhances soil water-holding capacity and nutrient content (4, 39), which are especially critical in young ecosystems, where runoff can remove water and nutrients before they can be taken up by plants. The highly interdependent nature of these and other processes makes it unsurprising that rates of biomass accumulation, soil formation, and even community compositional change respond steeply and similarly to temperature (Table 1 and Fig. 2).

Because of these feedbacks, primary succession on Mauna Loa exhibits a temperature dependence ($\varepsilon = 1.8$; $Q_{10} \approx 12$) that dwarfs those of most metabolically mediated biological rate processes (Fig. 4). The overall rate of primary succession in-

creases >50 -fold over the 16°C temperature gradient between the highest (2,480 m) and lowest (60 m) elevations for which data are available. Lava flows only about a century old in the wet lowlands have already accumulated a relatively productive (ANPP ≈ 400 –600 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) developing forest with substantial aboveground biomass (1–3 $\text{kg}\cdot\text{m}^{-2}$) and numerous species (6, 9), whereas flows the same age above a 2,000-m elevation support little or no vegetation and soil (6, 7, 23).

Amplification of temperature dependence, such as that observed here, should be general to systems whose dynamics are strongly shaped by positive feedbacks. An obvious application is to other cases of primary succession, whose rates do exhibit temperature dependence. For example, primary succession rate after the eruption of Mount St. Helens exhibits temperature dependence along an elevational gradient (8), and substantial differences in succession rate may be seen on recently formed volcanic islands, where the difference in temperature is due to latitude rather than elevation (40, 41). Subarctic Surtsey (33 km from Iceland; $\bar{T} \approx 5^\circ\text{C}$) has remained relatively depauperate of vegetation for four decades after eruption (42), whereas tropical Anak Krakatau (40 km from Sumatra; $\bar{T} \approx 26^\circ\text{C}$) supported forest vegetation exceeding 10 m in height only two decades after eruption (43). Although it remains to be seen whether these and other developing ecosystems will exhibit approximately the same magnitude of temperature dependence observed here, the underlying mechanisms should hold. Such amplified temperature dependence also is likely to be seen on land exposed by receding ice sheets and where ecosystem restoration involves multiple processes of soil and vegetation development.

More broadly, ecosystem development on Mauna Loa provides an example of how temperature-driven, biologically mediated gradients in resource availability can alter the effective temperature dependence of ecological processes. Such phenomena are not uncommon in ecology; for example, ε values of ecosystem respiration may be inflated by temperature-driven gradients in photosynthate supply to root growth or litterfall (44–46). Our model goes beyond the straightforward effect of temperature on constituent metabolic processes (1, 11) to describe cases where interactions among multiple processes affect the kinetics by altering resource concentrations. In an era of global warming, a mechanistic theory based on first principles of chemical kinetics could contribute to understanding the complex effects of temperature on the structure and dynamics of ecological systems.

Methods

All data were collected previously on the slopes of Mauna Loa, HI ($19^\circ29'$ N, $155^\circ36'$ W). Mauna Loa is an active shield volcano whose broad, gentle slopes are covered by lava flows of various ages. Lava flows differ in form, including chunky 'a'a and smooth, ropy pāhoehoe flows, but vary little in chemistry. Average annual temperature (\bar{T}) decreases at a lapse rate of 6.4°C per kilometer (47), resulting in a decrease of $\approx 17^\circ\text{C}$ between sea level and the upper range of vegetation around 2,400 m. Precipitation varies dramatically between the wet windward NE flank of Mauna Loa and its dry NW flank (48, 49). On the wet side, precipitation increases from $\approx 3,600$ $\text{mm}\cdot\text{yr}^{-1}$ at sea level to a peak of $\approx 5,700$ $\text{mm}\cdot\text{yr}^{-1}$ near 700 m and then declines as a roughly exponential function (7, 48). On the dry side, precipitation averages <750 $\text{mm}\cdot\text{yr}^{-1}$ over the entire altitudinal gradient, with a peak between 900 and 1,600 m (49).

The data sources and analytical methods that we used are given below and in the *SI Tables 5 and 6* and *SI Methods*). The data provided challenges in sorting out the separate and interactive effects age, temperature, precipitation, and lava type. Although there is no single "right" way to analyze these data, we tried to use the most statistically rigorous and ecologically realistic methods. We also tried alternative analytical procedures, which gave similar results. In general, we report analyses that give conservative estimates of ε .

Rates of aboveground biomass and soil accumulation were calculated as the slopes of linear regressions as a function of age (3), which were forced through the origin to enforce the assumption that initial values were zero. Data for these processes were available for both 'a'a and pāhoehoe sites between 80 and 2,480 m on both the wet and dry sides of Mauna Loa (*SI Table 5*). For biomass, ages

