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Paradoxical role of the spatial heterogeneity in the functioning of drylands

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Abstract

Erosive soil processes in arid ecosystems create local heterogeneities and associated ecological and hydrological diversities within the landscape. Spatial heterogeneity exhibits simultaneous opposing degrading and developing conditions with varying degrees of resilience. While it would have been expected that heterogeneity-induced response diversity should increase the ecosystem resilience, highly heterogeneous ecosystems promote irreversible shifts. The major question is whether heterogeneity accelerates dryland degradation or provides an opportunity for increasing sustainability. To understand this paradox, recent studies were reviewed to answer (1) the causes of spatial heterogeneity in patterns of soil biotic-abiotic properties; (2) how heterogeneity simultaneously exhibits seemingly opposite effects in dryland dynamics through the emergence of resilience thresholds. Until heterogeneity can retain multiple resilience thresholds, it will have facilitative effects on resilience of the landscape. When the distance between fragments exceeds a dispersal threshold, the disappearance of resilience thresholds promotes destructive effects of the heterogeneity, stimulating irreversible transitions. It is hoped that this review, in emphasizing the importance of the relationship between erosive soil disturbances and soil biotic-abiotic variables in the dynamics of spatial heterogeneity can provide an effective basis to quantify critical heterogeneity thresholds as an early warning sign for anticipating the future evolution trend of landscape.

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Introduction

Dryland soilscapes are composed of mosaics exhibiting an intense heterogeneity of biotic-abiotic properties and processes at a local scale. The spatial heterogeneity within the dryland regions is defined as local scale variability in soil biotic-abiotic components (here expressed as pedoheterogeneity), which promotes the growing distance between vegetated and barren mosaics. For instance, the heterogeneity in particle size distribution (affected by hydro-aeolian processes) in small spatial scales within patchy structures can encourage the emergence of tiny variations in the physical, chemical, and biological properties (e.g. pH, EC, available water capacity, soil organic matter, soil nutrients, vegetation density distribution, and soil microorganism diversity) of arid and semiarid areas soils. These characteristics are critical to the functioning of the ecosystem. Although it has been documented that landscape heterogeneity is one of the major determinants of biodiversity (Gillespie, 2005; Pop and Chitu, 2013; de Souza Júnior et al., 2014; Katayama et al., 2014), studies report that spatial heterogeneity has both negative and positive impacts on dynamic of ecological systems (Benton et al., 2003; Fahrig, 2003; Levin et al., 2007; Ricketts et al., 2008). The negative effects of landscape heterogeneity are often reported as a consequence of landscape fragmentation, particularly with regard to dryland landscapes (Foley et al., 2005; Fischer and Lindenmayer, 2007; Bailey et al., 2010). The spatial heterogeneity implies that in a patchy environment, control parameters may differ from one patch to another, for a variety of reasons (Poggiale et al., 2008). The conditions that create heterogeneous patches exhibit different resilience degrees (i.e., the ability of a system to maintain certain functions, processes, or populations after experiencing a disturbance) in the face of perturbations. In drylands the heterogeneous redistribution of resources such as water, nutrients, and sediment is the most important reason for expansion of spatially heterogeneous patterns of soil properties and vegetation (van de Koppel et al., 2002; van de Koppel and Rietkerk, 2004; Ludwig et al., 2005; D'Odorico and Porporato, 2006; Breshears et al., 2009; Turnbull et al., 2012). Alternatively, the distribution structure of soil biotic (organization of vegetation) and abiotic (physiochemical attributes) components, in turn, promotes the heterogeneous redistribution of limited resources within drylands (Housman et al., 2007). What conditions enhance the contrasts within heterogeneous mosaics? Through such fragmentation, the landscape exhibits strongly-defined adjacent contrasts of vegetation and barrenness within a single environment reflecting the varied functioning within heterogeneous mosaics. In the vegetated mosaics, higher plant density leads to an increase in water infiltration and nutrient availability (Bhark and Small, 2003; Bedford and Small, 2008; Ravi et al., 2008; Kéfi et al., 2010; Wu et al., 2016). Also this increased water availability can be attributed to reduced evaporation from the top soil by shading plants (Blasius et al., 2007). These conditions encourage greater plant stability on vegetated mosaics facing perturbations. However, such favorable conditions promoting vegetation do not occur on barren soil areas.

Spatial heterogeneity can simultaneously create multiple states with different resilience degrees within the landscape, as desertified fragments (barren or sparsely vegetated state) and desertification-prone patches (vegetated state). In this condition, every state within the landscape may be at a different developmental stage (Chapin et al., 2011). Therefore, each state can respond in different ways to environmental disturbances. Multiple examples of such transitions due to variation in spatial scale of heterogeneity are recognized in many studies. Theoretical and empirical studies have shown that the spatial redistribution of surface water may explain the occurrence of patterns of alternating vegetated and degraded patches in semiarid regions (von Hardenberg et al., 2001; Rietkerk et al., 2002; Rietkerk et al., 2004; Kéfiet al., 2010; Dakos et al., 2011; Meron, 2012; Kéfi et al., 2016). Further, the studies showed interaction between hydrologic–aeolian erosion and vegetation dynamic processes can accelerate land degradation in dryland through the emergence of such patterns (van de Koppel et al., 2002; Ravi et al., 2010). The condition can lead to irreversible vegetation collapse into degraded states, over time.

Among a wide range of environmental abiotic controls, since soil is both physically and chemically the foundation of ecosystems (McAuliffe, 1994; Monger and Bestelmeyer, 2006), any subtle change in its biotic and abiotic properties may affect the resilience trends of the ecosystem. Erosive soil disturbances and expansion of the distance between vegetation patches that are separated by barren patches are the most widespread cause and form of soil degradation in drylands (Bochet et al., 2009). The change in connectivity rates between homogeneous patches creates an index for forecasting future arid land dynamics. Different factors and processes impose soil degradation in arid and semiarid regions which are prone to rapid degradation. A pedogeomorphic approach stressing the interaction between pedologic and geomorphic properties and processes can provide a good perspective for a better understanding of the role played by factors and processes involved in the dynamics of spatial biotic-abiotic heterogeneity within drylands (Figure 1). The approach considers a set of unobserved, intrinsic and observable extrinsic environmental factors of the physical landscape (Phillips, 2001; Michaud et al., 2013; Dronova, 2017). Intrinsic factors or internal soil properties, including soil physiochemical attributes such as clay content (Yao et al., 2006), infiltration (Breshears and Barnes, 1999; Hamerlynck et al., 2002; Herrick et al., 2002), available water retention capacity (Duniway et al., 2007), and salinity (Dregne, 1991) cause gradients in the structure and function of the ecosystem (Bestelmeyer et al., 2006). Alternatively, extrinsic controls include geomorphic factors such as topography (Cammeraat, 2002; Parsons et al., 2003), and geomorphic processes such as hydrologic-aeolian erosion (Ravi et al., 2011; Turnbull et al., 2012; Wang et al., 2015), soil salinization (Runyan and D'Odorico, 2010; D’Odorico et al., 2013), landslides (Geertsema and Pojar, 2007; Geertsema et al., 2009), and land subsidence (Mohseni et al., 2017b). On the local scale, the distribution structure of soil biotic and abiotic components is directly and indirectly affected by extrinsic controls.

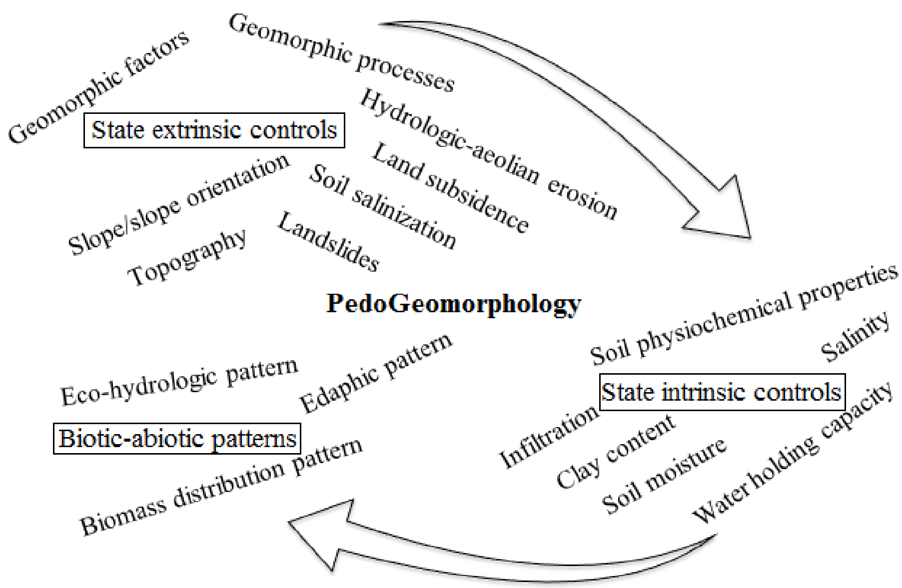

Figure 1. The pedogeomorphic approach considering the impacts of the interactions among abiotic extrinsic-intrinsic factors and processes on dryland degradation dynamics (source: authors).

From the geomorphological perspective, soil erosion refers to the natural processes that detach, transport, and deposit sediment (Boardman and Poesen, 2007; García-Ruiz et al., 2017). Erosive soil disturbances, such as many geomorphic processes and their interactions with extrinsic factors such as topography, render fine-scale variations described as pedoheterogeneity in soil biotic-abiotic properties (Taylor et al., 1993; Petersen et al., 2010), classifying landscape into distinct patches (vegetated patches vs. barren patches) and exhibiting multiple resilience thresholds. As a result, pedoheterogeneity, reflecting the influences of many environmental extrinsic controls can be the best predictor of dryland degradation (Ibáñez et al., 2005; Petersen et al., 2010). Therefore, examining the interactions between heterogeneous biotic-abiotic patterns and extrinsic controls, and their impacts on the functioning of ecosystems can be a preferential approach for gaining insights into the resilience dynamics of drylands.

In recent years, many studies examined the importance of interactions between different forms of soil erosion such as hydrologic–aeolian erosion (Ravi et al., 2007; Ravi et al., 2008; Ravi et al., 2010a; Ravi et al., 2011), fire (Turner et al., 1994; D'Odorico and Porporato, 2006; Ravi et al., 2009a), overgrazing (Anderies et al., 2002; van de Koppel et al., 2002; Neff et al., 2005), and biotic-abiotic structures, in the acceleration of drylands degradation. Few of these studies have shown the impacts of landform-dependent geomorphic processes, or anthropogenic disturbances other than the overgrazing and fire, on the dynamics of dryland resilience (Mohseni et al., 2017a; Mohseni et al., 2017b). In the present paper, using a selection of two erosive soil disturbances (landslide and land subsidence) which have been less studied in drylands, we reviewed how the processes promoting fine-scale variations in soil biotic-abiotic properties can affect the functioning of ecosystem. Additionally, we ask how resilience of drylands is influenced by such changes in the functioning of ecosystems. The research specifically addresses:

(1) Some causes and eventualities of spatial heterogeneity in drylands.
(2) The relative importance of pedoheterogeneity in dryland resilience.
(3) Insights into the paradox of spatial heterogeneity as an environmental control, which can be both degrading and developing.

Causes of the spatial heterogeneity and impact on the functioning of dryland

Environmental biotic-abiotic heterogeneity is a fundamental driver of change in ecosystem functioning on a local scale (Gaston, 1996; Loreau et al., 2001). Landscape fragmentation in resource-limited ecosystems can cause local scale variation in the distribution of soil resources (van de Koppel and Rietkerk, 2004; D'Odorico et al., 2007; Turnbull et al., 2012). Subsequently, such local scale variation in the distribution of soil resources can promote fragmentation across landscape over time. Thus, any disturbance which disrupts the processes of homogenization of resource distribution trends can promote biotic-abiotic heterogeneity within the landscape. The relative importance of disturbance drivers varies between systems, dependent on the inherent characteristics of each ecosystem (Turner, 2010; Crum et al., 2016). In the case of drylands, disturbances driving soil erosion may be the foremost source of the spatial heterogeneity in the organization of biotic-abiotic structures (Turner, 2010), and due to inherent dryland environmental conditions such as high aridity, low or intensive precipitation, diffuse vegetation cover, and low moisture availability promotes the high sensitivity of the dryland soilscape to erosion processes. Apart from climatic changes leading to increased aridity, which enhance losses of soil resources and biodiversity (Ravi et al., 2010a), geomorphic disturbances are the most widespread drivers of soil degradation in drylands. These disturbances impact on the stability of soil variables at any given location, and over time can affect the sustainability of the whole landscape. But how do these disturbances lead to spatial heterogeneity within the landscape?

Erosive soil geomorphic processes involving the separation, transportation, and depositing of soil particles play the critical role in the structuring and functioning of ecosystems, through their impacts on changing the functioning of ecosystems. In dryland systems where erosion and redistribution of sediment are active, detached surface soil removes nutrients and organic matter from particular mosaics, depositing them on others and causing spatial heterogeneity in edaphic patterns and associated ecological and hydrological structures, over short distances within the landscape (Puigdefábregas, 2005).

Interactions between intrinsic and extrinsic environmental controls determine the natural matrix of the spatial heterogeneity within ecosystems (Holling, 1992; Turner and Chapin, 2005). Apart from hydro-aeolian physical processes that directly disrupt homogeneity in the distribution of biotic-abiotic structures via the separation, transportation, and depositing of soil resources (Lal, 2001; Breshears et al., 2003; Ravi et al., 2008; Ravi et al., 2009b), landform–dependent processes (Bedford and Small, 2008) are the best example of the interactions between intrinsic (e.g., soil biotic and abiotic components) and extrinsic (e.g., landform topographic position) environmental controls, causing the spatial heterogeneity in patterns of soil biotic-abiotic properties (Wondzell et al., 1996). Few works have focused on the impacts of the interactions between landform-dependent processes and biotic-abiotic structures in the dynamics of the spatial heterogeneity in dryland landforms (Geertsema and Pojar, 2007; Mohseni et al., 2017a; Mohseni et al., 2017b).

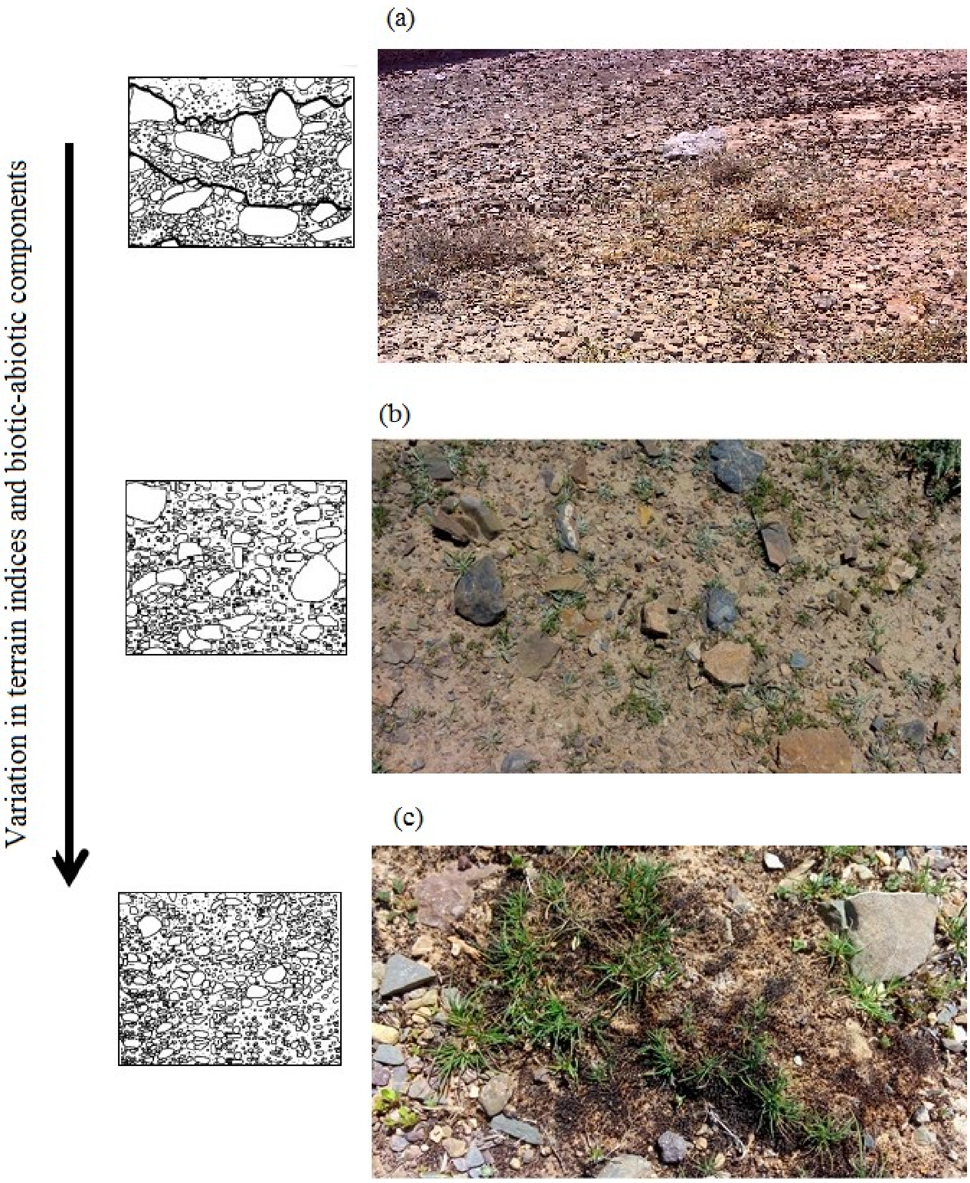

Figure 2. An example of the impacts of the interactions of extrinsic (topography) and intrinsic (soil physical properties) controls and processes (landslide) on the emergence of the spatial heterogeneity within drylands. The heterogeneous redistribution of debris flow-related sediments along fine-scale topographic variations (a-c) and the emergence of pedoheterogeneity and associated ecological (c: biological soil crust) and hydrological patterns within different topographic positions (modified from Mohseni et al. 2019).

For example, debris flows; the most widespread functional processes on the alluvial fan landforms, are strongly controlled by the topography that provides the physical pathway for the redistribution of sediments. Consequential to geomorphic disturbances are in situ variations of biotic-abiotic conditions at any given location (Walker and Shiels, 2012). Field observations illustrate the irregular redistribution of debris flow sediments along fine-scale changes in slope gradient, leading to the emergence of different patterns in internal and external soil properties (pedoheterogeneity) over short distances and restricted areas (Mohseni et al., 2017a).

Alternatively, since ecosystem processes are strongly sensitive to the distribution patterns of biotic-abiotic environment components (Hooper and Vitousek, 1998; Reich et al., 2005), pedoheterogeneity appearing within alluvial fans can affect the functioning of ecosystems through changing feedback processes (Kie et al., 2002). Local variations in internal soil properties (e.g., particle size distribution) cause micro-scale preferential nodes of infiltration which stimulate variations in ecohydrological processes within landforms (Figure 2).

Small variations occur in water content that, in turn, lead to huge differences in hydraulic conductivity trends stimulating the spatial heterogeneity in the distribution patterns of vegetation metrics within different landform positions (Mohseni et al., 2017a). The emergence of such localized variations promotes site condition in different positions of the upper, middle, and lower fan along slope. The consequences of such landform-dependent processes suggest that a high sensitivity level of dryland soilscapes to initial minor variations depends on the extrinsic characteristics of the landform.

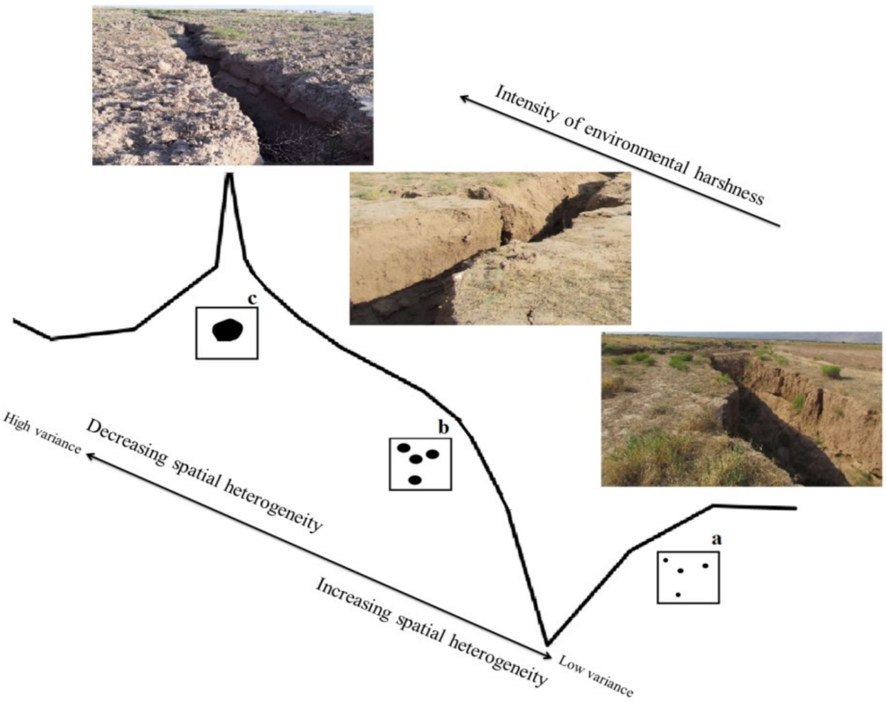

Figure 3. Conceptual diagram showing the variance of vegetation density distribution as an indicator for monitoring critical threshold of spatial heterogeneity. Snapshots show expansion of eco-edaphic heterogeneities within a landscape encouraging transformation between developed and degraded states along the development of earth fissures related to land subsidence. The black circles indicate the degree of connectivity of homogeneous eco-edaphic patterns. a: initiation of heterogeneities within soil biotic-abiotic patterns along with high resilience and decreasing variance, b: increasing the distance between vegetated and barren patches along with decreasing resilience and gradual increasing in variance trends, c: significant heterogeneity losses and the emergence of homogeneous degraded state showing imminence of irreversible transitions (peak of variance) (source: authors).

Some erosive soil processes, without material transporting and depositing mechanisms, indirectly disturb distribution of soil resources via their impacts on the structuring of ecosystem. Land subsidence is an example of such processes. Over-exploiting groundwater is one of the most negative environmentally-depleting practices of arid and semi-arid regions. Water depletion related to such practice causes deformation of the earth through the emergence of land subsidence and the associated ground fissures (Burbey, 2002; Pacheco-Martínez et al., 2013). This anthropogenic disturbance mostly occurs on piedmont plain landform covered by alluvial and fluvial sediments, which have a low degree of consolidation and are potentially prone to divergence. Field observations illustrate that the different dynamics of ground fissures (Figure 3) are important contributors to the occurrence of spatial heterogeneity in soil biotic-abiotic patterns (Mohseni et al., 2017b), in that vegetation metrics (e.g., density and size distribution) and abiotic soil characteristics (e.g., $CaCO_3$, EC, clay content, and infiltration rate) express a spatial relationship to the variations of the ground fissures in terms of length and width. Over-exploitation of groundwater leads to soil compaction and subsequently drainage reduction. This process stimulates the emergence of impermeable soils around the fissures. In the early stages of the formation of ground fissures following an intense rainfall event, water flows into surface fissures causing lateral washing of silt and clay which expand the fissures, over time becoming eroded gullies. The extended fissures increase the instability of the surrounding plants due to the collapse of vegetation into gullies.

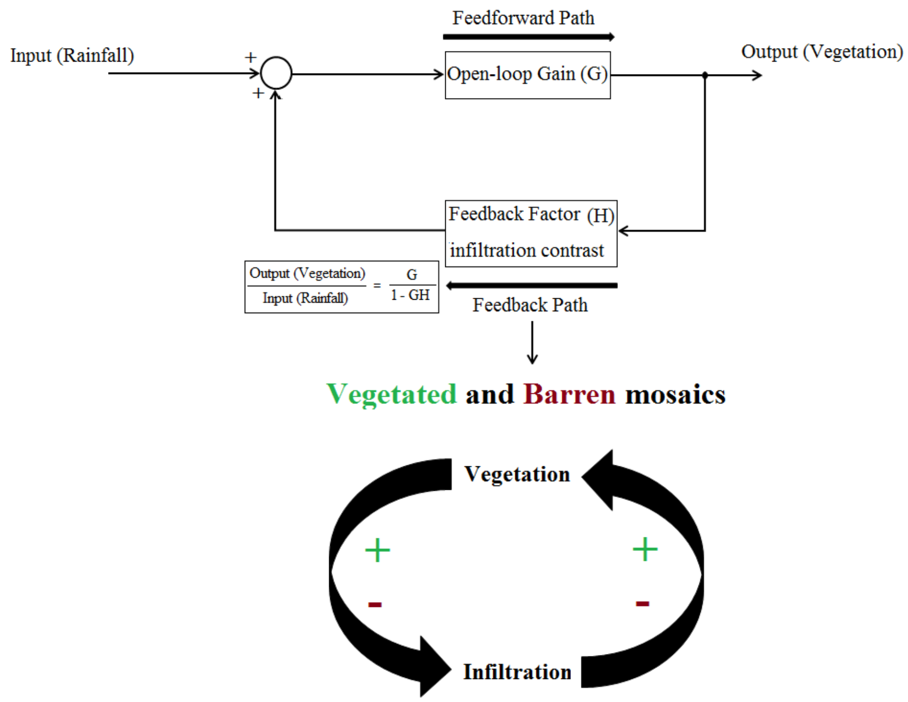

Figure 4. Conceptual diagram of positive plant-water feedback loop in arid ecosystems showing shift between two different states (developed and degraded states) caused by shift between two different sets of positive feedback loops amid two limited environmental elements in arid ecosystems (source: authors).

The condition occurs in the emergence of barren soils around gullies. This ultimately promotes inappropriate soil physiochemical attributes accelerating soil degradation trends. Such hostile conditions do not occur around surface fissures (the fissures that are small in terms of length and width). Local pedoheterogeneity induced by various spatial extent of ground fissures affect the functioning of the ecosystem through changing ecohydrological feedback processes (Figure 4), based on the dynamic relationship of soil-vegetation structures and runoff. Removal of vegetation, followed by expansion of ground fissures and the emergence of degraded soils, allow barren patches to connect as pathways of runoff and water erosion. Under sufficient rainfall, water is redistributed by surface flow from the barren soil surrounding extended ground fissures to the vegetated patches. This event simultaneously engage in a positive resource concentration feedback loop that emanates from the vegetated soil and a resource loss feedback sourced in barren soil (Figure 4), which may be defined as a horizontal resource redistribution over the short distances between the patches (Rietkerk and van de Koppel, 1997; Rietkerk et al., 2002; Rietkerk et al., 2004; Puigdefábregas, 2005; Saco et al., 2007; King et al., 2012). Thus, the expansion of the ground fissure and subsequent changes in soil biotic-abiotic components activate destabilizing positive feedback mechanisms, which stimulate the critical spatial heterogeneity encouraging collapse of the landscape into degraded state.

Consequence of landscape heterogeneity

The uneven redistribution of resources induced by erosive soil disturbances generates fragmented soilscapes with heterogeneous edaphic, ecological, and hydrological patterns (Box, 1961) within different arid land landform positions. The presence of patches with different biotic-abiotic properties causes the landscape to exhibit simultaneous contradictory states with different resilience degrees, which due to their inherent differences in structuring and functioning respond differently to environmental stresses. Thus, shifts of patches to alternative states of equilibrium occur, based on the different values of control variables (van Nes and Scheffer, 2005). The resilience hot spots include soil patches that preferentially acquire nutrients and other limited resources from the surrounding patches (McClain et al., 2003; van der Valk and Warner, 2009; Leon et al., 2014; Ma et al., 2017). It is fundamental to understand the conditions which continue to facilitate the establishment of more hot spot patches under intensifying pressures, as opposed to resilience blind spots. In water-limited ecosystems such as drylands, hot spots are mostly linked to the concentrations of soil water (Laudon et al., 2016) and are, thus, strongly correlated to the pedotaxa (Ibáñez et al., 2014), particularly soil texture (Cable et al., 2008), soil organic matter fractions (Almagro et al., 2013), biotic soil components such as vegetation compositions (Maestre and Cortina, 2003; Vargas et al., 2011), and all biotic-abiotic attributes which promote absorption and retention of moisture by soil (Morse et al., 2014). A high frequency of soil patches with resilient hot spot features within a landscape elevates hot spots to hotscapes, with a preferential impact on resilience level at the landscape scale.

Landform structure-dependent processes such as debris flows that occur on alluvial fans facilitate the heterogeneous redistribution of soil particles with different sizes, which produce variations in soil texture and associated infiltration rate (Graetz and Tongway, 1986; Wood et al., 1987) within different topographic positions. Contrasting factors such as drier or wetter conditions due to varying degrees of hydraulic conductivity, and stonier or softer soil due to varying particle size distribution, divide the landform into segments with relative uniformity of edaphic, ecological, and hydrological patterns. The contrasted localized conditions within the landform exhibit multiple resilience thresholds. This implies that each position exists under a different combination of transitory localized conditioning factors, shifting to alternate stable states at different values of control variables, displaying varying resilience levels in the face of environmental stresses. Field and modeling studies have indicated that significant functional and structural differences between different alluvial fan positions arise from the interactions of geomorphic process-control and biotic-abiotic soil variables, which display different responses to the increasing levels of aridity, in such a way that critical transitions occur according to the different levels of rainfall (Mohseni et al., 2017a). Positions with more desirable environmental conditions, such as higher levels of permeable soil particles and hydraulic conductivity, qualify as resilient hot spots due to their greater degree of self-organization in the face of intensifying aridity, compared with other positions. Conversely, positions with significant differences in the spatial patterns of soil biotic-abiotic properties cannot sustain high aridity levels, and therefore irreversible transitions occur under higher rainfall than in the case of the hot spots. As a result, the emergence of multiple resilience thresholds, and associated varied responses, displays a gradual and predictable degradation of drylands to a critical level, rather than catastrophically (Meron, 2012). Alternatively, the presence of soil patches with resilience hot spot features provides an opportunity for increasing the resilience level of fragmented landscape.

The findings of other studies show that variations in the architecture of ground fissures can promote dryland fragmentation into a range of developed (vegetated patches) and degraded (barren patches) states exhibiting multiple resilience thresholds (Fig. 4). The coexistence of the heterogeneous states, depending on ground fissure architecture, with amplifying ecohydrological feedback mechanisms between biotic-abiotic components of diverse states can further disturb landscape stability (Peters et al., 2004; D'Odorico and Porporato, 2006; D'Odorico et al., 2006; Borgogno et al., 2009). The importance of the interactions between the local scale heterogeneous patches in dryland resilience dynamics depends on their hierarchical positioning as functions at the higher scale. Developed mosaics around surface fissures display a higher proportion of fine covers, such as clay content, high vegetation cover, more organic matter, and subsequently a superior water-retention capacity, that all play role in resilience hot spots. Plants shelter the ground surface from the erosive wind and water actions, thereby preventing moisture evaporation from the soil surface (Schlesinger et al., 1990; Greene, 1992; Bhark and Small, 2003). Therefore, on vegetated patches around surface fissures or mosaics with no ground fissures, preferentially ecohydrological interactions (Kuzyakov and Blagodatskaya, 2015) guarantee more resilience of vegetation compositions and consequently maintain more desirable biotic-abiotic properties of soil than other patches. Changes in soil properties induced by land subsidence-related soil compaction around extended ground fissures lead to the mortality of the plants and stimulate the emergence of hydrophobic soils with inappropriate physiochemical attributes. This condition encourages the emergence of mosaics with a lower resilience. As a result, extended ground fissures can make pathways for the accumulation of soil resources and runoff toward developed patches (Ludwig et al., 2005; Gabet and Sternberg, 2008), providing an opportunity for strengthening resilience of these states. The pathways initially appear as diffusely degraded patches. In time, the extension of surface fissures by water erosion, encourages greater connectivity of the redistribution pathways of soil resources, reducing the resilience level of developed states due to increased distance from the nutrient source. The development of extended ground fissures across landscape and subsequently increasing connectivity of eroded soil patches leads to the gradual disappearance of multiple resilience thresholds that stimulate catastrophic shifts (Fig. 4). Although numerous resilience thresholds appear simultaneously at patch scale, their cumulative effects on the dynamics of fluxes and resources can affect the resilience at broader scales, including the landscape scale.

Paradox of the effect of spatial heterogeneity on ecosystem resilience

Spatial heterogeneity is the response of systems prone to critical degradation for maintaining their stability in the face of disturbances. The different functioning of mosaics with heterogeneous biotic-abiotic patterns causes them to respond differently to environmental stresses (Mohseni et al., 2017a). The response diversity provides an opportunity for increasing the resilience of the whole landscape (Downing et al., 2012). The heterogeneity may be expected to increase the resilience of ecosystems in the face of stressful conditions. From another perspective, the spatial heterogeneity amplifies small disturbances through activation of destabilizing positive feedback mechanisms (Turnbull et al., 2008; Turnbull et al., 2012; Kéfi et al., 2016), discussed in the previous sections. Given this paradox, is the spatial heterogeneity developing or degrading control of ecosystem state?

The opposing dynamics of heterogeneous biotic-abiotic structures impose a complexity of forces comprising dryland ecosystems. The dynamics of fragmented drylands and transitions between alternative stable states are strongly controlled by the spatial connectivity scale between homogenous patches (Western et al., 2001), in relation to the expansion of disturbances (Turner et al., 2001). The spatial heterogeneity initially utilizes the pathways of interconnected bare soil patches as corridors for the flow of water and soil resources from impenetrable barren patches toward permeable vegetated patches (Belnap et al., 2005; Okin et al., 2009; Ravi et al., 2010b). Disturbances change length of the connected hydrological pathways and thereby affect resilience of fragmented landscapes. When the frequency and development of disturbance is low, the distance between homogeneous patches is small. Since the ability of an organism to complement its resource requirements depends on the distance of those resource patches (Dunning et al., 1992; Taylor et al., 1993), short pathways between source patches (barren soils) and sink patches (vegetated soils) promote a stabilizing feedback mechanism increasing the availability of moisture and nutrients to vegetated patches (Ludwig et al., 2005; Ravi et al., 2010a). This condition maintains the preferential soil biotic-abiotic properties bolstering the resilience of the ecosystem. Once the gap between ecosystem fragments exceeds a dispersal threshold- point in which spatial heterogeneity cannot maintain resilience of ecosystem to combat perturbation and therefore ecosystem collapse to irreversible degraded state- and disturbances such as droughts and grazing continue to increase, significant increased distance between the heterogeneous patches limits the availability of vegetated patches to their nutrient sources, destabilizing the positive feedback mechanism. This condition allows the shrinking of the developed states (Fig. 4). As a result, significant degradation of soil biotic-abiotic properties and subsequently more connectivity of barren patches provides a condition for predomination of degraded state (Alados et al., 2009; Ravi et al., 2009b; Alados et al., 2011). This implies that while disturbances are promoting destabilization of a landscape, the emergence of multiple resilience thresholds, together with highly heterogeneous biotic-abiotic components, can result in a time-delay in response to intensifying stresses. In this condition, the spatial heterogeneity provides an opportunity for landscape renewal, provided that a critical heterogeneity threshold does not appear (Colombaroli et al., 2013) (Fig. 4). Therefore, changes in the rate of connectivity or length of connected pathways provide an indicator for measuring the critical heterogeneity threshold, defining the point at which resource losses are equally balanced across landscape.

In conclusion, spatial heterogeneity may reduce the tendency to catastrophic shifts, depending on dispersal heterogeneity scale, assuming dispersion is important and local environmental characteristics are not linear in variation. This framework provides a basis for anticipating future landscape dynamic trends, and guiding ecological management and remediation efforts.

Conclusions

Dryland soilscapes include patches with extremely high differentiations of edaphic, ecological, and hydrological properties and processes. Small scale heterogeneity in soil biotic and abiotic properties within landscape plays a major role in the operation of geomorphologic and ecohydrologic processes by controlling runoff and sediment dynamics and the associated feedback mechanisms (Dickie and Parsons, 2012). Since dryland degradation strongly affects these interactions, understanding the spatial linkages between the processes and drivers inducing spatial heterogeneity can be a preferential approach for simplifying and grasping the dynamic trends of ecosystem resilience. This paper reviewed the causes and effects of spatial heterogeneity and their impact on ecosystem functioning, underlining the importance of local scale soil biotic-abiotic imbalances in the dynamics of dryland resilience at the landscape scale. Spatial heterogeneity depending on connectivity scale of homogeneous patches can exhibit the contradictory reducing and enhancing effects of landscape resilience. As such, changes in the rate of connectivity or length of the connected pathways provide an indicator for measuring the critical heterogeneity threshold, defining the point at which resource losses are equally balanced across landscape. Although the spatial heterogeneity is a warning sign of critical soil degradation, the occurrence of multiple resilience thresholds induced by spatial heterogeneity boosts response diversity, which can engender greater resilience of the ecosystem as a whole and thereby stimulate gradual and predicable shifts instead of catastrophic transition.

Disclosure statement

No potential conflict of interest was reported by the authors.

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