Vol 439|26 January 2006|doi:10.1038/nature04452

nature

The search for a topographic signature of life

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Landscapes are shaped by the uplift, deformation and breakdown of bedrock and the erosion, transport and deposition of sediment. Life is important in all of these processes. Over short timescales, the impact of life is quite apparent: rock weathering, soil formation and erosion, slope stability and river dynamics are directly influenced by biotic processes that mediate chemical reactions, dilate soil, disrupt the ground surface and add strength with a weave of roots. Over geologic time, biotic effects are less obvious but equally important: biota affect climate, and climatic conditions dictate the mechanisms and rates of erosion that control topographic evolution. Apart from the obvious influence of humans, does the resulting landscape bear an unmistakable stamp of life? The influence of life on topography is a topic that has remained largely unexplored. Erosion laws that explicitly include biotic effects are needed to explore how intrinsically small-scale biotic processes can influence the form of entire landscapes, and to determine whether these processes create a distinctive topography.

Do biota affect landscape form and evolution? One way to think about this question is to imagine a very high-resolution topographic map of the Earth (for example, 1 m^{-2} data density) from which all artefacts of human activity have been removed and all vegetation has been cleared, and consider if a unique topographic signature of life would be evident in such a map. In other words, has the emergence of life so fundamentally altered erosion mechanics that there are features of the landscape that could only exist owing to biotic influences—if life had not arisen, would the tectonic and climatic processes that drive uplift and erosion of landscapes be significantly different? The simple question about the effect of biota on landscape development therefore raises several essential issues about the mechanisms underlying Earth's evolution.

Anyone who has tended a garden knows that vegetation affects erosion processes. Remove it, baring the soil, and surface erosion is likely. Much practical work has been done to quantify the influence of biota on erosion[1]. But over the long geologic timescales of landscape evolution, as mountain ranges emerge and climb towards an erosional equilibrium with the mass flux due to colliding plates, are biogenic processes significant? Would the Appalachians, Alps, Andes or Himalayas have distinctly different topography in the absence of biotic processes? Would the deeply weathered landscapes of Australia, South America or Africa have formed in the absence of life? Are river networks, now widely recognized as large-scale examples of self-organization[2], influenced by biotic processes? Despite the fact that all current landscapes emerged in a biotic world, few landscape evolution models explicitly include the effects of life[3–7].

In this Review, we explore these questions in three ways. First, we consider how biotic processes influence weathering, erosion, and sediment transport mechanisms, and how such influences could be manifest in landscape-scale morphology. Second, we consider how biotic processes affect climate and tectonics, which drive landscape evolution. Last, we consider landscapes on an Earth on which life never arose and examine the topographies of Venus and Mars.

Erosion, biotic processes and landscapes

Recently, numerical modelling has become an important tool in the study of landscape form and evolution. Numerical models have been used to investigate the process controls on landscape form[8–10], the coupling of tectonics and erosion[11–14], and the relationships among climate, tectonics and topography[14,15]. Some studies have specifically explored the effects of vegetation on landscape processes and form[3–7]. These modelling studies have provided valuable new insight into landscape dynamics, but their applicability is limited by a lack of mechanistic mathematical expressions for modelling specific erosion processes. All landscapes must obey an equation for the conservation of mass[16,17]:

$$\frac{\partial z}{\partial t} = U - E - \nabla\cdot\mathbf{q}_s \qquad (1)$$

in which z is the elevation of the ground surface, t is time, U is uplift rate, E is the incision rate into bedrock, and $\mathbf{q}_s$ is the volume flux of stored sediment (soil, colluvium, alluvium, and so on) per unit width. This is a simplified form of the conservation equation in which changes in bulk density have been ignored and, correspondingly, solute losses are not considered. To solve equation (1), we require an understanding of the tectonic processes (U) operating on the landscape as well as 'geomorphic transport laws'[17] (E and $\mathbf{q}_s$), which describe the rates of different transport, bedrock-to-soil conversion, and erosion processes in terms of material properties, climatic influences and attributes of the topography and subsurface. In this Review, we make the case that all three terms on the right-hand side of equation (1) are influenced by biota.

To understand the role of transport laws in shaping landscapes, look out of any aeroplane window as you travel across the world. What you will most commonly see is a landscape composed of ridges and valleys, forming a hierarchical structure in which smaller valleys drain to successively larger ones (Fig. 1). Why are there ridges and valleys? What controls their size? What sets the height and steepness of the hills?

The seminal paper by Smith and Bretherton[18] took an important step towards answering these questions by showing how two simple

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approximations for geomorphic transport laws ($\mathbf{q}_s$ in equation (1)—in this simple case, the bedrock erosion term E is ignored) give rise to either ridges or valleys (Fig. 1). For each transport law, they first solved equation (1) for the steady-state case ($\partial z/\partial t = 0$) and then introduced lateral perturbations to the topography. If $\mathbf{q}_s = KS$, where K is a diffusion-like coefficient and S is the local topographic slope, the resulting steady-state hillslope is convex-up (Fig. 1). Lateral topographic perturbations to this surface are damped by the diffusive sediment transport. Now consider the case in which sediment transport is proportional to both local water discharge (q_w) and slope, that is, $\mathbf{q}_s = F(q_w, S)$. Because the water discharge at a point on the landscape increases with the size of the area that drains to that point (A), gentler slopes are sufficient to transport sediment further from the topographic divide, and the resulting steady-state landform is concave-up (Fig. 1). Perturbations to this surface are unstable, however, because local concavities cause an increase in drainage area, which in turn accelerates incision and valley growth. Thus, ridge-and-valley topography emerges from a competition between diffusion-like and advective erosion processes. If we replace $F(q_w, S)$ with cA^mS^n (which assumes that incision varies with runoff energy expenditure or flow shear stress), with c, m and n empirical parameters, we can write in general $\mathbf{q}_s = KS + cA^mS^n$ and solve equation (1) to produce ridge and valley topography. This is, in essence, what nearly all landscape evolution models currently do. But the two proposed transport laws are not deeply mechanistic. What are the mechanics of erosion, and how does life fit in?

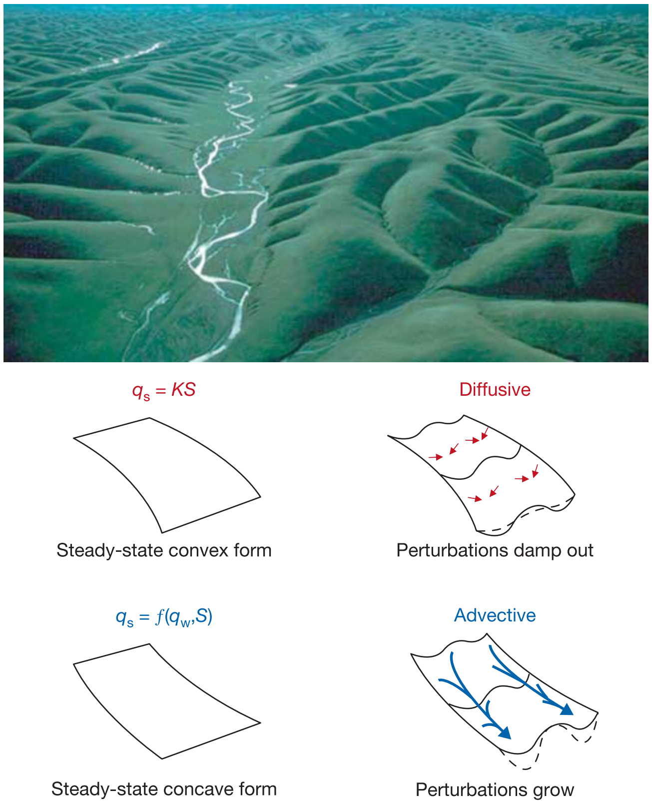

Figure 1 | An explanation for the origin of ridges and valleys. Top, photograph of a grass-covered, soil-mantled landscape finely divided into ridge-and-valley topography near Orland, California. Photo courtesy of J. Kirchner. Bottom, an explanation, first proposed by Smith and Bretherton[18], of why such topography emerges during landscape evolution (see text for a summary of their analysis). Slope-dependent (diffusive) transport leads to convex hillslopes, and when the topography is laterally perturbed, the transport direction (red arrows) causes the high points to lower and low points to fill in. This results in smooth topography, as suggested by the dashed line. In contrast, transport that depends on water flow and slope advects sediment, and produces concave-up hillslopes. Flow concentrations (blue flow paths) resulting from lateral topographic perturbation lead to incision, as suggested by the dashed lines. The competition of these two processes leads to diffusion-dominated ridges and advection-dominated valleys.

Recent reviews[17,19,20] discuss the current state of knowledge about geomorphic transport laws, so we can summarize here and focus on the biotic influence. Table 1 lists the primary erosion processes driving landscape evolution, the corresponding geomorphic transport laws, and the abiotic and biotic mechanisms that influence those laws. Here we discuss some of the critical processes in more detail.

Massive bedrock must break down into smaller fragments before it can be eroded and transported away. Abiotic processes such as chemical weathering, salt growth, freezing, stress release fracturing and chemical dissolution can produce loosened particles. So, too, can bedrock landslides. Field studies[17,20,21] have shown, however, that in a wide range of soil-mantled landscapes, soil production (the production of loose, transportable material from bedrock) is primarily due to biogenic disturbance. Root growth and animal burrowing disrupt bedrock that is weathered but structurally intact, creating a loose material free to move downslope[20]. The probability of biotic contact with the rock should decline with increasing soil mantle thickness, and this expectation is borne out in field studies of soil production rates. Using cosmogenic radionuclide dating, Heimsath *et al.*[21] documented an exponential decline in the rate of soil production with depth ($P = P_0e^{-\alpha h}$, in which P is the production rate with units of $\mathrm{L\,T^{-1}}$, h is soil depth, P_0 is the production rate on exposed bedrock, and α is a parameter with units of $\mathrm{L^{-1}}$; note that P is part of E in equation (1)). The production rate of soil is also strongly influenced by the degree of weathering of the bedrock; and biotic processes, especially microbial activity, can strongly affect weathering rates[22,23]. Where soil erosion outstrips soil production, bedrock emerges and the role of biota is greatly diminished.

Granular soils on inclined surfaces experience net downslope movement when they are dilationally disturbed[24]. The source of disturbance can be abiotic, as in the case of freeze–thaw, wetting–drying, or salt growth processes. Some clay-rich soils can swell and flow downslope[25]. On soil-mantled landscapes, however, dilational disturbance by burrowing organisms and displacement by falling trees often appears to dominate motion[24,26]. This can lead to a linear or nonlinear dependence of soil flux on local slope[27,28]. Despite the observation that biotic processes may dominate the downslope movement of soil, there are currently no data available to define quantitative relationships between flux law parameters and specific biotic processes (although significant work has begun[20]). Most commonly it is assumed that the proportionality constant between flux and slope (K or K_{nl} in Table 1) depends in some way on biotic activity.

In semi-arid to arid landscapes, where vegetation is sparse, precipitation rates can exceed the meagre infiltration rate into unvegetated ground and generate overland flow and surface wash. Where vegetation is sufficiently dense, it dictates the rate and pattern of surface wash and strongly limits its efficacy[1]. Currently there are no geomorphic transport laws that describe these processes, although empirical expressions for land management do explicitly account for biotic influences on surface wash[1]. Nonetheless, we can reason that in a wet abiotic world, loose particles on hillslopes would be washed away, hindering the development of a soil mantle.

River incision into bedrock drives landscape evolution, and thus a geomorphic transport law for this process is crucial to exploring linkages between tectonics, climate and erosion. Over the past two decades, theory, experiments and field studies have shown that an initial hypothesis[29–31]—that the rate of erosion is proportional to the rate of energy expenditure—while very useful[19], is incomplete. Recent work emphasizes the role of sediment grain size and quantity in controlling incision rates[19,32,33]. The sediment load carried along the bed of a river acts as an abrasive tool (more of it leads to more wear) as well as a cover (the more of it, the more protected the bed). The larger the rocks entering the channel from adjacent hillslopes, the steeper the channel must become to transmit them downstream. Biotic processes generally reduce the size of the grains entering the channel. Biotic effects tend to increase the weathered state of the rock, which accelerates the breakdown of grains once they enter the channel. Weathering of the bedrock beds of rivers (perhaps facilitated by biotic processes) would also increase their erodibility. Other primary erosion processes (landsliding, debris flows, glaciers and wind) and the associated biotic effects are summarized in Table 1.

As indicated in Table 1, then, biotic processes strongly influence the production and transport of debris, yet the few geomorphic transport laws that have been proposed do not account explicitly for these processes. Landscape evolution models that explore the relationships among climate, topography and tectonics rely on these transport laws. The absence of transport laws for many processes and the lack of accounting for biotic effects make the interpretations derived from these models less reliable. Nonetheless, we have sufficient understanding to explore qualitatively how erosion processes and the resulting landforms might differ in the absence of life.

Landscape evolution in the absence of life

What would happen if all life suddenly disappeared and the artefacts of humankind (roads, dams and so on) had never been constructed (Fig. 2)? For the moment, we assume that the oceans, Earth's climate and tectonics remain unchanged; we will consider these interactions below. Three distinctive responses would be likely.

The most obvious and certain effect of the sudden absence of life on Earth would be the rapid erosion of the soil mantle that covers semi-arid to wet landscapes. The absence of vegetative root strength would permit landsliding in loose soil on steep slopes during intense rainstorms. Soil consolidation owing to a lack of dilational disturbance by root growth and animal burrowing would lower infiltration rates, promoting overland flow, sheetwash and gullying. Rocky scree slopes fringing steep mountains would remain relatively unchanged.

Our first hypothesis, then, is that in an abiotic world, the soil mantle that drapes many hilly and mountainous landscapes would be stripped, and rough, poorly weathered, bedrock surfaces would emerge (Fig. 3a). The deep weathering profiles that develop on bedrock in wet tropical areas would be absent. One might speculate, therefore, that smooth, rounded, soil-mantled hilltops are a topographic signature of a biotic world. The landscape of the Atacama Desert of Chile proves that this is untrue as a universal generalization (Fig. 3b). In the hyperarid inland region of the Atacama referred to as the Central Depression[34], there are extensive areas of rounded, soil-mantled topography in which biotic processes are essentially absent. Intensive salt weathering breaks down bedrock to produce soil, and the surface mantle receives an input of wind-blown sediment[35]. The

Table 1 | A summary of geomorphic transport laws and biotic effects

Process	Geomorphic transport law, GTL*	Abiotic mechanisms	Biotic mechanisms
Soil production rate	$P = P_0 e^{-\alpha h}$ (ref. 21); other expressions proposed in refs 67–69	Salt and freeze–thaw weathering, atmospheric dust input, mineral alteration leading to loss of physical strength	Animal burrowing, root growth and tree throw; microbially mediated geochemical reactions; P_0 (through weathering) and α depend on biota
Slope-dependent downslope movement (creep)	$\mathbf{q}_s = -K\nabla z$ (refs 70, 28); $\mathbf{q}_s = \frac{-K_{nl}\nabla z}{1-(\nabla z/S_c)^2}$ (ref. 27); see ref. 20 for equations explicitly including biogenic mechanisms	Wetting and drying, freezing and thawing[69,71], shear flow	Animal burrowing and tree throw that cause dilational disturbance; both K_{nl} and S_c depend on biota
Landsliding	None available, but important starts for earthflows[72], deep-seated landslides[73] and landslide dynamics[74]	Stress exceeds material strength owing to earthquakes, elevated pore pressures derived from precipitation or from undermining of toe; released sediment travels downslope	Roots add strength and vegetation canopy reduces peak rainfall intensity (especially important in colluvial soil failures); evapotranspiration may reduce water levels in potential deep-seated landslides; vegetation may affect travel distance
Surface wash and splash (Horton mechanisms)	Many short-term empirical and mechanistic expressions[1], but no GTL available	Rainsplash and overland flow displace and remove particles; rill and gully incision	Strongly affects all aspects of runoff and erosion processes
River incision into bedrock	$E = k_b A^m S^n$ (refs 17,19, 29); $E = k_1 \frac{q_{sp}}{(T-1)^{1/2}} - k_2 \frac{q_{sp}^2}{D^{3/2}(T-1)^2}$ (ref. 33)	Plucking and particle wear due to river flow and sediment transport	Indirect effect through influence on sediment grain size and bank strength (which affects channel width); large woody debris may hold sediment and retard incision rate
Debris flow incision into bedrock	$E = k_d f \left[\rho_s D^2 \left(\frac{\partial u}{\partial y}\right)^a L_s\right]^p$ (ref. 75)	Particle impact and sliding wear of bedrock during mass transport	Large woody debris may halt debris flow movement, or enhance erosion
Glacial scour	$E = cU_b$ (ref. 76); more mechanistic expressions proposed[77]	Sediment-rich basal sliding wears bedrock	No apparent influence
Wind transport and scour	Extensive theory for sediment transport by wind[78–80], some theory for rock abrasion[81]	Abrasion by wind-suspended particles	Biotic ground cover eliminates process[82]

Details about each process and transport law can be found in the cited references. See ref. 17 for a discussion of GTLs. Note that none of the proposed GTLs define terms that are specific to biotic mechanisms.

* Approximate definitions of terms (see cited references for details): P, soil production rate from bedrock (contributes to E in equation (1)); P_0, soil production from exposed rock; h, soil thickness; α, constant; $\mathbf{q}_s$, volumetric sediment transport rate per unit width; K, constant; z, elevation; K_{nl}, constant; S_c, threshold slope at which transport rate becomes infinite; E, incision rate into bedrock; k_b, constant that may depend on uplift rate and rock strength; A, drainage area; S, local slope; m, n, constants; k_1, constant that depends on bedrock strength; k_2, constant that depends on bedrock strength and force needed to initiate sediment transport; q_{sp}, bedload supply; T, ratio of shear stress to critical shear stress for initial motion; D, representative grain diameter; k_d, constant that depends on bedrock properties; f, frequency of debris flows; ρ_s, bulk density of debris flow; u, debris flow velocity as a function of distance y above the bed; L_s, length of debris flow 'snout', a, p, constants; U_b, basal ice velocity; and c, constant.

resulting topography appears almost identical to that developed in the presence of active biotic processes (Fig. 1). This similarity in form is measurable: the curvature (a quantitative measure of hillslope 'roundness', usually expressed as the laplacian of elevation, $\nabla^2 z$) of the hillslope in Fig. 3b is similar to that commonly observed[21,36,37] in well-vegetated environments (Chilean data; J. Owen, personal communication). We can conclude that, whereas rough bedrock surfaces would be more typical of an abiotic world, rounded, soil-mantled landscapes could also occur. Figure 3a and b also illustrates that exposed bedrock is more likely where hillslopes are bordered by actively incising channels.

The stripping of the soil mantle and the emergence of bedrock on hillslopes should introduce coarser, less weathered sediment to channels. Our second hypothesis, then, is that river beds in an abiotic world would be coarser. This coarsening would cause the channels to steepen, and the longitudinal profiles of rivers would rise to greater heights in the mountains. This implies that the adjacent ridges would also be higher. While the occurrence of steep, rocky channels would increase and mountains might be somewhat higher in an abiotic world, these features are not unique and would not constitute a distinctive biotic signature when compared to the world we live in.

The tendency of river channels to meander (shift laterally along curved paths) or braid (form multiple channel paths) depends in part on the mechanical strength of the river banks, which is influenced by vegetation. Weak channel banks allow high flows to erode laterally, widening the channel and giving rise to multiple channel paths separated by bars (braiding). This realization has led some to propose that meandering is a signature of the influence of land plants[38,39]. Our third hypothesis, then, is that meandering rivers would be rare or absent in an abiotic world. While the influence of vegetation on bank strength is well documented[40,41], it is important to note that other sources of strength can lead to meandering. Bedrock can provide the appropriate strength[42], and meandering bedrock canyons are observed on both Earth and Mars[43]. But what about the case of meandering channels with banks composed of their own alluvial floodplain sediments? Recent observations[44–46] demonstrate that large-scale meanders with cut-off loops developed on a deltaic fan surface on Mars in the absence of vegetation. The source of strength there may have been frozen ground[44]. It is likely that meandering rivers would be less common on an abiotic Earth, but we cannot conclude that they would be absent.

These three hypotheses have helped us to explore the ways in which landscapes would differ in the absence of biota, but none have led us to identify a landform that cannot exist without life. We now turn our attention to the influence of biota on climate and, consequently, large-scale erosion and tectonics.

Landscapes if life influences climate

Life mediates atmospheric and ocean chemistry. Vegetation, in particular, influences heat transfer, water transport and characteristics of the land surface that affect atmospheric turbulence. How

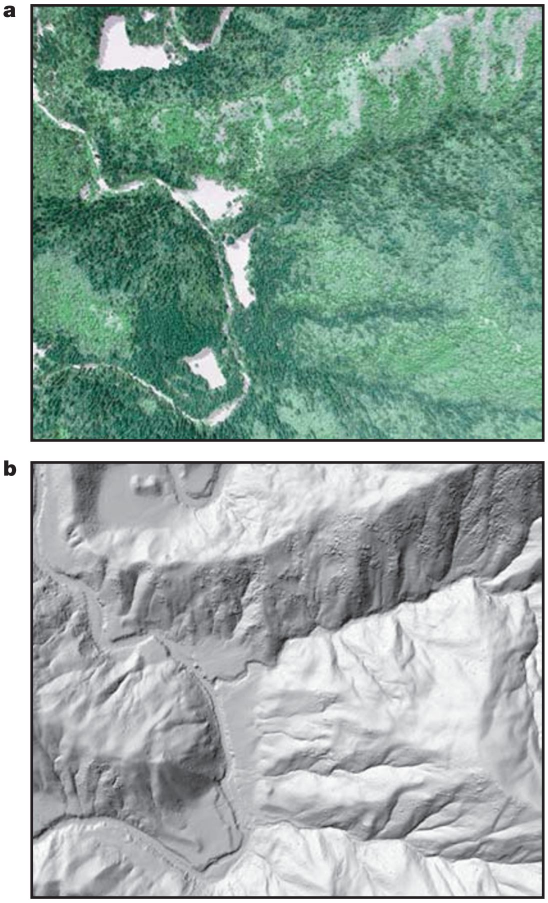

Figure 2 | Shaded relief images derived from airborne laser swath mapping (ALSM) data. Panel **a** includes vegetation, with colours based on canopy heights; panel **b** has been filtered to an approximate bare-earth surface. Width of the images is 2.3 km, and horizontal resolution of the data is about 1 m. ALSM data were collected and processed by the National Center for Airborne Laser Mapping (NCALM). Area shown is in the Angelo Coast Range Reserve along the South Fork Eel River, California (part of the University of California Natural Reserve System and a National Center for Earth-surface Dynamics research area).

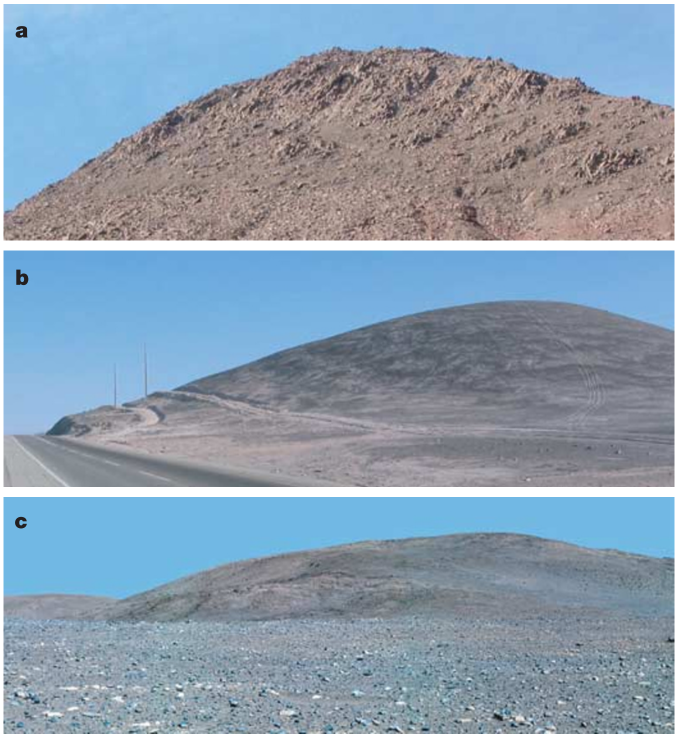

Figure 3 | Hillslopes on which soil formation appears to be driven entirely by abiotic processes. a, Bedrock hillslope in an area of active channel incision in the hyperarid Atacama Desert, Chile. **b**, Rounded, soil-mantled hillslope in the Atacama Desert bordered by an aggrading plain. Hillslopes in both **a** and **b** are about 40 m high. **c**, Image mosaic (artificially coloured) of the Columbia Hills, Mars, acquired by Spirit, one of the two Mars Exploration Rovers, from positions approximately 300 m from the base of the hills. Once the sky has been artificially coloured blue (the true colour is yellowish grey) and the red colour of the rocks (due to the presence of oxidized iron) has been removed, the rounded, soil-mantled hillslopes in **c** can hardly be distinguished from the terrestrial landscape in **b**. Mars image courtesy of NASA/JPL/Cornell University.

might life shape the pattern of precipitation, which is one of the major drivers of landscape evolution? One way to address this question is to perform a virtual experiment: remove all vegetation from a global climate model and document the effects on the predicted spatial patterns of rainfall and temperature. Kleidon *et al.*[47] report just such an experiment. A key finding is that the removal of vegetation leads to large changes in mean annual precipitation over extensive geographic regions.

Recent modelling studies, which have given rise to numerous field investigations, suggest that uplift, erosion and climate are strongly coupled in evolving mountain belts[14,48,49]. Figure 4 illustrates this proposed coupling. Crustal thickening at convergent plate boundaries causes uplift of the land surface, which steepens regional topographic gradients. In response, rivers carve canyons, steepening local slopes and inducing further landscape erosion. This erosional mass removal alters the force balance across the collisional zone and ultimately influences the height to which the mountains climb, the breadth of the uplifted region and the overall shape of the orogen. Through this feedback mechanism, the uneven distribution of precipitation across most mountain ranges exerts an important control on the dynamics of mountain growth: if erosion is positively correlated with precipitation, the wetter sides of mountains will erode more rapidly, accelerating the uplift of the underlying bedrock. This analysis suggests that biota, by influencing the pattern of precipitation, affect the height, width and symmetry of mountain ranges. Yet we still cannot argue that there is a unique mark of life upon the landscape.

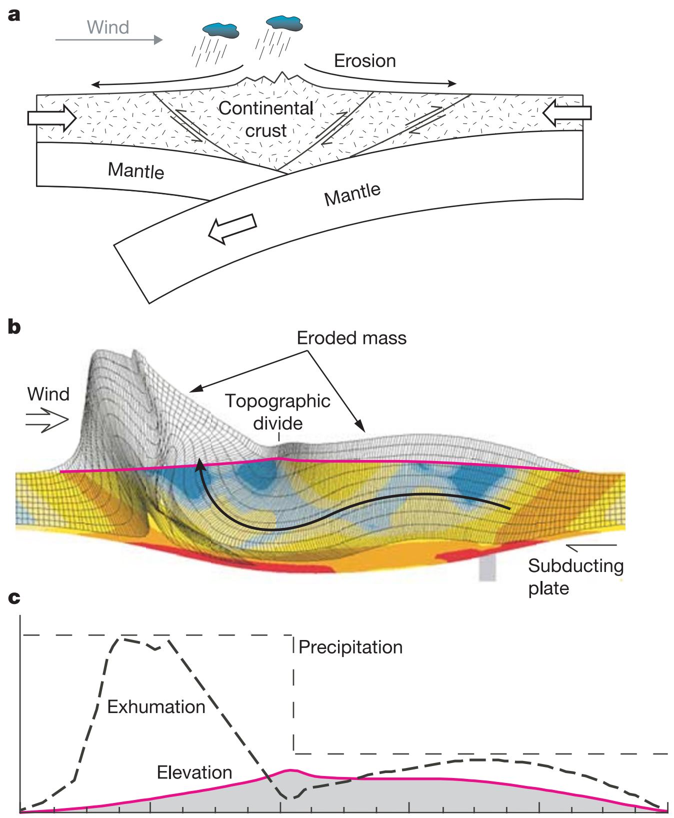

Figure 4 | Links among tectonics, climate, erosion and topography at convergent plate boundaries. **a**, Hypothetical cross-section of convergent plates (composed of continental crust overlying flowing mantle, with the plate on the right subducting beneath that on the left) and the resulting mountain range, as influenced by climatically controlled, spatially varying erosion. Open arrows show direction of motion; smaller coupled arrows show faulting arising from the convergence. **b**, Result of a finite-element numerical model of the scenario in **a** developed under strongly asymmetric rainfall across the mountain range in which wind-driven storms drop more precipitation on the left side of the mountain, leading to greater river incision and landscape erosion. The asymmetric rainfall pattern causes the topographic divide to shift towards the side of the mountain that receives more rainfall. Warmer colours correspond to higher strain rates. The magenta line marks the topographic surface, and the portion of the mesh above this line shows the eroded mass. The curved black arrow shows the path of bedrock through time. **c**, Simplified plot of exhumation, elevation and precipitation for the model result in **b**. Figure modified from Willett[14].

The numerical experiment of Kleidon *et al.* also predicts changes in near-surface air temperature of ±4 K, with some high mountain areas (parts of the Andes and Rocky Mountains, for example) experiencing strong cooling. Such a temperature drop would expand the area of freeze–thaw activity, which may increase erosion rates, but the net effect on topography will depend on the rate of debris removal by receiving streams. Again, this effect may lead to a change in the local erosion rate, but it would not make an abiotic Earth topographically distinct.

What if life never arose?

From a landscape evolution perspective, the question to ask is, if life had never emerged on Earth, how would the coupled climate–lithosphere system have evolved? No consensus was found in the literature on this issue; in fact, very little has been written about the evolution of Earth in the absence of life. The role of life in the evolution of the Earth is debated, as summarized in Box 1. To gain some insight into this problem, we can look to other Solar System bodies, particularly our neighbours Venus and Mars.

On Earth, plate tectonics depends on an upper mantle low-viscosity zone on which plates can glide, and it has been proposed that this zone arises from injections of water at subduction zones[50]. This insight suggests that the scarcity of water on the surface and in the interior of Venus may be responsible for the absence of plate tectonics there, despite internal dynamics that triggered a magmatic resurfacing of the planet within the past 700 million years[51]. Venus is relatively smooth (80% of the planet lies within 1 km of the mean planetary radius[50]) and lacks any evidence of non-volcanic surface channels. Early Venus would have received roughly the same amount of insolation as the present-day Earth. Is it possible that the emergence of life on Earth prevented the development of atmospheric conditions favourable to the loss of water via solar wind erosion, keeping the planet 'wet' and enabling plate tectonics? Is plate tectonics on Earth a consequence of life on Earth? One contributing effect is certainly the biologically mediated sequestration and burial of carbonate in the oceans, which prevents a runaway build-up of atmospheric carbon dioxide like that found on Venus. As noted by Chyba[52], the current understanding of early Earth's atmospheric chemistry and the development of life is experiencing a productive turmoil. This will also lead to better insight about how the Earth could have evolved in the absence of life.

Perhaps the greatest surprise to those who have examined the wonderfully detailed images of Mars acquired by robotic orbiters and rovers is how familiar the landscape feels, particularly at the local scale. Channel networks are widespread[53–55], river meanders in bedrock canyons and in alluvium have been found, and large alluvial fans have recently been mapped[56]. Rocky ridges similar to the one in Fig. 3a are common on Mars, but convex, debris-mantled hillslopes like the one in Fig. 3b can also be found (Fig. 3c). Wind-formed dunes are a pervasive feature of the landscape, extensive glacial features have been mapped[57] and numerous volcanoes exist.

Of course, Mars' topography does look different: impact craters abound, undissected plains are extensive, and there are some features, believed to be glacial in origin, that do not appear to have any analogues on Earth[58,59]. Mars is a one-plate planet with a very different large-scale structure, such as the enormous Tharsis bulge and the striking hemispheric dichotomy. This suggests that the question on Mars should be turned around: are there any features found there that could not occur in the presence of significant biotic influences? Perhaps some glacial features require ice-forming conditions incompatible with extensive life, but otherwise we are unable to identify any such features. The surface of Mars contains an abundance of familiar landforms, and we are beginning to see that Mars is not unique among Solar System objects in this respect. It is particularly noteworthy, for example, that the most prominent landscape features revealed during the descent of the Huygens probe to the surface of Titan are valley networks[60], which dominate the surface of the Earth.

The importance of life in landscape processes

Life permeates the Earth's surface and controls or mediates erosion and transport processes. Biotic processes influence long-term landscape evolution, even to the extent that they affect the height, width and symmetry of mountain ranges. Yet the answer to the question 'Is there a unique topographic signature of life on Earth?' seems to be 'no'. By 'unique' we mean a landform that could only exist in the presence of life. Even a single occurrence of broadly convex hillslopes on Mars (Fig. 3), for example, indicates that this landform is not a unique signature of life. This does not mean that life has not profoundly altered the course of Earth's evolution or its landscapes. Indeed, we expect that there is a topographic signature of life, but it may be more subtle than the presence of certain diagnostic landforms. This subtlety is likely to be one of frequency of occurrence and of scale.

Figure 5 illustrates the issue of frequency of occurrence. If we were to make quantitative measurements of landscape properties (for example, slopes, heights or curvatures) on an abiotic Earth and compare them to measurements of the Earth we know, the analysis presented above suggests that the frequency distributions of these measurements would be very different, even though all observed landform types would be found in both worlds. If we were to walk around an abiotic Earth, it would look different from ours, but it would not exhibit landforms unfamiliar to us, nor would we find any landform missing from our past experience. Mountainous landscapes would be rocky and irregular, and most rivers would have coarse beds and braided channels, but such features are observed on Earth today. The difference would lie in the frequency distributions of certain landform properties.

What might be the properties to plot on the abscissa in Fig. 5? Process models predict[9,61], and empirical analyses of high-resolution topography show[17], that slopes generally steepen with increasing drainage area on hillslopes and become more gentle with increasing drainage area in valleys, with the steepest slopes occurring at the transition from hillslopes to valleys. Analysis of the slope–area relationship has proven useful as a means of examining the results of landscape evolution models[7–10,61]. The inset in Fig. 5 shows slope–area curves for three landscapes, one in which biota have a significant influence on erosion processes, and two in which the biotic influence on erosion is minimal. These plots suggest four properties of the slope–area relationship whose frequency distributions could be used to distinguish biotic and abiotic landscapes. These properties are the power-law exponents for hillslopes (small areas) and valleys (large areas), and the area and slope at the transition point between hillslopes and valleys. At larger drainage areas and gentler slopes, further changes in erosion processes may produce additional breaks in the slope–area relationship[62]. The slope–area properties of the biotically-influenced landscape in Fig. 5 clearly differ from those of the landscapes with minimal biotic influence. The high-resolution topographic data needed to perform these analyses are currently available for very limited portions of the Earth's surface, but as airborne laser swath mapping surveys expand this coverage, it will

Box 1 | The influence of life on Earth's evolution

When the Solar System was young, conditions at the surface of our planet were very different from what they are today. The Earth was being bombarded by chemically reactive comets and asteroids, and mantle convection was more vigorous while continental crust was accumulating[83–85]. The chemistries of the mantle, crust and atmosphere were co-evolving[83–85]. Life appears to have arisen by 3.5 billion years ago (although the earliest dates are controversial[86,87]) and there is evidence that by this time oceans and sediments had formed[84,85], despite the fact that the Sun's luminosity was ~30% lower than its present value. Today, such a large reduction in insolation would cause the oceans to freeze, and so the evidence that the early Earth was not frozen has prompted many proposed solutions to the 'faint young Sun paradox'[85]. It has been argued that before 3.5 Gyr ago, when impacts were common, the Earth was indeed frozen, as the impactors reacted with the atmosphere and consumed carbon dioxide that would have produced a greenhouse effect[83]. Some suggest that elevated levels of greenhouse gases, most notably methane, prevented freezing[83]. Methane sources may have included mantle degassing and impacting bodies[83,85]. Others have proposed that solar ultraviolet radiation would cause rapid loss of methane and ammonia, and instead early Earth had a carbon dioxide- and hydrogen-rich atmosphere[88]. Once methanogenic bacteria arose, the Earth may have been covered in a biogenic methane haze with surface temperatures higher than those we experience today[85]. With the rise of oxygen levels roughly 2.3 Gyr ago and the corresponding loss of methane, the first global glaciation occurred[84–86]. Biotic sequestration of carbon to form carbonate deposits and periodic release upon subduction may be the primary driver in the subsequent 'ice house'–'hot house' oscillations in climate[89,90]. Hence, the emergence of life on Earth seems to have fundamentally altered the evolution of the planet.

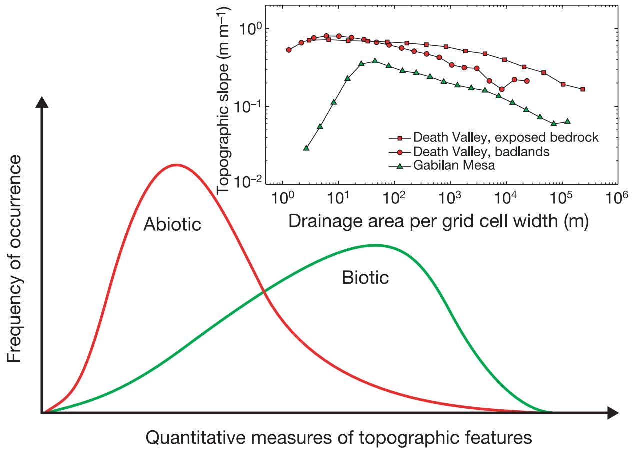

Figure 5 | Hypothetical frequency distributions of landform properties for the present Earth and an abiotic Earth. Whereas the same range of landform types would probably be present in both scenarios (provided the abiotic Earth retains its water, thereby permitting plate tectonics to occur), the frequency distributions of measurable landform properties (such as mountain height, steepness or curvature; the sinuosity of rivers; the extent of the landscape with a soil mantle; slope–area characteristics) might differ. Inset, relationships between slope (the magnitude of the topographic gradient) and drainage area per grid cell width for three landscapes. Biotic processes are of minimal erosional importance in areas of badlands and exposed bedrock in Death Valley, California, but are significant in the Gabilan Mesa, California, a landscape similar to that shown in Fig. 1. The differences between the slope–area relationships suggest several variables whose frequency distributions should differ in biotic and abiotic landscapes. Comparisons between landscapes with different spatial scales could also be made by normalizing the horizontal axis by topographic relief (the elevation difference between the highest and lowest points). Drainage area and slope were calculated from ALSM data with a horizontal resolution (grid cell width) of 2 m (provided by NCALM). Points are the mean slopes within logarithmically spaced, non-overlapping bins. Bars showing the standard errors of the binned values are smaller than the symbols. Areas sampled are 2.7 km^2 for Death Valley bedrock, 0.24 km^2 for Death Valley badlands, and 5.8 km^2 for the Gabilan Mesa.

become possible to define the frequency distributions of these attributes for Earth. Future missions to Mars will acquire data with sufficient resolution, and perhaps sufficient areal coverage, to permit a reasonably thorough survey of an abiotic landscape[63]. Hence, we cannot at present compare the distributions of slope–area attributes or other landscape properties in biotic and abiotic landscapes, but it may become possible to do so in the near future.

There may be a unique topographic signature of life at the submetre scale. Burrowing organisms often create small mounds at the surface (for example, gopher mounds, worm castings, termite mounds and crab mounds). When trees topple, their root systems can pull up wads of soil, creating pit-and-mound topography. Constructional biotic features might have distinct forms and densities of occurrence, but until the resolution of topographic data becomes at least an order of magnitude finer than what is currently available, such features will remain virtually undetectable. The largest biotic constructional features on Earth, coral reefs, are effectively life itself rather than the influence of life on topography, and hence are not considered here.

Once biotic processes are explicitly included in geomorphic transport laws, landscape evolution models can be used to perform numerical experiments that quantitatively explore the effects of life's presence or absence on landscape form, in a manner analogous to modelling the climatic effects of a twofold increase in atmospheric CO_2. Initial experiments of this kind[7], using current knowledge of geomorphic transport laws and approximations for the dynamics and erosional influence of vegetation, suggest that vegetation can affect landscape form by changing the dominant erosion process from overland flow under abiotic conditions to landsliding in well-vegetated states. While it may be difficult to test these predictions empirically on Earth, the ever-increasing volume of data for Mars should soon provide an opportunity for quantitative comparisons.

We currently lack most of the geomorphic transport laws required to formulate mechanistic landscape evolution models. Thus, the summary in Table 1 is both a tabulation of the current state of knowledge of geomorphic transport laws and, effectively, a list of future research directions. The role of biotic processes in existing laws is beginning to be quantified. Soil mass transport has been expressed in terms of the number density and energy expenditure of soil-moving organisms[64]. Field and modelling studies of the effects of fire[65,66] are revealing the role of vegetation in controlling the resisting forces in slope-dependent transport and shallow landsliding. Numerical experiments have begun to explore how vegetation influences erosion processes and landscape form[6,7]. These early efforts point the way towards a mechanistic understanding of the role of biotic processes in landscape evolution and the possibility of identifying the topographic signature of life.

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Acknowledgements Many colleagues offered advice and direction in preparation of this review, especially I. Fung, D. Schrag, N. Sleep, L. Sklar and L. Kump. A. Howard, D. Furbish, M. Power and G. Hilley gave comments on earlier drafts of the paper. M. Gabet made several suggestions. A. Kleidon shared unpublished data. N. Snyder and the NSF National Center for Airborne Laser Mapping provided the topographic data for Death Valley. Aspects of this work were supported by the NSF National Center for Earth Surface Dynamics, the NSF Graduate Research Fellowship Program, and NASA (for work in the Atacama Desert with R. Amundson).

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