Connectivity in dryland landscapes: shifting concepts of spatial interactions

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Dryland ecosystems are often characterized by patchy vegetation and exposed soil. This structure enhances transport of soil resources and seeds through the landscape (primarily by wind and water, but also by animals), thus emphasizing the importance of connectivity – given its relation to the flow of these materials – as a component of dryland ecosystem function. We argue that, as with the fertile-islands conceptual model before it, the concept of connectivity explains many phenomena observed in drylands. Further, it serves as an organizing principle to understand dryland structure and function at scales from individual plants to entire landscapes. The concept of connectivity also helps to organize thinking about interactions among processes occurring at different scales, such as when processes at one scale are overridden by processes at another. In these cases, we suggest that state change occurs when fine-scale processes fail to adjust to new external conditions through resource use or redistribution at the finer scale. The connectivity framework has practical implications for land management, especially with respect to decision making concerning the scale and location of agricultural production or habitat restoration in the world's drylands.

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Drylands, which constitute approximately 40% of the Earth's land surface (Reynolds *et al.* 2007) but are discussed in only about 6% of the terrestrial ecological literature, are unusual among terrestrial ecosystems because of the patchy distribution of vegetation and the high proportion of bare (unvegetated) soil that characterize such systems (of journal articles in the Web of Science index on terrestrial ecology, only 6% also reference "arid", "semiarid", "subhumid", "desert", or "dryland", as of April 2014). Low annual precipitation and high temperatures during the growing season lead to relatively small amounts of plant-available water, which translates into landscapes consisting of individual herbaceous or woody plants separated by bare soil interspaces that range in average diameter from < 1 m (grasslands) to > 5 m (shrublands). Given their characteristic patchy structure, the functioning of dryland landscapes has been based predominantly on individual plants and their associated bare interspaces (ie islands of fertility; Schlesinger *et al.* 1990). Although this plant–interspace perspective has led to insights into the structure and function of drylands (eg Schlesinger and Pilmanis 1998; Aguiar and Sala 1999; Reynolds *et al.* 1999), the model fails to explain some of the dynamics of these systems (Peters *et al.* 2006). A framework – one that focuses on the spatial interactions that link patterns and processes across multiple, interacting scales – is therefore being adopted (Peters *et al.* 2007). Here, we synthesize and extend recent developments in our understanding of these spatial interactions.

In a nutshell:

- Drylands are strongly shaped by the transport of soil resources and seeds through connected pathways
- An emerging conceptual model for understanding drylands relies on the idea of "connectivity", or how locations within the landscape are connected through the transfer of materials or energy
- The extent to which landscape units are physically linked to one another (structural connectivity) differs from connections that develop during individual events (functional or process-based connectivity) because in the latter, the degree of connectivity depends on the magnitude of the event
- Connectivity exists at a range of scales and, as an organizing concept for dryland landscapes, serves to explain how processes at one scale interact with processes at other scales, resulting in many of the observed features of drylands, including patterned vegetation, catastrophic events, state changes, and regime shifts
- Connectivity can be deliberately or inadvertently altered; consideration of the scale and distribution of connected pathways is crucial for the sustainable management and restoration of drylands

The concept of "connectivity" is currently being usefully applied to dryland ecology, building on the earlier use of the term in other scientific fields. Connectivity in hydrological sciences, for instance, reflects the transport of water and water-borne materials between locations on or beneath the soil surface (eg Ali and Roy 2009), and has typically been used in the analysis of systems involving substantial water movement, including groundwater systems, channel systems, and hillslopes in mesic (moderately moist) environments (eg Bracken *et al.* 2013). By way of comparison, connectivity in landscape ecology has generally referred to the movement of organisms between locations within the landscape (eg Taylor *et al.* 1993). The repurposing of this concept for application in dry-

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land ecology has not only yielded a new understanding of dryland ecology, but has also highlighted new questions and avenues for research.

For our purposes, connectivity is defined as the extent to which materials can move, spread, or be redistributed from one place to another within the landscape (sensu Peters *et al.* 2008). In drylands, connectivity is emerging as a useful analytical tool for understanding systems that are shaped by various interacting transport vectors that are, in turn, driven by patterns and processes operating across a range of spatial and temporal scales.

The historical view

The concept of fertile islands, as originally presented by Garcia-Moya and McKell (1970) and later expanded by Schlesinger *et al.* (1990), considers horizontal transport of sediments, leaf litter, and nutrients as mechanisms for accumulation of soil resources under individual plant canopies. Despite the early acknowledgement of the importance of transport processes, the concept has generally been reduced to a description of processes and patterns at the plant–interspace scale (eg Burke *et al.* 1998; Schlesinger and Pilmanis 1998; Yang *et al.* 2011; Klass *et al.* 2012; Parker *et al.* 2012). In three recent review papers summarizing the patterns of biogeochemical processes in shrub-encroached dryland landscapes (Barger *et al.* 2011; Eldridge *et al.* 2011; de Graaff *et al.* 2014), none quantitatively addressed the potential role of transport processes in the development or maintenance of spatial heterogeneity. Although the fertile-islands model provides an extremely useful conceptual framework to guide research in drylands globally, its restricted application to plant–interspace interactions (see above) is a limitation.

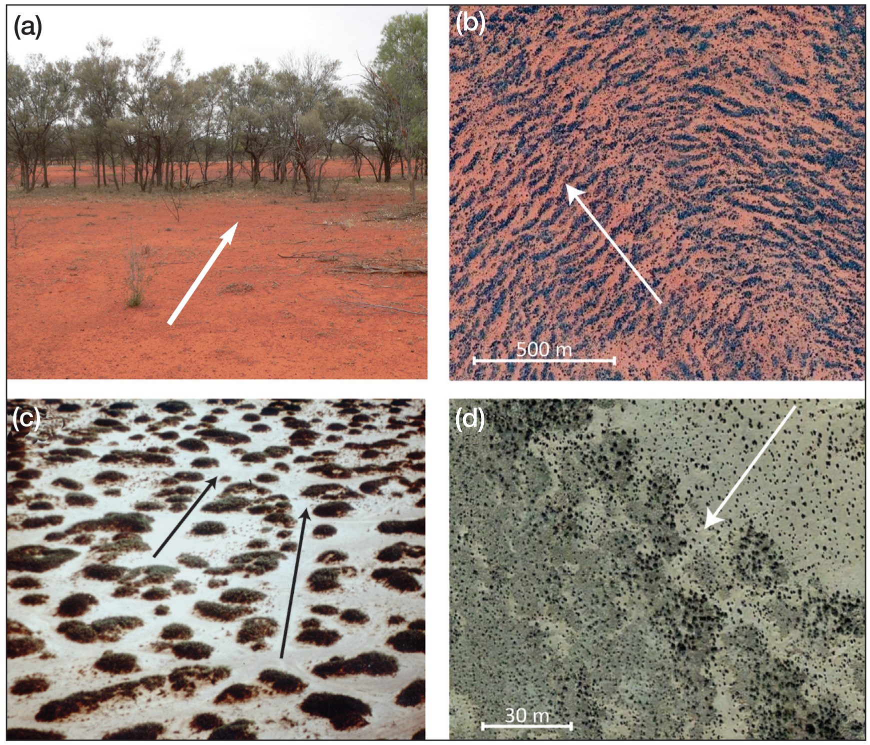

Figure 1. *Cases where the structure and function of ecosystems are influenced by connectivity and the spatial arrangement of vegetation. (a and b) Ground-level and overhead views, respectively, of mulga (*Acacia aneura*) groves in Australia, showing their characteristic banded structure (adapted from Moreno-de las Heras* et al. *2011b). (c) "Streets" (indicated by arrows) in mesquite (*Prosopis glandulosa*) nebkha fields of the Jornada Experimental Range, New Mexico (from Okin and Gillette 2001). (d) An ecotone between a shrubland (top right) with high hydrological connectivity and a grassland (bottom left) with low hydrological connectivity (Mueller* et al. *2007). For all images, arrows indicate the direction of water or wind flow.*

Spatial interactions beyond the fertile island

Despite the success of the fertile-islands model in explaining aspects of dryland patterns, there are many phenomena that cannot be explained by a plant–interspace interpretation. One such example is banded or patterned vegetation (Figure 1, a and b; eg Tongway and Ludwig 2001). The structure and function of these systems are strongly linked to the redistribution of water from mostly bare source areas to vegetated sink areas with high infiltration rates. Water redistribution in the banded mulga (*Acacia aneura*) systems of Australia, for instance, occurs at scales ranging from a few meters to hundreds of meters, well beyond the scale of plants and interspaces (Ludwig *et al.* 2005).

The organization observed in nebkha fields (sand mounds formed by trapping of sand by the branches of a plant; Figure 1c) provides another example where dynamics cannot be explained by redistribution of resources at the plant–interspace scale. In some dryland environments with deep sandy soils and large areas of bare ground, aeolian (wind-borne) transport leads to erosion in interspaces and redeposition of sediment around woody plants. The result of this erosion–deposition process is a landscape consisting of nebkhas enveloping woody plants separated by large bare spaces between dunes (Tengberg 1995; Rango *et al.* 2000). These interdunes constitute areas of large (> 2 m) fetch (the distance over which wind blows) that allow a considerable amount of sediment transport through, within, and out of the system, at scales exceeding that of the plant interspace. Some nebkha fields exhibit large-scale organization, with extended bare areas aligned with prevailing wind patterns into "streets" (eg Okin and Gillette 2001).

In these two cases, a linear scaling-up of plant–inter-

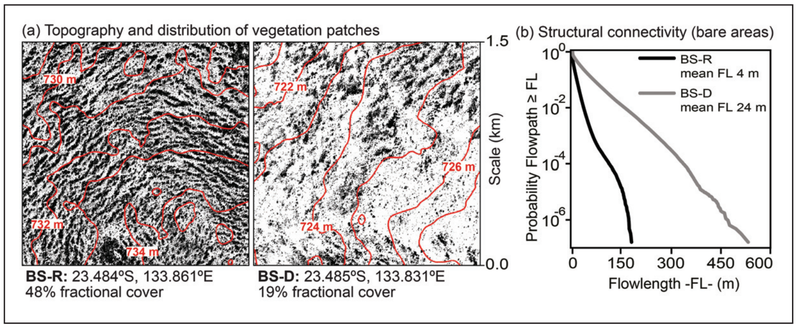

Figure 2. *Differences in structural connectivity, as measured by flowpath. (a) Two slopes in Australia with different vegetation cover (black polygons). Topographic contours are indicated by red lines. The plots are 1.5 km × 1.5 km. (b) Flowpath distribution for the two slopes (BS-R – high cover, low structural connectivity; BS-D – low cover, high structural connectivity; after Moreno-de las Heras* et al. *2012).*

space dynamics fails to explain the broader patterns because the spatial arrangement (rather than just the amount) of vegetation and interspaces controls these systems. The importance of spatial arrangement is further evident at ecotones (transition zones between adjacent communities; eg shrubland to grassland), where water flow and spatial connectivity within each plant community (ie high versus low hydrological connectivity for shrublands and grasslands, respectively) influence the location and behavior of the ecotone (Figure 1d). The effect of vegetation arrangement on ecosystem function can also be seen in the response of vegetation to precipitation events, where rainfall-use efficiency (ie the vegetation response per unit amount of precipitation, eg grams of biomass per millimeter of rainfall) varies with hydrological connectivity (WebFigure 1; Moreno-de las Heras *et al.* 2012). This relationship suggests two alternative states with a critical threshold between them: one alternative state consists of functional landscapes with low hydrological connectivity and high rainfall-use efficiency, whereas the other alternative state consists of dysfunctional or leaky landscapes with high hydrological connectivity and low rainfall-use efficiency.

■ The emerging conceptual framework: connectivity and its role in dryland function

Connectivity is defined by the movement of a substance (eg seeds, water, sediment, nutrients, fire) by some means (eg wind, water, animals) through a transport pathway. Connectivity plays an important role in landscape change because a given location is connected by transport processes to other locations with which it can exchange material (eg seeds, water, soil resources) in one or both directions. These pathways result in a landscape composed of locations that are interconnected at a range of temporal and spatial scales. The dynamics of any one location are therefore tightly coupled with the current state and dynamics of the other areas with which it is connected (Stewart *et al.* 2014).

Recently, two useful components – structural connectivity and functional (or process-based) connectivity (Bracken *et al.* 2013) – have been identified that may help disentangle the spatiotemporal aspects of connectivity and clarify the degree and temporal patterns of connections among locations (Bracken and Croke 2007; Turnbull *et al.* 2008; Wainwright *et al.* 2011). Structural connectivity is a form of heterogeneity that refers to the extent to which spatial units are physically linked to one another. It can be quantified through the use of contiguity indices, such as "leakiness" (Ludwig *et al.* 2007) and "flowlength" (Mayor *et al.* 2008); these account for the potential movement of substances in bare and low-cover areas in relation to the spatial organization of vegetation and local topography (Figure 2). In contrast, functional (or process-based) connectivity refers to the connections that arise during a particular transport event (eg a storm). Thus, for example, in a small runoff event in which overland flow is low, connectivity between locations will be dominated by microtopography (ie very small differences in soil-surface height). Locally high points may remain largely unconnected as water and sediments pass from one connected low point to another. In larger runoff events, much of this microtopographic control may be overwhelmed by increased runoff so that connectedness and consequent erosion are driven more by hillslope-scale macrotopography (Figure 3). Although structural connectivity can be easily measured, there is little consensus on how to quantify functional connectivity or indeed whether a simplified index-based approach is useful or could be universal (Moreno-de las Heras *et al.* 2010a; Mayor *et al.* 2011; Larsen *et al.* 2012; Bracken *et al.* 2013).

Both structural and functional connectivity are dynamic, although they change at different temporal scales. Landscape spatial patterns, which determine structural connectivity, change slowly (ie over weeks, months, and years) as a response to the dynamics of vegetation and soil processes (Turnbull *et al.* 2008). Conversely, functional connectivity varies between and within transport events (Bracken and Croke 2007; Wainwright *et al.* 2011).

The spatiotemporal interactions between structural and functional connectivity have a net impact on dryland ecosystems (Wilcox *et al.* 2003; Moreno-de las Heras *et al.* 2011a). Landscapes characterized by reduced structural connectivity will have negligible rates of water transport as well as limited wind- and water-borne transport of nutrients. Under such conditions, fine-scale redistribution of resources between bare and densely vegetated patches would increase water and nutrient availability, thereby facilitating plant growth and, ultimately, reinforcing the landscape's low-connectivity state. Alternatively, landscapes with high structural connectivity will exhibit higher rates of water and nutrient transport at broader scales, reducing the availability of resources and thus discouraging plant growth. This can directly affect plant viability and, as a result, influence vegetation presence and heterogeneity. Further positive feedbacks between structural and functional connectivity may exacerbate the degradation of highly connected landscapes, and ultimately promote regime shifts (sensu Bestelmeyer *et al.* 2015). Barring active management, these changes will most likely become irreversible in landscapes with extensively developed drainage networks (eg rills, gullies) or highly developed aeolian topography (eg nebkhas) that provide permanent structural pathways for the routing of soil resources (Wainwright *et al.* 2008; Moreno-de las Heras *et al.* 2011a; D'Odorico *et al.* 2012).

Connectivity is a fundamental part of many ecosystem feedbacks in drylands. For example, fire propagates along pathways of herbaceous plant material and controls the growth of woody vegetation; by causing seedling mortality among woody plant competitors, fire facilitates the growth of fire-adapted grasses (Hodgkinson 1986), which in turn provide fuel for future fires that maintain woody vegetation below densities where they could outcompete grasses. Interruption of this fire–grass feedback through drought or livestock grazing that preferentially kills or removes grasses and thereby disconnects herbaceous fuel pathways can result in woody encroachment and shifts to woody plant dominance.

Connectivity occurs across a range of spatial scales: from plants and their associated interspaces, to patches, landscape units, or plant community types, as well as among regions and continents (Peters *et al.* 2008). From an ecogeomorphic perspective (that is, in terms of the interactions between organisms and landforms), the connectivity conceptual model most closely resembles the fertile-islands model at the smallest scale (ie the plant-interspace scale). In the fertile-islands model, heterogeneity of vegetation cover in drylands is related to the concentration of nutrients beneath plants through biogeochemical cycling and deposition of material moved from interspaces as a result of wind and water erosion. Under the connectivity model, plants and their interspaces are linked through the transfer of material between them, and in this sense, the fertile-islands model can be seen as a specialized version of the connectivity model. At the plant–interspace scale, connectivity is not solely an aboveground phenomenon but may also include the exchange of carbon, water, and energy through the activity of soil microbes and plant roots (Klass *et al.* 2012). As the scale of heterogeneity increases, so does the length of connected pathways; this is related to dryland degradation in both conceptual models (eg Schlesinger and Pilmanis 1998; Ludwig *et al.* 2007; Okin *et al.* 2009).

At a larger scale, plant patches of similar productivity or species composition can serve as sources or sinks of material moved along connected pathways. Patches play an important ecological role; for instance, their spatial arrangement influences animal movement and foraging

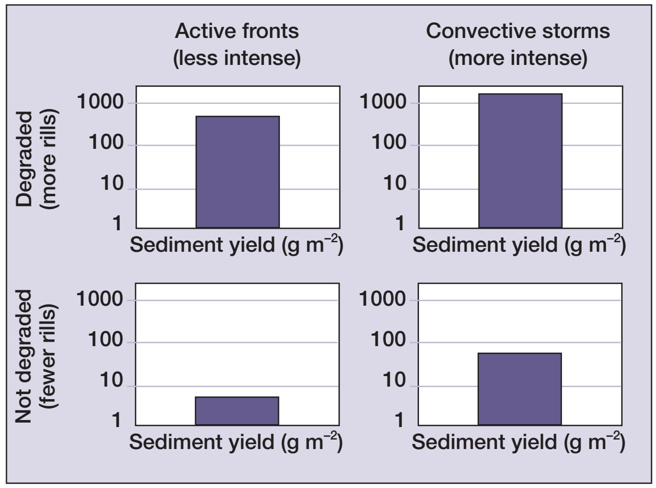

Figure 3. *Comparison of sediment yield (grams of sediment per square meter) from runoff events generated on degraded and undegraded hillslopes (both 20° on the same substrate) by low-intensity active Atlantic fronts and high-intensity convective storms (note log scale on sediment yield graphs; data from Moreno-de las Heras* et al*. 2010b).*

patterns (Sanchez and Parmenter 2002). Although plant-interspace interactions occur within each patch, the movement of materials and energy (ie the connectivity) among patches can overwhelm these finer-scale interactions and may come to dominate plant–interspace dynamics.

In this context, we argue that the dominance of coarser-scale (eg patch) over finer-scale (eg plant–interspace) processes occurs when the finer system cannot fully adjust to changes driven from the coarser scale. A small change in resources caused by (connected) coarse-scale transport, for instance, may allow the finer system to buffer the change by adjusting resource use or distribution (eg D'Odorico *et al.* 2006, 2010). But if the forcing is too large, the finer system may not be able to adjust without a regime shift (sensu Bestelmeyer *et al.* 2015). Indeed, we suggest that a state change often occurs when rates at the two scales are incompatible (WebFigure 2; Bestelmeyer *et al.* 2015).

Plant communities (eg upland or lowland grasslands, shrublands) at the landscape scale consist of each of the finer-scale systems (ie plant–interspace, patch). Redistribution of materials across the landscape through connected pathways at all scales influences the location and evolution of these plant communities, depending on the balance between landscape-scale additions/removals and finer-scale capacity to accommodate these changes. The contribution of runoff, sediment, and groundwater from the upper portions of hillslopes along connected pathways to lowlands that are sustained by these resources illustrates the importance of this landscape-scale connectivity.

■ Why is connectivity important?

The connectivity model for dryland function represents a spatial reorientation and expansion beyond the fertile-islands concept. Through the lens of connectivity, we are better able to explain and understand phenomena that do not easily fit into a perspective focused on plants and their associated interspaces. For example, decomposition rates of organic matter have traditionally been perceived as being controlled by in situ drivers; recent research, however, indicates that the mixing of leaf litter with soil particles transported horizontally by wind or water appears to be a key contribution to dryland decomposition (Throop and Archer 2009; Hewins *et al.* 2012). This suggests that decomposition can be influenced by landscape-scale patterns that affect wind and water transport.

Connectivity also provides a means to evaluate cross-scale interactions in drylands, which is often essential in cases where catastrophic events or transitions are observed (Peters *et al.* 2004). Primary among these are instances in which coarse-scale processes override smaller-scale processes, as when coarser-scale changes in resources exceed the capacity of finer-scale processes to buffer (through use or redistribution) the new external forcing without a regime shift. The Dust Bowl, which occurred after perennial grasslands were converted to cultivated croplands in the Great Plains of the US, is an example. Widespread drought (ie water deficit) in the 1930s led to crop failures (ie inability to cope with the water deficit) that increased the connectivity of erodible soil (ie a regime shift), particularly in nearby or adjacent fields (Peters *et al.* 2004). The new, highly connected state led to major wind erosion/dust emission events throughout the region, with these "black blizzards" negatively affecting air quality throughout the central and eastern US (Worster 2004). The Dust Bowl case shows how both large-scale climatological and land-use patterns can interact to influence local-scale processes (wind erosion/dust emission, mediated by connectivity of bare soil; eg Okin *et al.* 1999; Okin and Gillette 2001; Okin 2008). Furthermore, it demonstrates the impact of local-scale connectivity on larger-scale connectivity: namely, the connectedness of erodible bare areas resulted in wind erosion/dust emission, leading to dust transport through the atmosphere.

The idea that landscapes are affected by connectivity is not new. The fundamental concept in soil science of the "catena" (the sequence of related soils on a slope) and groundwater flow both require connected pathways, and the importance of connectivity in landscape ecology has been recognized for decades (eg Taylor *et al.* 1993). But we argue that the usefulness of connectivity as a general organizing principle of drylands has been underappreciated. We believe that, going forward, the idea of connectivity will serve as the platform on which new advances in dryland ecology will emerge, particularly in regard to understanding cross-scale interactions.

The development of the connectivity conceptual model has, in fact, highlighted how much we do not understand about the evolution of dryland systems. For instance, how do water and wind transport pathways interact with one another to shape dryland ecosystems?

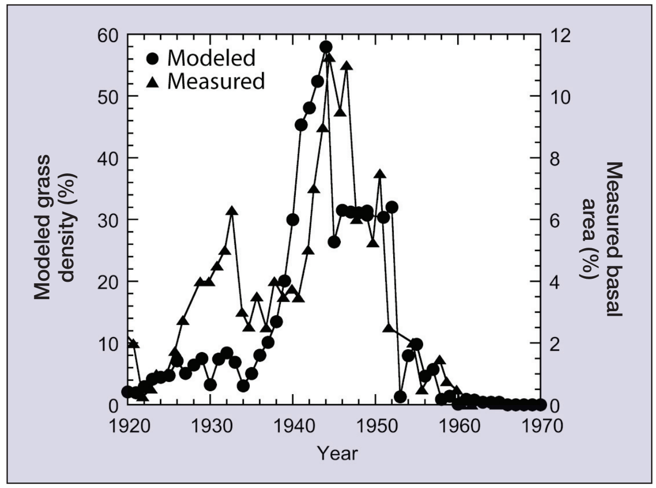

Figure 4. *Results from the model of Stewart* et al. *(2014) that used a framework in which transport and vegetation are linked through connectivity and affected by externalities such as climate, landscape position, and disturbance. These results show collapse of grass cover in the Jornada Experimental Range, New Mexico, during the severe 1950s drought, which agrees well with measured grass cover (shown) and spatial distribution of shrubs and grasses (see also WebFigure 3).*

What determines whether fine-scale processes can adjust to coarse-scale changes – for example, when does a regional drought trigger the erosion–vegetation feedback (D'Odorico *et al.* 2012)? These are critical questions in ecosystem science. Exploration of such ("macrosystem-type") multi-vector and multiscale subjects will likely prove to be a productive area of research. One recent example of such multi-vector/multiscale work is that of Stewart *et al.* (2014), who were able to predict emergent vegetation patterns in drylands, and show how these patterns vary with changing broad-scale drivers (eg climate, grazing), using a model that explicitly considers the connectivity of the landscape with respect to several transport vectors (wind, water, and animals) and the redistribution of resources at the plant–interspace scale (Figure 4; WebFigure 3). Because connectivity applies to a variety of transport vectors, the development of the connectivity model sets the stage for additional multi-vector/multi-scale approaches that, ultimately, will be necessary in order to understand the evolution of dryland landscapes (eg Tongway and Ludwig 2011).

The connectivity concept can also be used to guide experimental design. A cross-scale connectivity experiment on wind and water transport is currently underway in a 10 000-ha area of the Jornada Experimental Range in New Mexico. Focusing on interacting processes that might lead to the transition of shrub-dominated states back to grass-dominated states, this experiment includes treatments that are designed to separate plant-scale processes from larger, patch-scale connectivity-controlled processes (eg wind erosion). Plant-scale manipulations consist of removing mesquite plants from plots to reduce competition with grasses for soil water and nitrogen.

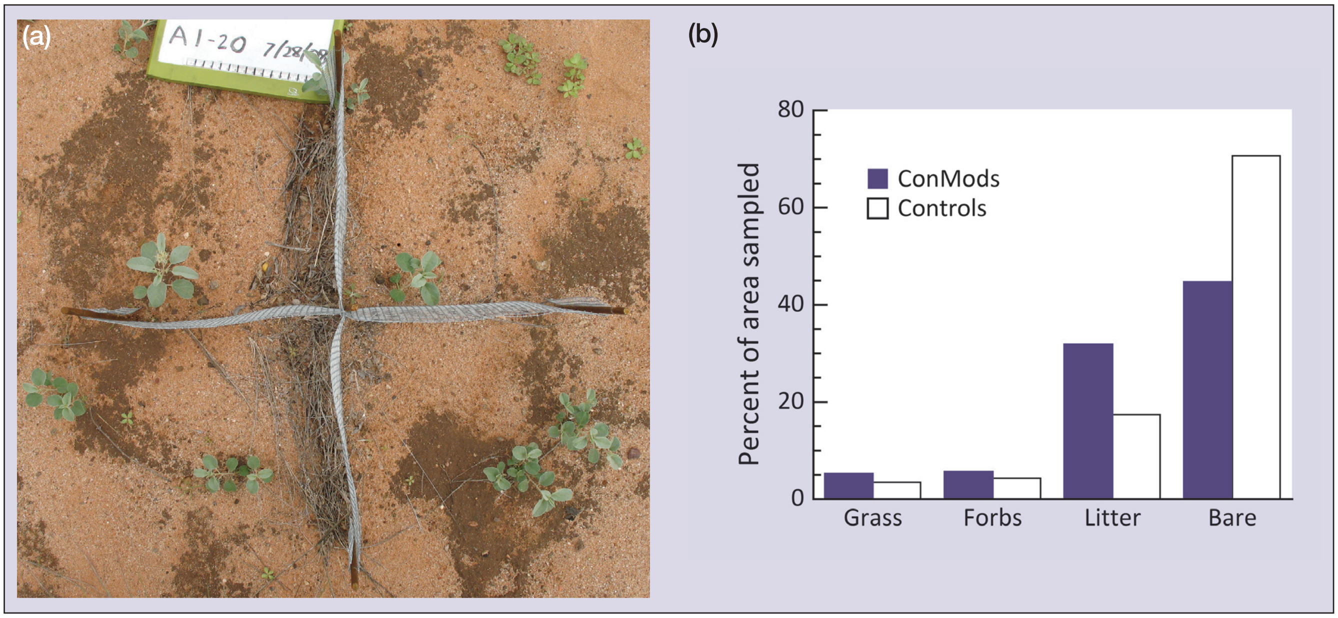

Figure 5. *(a) Connectivity modifier (ConMod) from pilot study after one growing season showing foliar litter collection at base of mesh and germination of forbs within the affected area. (b) Litter increased and bare soil decreased (P < 0.05) by using ConMods as compared with controls based on photographic analysis. Meteorological conditions did not favor grass establishment during the single year of the experiment. Future grass growth is expected when meteorological conditions are more favorable.*

Patch-scale manipulations involve placing connectivity modifiers ("ConMods") in bare soil spaces in each plot (Peters *et al.* 2011). ConMods (Figure 5) effectively reduce the size of connected pathways for wind and water transport on bare soil but do not directly increase plant cover or directly affect biotic processes, although indirect effects of ConMods on biotic processes are expected (eg enhanced carbon and nitrogen mineralization due to greater litter cover).

Practical implications

The connectivity conceptual model builds on the fertile-islands plant–interspace-dominated perspective, and thus has an expanded applicability to landscape management in drylands. In particular, this model has the potential to alter how the landscape is viewed with respect to agricultural production. New methods of production might consider locations on the landscape that are more suitable for crops in terms of water availability or protection from wind erosion. People in some drylands worldwide have been implicitly managing connectivity for millennia by allocating only selected portions of the landscape for production, namely those that can be actively managed to control water runoff and infiltration. The large fields and pastures/paddocks used in modern agriculture are perhaps inconsistent with evaluation and management of the landscape at finer scales, where connectivity is appropriate, but these "back-to-the-future" modes of production may become more necessary with increasing aridity. Nevertheless, modern practices such as no-till agriculture and grazing approaches that minimize denudation of cover exemplify ways to manage for connectivity.

Consideration of connectivity also allows for restoration options in drylands to be re-examined. Just as certain portions of the landscape (due to their connectedness to hillslope water-harvesting potential) might be regarded as suitable for a certain type of agriculture, it may prove useful to evaluate locations within the landscape for their suitability for restoration. Sites characterized by wind-erodible sands with highly connected bare areas and nebkhas may be irreversibly fixed in that state (eg D'Odorico *et al.* 2012) and the costs of restoration efforts could be prohibitive, whereas areas connected to hillslopes that contribute runoff may have soil-moisture conditions more suitable for restoration efforts. However, this notion of the landscape as a mosaic of (more or less) connected areas that are (more or less) suitable for restoration requires knowledge and management of the landscape at scales finer than those typically associated with agricultural production, at least in developed countries.

Managing directly for connectivity may also play a key role in both landscape conservation and the restoration of degraded drylands. For instance, the recovery capacity of degraded mulga shrublands in arid and semi-arid Australia is generally very low. About 20 years ago, however, David Tongway and John Ludwig initiated an experiment to rebuild vegetation patchiness in a grazed mulga landscape by laying brush piles parallel to the land contours in an attempt to break up long-connected runoff pathways and to generate sinks of resources, including seeds, that could facilitate the recovery of vegetation. Those flow obstructions facilitated the establishment of grass and forb species (Ludwig and Tongway 1996). Since then, woody vegetation (mulga trees) has successfully established in these areas (DJ Tongway pers comm).

Conclusions

As our understanding of dryland ecology has improved over the past several decades, researchers have turned their attention to processes and patterns at ever larger scales, perhaps echoing the increasingly large-scale study of many ecosystems, from early plot-level work to more recent continental-scale networks. But drylands remain unusual among terrestrial ecosystems in terms of the considerable abiotic transport through connected pathways made possible by the patchy distribution of vegetation and the high proportion of bare soil. Consideration of this connectivity as an organizing principle for evaluating landscape change and cross-scale interactions is yielding important insights into the form and function of the world's drylands. Perhaps counterintuitively, the advancement of ecological theory in drylands to incorporate connectivity has led to a re-examination of older management practices that took advantage of connectivity without necessarily having the explicit ecological theory to match. We are now developing the theoretical basis to support and, more importantly, to improve those practices.

Acknowledgements

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