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# BIOPHYSICAL LANDSCAPE INTERACTIONS: BRIDGING DISCIPLINES AND SCALE WITH CONNECTIVITY

**Short Title: CONNECTIVITY FOR BIOPHYSICAL LANDSCAPE INTERACTIONS**

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Abstract
Landscape composition and land use impact the interactions between soil and vegetation. Differences in micro-behaviour, driven by the interplay of heterogeneous soil and vegetation dynamics, affect emergent characteristics across a landscape. Scaling approaches to understand the drivers of these emergent characteristics have been attempted, but the blueprint of interacting biophysical processes in landscapes is inherently messy and often still unknown. A complicating factor is single disciplinary focus in environmental sciences. Integrated knowledge is vital especially in view of future challenges posed by climate change, population growth and soil threats. In this paper we give examples of biophysical interactions which occur across various temporal and spatial scales and discuss how connectivity can be useful for bridging disciplines and scales to increase our understanding.

## 1 INTRODUCTION

The combination of climate change, population growth and soil threats including carbon loss, biodiversity decline and erosion increasingly challenge the global community (Schwilch et al., 2016). A major scientific challenge in understanding processes involved in soil threats, landscape resilience, ecosystem stability, sustainable land management and the economic consequences, is that it is an interdisciplinary field (Pelletier et al., 2012), requiring more openness between scientific disciplines (Liu et al., 2007). As a result of single disciplinary focus, ambiguity arises in the understanding of landscape interactions, especially interactions between biological and physical processes in a landscape (Cook & Hauer, 2007).

We think that integrated concepts of biophysical landscape interactions are needed to preserve ecosystem functioning in landscapes, especially in light of soil threats, population growth, climate change, and global water scarcity (Falkenmark, 1990; Schwilch et al., 2016). This requires interdisciplinary collaboration. An integrated concept can only be established by bridging the gap between several disciplines (Schulz et al., 2006; Seppelt et al., 2009), in a way that is appealing to those disciplines at the same time. Unfortunately, as evidence suggests, interdisciplinary work is more challenging to get funded (Bromham et al., 2016). The paper discusses how interdisciplinary challenges in biophysical landscape interactions at several scales can benefit from a connectivity approach.

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Biophysical landscape interactions are those biotic and abiotic processes in a landscape that have an influence on the developments within and evolution of a landscape. Examples are the impact of soil heterogeneity on promoting coexistence of microbial life in the vadose zone (Long and Or, 2005), interaction between soil structure, hydraulics and climate and related effects of vegetation (Robinson et al., 2016; Reinsch et al., 2017), and cloud cover enhancement over forests (Teuling et al. 2017). An important aspect of biophysical landscape interactions is the different scales at which the various processes occur.

Scaling of environmental processes is possible, as long as the specific processes under consideration can be described by the same set of differential equations (Roth, 2008). Biophysical landscape interactions pose problems in this regard, because the combined physical and biochemical processes at different scales cannot be described by the same set of differential equations. For example, the description of the flow domain is scale dependent (Gelhar, 1986; Sánchez-Vila et al., 1996, Nieman & Rovey, 2009). The flow domain is that part of the system that can be mathematically described with one set of equations, such as the preferential flow domain, the groundwater flow domain, and the river channel flow domain. However, in scaling up, these domains may coincide and therefore no longer be described by the same equations.

There are two other complicating factors in understanding biophysical landscape interactions as well. While vegetation in many soil and hydrological models is approached physically, for example as a sink term in many soil water models, plant biology depends on more than physics alone (e.g. Wassen et al., 2013; Moreno de Las-Heras et al., 2016). And the response of vegetation to changing environmental conditions can include a possible, and often unknown, time-lag (e.g. Metzger et al., 2009). The interplay between the physical landscape and vegetation, which often co-evolve, and the resulting heterogeneity and emerging patterns is the reason it is so challenging to establish a theoretical basis for describing biophysical processes in landscapes.

In view of the considerable complexity of soil, numerical modelling is widely used to understand processes in soils, however the intricacies of biological responses in plants are mostly ignored. An integrative description for modelling biophysical interactions has been a long-standing goal in soil science (Vereecken et al., 2016). Figure 1 shows the scales involved in biophysical landscape interactions and examples of interdisciplinary challenges. In order to capture biophysical landscape interactions in models, it is important to find ways of dealing with feedbacks, the evolving heterogeneity when feedbacks play out differently, and with different scales. Interactions between ecology, hydrology, and geomorphology may be widely recognized, but they present grand challenges in themselves, especially the incorporation of feedbacks to understand system-level characteristics of landscapes.

Many disciplines involved in environmental research acknowledge spatial structure and heterogeneity in environmental systems (e.g. Schröder & Seppelt, 2006). Much research is focused on quantifying spatial structure and heterogeneity, such as climate variability, urban sprawl, deforestation and habitat loss (Ahlqvist & Shortridge, 2010). To be able to better understand the emerging patterns resulting from spatial structure and heterogeneity, connectivity has been acknowledged as a useful theoretical concept.

The concept has already been used in several (sub)disciplines: From an ecologists' perspective connectivity describes the understanding of water-mediated transfers of matter, energy and organisms (Pringle, 2001). Biologists often define connectivity as the degree to which a landscape facilitates or impedes the movement of individuals (Taylor et al., 1993). For hydrologists one definition is linked to how the hillslope's macropore network controls the flow through, replenishment of, and drainage from certain spots within the hillslope. This could lead to a hillslope scale connectedness of areas with relatively high hydraulic conductivity (Gomi et al., 2008). For soil scientists, connectivity may for example relate pore structure and effective properties for solute transport (Vogel, 2000). For geomorphologists connectivity can be described as the physical (de)coupling of landforms (Baartman et al., 2013). Finally, for sedimentologists in erosion research, connectivity relates to the transfer of sediments through a basin (Bracken & Croke, 2007), either by wind or water movement.

This paper will apply connectivity to the challenges of integrated concepts for biophysical landscape interactions. We do this by briefly reviewing examples of (a) existing studies of biophysical interactions and (b) various scales at which these interactions take place. We then (c) introduce connectivity and outline how we think it can be used to bridge disciplines, (d) assess the connectivity concept for sustainable landscape management, and (e) address challenges across scales, including examples and ideas on how to quantify connectivity.

## 2 BIOPHYSICAL INTERACTIONS

Habitat manifestation is an expression of its evolutionary history. While the spatial distribution of habitats is largely driven by current climates and management, a soil's depth and water holding capacity will have played a role as the plant-soil system coevolves over time.

Within a landscape, microclimate and soil composition may differ, resulting in species adaptation to local conditions (Schenk & Jackson, 2002). Plants also exhibit adaptivity depending on environmental conditions; this was shown for African savannah grasses (Hartnett et al., 2013) and an alpine perennial herb (von Arx et al., 2012). Plants may even develop habitat specific, symbiotically-conferred stress tolerance (Rodiguez et al., 2008). Differences in drought sensitivity shape tree and shrub distribution in tropical forests at local and regional scales (Engelbrecht et al., 2007). Plants scan their environment biochemically, resulting in a myriad of internal information that specify its ecological niche (Trewavas, 2002).

Correlations between soil water availability and species distribution have been recognized since the last century (Schimper, 1903); and nowadays hydrogeophysical soil mapping enables visualization of above and below ground spatial connectivity patterns (Robinson et al., 2008). It is becoming increasingly clear that root-sourced signals appear to play a key role in regulating stomatal aperture in response to soil water availability (Bacon, 2004). Constant exposure to environmental stresses, biotic or abiotic, influences plant physiology, gene adaptations, and flexibility in gene adaptation (Van der Ploeg & Teuling, 2013). Addressing gene-expression and genotype adaptation is challenging as it may complicate modelling efforts in for example climate change impacts, because the precise response to changing conditions is unknown (e.g Rodriguez et al., 2008). Yet, climate change is expected to lead to more spatiotemporal variability and intensity in the water cycle (e.g. Vereecken et al., 2016). Productivity and survival are therefore not only the result of a plant's genotype, but depend critically on how fast and how severe environmental conditions change (Jones, 2007). Understanding the feedbacks between environmental change, and the subsequent signals and responses in a plant species, is crucial for understanding the effects of environmental stresses on vegetation in landscapes.

Many of these feedbacks come together in the concept of coevolution, which is being used in the context of evolving non-linear trends in the landscape (Pelletier et al. 2013). The coevolution concept includes the change in topography or morphology of the landscape in interaction with the climate, vegetation and hydrology. Related, catchment coevolution has been defined as the process of spatial and temporal interactions between water, energy, bedrock, sediments, carbon, ecosystems and anthropogenic influences that lead to changes in catchment characteristics and responses (Troch et al., 2015). There is growing recognition of the importance of coevolution and biophysical interactions, which is needed to be able to better understand and sustainably manage our (natural) environment.

Pelletier et al. (2012) assessed coevolution within vegetation dynamics, pedogenesis and topographic development in southern California using a landscape modelling approach. They found strong correlations between Effective Energy and Mass Transfer (EEMT), above-ground biomass, soil thickness, hillslope-scale relief and mean distance-to-valley. Saco & Moreno de las Heras (2013) quantified the coevolution of vegetation and topography in semiarid areas. There, nonlinear interactions between physical and biological factors result in the emergence of remarkable landform related vegetation patterns such as striped and banded patterns. They found that variations in slope and abiotic or biotic factors can affect the vegetation patterns and resulting (micro)topography. Other work on coevolution includes e.g. D'Alpaos et al. (2007), who modelled the interplay of erosion, sedimentation and vegetation dynamics in tidal embayments; Perdigão & Bloeschl (2014) who investigated and quantified landscape-climate coevolution in Austria; and Jefferson et al. (2010) who studied the coevolution of hydrology and topography in a basalt topo-chronosequence landscape in Oregon, USA.

Coevolution is increasingly incorporated into models that simulate biophysical interactions. For example, a few models have started to treat soil formation as coevolution of a large number of soil parameters (Finke & Hutson, 2008). Other approaches include temporal changes of soil structure, a major determinant of water partitioning in the (sub)surface, and driver of biological activity, root growth and soil erosion (Leij et al., 2002; Stamati et al., 2013). A few models fully incorporate interactions between physical and biological processes (e.g. Laudone et al., 2011).

## 3. SCALES

Environmental and societal problems require an understanding of how processes operate at different scales, and how they can be linked across scales. Processes relevant in biophysical interactions in landscapes play a role at spatial scales ranging from millimetres to kilometres, i.e. from microbiology, such as soil microorganisms, to regional groundwater flow and landscape morphology, and at temporal scales ranging from seconds, e.g. earthquakes, to millennia, e.g. erosion and sculpting of landscapes by glaciers.

"Scaling refers to the transfer of understanding and of quantitative results from one spatial or temporal scale to another." according to Roth (2008). Most properties in landscapes have some degree of correlation, but that depends on the scale at which observations have been made. Considering the scale at which processes occur and become visible, heterogeneity in biotic and abiotic processes is the most defining property of a landscape. Landscape heterogeneity accounts for markedly different system responses (e.g. Laudon et al., 2016). One striking example in hydrology is the emergence of scale dependency in transmissivity, which leads to an increase in effective transmissivity (or hydraulic conductivity) with an increase in observation scale (Sanchez et al., 1996; Schulze-Makuch et al., 1999; Nieman & Rovey, 2009; Fodor et al., 2011).

For biophysical processes an important factor for scaling is the soil moisture, which is dependent on soil physical properties (Robinson et al., 2016), landscape (Charpentier & Groffman, 1992), vegetation (Mohanty & Skaggs, 2001; Scanlon et al., 2007), and atmospheric conditions (Teuling et al., 2005). Combined, these factors regulate vadose zone processes including infiltration, permeability, water holding capacity and moisture loss rates. Techniques to monitor the resulting variables of heterogeneity become increasingly available, for example remote sensing allows surveys covering large extents carried out at different scales (Lillesand et al., 2015) and hydrogeophysics allows mapping of the subsurface (Binley et al., 2015).

Scaling in time depends largely on the time-span involved because variables of a landscape system can change status from time independent to dependent or even be irrelevant (Schumm & Lichty, 1965). On a millennial timescale, the independent variables are, for instance, lithology, climate and vegetation, while hillslope and channel morphology are dependent variables and observed discharge and flow characteristics are considered indeterminable. Yet, on a short timescale (< 1 year), these indeterminable variables become the dependent ones.

Additionally, there is often a time-lag between an event (e.g. an extreme rainfall event, flood or landslide) and landscape or biophysical response (Phillips, 2003; Temme & Veldkamp, 2009). An extreme example is an earthquake, which may last only seconds, but may cause millennial-scale landscape responses, including increased erosion and catchment adjustment. In landscape ecology, time-lagged responses of biological variables to landscape modifications are widely recognised (e.g. Metzger et al., 2009). However, these are rarely considered in management plans. Understanding the ecological impacts of time-lagged responses to landscape modifications is critical for interpreting contemporary patterns of biodiversity (Royo et al., 2010).

## 4 POTENTIAL ROLE OF CONNECTIVITY

Connectivity is increasingly recognised as a major issue facing a hot, flat and crowded digital society (Friedman, 2009). In economics Didier Sornette has developed a new Dragon King (DK) theory for events that are generated by, or correspond to, changes in connectivity related mechanisms such as positive feedbacks, tipping points, bifurcations, and phase transitions. These phenomena are at the heart of connectivity and occur in nonlinear and complex systems, serving to amplify DK events to extreme levels, such as financial bubbles (Sornette and von der Berke, 2011).

What does the concept of connectivity offer for a better understanding of biophysical landscape interactions across various spatial and temporal scales? The key aspect of the connectivity concept is that it can create pathways for feedbacks which are often missing in soil models. Connectivity could thus play an important role in bridging disciplines and scales (Turnbull et al., 2008; Fryirs, 2012; Okin et al., 2015). Connectivity is dynamic over time and may change slowly or quickly, depending on the system and properties that are assessed. For example, connectivity in spatial landscape patterns changes slowly in response to dynamics of vegetation and soil processes, while connectivity changes quickly for example between and during rainfall events (Bracken & Croke, 2007; Wainwright et al., 2011).

The connectivity concept is a spatially explicit approach, by inclusion of neighbourhood effects (Peters et al., 2004), and therefore calls for inclusive information on flows or fluxes that connect different spatial units. Yet, connectivity has an advantage over spatially explicit modelling, where neighbourhood effects yield an increased parameter set and increased prediction uncertainty compared to non-spatial modelling. Instead, connectivity can be used to determine which spatial and temporal processes are likely to have an impact, and therefore the resulting modelling exercise can be simplified (Paola & Leeder, 2011). In modelling studies the connectivity concept is illustrated by using simple models and connecting different components of the system to learn more about the processes and feedbacks, for example for ecology (e.g. Tilman, 1994), hydrology (e.g. Porporato et al., 2003) and geomorphology (e.g. Saco et al., 2007).

Quantifying connectivity is challenging, according to recent discussion with scientists within the EU network project focussed on connectivity (COST1306 Action 'Connecteur' http://connecteur.info/). Connectivity is not often directly measured, but instead is inferred from other properties, such as soil texture distribution, moisture dynamics or the amount of discharge or sediment. We need to develop models where connectivity becomes a major part of the formulation, and tools that allow us to measure what we need to parameterise.

For biophysical landscape interactions, connectivity can be considered in terms of 'high', 'medium' and 'low' for the various processes at various scales, leading to various possible (sub)systems. Subsequently, for each (sub)system a particular process under consideration can be defined in terms of its connectivity status (i.e. high, medium, low), if it is related to other (sub)systems, and if it is relevant for the objective under investigation.

The classical example in which feedbacks between biotic and abiotic processes as well as (dis)connectivity play an important role is the vegetation patterns in semiarid landscapes, where isolated vegetation bands act as local sinks for water and nutrient flow, thereby disrupting sediment and hydrologic connectivity (e.g. Deblauwe et al., 2012). These banded patterns, consisting of alternating vegetated and bare bands, are formed because of an ecohydrological feedback system (Stewart et al., 2013). Differences in infiltration rates due to presence/absence of roots, macropores and soil aggregation in the vegetated/bare areas (Mora & Lazaro, 2013) lead to a runoff-runon mechanism (Saco et al., 2007). The runoff-runon mechanism is key for productivity, and disturbance of this ecohydrological feedback system can lead to severe land degradation (Okin et al., 2009; Moreno-de las Heras et al., 2011). Within this system, connectivity can be defined at several scales (see also Okin et al., 2015): (1) at the landscape scale, connectivity is low when the system is intact (Fig. 2a), because flow is limited to between two vegetated bands. Flow does not, or hardly, reaches the end of the hillslope or outlet of the catchment. If the system is disrupted, connectivity on the landscape scale is significantly increased (Fig. 2b) and could lead to rill or gully erosion. (2) At a local scale, connectivity between individual plants is medium to high: on the one hand they compete for water, on the other hand, they help each other by providing e.g. increased organic matter underneath the plant patches (Verwijmeren et al., 2014). Finally, (3) at a micro scale, connectivity in the bare areas is relatively low because of crusting which inhibits. percolation and infiltration, but high in the vegetated areas because of bioturbation (Klass et al., 2012).

Another example where connectivity can be quantified between the various (sub)systems is the agricultural system in NW Ethiopia (Tebebu et al., 2015; Zegeye et al., 2016) where soil erosion and sediment transfer to downstream reservoirs is an acute problem. Extensive soil and water conservation (SWC) measures have been introduced throughout the watershed to mitigate soil erosion. These measures are targeted at preventing erosion by on-field interventions such as soil bunds and grass barriers, and reducing sediment transfer pathways with sediment storage dams in gullies (Mekonnen et al., 2015). These interventions promote infiltration of precipitation into the soil and thereby reduce runoff and erosion. However, the side effect of increased infiltration is an increase in interflow from upstream to downstream parts of the catchment leading to shallower groundwater tables in the bottom of the catchment and faster saturation of the Vertisols during precipitation events (Tebebu et al., 2015). Therefore the upstream SWC measures in the hillslopes, eventually promote gully formation and expansion in the valleys (Zegeye et al., 2016). In this example connectivity can also be defined at various scales: (1) at the local scale, both the on-field (bunds and grass barrier) and between-fields (storage dams) SWC measures aim to reduce connectivity within the catchment as much as possible; however (2) at the landscape scale this resulted in increased connectivity between the upper and lower parts of the catchments through interflow processes, enhanced by the SWC measures.

Several studies have shown the usefulness of describing biophysical landscape interactions in terms of connectivity for more humid conditions as well. For intermontane depressional wetlands, landscape (sub-)surface hydrology, water chemistry and vegetation structure were highly connected to landscape scale processes (Cook & Hauer, 2007). Small but connected wetlands, stored more water longer, had higher productivity and different plant community composition compared to larger but isolated wetlands. At a more local scale, a wetland's ecology is determined by both frequency and duration of saturation and local groundwater quality, and species preference can thus be highly driven by microtopographical features (Van der Ploeg et al., 2012). In these systems the hydrology and vegetation are adjusted to each other. Despite such interplay between species distribution and complex patterning of ephemeral channels and streams, a relatively simple reservoir approach can capture the essence of drought and flood hazards (Van der Ploeg et al., 2012). Drier conditions trigger local connections between hummocks and hollows for hydrological routing, while wet conditions show a connected catchment response (Oosterwoud et al. 2017). Emergent vegetation properties can thus also be an indication of lateral hydrologic connectivity in addition to other controls (Hwang et al., 2012).

## 5 CONNECTIVITY FOR SUSTAINABLE LANDSCAPE MANAGEMENT

According to Venter et al. (2016), 75% of all terrestrial surface is experiencing human pressure, leading to declines of natural systems and biodiversity. Hydrological connectivity in the landscape itself is often declining due to anthropogenic influences such as dams and water diversions (Pringle, 2001). However, landscapes are also increasingly connected in terms of wind erosion when desertification comes into play (Okin et al., 2009). To manage these pressures, frameworks are being proposed for incorporating ecosystem services into land-management decision making (Schwilch et al., 2016). However, this remains challenging. The growing link between humans and ecosystem services necessitates a bridge between the question-driven, bioecology-centered spatial view and solution-driven society-centered holistic view (Wu, 2006).

In this sense, connectivity can be a very useful tool to assess how resilient a landscape is to change, and directs how it can be sustainably managed. For example, Jackson et al. (2013) applied connectivity in ecosystem service modelling to understand the impact of interventions like tree planting on flows of mass and energy.

## 6 CONNECTIVITY FOR EARTH-SYSTEM CHALLENGES

While connectivity is an ongoing area of research in ecology it has yet to fully migrate into our earth system science thinking. The problems humanity faces, such as climate change, require insight into the consequences of drivers such as extreme weather events and impacts on earth systems, their management and interventions we employ. Therefore, connectivity can be not only an interesting concept to describe emergent properties, but also a tool to evaluate management and mitigation strategies for sustainable land management (Okin et al., 2009, 2015; Bracken et al., 2013).

Insight into and acknowledgement of connectivity can be helpful, if not essential, for addressing key earth-system challenges, for example:

1. Natural flood management (NFM): To what extent can NFM alleviate flood risk? Research shows that the manipulation of the landscape at the hectare scale using shelter belts for example can reduce local flood risk (Marshall et al., 2009). However, the arrangement of vegetation and infrastructure features across the landscape speed up or slow down water and sediment movement, how this scales, and how this either synchronises, or desynchronises flows downstream remains

unknown. Quantifying connectivity within the arrangement of vegetation and infrastructure features would shed light on the most optimal design and therefore the benefits of natural flood management.

2. Soil carbon and nutrient cycling: What are the feedbacks from soil to climate and how will they impact change over the next century? Soils are estimated to store three times more carbon than plants or the atmosphere (Fischlin et al., 2007) and yet the connection between soils and global circulation models remains poor (Schmidt et al. 2011). Our understanding of the links between physics and biology to impact greenhouse gas emissions from soil is also limited (Reichstein et al., 2011; Blagodosky and Smith, 2012). Here connectivity could play an important role in understanding how carbon cycling is affected when soil hydraulics changes from uniform piston flow to bypass flow induced by soil water repellency.

Other challenges where connectivity concepts have already been successfully used include restoration of rivers (Reckendorfer et al., 2006; Jansson et al., 2007). In addition, dryland communities worldwide have implicitly used connectivity for their production systems for millennia (Okin et al., 2015). The scientific challenge will be to determine when complexity is important in biophysical landscape interactions and when it can essentially be ignored in models. Only as our modelling capability and understanding of complex phenomena increases will we be able to address this challenge. Remote sensing measurement techniques, such as LiDAR, UAVs, radar interferometry, hydrogeophysics and analysis of optical image data facilitate non-interfering observation of biophysical interactions on a landscape scale (e.g. Vogelmann et al., 2016; Lausch et al., 2013; Brake et al., 2013). A joint effort to connect Earth's (sub)surface processes by a combination of innovative big data-assimilation, measurement and modelling techniques will enable the scientific community to accurately address vital issues.

## 7 OUTLOOK

In this paper we have discussed how connectivity can be used to understand and connect biophysical processes at different spatial and temporal scales and why such a unifying concept is essential. Connectivity can bridge (sub)disciplines, although the differences in definitions and understanding need to be addressed: for example in ecology increased connectivity of ecosystems is seen as positive, while in soil science increased connectivity in erosion is negative. We need the next generation of models to incorporate connectivity and allow for the feedbacks that make earth system infrastructure so dynamic. This calls for development of models that are less focussed on detailed mechanistic understanding, and more focused on networks, connectivity and feedbacks while still incorporating the most important aspects of detailed mechanistic modelling (Paola & Leeder, 2011). Connectivity focused models hold promise for dealing with unprecedented levels of uncertainty in future trends of climate, population dynamics, economic development, and international trade barriers.

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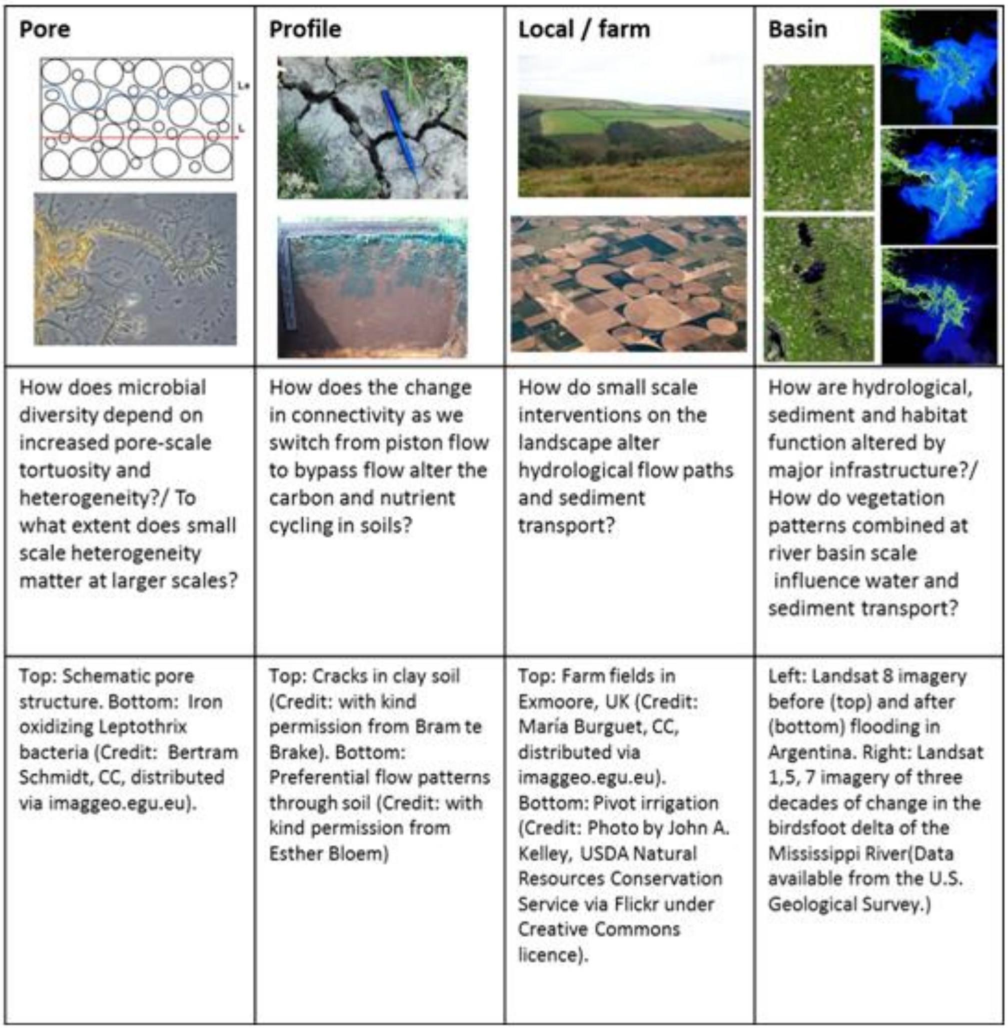


Figure 1: Illustration of challenges in biophysical landscape interactions where process understanding would benefit from bridging scales and disciplines.

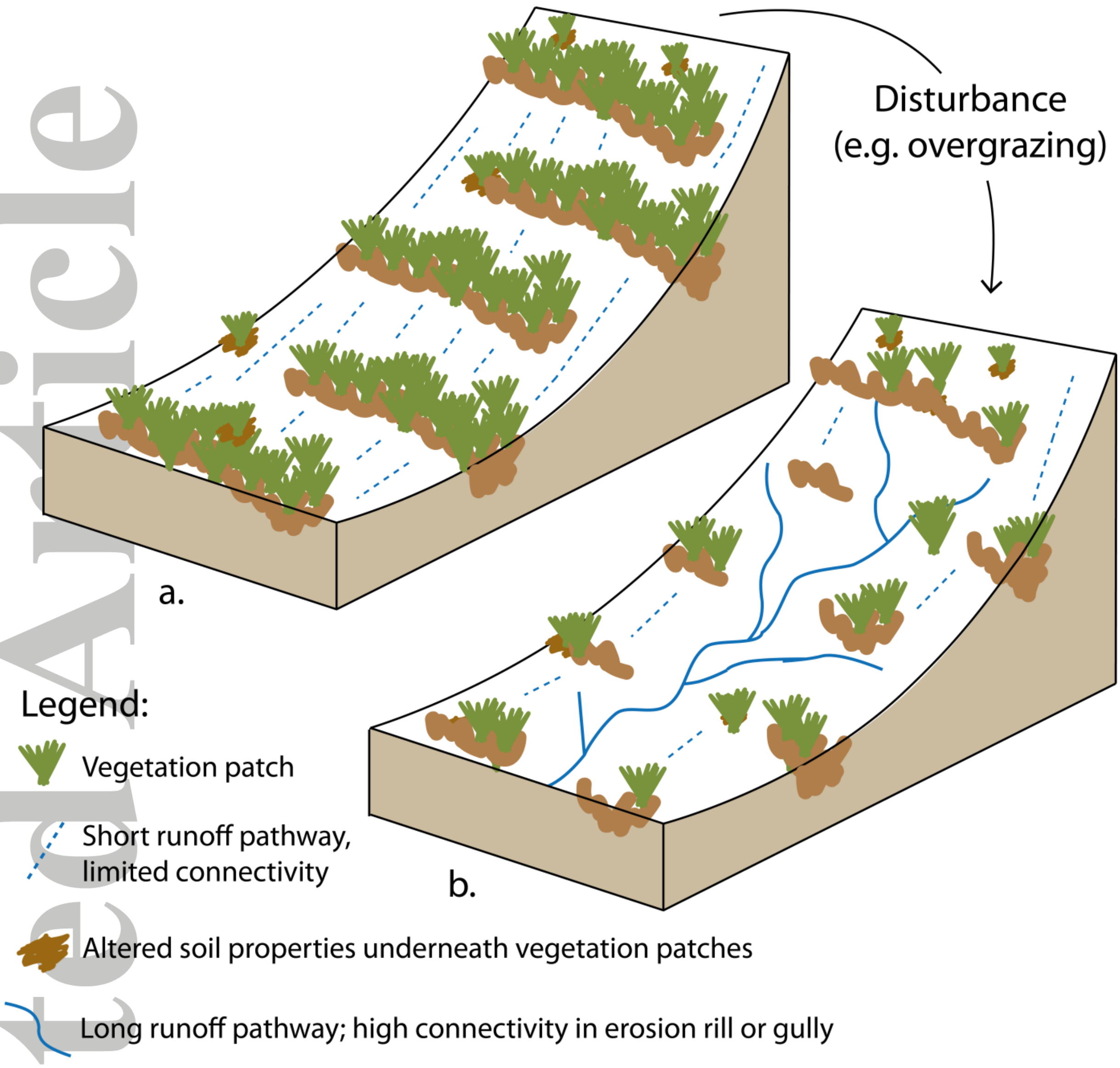


Figure 2: Sketch representing a dryland banded vegetation system with two potential system states: a) intact banded system with relatively short runoff pathways and limited hydrological connectivity (dashed lines) and b) disturbed system with longer runoff pathways and increased hydrological connectivity (continuous line) in rills or gullies.