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.

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

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

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 \( \approx 0.3 \) eV (equivalent to \( Q_{10} \approx 1.5 \)) over the temperature range 0–30°C, reflecting the temperature dependence of Rubisco-limited C3 photosynthesis (2). In contrast, respiration-fueled rates, including heterotrophic respiration and growth (11, 17), typically exhibit \( E_a \) values of \( \approx 0.65 \) 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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limiting “reactants” produced by other processes. Specifically, if the concentrations of reactants in Eq. 1 increase with temperature (e.g., \([R] \sim e^{-\frac{E[R]}{RT}}\)), where \(E[R]\) is a parameter characterizing the temperature dependence of \([R]\) and we assume \(m = 1\), then the temperature terms (e.g., \(e^{-\frac{E[R]}{RT}}\) and \(e^{-\frac{E[R]}{RT'}}\)) will combine multiplicatively such that the exponents sum to characterize the overall temperature dependence of the process. For notation, we refer to the new effective “activation energy” as \(\varepsilon\):

\[
\varepsilon = E_a + E[R] + \ldots + E[R],
\]

Thus, whenever a limiting reactant concentration increases with temperature (i.e., \(E[R] > 0\)), the overall temperature dependence will be increased (i.e., \(\varepsilon > E_a\)). In systems dominated by positive feedbacks, these effects will be compounded through time as the products from each time step move on to serve as reactants in the next.

Consideration of the pertinent reactants shows why primary succession is a prime candidate for the sort of dynamics described above. To apply Eq. 1 to an ecosystem context, we define three categories of reactants. First, the densities (g m\(^{-2}\)) of the structures that are sites of reactions (e.g., leaves, roots, and soil; g m\(^{-2}\)) contribute to the \([R]\) values. Second, concentrations (g m\(^{-3}\)) of key enzymes, organelles (e.g., chloroplasts and mitochondria), or microbes, which are often correlated with leaf or soil N and P (20, 21), represent key reactants. Finally, pools of biologically available limiting resources (e.g., nitrate, phosphate, organic C, and water; g m\(^{-2}\)) represent the most ephemeral category of reactants. The last category may not display a predictable relationship with temperature (although throughput rates generally do increase with temperature), but the two former categories, which represent products of temperature-dependent biotic growth, should increase more rapidly in warmer climates and, in so doing, feed back to affect the overall kinetics of early primary succession.

Here, we evaluate the hypothesis that the temperature dependence of early primary succession is amplified by more rapid accumulation of reactants at higher temperatures. During the initial rapidly accelerating phase of ecosystem development (i.e., before biomass accumulation plateaus), this mechanism should produce observable patterns. First, long-term rates of net ecosystem development—measured in terms of accumulation rates of biomass or soil (g m\(^{-2}\) yr\(^{-1}\)) or rates of community compositional change (species per year)—should display a temperature dependence much stronger than that of any of the constituent processes (i.e., \(\varepsilon > E_a\)) as described above because \(\varepsilon\) should be an aggregate of the activation energies of the constituent processes (Eq. 2) and should be inflated through time as feedback effects accrue. Second, at any point in time, concentrations of critical reactants should increase with temperature (i.e., \(E[R]\) values > 0; see Eq. 2) as a result of their more rapid accumulation at higher temperatures. Third, because of these gradients in resource concentration, biogeochemical fluxes (g m\(^{-2}\) yr\(^{-1}\)) should also exhibit inflated apparent temperature dependence (i.e., \(\varepsilon > E_a\); see Eq. 2).

We test these predictions by using data from the active volcano of Mauna Loa, HI, which is an ideal system in which to study the temperature dependence of ecosystem development. Lava flows of various ages span a broad elevational gradient, creating a matrix of sites with different combinations of age, climate, and lava type that lends itself to the study of climatic effects on succession (6, 7). The first \(>3,000\) yr of ecosystem development are well characterized. Carbon pools in live vegetation, detritus, and soil all increase (5–7, 9, 22, 23). Nitrogen, which enters the ecosystem through atmospheric deposition and biological fixation, and phosphorus, which is released from weathering lava, accumulate in the soil and vegetation (5, 9, 22–24). We use the wealth of data from this system to quantify the temperature dependence of aboveground biomass, soil, and soil nutrient accumulation rates (g m\(^{-2}\) yr\(^{-1}\)) and of rates of species colonization, loss, and turnover (species per year) during the initial rapidly accelerating phase of primary succession. Additionally, using data from relatively young ecosystems (109–138 yr), we test for a temperature gradient in reactant concentrations (leaf biomass, N, and P; g m\(^{-2}\)) and consider the temperature dependence of biogeochemical fluxes (e.g., aboveground net primary production (ANPP) and decomposi-
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 páhoehoe 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 ($v = 1.6–2.6; R^2 = 85.5–93.7$). 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 $v = 1.8$, 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 $t > 4.9; P < 0.0001$) 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, $1.31 \pm 0.49$ for soil N, and $1.12 \pm 0.34$ 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 $v$ for rates of aboveground net primary production, litterfall, N and P uptake by plants ($g m^{-2} y^{-1}; v = 1.10–1.53$), and decomposition ($k; v = 0.90$).

**Discussion**

The strong temperature dependence of the rate of early primary succession, together with observed gradients in resource con-
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 is greater than that inherent to any of its constituent processes \( (e > E_a) \). Accumulation rates of aboveground biomass and soil (Fig. 1) and rates of species compositional changes have effective activation energies, \( e \), ranging from 1.4 to 2.8 \( (Q_{10} \approx 7-50) \) (Table 1), and the overall temperature dependence (estimated from a combination of all rates) is similarly strong \( (e = 1.8; Q_{10} \approx 12) \) (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 \( (E_a \approx 0.3–0.7 \text{ eV}; Q_{10} \approx 1.5–3.0) \) (Fig. 4) and is much greater than that of biomass accumulation during secondary succession \( (E_a \approx 0.3 \text{ eV}; Q_{10} \approx 1.5) \), 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 \( e \) is nitrogen fixation; it has a very high activation energy \( (E_a = 2.18 \text{ eV below } 22\degree \text{C}) \) (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 \( (E_a \approx 0.95 \text{ eV}) \) (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.,

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

<table>
<thead>
<tr>
<th>Fluxes</th>
<th>Temperature response</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANPP</td>
<td>( e \geq \text{SE} )</td>
</tr>
<tr>
<td>Litterfall</td>
<td>( t )</td>
</tr>
<tr>
<td>N uptake</td>
<td>( p )</td>
</tr>
<tr>
<td>P uptake</td>
<td>( R^2 )</td>
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<tr>
<td>Decomposition</td>
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<th>Fluxes</th>
<th>( e \geq \text{SE} )</th>
<th>( t )</th>
<th>( p )</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANPP</td>
<td>1.53 ± 0.42</td>
<td>-3.6</td>
<td>0.07</td>
<td>86.9</td>
</tr>
<tr>
<td>Litterfall</td>
<td>1.24 ± 0.24</td>
<td>-5.1</td>
<td>0.04</td>
<td>92.9</td>
</tr>
<tr>
<td>N uptake</td>
<td>1.27 ± 0.19</td>
<td>-6.7</td>
<td>0.02</td>
<td>95.7</td>
</tr>
<tr>
<td>P uptake</td>
<td>1.10 ± 0.12</td>
<td>-8.9</td>
<td>0.01</td>
<td>97.6</td>
</tr>
<tr>
<td>Decomposition</td>
<td>0.90 ± 0.14</td>
<td>-6.3</td>
<td>0.02</td>
<td>95.2</td>
</tr>
</tbody>
</table>

All fluxes are measured in g m\(^{-2}\) yr\(^{-1}\), except decomposition, which is measured as k. Small sample sizes (all \( n = 4 \)) precluded consideration of the effects of precipitation.
increases >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 g m⁻² yr⁻¹) developing forest with substantial aboveground biomass mass (~3 g m⁻²) of 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; T = 5°C) has remained relatively depauperate of vegetation for four decades after eruption (42), whereas tropical Anak Krakatau (40 km from Sumatra; T = 26°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 would be similar. Such 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 photosynthetic 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°29’ N, 155°36’ 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 (T) decreases at a lapse rate of 6.4°C per kilometer (47), resulting in a decrease of ~17°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 ~3,600 mm yr⁻¹ at sea level to a peak of ~5,700 mm yr⁻¹ near 700 m and then declines as a roughly exponential function (7, 48). On the dry side, precipitation averages ~750 mm 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 S and S 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 slope 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 S). For biomass, ages
ranged from 5 to 4,000 years, but many old sites, particularly at low elevations, were excluded because accumulation of biomass had already decelerated. Calculations of the biomass accumulation rate are detailed in SI Methods and SI Table 6. For soil and its components, all data were from young ecosystems (109–140 yr), so rate was simply mass divided by age. Data for soil accumulation contained zero-values (primarily at high elevations), which we were forced to exclude from our analyses. Replacing these zeros with any value less than or equal to the lowest measured value resulted in a higher value.

Changes in species composition were determined by using presence–absence data for wet side ‘a’ flows of five ages (5–3,400 yr) and five elevations (1,219–2,438 m) (SI Table 5) (9, 30). Average colonization and loss rates were defined as the total number of species gained or lost along the entire chronosequence divided by chronosequence age (3,400 yr), and turnover rate is defined as the total number of species gained or lost along the entire chronosequence (15% of all absences) were attributed to sampling error or stochasticity and counted as absences. Data were insufficient to test for effects of precipitation.

Leaf and soil nutrient data from Vitousek et al. (23) were reanalyzed. Age-related variation was determined by using a paired t test for soil nutrients and an ANOVA for leaf nutrients. Temperature-related variation was analyzed for young (109–138 yr) sites (SI Tables 4 and S).

Data on biogeochemical fluxes (ANPP, litterfall, N and P uptake, and decomposition) from four relatively young (110–136 yr) paohoe flows on the wet side (SI Table 5) (9, 30) were used to estimate temperature dependency from four relatively young (110–136 yr) paohoe flows on the wet side (SI Table 5) (9, 30) were used to estimate temperature dependence of these processes. Again, data were insufficient to test for effects of precipitation.

We used multiple linear regression (Type III SS) to characterize the response of the above rates to three environmental variables: temperature, precipitation, and soil type. Average annual temperature (°F, Kelvin) was expressed as $1/kT$ (see Eq. 1), so $-e$ is the slope of the Arrhenius plot of ln [rate] as a function of $1/kT$ (Fig. 2A). Precipitation covaries nonlinearly with temperature along the altitudinal gradient, so there is no straightforward method to isolate its effects from those of temperature. We assessed the effect of precipitation in two ways: (i) We categorized precipitation regimes as wet (<900 mm yr$^{-1}$) or dry (<750 mm yr$^{-1}$), corresponding to the windward NE and the leeward NW slopes of Mauna Loa, respectively; (ii) we analyzed precipitation (w; mm yr$^{-1}$) as a covariate in our quantitative variation model that can capture complex curvilinear and peaked functions (SI Methods):

$$\text{rate} = ce^{-\frac{e}{kT}(w^{\alpha}+\beta)}.$$  

[3]

Here, $\alpha$ and $\beta$ can be either positive or negative exponents and $c$ is a normalization constant containing any differences between lawn flow types.

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