



RESEARCH LETTER

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Key Points:

- Weathering rates decrease at elevation partially due to a thick soil organic layer
- If global climate is perturbed, montane ecosystems may buffer perturbations
- We show two tectonic events when this may have occurred

Supporting Information:

- Readme
- Supplemental Figures S1-S6

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Montane forest root growth and soil organic layer depth as potential factors stabilizing Cenozoic global change

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Abstract Tree roots and their symbiotic fungal partners are believed to play a major role in regulating long-term global climate, but feedbacks between global temperature and biotic weathering have not yet been explored in detail. In situ field data from a 3000 m altitudinal transect in Peru show fine root growth decreases and organic layer depth increases with the cooler temperatures that prevail at increased altitude. We hypothesize that this observation suggests a negative feedback: as global temperatures rise, the soil organic layer will shrink, and more roots will grow in the mineral layer, thereby accelerating weathering and reducing atmospheric CO₂. We examine this mechanism with a process-based biological weathering model and demonstrate that this negative feedback could have contributed to moderating long-term global Cenozoic climate during major Cenozoic CO₂ changes linked to volcanic degassing and tectonic uplift events.

1. Introduction

Over millions of years, the Earth's atmospheric CO₂ and climate history are regulated by the balance between CO₂ removal via silicate rock weathering and organic carbon burial, and its return to the atmosphere by volcanic and metamorphic degassing [Berner and Kothavala, 2001]. Field and experimental studies indicate that tree root growth and root-associating symbiotic mycorrhizal fungi play an important role in controlling long-term continental weathering rates and therefore atmospheric CO₂ concentrations ((CO₂)_a) [Berner *et al.*, 2003; Taylor *et al.*, 2009a]. Tree roots and mycorrhizal fungi accelerate weathering and leaching of cations from the soil by acidifying the weathering environment in the microscopic regions around roots and fungal mycelia through respiration, active proton extrusion during nutrient uptake, and by the decomposition of organic matter [Arthur and Fahey, 1993; Banwart *et al.*, 2009]. Forest canopies, like those in the Amazonian rainforest, also increase the recirculation of rainfall via evapotranspiration [Shukla and Mintz, 1982], replacing saturated soil solution with fresh unsaturated water. These biota-controlled weathering processes provide a series of feedback on (CO₂)_a and climate over geological time scales by regulating the strength of the long-term CO₂ sink [Berner and Kothavala, 2001]. Since temperature is one of the controls on the productivity of land vegetation, there is a strong relationship between the global biosphere activity and the global temperature, and hence, it is likely that a strong biotic feedback exists between global temperature and the rate of biological weathering and CO₂ drawdown. However, previous geochemical carbon cycle modeling efforts [Bergman *et al.*, 2004; Berner *et al.*, 2003; Berner and Kothavala, 2001; Taylor *et al.*, 2011] have overlooked the feedback between temperature, soils, and root activity.

Here we propose the montane forest root-soil system as the major locus of the feedback between the global temperature and biotic weathering. We describe how montane forest feedbacks on Cenozoic (CO₂)_a and climate are likely mediated by rooting activity and the depth of the soil organic layer. Montane regions may be particularly important contributors to global terrestrial weathering because they are distributed on zones of active uplift where fresh unweathered rock undergoes rapid chemical weathering. Field studies of high-elevation temperate forest watersheds in the Swiss Alps and Rocky Mountain Park, north central Colorado [Arthur and Fahey, 1993] indicate they typically enhance weathering rates by a factor of 4. However, no studies have quantified weathering by tropical montane forests or the role of mountain forests worldwide in regulating long-term (CO₂)_a and climate via weathering processes [Berner *et al.*, 2003; Taylor *et al.*, 2009b]. We therefore developed a new quantitative mechanistic understanding of these issues by exploiting insights from a well-described montane forest transect in Peru along an elevation gradient (210 to 3020 m above sea level)

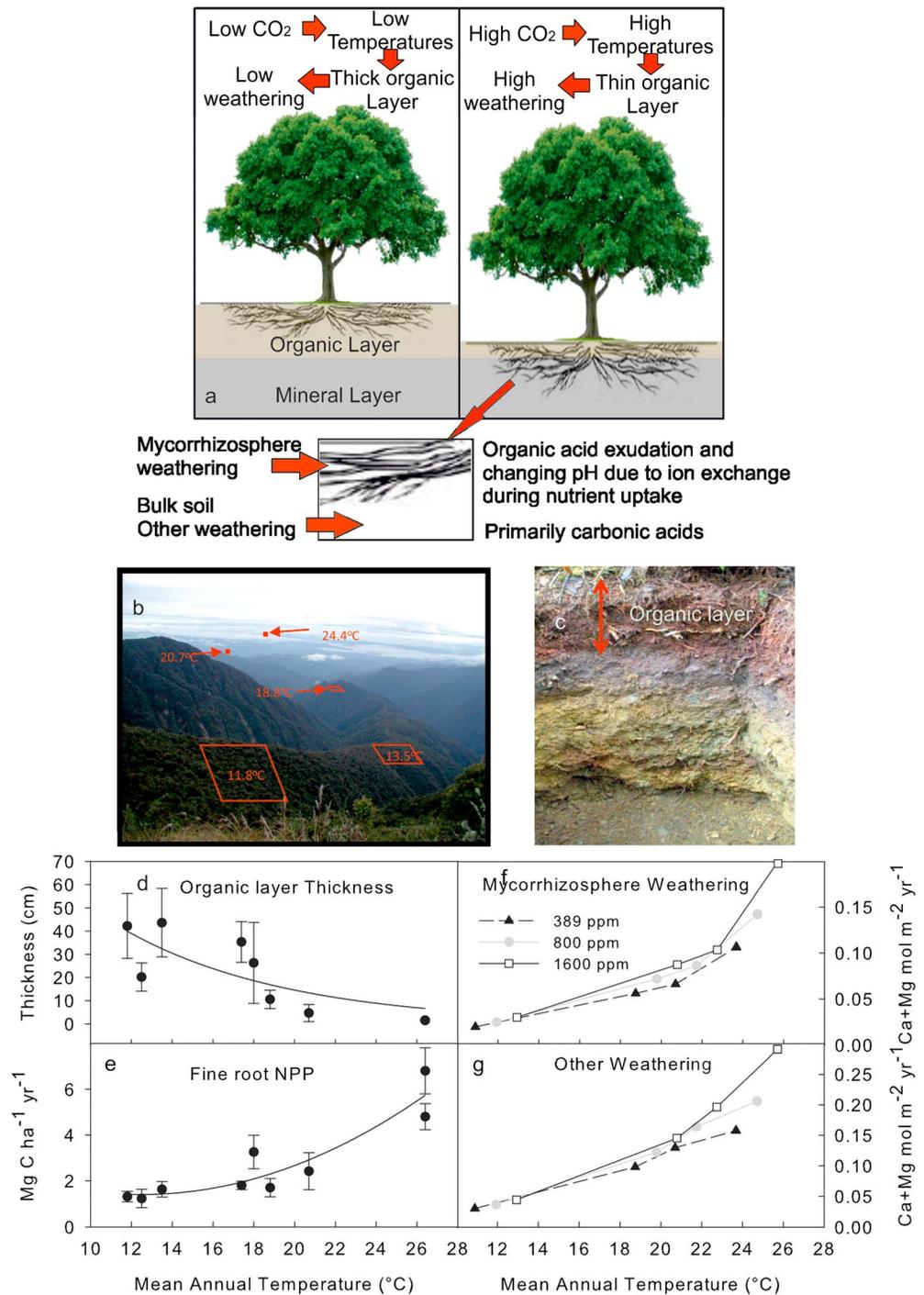


Figure 1. Observed and simulated Peruvian forest biogeochemical processes. (a) A conceptual diagram of a negative weathering feedback. Mycorrhizosphere weathering takes place in the few millimeter surrounding the mycorrhizosphere and collectively increases total weathering by between 14 and 52%, and other weathering, mainly driven by carbonic acids, occurs in the bulk soil. (b) A picture of our field sites showing some of the plots and average temperatures of the plots shown in the red squares. (c) Depth profile of the 3020 m plot (photo C. Quesada). The red arrow represents the organic layer, termed the O-horizon. (d) Organic layer thickness (cm) as a function of average yearly air temperatures ($OL = 802e^{0.23^*T}$, $r^2 = 0.847$). (e) Fine root growth to 30 cm depth ($Mg\ C\ ha^{-1}\ yr^{-1}$) as a function of average yearly air temperatures ($NPP_{fr} = 0.3697e^{0.1002^*T}$, $r^2 = 0.845$). In Figures 1d and 1e, values are means \pm 1 SE. (f and g) A process-based model of weathering rates for a granite substrate based on data from the Peruvian elevation transect at atmospheric CO₂ concentrations of 389, 800, and 1600 ppm. (Figure 1f) Mycorrhizosphere weathering is the difference between weathering computed with and without a chemically distinct mycorrhizosphere. (Figure 1g) Other weathering is an estimate of weathering rates along the transect without a chemically distinct rhizosphere.

(Figure 1b) [Girardin *et al.*, 2010; Malhi *et al.*, 2010; Salinas *et al.*, 2011]. The Peruvian transect has relatively homogeneous soil moisture conditions coupled with a marked mean annual temperature (MAT) gradient of 12.5 to 25°C, which suggests that the temperature is the main driver of changes in forest growth and soil development [Girardin *et al.*, 2010; Salinas *et al.*, 2011].

We use a modeling framework constrained by the observations of the Peruvian transect to investigate and quantify the potential role of montane tropical forests in stabilizing major Cenozoic (CO₂)_a and climate change for two illustrative tectonic events: first, during a major episode of CO₂ degassing with the end-Cretaceous emplacement of the basaltic Deccan traps (65 Myr ago) and second, during increased tectonic uplift of the past 45 Myr [Garzzone *et al.*, 2006; Pagani *et al.*, 2009; Rowley and Currie, 2006]. Our focus is on the Cenozoic, as the time when major clades of tropical forest trees originated and became established [Davis *et al.*, 2005; Wang *et al.*, 2009], including the tropical evergreen angiosperm tree lineages within the Rosids that dominate the Peruvian forests. Tree lineages within these forests form arbuscular mycorrhizal (AM) fungal partnerships that actively weather silicate minerals in soils [Quirk *et al.*, 2012].

2. Materials and Methods

We established nine experimental plots in the southern Peruvian Andes and adjacent lowlands, where we estimated fine root production per unit area and time (Mg C ha⁻¹ yr⁻¹) by allowing roots to grow in 9–16, 30 cm deep cores per plot of originally root-free soil surrounded by mesh, which we collected and counted every three months [Girardin *et al.*, 2010]. In addition, we measured organic layer depth (leaf litter layer and O-horizon comprised exclusively of decomposing plant material with no weatherable material), soil respiration, total net primary production (NPP), and climate with weather stations at three points (3020 m, 1500 m, and 210 m) along the elevation transect. We use the results of those measurements to constrain a process-based “biological proton cycle” model (it accounts for changing H⁺ to predict pH) [Taylor *et al.*, 2011; Taylor *et al.*, 2012] combined with the Sheffield dynamic global vegetation model [Beerling *et al.*, 1997] to simulate growth along the transect under a range of (CO₂)_a from 389 to 1600 ppm (Figures 1f and 1g). This process-based dynamic global vegetation model of terrestrial carbon and nitrogen cycling and the resulting simulated silicate weathering fluxes has produced accurate results when compared with observations from other forested watersheds, including those dominated by AM tropical trees [Taylor *et al.*, 2012].

Field data, such as fine root NPP, organic layer depth, mean monthly temperature, humidity, precipitation, soil moisture, and soil respiration along with (CO₂)_a inform the biological weathering model, which assumes an exponential distribution of fine roots and CO₂ in the soil (total root mass decreases exponentially with depth). Using kinetic rate laws and equilibrium chemistry, the model calculates weathering of silicate rocks (basalt and granite) as a function of temperature, soil pH, and concentration of low molecular weight organic chelators (modeled as oxalate) [Taylor *et al.*, 2011]. Minerals are weathered throughout the soil profile by carbonic and organic acids. However, within a few millimeters of fine roots and their mycorrhizal hyphae (the mycorrhizosphere), weathering is dominated by organic acid exudation and changing pH due to ion exchange during nutrient uptake (Figure 1a). Model runs with and without such a chemically distinct mycorrhizosphere suggest that the mycorrhizosphere increases the total soil weathering flux by 14 to 52%, with the greatest enhancement occurring on granite at high atmospheric CO₂, high temperature, and thin organic layer.

We then compute the global weathering rates by applying our simulations of weathering rates as a function of temperature and organic layer thickness from the transect to areas with elevations exceeding 250 m under two scenarios: (1) increased CO₂ degassing from volcanism during the end-Cretaceous emplacement of the Deccan traps (65 Myr) and (2) during the increased tectonic uplift during the past 45 Myr of the Cenozoic [Garzzone *et al.*, 2006; Pagani *et al.*, 2009; Rowley and Currie, 2006]. We limit these global simulations to igneous areas above 250 m because of the greater abundance of weatherable materials in uplifted regions and call these regions “montane” even though they may consist of plateaus. For each montane pixel, monthly temperature is determined based on climate simulations, elevation, and atmospheric CO₂ concentration. Based on this temperature, we calculate organic layer depth, fine root NPP, and percentage of the roots in the mineral layer. We then estimate weathering rates for each pixel, which we sum globally separating “mycorrhizosphere” (with a chemically distinct mycorrhizosphere) and “other” (without a chemically distinct mycorrhizosphere) weathering (Figures 1f and 1g). Mycorrhizosphere weathering includes only the

organic acid exudation and changing pH that affect weathering within a few millimeter of fine roots and their mycorrhizal hyphae whereas other includes all other types of weathering in the bulk soil solution, but is primarily weathering from carbonic acids (see Supporting Information for further methodological details and Figure 1a).

3. Results and Discussion

Soil organic layer depth sharply decreased with increased mean annual temperatures between the upland and lowland sites across the Peruvian transect indicating organic layer depth is a strongly temperature-dependent ecosystem property (Figure 1d). This thinning of the organic layer led to an estimated ~3-fold increase in the penetration of roots into the mineral layer at the bottom of the elevation gradient versus the top. Measured root growth indicates that the roots do not preferentially grow below the organic layer into the mineral layer to access nutrients (Figure S1 of the Supporting Information). As soil organic layer depth decreased with increased temperatures along the transect, net primary production of fine roots, as measured using soil in-growth cores, increased, due to warmer temperatures and increased growth rates, which further increased the surface area of roots in the mineral layer (Figure 1e). We hypothesize that the depth of the soil organic layer is a potentially important, but largely overlooked, control on biological weathering rates because only fine roots and mycorrhizal fungal networks that reach the mineral layer can contribute directly to weathering (Figure 1a).

Roots take up cations, which will lead to lower rhizosphere pH, enhancing weathering nonlinearly in the few millimeters surrounding the root system. Therefore, the regions surrounding root systems contribute substantially to the total weathering of the soil when these roots are in proximity to weatherable rock materials but not if the roots are growing within the organic layer of the soil (see Supplementary Online Material (SOM) for further details). The lack of primary mineral grains in the upper organic layer (O-horizon) of soils (Figures 1a and 1d) means there is no major weathering in that layer [Rosling *et al.*, 2004]. Root, fungal, and microbial respiration increases the partial pressure of CO₂ throughout the soil profile. Because carbonic acid weathering is not restricted to the mycorrhizosphere, we classify it as other weathering.

The field data were combined with a process-based weathering model to estimate a likely ~5.5-fold increase in biological weathering rates from the top of our elevation gradient to the bottom (not including CO₂ fertilization which could increase weathering by ~50% from 389 ppm to 1000 ppm) (Figure 1f) [Taylor *et al.*, 2011; Taylor *et al.*, 2012]. This is greater than the threefold increase estimated for the Swiss Alps across a narrower altitudinal gradient (2400–220 m above sea level) [Berner *et al.*, 2003]. These modeling results and field site data provide evidence that climate changes across the elevation gradient may moderate the penetration of roots into the soil mineral layer below, thus reducing weathering during cold periods and accelerating it during warm periods.

We used our synthetic modeling framework to assess the contribution of montane forest ecosystems worldwide (further justified in the SOM) to terrestrial weathering of granite and basalt-dominated terrains under a contemporary CO₂ (362 ppm) and modern observational climate (1992–2002). Globally, we estimate weathering on granitic or basaltic montane regions (>250 m above sea level) currently accounts for ~79% of the total weathering flux of Ca and Mg base cations (after correcting for relief and runoff [Taylor *et al.*, 2012]), even though such regions cover only ~7% of the global surface. These results highlight the potential for montane forest ecosystems to exert large effects at the global scale and play a key role in Cenozoic (CO₂)_a and climate stabilization during geotectonic perturbations of the geochemical carbon cycle.

We then investigated the potential feedback of montane forest weathering (i.e., in orographic regions >250 m elevation, see Figure 2a) on (CO₂)_a and climate during the eruption of the basaltic Deccan traps, 65 Myr ago, a major episode of volcanism that added an estimated 1.6×10^{18} moles CO₂ to the atmosphere over a period of ~1.2 Myr [Dessert *et al.*, 2001]. We calculate changes in (CO₂)_a during this period using a simple geochemical carbon cycle model [Dessert *et al.*, 2001] combined with geography, orography and a baseline late-Cretaceous global climate simulation [Pope *et al.*, 2000]. Simulations indicate that the peak (CO₂)_a increased average global temperatures by ~1.73°C which, through increased temperature driven decomposition, decreased the thickness of the soil organic layer globally by an average of ~10%. Our simulations indicate that this decrease in the thickness of the organic layer allowed 19% more fine root NPP in the mineral layer and thereby increased weathering (Figures 2b and 2c). These effects, together with increased forest NPP and geographical extent,

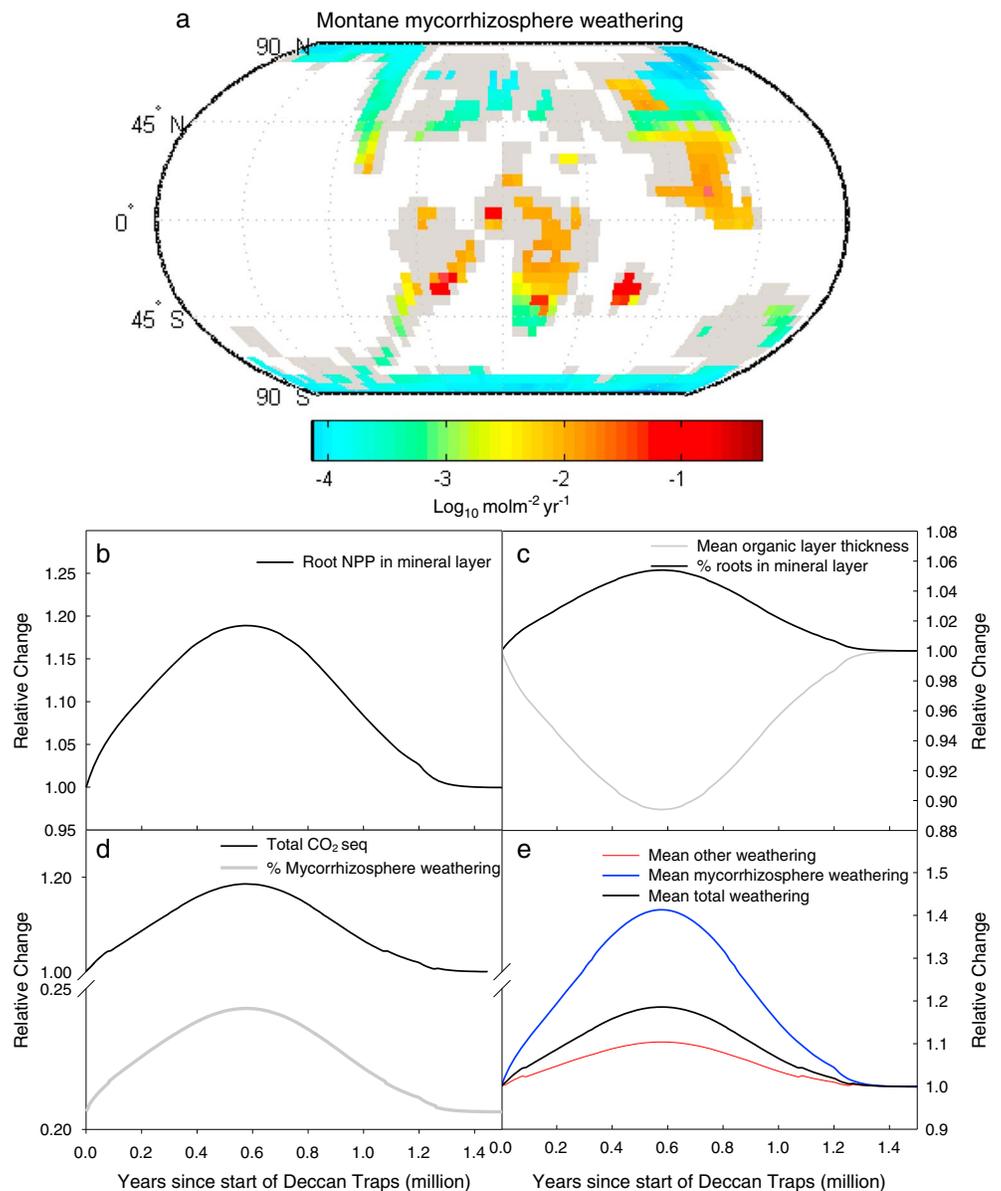


Figure 2. Simulated global forest and other weathering responses to end-Cretaceous volcanism. (a) Map of global montane (>250 m elevation) biological weathering ($\log_{10} \text{ mol Ca} + \text{Mg m}^{-2} \text{ yr}^{-1}$) ~65 Myr ago. (b) Change in global average fine root NPP in the mineral layer (black line) with 1 equal to the levels at ~65 Myr ago. (c) Change in global average organic layer thickness (gray line) and root penetration in the mineral layer (black line). (d) Change in the total CO_2 sequestered (black line) and percent mycorrhizosphere/total weathering (gray line). (e) Change in the global average mycorrhizosphere (blue), other (red), and total weathering (black) over a 1.5 Myr period.

increased biological silicate weathering rates by 42% (40–44%) (Figure 2e). Overall, our simulations indicate that the total global CO_2 sequestered through montane weathering increased by ~19% or 50 ppm Myr^{-1} (Figure 2d). This compares to an estimated 57 ppmv decrease in $(\text{CO}_2)_a$ from increased weathering due to the basalt from the Deccan traps themselves [Dessert *et al.*, 2001]. These simulations suggest that montane forest-driven silicate weathering probably exerted an important stabilizing climate feedback during the eruption of the Deccan traps by increasing the biological component to almost 25% of the total weathering (Figure 2d) and root penetration of the mineral layer by ~20% (Figure 2c), reducing peak $(\text{CO}_2)_a$ and temperatures during the extreme volcanism.

We next simulated the geochemical carbon cycle effects of global montane forest-silicate weathering responses to the uplift of the Himalayas, the Rockies, the Andes, and the New Guinea arc over the past 45 Myr (see red boxes in Figure 3a) [Garziona *et al.*, 2006; Pagani *et al.*, 2009; Rowley and Currie, 2006], assuming a

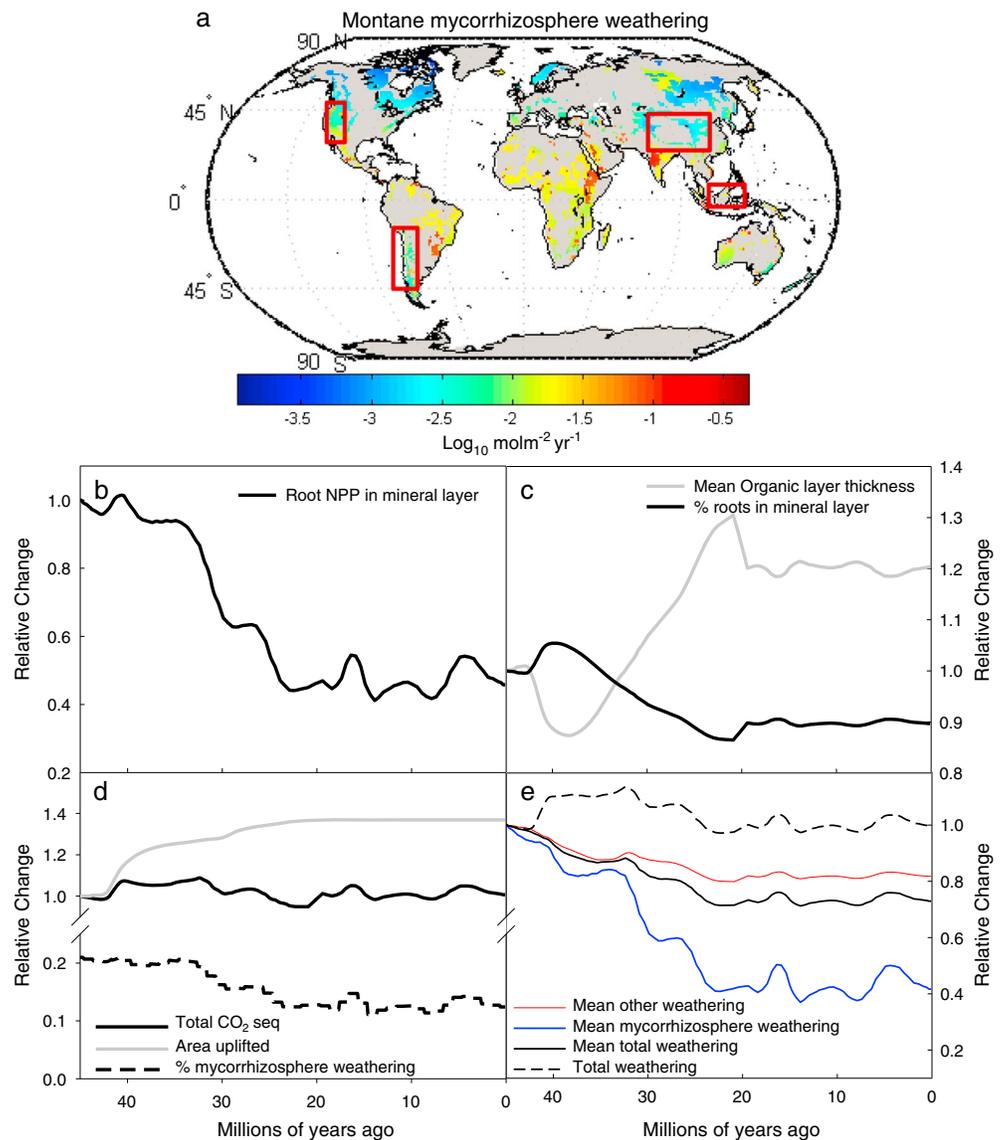


Figure 3. Simulated global forest and abiotic weathering responses to Cenozoic uplift events. (a) Map of current global montane (>250 m elevation) biological weathering ($\text{log}_{10} \text{ mol Ca} + \text{Mg m}^{-2} \text{ yr}^{-1}$). Red boxes show areas of uplift including the Himalaya (uplift from 40 Myr ago and continuing for 20 Myr), the Rockies (40 Myr ago and continuing for 10 Myr), the Andes (25 Myr ago and continuing for 10 Myr), and the New Guinea arc (15 Myr ago and continuing for 5 Myr). (b) Change in the global average fine root NPP in the mineral layer (black line) with 1 equal to the levels at 45 Myr ago. (c) Change in the global average soil organic layer depth thickness (gray line) and root penetration in the mineral layer (black line). (d) Change in the total CO₂ sequestered (black line), the total area uplifted (>250 m) (gray line), and the percent biological/total weathering (black dashed line). (e) Change in the total summed weathering (black stippled line) and per pixel averaged (solid lines) mycorrhizosphere (with mycorrhizosphere, blue), other (without mycorrhizosphere, red), and total (black) weathering rates from (left column) 45 Myr ago to today.

mean initial $(\text{CO}_2)_a$ based on proxy data sets (~1100 ppm) [Beerling and Royer, 2011]. Total uplifted area (>250 m) increased in our model by ~37% (Figures 3a and 3d), leading to more surface area for weathering, CO₂ removal and a 4.2°C decline in MAT in our simulation. Our simulations indicate that falling $(\text{CO}_2)_a$ and a cooling from mountain building slowed soil organic matter decomposition and increased the organic layer depth (Figure 3c), thereby reducing root penetration into the mineral layer (Figures 3b and 3c) and decreasing per pixel biological weathering by 43% (41–46%) (Figure 3e). We estimate that the total summed weathering initially increased by ~10%, leading to a drawdown of $(\text{CO}_2)_a$ as new weatherable material was exposed through uplift, but then stabilized ~20 Myr ago as per pixel weathering rates decreased (Figure 3e). Our simulations indicate that without the effect of the montane vegetation feedback, $(\text{CO}_2)_a$ would have

continued to decline as global weathering rates continued to exceed $(\text{CO}_2)_a$ sources (Figure 3e). Montane forests therefore may have played an important role in stabilizing $(\text{CO}_2)_a$ and climate over the past 45 Myr. Sensitivity analyses indicate that ~50% of the total decrease in weathering in Figure 3b is due to the biological weathering feedback (Figure S6 of the Supporting Information). Although abiotic weathering is a larger percentage of total weathering (initially ~78%) (Figure 3d), biological weathering is much more sensitive to $(\text{CO}_2)_a$ and climate (Figure 3e) leading to important climate stabilizing roles for both.

The strength of the negative feedback (i.e., higher temperatures leading to increased weathering rates) simulated here are partially dependent on how trees allocate their carbon (i.e., whether they allocate fixed carbon toward more leaves or more fine roots) under conditions of stress, such as cold temperatures or low $(\text{CO}_2)_a$. Predicting changing root growth with diminished NPP can be difficult because root growth may respond to precipitation or nutrient status as well as temperature and $(\text{CO}_2)_a$ [Liu and Greaver, 2010; Metcalfe et al., 2008]. To test the sensitivity of our study to different root growth scenarios, we repeated the simulations reported in Figures 2 and 3 (Figures S4 and S5 of the Supporting Information) assuming 50% of the area is dominated by regions where root growth decreases with warmer temperatures. However, we obtain broadly similar results as before because decreasing temperatures caused the soil organic layer to thicken, thereby preventing additional root growth from penetrating into the mineral layer. Moreover, any $(\text{CO}_2)_a$ fertilization would further strengthen the negative climate feedback by increasing the total NPP available for root growth. This indicates that the changing organic layer depth plays a larger role in climate stabilization than changing fine root NPP. The decrease in organic layer depth with increased temperatures occurs because although leaf production at the bottom of the elevation gradient is ~double that at the top, the residence time of litter is ~4 times less [Salinas et al., 2011], which leads to the depletion of organic material. In addition, processes of organic matter production and associated autotrophic respiration are generally less sensitive to warmer temperatures than heterotrophic respiration, which drives further reductions in organic soil thickness [Kerckhoff et al., 2005].

Our simulations highlight the important yet previously overlooked role that the decomposition of the organic layer could have played in buffering global Cenozoic geochemical carbon cycle perturbations. Decomposition processes have previously been shown to impact weathering rates as warmer conditions increase dissolved organic carbon release from decomposition, influencing soil pH, and dampening the feedback between productivity and weathering [Banwart et al., 2009]. However, we have demonstrated a different process where cooler temperatures slow decomposition, allowing a thick litter layer to accumulate which may prevent roots from actively weathering rocks in the mineral layer of soils. This negative feedback is likely to be robust both spatially and temporally because it is dependent on decomposition processes that are largely environmentally driven [Salinas et al., 2011] and stable through time [Robinson, 1990].

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