Legacy effects in linked ecological–soil–geomorphic systems of drylands

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A legacy effect refers to the impacts that previous conditions have on current processes or properties. Legacies have been recognized by many disciplines, from physiology and ecology to anthropology and geology. Within the context of climatic change, ecological legacies in drylands (eg vegetative patterns) result from feedbacks between biotic, soil, and geomorphic processes that operate at multiple spatial and temporal scales. Legacy effects depend on (1) the magnitude of the original phenomenon, (2) the time since the occurrence of the phenomenon, and (3) the sensitivity of the ecological–soil–geomorphic system to change. Here we present a conceptual framework for legacy effects at short-term (days to months), medium-term (years to decades), and long-term (centuries to millennia) timescales, which reveals the ubiquity of such effects in drylands across research disciplines.

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Legacies are well-known as key factors in many scientific disciplines. Ecologists, for instance, recognize the importance of previous-year precipitation on current-year net primary production (Sala *et al*. 2012). Likewise, natural resource managers and environmental scientists recognize the importance of legacies on ecosystem structure and function (Foster *et al*. 2003), while anthropologists are familiar with the effects of historical land use on current vegetative patterns (Figure 1).

Scientists from numerous disciplines also acknowledge the role of legacies in the following triad: "environment → processes → properties" (eg Birkeland 1999; Turner *et al*. 2001). In drylands, ecologists, soil scientists, and geomorphologists have shown that environmental conditions govern processes that, in turn, generate properties. Examples include rainfall → photosynthesis → net primary production (in ecology); vegetative cover → organic matter accumulation → pH (in soil science); and mountain building → erosion → landforms (in geomorphology). The "environment → processes → properties" triad can also be investigated in reverse to understand paleoenvironments (eg Targulian and Goryachkin 2004). Such studies have shown that some properties have better "memories" than others. For example, the $^{13}C/^{12}C$ ratio in soil organic matter in a shrubland may "remember" a former grassland, but its memory will fade more quickly than the $^{13}C/^{12}C$ ratio in carbonate minerals of that same soil (Monger *et al*. 2009).

In a nutshell:

- Ecological legacies are the impacts of past conditions on current landscapes
- Such legacies may represent short-, medium-, or long-term effects
- Impacts also depend on the severity of the originating condition

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The emerging legacy paradigm

Legacies in drylands occur across disciplines and scales, and are a function of three variables: (1) the magnitude of the historical phenomenon, (2) the time elapsed since its occurrence, and (3) the sensitivity of the ecological–soil–geomorphic system to change (Rachal *et al*. 2012; Sala *et al*. 2012; Monger and Rachal 2013). Feedbacks within an "ecogeomorphic" system are illustrated in the following three examples and summarized in a conceptual model (Figure 2). (1) In a semi-desert region of southern New Mexico, overgrazing by domestic cattle resulted in selective herbivory of grasses, giving unpalatable shrubs a competitive advantage (Buffington and Herbel 1965). Eventually forced to eat the pods of mesquite (*Prosopis* spp), cattle also became an agent of seed dispersal, which led to greater abundance of mesquite shrubs and areas of bare ground that are typically larger between shrubs than between grasses. The increased bare ground promoted soil erosion (gully cutting in the case of water erosion and removal of silt, sand, and fine particles of organic matter

Figure 1. Ruins associated with a Roman–Byzantine-era farm near the ancient city of Shivta in the Negev Desert, an example of water harvesting techniques that have created a legacy effect on the desert landscape. Though long abandoned, the ancient structures still capture runoff water as reflected by lush seasonal vegetation.

in the case of wind erosion), thus altering topography. (2) In the Mojave Desert, the topography was altered by the construction of a railroad line that acted as a barrier to water moving downslope. The barrier enhanced water capture upslope along the railroad and reduced the amount of water available to vegetation downslope of the line (Schwinning *et al.* 2010). When framed in terms of the conceptual model (Figure 2), the railroad line affected the lateral redistribution of water, changing soil moisture, which resulted in a higher density of vegetation (*Larrea tridentata*) in areas with enhanced water on the upslope side of the railroad. In contrast, areas with reduced water levels downslope of the railroad saw a shift in plant community to a drought deciduous species (*Ambrosia dumosa*). (3) In the Ebro Valley of Spain, one of the driest regions in Europe, the soil itself creates changes in soil climate. Differences in soil moisture occur along the perimeters of polygonally shaped plates that form in periodically flooded playa lakes (Dominguez-Beisiegel *et al.* 2012). The cracks between the plates hold greater soil moisture, which allows the glaucous glasswort (*Arthrocnemum macrostachyum*) to germinate there, adding more propagules, increasing organic matter, and changing the soil properties along the edges of the plates.

Continuum of spatial and temporal scales

Spatially, ecological–soil–geomorphic legacy effects can be seen from continental to experimental-plot scales. At the continental scale, the dry climate that creates the Chihuahuan Desert of North America is a legacy effect of mountain ranges that deplete the moisture in air masses combined with its 30°-latitude location resulting from plate tectonics (Figure 3a; Schmidt 1979). At the physiographic scale, a piedmont slope is a legacy effect of sediments deposited along the fronts of uplifted mountains (Figure 3b; Seager 1981). Sand sheets at the landscape scale are a legacy of sand movement along the prevailing wind direction (Figure 3c; Gile 1999). At the finer landform scale, crescent-shaped banded vegetation is a legacy of wind-blown sand interacting with sediments carried downslope by water (Figure 3d; Weems and Monger 2012). Finally, plot-scale studies have shown that hydrologically enhanced zones of grass productivity are a legacy left by the construction of dikes that capture flowing water and sediments (Figure 3e; Rango *et al.* 2006).

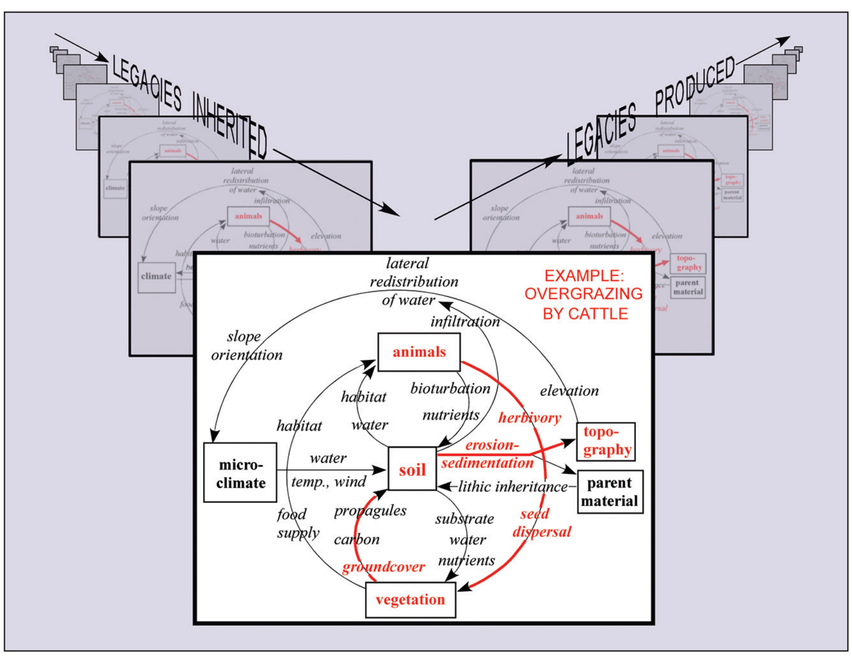

Figure 2. Conceptual framework showing linkages between ecological (animals and vegetation), soil, and geomorphic (topography and parent material) factors and processes, and their interactions with microclimate in dryland systems. The interactions altered by cattle overgrazing are shown in red; black arrows highlight interactions that are still present, but less affected by overgrazing (after Monger and Bestelmeyer 2006).

Temporally, ecological–soil–geomorphic legacies can be seen from millennial to diurnal scales (Table 1). In the next section, we provide examples – organized along timescales from the very short to the very long – that were developed under different disciplines but are grouped here within the same conceptual framework.

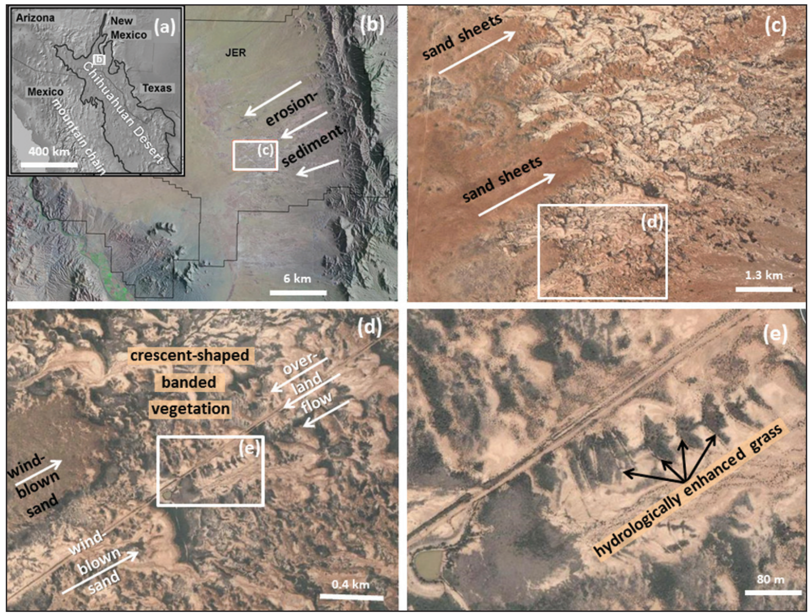

Figure 3. *Examples of legacy effects at progressively finer spatial scales. Image data provided by Google, Image Landsat, INEGI, © 2014.*

Short term (days to months)

Ecological legacy – stomatal conductance

Stomatal conductance is a short-term legacy from prior rainfall that may persist when plants are rewetted after a prolonged drought, leading to "memory" of past rainfall events. Stomatal conductance in the grass *Bouteloua gracilis* in a semi-arid shortgrass steppe in Colorado, for example, remained relatively low for one week after the end of such a drought (Sala *et al.* 1982). Leaf water potential in the same system recovered quickly, however, suggesting that legacy effects maintain control over stomatal behavior. Similar effects were reported in a semi-arid grassland in Arizona. There, following a precipitation pulse, stomatal conductance took 1–15 days to reach maximum values (Ignace *et al.* 2007); this is because, during drought periods, plants accumulate abscisic acid, which limits stomatal aperture even after turgor pressure recovers (McAinsh *et al.* 1990).

Soil legacy – soil moisture

Soil horizons serve as reservoirs that retain water and buffer vegetation against low and variable precipitation (eg Duniway *et al.* 2010; Mahmood and Vivoni 2014). Thus, soil moisture at a given point in time can be viewed as a legacy of previous meteorological and biological processes (eg Gutierrez-Jurado *et al.* 2013). Depending on these interacting and often conflicting processes, the legacy effects of soil moisture can range from hours to months (Figure 4).

Geomorphic legacy – impacts of roads

Road networks within dryland areas alter surface hydrology and concentrate overland flows (Duniway and Herrick 2011). Roads running across a slope (ie with elevation contours) can divert water laterally, releasing the flows through cross-drains and creating erosion downslope of the roads. Similarly, roads running with the slope (ie longitudinally) tend to capture, concentrate, and alter overland flow. This concentration of dispersed overland flow can change geomorphic processes related to hydrology and sediment transport, thereby generating legacy effects (Figure 5).

Medium term (years to decades)

Ecological legacy – precipitation

Sala *et al.* (2012) characterized medium-term legacies of precipitation in drylands as the negative effect of a drought event after the drought is over or as the positive effect of an extremely wet event after it has occurred. Medium-term legacy responses of aboveground net primary production (ANPP) are estimated as the difference

Table 1. Examples of legacy effects and their antecedent environmental factors operating at short-, medium-, and long-term timescales in dryland landscapes

Timescales	Ecological	Soil	Geomorphic
Short term (days to months)	*Soil moisture →* **stomatal conductance**	*Rainfall →* **soil moisture recharge**	*Road construction →* **altered overland flow**
	Fire → **shrub mortality**	*Diurnal solar cycles →* **soil temperature change**	*Strong winds →* **dust storms**
Medium term (years to decades)	*Drought episodes →* **net primary production**	*Herbaceous to woody →* **more heterogeneous soil organic matter**	*High aeolian deposition →* **coppice dune formation**
	Gasoline combustion → **nitrogen fertilization**	*Improper irrigation →* **salinity and sodicity**	*Bare ground →* **gully networks**
Long term (centuries to millennia)	*Climate change →* **biome migration**	*Cultivated agriculture →* **topsoil loss**	*Water harvesting →* **dune stabilization**
	Paleo-Indian overkill → **faunal extinctions**	*Climate change →* **soil $CaCO_3$ dissolution**	*Climate change →* **fluvial base-level**

Notes: Words in italics represent environmental conditions; the arrows point toward the effect on ecological, soil, or geomorphic legacies (in bold).

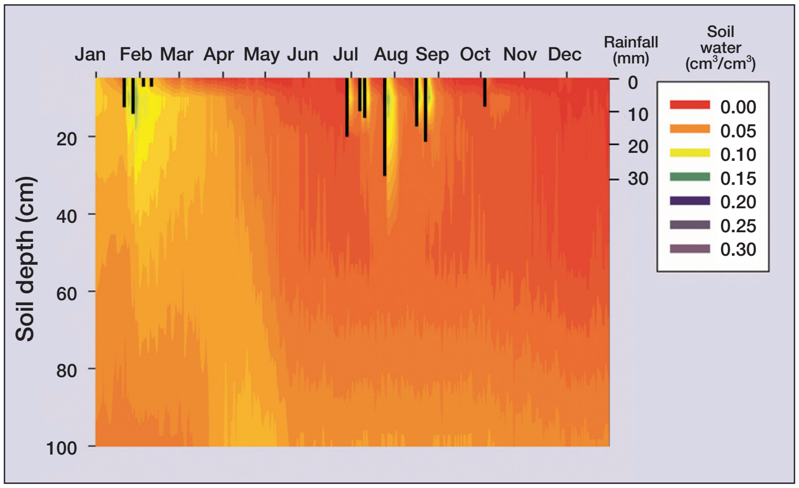

Figure 4. *Soil moisture as a short-term legacy effect of rainfall events. Data are daily measurements of volumetric soil moisture in a loamy sand soil at the Jornada LTER in southern New Mexico. Rainfall events are shown as inverted black vertical lines. Note the more effective wetting during winter rainfall in contrast to summer when evapotranspiration is greater.*

between observed ANPP and expected ANPP, which is calculated based on current precipitation and a long-term precipitation–production relationship. Positive legacies result when observed ANPP is higher than expected ANPP; this type of legacy occurs during the transition from wet to dry conditions. Negative legacies result when observed ANPP is lower than expected ANPP during dry to wet transitions, such as the observed lags in ecosystem responses in a Chihuahuan Desert grassland experiment (Reichmann *et al.* 2013). Legacy magnitude was linearly proportional to the difference in annual precipitation between the current year and the previous year. Moreover, the magnitude of a negative legacy was inversely equivalent to the magnitude of a positive legacy. Legacies account for an important fraction of annual primary production. In the Chihuahuan Desert grasslands, legacies represent 20% of annual net primary production, with the density of tillers (lateral shoots characteristic of grass species) identified as the mechanism promoting legacies in this ecosystem type (Reichmann and Sala 2014). Tiller density at the beginning of the growing season was determined by the precipitation or production levels in the previous year and shaped the ecosystem's ability to utilize available water. A previous dry year results in low tiller density, which constrains production, whereas a previous wet year yields high tiller density, which enhances production.

Soil legacy – changes in vegetation and soil organic carbon

Spatial distribution of soil organic carbon (SOC) typically changes as shrubs advance into and replace grasslands. For example, SOC accumulates over time as woody plants grow and deposit above- and belowground litter and root exudates. Following woody plant mortality, slow declines in SOC mirror the slow accretion rate under live plants, which creates strong legacy effects on organic carbon that may persist for decades (Throop and Archer 2008). For instance, elevated levels of SOC persisted for at least 40 years after aerial herbicide applications to remove velvet mesquite (*Prosopis velutina*) in a semi-desert grassland in Arizona (McClaran *et al.* 2008).

Geomorphic legacy – formation of coppice dunes

Coppice dunes are dome-shaped mounds of sand, 0.5–2 m in height, that form when wind-blown sand accumulates around shrubs such as honey mesquite (*Prosopis glandulosa*), which continue to grow upward with the rising sand. In many dryland areas of the US Southwest, coppice dunes have resulted from overgrazing and drought that caused topographically uniform perennial grasslands to convert to steep-sided dunes separated by bare ground (Buffington and Herbel 1965; Gile 1966). However, coppice dunes can form in any dryland where aeolian (wind-driven) sand movement is pronounced and shrubs are available to trap the sand; in addition to the US Southwest, such areas include deserts in China, the Middle East, and Africa (eg Dougill and Thomas 2002; Saqqa and Atallah 2004; Wang *et al.* 2006).

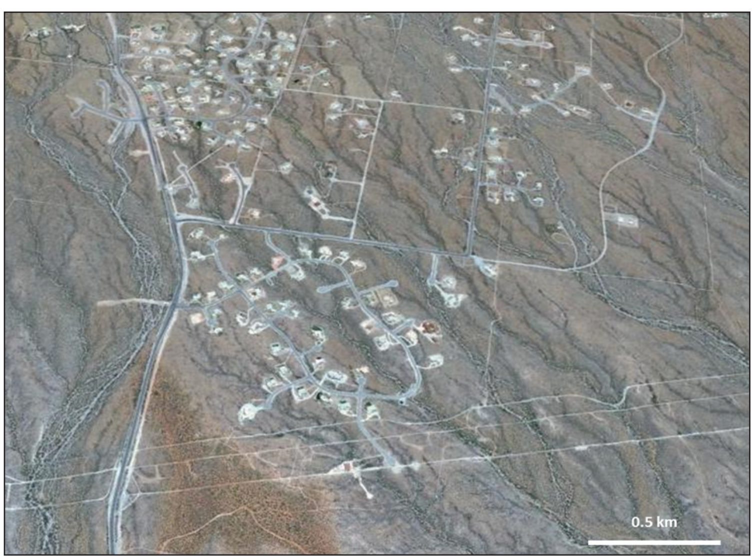

Figure 5. *Short-term geomorphic legacy effect created by roads and houses superimposed on a drainage network on a piedmont slope in southern New Mexico. Image data provided by Google, INEGI, © 2014.*

Long term (centuries to millennia)

Ecological legacy – biome migration driven by climate change

Over long timescales, imprints of the cooler and wetter Pleistocene climate in much of the now hot and dry US Southwest can be observed as topographic characteristics, such as hillslope profile and channel drainage network density (Istanbulluoglu *et al.* 2008; Gutierrez-Jurado and Vivoni 2013). In some regions, banded vegetation has also been interpreted as the legacy of a different climate (Weems and Monger 2012). Similarly, some black grama (*Bouteloua eriopoda*) grasslands have been described as vestiges of the Little Ice Age (ca 1500–1850 CE; Neilson 1986), with soaptree yucca (*Yucca elata*) representing a remnant species from that slightly cooler and moister climate (Figure 6).

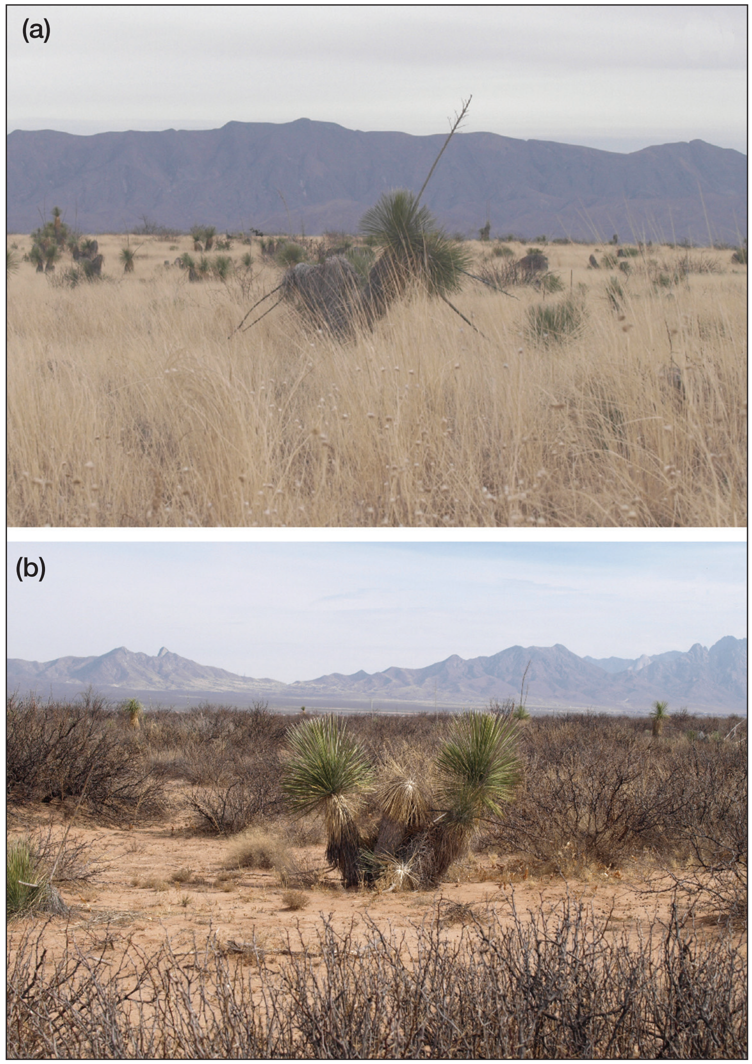

Figure 6. *Soaptree yuccas (*Yucca elata*) as a relict species (ie legacy) of former climatic and vegetative conditions (Dick-Peddie 1993). (a) Soaptree yuccas as a subdominant species in an intact grassland. (b) Yucca in an area that was formerly a grassland, according to vegetation maps from the 1920s.*

Soil legacy – topsoil loss from ancient land use

Dryland sites within the Mediterranean Basin offer a prime example of erosion caused by intensive land use over millennia (García Badell 1951; Hughes and Thirgood 1982; Boixadera *et al.* 2014). Since ancient Roman times, the maintenance of historical crops (eg grape vines, olive trees) necessitated a weed-free (bare) soil surface, which was vulnerable to erosion; this was maintained by repeated plowing (Butzer 2005). Erosion subsequently impoverished the soil, causing thinning of the fertile soil horizons and degradation of soil structure. Consequently, many contemporary grape vines and olive trees now grow in shallow, organic-poor soils with reduced water-holding capacity. To counterbalance such erosion, farmers historically built stone-wall terraces, thereby illustrating another long-term soil legacy. These stone-wall terraces have been documented in the Mediterranean Basin since the Bronze Age (Asins-Velis 2006) and, where properly maintained, have allowed full use of the land for agriculture without noticeable erosion. When used extensively, such terraces contribute to important changes in soils by slowing erosion and accumulating soil through sediment retention (Roquero 1964). The result is a soil with greater rooting depth and water-holding capacity. From a hydrological point of view, stone-wall terraces impede overland flow and create saturation areas, changing the hydrological network and reducing runoff (Abu Hammad *et al.* 2004). During intense storms, these terraces can even encourage saturation flow by capturing water that would otherwise run off without infiltrating the soil (Gallart *et al.* 1994). For instance, a large part of the semi-arid area of Les Garrigues, in southwestern Spain, is composed of stone-wall terraces, which date from the 18th century and are linked to the expansion of olive cultivation.

Geomorphic legacy – dune stabilization by ancient infrastructure

The Negev Desert and the broader Levant witnessed a thousand-year Hellenistic–Roman–Byzantine continuum, characterized by intense development of water collection and storage infrastructures. This infrastructure allowed commercial caravans, composed of people and beasts of burden, to travel along established routes dotted by natural springs and water cisterns, fortresses, and inns. It also permitted the subsequent development of thriving permanent settlements, based partly on agriculture. Understanding the interactions between water and soils enabled the development of dry riverbed terracing that retained floodwater long enough to allow its slow percolation underground. Where water flows, soil comes with it; terrace soil gradually deepened to allow a diversification of and transition in crops, from wheat and barley to grape vines and pomegranates, and then to larger trees with bigger root systems. By continuing to contain runoff water, the terraces acted as a flood-control system, slowing erosion and gully incision processes (Avni *et al.* 2013). This also encouraged the continuous growth of dense vegetation that, in turn, prevented the intrusion of sand dunes into settlements (Issar 1990).

Conclusions

Desert ecologists have long recognized the importance of abiotic factors in dryland systems. Likewise, desert geomorphologists and pedologists have widely acknowledged the necessity of integrating biotic factors into their models. The concept of legacy effects adds to our knowledge about the tight linkages between these systems and enables researchers to understand current processes and properties in the context of past environments. Although legacy effects have been primarily of academic interest, the pervasive signature of past conditions in dryland vegetation patterns, soil properties, and landscape features has highlighted the importance of legacy effects in dryland management as well. It is very useful to know an ecosystem's past to properly manage for its future (Swetnam *et al.* 1999; Bestelmeyer *et al.* 2003, 2015; Foster *et al.* 2003).

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