Bedrock composition regulates mountain ecosystems and landscape evolution

W. Jesse Hahm[1], Clifford S. Riebe[1], Claire E. Lukens, and Sayaka Araki

Department of Geology and Geophysics, University of Wyoming, Laramie, WY 82071

Edited by Peter M. Vitousek, Stanford University, Stanford, CA, and approved December 20, 2013 (received for review August 24, 2013)

Earth's land surface teems with life. Although the distribution of ecosystems is largely explained by temperature and precipitation, vegetation can vary markedly with little variation in climate. Here we explore the role of bedrock in governing the distribution of forest cover across the Sierra Nevada Batholith, California. Our sites span a narrow range of elevations and thus a narrow range in climate. However, land cover varies from Giant Sequoia (*Sequoiadendron giganteum*), the largest trees on Earth, to vegetation-free swaths that are visible from space. Meanwhile, underlying bedrock spans nearly the entire compositional range of granitic bedrock in the western North American cordillera. We explored connections between lithology and vegetation using measurements of bedrock geochemistry and forest productivity. Tree-canopy cover, a proxy for forest productivity, varies by more than an order of magnitude across our sites, changing abruptly at mapped contacts between plutons and correlating with bedrock concentrations of major and minor elements, including the plant-essential nutrient phosphorus. Nutrient-poor areas that lack vegetation and soil are eroding more than two times slower on average than surrounding, more nutrient-rich, soil-mantled bedrock. This suggests that bedrock geochemistry can influence landscape evolution through an intrinsic limitation on primary productivity. Our results are consistent with widespread bottom-up lithologic control on the distribution and diversity of vegetation in mountainous terrain.

erosion rates | bedrock weathering | critical zone | forest distribution

Vegetation captures solar energy and sends it cascading through ecosystems, creating habitats for other organisms and fixing nutrients and carbon from the atmosphere. Vegetation also plays an important although still incompletely understood role in the breakdown and erosion of rock (1–3) and thus the evolution of Earth's topography (4). Understanding the factors that determine where vegetation thrives—and where it does not—is therefore fundamental to many disciplines, including ecology, geomorphology, geochemistry, and pedology. As a substrate for life, lithology can influence overlying vegetation, spurring endemism due to the presence of toxins (5, 6) and limiting productivity where rock-derived nutrients are scarce (7–9). However, lithologic effects on vegetation are generally considered secondary to climatic factors such as the length of the growing season and the amount of moisture available for plant growth (10). Here we show that bedrock composition can drive differences in vegetation on par with the systematic altitudinal differences found in mountains between their hot, dry foothills and cold, wet alpine summits.

Evidence for Bottom-Up Regulation of Vegetation

Our study area, the Sierra Nevada Batholith, is a collection of geochemically diverse but genetically related plutons that form the core of California's most prominent mountain range (Fig. 1 *A*–*D*). The Sierra Nevada exhibits sharp altitudinal contrasts in vegetation (Fig. 1*B*): starting in the west at low elevations and moving east and upward, discontinuous oak woodlands grade into dense conifer forests and finally to nearly barren alpine slopes, consistent with gradients in temperature and moisture (Fig. 1*E*). Primary productivity and evapotranspiration are optimized at midelevations, reflecting a tradeoff between decreasing temperature and increasing precipitation with altitude (15). However, even at the highly productive midelevations, vegetation varies markedly without major differences in climate. For example, Giant Sequoia, the largest trees on Earth, grow in groves adjacent to barren patches where soil is absent and bedrock is exposed (Fig. 1 *C* and *D*). The bare and vegetated areas lie at similar elevations, ruling out altitudinal differences in climate as a plausible explanation for the variations in canopy cover (Fig. 1*E*). Rather, it appears that vegetation is strongly influenced by underlying bedrock; the contacts between different plutons (13, 14) often coincide with sharp ecotones between densely forested, soil-mantled slopes and sparsely vegetated, mostly soil-free bedrock (Fig. 1 *C* and *D*).

Other factors besides lithology fail to explain observed differences in vegetation. For example, Shuteye Peak, Bald Mountain, and Snow Corral Meadow were not glaciated in the Pleistocene (12). However, today they stand largely devoid of vegetation (Fig. 1 *C* and *D*). Moreover, we observe no evidence of recent high-intensity fire or widespread anthropogenic disturbance that might explain the variable presence–absence of vegetation and soil (*SI Text*). To rule out local variations in climate and topography as possible explanations, we polled the Kings and San Joaquin watersheds for areas that have the same multivariate probability distribution of elevation, aspect, and slope as the Bald Mountain Granite (Fig. 1*D*), which is exposed immediately next to the Southern Sierra Critical Zone Observatory (CZO). Thus, we sampled the landscape outside a prominent bald spot in a way that mimics the underlying pluton as closely as possible in climatic and topographic factors that might influence overlying vegetation and soil. If these factors were important in explaining the differences shown in Fig. 1*D*, then the sampled outlying area would closely resemble the Bald

Significance

This investigation focused on the factors that influence forest cover in the Sierra Nevada, California, where Giant Sequoia, the largest trees on Earth, grow in groves immediately next to expanses of rock devoid of soil and vegetation. The differences in forest cover correspond to twofold differences in erosion rates, suggesting that vegetation is an important regulator of landscape evolution across the region. Analyses presented here show that differences in forest cover can be explained by variations in geochemical composition of underlying bedrock. These results are important because they demonstrate that bedrock geochemistry is on par with climate as a regulator of vegetation in the Sierra Nevada and likely in other granitic mountain ranges around the world.

Author contributions: W.J.H. and C.S.R. designed research; W.J.H., C.S.R., C.E.L., and S.A. performed research; W.J.H. contributed new analytic tools; W.J.H., C.S.R., C.E.L., and S.A. analyzed data; and W.J.H. and C.S.R. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1] To whom correspondence may be addressed. E-mail: whahm@uwyo.edu or criebe@uwyo.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1315667111/-/DCSupplemental.

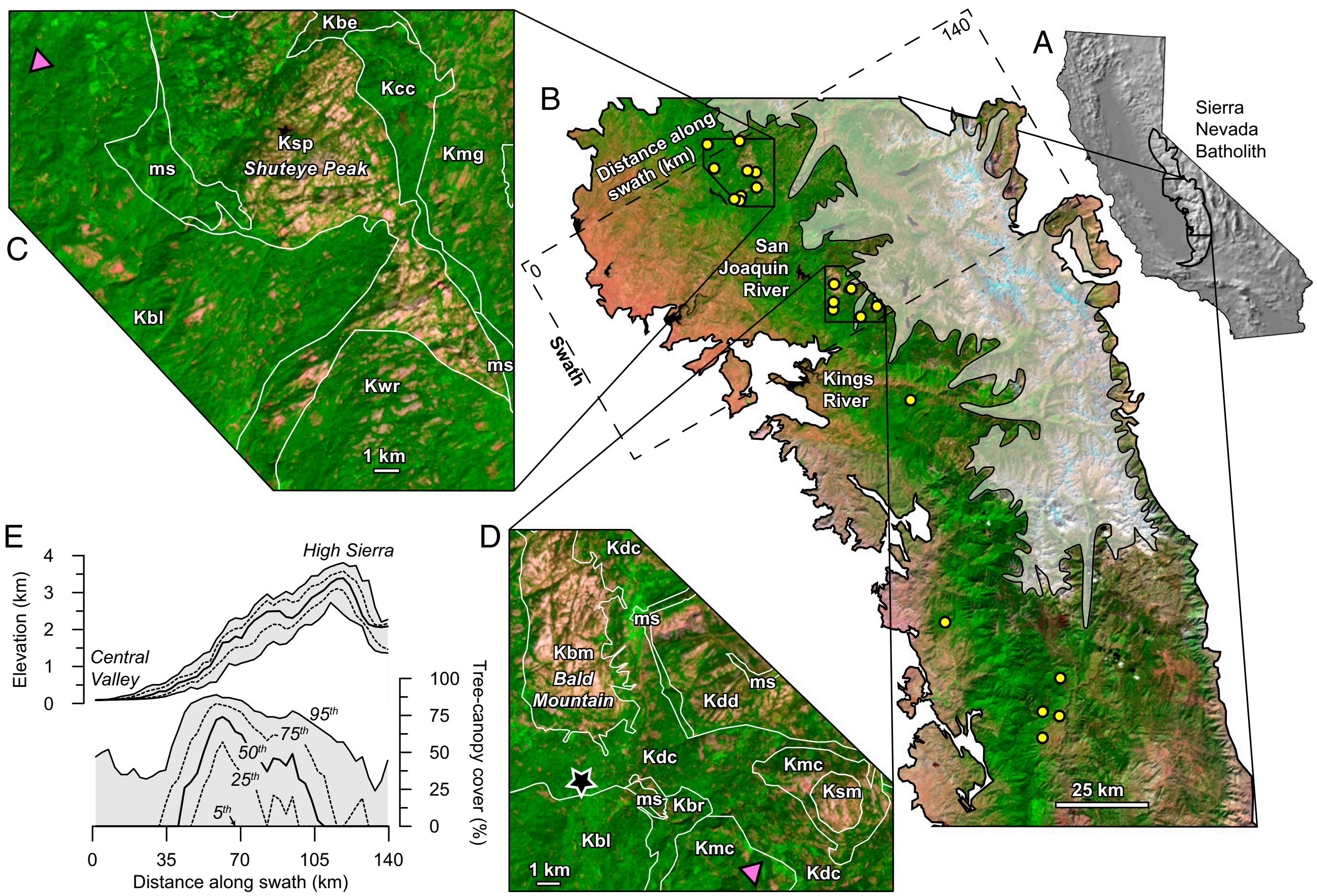

Fig. 1. Vegetation, climate, and bedrock of Sierra Nevada study sites. (*A*) Shaded-relief map of California with Sierra Nevada Batholith (outlined in black; after ref. 11). (*B*) False-color Landsat mosaic (*SI Text*) of central Sierra Nevada Batholith showing sharp altitudinal contrasts in vegetation. Bedrock sampling sites (circles) lie outside the limits of Pleistocene glaciation (transparency; after ref. 12). (*C* and *D*) Detailed view of two sampling regions showing simplified bedrock contacts (lines; after refs. 13 and 14), which often separate sparsely and densely canopied plutons. Triangles mark Giant Sequoia groves; star marks Southern Sierra CZO. Letters denote rock types: Granites (Bald Mountain, Kbm; Shuteye Peak, Ksp; Snow Corral Meadow, Ksm; Bear Creek, Kbr; Dinkey Dome, Kdd); Tonalites (Bass Lake, Kbl); Granodiorites (Dinkey Creek, Kdc; Whiskey Ridge, Kwr; Beasore Meadow, Kbe; Camino Creek, Kcc; Mount Givens, Kmg; McKinley Grove, Kmc); Metasediments (ms). (*E*) Typical range-perpendicular trend in elevation and tree-canopy cover with labels showing percentiles of values observed at each distance along the swath shown in *B*.

Mountain pluton in tree-canopy cover. However, we find that just 10% of the outlying area is bare, compared with roughly 45% of the Bald Mountain Granite (Fig. S1). Thus, we can be reasonably certain that differences in the underlying plutons—not elevation, slope, or aspect—govern the sharp contrast in vegetation shown in Fig. 1*D*.

Possible Lithologic Controls on Vegetation

Several physical and chemical properties of bedrock could act as bottom-up regulators of the distribution of vegetation, including (*i*) toxin concentrations, which could inhibit growth; (*ii*) concentrations of rapidly weatherable minerals, which could influence porosity generation in regolith; (*iii*) concentrations of clay-forming primary minerals, which could affect the retention of plant-available nutrients and water; (*iv*) nutrient concentrations, which could limit plant growth; and (*v*) fracture density, which could govern access to water, nutrients, and anchor points for roots. These properties influence the hydrology or chemistry (or both) of regolith and hence are possible contributors to lithologic regulation of overlying vegetation. Next we discuss how each of these properties varies with vegetation across a lithosequence in the western Sierra Nevada. We show that the available evidence is consistent with a bottom-up control of vegetation by bedrock composition.

Bedrock Geochemistry. To explore connections between vegetation and bedrock geochemistry, we collected 235 samples of bedrock from 21 sites and measured bulk geochemistry using X-ray fluorescence (Fig. 1*B* and *Methods*). The geographic coordinates of our samples allowed us to pair the geochemical results with remotely sensed tree-canopy cover from the National Land Cover Database (16). Tree-canopy cover reflects leaf area, which should correspond with primary productivity, as long as the canopy is partly open to the sky (i.e., not saturated in its leaf cover). This is the case across much of the Sierra Nevada (17) and all of our study sites (Fig. 1*E*). The assumed connection between forest productivity and tree-canopy cover is corroborated by stand-scale estimates we made of primary productivity from tree rings and biomass at two sites (Fig. 2 for locations; *SI Text* and Datasets S1 and S2).

Our analyses show that rocks underlying the bare and vegetated areas have starkly different bulk geochemistry. For example, phosphorus in individual samples varies by a factor of 20 across the sites (Dataset S3). Moreover, geochemical differences between plutons are large compared with differences within them; for example, both in the CZO vicinity and elsewhere, bedrock P concentrations change abruptly at boundaries between rock types, where vegetation contrasts are likewise sharp (Fig. 2). Moreover, the sparsely vegetated Bald Mountain Granite (Kbm) has seven times less bedrock P than the neighboring,

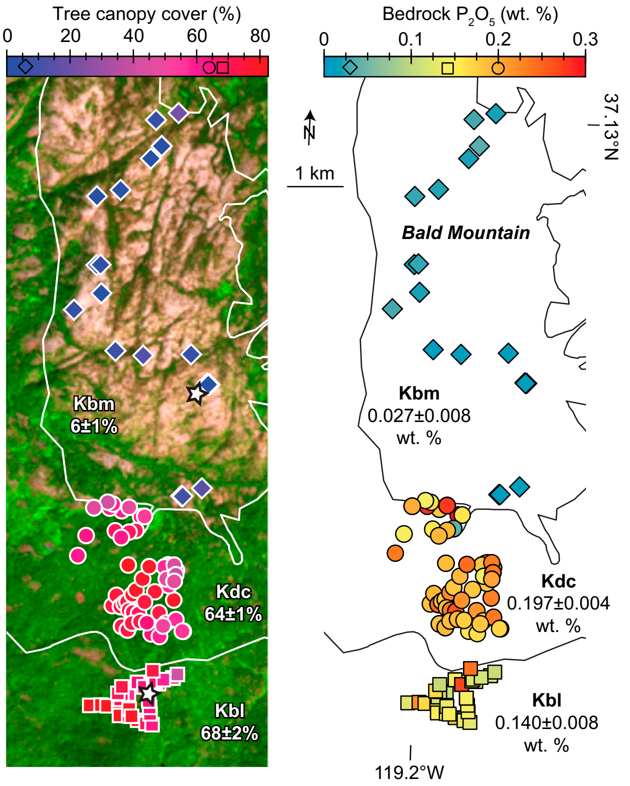

Fig. 2. Distribution of vegetation across bedrock with differing phosphorus content. (*Left*) False-color Landsat image of CZO vicinity with georeferenced bedrock contacts from simplified geologic map shown at *Right* (after ref. 14). Symbol colors match colorbar scales of Landsat-derived, remotely sensed tree-canopy cover (16; Dataset S3 and *SI Text*), a proxy for primary productivity (*Left*), and bedrock P concentrations (*Right*). Vegetated–unvegetated ecotone coincides with boundary of Bald Mountain Granite (Kbm; diamonds), a desert in bedrock P relative to more heavily forested Dinkey Creek Granodiorite (Kdc; circles) and Bass Lake Tonalite (Kbl; squares). Labels show average (±SEM) tree-canopy cover (*Left*) and bedrock P concentration (*Right*) by rock type. Stars at *Left* pinpoint productivity surveys (*SI Text*).

heavily vegetated Dinkey Creek Granodiorite (Kdc; Fig. 2 and Dataset S4).

The strong bedrock control of vegetation near the CZO (Fig. 2) prevails across our entire lithosequence of midelevation sites (Fig. 3). Tree-canopy cover varies from 6% to 81% on average but is uncorrelated with average temperature and precipitation (Fig. S2 and Dataset S4). Instead, differences in vegetation can be explained by differences in bulk geochemistry of bedrock. Site-wide average concentrations of Si, Al, Fe, Ca, K, Mg, and P in bedrock are all significantly correlated with average tree-canopy cover (Fig. 3); Si, Fe, and Ca have the largest absolute ranges (>5 wt % oxide; Fig. 3), whereas Mg and P have the largest relative ranges, differing by up to 50-fold in concentration across the sites (Fig. S3). In contrast, trace elements As, Se, and Cd, which are toxic to plants in high concentrations (18), do not explain observed contrasts in canopy cover (Dataset S4).

The overlay of geologic maps and Landsat imagery reveals sharp differences in vegetation across bedrock contacts (Figs. 1 and 2), consistent with a threshold response. In contrast, the correlations that emerge across the entire lithosequence are consistent with a continuous gradient in vegetation with changes in bedrock composition. These correlations explain up to ~60% of the variance in tree-canopy cover (Fig. 3), indicating that bedrock composition is a dominant explanatory variable. The unexplained variance may reflect many factors including differences in response to natural and anthropogenic disturbances, which were not accounted for in our analysis.

Bedrock Mineralogy and Weathering. The correlations between geochemistry and canopy cover point to several possible mechanisms of bedrock control on vegetation. Mineralogy covaries strongly with bedrock geochemistry (Fig. S4 and Dataset S5) in ways that might account for differences in weathering (19), subsurface water-holding capacity, and thus the regolith's suitability as a substrate for vegetation (20). Increases in Si concentrations correspond to increases in quartz and K-feldspar concentrations and decreases in both plagioclase content and color index, a measure of mafic minerals (21; Fig. S4). Quartz and K-feldspar are more resistant to weathering than plagioclase (22, 23), and weathering of the mafic mineral biotite has commonly been implicated in the disaggregation of granitic bedrock (19, 24). Thus, decreasing canopy cover with increasing Si concentrations (Fig. 3) could reflect differences in weathering, which could influence subsurface porosity and rates of soil production. In addition, the decrease in plagioclase, biotite, and hornblende with increasing Si across our sites suggests that the production of clay via weathering of these minerals may be positively correlated with canopy cover. If so, it would be consistent with clay-content control of nutrient and water retention.

Nutrient Concentrations in Bedrock. In addition to producing secondary minerals, weathering also liberates plant-essential nutrients into soil solution (25). Many nutrients including P are derived exclusively from minerals. Among the mineral-derived macronutrients that are essential for plants, P is required in the highest concentrations relative to its abundance in the upper continental crust (26, 27; Table 1). Thus, P is the most common rock-derived limiting nutrient in terrestrial ecosystems (28). It has recently been proposed that P limitations can arise because of low P in underlying bedrock in eroding landscapes (25, 29, 30). Across our sites, bedrock P concentrations span more than an order of magnitude (Dataset S3) and correlate strongly with tree-canopy cover (Figs. 2 and 3). This is consistent with a widespread phosphorus limitation; although P makes up less than one part per thousand of bedrock underlying our sites, it may regulate ecosystem productivity and vegetation distributions at the scale of the entire batholith (Fig. 1 *B* and *E*). If this were the case, it would be evidence for a previously unidentified but nevertheless widespread intrinsic (i.e., bedrock-related) P limitation; previous examples of P limitations have been linked to chemical leaching processes that deplete bedrock of nutrients (e.g., 31, 32), not the initial composition of the bedrock. Such an intrinsic limitation, if present, could be more definitively documented via fertilization experiments performed along the lithosequence.

Density of Bedrock Fractures. Higher bedrock fracture density could promote vegetation by providing footholds for roots and reservoirs for water storage (20, 33). Thus, differences in fracture density could help explain the lithologic control of vegetation shown in Fig. 3. However, for this to be the case, fracture density would need to correlate strongly with bedrock geochemistry. Fracture production in the Sierra Nevada has been attributed to variations in grain size (34); dike occurrence (35); volatile expulsion (36); frost cracking (37); and thermal, topographic, and regional stresses (38–40). The relative importance of these mechanisms in different plutons is a subject of active research. None of them has ever been linked to bedrock geochemistry in a way that would explain Fig. 3 (*SI Text*). However, we cannot rule out control of vegetation by fractures in the absence of fracture density measurements across the sampling sites.

Bedrock–Regolith Connections. Our analysis exposes a widespread bottom-up control of lithology on the distribution of vegetation in the Sierra Nevada. Mechanistically, the connection presumably occurs in weathered bedrock (i.e., regolith), where nutrients and water are accessible to plants. Hence the strong plant–bedrock connection shown in Fig. 3 is likely filtered through regolith. This would be consistent with the well-established, crucial role of deep regolith in sustaining ecosystems in California's granitic mountain

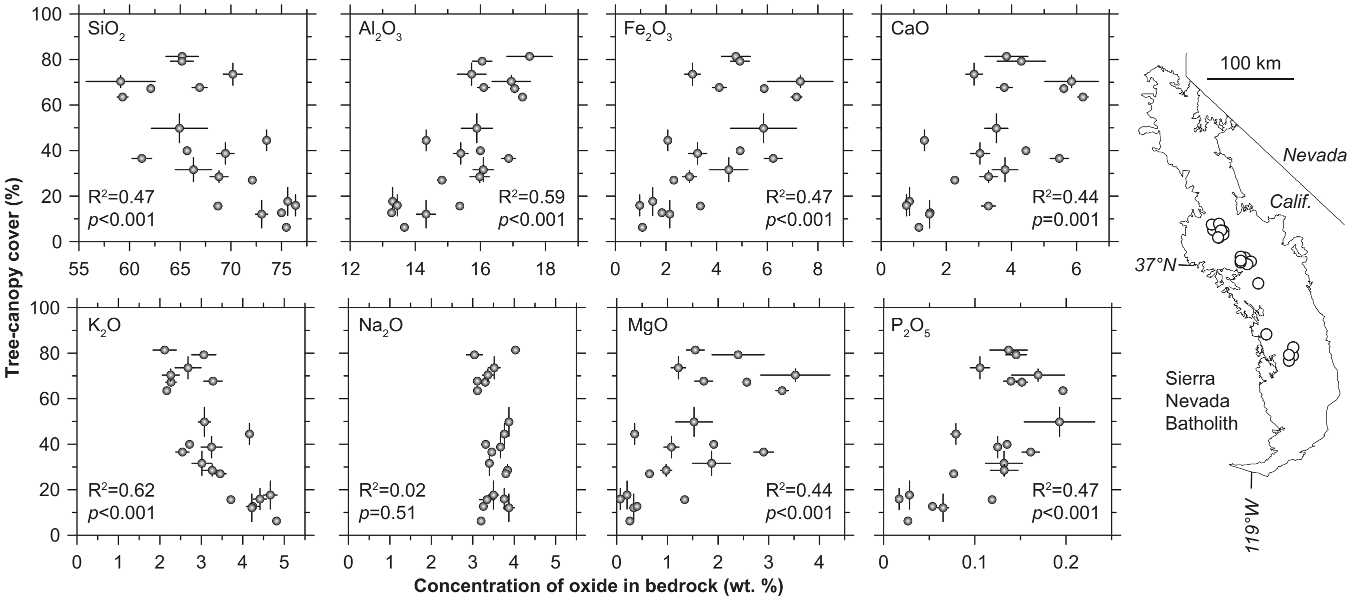

Fig. 3. Vegetation correlates with bulk geochemistry. Site-wide average tree-canopy cover covaries with average bedrock composition for all elements shown except Na. Error bars are ±SEM. Labels show coefficients of determination (R^2) and *P* values on the correlations based on two-tailed *t* tests (Dataset S4). Sites span a 186 km lithosequence (*Right*) of similar elevation and climate through plutons ranging from tonalite to granite.

ranges; studies have shown that plant roots often receive nutrients and water from mycorrhizal fungi at depth (41) and that ecosystem productivity can persist on deep water stores during the summer dry season, long after shallow soils are dry (15, 17, 33, 42).

Regolith nutrient content and water-holding capacity could vary as a function of bedrock composition (e.g., 43) and thus explain the correlations in Fig. 3, but the functional relationships have rarely been documented in granitic landscapes. There is some indication from the vicinity of the CZO that variations in regolith can be high within a single geochemically homogeneous pluton. For example, seismic refraction surveys indicate that depth-integrated regolith water-holding capacity can vary by more than an order of magnitude in the space of 100 m on a single slope (44). This intrapluton variability appears to be widespread based on road cuts in the area. Hence, unless differences between plutons are very large, they will be difficult to detect without analyses that average over intrasite variability in regolith water-holding capacity. Nevertheless, catchment-scale surveys of water fluxes and subsurface properties (from geophysical surveys and drilling) should help determine whether bedrock composition is an important regulator of regolith water-holding capacity. In addition, fertilization experiments and measurements of plant-accessible nutrients should determine the extent to which regolith nutrient content is regulated by bedrock composition. However, it will be important in any such analysis to account for top-down biotic influences (e.g., nutrient cycling and soil retention), which may otherwise obscure bottom-up effects of bedrock composition.

Table 1. Nutrients in Earth's crust and conifer foliage

Element	Concentration in continental crust (mg g^{-1}) (27)	Relative weight in plants (26)	Ratio plant:crust
P	0.67	10	15
S	0.95	5	5.2
K	28.6	35	1.2
Mg	13.5	4	0.3
Ca	29.5	2.5	0.1

Weight relative to weight of N in spruce foliage from laboratory and field experiments where nutrients were not limiting (26).

Implications for Landscape Evolution

Whatever their cause, the variations in vegetation across the lithosequence likely result in differences in geomorphic processes and thus landscape evolution (4). For example, increases in forest cover might cause systematic variations in soil retention (45) and bedrock weathering (2) due to differences in rooting and organic ligand release (1). This should lead to differences in soil production and erosion by chemical, physical, and biological processes (46). Cosmogenic nuclides in quartz from bedrock surfaces and stream sediment help quantify these relationships (*Methods* and *SI Text*). Across our sites, bedrock catchments and surfaces with little overlying vegetation and soil are eroding more than two times slower on average than more densely canopied, soil-mantled areas (Fig. 4). This difference persists across catchments spanning a range of average hillslope gradients, from 6 to 33° (Fig. S5), evidently because exposed bedrock weathers slower than bedrock covered by soil in the Sierra Nevada (19, 48). Previous cosmogenic nuclide studies of other granitic landscapes (e.g., 47) have shown that this is common (Fig. 4). Over time, such differences in erosion rates should cause relief change, leaving soil-free bedrock as highpoints in the landscape, consistent with the observation that barren patches are often higher than their surroundings in the western Sierra Nevada (Fig. 1 *C* and *D*). Hence, the lithological contrasts that drive the presence and absence of soil evidently provoke a weathering limitation on landscape evolution (in the sense of ref. 49) as well as a productivity limitation on ecosystems (Fig. 3). This is consistent with a geochemically mediated biotic control on erosion rates that may reflect differences in bedrock P concentrations; the bare, slowly eroding Shuteye Peak, Snow Corral Meadow and Bald Mountain plutons (Fig. 1 *C* and *D*) have P concentrations roughly five times lower than the average continental crust (Fig. 2; cf. Table 1 and Dataset S4). If deficiencies in bedrock P inhibit vegetation and soil at these sites, it would imply that a minor component of the bedrock has significant influence on pluton-scale landscape evolution.

Lithologic Control of Vegetation in Other Landscapes

We interpret the correlations in Fig. 3 and the differences in Fig. 4 to reflect the fundamental role of bedrock composition in governing distributions of vegetation and patterns of landscape evolution within the sampled midelevation climate zone. The intrinsic geochemical diversity that apparently influences vegetation and erosion at the surface today arose roughly 100 million years ago due to magmatic processes that distributed rock-forming elements along an active arc during the convergence of the Farallon and North American plates (13). The entire batholith shares this common intrusive origin. Thus, it seems likely that bedrock composition is an important regulator of vegetation and erosion elsewhere in the Sierra Nevada. If so, then the relationships identified here may have implications for predicting the upward (and thus eastward) migration of vegetation under a warming climate (50). The long-recognized eastward increase in bedrock K concentrations across the batholith (13) implies that plutons at higher elevations may be less habitable (Fig. 3) than plutons within the current altitudinal optimum for ecosystem productivity (Fig. 1*E*). If so, it could influence future distributions of snowpack and the timing of snow melt and runoff (e.g., 51) from a mountain range that collectively supplies roughly 10% of the US population with vital water resources (52).

The plutons sampled in our study span nearly the entire compositional range of the granitic core of the western North American cordillera (Fig. 5). This broad group of rocks shares a subduction-related origin with the Sierra Nevada Batholith (53), implying that mountains throughout the western United States, Canada, and Mexico may manifest the lithologic effects identified here. Globally, plutonic rocks like those in Fig. 5 underlie 5.7% of the land surface (55) and are especially concentrated in mountain ranges. Thus, the control of ecosystem productivity and landscape evolution by bedrock composition may be widespread in mountain landscapes around the world.

Connections between bedrock and overlying vegetation have been recognized for hundreds of years and underpin many publications on species distributions and endemism in different lithologies (5). For example, so-called “serpentine syndrome,” which occurs in ultramafic rocks with high Mg concentrations, manifests in sparse, stunted forests dominated by species unique to serpentinite (6). Meanwhile, low bedrock P has been implicated in the nutrient-limited fynbos ecosystem of South Africa (8) and some vegetation-free bedrock of the Colorado Plateau (7); each of these nutrient-limited landscapes are developed on quartz arenites with P concentrations similar to the barren granite in Fig. 1 *C* and *D*. However, in granitic terrain, the evidently crucial role of lithology in regulating pedogenesis, erosion, weathering, and ecosystem development has gone undetected until now, perhaps because previous studies have largely focused on quantifying effects of gradients in climate, tectonics, and time (e.g., 15, 56–59). Here, we held these state factors (60) constant across a lithosequence of varying granitic bedrock. We detected connections between bedrock geochemistry, vegetation, and landscape evolution across the lithosequence by coupling old and new datasets of georeferenced climate, topography, geology, geochemistry, landscape erosion, and remotely sensed vegetation.

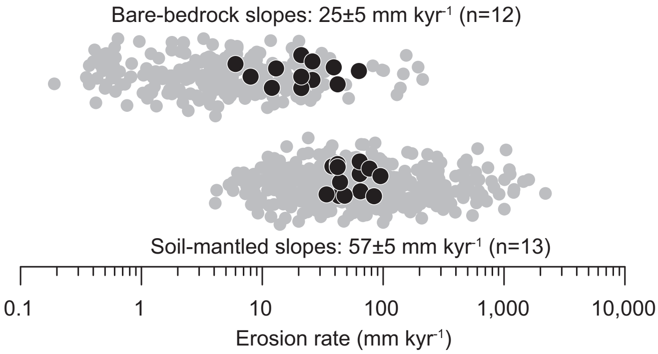

Fig. 4. Erosion rates versus land cover. A global compilation of cosmogenic nuclide data (gray, after ref. 47) demonstrates that erosion from soil-mantled granitic terrain (*Bottom*; $n = 416$) is typically faster than it is from exposed granitic bedrock (*Top*; $n = 250$). This is consistent with cosmogenic nuclides in samples from the Sierra Nevada study region (black, with labeled averages ± SEM and number of samples); erosion is more than two times faster on average in soil-mantled terrain (*Bottom*) than it is in bare rock (*Top*). Erosion rates (Datasets S6 and S7) are jittered to display their distributions.

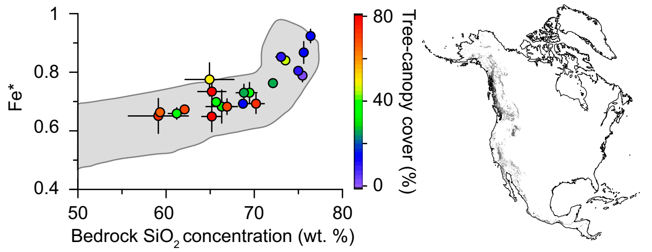

Fig. 5. Bedrock composition of study sites (circles) and cordilleran granites (gray) of western North America. Average (±SEM) bedrock Fe*, defined as total FeO/(total FeO + MgO), versus average (±SEM) SiO_2 for study sites (color shows mean tree-canopy cover). Shading in plot shows inner 95% of 538 analyses (after ref. 53) of plutonic rocks in North America’s western mountain ranges (map, after ref. 54). Our lithosequence spans nearly the entire compositional range of granitic bedrock in the cordillera.

Conclusions

The connections between bedrock composition and surface processes are strong enough to produce differences in vegetation that can be seen from space (Fig. 1 *B*–*D*) and moreover are as large as the differences that arise from altitudinal variations in climate across an entire mountain range (Fig. 1*E*). Thus, they have the potential to obscure or distort trends in chrono-, climo-, and toposequence studies of ecosystems and landscape processes. In the Sierra Nevada, large vegetation differences apparently arise due to compositional differences across granitic rock types that have traditionally been regarded as a geochemically homogeneous class of bedrock in state-factor studies of landscape processes. Our results suggest that such studies can minimize confounding variations by choosing sites with a narrow range in bedrock composition. Alternatively, the effects of lithology on vegetation and erosion can be quantified and thus accounted for using the approach outlined here. We found hitherto undetected connections among bedrock composition, mountain ecosystem productivity, and landscape evolution across the Sierra Nevada Batholith. Evidence presented here shows that these connections are strong, underscoring the need for a better understanding of how life and landscapes are linked across lithosequences of variable bedrock composition.

Methods

Linking Bedrock Geochemistry, Mapped Geology, and Forest Cover. We sampled fresh bedrock by sledgehammer or drill and quantified bulk geochemistry via X-ray fluorescence. Sample locations were georeferenced with digitized geologic maps (13, 14) and a raster of tree-canopy cover based on Landsat 5 and 7 imagery (16). Thus, we paired bedrock geochemistry with mapped geology and tree-canopy cover (Figs. 1, 2, 3, and 5). Our analysis of climatic and topographic effects on tree-canopy cover (Figs. S1 and S2) was based on 10-m elevation data and climate data from ref. 61.

Measuring Long-Term Average Erosion Rates. We used cosmogenic ^{10}Be in quartz from soil-mantled and exposed-bedrock slopes to measure millennial-averaged erosion rates (62). We used University of Wyoming (UW) facilities to purify quartz, dissolve it, and separate Be for analysis. ^{10}Be/^{9}Be ratios were measured by accelerator mass spectrometry (see *SI Text*). We corrected ^{10}Be production rates for latitude and mass shielding due to the atmosphere, topography, biomass, and snow. Inferred denudation rates were corrected for effects of chemical erosion (63).

ACKNOWLEDGMENTS. We thank C. Bechtel, A. Dosseto, B. Jessup, J. Jessup, M. Johnson, H. Rogers, and M. Smith for field assistance; M. Cargill, N. Swoboda-Colberg, B. Jessup, T. O'Flannigan, J. Schmidt, S. Swapp, D. Tinker, R. Valenzuela, and W. White for laboratory assistance; and B. Cubrich, K. Ferrier, R. Frost, D. Granger, B. John, A. Kelly, R. Mahon, T. Minckley, H. Rogers, L. Sklar, C. Wilkin, and anonymous reviewers for constructive comments. This work was funded by National Science Foundation Grants EAR 0725097 and 1239521 (to C.S.R.) and a UW Shlemon Scholarship (to W.J.H.)

1. Drever JI (1994) The effect of land plants on weathering rates of silicate minerals. *Geochim Cosmochim Acta* 58(10):2325–2332.
2. Roering JJ, Marshall JA, Booth AM, Mort M, Jin Q (2010) Evidence for biotic controls on topography and soil production. *Earth Planet Sci Lett* 298(1-2):183–190.
3. Brantley SL, et al. (2011) Twelve testable hypotheses on the geobiology of weathering. *Geobiology* 9(2):140–165.
4. Dietrich WE, Perron JT (2006) The search for a topographic signature of life. *Nature* 439(7075):411–418.
5. Kruckeberg AR (2004) *Geology and Plant Life: The Effects of Landforms and Rock Types on Plants* (Univ of Wash Press, Seattle).
6. Brady KU, Kruckeberg AR, Bradshaw HD, Jr. (2005) Evolutionary ecology of plant adaptation to serpentine soils. *Annu Rev Ecol Evol Syst* 36(1):243–266.
7. Neff JC, Reynolds RL, Sanford RL, Jr., Fernandez DP, Lamothe P (2006) Controls of bedrock geochemistry on soil and plant nutrients in southeastern Utah. *Ecosystems* 9(6):879–893.
8. Soderberg K, Compton JS (2007) Dust as a nutrient source for fynbos ecosystems, South Africa. *Ecosystems* 10(4):550–561.
9. Morford SL, Houlton BZ, Dahlgren RA (2011) Increased forest ecosystem carbon and nitrogen storage from nitrogen rich bedrock. *Nature* 477(7362):78–81.
10. Stephenson NL (1990) Climatic control of vegetation distribution: The role of the water balance. *Am Nat* 135(5):649–670.
11. Irwin WP, Wooden JL (2001) *Map Showing Plutons and Accreted Terranes of the Sierra Nevada, California, with a Tabulation of U/Pb Isotopic Ages* (US Dept of the Interior, US Geol Surv, Washington, DC).
12. Gillespie AR, Zehfuss PH (2004) *Quaternary Glaciations—Extent and Chronology, Part II*, eds Ehlers J, Gibbard PL (Elsevier, Amsterdam), pp 51–62.
13. Bateman PC (1992) *Plutonism in the Central Part of the Sierra Nevada Batholith* (US Govt Print Off, Washington, DC).
14. Bateman PC, Wones DR (1972) *Geologic Map of the Huntington Lake Quadrangle, Central Sierra Nevada, California. US Geol Surv Geol Quad Map.* (US Geol Surv, Washington, DC).
15. Goulden ML, et al. (2012) Evapotranspiration along an elevation gradient in California's Sierra Nevada. *J Geophys Res* 117(G3):G03028, 10.1029/2012JG002027.
16. Homer C,, et al. (2007) Completion of the 2001 National Land Cover Database for the conterminous United States. *Photogramm Eng Remote Sens* 73(4):1–5.
17. Bales RC, et al. (2011) Soil moisture response to snowmelt and rainfall in a Sierra Nevada mixed-conifer forest. *Vadose Zone J* 10(3):786–799.
18. Clemens S (2006) Toxic metal accumulation, responses to exposure and mechanisms of tolerance in plants. *Biochimie* 88(11):1707–1719.
19. Wahrhaftig C (1965) Stepped topography of southern Sierra Nevada, California. *Geol Soc Am Bull* 76(10):1165–1189.
20. Graham RC, Rossi A, Hubbert KR (2010) Rock to regolith conversion: Producing hospitable substrates for terrestrial ecosystems. *GSA Today* 20(2):4–9.
21. Bateman PC, Dodge FCW, Bruggman PE (1984) *Major Oxide Analyses, CIPW Norms, Modes, and Bulk Specific Gravities of Plutonic Rocks from the Mariposa 1° X 2° Sheet, Central Sierra Nevada, California* (US Dept of the Interior, US Geol Surv, Washington, DC).
22. Schulz MS, White AF (1999) Chemical weathering in a tropical watershed, Luquillo Mountains, Puerto Rico III: quartz dissolution rates. *Geochim Cosmochim Acta* 63(3-4): 337–350.
23. White AF, et al. (2001) Differential rates of feldspar weathering in granitic regoliths. *Geochim Cosmochim Acta* 65(6):847–869.
24. Buss HL, Sak P, Webb S, Brantley SL (2008) Weathering of the Rio Blanco quartz diorite, Luquillo Mountains, Puerto Rico: Coupling oxidation, dissolution, and fracturing. *Geochim Cosmochim Acta* 72(18):4488–4507.
25. Porder S, Hilley GE, Chadwick OA (2007) Chemical weathering, mass loss, and dust inputs across a climate by time matrix in the Hawaiian Islands. *Earth Planet Sci Lett* 258(3-4):414–427.
26. Linder S (1995) Foliar analysis for detecting and correcting nutrient imbalances in Norway spruce. *Ecol Bull* 44(1):178–190.
27. Wedepohl KH (1995) The composition of the continental crust. *Geochim Cosmochim Acta* 59(7):1217–1232.
28. Elser JJ, et al. (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol Lett* 10(12): 1135–1142.
29. Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecol Appl* 20(1):5–15.
30. Porder S, Ramachandran S (2012) The phosphorus concentration of common rocks—a potential driver of ecosystem P status. *Plant Soil* 367(1-2):1–15.
31. Walker T, Syers JK (1976) The fate of phosphorus during pedogenesis. *Geoderma* 15(1):1–19.
32. Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO (1999) Changing sources of nutrients during four million years of ecosystem development. *Nature* 397(6719): 491–497.
33. Arkley RJ (1981) Soil moisture use by mixed conifer forest in a summer-dry climate. *Soil Sci Soc Am J* 45(2):423–427.
34. Hamilton WB (1956) Variations in plutons of granitic rocks of the Huntington Lake area of the Sierra Nevada, California. *Geol Soc Am Bull* 67(12):1585–1598.
35. Christiansen PP, Pollard DD (1997) Nucleation, growth and structural development of mylonitic shear zones in granitic rock. *J Struct Geol* 19(9):1159–1172.
36. Riley P, Tikoff B (2010) Tabular fracture clusters: Dynamic fracturing produced by volatile expulsion, Sierra Nevada Batholith, California. *J Struct Geol* 32(10):1488–1499.
37. Dühnforth M, Anderson RS, Ward DJ, Stock GM (2010) Bedrock fracture control of glacial erosion processes and rates. *Geology* 38(5):423–426.
38. Bergbauer S, Martel SJ (1999) Formation of joints in cooling plutons. *J Struct Geol* 21(7):821–835.
39. Martel SJ (2011) Mechanics of curved surfaces, with application to surface-parallel cracks. *Geophys Res Lett* 38(20):L20303.
40. Martel SJ, Pollard DD (1989) Mechanics of slip and fracture along small faults and simple strike–slip fault zones in granitic rock. *J Geophys Res Solid Earth* 94(B7): 9417–9428.
41. Egerton-Warburton LM, Graham RC, Hubbert KR (2003) Spatial variability in mycorrhizal hyphae and nutrient and water availability in a soil-weathered bedrock profile. *Plant Soil* 249(2):331–342.
42. Anderson MA, Graham RC, Alyanakian GJ, Martynn DZ (1995) Late summer water status of soils and weathered bedrock in a giant sequoia grove. *Soil Sci* 160(6): 415–422.
43. Onda Y (1992) Influence of water storage capacity in the regolith zone on hydrological characteristics, slope processes, and slope form. *Z Geomorphol* 36(2):165–178.
44. Holbrook WS, et al. (2014) Geophysical constraints on deep weathering and water storage potential in the Southern Sierra Critical Zone Observatory. *Earth Surf Proc Landf*, 10.1002/esp.3502.
45. Vanacker V, et al. (2007) Restoring dense vegetation can slow mountain erosion to near natural benchmark levels. *Geology* 35(4):303–306.
46. Dixon JL, Heimsath AM, Amundson RC (2009) The critical role of climate and saprolite weathering in landscape evolution. *Earth Surf Process Landf* 34(11):1507–1521.
47. Portenga EW, Bierman PR (2011) Understanding Earth's eroding surface with Be-10. *GSA Today* 21(8):4–10.
48. Granger DE, Riebe CS, Kirchner JW, Finkel RC (2001) Modulation of erosion on steep granitic slopes by boulder armoring, as revealed by cosmogenic Al-26 and Be-10. *Earth Planet Sci Lett* 186(2):269–281.
49. Carson MA, Kirkby MJ (1972) *Hillslope Form and Process* (Cambridge Univ Press, London).
50. Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proc Natl Acad Sci USA* 105(33):11823–11826.
51. Musselman KN, Molotch NP, Margulis SA, Kirchner PB, Bales RC (2012) Influence of canopy structure and direct beam solar irradiance on snowmelt rates in a mixed conifer forest. *Agric For Meteorol* 161:46–56.
52. Null SE, Viers JH, Mount JF (2010) Hydrologic response and watershed sensitivity to climate warming in California's Sierra Nevada. *PLoS ONE* 5(4):e9932.
53. Frost BR, et al. (2001) A geochemical classification for granitic rocks. *J Petrol* 42(11): 2033–2048.
54. Garrity CP, Soller DR (2009) Database of the Geologic Map of North America; adapted from the map by J.C. Reed, Jr. and others (2005). Available at http://pubs.usgs.gov/ds/424/. Accessed August 24, 2013.
55. Hartmann J, Moosdorf N (2012) The new global lithological map database GLiM: A representation of rock properties at the Earth surface. *Geochem Geophys Geosyst* 13(12):1–37.
56. Dahlgren RA, Boettinger JL, Huntington GL, Amundson RC (1997) Soil development along an elevational transect in the western Sierra Nevada, California. *Geoderma* 78(3-4):207–236.
57. Dixon JL, Heimsath AM, Kaste JM, Amundson RC (2009) Climate-driven processes of hillslope weathering. *Geology* 37(11):975–978.
58. Riebe CS, Kirchner JW, Granger DE, Finkel RC (2000) Erosional equilibrium and disequilibrium in the Sierra Nevada, inferred from cosmogenic Al-26 and Be-10 in alluvial sediment. *Geology* 28(9):803–806.
59. Harden JW (1987) Soils developed in granitic alluvium near Merced, California. *Geol Surv Bull* 1590:1–66.
60. Jenny H (1941) *Factors of Soil Formation: A System of Quantitative Pedology* (McGraw-Hill., New York).
61. PRISM Climate Group (2013) Climate data. Available at www.prismclimate.org.
62. Granger DE, Riebe CS (2014) *Treatise on Geochemistry*, ed Drever JI (Elsevier, Oxford), 2nd Ed, pp 401–436.
63. Riebe CS, Granger DE (2013) Quantifying effects of deep and near-surface chemical erosion on cosmogenic nuclides in soils, saprolite, and sediment. *Earth Surf Process Landf* 38(5):523–533.