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Global Environmental Changes Impact Soil Hydraulic Functions through Biophysical Feedbacks

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Running Head: Alternative stable soil moisture states

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Abstract

Although only representing 0.05% of global freshwater, or 0.001% of all global water, soil water supports all terrestrial biological life. Soil moisture behaviour in most models is constrained by hydraulic parameters that do not change. Here we argue that biological feedbacks from plants, macro-fauna and the microbiome influence soil structure, and thus the soil hydraulic parameters and the soil water content signals we observe. Incorporating biological feedbacks into soil hydrological models is therefore important for understanding environmental change and its impacts on ecosystems. We anticipate that environmental change will accelerate and modify soil hydraulic function. Increasingly we understand the vital role that soil moisture exerts on the carbon cycle and other environmental threats such as heatwaves, droughts and floods, wildfires, regional precipitation patterns, disease regulation and infrastructure stability, in addition to agricultural production. Biological feedbacks may result in changes to soil hydraulic function that could be irreversible, resulting in alternative stable states (ASS) of soil moisture. To explore this, we need models that consider all the major feedbacks between soil properties and soil-plant-faunal-microbial-atmospheric processes, which is something we currently do not have. Therefore, a new direction is required to incorporate a dynamic description of soil structure and hydraulic property evolution into soil-plant-atmosphere, or land surface, models that consider feedbacks from land use and climate drivers of change, so as to better model ecosystem dynamics.

Soil moisture and global environmental change

In the last 15 years, the importance of soil moisture has been recognized by earth system science involved with understanding the consequences of environmental change on the earth system (Green et al., 2019, Seneviratne et al., 2010). For example, soil moisture has been included in the list of the 50 most essential climate variables (Dorigo et al., 2015) in order to support international organizations with the assessment of climate change impacts. In 2010, the Global Climate Observing System (GCOS) initiative has defined soil moisture as a fundamental climate variable (GCOS, 2010). Fundamentally, soil moisture provides the water resource for plants and primary food production, while it also affects a range of hydrological processes such as recharge of aquifers through the vadose zone. Soil moisture is also an important source of atmospheric water at continental scales as it is transpired by plants and evaporates from the soil surface, a proportion of which falls as precipitation back on the land surface downwind from the site of the original evapotranspiration (Entekhabi et al., 1996, Koster et al., 2004, Taylor et al., 2011). Thus, soil moisture contributes to regulating the global energy balance of terrestrial ecosystems, also controlling soil temperature, air humidity and surface albedo (Robinson et al., 2008, Seneviratne et al., 2010, Vereecken et al., 2008). A deficit of soil moisture leads to drought (Dai et al., 2004, Sheffield & Wood, 2008); moreover, prior to deficit soil
moisture acts as a shock absorber reducing the magnitude of heatwaves (Rasmijn et al., 2018, Seneviratne et al., 2006).

From a biogeochemical perspective, soil moisture influences redox conditions (Keiluweit et al., 2017, Veneman et al., 1998) thereby changing the availability of nutrients for plants, fauna and microbes. Soil moisture indirectly influences microbial activity and respiration as it changes carbon and nutrient availability (Evans & Wallenstein, 2014, Frank et al., 2015, He & Dijkstra, 2014, Vicca et al., 2014), and directly by soil moisture availability and excess (Davidson et al., 1998, Orchard & Cook, 1983, Reinsch et al., 2017, Skopp et al., 1990). Among the important processes, soil moisture regulates nitrification, denitrification and CO₂ production via soil microbial and plant root respiration (Homyak et al., 2017, Manzoni et al., 2012, Vicca et al., 2014).

Long-term changes in soil moisture can have drastic impacts on the biosphere (Manzoni et al., 2012, Wu et al., 2011). Long-term reductions in soil moisture can cause desertification and tree mortality (Van Mantgem et al., 2009), thereby completely changing the landscape. Soil moisture is also linked to wildfires, often in complex ways (Westerling et al., 2003). Soil, and associated ecosystem degradation and accelerated desertification can also cause severe dust storms, which can lead to respiratory diseases and other health problems (Stacy et al., 2012). Given the importance of soil moisture dynamics within the biosphere, the objective of this opinion paper is to highlight the links between environmental change, impacts on biological systems and potentially irreversible or slowly reversible alterations in soil hydraulic function. Our work considers feedbacks between the soil-plant-faunal-microbial system and soil structure, which modify soil hydraulic function in response to environmental change.

Here we define soil hydraulic function as the ability of soils to infiltrate and retain water to provide the moisture pool that sustains the soil-plant-faunal-microbial system. Mathematically, soil hydraulic functions are usually described with static values of hydraulic parameters, such as those governing hydraulic conductivity and soil water retention. This simplification neglects the co-evolution of the soil-plant-faunal-microbial system; especially the different strategies that living soil organisms adopt, to modify or adapt to soil structural and moisture changes. Thus, physico-chemical processes and biological activity can modify the soil properties resulting in a shift from one soil moisture regime to another. Before going further, it is important to stress that these phenomena, which lead to permanent alterations of the soil pore structure, should be distinguished from the hysteresis (i.e. the non-uniqueness of water/air distributions in soil) due to soil structure at the pore-scale that arises from the
history of wetting and drying (Dane & Lenhard, 2005). This classical phenomenon of hysteresis, which has been studied in soil physics for nearly a century (Haines, 1930), is not the subject of this opinion paper. Here, we examine biological factors and processes that change the soil architecture (i.e. the geometry and topology of soil pore space and solid matter) or the properties of the solid surfaces (e.g. hydrophobicity) that influence the soil hydrology. The focus of this opinion piece is therefore on physico-chemical and biological processes mediated by environmental change that have irreversible or slowly reversible direct or indirect impacts on soil structure and therefore soil moisture states and hydraulic behaviour.

Biology has a number of direct effects on hydraulic function. Given that soils and vegetation often co-evolve, it is unsurprising that changes to vegetation through land use or climate change affect soil properties. Broadly, we might recognise four primary pathways through which flora (Rabbi et al., 2018), fauna (Smettem, 1992) and soil microbes (Hallett, 2008) alter hydraulic function through changes in:

1) organic matter inputs changing bulk density, porosity and/or pore size distribution (Franzluebbers, 2002, Jarvis et al., 2017, Rawls et al., 2004, Yang et al., 2014);
2) rooting structure and decreases in porosity through compression induced by new root growth, or macropore generation when roots decay (Bodner et al., 2014, Fischer et al., 2015, Koestel & Schlüter, 2019);
3) biopore characteristics and abundance resulting from the activity of macrofauna, the 'ecosystem engineers' (Berry, 2018, Smettem, 1992); and
4) microbial activity, especially in the rhizosphere, which impacts hydrophobicity (Hallett, 2008).

Biology is also involved in a variety of indirect climate-mediated impacts. Pedotransfer functions traditionally use soil texture as the only model input to estimate hydraulic properties in landscape- and global scale models. However, although biological and climatic factors are rarely considered, the ability of organisms to modulate soil hydrology may overwrite these intrinsic soil properties. Jarvis et al. (2013) found that saturated and near-saturated hydraulic conductivity could be better explained by land use, organic carbon content, bulk density and climatic factors (average annual precipitation, temperature), rather than the classical emphasis on soil texture (i.e. sand, silt and clay contents). More recent, continental scale research has also established links between climate and soil hydraulic function. Hirmas et al. (2018) provided evidence that macroporosity increases in drier climates on decadal time scales, which they suggest may lead to 'unexplored feedbacks between climate and the land surface.' Robinson et al. (2016) presented evidence of a connection between climate change and
soil hydraulic function through a long-term drought manipulation experiment, with a shift to an alternative, more permanent, soil moisture state. The soil moisture state shift was attributed to a drought-induced alteration of soil structure. Climate and other environmental stresses may initiate these soil responses. It is critical to consider the effects of biological processes on soil hydrology if the key drivers (climate and land use) change. Therefore, developing a new ‘dynamic’ paradigm for soil hydraulic functioning by linking biological and climate feedbacks to soil hydraulic behaviour must be an important direction for understanding impacts of global environmental change, as well as for developing policies that mitigate soil threats such as erosion, compaction or salinization.

Alternative stable states in relation to soil hydraulic function

Rapid global change, through either land use or climate, raises the concern that hydrological systems may begin to experience abrupt state shifts. About 40 years ago, ecologists (Beisner et al., 2003, Holling, 1973, Lewontin, 1969) first proposed that communities or ecosystems can be found in one of several possible alternative stable states (ASS). The theory of ASS (Petraitis, 2013) predicts that under the same environmental conditions an ecological system can potentially exist in different, but stable, states following a ‘disruptive’ perturbation (Carpenter et al., 2011, Scheffer et al., 2012, Schröder et al., 2005). This has been explored in soils research in the context of fire-vegetation-soil (Wood & Bowman, 2012) and in ecohydrology to explain abrupt changes of plant communities (Borgogno et al., 2007, D’Odorico et al., 2007, Zeng & Zeng, 1996, Zeng et al., 2004). Feedback mechanisms between vegetation and soil moisture may induce a transition between soil moisture states. The existence of ASS has profound implications for management with a seemingly stable vegetated state suddenly, following a perturbation, crossing a critical threshold and moving to a new, often degraded, state. Once this has occurred, the system does not return to the former state after the perturbation has ceased, resulting in an irreversible state change. The existence of such states has been proposed for a variety of ecosystems and a useful conceptual framework is presented in (Bestelmeyer et al., 2011). It is particularly relevant to the world’s rangelands, where the threat of a shift from a state that sustains life, to a degraded one that does not, is a constant concern.

There is only limited evidence for shifts for different ecosystems Schröder et al. (2005). They argued that evidence of state shifts has been largely derived from analyses of historical records and rarely from manipulation experiments, thus offering only indirect evidence, which remains open to alternative explanations. They found 13 experiments showing direct evidence of ecological state shifts. Much of the work on dryland ecohydrology (Borgogno et al., 2007, D’Odorico et al., 2007, Zeng & Zeng, 1996) is based on modelling, as manipulating ecosystems experimentally is a considerable challenge. The ‘tipping point’ concept, where a change at the tipping point sets in motion
mutually reinforcing feedback loops that force the system on a new course, is garnering interest. Aligned with this are studies that suggest the need to search for “critical slowing down points” in modelling that will indicate a regime shift; see for example (Van Nes & Scheffer, 2007). Given that modelling and experimental evidence of shifts in soil hydraulic function are emerging (Robinson et al., 2016, Zeng et al., 2004), largely connected to alterations in biological factors, we must determine the processes leading to such changes and ASS.

**Evidence for alternative states in soils: some illustrative examples**

We propose that it is important to identify and gather evidence for ASS in soils (Dekker et al., 2007, Rietkerk et al., 2004, Robinson et al., 2016, Zeng et al., 2004), which we now consider. Soil structure may deform by exertion of outside force by machinery or livestock trampling, leading to a change in infiltration response of the soil (Logsdon, 2012, Messing & Jarvis, 1993, Moret & Arrue, 2007). Reversing such deformation by for example no-tillage practices may take years (Horn, 2004). If soils contain clay, they may exhibit shrink and swell behaviour because of soil moisture availability. Te Brake et al. (2013) provides an example of a loam soil where very dry spring conditions resulted in shrinkage of 20 mm over a soil depth of 60 cm. For marshes and wetlands seasonal elevation changes have been observed, while drought led to increased consolidation of the soil, thereby reducing the resilience of these ecosystems (Cahoon et al., 2011). Such soils may exhibit hysteresis effects through multiple drying/wetting or freezing/thawing cycles, thereby impacting soil water storage, root water uptake, and the ability of roots to penetrate the soil. Roots themselves impact soil structure (Fischer et al., 2015, Koestel & Schlüter, 2019) and vegetation changes such as deforestation may lead to irreversible changes in soil water retention (Ramírez et al., 2017). For soils containing high organic matter, such as peat soils, ponding of surface water upstream from hummocks combined with positive feedbacks between hummock occurrence and water table depth can lead to string patterns (Swanson & Grigal, 1988).

Water resource concentration mechanisms can lead to ASS (Rietkerk et al., 2004). In particular, feedbacks and self-organized pattern development have been documented and modelled, explaining the occurrence of vegetation patterns (e.g., tiger bush) in dryland ecosystem functioning (Rietkerk et al., 2002, Rietkerk et al., 2004). Another water concentration mechanism widely studied in soil science is soil hydrophobicity (Doerr et al., 2000, Hallett, 2008). Extensive work has been conducted on soil hydrophobicity, which was initially associated with wildfires (DeBano, 2000). Increasingly, hydrophobicity is observed across soil types and across biomes globally, although the exact extent remains unclear (Doerr et al., 2000). Hydrophobicity changes solid-water contact angles and thus the way water infiltrates into soil (Filipović et al., 2018, Ritsema et al., 1998). Water infiltrates into dry
soil due to capillary and gravitational forces, normally with small pores filling first and large pores last. Hydrophobicity reverses this sequence with large pores filling first and small ones last, or not at all. This creates both non-homogeneous wetting through preferential flow, as well as increased air entrapment, infiltrating (or channelling) water further downwards into the soil without wetting the surface soil (Jarvis et al., 2016). There is growing consensus that hydrophobicity derives from multiple sources (Hallett, 2008). These include geochemical, e.g. through alteration by fire (DeBano, 2000, Stoof et al., 2010, Weninger et al., 2019); biochemical; leaf litter, plant degradation products, root exudates (Doerr et al., 2000, Hallett, 2008); biological where the organisms themselves are hydrophobic like fungi (Unestam, 1991, Wessels, 1993), and physical, simply through microscopically rough, rugose, or wrinkled surfaces (Quéré, 2008). However, the mechanisms that stimulate the development and persistence of soil hydrophobicity remain poorly understood; especially links to climate change (Goebel et al., 2011). The role of soil organisms and their contribution to the development and persistence of hydrophobicity and soil structure are only now being uncovered. Pioneering work on mycorrhizae (Unestam, 1991) indicated some organisms are hydrophilic, some aren’t, and some change, making the study of such phenomena challenging.

In a study in Utah, Robinson et al. (2010) found that hydrophobic compounds were associated with pinyon - juniper woodlands, resulting in a water concentration mechanism under the trees (Figure 1). Anecdotal evidence indicated that soils under trees further away from water flow paths were more hydrophobic, suggesting a feedback of increasing hydrophobicity with increasing stress. Hydrophobicity could have several beneficial effects; i) leaving topsoil like a dry mulch, creating an evaporation barrier and reducing competition from seed germination; ii) altering the infiltration behaviour of the soil and so effectively increasing the amount of moisture infiltrating deeper into the soil, developing a potential soil moisture maintenance pool for vegetation. For example, the way in which hydrophobicity impacts water infiltration is illustrated based on Hydrus 2D simulations depicted in Figure 1 (adapted from Robinson et al. (2010)). The left side of Figure 1 illustrates infiltration under a tree canopy where hydrophobic conditions dominate, whereas the right side shows infiltration into hydrophilic bare soil conditions. The water infiltrates twice as deep in the 24 hr simulation period under hydrophobic conditions forming small wet bulbs. Furthermore, these wetted bulbs are less connected to the soil surface, thus reducing evaporative losses. Understanding the link between the soil-plant-faunal-microbial system in response to environmental stress and the development and persistence of hydrophobicity represents a distinct research gap.
Plants, through their rooting behaviour, can modify the soil below plants and in their immediate vicinity, thereby altering the hydraulic conductivity and infiltration behaviour of the soil leading to water concentration. Franz et al. (2011) was able to demonstrate with a combination of measurements and modelling that the proliferation of the undesirable succulent, *S. volkensii* in central Kenya was a result of a positive feedback. Increased grazing led to smaller above-ground forage biomass and bare soil patches, such that water infiltrated preferentially where the remaining grass swards were growing. *S. volkensii* was then able to exploit this, growing water in run-on rather than runoff zones, developing self-organized patterns in the landscape with islands of *S. volkensii*. In addition to enhancing local infiltration, plants also shade soil, thereby locally reducing evaporation from the soil surface. Once established, plant islands preferentially concentrate water resources, whereas the bare soil patches in-between represent a drier, hotter, and more hostile environment for other plants to establish. This supports that the present state of the vegetation depends on its history (Rietkerk et al., 2004).

Changes to the hydraulic conductivity of an organo-mineral soil with perched water have also been proposed as a mechanism to explain the observed change in the soil moisture patterns recorded during a long-term climate change experiment subjected to drought (Robinson et al., 2016). The soil moisture storage in the top 10 cm (O horizon) of a podzol, with a 10 cm organic layer overlying an 18 cm thick mineral layer resulted in a substantial hydraulic contrast. The O horizon stopped rewetting fully after a summer drought (Figure 2). The figure shows two organic (O<sub>f</sub> and O<sub>h</sub>, 10 cm) horizons over a mineral layer (18 cm). The grey (before intense drought) and black (after intense drought) lines reflect the soil moisture storage in the O horizon (10 cm). The organic horizon transitions from fermented (O<sub>f</sub> = 5 cm), to humic (O<sub>h</sub> = 5 cm) then to a mineral horizon (18 cm). The hydraulic conductivity of the O<sub>h</sub> horizon was adjusted, from 1 cm day<sup>-1</sup> prior to the drought, to 10 cm day<sup>-1</sup> post drought, reflecting an increase in O<sub>h</sub> soil horizon hydraulic conductivity brought about by drought-induced soil structural change. What we do not know is whether this response to drought is a permanent shift to an ASS, or whether the soil will recover in the long-term.

Data from similar soils from long-term soil moisture storage monitoring programme at the Plynlimon experimental site (Hudson, 1988) provide some insight into the roles of vegetation and soil (Figure 3). A major drought occurred in 1976 and a minor one in 1984 in Wales (Hudson, 1988). The data for peat soils show that they dry and then rewet (Figure 3A), whereas the podzolic soil dries and rewets under grass, but not under forest (Figure 3B). We suggest that the latter is evidence of a shift to an ASS induced by the drought, cracking the subsoil and facilitating drainage of any perched soil water. The upward trajectory of the recovery in the forested soil, following the 1976 drought, suggests that the soil structure might rebound and perched water again collect, but a subsequent drought in 1984...
appears to stop this recovery. Hence, the data show intriguing patterns in soil moisture response to drought for different soils and vegetation. Clearly, there are feedbacks from the drought affecting the soil moisture retention through alteration of the soil structure.

**Synthesis and future direction**

Climate change is causing diverse effects, higher summer temperatures, droughts, fewer frost days and more intense rain events (Frich *et al.*, 2002, Thornton *et al.*, 2014). Based on the evidence compiled in this work, we propose that drier periods are likely to cause a number of biophysicochemical feedbacks to soil that alter the soil hydraulic function and moisture states. This is conceptualised at the top of Figure 4, where the climate gradient, or frequency of drought, leads to soils being subjected to longer and more intense dry spells (A, B, C). At the bottom, soil wetting scenarios and changes to the hydraulic function are shown as drying becomes stronger and more prolonged. Figure 4A is a soil profile with no macropores that is hydrophilic and exhibits uniform matrix flow, with winter wetting and summer drying. Figure 4B shows macropores developing, where, as summers become drier, plant roots penetrate deeper in search of water and the soil develops cracks. During rainfall, water infiltrates into the soil preferentially in macropores, resulting in a heterogeneous wetting of the soil profile (Jarvis *et al.*, 2016). Figure 4C highlights a more severe drought condition, inducing the ecosystem to a hydrophobic state. This alters the infiltration process so that even in an unsaturated state soil preferential flow may occur in macropores, capturing scarce water resources that would otherwise be quickly lost to evaporation from the soil surface. This may allow for the development of a soil moisture pool deeper in the soil profile that could form a maintenance moisture pool for vegetation during dry periods (4C). This conceptual framework proposes a number of feedbacks that result in changes to soil structure, hydrophobicity and moisture retention. The drought-induced feedbacks result in soil moisture shifts with ASS as a result. What we are yet to determine are the time scales over which these phenomena and feedbacks might occur, and how quickly the soil moisture state will recover, if at all. The evidence from Figure 3 suggests that these shifts might be long-term. These examples illustrate how climate, and especially drought, as a driver can lead to reinforcing feedback mechanisms and thus ASS. Land use and soil management may also alter soil hydraulic function, for example changes in cropping systems and soil management practices and systems can affect soil properties with consequences for hydraulic functions, water storage and movement, carbon cycling, biological activity, transport of nutrients and pollutants, and plant growth (Alletto *et al.*, 2015, Franzluebbers, 2002, Strudley *et al.*, 2008). These temporal changes are particularly seen in the near-
saturated range, where soil structure strongly influences water storage and flow (Daraghmeh et al., 2008, Or & Ghezzehei, 2002).

We need to change and develop models to meet the challenges of incorporating soil bio-physical feedbacks. Predicting the impacts of environmental change on soil functions and ecosystem services requires appropriately parameterized models that can account for the dynamic nature of soil hydraulic properties. However, applications of models in the literature generally make use of time invariant hydraulic parameters (Figure 5). The grey box shows the current approach to modelling soil hydraulic functions and soil moisture processes, which assumes they are ‘static’ and unresponsive to changes in environmental conditions. The required future direction is to move towards a dynamic concept of the soil so that soil processes susceptible to environmental change result in biophysical feedbacks to the soil system altering the hydraulic function. Modelling studies accounting for time-variable hydraulic properties in tilled soils have shown improved simulations of near-surface soil water storage (Alletto et al., 2015, Schwen et al., 2011). However, we know little about which parameters are constant, which change, and how. Alletto et al. (2015) observed that both hydraulic conductivity and saturated water content decreased with time in a tilled cropping system. They also refer to work indicating that the α parameter in the Van Genuchten (1980) water retention curve changes but the value of n related to pore size distribution does not. However, tilled systems likely represent transient behaviour brought about by management rather than a switch to an ASS.

Understanding i) the dynamics of environmental processes, ii) bio-physical feedbacks on soil, iii) the subsequent soil moisture state behaviour, and iv) impact on environmental processes, together represent a major challenge for modelling soil functions under future environmental change, as does the collection of data from long-term monitoring and manipulation experiments. The need for this new understanding is supported by recent calls to bring together biological and physical modelling of the soil system (Blagodatsky & Smith, 2012, Vereecken et al., 2016). If ecosystems respond as we propose, it suggests a continued dynamic co-evolution of hydrological properties and processes mediated by bio-physical-soil feedbacks, driven by global environmental change.

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Figure 1. Successive numerical simulations (from top to bottom) of infiltration and subsequent water redistribution: left hand side in hydrophobic soil and right hand side in none hydrophobic bare soil using Hydrus 2D (Šimůnek et al., 2008). The water infiltrates deeper in the soil profile in the hydrophobic soil forming wet bulbs. The reduced connectivity with the surface makes the water less likely to evaporate.

Figure 2. Soil moisture data (points) and Hydrus 1D modelling output (lines) for a soil moisture state shift (01/01/2004) at the Clocaenog (UK) long-term climate change experiment. The grey and black lines use three soil horizons, where the hydraulic conductivity of the O_h horizon is adjusted to 1 cm day\(^{-1}\) for the first 3 years, and 10 cm day\(^{-1}\) after that reflecting an order of magnitude increase in hydraulic conductivity following drought that caused cracking of the O_h horizon.

Figure 3. Soil moisture deficits measured on Peat and Podzol under different land uses at the long-term field site Y Foel (Neutron probe tubes 35-38) in Plynlimon, UK. A) The peat dries during the drought year of 1976 (pink bar) but recovers to its winter soil moisture values within a few years, the drying is greatest under the forest (black) and the recovery slower than under rough grass (red). B) The podzol on the other hand is not impacted by the same drought under the rough grass/heather/seedlings but appears to show an ASS under the forest which never returns to it’s original soil moisture state.

Figure 4. Conceptual model of soil moisture processes in response to increasingly drier summers. A) is characteristic matrix flow in non-hydrophobic soils, B) droughts may cause increased macroporosity and saturation resulting in excess infiltration that causes preferential flow, C) further drying induces feedback from plants (root exudates) and microbes producing hydrophobic compounds that allow for unsaturated preferential flow in cracks or biopores, as modelled in Figure 2.

Figure 5. Schematic view of both current modelling of soil hydraulic function (grey) and the proposed future direction that incorporates dynamic, time varying soil hydraulic parameters that result in ecosystem feedbacks (orange).
Current focus of soil hydraulic modelling

- ‘Static’ soil profile with time invariant hydraulic parameters
  - Soil moisture processes
  - Environmental processes
  - No feedbacks

Proposed future direction of soil hydraulic modelling incorporating feedbacks

- ‘Dynamic’ soil profile with time varying hydraulic parameters, sensitive to management and global change
  - Soil moisture processes
  - Ability to model transient and alternative states
  - Environmental processes susceptible to change from:
    - Management
    - Climate change
    - Land use change
    - Invasive species
  - Resulting in feedbacks

Deformation of the solid phase
Hydraulic conductance
Hydrophobicity
Water resource concentration
Biophysical Feedbacks