Landsliding and Its Multiscale Influence on Mountainscapes

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Landsliding is a complex process that modifies mountainscapes worldwide. Its severe and sometimes long-lasting negative effects contrast with the less-documented positive effects on ecosystems, raising numerous questions about the dual role of landsliding, the feedbacks between biotic and geomorphic processes, and, ultimately, the ecological and evolutionary responses of organisms. We present a conceptual model in which feedbacks between biotic and geomorphic processes, landslides, and ecosystem attributes are hypothesized to drive the dynamics of mountain ecosystems at multiple scales. This model is used to integrate and synthesize a rich, but fragmented, body of literature generated in different disciplines, and to highlight the need for profitable collaborations between biologists and geoscientists. Such efforts should help identify attributes that contribute to the resilience of mountain ecosystems, and also should help in conservation, restoration, and hazard assessment. Given the sensitivity of mountains to land-use and global climate change, these endeavors are both relevant and timely.

Keywords: landslides, biotic and geomorphic processes, mountains, conservation

Mountains cover roughly 25% of Earth's terrestrial surface, yet they harbor a disproportionately large number of unique species and human cultures (Price and Butts 2000). Mountains also play an important, albeit poorly understood, role in hydroclimatic and biogeochemical cycles that directly or indirectly sustain the livelihood of many people around the world (Schröter et al. 2005). Among the processes that continuously modify mountainscapes, landsliding stands out because of its severe and long-lasting negative effects on natural and human-dominated ecosystems (figure 1). Yet landsliding may influence ecosystems in positive ways through its effect on biodiversity and ecosystem function, raising questions about its dual role in mountainscapes and about the nature of the feedbacks between geomorphic and biotic processes. Furthermore, because landsliding has influenced mountainscapes over millions of years, questions arise about the ways in which organisms, including humans, have adapted to these dynamic landscapes. Answers to these questions are important for two reasons. First, they should help identify attributes that contribute to the resilience of natural and human-dominated mountain ecosystems. Second, they should have direct practical implications for conservation, restoration, and hazard assessment.

There is mounting evidence that the frequency and magnitude of landsliding is changing in many parts of the world in response to climate change (Lateltin et al. 1997). This is not surprising, given that precipitation is one of the two external triggering mechanisms—the other being seismic activity—involved in the formation of landslides. Evidence from the past clearly indicates that cycles of elevated landslide activity have been followed by cycles of low activity, and that these are correlated with climate fluctuations over a variety of timescales (González-Diez et al. 1996, Thomas 2000).

What sets current changes in landslide activity apart is the likely influence of anthropogenic factors, either acting alone or in concert with climate, which can further modify the process of landsliding and the nature of ecosystem responses. Among these factors, deforestation and land-use change have the potential to influence the frequency and magnitude of landsliding because of their direct effects on vegetation attributes that influence slope stability (Sidle and Ochiai 2006). The extent and conditions under which mountain ecosystems are resilient to these changes—that is, the amount of disturbance they can absorb before changing into states with different structure and function (Holling 1996)—are not known. Addressing this issue is crucial for the long-term conservation of mountainscapes.

Figure 1. Landslides influence the diversity and functioning of natural and human-dominated ecosystems worldwide. Depending on the material removed (columns) and mode of movement (rows) they can be classified into various types (modified after Cruden and Varnes 1996). (a) Translational debris slides in protected forests in the Podocarpus National Park, Ecuador. (b) Rotational debris slide partly transformed by subsequent gully erosion in pasturelands near Pucara, Cajamarca, Peru. (c) Debris flow entering a river channel near Zamora, Ecuador. (d) Translational earth slide influencing fallowland and roads, Chiapas, Mexico. (e) Rotational earth slide in annual croplands in Mbale, Mount Elgon, Uganda. (f) Earth flow with deposition zone extending and obliterating a river channel near Cuenca, Ecuador. Not illustrated are landslides involving rocks. Photographs: Michael Richter (a–d) and Lievens Claessens (e, f).

The interactions outlined above are summarized in a conceptual model that emphasizes important feedbacks between geomorphic and biotic processes at multiple scales (figure 2). The various components of this model have been studied separately by scientists from different disciplines, who are in turn often pursuing answers to an equally diverse set of questions. We argue that it is through the integration and synthesis of this knowledge across different scales that we will begin to
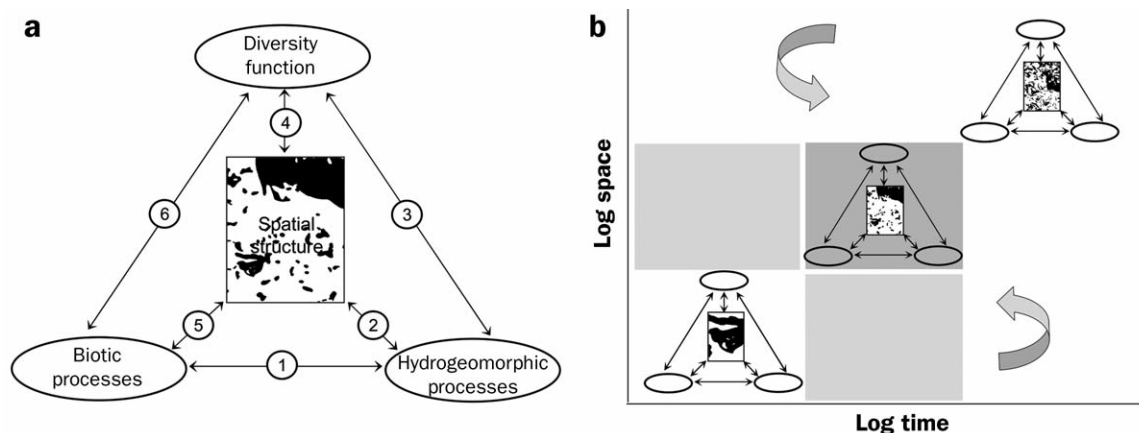
Figure 2. (a) Conceptual model illustrating the key elements (ovals and rectangle) and interactions among them (arrows) hypothesized to underlie the dynamics of mountainscapes mediated by landsliding. Human activities, such as deforestation, are included under biotic processes. (b) The same model placed in a space-time diagram to illustrate three scales at which these key components and interactions operate. The gray arrows represent cross-scale interactions, that is, the influence of one scale on another. At small scales (left and below the gray bars), interactions among neighboring slope units may determine the size, shape, and degree of spatial heterogeneity of individual landslides. At this scale, the availability of nutrients and propagules will influence landslide recovery rates, but landslide edges as well as landslide zones are likely to mediate the speed at which recovery occurs. Alien species may start their influence on landsliding at small scales. At intermediate scales (gray bars), the distribution of slopes, land cover, soils, and geologic substrates will determine the characteristics of landslide populations triggered by individual storms or earthquakes. At this scale, many of the same factors influencing the formation of landslides are likely to influence their recovery. For example, deforestation and land-use change may not only increase slope instability but also limit the availability of propagules to colonize landslides. At large scales (right and top of gray bars), the location of mountain ranges relative to zones of high rainfall or seismicity (or both) determines the frequency and magnitude of landsliding. Climate change has the potential to influence landsliding at this scale through its direct effect on regional patterns of rainfall and indirect effects on the distribution of organisms.

gain a deeper understanding of the large-scale dynamics of mountain ecosystems driven by landsliding.

We begin by reviewing a simple model of slope stability to establish a basic understanding of the biophysical processes underlying the formation of landslides (figure 2a, arrows 1–3), and proceed to characterize the resulting spatial structure of mountainscapes (figure 2a, center). We then examine the consequences of landsliding on the diversity and functioning of ecosystems, including recovery processes (figure 2a, arrows 4–6). In this section we show that most ecological work has focused on small scales (figure 2b, left), which contrast sharply with the scale at which humans may be altering the process of landsliding (figure 2b, center and right).

In the following sections, we describe the various mechanisms by which humans may directly and indirectly alter landsliding, and summarize strategies that have been developed to cope with landslides and conserve mountainscapes. We conclude by examining recent work that uses new tools and approaches to study landslides at large spatial and temporal scales, and we outline challenging avenues of ecological research on landsliding. We think that ecologists have an important yet largely unfulfilled contribution to make in understanding the feedbacks between biotic and hydrogeomorphic processes, of which landsliding is a prime example. This is particularly relevant in mountainscapes that are highly sensitive to human impacts at multiple scales, including altered land-use patterns and global climate change.

Landslide formation and the interaction between geomorphic and biotic processes

Landsliding is a complex process characterized by the downslope movement of vegetation, soil, saprolite, and rock under the influence of gravity. In dry environments, mass movements often involve rocks, whereas in humid environments they involve vegetation, soil, and deeply weathered bedrock. We focus mostly on humid environments because there the influence of biotic processes is most visible, and because these environments are the best studied.

A simple deterministic model can help show how biotic and geomorphic processes interact to drive the large-scale dynamics of mountainscapes influenced by landsliding (box 1; figure 2a, arrows 1 and 2). In this model, an individual and independent slope unit consisting of vegetation, soil, water, and saprolite resting on a slope is subject to two opposing forces: resisting forces and driving forces (box 1; Conforth 2005). A slope unit becomes susceptible to failure when the resisting and driving forces are of the same magnitude. At this stage, infiltrating rainfall or the ground acceleration of an earthquake can suddenly tip the balance between these two forces, inducing a slope unit to fail (box 1).

Box 1. Geomorphic thresholds in a vegetated world.

Slope stability analyses are performed using several approaches and incorporating vegetation attributes to different degrees. Of these, deterministic analyses that consider an individual and independent slope subject to limit equilibrium conditions (Conforth 2005) have been widely used to explore ways in which geomorphic and biotic attributes interact to increase or decrease slope stability (Sidle and Ochiai 2006). According to these analyses, any slope unit of vegetation soil, water, and saprolite along a slope is influenced by two groups of forces: those resisting failure (*S*, shear strength) and those driving instability (τ_f, stresses). The simplest of these models uses the ratio between these two sets of forces (*FS*, or factor of safety) to determine the likelihood of slope failure:

$$FS = \frac{S}{\tau_f} = \frac{C'/\cos\alpha + (\sigma_n - \mu)\tan\phi'}{\tau_f} \qquad (1)$$

When $FS \leq 1$, the slope unit is prone to failure, and it is assumed to be stable when $FS > 1$.

In general, the shear strength *S* is given in terms of the Coulomb failure criterion, in which the resisting force, *S*, is influenced by the effective cohesion or inherent strength (*C'*) and angle of internal friction (ϕ) of the soil, the normal stress (σ_n), the pore water pressure (μ), and the angle of the slope (α). Normal stress represents the perpendicular component of the weight of the material (*W*) at the point of failure, and the pore water pressure, the upward pressure exerted by the column of water (light gray in the figure below) once it starts to build up above the plane of failure during prolonged rainstorms. The driving force, τ_f, includes the contribution of the weight of the slope material *W* and seismic accelerations.

Plants can modify the mechanical and hydrological properties of soil, saprolite, and bedrock, all of which are important for slope stability. Examples of the former include (a) root reinforcement of soil; (b) root extension into joints and fractures in bedrock, contributing to physical and chemical weathering rates; and (c) vegetation weight, which contributes to surcharge. Examples of the latter include (d) rainfall interception, (e) water infiltration rates, and (f) evapotranspiration rates. Of these factors, (a) and (c) have received the most attention from geomorphologists, engineers, and foresters (for a review, see Sidle and Ochiai 2006). Equation 1 can be modified to incorporate (a) and (c) plus an earthquake component:

$$FS = \frac{C' + \Delta C + \left[(s' + b')(\cos^2\alpha - A\sin\alpha) - (w')(\cos^2\alpha)\right]\tan\phi'}{(s' + b')(\sin\alpha\cos\alpha + A\cos\alpha)}, \qquad (2)$$

where ΔC is the soil cohesion attributable to roots, *b'* is total plant biomass expressed as mass per unit area or force, and *A* is the horizontal acceleration component of earthquakes. The variables *s'* and *w'* are simplified notations for the unit weight of soil and water in the soil column.

The above version of *FS* shows how earthquakes and rainfall may increase the gravitational load and decrease soil strength, respectively, and why they are called landslide-triggering mechanisms. In addition, it shows the importance of soil attributes (*C* and ϕ) on slope stability; these attributes are known to vary with geological substrate and weathering products. Last, plant attributes influencing soil strength and gravitational load change as a function of multiple factors, including plant and stand age, substrate characteristics, and species composition. Most likely, these attributes also influence soil hydrological properties as well as weathering rates.

The approach outlined above illustrates the various ways in which geomorphic and ecological processes may interact, but it may have several limitations because many of the assumptions underlying such analyses may not hold when applied over large areas. Moreover, it can be difficult to obtain reliable values for the various parameters included in such models.
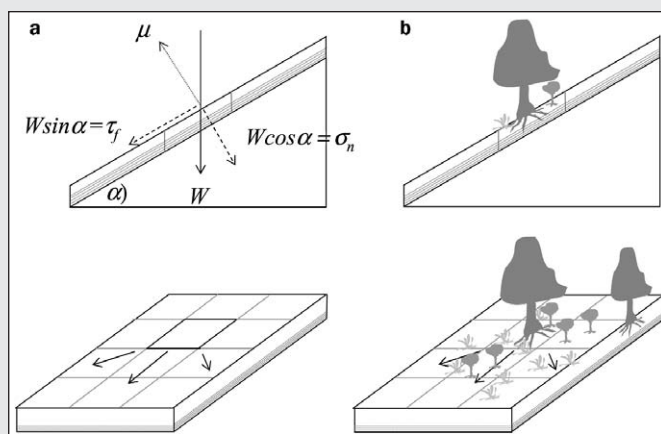
The forces operating on any slope unit (represented by grid cells in this diagram) differ in a world (a) devoid of vegetation and (b) with vegetation. Whereas the distribution and connectivity of multiple slope units that fail simultaneously will determine the size of individual landslides and spatial heterogeneity therein, the conditions of the set of slopes affected by a given storm or earthquake will determine the number, size, and spatial distribution of landslides formed at any given time. The light gray zone represents the upward pressure exerted by the column of water once it starts to build up above the plane of failure during prolonged rainstorms.

Vegetation can modify the magnitude of these forces and thus the threshold conditions that lead to slope instability, and when integrated over a landscape, it can also modify the spatial distribution of landslides (box 1). This raises the possibility that ecological and evolutionary processes could be operating to select traits that contribute to plant persistence on unstable slopes (figure 2a, arrow 3). Studies investigating the mechanical properties of plant roots (box 1) have shown that root strength is highly variable among species, functional groups, and vegetation types (Sidle and Ochiai 2006, Stokes et al. 2007). Root strength is a function of the tensile strength, density, and architecture of roots, attributes known to be phenotypically plastic and genetically variable, and therefore likely to be subjected to evolutionary forces. Other studies have advanced the concept of "landslide immunity" to describe the absence of landslide activity in areas already affected by landslides (Shimokawa 1984). This condition may result when soils and vegetation have not reached the threshold conditions for failure under the influence of rainfall or seismic events of a given frequency and magnitude. Therefore, lengthy ecosystem development after a landslide, relative to the frequency of triggering mechanisms, may protect against further landslides.

Landslides and the spatial structure of mountainscapes

Landsliding leaves a characteristic spatial signature that is likely to play a key role in the dynamics of mountainscapes and in the life of an unknown number of organisms (figure 2a, center). Because landslides represent suitable habitat patches for some species, they have important consequences for the diversity and functioning of ecosystems. Characterizing the spatial signature of landslides will help put the ecological work that will follow into a spatial context (figure 3).

At the scale of individual landslides, the down-slope movement of material produces zones that are quite distinctive from their surroundings (figure 3a–3c). The initial failure zone, commonly known as the scar, typically has the steepest slope and is the area from which vegetation, soil, and saprolite are removed. The deposition zone, or toe, develops in more gentle slopes, and this is where the majority of the displaced material comes to rest. In some instances, a distinctive transport zone or chute forms when additional material is scoured between the initiation and deposition zones (Martin et al. 2002). In addition to this down-slope gradient in environmental conditions, the removal of vegetation and soil also creates horizontal gradients between the center of a landslide and the nearby undisturbed substrate. Conditions are usually the mildest at the edges of a landslide, and the harshest at the center.

At an intermediate scale, the tens to thousands of landslides triggered by single rainstorms or earthquakes collectively belong to a population of landslides (figure 3d–3g). At this scale, differences among, rather than within, individual landslides may become more important for understanding the influence of landsliding on mountainscapes. Landslides within a population may vary greatly in the type of material

mobilized and their mode of movement (figure 1; e.g., Cruden and Varnes 1996), morphology (Crozier 1973), size (Stark and Hovius 2001), and spatial distribution. The first two attributes, which are widely used by geomorphologists to classify landslides, may reveal something about prevailing climates and bedrock weathering rates—two factors that influence and may be influenced by vegetation—and the processes behind landslide formation (box 1). Landslide size, on the other hand, can be used to describe the integrated effect of the many small and the few large landslides in any given population (Stark and Hovius 2001). In particular, the inverse cumulative density functions of landslide size often take the form of a power law (figure 3g), a property also observed in theoretical systems that are far from equilibrium and that self-organize into a critical state (Bak et al. 1988). One possibility is that mountainscapes may have the same properties as these systems, and if this is true, we might have a powerful theoretical framework to look at mountains in different ways.

Landslide populations can also be characterized by their spatial arrangement, including relationships with the location and magnitude of triggering events and a diverse array of landscape variables (figure 3e, 3f). For example, landslide density may be highest near the epicenter of an earthquake or on certain lithologies and land covers (Murthy et al. 2004, Meunier et al. 2007). On the other hand, the distribution of landslides relative to stream networks can be important for understanding linkages between the hill slope and fluvial systems (Korup 2005), and therefore their extended influence on mountain ecosystems (Reeves 1995).

At large scales, landslide populations overlap in space and time because of the recurrence of rainfall and seismic landslide-triggering events in the same region (figure 3h–3j). We refer to these overlapping populations as landslide assemblages. In Central America, for example, within a 110-year period at least 56 earthquakes and 6 storms triggered populations of landslides, each consisting of hundreds to thousands of landslides that denuded areas ranging from 3 to 383 square kilometers (figure 3i; Restrepo and Alvarez 2006). At this scale, the influence of landsliding on ecosystems can be expressed in terms of magnitude-frequency curves that relate the total area denuded by landslides to the frequency of triggering events of known magnitude (figure 3j; Wolman and Miller 1960, Garwood et al. 1979). We foresee that the increasing availability of remote-sensing data will help characterize the dynamics of landsliding in realistic ways.

Landslides, ecosystem function, and diversity

The spatial and temporal variability of landslides, whether at the individual, population, or assemblage level, is likely to influence ecosystem function and diversity in profound ways (figure 2a, arrows 4–6). First, landsliding, unlike other disturbances (Pickett and White 1985), transforms substrates in complex ways through the sudden down-slope transport of vegetation, soil, and saprolite (Furian et al. 1999, Geertsema and Pojar 2007). Second, landsliding results in highly heterogeneous landscapes in which landslide size and proximity may

Individual landslides
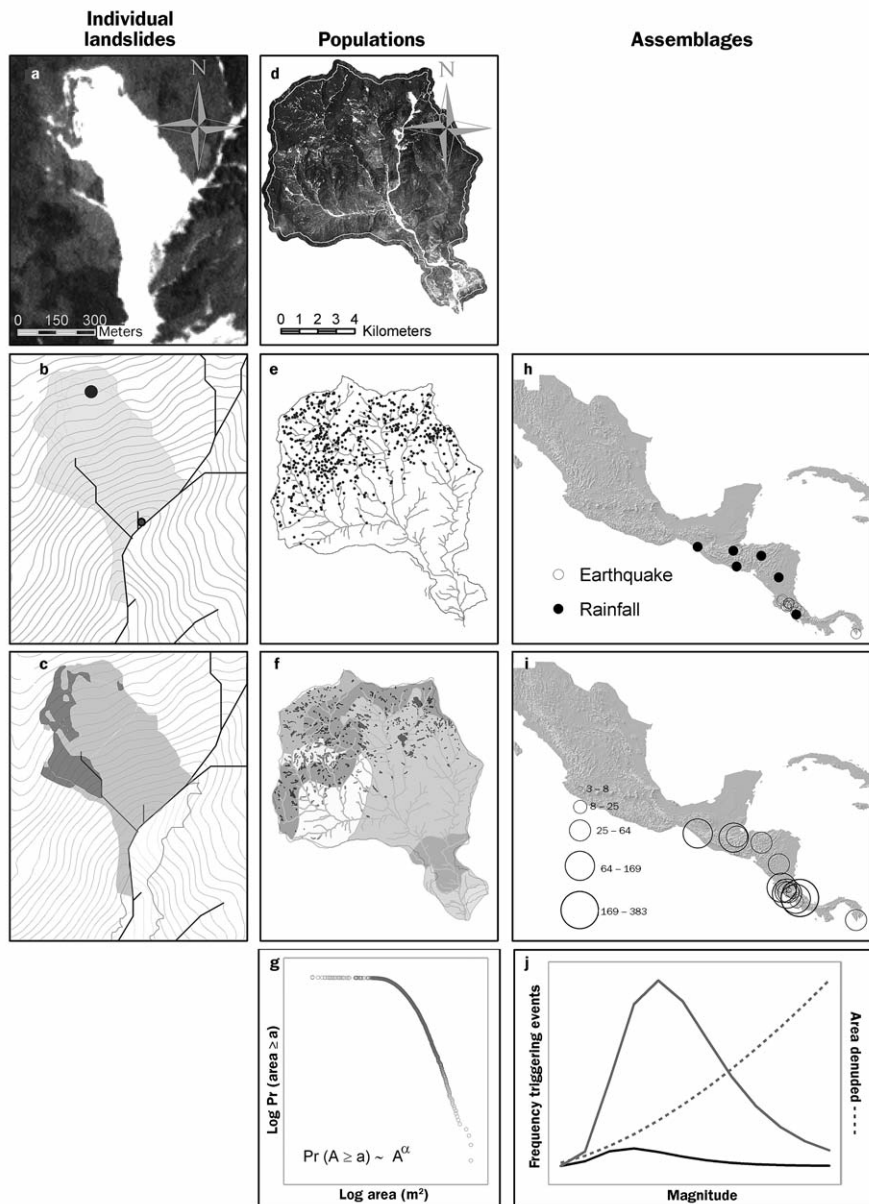
Populations

Assemblages

Figure 3. Landslides can be examined as (a–c) individual events, (d–f) populations triggered by known rainfall or earthquake events (or both), and (g–i) assemblages triggered in a given region by multiple rainfall and earthquake events. (a) A large landslide triggered in 1998 by Hurricane Mitch, Sierra de Las Minas, Guatemala. Landslide initiation or deposition zones may be mapped as (b) points or (c) polygons. In (c), the initiation, or source, shows the newly exposed substrates (light gray), as well as island-like patches of vegetation and organic material (dark gray) that contribute greatly to the within-landslide heterogeneity. (d) A subsample of a large population of landslides (> 6000) triggered by a hurricane in the Sierra de las Minas, Guatemala. Mapping (e) the initiation points or (f) the landslides themselves may help understanding the causes of landsliding, the functional role of landslides in mountainscapes, and their statistical and spatial attributes. (g) Inverse cumulative distribution of landslides triggered by the Guatemala's 1976 earthquake with the epicenter at the Sierra de las Minas. The power-law behavior (straight line) describing the enormous variability in size represents an emergent property of systems that self-organize into a nonequilibrium state. (h) During the last 50 years, storms (filled circles) and earthquakes (open circles) of variable magnitude have triggered multiple populations of landslides in Central America. (i) The populations of landslides described in (h) differ in terms of the total denuded area represented by the size of the circles. (j) Magnitude-frequency curves (continuous, dark gray line) provide an estimate of the overall impact of landsliding on mountainscapes. These curves are obtained by multiplying the functions describing the distribution of landslide-triggering event magnitudes (continuous, black line) and the relationship between triggering-event magnitudes and the total area denuded by them (discontinuous, dark gray line).

influence the movement of organisms and ecosystem development (Hupp 1983), as has been documented for other disturbances (Paine and Levin 1981). Third, ecosystems reorganize on these quasi-primary substrates, and this entails the rejuvenation of soils and the colonization of landslides by an unknown array of organisms (Walker et al. 1996, Wilcke et al. 2003).

The study of individual landslides, including chronosequences, from which temporal change is inferred, has so far generated most of the data upon which we base our understanding of the influence of landslides on ecosystem function and diversity. In particular, soil formation and propagule dispersal vary greatly within landslides, mirroring the existing horizontal and down-slope environmental gradients. Landslide edges often have relatively fertile and humid soils compared with the center, which might be more deeply or frequently scoured (Walker et al. 1996). Plant propagules may be more abundant at the edges than at the center of the landslide because dispersal is limited (Walker et al. 1996, Velázquez and Gómez-Sal 2007). For plants that are dependent on vertebrates for seed dispersal, landslide edges may prevent the movement of propagules altogether if vertebrates do not move across them, and this may delay colonization rates at the center of landslides (Samaniego 2003, Shiels and Walker 2003). Likewise, the initiation

zone of a landslide typically has mineral-rich, poorly weathered substrates, and the arrival of propagules may become crucial for plant recovery because of minimal biological legacy and continued small-scale erosion (Guariguata 1990). On the other hand, the deposition zones have a relatively high content of organic matter that reflects the rich mixture of displaced vegetation, soil, and saprolite. Here, the presence of a seed bank and plant remains with vegetative growth may quicken plant recovery rates (Guariguata 1990, Wilcke et al. 2003). Ultimately, these differences in soil conditions and propagule dispersal may explain species preferences within individual landslides, as shown by work in Brazil's Mata Atlántica (box 2).

Ecosystems reorganize on landslides over time. Studies documenting changes in species composition and abundance over short timescales (< 5 years) show that species trajectories, and therefore some assemblage-level attributes, may vary widely, and sometimes in unpredictable ways (Dale et al. 2005, Velázquez and Gómez-Sal 2007). Additionally, in some temperate sites, tree species that are characteristic of nearby mature forests can potentially colonize and establish within months after landslide formation (Hupp 1983, Dale et al. 2005), and trees characteristic of early succession may persist for more than 70 years, albeit with no recruitment (Mark and Dickinson 1989). On the other hand, studies examining changes in species richness (Dale et al. 2005), plant abundance (Lundgren 1978, Mark and Dickinson 1989), or soil nutrients (Zarin and Johnson 1995) over long time scales (≥ 5 years) show nonlinear, often predictable trajectories (figure 4a, top).

The form of these trajectories may be explained by time lags introduced by the changing nature of the interactions taking place among organisms, as well as by feedbacks between the biota and substrate attributes. For example, the colonization

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Box 2. Landslide heterogeneity influences palm demography in Brazil's Serra do Mar.

The Serra do Mar, located in southeastern Brazil within the Mata Atlántica, is a mountain range well known for its high diversity, endemism, and documented history of landsliding. Large storms during the austral summer season, together with sandy, loamy soils with local thicknesses up to 15 meters derived from deeply weathered Precambrian rocks, largely explain landslide prevalence (Furian et al. 1999). In February 1996, severe landsliding in the Santa Virginia Reserve provided a unique opportunity to investigate the role of landslide heterogeneity on palm demography. Seedlings, juveniles, and adults of five palm species were censused in 2006 in two landslides triggered in 1996 and two adjacent undisturbed forest sites and classified according to habitat (landslide edge and forest interior) and slope position (middle and bottom) (Bastos-Neto and Fisch 2007). The abundance of these five species and their patterns of regeneration differed in the 10-year-old landslide areas and forest sites. Seedlings of *Euterpe edulis* and *Geonoma schottiana* were more abundant in the forest interior than on the landslide-edge plots; within the forest interior, the seedlings were most abundant in valleys. As juveniles and adults, they became more abundant at landslide edges. These results suggest that *E. edulis* and *G. schottiana* experience dispersal limitation into landslides, but once there, they benefit from landslide conditions. On the other hand, seedlings, juveniles, and adults of *Geonoma gamiova* were more abundant in the forest interior than at the landslide edge; as these palms aged, however, proportionally more individuals were found at forest interior plots primarily on the slopes rather than in the valleys. Although *G. gamiova* seedlings established along landslide edges, their reduced survival at later stages suggests that this species avoids landslides.
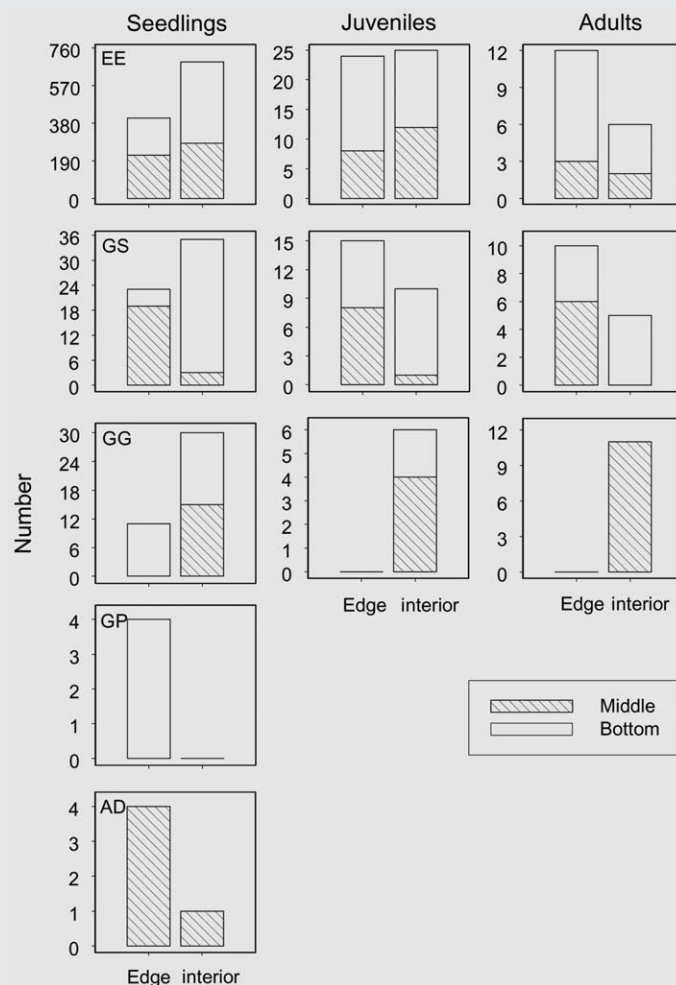
Abundance of five palm species as a function of habitat (landslide edge [edge] and adjacent forest [interior]) and slope position (middle and bottom). The species regenerating on landslides in the Serra do Mar include Geonoma schottiana *(GS),* Euterpe edulis *(EE),* Geonoma gamiova *(GG),* Geonoma pohliana *(GP), and* Attalea dubia *(AD).*
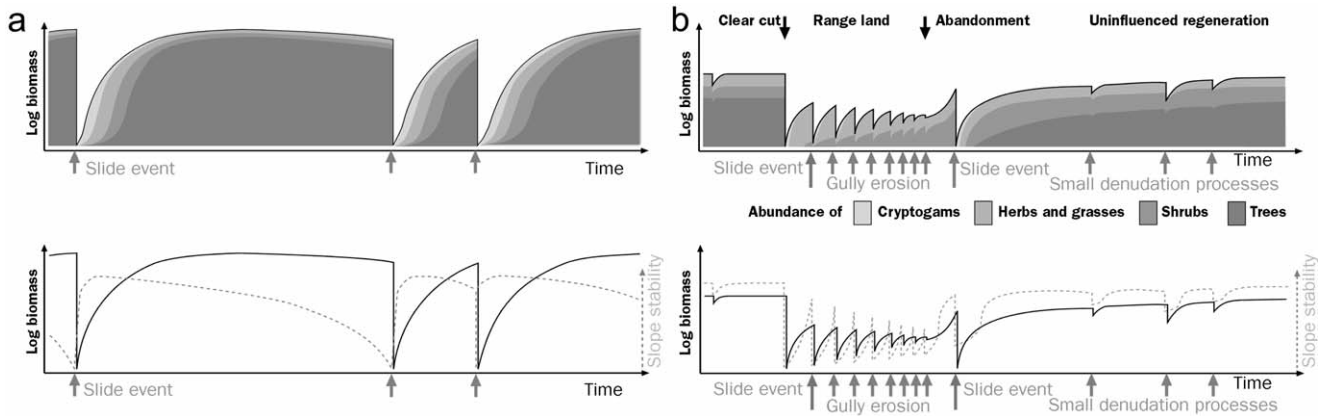

Figure 4. Ecosystems develop on quasi-primary substrates generated by landsliding activity. The top figures illustrate the non-linear trajectories describing changes in the abundance of different functional groups of plants through time (area under each curve) in (a) montane rain forest and (b) pastures or areas dominated by annual crops in drier environments. Note that cryptograms, common early colonizers of landslides, are generally absent from landslides in pastures. The bottom figures illustrate the relationship between total plant biomass (solid black line) and slope stability (dotted gray line) for each of the two environments. In (a), biomass may increase surcharge and therefore the driving forces leading to slope instability. In (b), reduced biomass following human influences on the landscape may lead to the formation of translational landslides and subsequent interactions with sheet erosion, gullying, and further landsliding. The arrows indicate the occurrence of landslide-triggering events that may result in the fast, and almost total, removal of vegetation and soil from slopes. The timescale in (a) is on the order of centuries, and in (b), decades.

of landslides by propagules and the *in situ* growth of surviving plants represent crucial aboveground processes that mark the beginning of ecosystem development in the Luquillo Mountains of Puerto Rico (Walker et al. 1996). Birds and bats commonly introduce late successional species, especially if perches are available (Shiels and Walker 2003). In other instances, the vegetative propagation of forking ferns (*Dicranopteris*) may delay forest development on landslides for decades. Later, dense stands of tree ferns and other landslide colonizers such as *Cecropia, Piper,* or *Miconia* tend to inhibit the growth of grasses and herbs, thereby indirectly facilitating the establishment of later successional trees. These changes are mirrored by those that take place belowground and manifest themselves as an increase in carbon and nitrogen and a decline in phosphorus as landslides age (Zarin and Johnson 1995).

Differences in initial abiotic and biotic conditions within landslides may produce divergent developmental trajectories, as shown in the Luquillo Mountains of Puerto Rico. Here, a landslide chronosequence revealed that slight differences in adult plant density and seedling abundance between the deposition and initiation zones were magnified through time (Guariguata 1990). Similarly, in Nicaragua, a study of a single large landslide spanning a wide elevation range (250 to 1090 meters) showed that species richness and composition, as well as plant size, diverged considerably among landslide zones during the first four years of ecosystem development (Velázquez and Gómez-Sal 2008). More broadly speaking, the time that it takes a given attribute to reach prelandslide levels (represented in figure 4a by the point at which no further changes are observable) may be used as a measure of

stability, but as table 1 shows, these times vary greatly among sites and ecosystem attributes. This concept of stability, however, may lose its relevance in view of the influence of deforestation, land use, and climatic change, which maintain the system in a permanent transient state.

Studies at the scale of landslide populations and assemblages are scarce, yet the greater availability of spatial data and modeling tools may open new possibilities for addressing questions at these scales. Field studies indicate that there is enormous variation in plant and ecosystem responses among landslides in any given population or assemblage. For example, more than 100 landslides triggered by a storm (rainfall intensity of approximately 17 millimeters per hour) in 2003 were distributed across a wide elevation gradient and different lithologies in the Luquillo Mountains of Puerto Rico (Shiels et al. 2008). A subsample of landslides from this population revealed that major differences in soil characteristics (e.g., soil nitrogen, particle size, water-holding capacity) accounted for differences in plant life form, patterns of litterfall, and the accumulation of plant biomass (Shiels et al. 2008). Similarly, in Ecuador's Podocarpus National Park, species composition varied greatly in an assemblage of 92 landslides, reflecting to some extent well-known environmental gradients (box 3).

Such studies suggest that landslides are important for many organisms that regenerate and complete most, if not all, of their life cycles on them (boxes 2, 3; Kessler 1999). Landslides represent new and ephemeral substrates characterized by increased solar radiation and variable nutrient conditions and substrate stability (Shiels et al. 2006). Pioneer species such as *Cecropia* may benefit from landslides because their seeds germinate when exposed to more light and a

Table 1. Recovery time (years) to prelandslide levels of various ecosystem-level attributes.

Ecosystem attribute	Subtropical lower montane forest (reference)	Temperate moist oak forest (reference)	Temperate pine forest (reference)	Temperate rain forest (reference)
Tree-stem density		> 40 (Pandey and Singh 1985)		78 (Mark and Dickinson 1989)
Tree basal area	Approximately 52[a] (Guariguata 1990)	> 40 (Pandey and Singh 1985)		> 100 (Mark and Dickinson 1989)
Stand-level basal area	> 124 (Restrepo et al. 2003)	> 40 (Pandey and Singh 1985), > 120 (Reddy and Singh 1993)	> 25 (Restrepo et al. 2003)	
Soil nutrients				
Nitrogen	Approximately 37 (Zarin and Johnson 1995)	Approximately 40 (Pandey and Singh 1985); approximately 120 (Reddy and Singh 1993)	> 25 (Reddy and Singh 1993)	
Carbon	> 59 (Zarin and Johnson 1995)	Approximately 40 (Pandey and Singh 1985); 35 (Reddy and Singh 1993)	Approximately 25 (Reddy and Singh 1993)	
Phosphorus		Approximately 40 (Pandey and Singh 1985); 60 (Reddy and Singh 1993)	Approximately 25 (Reddy and Singh 1993)	

Note: All of the studies cited, except the one by Mark and Dickinson (1989), are based on chronosequence studies.
a. Deposition zone.

higher temperature. Hardy perennials, such as forking ferns (*Dicranopteris, Diplopterygium,* and *Sticherus* in the Gleicheniaceae), bamboos (*Chusquea*), and blackberry (*Rubus*), benefit in the dry and unstable conditions found in the initiation zones of landslides because they can outcompete more ephemeral plants through extensive vegetative growth (Miles and Swanson 1986, Walker et al. 1996, Kessler 1999). On the other hand, in the stable, high-nutrient conditions of the deposition zones, fast-growing trees may rapidly increase in abundance (e.g., *Trema micrantha* in Central America; Velázquez and Gómez-Sal 2007). In other instances, plants colonizing landslides (e.g., *Desmodium, Alnus,* several Ericaceae; box 3) adapt to the altered soil nutrient conditions by developing symbiotic (Dale et al. 2005) and parasitic (*Gaidendron punctatum*; box 3) relationships.

Landsliding is influenced by human activities

Humans have influenced the process of landsliding in different ways and at multiple scales (figures 2b, 4b). Exotic species (figure 2a, top) are an example of a small-scale influence that can potentially propagate at larger scales (figure 2a, arrow 3). The tree *Miconia calvescens* was introduced to Tahiti in the early 1900s as an ornamental species and now covers two-thirds of the island (Meyer and Florence 1996). A combination of fast growth rates and shallow root systems has led to the formation of dense, extensive stands of *M. calvescens* that may have reduced the magnitude of the forces contributing to slope stability, and ultimately increased the frequency of landsliding (Meyer and Florence 1996). The grass *Hyparrhenia rufa* was introduced for cattle fodder in Central America, and now it is widely spread in dry parts of that continent. Its perennial habits, fast growth, and resistance to fire may explain why it became the most abundant grass colonizing Nicaragua's Casita landslide, which was triggered by Hurricane Mitch in 1998 (Velázquez and Gómez-Sal 2007). This species appeared at elevations higher than those at which it normally occurs;

it most likely contributed to the spread of human-induced fires into the landslide, thereby influencing vegetation recovery and promoting grass-fire cycles that make this species progressively more abundant.

Humans may also influence landsliding through the small-scale modification of natural disturbance regimes resulting from deliberate changes in species composition (figure 2, arrow 6). In the fire-prone ecosystems of southern California, slope aspect strongly influences vegetation and fire regimes. In particular, the northerly, mesic slopes are covered by broad-leaved chaparral, and the southerly, more xeric slopes by sagebrush (Rice et al. 1969). The replacement of sagebrush by perennial and annual grasses in an effort to reduce surface erosion following fire led to extensive landsliding after major winter storms in the mid 1960s. In addition, unconverted areas of chamise and sagebrush exhibited a higher density of landslides than broad-leaved chaparral.

Road construction influences landsliding directly and indirectly through the modification of land cover and hydrogeomophic processes, respectively (figure 2a, center and bottom left). This includes the creation of new and unstable surfaces, the undercutting of hillslopes, the modification of hill-slope hydrology, and ground shaking (box 1). The consequences of a higher density of road-associated landslides include soil losses (25 to 350 times higher than in undisturbed forest; Sidle et al. 2006), changes in ecosystem processes (Shiels et al. 2008), and the arrival and establishment of exotic species, which is of particular concern in protected areas. Although road construction may represent a small- to intermediate-scale human influence on landsliding, the worldwide expansion of road networks in mountainous terrain has the potential to make this influence global.

Land-use change, which operates at intermediate scales, is perhaps the most-cited human influence on landsliding. Land-use change not only involves changes in species composition and ecosystem function (figure 2a, top), but, most

Box 3. Landslide assemblages and species composition in Ecuador's Podocarpus National Park.

The Podocarpus National Park (PNP), located in the Cordillera Real of southeastern Ecuador, is characterized by steep temperature and precipitation gradients. Depending on the elevation of the site, the eastern flank draining into the Amazon basin may receive between 2000 and 6000 millimeters (mm) or more of total annual precipitation, whereas the western flank draining into the Inter-Andean valley of Ecuador receives between 750 and 4000 mm. The PNP is underlain by Paleozoic schists and sandstones, which make the terrain highly susceptible to slope failure. The construction of roads and conversion of forests into pastures dominated by exotic species have added an

additional layer of complexity. Sampling of all plants in plots established on landslides in natural (92 landslides, 115 plots in forest areas within the PNP; 2100–3200 meters [m]; landslides in undisturbed areas) and human-disturbed (43 landslides, 104 plots, in buffer areas of the PNP and roads; 1900–2800 m; landslides in disturbed areas) habitats yielded a total of 231 species, 7 of which were found in more than 75 plots, and 100 of which were found only once (Lozano and Bussmann 2005). A detrended correspondence analysis separated the plots on the basis of presence/absence data, and further cluster and regression tree analyses grouped them into 14 clusters that could be distinguished by their location along the northeast-southwest precipitation gradient (plots located on the eastern versus western flank of the cordillera), degree of disturbance (natural versus human-disturbed habitats), and elevation (low versus high elevation). The latter variable was important for characterizing plots at finer scales (tips of the regression tree). The species that were highly correlated with the ordination axes may represent suites of species adapted to landslide conditions along the complex environmental conditions of the PNP.
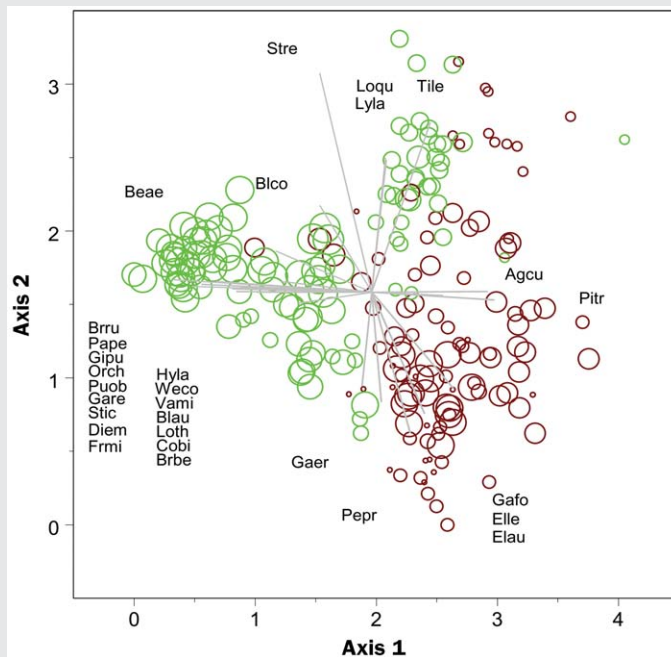
Bivariate plots classified according to cluster affiliation (14 clusters, indicated by different-sized circles) and degree of disturbance (natural [green] and human-disturbed [red] habitats). The gray lines represent the species that were highly correlated with the axes: Agcu (Ageratina cutervensis), Beae (Bejaria aestuans), Blau (Blechnum auratum), Blco (Blechnum cordatum), Brbe (Brachyotum bentharnianum), Brru (Brachyotum rugosum), Cobi (Cortaderia bifida), Diem (Disterigma empetrifolium), Elle (Elaphoglossum lepidotum), Elau (Elleanthus aurantiacus), Frmi (Freziera minima), Gapu (Gaiadendron punctatum), Gafo (Gaultheria foliolosa), Gare (Gaultheria reticulata), Gaer (Gaultheria erecta), Hyla (Hypericum lancioides), Lygl (Lycopodiella glaucescens), Loqu (Lophosoria quadripinnata), Loth (Loricaria thyoides), Otch (Orthosanthus chimborancensis), Pape (Paepalanthus ensifolius), Pepr (Pernettya prostrata), Pitr (Pitcairnia trianae), Puob (Puya obconica), Stre (Sticherus revolutus), Stic (Stipa ichu), Tile (Tibouchina lepidota), Vami (Valeriana microphylla), and Weco (Weinmannia cochensis).

important, it modifies landscape structure (figure 2a, middle) and therefore the propagation of slope instability along hillslopes (box 1). In addition, changes in land use may delay the recovery of ecosystems in landslide areas, and this may enhance other processes such as gully erosion (figure 4b).

Surprisingly, there are contradictory reports about landslide prevalence under different land uses in mountainscapes. In many instances it has been shown that slope instability and the total area affected by landslides may increase in areas where forests are managed for timber production or converted to other land uses (figure 1; Sidle et al. 2006). In other instances, however, landslide activity may be higher under dense natural forest cover than in areas affected by human activities (Pain and Bowler 1973), or it may vary depending on forest age and type (Crozier et al. 1981, Murthy et al. 2004). The loss

of the effective root strength that vegetation imparts to the soil is the mechanism behind the greater density of landslides after logging or the conversion of forest to other land uses (box 1; Sidle and Ochiai 2006, Sidle et al. 2006). Soil cohesion attributed to root strength may decrease as roots die and decay, and in temperate areas these effects may be noticed over prolonged periods of time (15 to 100 years; Schmidt et al. 2001, Sidle et al. 2006).

Last, human-induced climate change can alter landsliding regimes (Lateltin et al. 1997) through its direct influence on hydrogeomorphic and biotic processes (figure 2a, bottom). Changes in precipitation patterns over a variety of timescales are correlated with cyclical patterns in landslide activity (González-Diez et al. 1996, Thomas 2000). Yet some of this variability may be attributable to the direct influence of cli-

mate on biome distribution, and ultimately to plant properties controlling slope stability.

Landsliding and the conservation of mountainscapes

Landsliding poses numerous challenges for the management and conservation of mountainscapes. The productivity of human-dominated ecosystems, whether for timber, agriculture, cattle, or water production, may decrease as a result of increased landsliding. Also, losses of infrastructure and human lives are an undeniable consequence of landsliding. Management strategies have therefore emphasized slope stabilization, including the control of soil losses and sediment production, as well as elaboration of hazard assessment plans (Luckman et al. 1999, Stokes et al. 2007). These and other studies have revealed the importance of plant diversity at the level of root systems, functional groups, and stand age, and of planting and harvesting practices to manage landsliding in human-dominated ecosystems.

In areas little affected by human activities, such as those targeted for the conservation of biodiversity, ecosystem function, and landscape structuring processes, landsliding is also perceived as having negative effects on ecosystems. Not surprisingly, a variety of pre- and postlandslide conservation strategies have been proposed to prevent or ameliorate the effects of landsliding activity. Prelandslide conservation includes road decommissioning (Davis et al. 2004), whereas postlandslide conservation includes various restoration techniques aimed at stabilizing the soil and accelerating the revegetation of landslides through the construction of retention walls (Sidle and Ochiai 2006), the application of organic and inorganic fertilizers (Shiels et al. 2006), hand and aerial seeding with fast-growing species (Davis et al. 2004), outplanting of late successional species (Davis et al. 2004), the promotion of natural seed dispersers (Shiels and Walker 2003), and the removal of species that may arrest succession (Walker et al. 1996). Yet measures to accelerate conditions to mature stages of development may take away the ecological benefits of succession and greatly reduce the heterogeneity and diversity of the landslide-dominated area. Therefore, the implementation of any of these techniques in protected areas should be preceded by studies that consider the impact of these activities on the species that establish and thrive on landslides and on the rates of ecosystem processes, which can ultimately have an impact on "landslide immunity" (figure 4).

New tools and approaches

The greater availability of remotely sensed data and the development of spatial modeling tools and GIS (geographic information system) techniques have made it possible to begin to address several questions at the levels of landslide populations and assemblages. A first set of studies has successfully examined landslide vegetation recovery rates in the Andes of northwestern Argentina (Paolini 2006), the Jou-Jou mountains of Taiwan (Lin et al. 2004), and Lyell Island in Canada (Davis et al. 2004). In the first study, a combination of mul-titemporal Landsat TM and ETM+ images with dendrochronological data revealed a reduction in the number of landslides over a 16-year period that was consistent with a decrease in precipitation in the area. This work also showed that patterns of landslide colonization were determined mainly by the characteristics of the surrounding vegetation, with the exception of landslides occurring in high-altitude, grass-dominated areas where the tree *Alnus acuminata* successfully colonized landslides. In the second study, the analysis of the normalized vegetation index derived from SPOT satellite images showed that within one year of formation, 37% of the total area denuded by earthquake-triggered landslides (909 hectares) had good to excellent recovery rates. On the other hand, 36% and 27% of the area had average or poor recovery rates, respectively. Finally, the use of oblique aerial video imagery at Lyell Island revealed a reduction in the number of landslides five years after the initial phase of a large-scale restoration program that air seeded and fertilized slopes in an effort to stabilize them. This approach demonstrated an effective way to monitor restoration efforts in areas affected by landslides that would have otherwise been very difficult to access.

A second set of studies focuses on the process of landsliding (box 1, figure 2, arrows 1 and 2). The combination of a slope stability and vegetation growth models in a spatially-explicit context showed that topography and timber-harvesting methods exerted a strong control on the initiation of landslides (Wu and Sidle 1995). Using a slightly different approach, Basu and Roy (2004) developed a model to examine the long-term effects of earthquake- and rainfall-induced landslides on forest productivity. In an interesting application of remotely sensed data, Hales and colleagues (2008) combined root-strength data for *Rhododendron maximum* with a map of the species' distribution to determine how subtle changes in forest composition in Appalachian forests could affect the large-scale distribution of root strength and thus slope stability.

A third set of applications relies on spatial modeling to investigate the large-scale effects of landsliding on diversity and ecosystem function (figure 2a, arrows 4–6). Claessens and colleagues (2006) combined a slope stability (box 1) and a simple hydrological model and demonstrated that kauri trees (*Agathis australis*) in New Zealand tended to establish preferentially on sites of moderate to high landslide hazard, highlighting the importance of landslides in the dynamics of native forests. Landsliding may also have a major impact on carbon budgets, as suggested by the work of Restrepo and colleagues (2003) in the Ninole ridges of Hawaii. The integration of infrared aerial photographs and biomass data showed that landsliding can mobilize large amounts of biomass in relatively short periods of time.

Future research challenges and needs

Landsliding strongly influences the dynamics of mountainscapes at a variety of scales. Multiple factors are altering this process, and with it, the diversity and functioning of natural and human-dominated mountain ecosystems (figure 2).

Coping with these changes will require research aimed at better understanding interactions between biotic and hydrogeomorphic processes, and an examination of these interactions across a diverse range of environmental conditions and scales (figure 2). The research needs can be grouped into four broad themes that overlap with the components of our conceptual model (figure 2)—ecosystem attributes and geomorphic thresholds, ecosystem recovery following landslides, landslides and landscape structure, and the resilience of mountainscapes influenced by landsliding. Advancing landslide research along these themes can make a great contribution to an array of applied issues ranging from conservation and restoration to hazard assessment.

Ecosystem attributes and geomorphic thresholds. The extent to which individual and stand-level plant attributes have been influenced by, and in turn have influenced, ecosystem function and geomorphic thresholds remains little known (box 1). We foresee that research using biomass as a currency to investigate these interactions will shed light into evolutionary processes that may have shaped allocation patterns, allometries, and the architecture of plants in mountains. Likewise, research in this area may contribute to an understanding of ecological processes that influence the composition, abundance, and spatial distribution of plants within natural and human-dominated ecosystems. For example, can we identify functional groups of plants on the basis of their influence on slope stability? Can we identify plant species that are indicators of stable and unstable slopes? How do plant attributes vary among areas that differ in their susceptibility to slope failure? How do plants influence hydrological and mechanical processes that contribute to slope stability? How do changes in the vegetation over time influence geomorphic thresholds?

Ecosystem recovery following landslides. Although we have described several studies assessing landslide recovery, the extent to which climate, geologic substrate, land use, invasive species, and even biogeography influence the recovery of landslides is little understood. In addition, fundamental aspects of ecosystem recovery involving biogeochemical cycles have been little investigated. Research focusing on these topics and on changes in species composition and abundance will ultimately shed light on the contribution of landsliding to the diversity and functioning of mountainscapes. For example, can we identify species or suites of species truly adapted to landslides? Can these be used as bioindicators of past landslide activity? How do these species handle the conditions created by landslides? Are landslide species the same ones that colonize human-altered environments? To what extent do ecosystem developmental trajectories vary within landslide populations and assemblages?

Landslides and structure of mountainscapes. Landsliding transforms the spatial structure of mountainscapes, and with it, the movement of water, nutrients, and propagules. More-

over, landsliding extends its influence to riverscapes through the transfer of hillslope material into streams. In turn, the spatial arrangement of variables that influence slope stability may explain the likelihood of landslides. Research on this theme may help address questions about landslide immunity, mountainscape dynamics, coupling between natural and human-dominated systems, and coupling between hillslope and river systems. For example, does the power-law distribution of landslides in space arise from the multifractal spatial distribution of rainfall over mountainous terrain, the fractal nature of topography, the fractal structure and hydraulic properties of soils, the fractal nature of the vegetation, or from the coupling among all of these?

Resilience of mountainscapes influenced by landsliding. Humans have lived in mountains for millennia. Drawing parallels between natural and human-dominated systems may help elucidate basic principles governing the response of organisms to disturbance, including adaptations to cope with unstable substrates as well as areas already disturbed by landslides. These principles in turn may help clarify the extent and conditions under which mountain ecosystems are resilient to change. For example, can we use the size distribution of landslides to describe the state of a given mountainscape? To what extent do human activities interact with landsliding to shift the state of these systems to one characterized by a different structure and function? How do other disturbances interact with landsliding and contribute to the reorganization of mountainscapes? How do interactions at multiple spatial and temporal scales influence landsliding? How do we manage mountainscapes for resilience?

We expect that increased human pressure on mountainscapes will prompt new studies, which will prove more effective if they integrate knowledge on biotic and geomorphic interactions at multiple scales.