

The soil-geomorphic template and biotic change in arid and semi-arid ecosystems[☆]

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Abstract

The objective of this paper is to illustrate the concept of the soil-geomorphic template and its relationship to biotic change in arid and semi-arid regions. Such biotic change is typically accompanied by and linked to geomorphic change that involves soil, topography, and soil parent material, which together form the *soil-geomorphic template*. Soil is a factor in biotic change because it is the substrate that provides water, nutrients, anchorage for plants, and habitat for burrowing animals. Topography is a factor in biotic change because it influences local microclimate by means of elevation, lateral redistribution of water, and slope orientation. Soil parent material is a factor in biotic change because it provides the lithic inheritance from the geologic landscape that gives rise to soils with different particle size distribution (i.e. available water holding capacity) and nutrient status. Numerous linkages and feedback loops occur between the soil-geomorphic template, microclimate, vegetation, and animals. A perturbation in any of these factors can steer an ecosystem from one state to another. The integral relationship between the soil-geomorphic template and biotic change is an example of how biological and geological systems are coupled and co-evolve over long-term (Quaternary landscape evolution) and short-term (human-induced desertification) time-scales.

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1. Introduction

Although biotic and geomorphic change, in a general sense, have occurred in arid and semi-arid regions of the world throughout geologic time (e.g. Williams, 1994; Atalay, 1998; Brook et al., 1998; Glennie, 1998), many desert grasslands have experienced a dramatic invasion by woody shrubs and an increase in soil erosion during the last century (Lal, 2001). Thus, superimposed on the natural cycles of biotic and geomorphic change is biotic and geomorphic change caused by desertification resulting from human land use. The soil-geomorphic template applies to both natural and human-induced change.

Natural cycles of biotic change in the Chihuahuan Desert of North America, for example, are based on fossil packrat middens (Van Devender, 1990), fossil pollen (Hall, 1997), fossil animals (Harris, 1987), and carbon isotopes (Buck and Monger, 1999). These studies indicate a peak in mesic vegetation during the last glacial maximum (approximately 20,000 years ago) followed by a peak in xeric vegetation during the altithermal period (approximately 6000 years ago; Antevs, 1955; Hawley, 1975; Gile et al., 1981; Monger, 2003).

Natural cycles of geomorphic change in this region are based on studies of alluvial fan formation along mountain fronts (Gile and Hawley, 1966), fan-terrace formation along rivers (Hawley and Kottowski, 1969), dune deposition on the leeward sides of pluvial lakes (Hawley, 1993), and pedogenic carbonate precipitation/dissolution in soil profiles (Gile, 1975). Timing of these events is based on radiocarbon dates (Gile et al., 1981), biostratigraphic dates (Hawley et al., 1969), paleomagnetic dates (Mack et al., 1993), and tephrochronologic dates (Mack et al., 1996). These studies indicate greater erosion and sedimentation during relatively dry interglacial periods with diminished vegetative cover followed by greater landscape stability and soil formation during wetter glacial periods when vegetative cover increased (Ruhe, 1962; Hawley, 1975; Gile et al., 1981).

Human-induced biotic changes in this region on a time-scale of about 150 years are based on land survey notes (Buffington and Herbel, 1965), vegetation maps (Gibbens et al., 2005), repeat photography (Buffington and Herbel, 1965; Gile et al., 2003), and interviews with long-time residents (Gardner, 1951). These studies indicate a decline in grasses and an increase in shrubs beginning in the late 1850s as a consequence of human-induced biotic changes. The most prominent human-induced geomorphic changes accompanying this biotic change were the cutting of deep arroyos (Bryan, 1925) and the deposition of coppice dunes (Gile, 1966).

The objective of this paper is to describe the linkages and feedback loops that occur between biotic change and geomorphic change. To this end, we develop the concept of the geomorphic template, which accounts for the combined influences of soil, topography, and soil parent material on vegetation patterns and dynamics. Of particular importance in our example is how soil-geomorphic templates influence the encroachment of woody shrubs into grasslands (see Peters and Havstad, 2006). Our examples are most pertinent to the climatic zones where desert boundaries transition into steppe boundaries (i.e. where arid and semi-arid climates meet). We suggest that understanding the relationships between the soil-geomorphic template and factors traditionally emphasized by ecologists (e.g. plant cover and climate), is essential to understanding biotic change and landscape heterogeneity in arid and semi-arid systems.

2. The soil-geomorphic template

As defined in this manuscript, the *soil-geomorphic template* is the soil, topography, and soil parent material. *Soil* is the physical and chemical substrate on which ecosystems reside and to which they are linked (Stafford Smith and Morton, 1990; McAuliffe, 1994). *Geomorphic*, as used in this context, accounts for both topography of the landscape and the geologic or lithic composition that serves as soil parent material. The term *template* is used to convey the concept of a pattern serving as a foundation upon which a biotic community generates a related pattern.

The size of the soil-geomorphic template is variable; however, it requires an area that is heterogeneous with respect to landforms and soil types. The template may be less than 1 km², as in the case of playettes on alluvial plains (Rango et al., 2006), or greater than 1000 km², as in the case of mountain ranges separated by bajadas and intermontane basin floors (Hawley, 2004). The main criterion for template size is resolution, i.e. at what scale is it most clearly apparent that landforms and soil types influence vegetation patterns? In the case of woody shrub encroachment at the Jornada Experimental Range, the size of the soil-geomorphic template is typically a few hundred km² (Fig. 1).

Linkages among the soil-geomorphic template, microclimate, vegetation, and animals are illustrated sequentially, with factors and linkages added at each step shown in red (Fig. 2). The model contains a combination of interacting entities, factors, and processes. Entities (i.e. things that exist as particular and discrete units) include soil, parent material, water, vegetation, propagules, and nutrients. Factors (i.e. conditions contributing to an outcome) include topography, microclimate, groundcover, and habitat. Processes (i.e. series of actions that elicit a result) include erosion, sedimentation, lateral redistribution of water, infiltration, bioturbation, and herbivory.

Depending on the focus, however, entities can also be factors. For example, soil is a factor for vegetation type and parent material is a factor for soil formation (Jenny, 1941). Likewise, processes can also be factors, depending on the context. For example, erosion is a factor for topographic development and herbivory is a factor for shrub establishment. In addition to the dual function of these words, it is also important to emphasize that the soil-geomorphic template model (Fig. 2) is implicitly about change.

3. Linkages within the soil-geomorphic template

The three components of the soil-geomorphic template (soil, topography, and soil parent material) and linkages (arrows) among them are shown in Fig. 2a. The linkage between parent material and soil entails the pedogenic transformation of lithic material from which soils develop (Fig. 2a). This lithic inheritance is more readily observed in arid climates than in humid climates because greater chemical weathering in humid climates erases much of the original fabric of the parent material (Buol et al., 1973). Soil, in turn, is linked to parent material by erosion-sedimentation because a soil eroded from one location becomes sediment (i.e. parent material) from which a new soil develops in a different location. Soil is also linked to topography (the three-dimensional configuration of a landscape) by erosion and sedimentation (Fig. 2a). Given enough time, soil erosion and the resulting sedimentation, in conjunction with deep-seated geologic processes of tectonic uplift and volcanism, will fashion a landscape and produce its topography (e.g. Hawley, 1986).

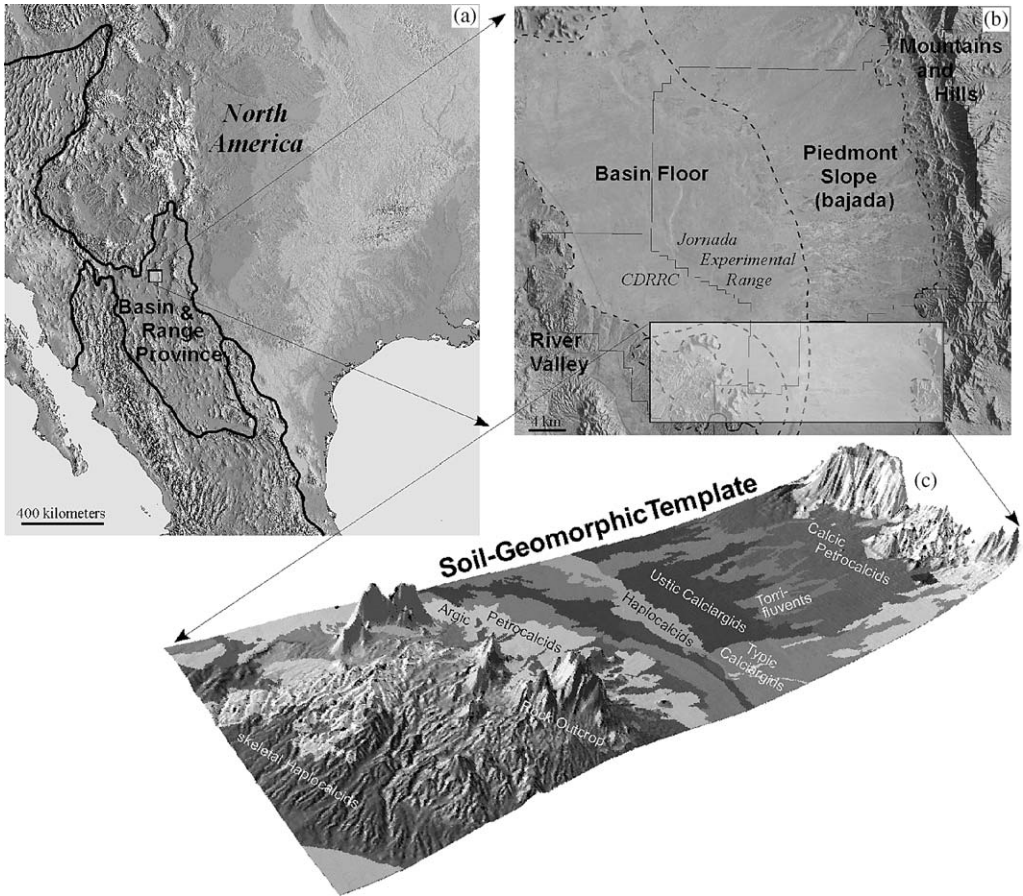


Fig. 1. Example of a soil-geomorphic template as it occurs within the context of the Basin and Range Province of North America. The effect of the soil-geomorphic template on biotic change results from the combined influence of soil type and landscape configuration. Soil types are classified using the Soil Taxonomy system (Soil Survey Staff, 1999) by Gile et al. (2003). The Jornada Experimental Range and CDRRC (Chihuahuan Desert Rangeland Research Center) are located in southern New Mexico, USA.

4. Linkages to microclimate

Microclimate is the climate near the ground, i.e. from the ground surface to the height of the plant canopy (Anthes et al., 1981; Strahler and Strahler, 1987). Within a regional climate that has a particular temperature and precipitation regime, microclimate varies as a result of local topography (Turner et al., 2001). The elements of local topography that affect microclimate are elevation, lateral redistribution of water, and aspect (Fig. 2b). At any point on the landscape, microclimate affects transmission and removal of heat and water to and from the soil (Fig. 2b). In addition, microclimate involves the effects of wind. Wind impacts soil by causing erosion, especially on bare sandy soil. Water also plays an important role as an agent of erosion, in addition to its role as an essential substance for plant and animal life.

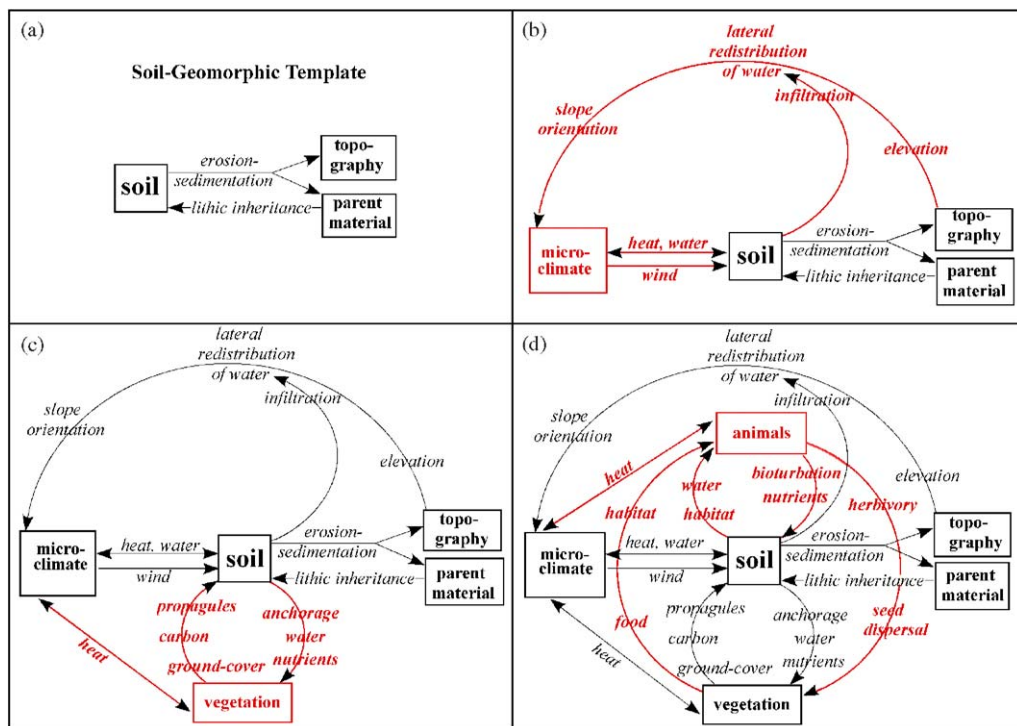


Fig. 2. Illustration that sequentially depicts linkages among the soil-geomorphic template, microclimate, vegetation, and animals. The first frame (a) shows components of the soil-geomorphic template. The second frame (b) indicates in red the linkages between the soil-geomorphic template and microclimate. Linkages to vegetation and animals are depicted in frames (c) and (d), respectively.

The effects of elevation on microclimate can be observed in deserts and steppes containing mountains. Because of the orographic relief of mountains, adiabatic properties of cooling air and water condensation affect temperature and precipitation. For example, in the Chihuahuan Desert a decrease in mean annual temperature of 3 °C and an increase in mean annual precipitation of 100 mm occur for each 500 m rise in elevation (calculated from data for Alamogordo and Cloudcroft, NM; Western Regional Climate Center, <http://www.wrcc.dri.edu/>). These climatic factors exert important constraints on biotic change because vegetation zones in this terrain are restricted at lower elevations by soil moisture and at higher elevations by low temperatures (Dick-Peddie, 1993).

The effects of lateral redistribution of water are evident along mountain bajadas in deserts and steppes. Soil at the top of a bajada in a runoff position contains less water than soil downslope in a run-in position, even though both receive the same mean annual precipitation (Herbel and Gile, 1973; Herbel et al., 1994). Infiltration influences this relationship (Fig. 2b) because runoff decreases as infiltration increases. This effect can be observed on the bajada at the Jornada Experimental Range (Fig. 1b). Alluvial fans debouched from mountains on the northern half of the bajada are buried by sand blown from the basin floor, while the debouched fans are exposed on the southern half of the bajada. Because of greater infiltration, the sandy area to the north lacks the complex

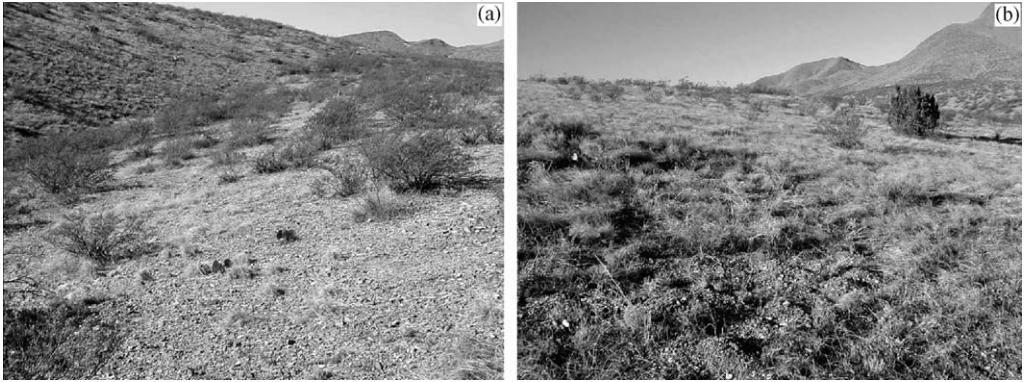


Fig. 3. The effect of aspect on plant communities of Nickel gravelly sandy loam (Typic Haplocalcid) in an area that has been ungrazed for decades (Bosque del Apache National Wildlife Refuge, New Mexico, USA). (a) South-facing slope of a ballena landform dominated by creosotebush (*Larrea tridentata*) and patchy grass (*Muhlenbergia porteri*). (b) North-facing slope of the same ballena dominated by black grama (*Bouteloua eriopoda*) grass with a few creosotebush and juniper (*Juniperus monosperma*). Thus, the shift from desert grassland to a desertified state occurred over tens of meters and the pattern repeats within each of the parallel ballenas. The slope of south-facing aspects of ballenas is often greater than that of the north-facing aspect, reflecting the effect of microclimate on feedback between vegetation cover and soil erosion rate.

drainage network of rills, gullies, and arroyos that characterizes the alluvial fans of the southern area. On a finer scale, desert pavement limits infiltration and delivers rainfall to nearby bare ground where shrubs cluster (Wood et al., 2002; Wood et al., 2005).

The effects of slope aspect on microclimate can be seen in deserts with complex topography. North-facing slopes (in the northern hemisphere) are cooler and moister than their south-facing counterparts. When elevation and lateral redistribution of water are held constant, mesic vegetation and soils with greater organic matter exist on northern slopes, while more xeric vegetation and soils containing less organic matter occur on southern slopes (Dick-Peddie, 1993). Even relatively small-scale changes in aspect that occur across low ridges can dictate whether a biotic community is desertified (Fig. 3). Slope aspect in mountains has a major effect on vegetation patterns. The same vegetation type will exist at a higher elevation on a south-facing mountain slope than on its north-facing counterpart (Brown, 1994).

5. Linkages to vegetation

Three major linkages exist from soil to vegetation: anchorage, water (i.e. plant-available water), and nutrients (Fig. 2c). Anchorage (i.e. attachment of plants to the land surface via rooting) is impacted by the depth of soil to bedrock or to the water table. Plant-available water is affected by the capability of soil to absorb, store, and release water to plants. For example, the available water holding capacity of silt loam textures is greater than coarse sands by a factor of 3.5 (Brady and Weil, 1999). Nutrients are impacted by soil in three ways. First, nutrients (e.g. calcium, phosphorus, and potassium) are derived directly from chemical weathering of soil minerals. Second, nitrogen is made available to plants by means of N fixation in soil, as well as from atmospheric inputs (Schlesinger and Schmidt,

in press). Third, nutrients are stored and released to plant roots from ion exchange sites on organic and mineral colloids. In addition to nutrients, chemical properties of soil, such as pH and salinity, exert important controls on vegetation in arid and semi-arid ecosystems (Fuller, 1975).

In addition to reduced anchorage capacity, shallow soils to bedrock also reduce available water holding and nutrient storage capacity (Hunt, 1972). Nevertheless, on some bedrock outcrops associated with hills and small mountains in deserts and steppes, trees are common. This paradox occurs because moisture that percolates into pockets of soil between rocks is concentrated into relatively small volumes of soil. Consequently, this water is held at tensions low enough for trees to extract (Dick-Peddie, 1993). Also, water runs off the impermeable rock in catchment areas into pockets of soil between rocks, further concentrating water in the soil.

Three major linkages exist from vegetation to soil (Fig. 2c). The first linkage, which is integrally related to geomorphic change, is vegetative ground cover. As ground cover decreases, bare ground and erosion increase (Bull, 1991; Wainwright et al., 2000). The second linkage is carbon. That vegetation contributes organic carbon to soils is clear, but in many situations, vegetation and micro-organisms also add inorganic carbon (Goudie, 1973; Monger et al., 1991). These carbon transfers influence the level of atmospheric carbon dioxide that in turn affects climate (Schlesinger, 2002; Berner, 2004). The third way vegetation affects soil and makes the vegetation-soil linkage perpetual is through the addition of seeds and other propagules that ultimately determine many soil processes. In addition to soil-vegetation linkages, the direct effect of heat on vegetation is also critical to biotic change (Fig. 2c).

6. Linkages to animals

The direct influence that soil exerts on animals relates to the habitat (i.e. shelter) soils provide for ants, termites, and other burrowing animals, and the water used by animals that is stored and released by soil (Fig. 2d). Soil serves as habitat by providing a physical and, to some extent, chemical environment for many animal species (Whitford, 2002). The role of soil as a water source ranges from thin water films in soil pores in which nematodes reside to large springs issuing from soil phreatic zones that provide drinking water to large animals.

In turn, animals affect soil through bioturbation of soil horizons and their role in nutrient cycling. Bioturbation by animals involves the transfer of soil particles to the land surface by insects, reptiles, and mammals (e.g. Anderson and Kay, 1999). Ants, for example, can transfer 80 g/m² of desert soil to the land surface per year (Whitford et al., 1986). Termites also bioturbate extensive amounts of soil and have been known to obliterate argillic horizons (Gile, 1975). Nutrient cycling by animals involves their role in decomposition of organic matter (Whitford, 1996) and movement of nutrients across the landscape, as in the case of feces from large herbivores.

Three other important linkages involve animals. First is the direct impact of heat on animals (Fig. 2d). Second is the direct impact of animals on vegetation by herbivory and seed dispersal (Fig. 2d). Third is the direct impact of vegetation on animals by serving as a food source and supplying habitat (e.g. woody shrubs for bird nesting).

7. Coupled biotic and geomorphic change

Coupled biotic-geomorphic change occurs at long-term time-scales, as with Quaternary landscape evolution (Wright, 1983), and at short-term time-scales, as with the desertification event that has been taking place in the Chihuahuan Desert during the last 150 years (Schlesinger et al., 1990). Beginning in the mid-1800s, the animal component in Fig. 2d was drastically changed, as tens of thousands of cattle were brought into the desert grassland (Fredrickson et al., 1998). Consequently, intense selective herbivory occurred and the most palatable grasses were consumed. Moreover, with elevated cattle numbers, honey mesquite (*Prosopis glandulosa*; a major competitor of grass) had a robust dispersing agent (see Fredrickson et al., 2006). Selective grazing of grass and replacement by shrubs greatly diminished overall ground cover (Buffington and Herbel, 1965). Reduced ground cover led to more bare soil and consequently to increased erosion. As erosion ensued, it changed the topography of many landscapes from smooth grass-covered sandy soils to hummocky mesquite dunes separated by bare and deflated soils. Deflated soils between shrubs are hostile environments for establishment of most plants due to frequent and severe disturbances associated with sand abrasion, erosion, burial, and high temperatures (Okin et al., 2006). As a result, there has been little success in reestablishing black grama on this type of soil-geomorphic template (Herrick et al., in press).

Yet, not all soil-geomorphic templates are equally prone to change. This point is illustrated by the fact that some grasslands in the northern Chihuahuan Desert did not become desertified after the introduction of cattle (e.g. tobosa grasslands on narrow alluvial flats with silty-clay soils). This resistance to desertification is attributed to interactions among (1) relatively high amounts of run-in water that these silty-clay soils receive from adjacent piedmont slopes, (2) differences in the seasonal palatability of perennial grasses, (3) differences in rooting strategies of these grasses (Gibbens and Lenz, 2001), and (4) differences in vulnerability of the soils to compaction, surface disturbance, and wind erosion due to soil texture (Bestelmeyer et al., in press).

On a broader scale, the soil-geomorphic template and its interactions with microclimate, vegetation, and animals (Fig. 2) are a component of the dynamic template (Peters and Havstad, 2006). This template represents an area in context with its surroundings, and contains changes occurring at very slow (e.g. geologic, climatic) rates to relatively fast (e.g. vegetation cover, animal density) rates. The soil-geomorphic template and its feedbacks are two of the five key elements identified by Peters and Havstad (2006) that interact across scales to explain heterogeneous vegetation patterns and nonlinear dynamics.

8. Conclusions

The factors, linkages, and feed-back loops illustrated in Fig. 2 are essentially a graphic depicting the interactions among the five soil-forming factors identified by Dokuchaev (1883) and expounded by Jenny (1941). The figure, however, demonstrates how a change in one factor or linkage can cause the entire system to respond, e.g. the formation of coppice dunes caused by altering the animal component.

A greater understanding of soil-geomorphic templates and how they are nested in broader scale templates that explain interactions across scales can help us explain and manage the variability inherent to arid and semi-arid ecosystems worldwide (McAuliffe,

2003). Because some soil-geomorphic templates (e.g. those in sandy landscapes) are more vulnerable than others (e.g. those in fine-textured landscapes that receive run-in water), management practices should be tailored to geomorphic settings. Work is also needed to quantify conditions in which the role of soil-geomorphic templates in regulating biotic change is diminished because climate or land use is the dominant process.

The soil-geomorphic template provides a framework within which to integrate ideas from multiple disciplines, including soil science, geomorphology, climatology, landscape ecology, ecosystem ecology, and organismal ecology. Attempts to explain the behavior of desert and steppe systems using only a subset of these disciplines have often been incomplete or misleading. Experimental and comparative work with the soil-geomorphic template concept will further our knowledge of how the biologic and geologic worlds are coupled and co-evolve in arid and semi-arid regions.

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