thickness (squared correlation coefficient = 0.997). Another way of saying this is that the degree of cortical folding increases with total cortical area (i.e., larger brains tend to be more folded) but increases more rapidly for thinner cortices. Other scientists had noted previously that, as brains become larger and more folded, surface area increases faster than thickness (*5*), but none had captured the relationship as precisely.

To explain their observed scaling rule, Mota and Herculano-Houzel crumpled sheets of paper varying in both thickness and area. Remarkably, these paper balls obey the same general scaling law as the neocortex (see the figure): Their degree of folding increases with total surface area, but folding increases faster for thinner sheets. Moreover, the scaling exponent is nearly identical for crumpled paper and folded cortices. On the basis of these observations, Mota and Herculano-Houzel modeled both kinds of structures as self-avoiding (i.e., nonintersecting) surfaces that minimize their effective free energy, which means that the structures move to

"...paper balls obey the same general scaling law as the neocortex..."

minimize the balance of internal and external stresses until, eventually, equilibrium is reached. In the case of the paper balls, the crumpled balls relax after being compressed. In the case of the cortex, the stresses are mainly internal; according to Mota and Herculano-Houzel, they result mainly from the tension generated by axons that connect the growing gray matter to (and through) the underlying white matter (*6*).

Although the physics of paper balls has been explored in several previous studies (*7*), the analogy to cortical folding is a new scientific proposal. Most existing models of cortical folding involve the tangential expansion of an outer layer that is bonded to a more slowly growing central core (or deeper layer); swelling composite hydrogels are of this class (*8*), as are some computational models (*9*). Folding in these other models results not from external compression but from differential tangential expansion, which causes buckling of the more rapidly expanding outer layer; axonal tension is thought to play at best a minor role. Although Mota and Herculano-Houzel's proposal is sure to reinvigorate a long debate about the importance of axons in shaping cortical folds (*10*), axonal tension is not essential to their model (after all, the crumpled paper sheets do not have little strings attached to them). The critical element of almost all current models is that folding minimizes overall stress, however it is created.

The principal problem with the paper ball analogy is that it describes the folding of a structure that no longer grows, whereas the cortex folds during development. The scaling laws likewise only describe relationships between adult parameters. For example, Mota and Herculano-Houzel note that cortical folding occurs in any taxonomic group for which total cortical surface area increases faster than the square of cortical thickness. This scaling rule sounds like a developmental rule, but it describes only adult relationships and may result from a variety of different developmental mechanisms. For instance, cortical area may increase faster than the square root of cortical thickness if species with larger cortices expand the surface area of their cortical progenitor zone but retain the ancestral program for how to transform a patch of progenitor zone into adult gray matter (*11*). Alternatively (or in addition), species with larger cortices may change neuronal migration in such a way that a patch of ventricular zone gives rise to gray matter with an expanded surface area, relative to the ancestral condition (*12*, *13*). Either way, cortical surface in the adult would expand without increasing cortical thickness, thus fulfilling this adult scaling rule.

The larger message is that adult scaling laws do not reveal what evolutionary changes in development generate those laws. Mota and Herculano-Houzel have beautifully described some adult morphological relationships—what D'Arcy Thompson called "form"—but much more work is needed to explain what types of changes in development—or "growth"—gave rise to them. ■

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GEOMORPHOLOGY

Landscapes in the lab

A table-top experiment can probe the processes of landscape evolution

By **Scott W. McCoy**

Rivers dissect much of Earth's surface into conspicuous networks of valleys and hillslopes. Viewed from an airplane, these erosional networks might appear fractal; a close look at a part presents a view indistinguishable from the whole (*1*). But meter-scale topographic measurements reveal that the extent of landscape dissection by downcarving streams is finite and limited by the size of smooth, undissected hillslopes that separate adjacent valleys (*1*, *2*). Within a drainage basin, hillslopes commonly have a characteristic size (see the figure), yet across different landscapes this scale can vary from meters to a kilometer (*1*, *3*). What imposes this scale on a landscape, and why does it change from one landscape to another? On page 51 of this issue, Sweeney *et al.* (*4*) demonstrate using controlled laboratory experiments that landscape scale is set by a competition between river incision that cuts valley networks and diffusive hillslope processes that fill them in. Their experiments highlight that the extent of valley incision is an emergent, dynamic landscape characteristic that depends on a delicate balance of forces shaping the landscape.

More than a century ago, Davis (*5*) and Gilbert (*6*) proposed that the limit of landscape dissection, and the point at which valleys transition to hillslopes, emerges from a competition between hillslope processes that smooth the landscape and channel processes that cut valleys. Hillslope processes that cause soil creep are biotic (for example, animal burrowing or tree throw) or abiotic (for example, frost heave or rain splash). Channel processes derive their incisional power from the concentrated action of flowing water and debris.

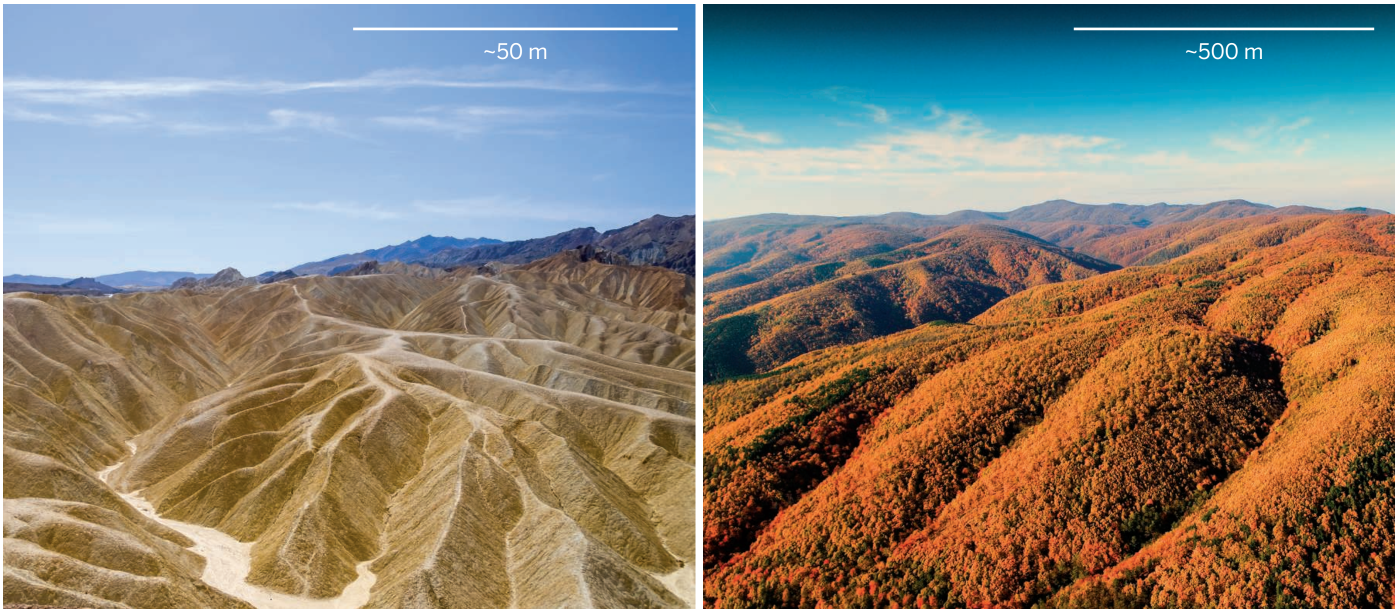
The evolution of soil-mantled landscapes can be modeled using an advection-diffusion equation derived by combining conservation of mass with physically based equations for sediment transport by creep and surface water flow (*7*). It has been shown (*2*, *3*) that the process competition of Davis can be encoded in one of the equation's nondimensional groups, its Péclet number, $Pe = KL^2/D$, which captures the relative vigor of advective channel processes, represented by the coefficient K, and diffusive hillslope processes, represented by D, at a given length scale, L. The framework predicts that in landscapes where Pe is larger at a chosen L, stream incision dominates erosion over an expanded fraction of the terrain; valley networks should be more extensive, and hillslopes should be smaller. Conversely, if Pe is smaller, stream incision dominates erosion over a reduced fraction of the terrain; hillslopes should be larger and the valley network less extensive. Perron *et al.* (*3*) showed, using a variety of soil-mantled field sites, that the theory predicted the characteristic size of hillslopes and valley spacing.

Before the experiments of Sweeney and colleagues, the advection-diffusion theory for the evolution of soil-mantled landscapes had not been subjected to tests in a controlled laboratory environment. Using a novel setup, Sweeney *et al.* added both diffusive and advective sediment transport processes into a controlled landscape evolution experiment. To produce hillslope disturbance mimicking soil creep, they bombarded the experimental landscape with large, energetic water drops that dislodged sediment upon impact. To produce channel incision without inducing additional hillslope transport, the landscape was misted. They then manipulated the relative rates of diffusive versus advective transport by changing the relative amount of water applied in the form of large drops versus mist. Precise control over imposed initial conditions, boundary conditions, and material properties, coupled with high temporal and spatial resolution topographic measurements, allowed them to document the emergence of hillslopes and valleys, as well as calculate time-averaged values for the process rate parameters, D and K. Sweeney *et al.* clearly demonstrate that the extent of valley incision increases with increasing values of Pe and, hence, is set by a balance between diffusive hillslope processes and advective channel processes, thereby confirming the theoretical predictions.

One implication of their results is that perturbations to this process-rate balance, driven by changes in climate or land use, for example, will change the reach of erosional valley networks. Thick, fertile soils and infrastructure are commonly located on soil-mantled hillslopes. Network expansion can transform fertile farmland into barren badlands by stripping away nourishing soil.

A topic of discussion regarding the experiments from Sweeney *et al.* will likely be the degree to which these miniature experiments are accurate models of real landscapes. A dynamic scale model for landscape evolution has never been realized (*8*), and the experiments conducted by Sweeney *et al.* are no exception. Scaling issues arise when squeezing an entire erosional network into a 0.5 m by 0.5 m box such that some care and caution may be needed before the results are declared definitive. But the benefits of controlled experimentation and the ability to manipulate a single variable while all others remain constant outweigh these scaling uncertainties (*8*).

Sweeney *et al.* add important experimental evidence demonstrating that the advective-diffusion equation is a useful description of how soil-mantled landscapes evolve and that the relative intensities of channel versus hillslope processes encoded in the Péclet number determine fundamental landscape properties. What is less clear, however, is the functional form of relationships that relate these important rate parameters, D and K, to measurable properties of process mechanics, climate, substrate, land use, life, and tectonics. Quantifying these relationships is necessary for geomorphology to be a truly predictive science. The experiments presented by Sweeney *et al.* point the way to opportunities in manipulated, controlled experimentation that should help to reveal controls on rate parameters as well as further probe the mechanics of landscape evolution. ■



A matter of scale. Sweeney *et al*. (*4*) show that the difference in scale that can arise between landscapes is because each landscape has a unique balance between the vigor of river incision that cuts valley networks and diffusive hillslope processes that fill them in.

PHOTOS: (LEFT) ELENA CHUKHLEBOVA/THINKSTOCK; (RIGHT) ROMULIC-STOJCIC/HORIZONTAL/LUMI IMAGES/CORBIS

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