COMMENTARY

Coevolution of life and landscapes

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The influence of organisms on landscapes, and of landscapes on organisms, has long been recognized. Darwin calculated that "if a small fraction of the layer of fine earth . . . annually brought to the surface by worms, is carried away, a great result cannot fail to be produced within a period which no geologist considers extremely long" (1). As our understanding of biogeochemistry, weathering, and geomorphology has grown, so have our observations of life's imprint on earth's surface morphology. It has been proposed that even plate tectonics (2) and the rise of continents (3) may be linked to the presence of life. Just as the land is shaped by life, life is shaped by the landscapes it inhabits (4). Geologic contacts often underlie ecological boundaries (5), and surface geology in soil-mantled landscapes is commonly inferred from the distribution of vegetation. In PNAS, Hahm et al. (6) provide an elegant illustration of

the two-way interaction between the evolution of life and land. The authors show that subtle variations in soil parent rock across the granitic core of the Sierra Nevada Mountains of California correlate with dramatic ecosystem differences, creating vegetation-free zones adjacent to groves of giant sequoias. Without substantial root activity, the vegetation-free zones denude more slowly than forested areas, leaving high bald mountain tops flanked by forests throughout the region (6).

Hahm et al.'s (6) work pieces together several emerging themes in geomorphology and biogeochemistry: (*i*) ecosystem access to water and nutrients can depend strongly on soil parent material (4); (*ii*) soil production from bedrock increases with increased biological activity (7); (*iii*) soil production is related to soil thickness (8); and (*iv*) soil thickness tends toward an inverse correlation with denuda-

tion rate as landscapes are lowered (9). The next step will be to determine the mechanisms underpinning the interactions between ecosystem and landscape evolution, and explore the relative importance of those mechanisms across Earth's varied tectonic and climatic settings (Fig. 1).

In the case of the Sierra Nevada, the observed correlations between biological communities and soil parent material suggest several plausible mechanisms. Intriguingly, Hahm et al. (6) suggest that the transition between soil-mantled hillslopes and exposed bedrock may result from variations in bedrock phosphorus (P) content. Of the rock-derived elements essential for life, P is the most concentrated in organisms relative to the lithosphere (10). Common crustal rocks vary by over two orders-of-magnitude in their P content, and the variation within a single rock type can be nearly this large (11). P limitation to plant production is thought to be widespread, both where soil P has been leached out through intense weathering and where soil parent material is particularly P deficient (12). Although P is not thought to widely limit production in the relatively lightly weathered soils of the Sierra Nevada, the P content of some of the granitic rocks underlying the bald mountain tops is as low as any common crustal rock type (11). In contrast, the P content of the rocks underlying the adjacent giant sequoias is much closer to that of average continental crust. If variation in P content controls the distribution of ecosystems in this landscape, and thus drives differences in weathering, soil formation, and denudation, it begs the question of how the large variation in parent-rock P observed within and between rock types has influenced the evolution of landscapes in the Sierra and beyond.

Variation in soil parent-rock P is not the only plausible explanation for the differences in vegetation cover in the Sierra Nevada. Although Hahm et al. (6) convincingly rule out aspect, elevation, and climate, they are not able to rule out the possibility that water retention varies among rock types. The region
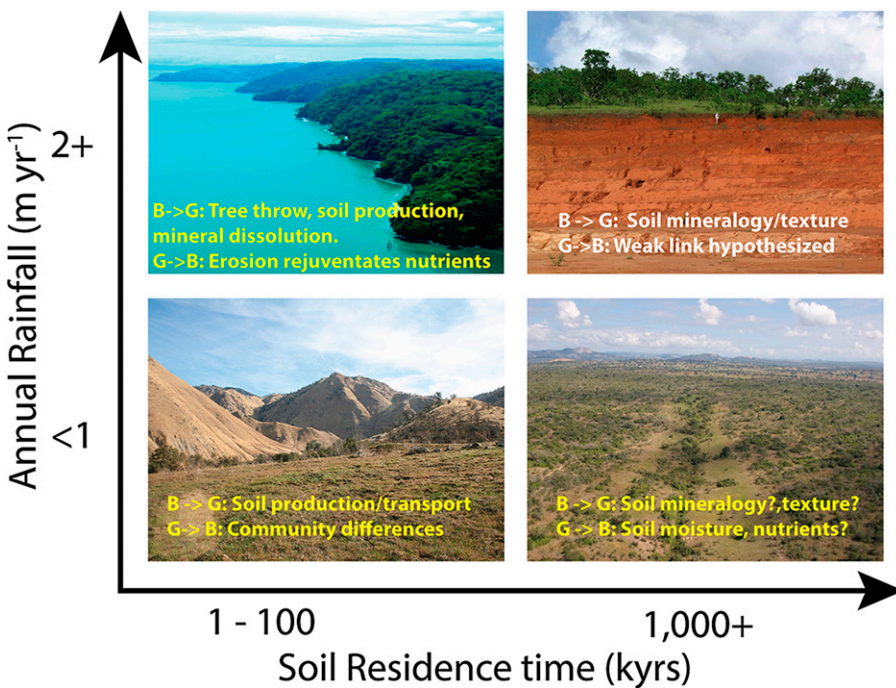

Fig. 1. Hypothesized important interactions between geomorphology and biota (G→B) and biota and geomorphology (B→G) in different climatic and geomorphic settings. Question marks indicate interactions that are possible but have not been well documented. Photos: (*Upper Left*) Osa Peninsula in Southern Costa Rica (photo credit: Alan Townsend, University of Colorado Boulder, Boulder, CO); (*Upper Right*) a deep road cut in the Upata Region of Venezuela; (*Lower Right*) Kruger National Park (photo credit: Shaun Levick, BGC Group, Jena, Germany); and (*Lower Left*) the Sierra Nevada (photo credit: George Hilley, Stanford University, Stanford, CA).

has long hot summers, and regolith water-holding capacity—mediated through rock fracture density, grain size, and plant/fungal-driven weathering of micas and feldspars—may be an alternative bedrock influence on the communities.

Whatever the mechanism, this work (6) highlights the little explored interplay between ecosystems and landscape evolution. Hahm et al. (6) consider a relatively dry landscape that varies between soil-mantled and bedrock-dominated hillslopes. However, even where soil cover is ubiquitous, several mechanisms exist that might influence the interaction between ecosystems and geomorphology. For example, plants on low P soils invest more heavily in fine root production and associations with mycorrhizal fungi, both of which increase the depth and volume of soil that can be exploited (13). Do P-poor but soil-mantled hillslopes show more rapid soil production and denudation as a result of plant adaptation to nutrient-poor conditions? If nutrient-poor forests erode more quickly, does more rapid lowering enhance the delivery of rock-derived nutrients to plants, and thus act as a negative feedback? Similarly, trees can grow tap roots many meters deep in response to water stress, particularly in systems that experience strong periodic drought (14). How and where might these roots play a role in regolith production, and the transport of material from hillslopes to channels? How do these root distributions affect the size of regolith—and the fraction of precipitation—that makes it to channels? Both factors may affect the rate of incision, and thus landscape evolution.

Our understanding of the mechanisms governing these two-way interactions is in its infancy. However, as Hahm et al. (6) illustrate, these mechanisms clearly exist. There is a wealth of evidence that soil parent rock can be a strong control of ecosystem properties (4). As Darwin pointed out, the imprint of biotic activity on the evolution of landscapes is also extensive (1), although there does not seem to be a unique topography that life alone can create (2). Fig. 1 puts forth some potentially important influences of biota on geomorphology (B→G) and of geomorphology on biota (G→B) in different climatic and geomorphic settings.

In theory, the influence of parent material on soils and ecosystems should diminish as soils age and atmospheric inputs homogenize soils across lithologic contrasts (15). Similarly, the influence of biotic communities on the evolution of geomorphology should diminish as regolith thickens and roots are separated from the base of the weathering zone (2). However, the available evidence

suggests that the influence of soil parent material on biotic and geomorphic properties can be long lived. The soils of semiarid Kruger National Park, South Africa [<700 mm·y^{-1} mean annual precipitation (MAP)] have a residence time of several million years. Even still, granite-derived soils host relatively tree-covered hillslopes with high channel density and basalt-derived soils host grass-dominated communities on flatter, more undulating topography (16). The more mesic Atherton Tablelands of Australia (1.5 m·y^{-1} MAP) have similar soil residence times to Kruger, and also show ecosystem differences across geologic contacts (17). Even the forests on the lower flanks of Mt. Kinabalu, Borneo (2.3 m·y^{-1} MAP) differ in productivity between sedimentary and ultramafic rock-derived soils (18). We do not know if these ecosystem differences feed back to differences in landscape evolution. Elucidating the mechanisms that underpin the correlations between ecosystems and bedrock will help us understand where and how to look for these feedbacks.

A reasonable working hypothesis is that the influence of soil parent material on ecosystem properties is reduced at the extremes of climate and soil age (Fig. 1), and thus the link illustrated by Hahm et al. (6) might be less important at these extremes. For example, in the Luquillo Mountains of Puerto Rico (4 m·y^{-1} MAP), ecosystems do not systematically differ across geologic contacts, despite variation in soil properties (19) and denudation rates (20). Perhaps under very high rainfall the influence of parent mate-

rial on ecosystems is diminished, although a hypothesis based on such limited data must certainly be viewed as preliminary. Similarly, there are broad swaths of the lowland tropics underlain by regolith that is many tens, if not hundreds, of meters thick (21). Under these circumstances, shifts in community composition (other than large, climate drivers differences) might have little or no effect on landscape evolution. Similarly, the geologic rejuvenation of nutrients via erosion is not possible if there is no unweathered material near the surface on hillslopes. Whether the hypothesis of weaker biology/geomorphology links in the highly weathered tropics holds up to the scrutiny afforded by Light Detection and Ranging (LIDAR)-based topographic measurements remains to be seen.

Ultimately, Hahm et al.'s work (6) leads us in two very important directions. First, the authors show that even small differences in rock properties can have dramatic ecosystem effects that feed back to landscape evolution. They highlight the need to generate and test hypotheses as to the mechanisms underpinning these correlations. Second, Hahm et al. (6) raise the question of how widely the coevolution of life and landscapes extends across the terrestrial biosphere. In doing so, the authors set a clear agenda for research at the interface of geomorphology and biogeochemistry.

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