

Organization of complexity in water limited ecohydrology

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ABSTRACT

Water limited ecohydrological systems (WLES), with their broad extent, large stores of global terrestrial carbon, potential for large instantaneous fluxes of carbon and water, sensitivity to environmental changes, and likely global expansion, are particularly important ecohydrological systems. Strong nonlinear responses to environmental variability characterize WLES, and the resulting complexity of system dynamics has challenged research focussed on general understanding and site specific predictions. To address this challenge our synthesis brings together current views of complexity from ecological and hydrological sciences to look towards a framework for understanding ecohydrological systems (in particular WLES) as complex adaptive systems (CAS). This synthesis suggests that WLES have many properties similar to CAS. In addition to exhibiting feedbacks, thresholds, and hysteresis, the functioning of WLES is strongly affected by self-organization of both vertical and horizontal structure across multiple scales. As a CAS, key variables for understanding WLES dynamics are related to their potential for adaptation, resistance to variability, and resilience to state changes. Several essential components of CAS, including potential for adaptation and rapid changes between states, pose challenges for modelling and generating predictions of WLES. Model evaluation and predictable quantities may need to focus more directly on temporal or spatial variance in contrast to mean state values for success at understanding system-level characteristics. How coupled climate and vegetation changes will alter available soil, surface and groundwater supplies, and overall biogeochemistry will reflect how self-organizational ecohydrological processes differentially partition precipitation and overall net metabolic functioning. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS complexity; water limitation; adaptation; self-organization

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INTRODUCTION

Water limited ecohydrological systems (WLES) are characterized hydrologically by potential rates of evapotranspiration greatly exceeding rainfall input (Allison and Hughes, 1983). These conditions include both arid and semi-arid lands, which cover 35–45% of the global terrestrial surface (Asner *et al.*, 2003; Reynolds *et al.*, 2007) and store about 241 Pg or 15.5% of world's total of 1550 Pg organic C to 1 m (Lal, 2004), approximately twice the amount stored in temperate forest ecosystems ~104–155 Pg (Post *et al.*, 1982). However, areas where WLES-like processes are prominent for some periods of the year are likely to extend much further (Figure 1). Run-off in these systems is rare and, when it does occur, is typically in the form of infiltration excess overland flow (Yair and Lavee, 1985) with transmission losses to the soil profile along the overland flowpath or subsurface stormflow via snowmelt following the connectivity

of storage element filling in the subsurface (Unnikrishna *et al.*, 1995; Kelleners *et al.*, 2010). While in most WLES the mean rate of hydrological cycling and biological functioning is low, these systems are characterized by large pulses of activity when water becomes available and resulting rates of activity can often exceed those from more humid environments (Birch, 1964; Noy-Meir, 1973; Lee *et al.*, 2004; Xu *et al.*, 2004; Jenerette *et al.*, 2008; Scott *et al.*, 2009). The propensity for pulsed dynamics leads to a strong nonlinear sensitivity to environmental variability. To a broad extent, large stores of global terrestrial carbon, potential for large instantaneous fluxes, sensitivity to environmental changes, and likely global expansion of WLES make them a particularly important ecohydrological system to understand. More specifically, there is a pressing need to better quantify coupled ecosystem and hydrologic functioning during periods of water limitation. Understanding the potential global feedbacks associated with the dynamics of WLES are essential in forecasting future rates and consequences of global changes.

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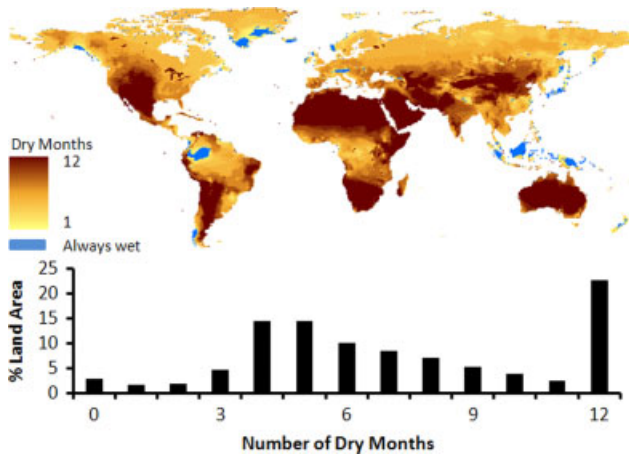


Figure 1. Distribution of the temporal extent of land surface water limitation. The map shows increasing darkness of brown with the number of months where potential evapotranspiration exceeds precipitation. Areas in blue have precipitation always exceeding potential evapotranspiration. These patterns are summarized below as the proportion of land area for each possible number of months. Only 2.9% of global land area is continually wet. On average the land surface is dry for 7.1 months of the year. Precipitation data are from a 30-year mean monthly climatology (Cramer and Leemans, 2001). Potential evapotranspiration data are from a modified Food and Agricultural—Penman—Monteith algorithm implemented using the WorldClim Global Climate Data (Trabucco and Zomer, 2009). Data were processed using ArcGIS 9.3.

Achieving the interdisciplinary synthesis required for ecohydrology will build on a reconciliation of how concepts and technical approaches used to generate knowledge have been defined across disciplines. This reconciliation needs to address the two contrasting science views influencing ecohydrology: the Newtonian view where understanding broadly applicable general mechanisms is desired and the Darwinian view where an understanding of the specific details of particular systems is sought (Harte, 2002). A hallmark of both ecology and hydrology has been an appeal to the generality of

a mechanistic understanding. However, research in both fields is faced with a reality where any given system has many idiosyncratic state dependencies. A comprehensive reductionist understanding in ecology or hydrology has infrequently been achieved and only after substantial effort towards resolving many individual processes intrinsic to the particular system (McDonnell *et al.*, 2007). Even when such detailed process information has been developed, surprises in ecohydrological trajectories still occur (Heffernan, 2008). To link across the multiple paradigms, ‘complexity science’ approaches may provide a useful framework (Prigogine and Stengers, 1984; Holland, 1992; Kauffman, 1993; Cowan *et al.*, 1994). In scope, complexity science links relatively simple relationships at relatively fine scales and allows interactions among networks of these discrete units to dominate system dynamics. The complexity of the network, described by the number, diversity, and connectivity of units, greatly influences how these systems behave. WLES are principally characterized as multiple-scaled, with high spatial and temporal variability; feedbacks of WLES extend to decadal (Scott *et al.*, 2009) and subcontinental (Dominguez *et al.*, 2009) scales. As such, these systems exhibit much complexity in both structure and functioning and probably a complexity science approach will be useful for synthesis (Table I).

The objective of our synthesis is to look towards a framework for understanding ecohydrological systems (in particular WLES) as complex adaptive systems (CAS). We bring together current views of complexity from ecological and hydrological sciences in this framework, suitable for understanding WLES water dynamics and how these water fluxes influence and respond to whole-ecosystem metabolism. We first organize key nonlinear ecohydrological mechanistic processes and incorporate them into a general understanding of whole system dynamics. We examine how complex ecohydrological

Table I. Examples of common properties associated with complex systems from both ecological and hydrological processes.

Property	Ecological example	Hydrological example
Self-organization	Microclimate effects; ecosystem engineering Soil development; vegetation patterns	Drainage network; flow path development
Threshold	Xylem embolism; leaf out; leaf fall; birth/death	Flooding; throughfall; snowmelt; saturated flow
Adaptation	Species shifts; phenotypic plasticity	Erosion, deposition
Nonlinearity	Temperature response curves	Soil–water retention curves; run-off generation; preferential flow; plant uptake of soil moisture
Irreversible	Growth curves Extinction	Erosion; weathering;
Scale-free behaviour	Patch distributions Patch boundaries	Stream networks
Scale-dependent behaviour	Boundary layer conductance	Dispersion
Legacy	Organismal regulation Reproductive effort	Antecedent soil-moisture conditions; geomorphology
Hysteresis	Nutrient/resource patches Soil respiration; delays in delivery of photosynthetic products to the roots due to phloem transport time	Soil–water retention
Feedbacks	Growth	Erosion

systems influence both local carbon and water cycles and in aggregate influence global earth system dynamics. Throughout, we use diverse examples to show the flexibility of complexity approaches in understanding WLES, highlighting key processes whose importance can only be understood in the context of the embedded system.

ECOHYDROLOGICAL SOURCES OF COMPLEXITY

Ecohydrological systems can be described as a set of whole-system-scale processes that result in a series of net exchanges with the environment and in the maintenance of the system's intrinsic organizational characteristics. *Net* exchanges between a system and its environment are determined by gross fluxes of individual components and partitioning of incoming fluxes into multiple effluxes. Such fluxes include mass, energy, and information exchanges, which differ in their conservation properties—with energy and material being conservative and information being non-conservative—and potential for recycling, with energy not recycled and materials continually recycled (Reiners and Driese, 2003). Examples of each flux include energy, CO₂, and biological species. The dynamics of these fluxes have many sources of complexity. Net and component fluxes respond nonlinearly to environmental variation, depend on traits of the biotic communities, and are influenced by historical legacies at multiple timescales (Figure 2). While nonlinear processes alone are insufficient to impart complex behaviour to a system, complex systems necessarily have many nonlinear interactions, and developing an understanding of these sources of nonlinearities is an essential foundation (Phillips, 2003). The environmental drivers provide an initial source of complexity with environmental variability occurring across all scales and legacies from past variability strongly influencing present states. Biological responses to environmental variation, including amplification, dampening, and nonlinear state changes, are another source of complexity. Finally, the structure of the interaction network provides a source for complexity with large numbers of components that vary in their individual characteristics and are richly connected.

Interactions between carbon, water, energy, and biology

Soil moisture is a fundamental constraint of most ecohydrological processes and, in particular, of ecosystem metabolism in water limited regions (Noy-Meir, 1973). How biological processes respond to soil moisture determines, to a large extent, ecosystem functioning. The dynamics of this fundamental ecohydrological variable have many sources of nonlinearities. For the same moisture input, local geomorphology and vegetation can affect groundwater recharge, access to groundwater, energy inputs, run-on and run-off (Wilcox *et al.*, 2003; Zou *et al.*, 2007; Goodrich *et al.*, 2008; Scott *et al.*, 2008b). Seasonality of precipitation can influence the amount of effective moisture available for biological processes

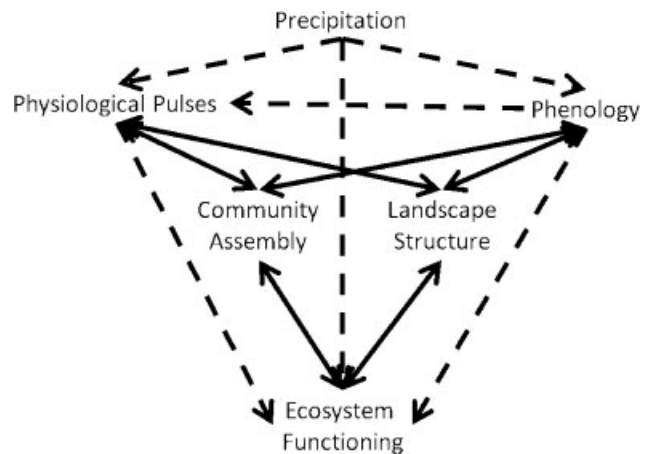


Figure 2. Conceptual relationship between precipitation variability and ecosystem functioning, with a particular emphasis on carbon cycling processes. Dashed lines denote direct effects and solid lines denote indirect effects of precipitation variability. This process-based conceptual model highlights strongly interactive meteorological and biological processes associated with ecosystem functional responses to precipitation variability.

and be directly related to temperature dependent enzymatic reactions (Goodrich *et al.*, 2008; Jenerette *et al.*, 2010). Plants and soil organisms differ markedly in their metabolic sensitivity to soil moisture (Huxman *et al.*, 2004; Williams *et al.*, 2009), which leads to large differences in respiratory and photosynthetic processes. Plant community composition can strongly regulate ecosystem sensitivity to moisture availability; with major differences including continua of C₃, C₄, and Crassulacean acid metabolism (CAM) photosynthetic pathways and dominance by wood and grass life-forms. Transitions from C₃ to C₄ and CAM lead to large increases in leaf-level water-use efficiency, accomplished through decoupling electron transport and carboxylation; however, these increases in efficiency come at an energetic cost that reduces maximum photosynthetic rates. Much research has examined potential differences among these life-forms, and even species differences within similar life-forms can lead to differences in whole-ecosystem functioning (Scott *et al.*, 2010). Another key life-form difference is the contrast between woody and grassy species. Woody plants generally have greater access to deeper water storage than grasses. However, grasses have more plastic phenological responses to precipitation variability. Shifts in community composition between woody and grass dominated vegetation communities alter vertical rooting distributions and depths (Schenk and Jackson, 2002), effectively altering ecosystem water and carbon balance (Huxman *et al.*, 2005; Hultine *et al.*, 2006; Scott *et al.*, 2009). These differences in access to deeper water sources complicate our understanding of how distinct plant functional types, such as C₃ versus C₄, or woody versus grass, will regulate ecosystem processes under altered climate regimes (Kirschbaum, 2004; Sage and Kubien, 2007).

In addition to direct effects on carbon and water dynamics, ecohydrological systems physically alter the micro-scale energy balance through increased attenuation of incoming solar radiation, which induces cooler

soil temperatures, reduces evaporative potentials (Scholes and Archer, 1997; Martens *et al.*, 2000; Breshears *et al.*, 2009a; Villegas *et al.*, 2010), and slows soil metabolic processes (Barron-Gafford *et al.*, 2011). During warm seasons, spatially variable energy partitioning can lead to surface soil temperatures varying by as much as 30 °C between inter-canopy and sub-canopy patches (Barron-Gafford *et al.*, 2011). Above ground, leaves may frequently warm beyond thermal optima to the point where electron transport capacity becomes limiting and/or Rubisco activase becomes heat labile, reducing photosynthetic capacity (A_{\max}) (Sage *et al.*, 2008) leading to both plant and ecosystem changes. Finally, energy partitioning within these systems contributes significantly to the total global warming potential associated with changes in semi-arid regions (Zeng *et al.*, 2002; Pielke *et al.*, 2007; Rotenberg and Yakir, 2010). Large uncertainties exist in understanding the influence of an ecosystem on its immediate microclimate, biological responses to micro-environmental variability, and the net partitioning of incoming radiation into sensible and latent heat flux.

Ecological responses vary at event, seasonal, annual, and inter-annual scales

Moisture availability varies in space, from sub-metre to continental scales and in time from individual wetting/drying cycles to decadal and longer oscillations. This variation is driven by strongly stochastic processes in most water limited regions (Porporato *et al.*, 2004; Katul *et al.*, 2007). The effects of changes in precipitation variability on net ecosystem carbon fluxes will depend on how constituent fluxes of photosynthesis and ecosystem respiration respond (Huxman *et al.*, 2004; Chen *et al.*, 2009; Williams *et al.*, 2009). Moisture variability affects ecosystems' net carbon balance at numerous scales and through multiple interacting pathways, including physiological, phenological, community structuring, and evolutionary (Weltzin *et al.*, 2003; Schwinning and Sala, 2004; Jenerette and Lal, 2005; Shen *et al.*, 2008). In WLES, moisture often arrives as discrete events leading to metabolic pulses of heterotrophic and autotrophic processes (Noy-Meir, 1973; Huxman *et al.*, 2004; Reynolds *et al.*, 2004). In many cases, the spatial and temporal distribution of events can be as important for ecohydrological functioning as the total magnitude. Timing of rainfall relative to other rainfall events, such as events separated by hours or weeks, and other seasonal cues, including plant activity or other meteorological conditions, is often as critical to ecosystem responses as the mean climate (Reynolds *et al.*, 2004; Bates *et al.*, 2006; Jentsch *et al.*, 2007). Such spatial and temporal variability can have large consequences for ecosystem functioning and overall partitioning of precipitation into E, T, and run-off (Weltzin *et al.*, 2003; Collins *et al.*, 2008).

At the scale of an individual event, large cascades of biological responses follow the wetting of a previously dry ecosystem. A mechanistic understanding of these

pulse dynamics is generally lacking, especially in scaling organismal processes to whole ecosystem functioning (Jentsch *et al.*, 2007). Micro-organisms often have immediate direct responses to wetting, which are then modulated by community interactions and substrate availability. Emergence from drought, in both plant and microbial organisms, results in rapid sub-cellular and whole organism responses coordinated through multiple signalling pathways leading to an overall metabolic upregulation. Sensitivity to these drying–wetting cycles may further be influenced by vegetation through variation in leaf physiology, phenology, local microclimate, whole plant hydraulics, and litter decomposition (Schwinning and Sala, 2004; Cornwell *et al.*, 2008; Jenerette *et al.*, 2009). In aggregate, these processes lead to whole community and ecosystem pulses with complex trajectories for the overall net exchanges of CO₂ and water.

Phenological dynamics of vegetation interact with seasonal changes in moisture and are drivers of individual rainfall event response variability. However, generating a predictive theory of phenological patterns for whole ecohydrological systems has been challenging. Phenological differences often vary with life-form with many constrained deciduous or dynamic exploitation strategies. Woody vegetation is usually more constrained and grasses are often more exploitative. Vegetation growth is generally limited by meristem tissue and the ability to transfer carbon between carbon storage tissue and meristems places a key biological constraint on ecosystem seasonal sensitivity to precipitation (Thornley, 1991; Knapp and Smith, 2001). In WLES, phenological dynamics are closely connected to precipitation regimes and exhibit complex dynamics with unexpected dependencies across multiple rain seasons (White *et al.*, 1997; Botta *et al.*, 2000; Picard *et al.*, 2005; Jenerette *et al.*, 2010).

Many WLES exhibit strong inter-annual variability in biological activity leading to large differences between actual biomass in a given year and what would be predicted as the 'steady-state' biomass (Arnone *et al.*, 2008; Scott *et al.*, 2009; Misson *et al.*, 2010). A year with unusually high precipitation preceded by several years of low precipitation will likely have reduced biological capacity to respond, and correspondingly, lower than expected functioning. Similarly, dry years following wetter periods will likely be associated with unexpectedly high whole ecosystem respiration rates (Arnone *et al.*, 2008; Scott *et al.*, 2009).

Ecohydrological networks

The direct linkages between individual components of ecohydrological carbon, water, and energy fluxes are embedded in a highly organized spatial, temporal, and organizational network both in the horizontal and vertical dimensions (Turnbull *et al.*, 2008). Ecohydrological systems are composed of units that range from micropores or individual cells through hillslopes and organisms, to watersheds and ecosystems. From ecological hierarchy theory (O'Neill *et al.*, 1986) the network of connections

among lower levels gives rise to higher-level phenomena, which, in turn, modify distributions at the lower levels. Separation of processes across a network of interactions often leads to a wide array of complex behaviours including feedbacks, thresholds, and hysteresis (Turnbull *et al.*, 2008). In many cases, these network properties can serve to dampen the large source of individual process nonlinearities that occur in the system (Sivapalan, 2003). The couplings among vegetation, soils, and hydrology create several feedbacks; for example, the formation of vegetation patches is self-reinforcing by leading to further accumulation of nutrients, organic matter, and soil moisture in the individual patches (Schlesinger *et al.*, 1990; Okin *et al.*, 2009). Thresholds are commonly crossed, leading to large changes in system configuration and functioning with prominent examples ranging from desertification (Rietkerk *et al.*, 2004) to the initiation of saturated flow (Tromp-van Meerveld and McDonnell, 2006b) where a hillslope goes from a state unconnected with the stream to one fully coupled via a continuously connected transient water table. Hysteresis effects, where multiple states of key output variables occur in response to proposed drivers, are observed in both hydrological and ecosystem processes and are commonly associated with interactions at the ecohydrological interface. Prominent examples for both include patterns of ecosystem respiration (Vargas and Allen, 2008) and the linkages between patterns of topography, soil moisture, transpiration, and species distribution at the hillslope scale (Tromp-van Meerveld and McDonnell, 2006a).

TOWARDS SYNTHETIC ECOHYDROLOGICAL THEORY: MERGING CONTINUOUS AND DISCRETE SCALING

A challenge for an ecohydrological synthesis is that primarily—although certainly with prominent counter examples of both—hydrologists have been examining scale-independent properties, whereas ecologists have been concerned with scale-dependent properties of ecohydrological systems, again reflecting differences in Newtonian and Darwinian research approaches. Consilience among theories is needed to bridge across sub-cellular to landscape processes, where over such scale ranges both properties are important. Key to this integration is the concept of spatial scale. Like the study of relationships and interactions among individuals, populations, and communities, the science of ecology may also be described by taking an object-oriented view of the world. A primary focus is on the tree or the forest, rather than a 'degree of treeness'. There are many such boundaries between scales of organization and much ecological research investigates processes within assumed homogeneous units, e.g. a tree, or crossing between scale boundaries, e.g. tree–forest interactions (O'Neill, 1989; Wu and Loucks, 1995). In contrast, the science of hydrology has traditionally taken a continuum perspective, with each point in space characterized by a variety of parameters and variables, e.g. porosity, degree of saturation,

and nitrate concentration (Beven, 1995). Variation among parameters and variables is often connected to dimensionless quantities with an emphasis on generating scaling approaches (Lyon and Troch, 2007; Harman and Sivapalan, 2009). One challenge for the emergent field of ecohydrology is bringing together these continuum and object-oriented perspectives. Research examining the ecological effects of precipitation variability highlight applications from both perspectives where descriptions of rainfall distribution regimes (Rodriguez-Iturbe *et al.*, 2001b; Porporato *et al.*, 2004) are being contrasted with description of responses to discrete events and sequences of events (Huxman *et al.*, 2004; Baldocchi *et al.*, 2006; Jenerette *et al.*, 2008).

A synthetic ecohydrological approach will incorporate continuous scaling within limited-scale domains and disjunctions in scaling relationships at the boundary of scale domains. Hierarchy theory organizes complex phenomena into components that are both constructed of and form other components at different scales (Allen and Starr, 1982; O'Neill *et al.*, 1986; Simon, 1996; Wu, 1999)—with much of these scale dependencies arising from the presence of organisms. Higher levels interact primarily with lower levels through constraints to processes and by imposing external regulation; higher levels provide the limits to the variation within a lower level. Within a hierarchical level, self-similar spatial patterns have been observed for many ecohydrological physical structures (Mandelbrot, 1983; Phillips, 1993; Nikora, 1994) and associated processes (Kirchner *et al.*, 2000; Harman and Sivapalan, 2009). Hierarchical breaks occur in biological mechanisms at cellular, organ, sub-canopy, organism, canopy, stand, community, and forest scales and in hydrological processes at the soil column, hillslope, catchment (where transport is dominated by landscape characteristics), and large river basin (where transport is dominated by river network characteristics) scales. Initial applications of hierarchical approaches have been used in several ecohydrological studies to identify linkages between terrestrial and aquatic components across a landscape (Fisher *et al.*, 1998; Dent *et al.*, 2001; Jenerette and Lal, 2005; Turnbull *et al.*, 2008).

In soil physics, the concept of the representative elementary volume (REV) is used to describe the spatial scale at which a soil sample, for example, is representative of the continuum. Meaning, the minimum scale at which it is appropriate to describe relevant characteristics such as hydraulic conductivity (Hillel, 1998). Similarly, in catchment hydrology, the representative elementary area (REA) concept has been quantified based on stream gauging, where a threshold catchment area defines the scale at which the variance in unit area discharge collapses to a single value (Woods *et al.*, 1995). This can describe, for instance, the appropriate minimum scale for gauging a stream for such results to be representative to streams elsewhere in the watershed system. In this sense of an REV or REA, there exists a range of scales for which the mathematical representations of processes are stable, and small changes in scale do not

greatly influence the dynamics of the system. The mathematical tools of self-similarity effectively describe those scales (as dimensionless groups of combinations of all variables), eliminate the functional dependence of certain dimensionless groups on the governing partial differential equation (i.e. reducing it to an ordinary differential equation), and can lead to analytical solutions of complex problems (Huppert and Woods, 1995; Barenblatt, 1996). Similarly, the REV and REA concepts can be extended to temporal scales to identify representative time domains where processes are nearly decoupled from much higher and lower frequencies of variability, which can then be effectively described as either noise or constant.

Many uses of the REV and REA are similar to ecological approaches of hierarchical partitioning. We frame a coupling between ecology and hydrology around these consistent concepts of the REV and REA and hierarchical partitioning. The fundamental unit, as such, is the ecohydrological patch, a relatively homogeneous spatially and temporally defined unit of a WLES (Figure 3) (Urban *et al.*, 1987; Pickett and Cadenasso, 1995). Applications of ecohydrological patch concepts should facilitate combining hierarchical partitioning and scale similarity in ecological and hydrological domains to better resolve scaling relations of complex WLES. This type of approach has been used recently to explore catchment scale REAs and how landscapes control the transit time of water in catchments, where catchments are analogous to soil cores and a particular size of catchment is defined as being representative of the continuum of conditions across all catchments (Hrachowitz *et al.*, 2010). As Sivapalan (2003) notes, in order to arrive at a satisfactory simplicity, we clearly need a mechanism in any such aggregation to whittle down the unnecessary process details and to transfer dominant process control from the hillslope to the watershed scale.

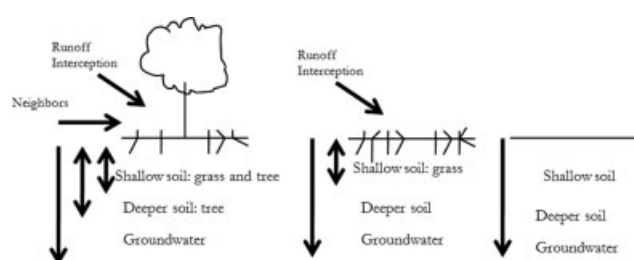


Figure 3. Self-organization of vertical structure and hydrologic fluxes (excluding evaporative losses) for three different patch types gives rise to whole landscape self-organization. The arrows show directional movements of water. Hydraulic redistribution occurs vertically and horizontally. This division of dryland ecosystem patches into these three types is a widely used simplification. Commonly, two soil depths (or three including a surface pool) are modelled where in the upper pool both grasses and trees can obtain water and in the lower pool only trees can obtain water. Much research on rooting depth shows that rooting profiles are dynamic thus making the actual depth of each pool variable, although perhaps predictable. This figure depicts the potential sources of water and possible movements through the soil and vegetation for each of these patch types. Changes in the vegetation community alter the vertical and horizontal connectivity at the individual patch scale. Across an ecohydrological landscape, the arrangement in these three patch types often generates self-organized waves and islands of distinct patch types and strong degrees of spatial correlations.

A direction for synthesis is the suggestion that ecohydrological systems, in part through self-organizing processes, create these nested hierarchical structures of patches consisting of both broad domains of similarity and discrete changes in functioning across scales. Considering the ecohydrological patch, one wonders if there are general principles that can be drawn out regarding the effect of vegetation on the appropriate spatial scales of hydrologic parameters and variables. This self-generating scaling occurs through ecohydrological self-modification of the environment with interacting positive and negative feedback mechanisms. For example, in the initial stages, shoot growth is a positive feedback, since more and larger leaves provide carbon to fuel further growth. At later stages, stomatal closure in response to soil drying is in turn a negative feedback constraining water loss and carbon uptake. Within this context, one emerging theme with respect to limiting resources is a pattern of positive feedbacks operating at spatial scales larger than the vegetation and negative feedback mechanisms operating at scales smaller than the vegetation. That is, through coupled positive and negative feedback mechanisms at alternate scales plants act to concentrate limiting resources to the scale of the vegetation and to homogenize those resources within the scale of the vegetation. This concentration and homogenizing within individual scales reinforces patch distributions. These notions of resource acquisition and homeostasis are foundational to ecology and may provide insight to the issue of scale in ecohydrology. The emphasis on self-organization as both a source of structure and a primary function for ecohydrological systems suggests that a CAS perspective may be helpful for improved understanding and generating future predictions.

COMPLEX ADAPTIVE ECOHYDROLOGICAL SYSTEMS

CAS characteristics of ecohydrological systems

We extend these ideas of complexity and self-organization across multiple scales by further suggesting an approach describing WLES as CAS, which may be as powerful, and provide complementary information, as a primarily reductionist approach (Railsback, 2001; Grimm *et al.*, 2005). CAS are those systems that exhibit complexity in both behaviour and structure and have the capacity for self-organization and adaptation to environmental conditions (Holland, 1992). Much of these approaches are extensions of general systems and cybernetic theories (Ashby, 1956; Simon, 1996). CAS are generally composed of many semi-autonomous units that interact through some, although not exclusively all, non-linear processes. A CAS depends on exchanges with an environment to maintain a state far from equilibrium characterized by the self-organized generation of multiple hierarchical relationships (Wu and Loucks, 1995). Across scales, a CAS has some capacity to alter its configuration and influence its own micro-environment. In addition to

the inherent properties of complex systems, CAS also have the capacity to modify the rules of interactions between components or the processes occurring within a single component (Kauffman, 1993; Cowan *et al.*, 1994; Levin, 1998; Chave and Levin, 2003). However, the potential for adaptation is strongly dependent on historical legacies. The approach of CAS extends hierarchical and other organizational theories that do not explicitly examine the sources of scale partitioning to a science that explicitly examines the generation and dynamics of hierarchical units as a fundamental function (Holling and Gunderson, 2002).

CAS can be described through several system-level properties including instantaneous state and whole system characteristics (Table II). Composition, broadly described as the number and diversity of units within and between hierarchical levels, and configuration, the arrangement of units both spatially and functionally, are the two primary characteristics influencing organization. Biological sources of diversity span genomic variability within species and across taxa to functional variability of responses to common drivers. Hydrologic sources of diversity at the patch to landscape scale include, but are not limited to, heterogeneity of soil texture, flow paths, and precipitation. Variations in ecohydrological configuration arise from root and shoot structure, flow paths, and concentration gradients, which in turn respond to environmental patterns and internal organization.

Self-organization

Like CAS, self-organization in ecohydrological systems provides a strong control over sensitivity to environmental variability. Ecohydrological self-organization can be found across space in both vertical profiles and horizontal surfaces with sources in both ecological and geomorphological processes (Figure 4). The scope of self-organizing processes in ecohydrological systems can be extensive with direct effects on primarily physical processes such as rates of infiltration (Thompson *et al.*, 2010) and precipitation regimes (Juang *et al.*, 2007; Konings *et al.*, 2010). These effects extend through the vegetation, which further influences magnitudes of soil moisture spatial variability and its spatial structure in response to wetting (Caylor *et al.*, 2005; Ivanov *et al.*, 2010).

In the vertical direction, from the top of the boundary layer to the bottom of the soil profile, ecohydrological self-organization influences functional responses to environmental variability. Such self-organization is indicative of the inter-annual consistency of the proportion of annual evaporation to the total soil moisture available within a site (Horton, 1933; Troch *et al.*, 2009). System-level mechanisms for these findings can be expected from trade-offs in plants maximizing efficiency and minimizing stress (Caylor *et al.*, 2009). As a direct consequence, rooting depth profiles adjust to patterns of precipitation characteristics and act as a feedback for balancing this trade-off (Guswa, 2010). Changes in vertical structure alter the zero flux plane, or the depth below soil

surface evaporation, influencing the rates of groundwater recharge. These coupled processes describe a self-organizing WLES that adjusts vertical spatial structure within an ecohydrological patch as a functional response to the environment. Adaptation of system configuration throughout the vertical profile can stabilize functioning in the face of environmental variability.

Ecohydrological landscapes also exhibit self-organizing tendencies in the horizontal distribution of landscape components (Rigon *et al.*, 1994; Rodriguez-Iturbe *et al.*, 1998; Phillips, 1999; Milne *et al.*, 2002). Across horizontal dimensions much organization can be found in the spatial structure of stream networks (Rodriguez-Iturbe *et al.*, 1994; Stolum, 1996; Phillips, 2001) and soil-moisture patterns (Rodriguez-Iturbe *et al.*, 2006; Ivanov *et al.*, 2010). Across a larger landscape of multiple patches, ecohydrological systems tend to self-organize the distribution of vegetation into well-defined local patches (Klausmeier, 1999; Rietkerk *et al.*, 2002) and a regular distribution of patches across the landscape (Kefi *et al.*, 2007; Scanlon, *et al.*, 2007; Borgogno *et al.*, 2009). In these cases and others, observed spatial patterns are generally insensitive to initial conditions and have consistent features arising across multiple environments. Often, stochastic noise in the environment is sufficient to cause self-organization processes to coalesce systems into organized patchy structures (D'Odorico *et al.*, 2006; Borgogno *et al.*, 2009).

Coupled self-organization in the vertical and horizontal dimensions can be shown in ecohydrological partitioning of precipitation inputs. Regardless of the mechanism (interception of overland flow, fog, or blowing snow), vegetation tends to concentrate water to the scale of the vegetation. Although imperfect, the hypothesis that vegetation concentrates limiting resources is consistent with observations of water (and nutrient) acquisition across a range of examples. In the coastal redwood forests of California, Dawson (1998) showed that the trees increase the interception of fog, an example of above-ground concentration of water by plants. The contribution of fog to the hydrologic budget in the redwood stands is double what it is without the trees (Dawson, 1998). In addition to the concentrating effect, plants also exhibit a propensity to homogenize water resources within the scale of the vegetation. Transpiration is a process with a negative feedback; as water is removed from the soil, the process of plant uptake is self-limiting as stomata close, whether via a hydraulic or chemical signalling mechanism. Thus, as the soil dries out, the spatial pattern changes from homogeneously wet, to an intermediate heterogeneous distribution of soil moisture that is eventually smoothed and homogenized through drying (Ivanov *et al.*, 2010). Additionally, there is now extensive evidence for hydraulic redistribution, both vertical and horizontal, which acts to eliminate gradients in soil moisture throughout the root zone (Dawson, 1993; Burgess *et al.*, 2001; Burgess and Bleby, 2006; Munoz *et al.*, 2008; Scott *et al.*, 2008a). The hydraulic network of roots moves

Table II. Measurable characteristics of CAS that can generally be quantified by degree (i.e. low to high), provided that space and time-scales are specified.

System characteristic	Ecological system	Ecological examples	Hydrological system	Hydrological examples
Diversity	Richness, variability, and evenness of biological components	Diversity of plant species, functional types	Richness, variability, and evenness of hydrologic parameters	Heterogeneity of soil texture, leaf-area-index, land-cover
Connectedness	Degree to which alike elements are adjacent in space	Pheontype clustering; root functioning	Degree to which alike elements are adjacent in space (particularly in the direction of flow)	Drainage network; preferential flowpaths
Dispersion	Degree to which concentrated loads are spread around	Seed dispersal, hydraulic redistribution of soil moisture	Degree to which concentrated loads are spread around	Attenuation of rainfall pulse; dispersion of solutes and contaminants
Concentrating	Degree to which diffuse resources are concentrated	Phosphorous in Everglades tree islands; nutrients and water in tiger bush landscapes; water in snow-drift landscapes	Degree to which diffuse resources are concentrated	Concentration of rain or fog by CA redwoods
Resistance	Magnitude of environmental variability that can be withstood without altered functioning	Stomatal regulation to manage water deficits	Magnitude of driving force needed to achieve specified rate	Inverse of hydraulic conductivity in soils; hydraulic resistance in plants;
Resilience	Magnitude of environmental variability that can be withstood without altering whole system organization	Leaf area adjustments to manage water deficits; Temperature acclimation	Ability of a system to return to original state following a disturbance	andscape adjustments to maintain consistent annual evaporative fractions

Neither binary variables nor more complex variables, that require more than one dimension to quantify are included. Notably, there are important differences in common ecological and hydrological uses of resistance and resilience. We have adapted the ecological perspective in the text for these terms, although the concepts associated with both ecological and hydrological uses relevant for WLES.

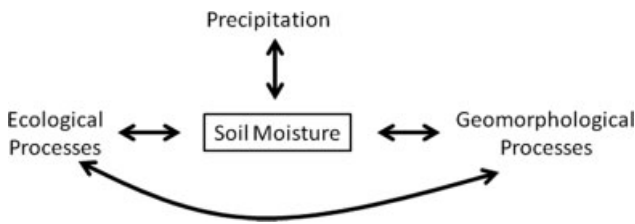


Figure 4. The pattern of soil moisture, a key ecohydrological state variable, is strongly controlled by self-organizational processes relating to coupled ecological and geomorphological processes across multiple scales. The feedbacks between ecological and geomorphological processes can occur at disparate timescales, and the relative importance of different processes can vary in response to multiple environmental gradients and self-organizational dynamics.

water from regions of higher to lower potential, accelerating the homogenizing effect of water extraction. Also relevant to the above discussion is the notion of temporal scale. In this section, we have focussed on timescales that are long relative to the diel forcing of solar radiation but short relative to the life-history of the vegetation. That is, the above discussion holds for timescales over which the vegetation can be thought of as stable. These timescales also correspond to the typical timescales of interest in water supply. Coupling these phenomena with processes occurring at temporal scales, where diel changes in solar radiation and other meteorological patterns are resolved, provides opportunities to more closely link ecohydrological processes to organismal physiology. Moving to longer timescales, such as those relevant to successional and erosional dynamics, may give rise to different behaviours with respect to the concentrating and homogenizing effects of vegetation.

Resilience, resistance, stability

Stability in functioning, defined generally as the inverse of variance over some temporal or spatial interval (Tilman *et al.*, 1998), is conceptually easy to measure although the information provided about system dynamics is unclear. More important for developing an understanding of system dynamics are variables describing resistance and resilience (Holling, 2001). The degree of each is dependent on self-organizational processes and is in response to specific environmental variability (Carpenter *et al.*, 2001). Resistance mechanisms lead to the maintenance of functional stability in the face of variability, whereas resilience mechanisms lead towards the maintenance of organizational structure and may amplify environmental variation. Often, there is a trade-off associated with the use of either strategy (Orwin *et al.*, 2006; Jenerette *et al.*, 2009). Increases in diversity have been associated with increased stability, resilience, resistance, and overall rates of functioning (Loreau *et al.*, 2001; Holling and Gunderson, 2002; Hooper *et al.*, 2005). Increasing the connectivity of a system similarly tends to increase resilience and stability (Suding *et al.*, 2004). Although, connectivity thresholds often exist where further increases lead to catastrophic reductions in resilience and stability (Holling and Gunderson, 2002).

In a brief article by John H. Holland (1992), he refers to CAS as striking balances between two types of behaviours: exploration versus exploitation or tracking versus averaging. In tracking, a system responds to environmental change rapidly whereas in averaging the response is dampened. This binary seems to be strongly tied to notions of resilience and resistance. In some ways, resistance is the ability to average out environmental variability—whether too much or too little (temperature, sunlight, water, etc.) Thus, systems with high resistance (in the ecological sense) are those operating from an averaging perspective. Benefits accrue when resources are homogenized. In contrast, systems that put more weight on ‘tracking’ kinds of behaviour need to be more resilient and continually adjust to environmental variability to use peaks or downregulate during minima of resource availabilities.

Understanding the biophysical mechanisms associated with these system traits is providing new insights into the maintenance of organization in ecohydrological systems. The balance of tracking versus averaging behaviour (or resilient vs resistant) will be time-dependent; for example, a deciduous tree may be resistant to water stress on the timescale of weeks and resilient with respect to light and temperature at the seasonal scale. The importance of resistance and resilience mechanisms for ecohydrological systems have been shown in overall net carbon flux at individual event (Potts *et al.*, 2006) and seasonal scales (Jenerette *et al.*, 2009). In these examples, below-ground processes exhibited more tracking through immediate responses than above-ground, and ecosystems dominated by grasses exhibited more tracking than those dominated by woody plants through differences in phenological sensitivity to precipitation.

Resistance and resilience mechanisms also lead to domains of system attractors and result in nonlinear shifts between alternate stable states. Once resilience thresholds are crossed, the system may enter new organizational states. These state-change-dynamics in drylands are most exemplified as alternative stable states between grass and woody dominated conditions (Carpenter *et al.*, 2001; D’Odorico *et al.*, 2007; Kefi *et al.*, 2007; Rietkerk and van de Koppe, 2008) and transitions in both directions have been observed (Briggs *et al.*, 2005; Cox and Allen, 2008). When near resilience thresholds, systems exhibit extreme sensitivity to the environment (Carpenter and Brock, 2006). These transitions often follow non-linear cusp-catastrophe behaviours and have been modelled using formal catastrophe theory approaches (Lockwood and Lockwood, 1993). Returning the system to the previous state requires changing the driving parameter much further than past the threshold for entering the new state as this new state also has self-organizational resilience and resistance processes (Rietkerk *et al.*, 2004; Scheffer *et al.*, 2009).

What is being optimized?

Progress in developing systems-level descriptions of ecohydrology commonly appeal to assumptions of optimization. A primary challenge for using optimization is the perceived goal-seeking behaviour of adaptation and the need for a clear objective function over which the system is optimizing. The classic examples of using optimization in ecohydrological theory are Eagleson's optimality hypotheses that have served as an initial approach for linking land surface dynamics with variations in precipitation (Eagleson, 1978, 1982). This theory was built around three hypotheses: (1) vegetation canopy density will rapidly equilibrate with climate and soil conditions to maximize soil moisture and thereby minimize plant water stress, (2) vegetation will maximize transpiration efficiency through succession, thus again maximizing soil water, and (3) vegetation will modify soil development to maximize canopy density. Recent critiques suggest that while the theory may provide some valuable insights, it also conflicts with some well-understood ecological processes (Hatton *et al.*, 1997; Kerkhoff *et al.*, 2004). Potential modifications to this theory include incorporating: (1) the dynamic interaction of water availability and C cycling, (2) physiologic differences between different plant functional types, and (3) spatial heterogeneity in vegetation–precipitation interactions (Rodriguez-Iturbe *et al.*, 1999; Kerkhoff *et al.*, 2004; Sankaran *et al.*, 2004).

More recent examples have developed optimality-based hypotheses to better describe vertical structure within an ecosystem for vegetation use of water (Guswa, 2008; Schymanski *et al.*, 2008b). At biophysical levels, stomata should adjust dynamically to maximize photosynthesis for a given water loss and this hypothesis has been supported in several studies (Wong *et al.*, 1985; Schymanski *et al.*, 2008a). Trade-offs in meeting the water use—carbon gain constraints lead to contrasting strategies of more intensive maximal use or more conservative maximum use efficiency (Rodriguez-Iturbe *et al.*, 2001a; Porporato *et al.*, 2004; Caylor *et al.*, 2009; Guswa, 2010). These trade-offs are consistent with common plant strategies (Grime, 2001). Other extensions have looked towards biophysical relationships between water-use efficiency and water stress and evaluated trade-offs as a multiple constraint problem (Caylor *et al.*, 2009). In these examples, reference is ultimately made to plant organismal fitness as a justification for optimization. Several alternative extensions of Eagleson's early hypotheses have successfully used thermodynamic justifications of entropy maximization (Kleidon and Schymanski, 2008; Kleidon, 2010). Other alternatives suggest that the rate of flow between distinct units is itself a cause of optimization (Bejan and Lorente, 2006, 2010). While a large degree of care is needed when assuming optimization, at present, several approaches have been developed where biological and physical objective functions have a mechanistic justification.

Predictability and modelling

While CAS can be understood, they pose several challenges for predictability. For many CAS, the future system state may be only loosely connected to current trajectories. Challenges are posed within individual state regimes, shifts between regimes, and potential for novelty through adaptation. Predicting even at short timescales when catastrophic changes between system regimes occur can be challenging (Carpenter *et al.*, 2008; Brock and Carpenter, 2010; Hastings and Wysham, 2010). An improved understanding of what can be predicted would help direct immediate research and move research towards a path of predicting what is possible (Sivapalan, 2009).

Predictability is complicated by the capacity for adaptation. Adaptive processes in CAS can lead to novel future processes and system configurations. Adaptation generates this novelty by adjusting parameters of processes, adjusting connections between components, and creating new processes and connections. WLES have many pathways for adaptation at multiple temporal and spatial scales (Figure 5). The means by which adaptation occurs can lead to enhanced resilience or resistance or lead to rapid shifts in system states. Even in the canonical examples, adaptation can rapidly change the rules of interactions that can be understood although poorly predicted if even at very short time horizons (Arthur, 1999).

A consequence of complexity suggests that predicting properties of system variability may be more successful than predicting state values. This predictive property is based on the dependence and internal propagation of disturbance events. One approach, self-organized criticality, suggests that CAS do not adjust mean properties but, rather, distributions of variances (Bak *et al.*, 1988; Kauffman, 1993; Bak, 1996; Turcotte and Rundle, 2002). The

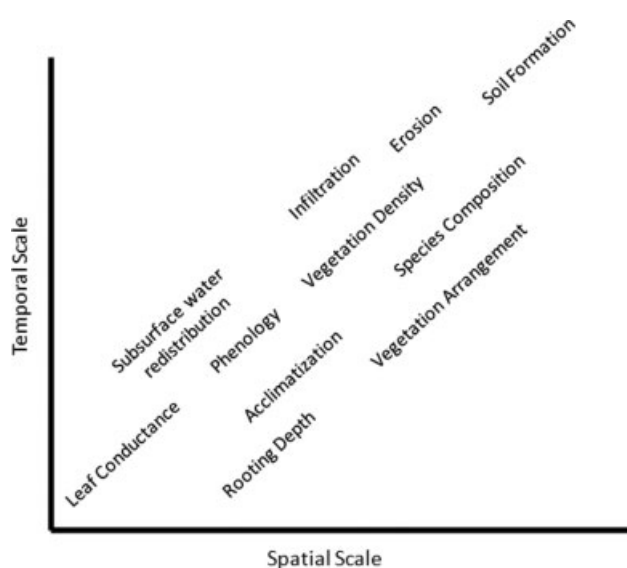


Figure 5. Stommel diagram of possible adaptation mechanisms loosely arranged across a broad range of temporal and spatial scales. At the finest scales, variation in leaf conductance can occur for an individual leaf within an hour. At broadest scales, soil formation can span regions and millennia.

theory predicts that in CAS the magnitude of individual dissipative events are more closely related to system self-organization than environmental variability. Large events are rare whereas small events are common; even in response to similar drivers, and although predictions of individual events is challenging, the frequency of all events is predicted by the scaling relationship between event frequency and size. Several ecohydrological examples evaluating variance distributions have been used to better understand flow paths (Rodríguez-Iturbe *et al.*, 1992; Stolum, 1996; Kirchner *et al.*, 2000) and vegetation structure (Kefi *et al.*, 2007; Scanlon *et al.*, 2007). Many of these variance distribution processes have specifically been used to examine systems that are continually adapting, such as evolutionary processes (Kauffman, 1993).

In overcoming the challenges with predictability, improved models and approaches to modelling will likely be necessary. Models that emphasize the coupling between environmental and system variability will allow better descriptions of system functioning in response to the environment. Several statistical approaches have been used successfully to identify such coherence in spatial and temporal dimensions between environmental and system variability including wavelet analysis (Keitt and Urban, 2005; Vargas *et al.*, 2010) and related spectral and power analyses (Keitt, 2000; Yu, 2006). Jointly applying these and other statistical approaches to mechanistic models that resolve fine scale temporal resolution would facilitate linking systems theory with new high-resolution data sets (Ruddell and Kumar, 2009). Such joint analyses would help change the direction of modelling dynamics from predicting mean system states to better tracking changes in the state. Recently, theory and data for coupling detailed physiological models with whole-ecosystem measurements at half-hourly scales have shown great success (Desai *et al.*, 2007; Jenerette *et al.*, 2009; Medvigy *et al.*, 2009). Expanding on this foundation by describing potentials for regime changes will be necessary for identifying systems that are at risk to such changes and the resulting consequences over decadal and longer timescales.

IMPLICATIONS AND FUTURE DIRECTIONS

Applications of similarity and hierarchical partitioning approaches to better understand WLES are challenging. Throughout, we have echoed a general suggestion (Lawton, 1999) that spatial scaling patterns provide opportunities for improved pattern-process couplings of WLES. Because of often-unique local combinations of environmental variables and intrinsic self-organization, which is in part a response to this variability, place-based science approaches are likely to provide opportunities to identify general mechanisms once location-specific variables are understood—a resolution of Newtonian and Darwinian scientific traditions. An approach recognizing the system-level organization processes complements and extends existing detailed process-level information and

can often suggest new directions for improved understanding of process. From a combined process-system science a more mechanistically grounded understanding of individual processes needs to be embedded in a systems approach to improve capacity for prediction, with particular emphasis on regime change dynamics.

Knowledge of ecohydrological system-level properties frequently suggests new avenues for improved process-based understanding of direct mechanistic controls. Celia and Guswa (2002) suggest that most, if not all, hysteresis in hydrologic systems comes from an incomplete description of the true functional dependence. These ideas hark to early cybernetic definitions of system dynamics and the necessity of single-valued transformations (Ashby, 1956). Identifying a hysteresis can suggest opportunities to better understand mechanistic relationships in the context of systems-level organization. For example, if soil moisture is reported only as an average over the soil column, then transpiration as a function of soil moisture will appear hysteretic; at the point scale in a soil, capillary pressure may be a function of not only average soil saturation but also the geometric arrangement of interfaces and voids. This is similar to the hysteresis commonly found between temperature and respiration—the hysteresis can result from changes in available substrate from daily (recent photosynthate) to seasonal (litter from senescence) timescales (Davidson *et al.*, 2006; Riveros-Iregui *et al.*, 2007; Vargas *et al.*, 2010) or from physical processes of heat and CO₂ transport alone (Phillips *et al.*, 2010).

A CAS approach should lead to a unified, mechanistic understanding of how changes in vegetation affect ecohydrological functioning. The phenomena of woody plant encroachment (WPE) (Huxman *et al.*, 2005; Knapp *et al.*, 2008) and widespread vegetation die-off (McDowell *et al.*, 2008; Breshears *et al.*, 2009b; Allen *et al.*, 2010) provide two examples in changes to the proportion of woody plant coverage that could illustrate general WLES system-level processes. Both of these changes cause large-scale reorganization of the ecohydrological system; however, their consequences for long-term sustainability of the system prior to the change may differ. WPE is a regime shift in the dominant organisms and resulting scale of variability associated with changing from grasses to trees. WPE is often described as a conversion between alternate stable states, and return to prior grassy states may be difficult. Predicting ecohydrological responses to WPE has been challenging. Expansion of woody plants commonly leads to reduced groundwater recharge (Huxman *et al.*, 2005); but, in some cases, woody expansion has been associated with improved recharge (Wilcox and Huang, 2010). In contrast, widespread mortality is a punctuated event across the entire system resulting in an immediate change in the dominant living vegetation. In contrast to WPE, a disturbance such as die-off may not fundamentally alter the system and allow re-colonization and succession to return the system to the prior state with little intervention. Immediately following the mortality event, however, the

system may be poised to enter alternate system attractors. Together, these two examples show how large-scale changes in woody cover can cause and result in substantial changes to system structure and self-organizational trajectories. At the same time such systems-level analyses can also lead to specific process level predictions suitable for empirical evaluation describing the mechanisms associated with both changes.

Improved understanding of WLES will be needed to better forecast potential terrestrial feedbacks to earth system dynamics. With limited buffering and predominant resource tracking, WLES may be more sensitive to environmental variability than more humid environments, as evidenced by recent observations of large-scale vegetation mortality associated with unusually warm droughts in drylands (Breshears *et al.*, 2005; Allen *et al.*, 2010). Such transitions may lead to smaller-scale shifts in the composition of subsequent species in these altered environments or larger-scale changes in the terrestrial energy balance (Rotenberg and Yakir, 2010) and rapid emissions of greenhouse gases as large stores of organic material are released with climate change induced drying (Reichstein *et al.*, 2002; Ciais *et al.*, 2005; Reichstein *et al.*, 2007). Many projections of future climates suggest that global warming will be accompanied by larger rates of evaporation and more variable precipitation regimes (Douville *et al.*, 2002; Min *et al.*, 2011). These combined changes to the water balance will likely lead to an expansion of WLES both spatially, as the area of mean water deficit increases, and temporally, as prolonged droughts place usually wet areas into an expanding window of water deficit. How coupled climate and vegetation changes alter available soil, surface and groundwater supplies, and overall biogeochemistry will reflect how self-organizational ecohydrological processes differentially partition precipitation and overall net metabolic functioning.

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