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A conceptual framework for understanding semi-arid land degradation: ecohydrological interactions across multiple-space and time scales

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1   **A conceptual framework for understanding semi-arid land**

2   **degradation: ecohydrological interactions across multiple-**

3   **space and time scales**

4

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11

12   **Short title:**

13   **A conceptual framework for understanding semi-arid land-degradation**

14

15   **ABSTRACT**

16   Land degradation is a problem prolific across semi-arid areas world-wide. Despite

17   being a complex process including both biotic and abiotic elements, previous attempts

18   to understand ecosystem dynamics have largely been carried out within the disparate

19   disciplines of ecology and hydrology which has led to significant limitations. Here, an

20   ecohydrological framework is outlined, to provide a new direction for the study of

21   land degradation in semi-arid ecosystems. Unlike other frameworks that draw upon

22   hierarchy theory to provide a broad, non-explicit conceptual framework, this new

23   framework is based upon the explicit linkage of processes operating over the

24   continuum of temporal and spatial scales by perceiving the ecosystem as a series of

25   structural and functional connections, within which interactions between biotic and

26   abiotic components of the landscape occur. It is hypothesised that semi-arid land

27   degradation conforms to a cusp-catastrophe model, in which the two controlling

28   variables are abiotic structural connectivity and abiotic functional connectivity, which

29   implicitly account for ecosystem resilience, and biotic structural and function

30   connectivity. It is suggested therefore that future research must (1) evaluate how

31   abiotic and biotic function (i.e. water, sediment and nutrient loss/redistribution) vary

32   over grass-shrub transitions and (2) quantify the biotic/abiotic structure over grass-

1 shrub transitions, to (3) determine the interactions between ecosystem structure and

2 function, and interactions/feedbacks between biotic and abiotic components of the

3 ecosystem.

4

5 **KEY WORDS**

6 Ecohydrology, vegetation transition, structure, function, biotic, abiotic, connectivity,

7 cusp catastrophe

8

9 **Introduction**

10 Semi-arid areas occupy approximately 17% of the global land mass (UNEP 1992). A

11 major form of land degradation in different semi-arid areas is the invasion of

12 grasslands by shrubs, for example, in the USA (Brown *et al.*, 1997; Van Auken,

13 2000), Australia (Krull *et al.*, 2005), Patagonia (Aguiar *et al.*, 1996) and China

14 (Cheng *et al.*, 2007). The degradation of grasslands typically affects herbaceous

15 productivity, and therefore the sustainability of pastoral, subsistence and commercial

16 livestock grazing (Fisher, 1950). In addition, invasion by shrub species induces a

17 change in surface processes, notably increased runoff and erosion (Abrahams *et al.*,

18 1995; Parsons *et al.*, 1996; Wainwright *et al.*, 2000) and a change in the spatial

19 distribution of soil properties that affect ecological and hydrological processes

20 (Müller *et al.*, in press; Schlesinger *et al.*, 1996). Biophysical and biogeochemical

21 changes that occur during the invasion of grasslands by shrubs may affect land

22 surface-atmospheric interactions, thus potentially affecting ecosystems world-wide

23 due to global biogeochemical feedbacks (Peterjohn and Schlesinger, 1990;

24 Schlesinger *et al.*, 1990). Given the consequences of grassland degradation at local,

25 regional and global scales, management strategies need to be developed for

26 rangelands to enable their sustainable use in order to prevent further grassland to

27 shrubland transitions, to reverse transitions where possible, and to provide policy

28 makers with relevant information about the ecological and hydrological implications

29 of land-management decisions that may accelerate grass to shrub transition (Wilcox

30 and Thurow, 2006).

31 It is widely acknowledged that grassland to shrubland transitions display non-

32 linear, threshold dynamics, which means that restoration of degraded landscapes is

33 unlikely to be feasible without substantial intervention and economic input (Friedel,

34 1991; Pardini *et al.*, 2003). Vegetation proxy data from the northern Chihuahuan

desert, USA, indicates that during the Holocene there were cycles of grassland to shrubland transitions that were proceeded by shrub-grass transitions (see review in Wainwright, 2005). Furthermore, other proxy data show recurrent droughts with a 100-130 year periodicity (Clark *et al.*, 2002). Thus, it is evident that shrubland to grassland transitions are possible under certain conditions; however, understanding of semi-arid degradation remains limited, particularly given the potential for grassland degradation to exhibit non-linear, threshold dynamics which hinders our ability to interpret and manage these ecosystems.

It is being increasingly recognised that to improve the present-day understanding of land-surface processes in semi-arid areas, an interdisciplinary approach is required, that transcends the boundaries between ecology and hydrology (for example Müller *et al.*, in press; Schlesinger and Pilmanis, 1998), in the hybrid discipline of *ecohydrology* (Kundzewicz, 2002; Newman *et al.*, 2006; Porporato and Rodriguez-Iturbe, 2002; Wainwright *et al.*, 1999; Wilcox and Newman, 2005). Early definitions of ecohydrology, for example, Rodriguez-Iturbe (2000), who defines ecohydrology as "the science which seeks to describe the hydrological mechanisms that underlie ecologic pattern and processes", focussed primarily on the hydrological influences upon ecology and little on the ecological influences on hydrology. Newman *et al.* (2006) define ecohydrology as being 'a hybrid discipline which seeks to elucidate how hydrological processes influence the distribution, structure, function and dynamics of biological communities and how feedbacks from biological communities affect the water cycle'. Although still somewhat hydrologically biased, the definition of ecohydrology of Newman *et al*. (2006) incorporates to a greater extent than most, the ecological feedbacks that influence hydrology. The increasing recognition of the importance of ecohydrological considerations in understanding semi-arid ecosystem dynamics has enforced the need for future research to consider the two-way interactions between and interdependence of ecological and hydrological processes.

The aim of this paper is to develop a framework to further understanding of semi-arid land degradation that explicitly considers the interactions between ecological (biotic) and hydrological (abiotic) processes, over the array of time/space scales over which these processes operate. In this paper, specific emphasis is placed on understanding the processes and dynamics of grassland degradation in the south-west USA, although broader ecohydrological issues that are globally relevant are also

addressed. This paper is split into four key sections. The first section outlines the basis for a new ecohydrological framework. The second section outlines the proposed ecohydrological framework. The third section outlines key features of semi-arid land-degradation, leading onto the identification of future research that needs to be carried out in order to fulfil the outlined ecohydrological framework. The fourth section presents the hypothesised dynamics of semi-arid land-degradation that explicitly takes into consideration the features outlined in the ecohydrological framework

Basis of an ecohydrological framework for understanding semi-arid land degradation

Semi-arid ecohydrology has largely focussed on the vertical interactions between the soil-plant-atmosphere interface, in particular, on soil moisture and plants (Caylor *et al.*, 2006; Porporato *et al.*, 2002; Porporato and Rodriguez-Iturbe, 2002; Rodriguez-Iturbe, 2000; Rodriguez-Iturbe *et al.*, 1999) since soil moisture is perceived to be at the heart of the hydrological cycle and plants are the main component of the terrestrial ecosystem (Porporato and Rodriguez-Iturbe, 2002). There is a common perception that plant-available soil moisture can be determined by sparse measurements of soil-moisture. However, this approach disregards the effects of other hydrological processes, namely runoff and runon infiltration in determining the spatial patterns and amount of available soil moisture. While soil moisture is a key ecohydrological variable, because it forms a crucial link between hydrological and biogeochemical processes (Rodriguez-Iturbe, 2000), consideration of soil moisture alone is insufficient to address the array of ecohydrological interactions that govern semi-arid vegetation dynamics (Huenneke and Schlesinger, 2004). However, even in more recent literature, such as D'Odorico and Porporato's edited book, *Dryland Ecohydrology* (2006), there is still insufficient recognition of the rôle of aspects of semi-arid hydrology other than soil moisture, in particular, surface runoff and its rôle in redistributing resources through the landscape is almost entirely neglected.

In semi-arid ecosystems, it is already well-established that hydrology exerts a profound influence over other abiotic components of the landscape, primarily erosion (Wainwright *et al.*, 2000), and the loss or redistribution of key plant-limiting nutrients such as nitrogen (Parsons *et al.*, 2003; Schlesinger *et al.*, 1999; Schlesinger *et al.*, 2000). It is therefore argued that semi-arid ecohydrology warrants consideration of ecological processes and the suite of hydrology-driven abiotic processes over space

1	and through time. The realisation that ecohydrology should consider biotic and abiotic
2	interactions through space and time is not new. For instance, Caylor *et al.* (2006:1)
3	stated that "the biotic pattern of vegetation serves to redistribute key abiotic resources
4	such as energy, water and nutrients in important ways that are critical to the dynamics
5	of the community through space and time". Thus, there has been recognition of the
6	importance of biotic/abiotic interactions on shaping ecosystem response, but in
7	practice, there has been little attempt to explore these interactions which are thought
8	to govern semi-arid vegetation dynamics. Newman *et al.* (2006) in their '*Scientific*
9	*vision*' of ecohydrology in water-limited systems, identified crosscutting
10	ecohydrological challenges that require further study: issues of spatial complexity,
11	scaling and thresholds, and feedbacks and interactions. The ecohydrological
12	challenges outlined by Newman *et al.* (2006) have already been addressed in various
13	guises within the disparate ecological and hydrological disciplines, broadly in terms
14	of hierarchy theory (for example Bergkamp, 1998; Cammeraat, 2002; Peters *et al.*,
15	2006; Peters and Havstad, 2006), non-linear dynamics within the catastrophe-theory
16	framework (for example Laycock, 1991; Lockwood and Lockwood, 1993; Scheffer *et*
17	*al.*, 2001; Scheffer and Carpenter, 2003), and varied interpretations of connectivity
18	within both ecology (for example Turner *et al.*, 1993; With *et al.*, 1997) and
19	hydrology (for example Bracken and Croke, 2007; Müller *et al.*, 2007; Western *et al.*,
20	2001).
21	The following discussion explores how previous studies seeking to understand
22	semi-arid vegetation transitions have drawn upon hierarchy theory, hydrological and
23	ecological connectivity and non-linear dynamics, and develops them within an
24	ecohydrological context, to form the basis for an ecohydrological framework to
25	understand semi-arid land degradation.
26	

27 ***Hierarchy theory***

28	Hierarchy theory is a theory of scaled systems (O'Neill *et al.*, 1989) which has been
29	widely adopted in ecology as a tool for transcending issues of scale, and has received
30	some recognition in geomorphology (for example Bergkamp, 1998; Cammeraat,
31	2002). With reference to hierarchy theory, O'Neill *et al.* (1989) proposed that spatial
32	and temporal scales are the natural consequence of nonlinear biotic and abiotic
33	interactions in complex ecological systems. Recent applications of hierarchy theory in
34	conceptual frameworks for studying grassland degradation (Peters *et al.*, 2006) have

focussed primarily on biotic characteristics of grassland to shrubland transitions over spatial scales, without explicit incorporation of the rôle of abiotic structure and function on ecosystem processes. Peters and Havstad (2006) recognised the rôle of resource distribution and feedbacks in their hierarchical conceptual framework for semi-arid systems. However, their framework retained a sufficiently high level of ambiguity so that it is not clear how it can be utilised and employed, to provide a new insight into the way in which we can study semi-arid ecosystems to overcome the existing limitations of our understanding of transition dynamics.

A limitation of hierarchy theory as the basis for understanding vegetation transitions is its consideration of discrete spatial and temporal entities that form spatial and temporal hierarchies which describe overall ecosystem dynamics. While hierarchy theory provides a methodical way of conceptualising the differences in patterns and processes at each level of the spatial and temporal hierarchy, it does not explicitly provide a means of transcending scales since it does not account for the spatial and temporal connectivity between scales. The spatial and temporal connectivity between scales is particularly important in semi-arid ecosystems (see Müller *et al.*, 2007; Peters and Havstad, 2006). Thus, since hierarchy theory cannot account for the spatial and temporal connectivity between scales, other approaches are needed in which connectivity is explicitly accounted for.

Hydrological and ecological connectivity
Connectivity among spatial units is an important determinant of system dynamics (Peters and Havstad, 2006). Within an ecological context, landscape connectivity refers to the degree to which the landscape facilitates or impedes (animal or propagule) movement among resource patches (Taylor *et al.*, 1993). In this context, movement is a key component of landscape connectivity (Turner *et al.*, 1993). Turner's (1993) interpretation of landscape connectivity is ultimately a process-orientated one, since it depends upon how processes link elements within the landscape (With and King, 1997). Landscape connectivity may be better described in terms of *structural connectivity*, that is the degree to which landscape elements are contiguous or physically linked to one another (Tischendorf and Fahrig, 2000; With *et al.*, 1997), and *functional connectivity*, the linkage of habitat site by a process (Belisle, 2005; Kimberly *et al.*, 1997; Uezu *et al.*, 2005; With *et al.*, 1997; With and King, 1997).

1   These structural and functional notions of connectivity are implicit in the

2 hydrological sciences, although they have not been explicitly referred to as such.

3 Within hydrology, the term hydrological connectivity has been used in two different

4 contexts, which are akin to use of the terms *structural* and *functional connectivity*

5 within ecology. Bracken and Croke (2007) conceptualised hydrological connectivity

6 as being static and dynamic. Their static conceptualisation of hydrological

7 connectivity refers to spatial patterns such as hydrological response units, while their

8 dynamic representation of hydrological connectivity refers to longer-term landscape

9 development and short-term variations in antecedent conditions and rainfall inputs to

10 the system that result in non-linearities in the hillslope and catchment response to

11 rainfall (Bracken and Croke, 2007). Hydrological connectivity has been used to refer

12 to the structure and heterogeneity of hydrological variables, such as the presence of

13 soils with low infiltration capacities, and high soil-moisture content which might

14 generate Hortonian overland flow, which is akin to the static representation of

15 hydrological connectivity of Bracken and Croke (2007). The importance of the

16 connectivity of patterns in affecting the hydrological response is being increasingly

17 recognised (Grayson *et al.*, 2002; Müller *et al.*, 2007; Western *et al.*, 2001: Bracken

18 and Croke, 2007), since heterogeneities, even when present in relatively small

19 proportions, often have drastic impacts on the overall behaviour of a system,

20 depending upon their spatial distribution (Cappelaere *et al.*, 2000). The overall

21 hydrological behaviour of a system, in terms of its hydrological connectivity (used in

22 this sense to describe how well runoff-producing areas interconnect to yield

23 continuous flows, and thus cause erosion and redistribute sediment and nutrients) can

24 also be considered in terms of functional connectivity. As with the ecological

25 interpretation of structural and functional connectivity, in hydrology, it is the

26 connectivity of structural attributes such as soil moisture that affect the functional

27 connectivity of the landscape in terms of its ability to yield continuous flows (Müller

28 *et al.*, 2007; Western *et al.*, 1998). Thus, it is the interaction between structural and

29 functional connectivity that results in the dynamic connectivity referred to in Bracken

30 and Croke (2007).

31

32 One key difference that exists between functional connectivity in relation to structural

33 connectivity in ecology and hydrology is the directional element of the connectivity.

34 Hydrological connectivity is broadly defined by how abiotic components of the

ecosystem which affect hydrological function, such as the spatial configuration of soil characteristics at finer scales (Müller *et al.*, 2007) and the configuration of hydrological response units (such as those defined by land-use) at the broader catchment scale (e.g. Kirkby *et al*. 2002), are connected along a topographic gradient. Ecological connectivity by contrast is not forced to be directional like hydrological connectivity, although certain components of ecological connectivity may be subject to abiotically imposed directionality, for instance seed dispersal by wind and water or biotically imposed directionality by animals. Furthermore, structural factors influenced by hydrology will impose some directional influence over ecological connectivity.

Ecological functional connectivity refers principally to the movement of biota (animals and propagules) around the ecosystem, and hydrological functional connectivity refers principally to the flow of water, sediment and nutrients over the landscape. Thus, ecological functional connectivity and hydrological functional connectivity have a common element, *movement*, which is in both cases determined by the structural connectivity of the ecosystem. The properties that determine the structural connectivity of the ecosystem within hydrology and ecology are broadly speaking the same, *biotic and abiotic components of the ecosystem*. Herein lies the difficulty in interpreting ecosystem dynamics in terms of disparate hydrological processes and ecological processes: biotic and abiotic structural components of the ecosystem cannot be disentangled, since they modify, and are modified by each other. The rôle of vegetation structure on modifying the hydrological response (in terms of its modification of abiotic properties through biotic-biotic feedbacks) is widely recognised (Abrahams *et al.*, 1995; Bochet *et al.*, 2000; Boer and Puigdefabregas, 2005; Pardini *et al.*, 2003; Parsons *et al.*, 1996; Puigdefabregas, 2005; Wainwright *et al.*, 2000) since vegetated and bare ground patches form interconnected units within the larger patch mosaic, which determines if, and how patches interact and strongly affects the downslope routing of water, sediments and nutrients (Imeson and Prinsen, 2004). Furthermore, it is not only the extent to which vegetation patches prevail on a hillslope that exert an influence on runoff and erosion (Boer and Puigdefabregas, 2005), but also the spatial organisation of bare and vegetated surfaces, such that it is the size, length and connectivity of bare areas that determines the processes in operation at the hillslope scale (Cammeraat, 2004). Implicit in the recognition that vegetation exerts a major influence over functional hydrological connectivity, are the

1 biotic-abiotic feedbacks that modify abiotic structural components of the landscape

2 that ultimately determine functional connectivity.

3 There are very clear, but previously unstated links between ecological and

4 hydrological interpretation and understanding of connectivity, since it is impossible to

5 disentangle biotic and abiotic interactions, as will be discussed further below. Thus,

6 the structural connectivity of the landscape determines the propensity of the landscape

7 to possess biotic and abiotic functional connectivity (but the degree of functional

8 connectivity that arises from structural connectivity will be species/vector specific),

9 which in turn modifies biotic and abiotic structural connectivity.

10

11 *Non-linear dynamics*

12 It has long been proposed that the dynamics of semi-arid grassland to shrubland

13 transitions conform to the threshold concept whereby perturbations cause a system to

14 cross a threshold and move toward another state (Laycock, 1991; Westoby *et al.*,

15 1989). Laycock (1991) advanced upon the transitional successional notions of

16 rangeland dynamics, by proposing the state-and-threshold model of grassland

17 degradation in which rangeland dynamics exhibit sudden, discontinuous changes, a

18 theory that was the precursor to subsequent non-equilibrium, catastrophic

19 conceptualisations of rangeland dynamics (for example Lockwood and Lockwood,

20 1993; Scheffer and Carpenter, 2003). Lockwood and Lockwood (1993) recognised

21 that in some cases disturbed or recovering rangelands move through a gradual,

22 continuous series of successional changes, which has no place in Laycock's state-and

23 threshold model, and therefore identified the need for a model of rangeland dynamics

24 that allows for both successional and state-and-threshold dynamics.

25 The concept of threshold is directly related to the concepts of catastrophe

26 theory, because in both cases abrupt changes occur across a defined boundary (Graf,

27 1988). Catastrophe theory, originally outlined by Thom (1975) has been drawn upon

28 to provide a qualitative description of the nature of system change, in both ecology

29 (Loehle, 1985; Ouimet and Legendre, 1988; Rietkerk *et al.*, 1996) and

30 geomorphology (Graf, 1983; 1988; Thornes, 1980) in systems that possess a tendency

31 to exhibit catastrophic behaviour (i.e semi-arid environments).

32 Consideration of grass to shrub transitions within the framework of the cusp

33 catastrophe model is relevant, because the cusp catastrophe model provides a clear,

34 conceptual outline for both the continuous (successional) and discontinuous (non-

1   linear) nature of grass-shrub transitions. Conceptualising semi-arid vegetation

2   transition dynamics as a cusp-catastrophe phenomenon gives rise to the recognition

3   that even very small incremental changes in conditions can trigger a large shift in

4   ecosystem state if a critical threshold, known as a catastrophic bifurcation is passed

5   (Scheffer and Carpenter, 2003). Catastrophic bifurcation is akin to the idea of

6   'criticality', which comprises a drastic shift in ecosystem state following only slight

7   changes in an underlying condition (Pascual and Guichard, 2005). One of the most

8   important ecosystem features, in consideration of catastrophic events is resilience,

9   which refers to the capacity of a system to absorb disturbance and reorganise while

10   undergoing change so as to retain essentially the same function, structure, identity and

11   feedbacks (Walker *et al.*, 2004). Hence, once the resilience of semi-arid grasslands is

12   exceeded, a catastrophic bifurcation is passed and the ecosystem will jump to a shrub-

13   dominated state.

14   There are five properties that indicate catastrophic cusp behaviour which have

15   been identified in grassland to shrubland transitions (outlined in Gilmore, 1981;

16   Lockwood and Lockwood, 1993; Rietkerk *et al.*, 1996) (Figure 1). Grass-shrub

17   transitions exhibit (1) *bimodality*, which is when an ecosystem has two distinct

18   vegetation states (represented by the two surfaces of the cusp), i.e. grassland and

19   shrubland. A region of (2) *inaccessibility* separates the grassland and shrubland states,

20   which is the folded part of the cusp that represents a region of inaccessibility;

21   therefore the system cannot be stable within that region, and so the ecosystem is

22   unlikely to persist in this state for very long, because of its propensity to make a (3)

23   *sudden jump* to an alternative state, seen when a trajectory reaches the edge of the

24   cusp (the area of inaccessibility). Thus, the ecosystem will exhibit (4) *divergence*,

25   which refers to relatively small changes in control variables that result in markedly

26   different behaviours of the systems. The ecosystem will exhibit (5) *hysteresis*, which

27   means that the trajectory of change in ecosystem structure and function associated

28   with a jump in one direction (i.e. grass-shrub) is different from the trajectory resulting

29   in a jump in the opposite direction (shrub-grass).

30   Laycock (1991) recognised the need to identify and understand the factors

31   which force a stable community across a threshold, thinking which is in line with the

32   more recent work of Scheffer *et al.* (2001) which suggests that the prevention of

33   significant perturbations is a major goal of ecosystem management. Therefore, the

34   majority of research into grass-shrub transitions has focussed solely on the

1 identification of thresholds, and not on developing understanding of the processes that
2 cause a threshold to be crossed. However, there exists a fundamental problem with
3 research being directed solely at the identification of thresholds: environmental
4 thresholds are not necessarily constant, since the position of a threshold along a
5 determining variable may change (Walker and Meyers, 2004), as would be predicted
6 by the cusp-catastrophe model. When there are several variables determining
7 ecosystem dynamics, it becomes evident that determining the position of the threshold
8 becomes somewhat more complex particularly when the resilience of an ecosystem is
9 considered (Walker *et al.*, 2004). Ecosystem resilience is a dynamic property, which
10 means that the position of a threshold may also be dynamic. Therefore, not only might
11 the position of a threshold change depending upon the resilience of the ecosystem, so
12 too might the depth of the basin of attraction, making it easier or harder to approach
13 the threshold (Walker and Meyers, 2004). Efforts to reduce the risk of grass-shrub
14 transitions should therefore address the gradual changes that affect resilience rather
15 than merely control disturbance (Scheffer *et al.*, 2001). Given the emphasis of
16 dynamism, in terms of resilience and the position of thresholds, what is needed to
17 understand and manage vegetation transitions is a more comprehensive mechanistic
18 knowledge of ecohydrological dynamics. Understanding ecohydrological dynamics
19 will enable changes in abiotic and biotic feedbacks, with reference to properties such
20 as resilience and the position of thresholds, to be determined under different external
21 environmental conditions and internal ecosystem dynamics.

22 While it is widely acknowledged that grassland to shrubland transitions exhibit
23 a catastrophic response, the changing processes and biotic/abiotic interactions
24 operating over space/time that underpin the transition dynamics remain largely
25 unknown. Understanding grass-shrub transitions as cusp-catastrophe phenomena
26 reinforces the requirement to understand ecohydrological interactions, since different
27 ecosystem states or dynamic regimes are enforced by positive feedbacks between
28 plants and their environment that ultimately creates high ecosystem resilience.
29 Didham and Watts (2005) proposed that systems with inherently strong abiotic
30 regimes, such as semi-arid grasslands and shrublands, may (1) be made prone to enter
31 resilient alternative states (2) switch more readily to an alternative stable state
32 following a lower level of perturbation or (3) be more difficult to restore than systems
33 that are weakly structured by environmental adversity. Therefore, given the non-
34 linear, threshold dynamics of grassland degradation, a full consideration of how

1 ecohydrological interactions vary over the course of shrubland invasion is required,
2 and perhaps even more importantly, how ecohydrological interactions vary as
3 grassland resilience is compromised.

4 Hierarchy theory presents a clear way of considering the suite of processes
5 operating over space and through time, and has been used previously as the basis for
6 several frameworks studying semi-arid ecosystem dynamics. While hierarchy theory
7 provides a clear conceptual outline of the scale-dependent nature of ecosystem
8 properties, in practical terms it does not lend itself to the explicit consideration of
9 abiotic and biotic interactions over a continuum of spatial and temporal scales.

10 The discussion of connectivity within ecology and hydrology has revealed that
11 although notions of connectivity have arisen relatively independently in these
12 disparate disciplines, both recognise two features of connectivity: structural and
13 functional connectivity. Consideration of ecosystem processes in terms of structural
14 and functional connectivity between abiotic and biotic components of the ecosystem,
15 over a continuum of space/time scales provides a direct means of explicitly
16 determining ecosystem dynamics in terms of both ecology and hydrology.

17 The current understanding of semi-arid land degradation may be developed by
18 exploring degradation within the cusp-catastrophe framework, but this requires that
19 biotic and abiotic elements of the ecosystem be understood, in terms of both their
20 structure and function, and the connectivity between these elements, in spatial and
21 temporal terms.

22 **The ecohydrological framework for understanding semi-arid land**
23 **degradation**

24 The proposed ecohydrological framework is based upon (1) interactions between
25 abiotic and biotic ecosystem components in terms of their structure and function, (2)
26 the connectivity of structure and function through time and space and (3) the
27 evolution of ecosystem structure and function over space/time scales as these are the
28 factors that have been identified as being paramount in understanding semi-arid land
29 degradation. An outline of the framework is presented in Figure 2.

30

31 *Interactions between ecosystem structure and function*

32 Ecosystem structure exerts a profound influence over ecosystem function, which in
33 turn determines ecosystem structure. Thus, it is the combined influence of biotic and

1   abiotic components of ecosystem structure that determine biotic and abiotic function

2   which in turn redefine biotic and abiotic structure. Therefore, it is necessary that the

3   ecohydrological framework considers structural connectivity in relation to functional

4   connectivity.

5

6   *Connectivity of structure and function through time and space and its evolution*

7   Ecosystem structure, and thus biotic and abiotic connectivity, evolves through time

8   and space, determined by functional processes operating over a continuum of

9   timescales. By drawing upon the notion of connectivity to transcend spatial and

10   temporal scales, thereby avoiding transposition of scale errors (O'Neill, 1988), there is

11   a recognition that structure and function at one scale is influenced (non-linearly) by

12   structure and function at other scales; thus a mechanistic interpretation of the

13   behaviour of a system can only be derived by assessment of the extent to which

14   ecosystem structure and function are connected through time and space.

15

16   *Adopting the outlined framework to understand semi-arid degradation*

17   The ecohydrological framework (Figure 2) depicts the key biotic/abiotic and

18   structural/functional interactions over space and time that need to be revealed if we

19   are to understand semi-arid land degradation. At present, the ecohydrological

20   understanding of semi-arid ecosystems remains very limited. Because previous field-

21   based experiments to understand semi-arid ecosystems have not been carried out

22   within an ecohydrological context, their experimental designs are largely reflective of

23   existing ecological or hydrological research structures which are not necessarily

24   conducive to studying biotic and abiotic *interactions*. For instance, most of the

25   current hydrological understanding in semi-arid areas is derived from small-scale plot

26   studies (for example Brazier *et al.*, 2007; Parsons *et al.*, 2006), understanding from

27   which needs to be coupled with other approaches so that consistent understanding of

28   ecohydrological systems over the continuum of space/time scales can be achieved

29   (Wainwright *et al.*, 2000). Thus, in view of the outlined framework, further

30   experimental approaches are required to achieve the advanced level of

31   ecohydrological understanding that is required for the comprehensive study of semi-

32   arid grass-shrub transitions. The following section provides a review of what is

33   already known about land degradation, focussing on research form the south-western

34   USA, to identify the future research that needs to be carried out in order to determine

1 the interactions and feedbacks between the components outlined in the
2 ecohydrological framework.

3

4 **Overview of land degradation in the south-western USA**

5 Degradation in semi-arid areas world-wide is often exemplified by a change in type,
6 cover and spatial distribution of vegetation (Boer and Puigdefabregas, 2005;
7 Huenneke *et al.*, 2002), and the concurrent increase in runoff and soil erosion
8 (Abrahams *et al.*, 1995; Boer and Puigdefabregas, 2005; Pardini *et al.*, 2003;
9 Wainwright *et al.*, 2000; Wainwright *et al.*, 2002), which are widespread land-
10 degradation problems because of their contributions to water and soil-fertility losses
11 (Lado and Ben-Hur, 2004; Martinez-Mena *et al.*, 2001). The complex interplay of
12 landscape feedbacks between the spatial distribution of vegetation, runoff and erosion
13 also results in the spatial redistribution of soil properties, including soil-moisture and
14 nutrient content (Cross and Schlesinger, 1999; Müller *et al.*, in press), particle-size
15 characteristics and soil organic matter content. An interrelated set of conditions
16 determines the susceptibility of land to degradation, which include, but are not
17 exclusively restricted to the seasonal distribution and amount of rainfall, vegetation
18 resilience, vegetation distribution, soil characteristics and topography (Dregne, 1977).

19

20 *Drivers of land degradation*

21 In the south-western United States, the invasion of grassland by shrubs has been
22 attributed to various driving forces, including overgrazing (Buffington and Herbel,
23 1965), increasing carbon dioxide concentrations (BassiriRad *et al.*, 1997) and
24 changing precipitation amount and distribution (Brown and Archer, 1999; Gao and
25 Reynolds, 2003; Neilson, 1986), although it is likely that a combination of driving
26 forces are responsible for land degradation. These driving forces are thought to induce
27 grass to shrub transitions because of the different responses that the species exhibit to
28 changing environmental conditions, due to their differing physiological and
29 phenological characteristics and the ways in which they modify, and are modified by
30 the structure of the environment they inhabit. For example, grass species such as black
31 grama (*Bouteloua eriopoda*) have a finely divided, well developed root system,
32 mainly located in the uppermost 25 cm of soil (Campbell and Bomberger, 1934). Thus
33 black grama can be very responsive to summer moisture and can greatly increase its

1   cover in enhanced moisture conditions (Gosz and Gosz, 1996; Noy-Meir, 1973).

2   However, the potential for plant growth in the summer is affected by the length of the

3   spring drought, because the death of the root and shoot tissue reduces the number of

4   growing points capable of utilizing the summer rainfall (Gao and Reynolds, 2003). In

5   contrast, shrubs, such as creosotebush (*Larrea tridentata*), are highly drought-resistant

6   and have deep tap roots that are able to access deeper soil-moisture reserves

7   (MartinezMeza and Whitford, 1996; Whitford *et al.*, 1997), therefore, even after

8   drought conditions, shrubs are able to establish readily (Herbel and Gibbens, 1996).

9   Furthermore, with regard to reproduction, the principal spread of black grama comes

10   from the lateral extension of individual tufts, as a result of new perennial stems from

11   rooted buds on the stolons (Nelson, 1934). Therefore, as black grama patches become

12   increasingly fragmented, their potential for vegetative reproduction is reduced

13   (Campbell and Bomberger, 1934). Although black grama has the potential to

14   reproduce via seed production, where black grama patches are co-dominated with

15   creosotebush, fewer seeds are produced per plant, and seeds that are produced are of

16   reduced viability (Peters, 2002). Creosotebush however are able to reproduce

17   whenever conditions are favourable, when resources are not limited, and reproductive

18   growth occurs in response to rainfall events (Kemp, 1983; Reynolds *et al.*, 1999;

19   Rossi *et al.*, 1999), hence the reproductive potential of creosotebush reduces the

20   potential impact of habitat fragmentation relative to black grama.

21

22   *Structural and functional changes*

23   Changes in the spatial configuration of vegetation (such as the examples detailed

24   above) occur during grass-shrub transitions. There may be a reduction in the basal

25   area of plant biomass, and perhaps more importantly, a redistribution of plant biomass

26   (Huenneke *et al.*, 2002), which impacts upon, and is affected by, fundamental

27   processes, including nutrient cycling and water and sediment fluxes (McCarron and

28   Knapp, 2001; Schlesinger *et al.*, 1990). The spatial configuration of vegetation has a

29   major impact upon water, sediment and nutrient fluxes in semiarid environments,

30   particularly under smaller runoff events, because of its role in providing resistance to

31   flow, thus forming potential sinks in the landscape (Bartley *et al.*, 2006) for runoff,

32   eroded sediment and nutrients (Ludwig and Tongway, 1995; Ludwig *et al.*, 1999).

33   During extreme runoff events, it is likely that runoff-generating areas will become

34   connected due to decreased transmission losses (Parsons *et al.*, 1996) which in turn

1 will increase the capacity of the runoff to entrain and transport sediment, thus

2 reinforcing the structural connectivity of the landscape that will dictate future

3 functional responses.

4   In the south-western USA, runoff is typically generated by high-intensity

5 rainfall events during the summer monsoon months, in which the infiltration capacity

6 of the soil is exceeded, leading to the generation of infiltration-excess overland flow.

7 It is thought that vegetation cover is one of the major factors governing runoff and

8 erosion over semi-arid hillslopes (Abrahams and Parsons, 1991; Calvo-Cases *et al.*,

9 2003; Cammeraat, 2004). The vegetation cover influences the magnitude and duration

10 of flow and amount of erosion that occurs by providing root cohesion to otherwise

11 unconsolidated sediment, thereby impeding near surface disturbance, affecting soil

12 infiltration characteristics and by providing resistance to flow that generally reduces

13 flow velocity (Abrahams *et al.*, 1994; Osterkamp and Friedman, 2000).

14   Numerous field-based studies have been carried out to investigate how the

15 hydrological response and associated nutrient and sediment fluxes vary over grassland

16 and shrubland (for example Abrahams *et al.*, 1994; Abrahams *et al.*, 1995; Neave and

17 Abrahams, 2002; Schlesinger *et al.*, 1999; Schlesinger *et al.*, 2000; Wainwright *et al.*,

18 2000; Wainwright *et al.*, 2002). The general findings of these investigations reveal

19 that runoff responses are much greater over shrubland, because of inter-rill overland

20 flow and ultimately the development of concentrated flow paths or rills. The high

21 connectivity of areas of reduced infiltration in intershrub areas promotes enhanced

22 runoff generation and flow connectivity as less runon (flow from upslope) infiltration

23 occurs. Erosion on semi-arid hillslopes is controlled by an interaction of raindrop-

24 erosion processes and surface-flow processes thus, where there is greater vegetation

25 cover, there is an increase in interception of raindrops, reducing their kinetic energy,

26 and increasing hydraulic roughness due to plant stems and an increase in plant roots

27 which bind the soil reducing its erodibility (Wainwright *et al.*, 2000). Thus, the

28 reduced or altered distribution of vegetation in shrubland environments, and the

29 increased connectivity of runoff-generating areas creates favourable conditions for

30 higher flow velocities to be reached, thereby increasing the erosive energy of the flow

31 and the capacity to transport sediment and nutrients leading to a net increase in

32 erosion.

33

1 *Functional and structural connectivity*

2 While most studies suggest an increase in the flow connectivity over shrubland at

3 small scales, the extent to which flows are connected has rarely, and not yet

4 adequately been investigated at the landscape scale, which is important in terms of

5 overall ecosystem dynamics because runoff in semi-arid environments plays a key

6 rôle in redistributing and/or removing nutrients. Plot-based studies have revealed

7 concentrations of nitrogen in runoff over shrubland are lower than concentrations over

8 grassland (Schlesinger *et al.*, 1999), but because of increased flow discharges over

9 shrubland relative to grassland, shrublands experience a greater overall loss of

10 nutrients (Schlesinger *et al.*, 2000). However, the very limited amount of research that

11 has been carried out into runoff-related nutrient dynamics has been primarily

12 conducted over small plots, under simulated rainfall conditions. It has since been

13 shown that observations of nutrient fluxes in runoff from natural rainfall events are

14 also scale-dependent (Brazier *et al.*, 2007), increasing with flow discharge, but at a

15 decreasing rate as slope length increases. Therefore, research into runoff-associated

16 nutrient fluxes warrants further consideration to overcome some of these scaling

17 limitations, and artefacts that may be introduced by simulated rainfall or small (and

18 short) scales of observation of natural rainfall.

19 Previous research has established that changes in the spatial structure of

20 vegetation, runoff and erosion response of the landscape are associated with a change

21 in spatial scale of the distribution of soil properties (for example Cross and

22 Schlesinger, 1999; Müller *et al.*, in press; Schlesinger *et al.*, 1996). The difference in

23 spatial distribution and connectivity of soil properties between grassland and

24 shrubland has both biotic and abiotic implications. The redistribution of soil resources

25 affects the potential for plant establishment and growth, and changes soil properties,

26 such as a change in the hydrological conductivity which affects infiltration rates, soil

27 moisture holding capacity, and thus impacts upon the hydrological response of the

28 landscape (Müller *et al.*, 2007; in press; Western *et al.*, 1998).

29

30 *Synthesis*

31 The differences in community structure, spatial and temporal utilisation and

32 modification of resources, hydrology and erosion are indicative of the complexity and

33 variation of ecohydrological interactions that occur over grass and shrublands.

34 Research to date has focussed on how ecological and hydrological processes vary at

1 the end-member stages of degradation, which is insufficient to ascertain how
2 processes interact and vary along the trajectory of degradation. An ecohydrological
3 framework for improving the present-day understanding of vegetation transitions must
4 consider not only the spatial changes in the distribution of plant biomass, but the
5 associated changes in soil properties, and how they vary spatially and temporally. The
6 feedbacks and interactions between structural and functional components of semi-arid
7 ecosystems operate over a continuum of spatial and temporal scales, which need to be
8 considered if we are to advance our ecohydrological understanding of semi-arid
9 ecosystems. Figure 3 illustrates the key components of semi-arid ecosystems that
10 require consideration in order for the ecohydrological framework to be realised (Table
11 1).

Hypothesised dynamics of semi-arid land-degradation

13 It is already well-established that grass-shrub transitions have the propensity to
14 display non-linear threshold dynamics which are not readily reversible, although
15 grass-shrub transitions have been observed that conform more to the successional
16 paradigm, in which transitions do not display hysteresis when reversed. From the
17 ecohydrological framework, and overview of the present-day understanding of land
18 degradation, it is hypothesised that dynamics of land degradation are conceptualised
19 by a cusp-catastrophe model (Figure 4), in which the two controlling variables are
20 abiotic structural connectivity and abiotic functional connectivity, which implicitly
21 account for ecosystem resilience, and biotic structural and function connectivity.

22   The rationale of conceptualising land degradation within a cusp catastrophe
23 model is that cusp catastrophe models have the capacity to explain both successional
24 and state-and-threshold ecosystem dynamics that apply in the case of grassland
25 degradation. In this hypothetical cusp-catastrophe model, when a driver of ecosystem
26 change modifies ecosystem state, the dynamics of vegetation change will be
27 determined by the biotic and abiotic structural connectivity, and the point at which the
28 ecosystem lies along the cusp fold (determined by the history of land use and extrinsic
29 conditions at a specific location), which will in turn determine the extent to which the
30 ecosystem is functionally connected in terms of biotic and abiotic components.

31   In scenario 1, the invasion of shrubs is not associated with a major increase in
32 abiotic structural connectivity, and so the degree of habitat fragmentation remains
33 relatively low. When shrubs become more dominant along the trajectory of

1   degradation, because abiotic structural connectivity remains low, the increase in

2   functional connectivity is not as high compared to scenario 2. Therefore, the extent to

3   which resources become redistributed over the ecosystem is limited. Reversal of the

4   transition is possible without the occurrence of a catastrophic jump.

5   In scenario 2, the grassland possesses high abiotic structural connectivity, for

6   example, well-connected flow lines that facilitate high runoff generation and

7   subsequent flow of high discharges. Under such conditions grass cover will be highly

8   fragmented. The high abiotic structural connectivity will increase the propensity for

9   vectors, such as wind and water to redistribute resources over the landscape as shrubs

10   invade which will cause a catastrophic jump from the area of inaccessibility to the

11   alternative shrub-dominated plane of the cusp catastrophe. Because the trajectory of

12   degradation in scenario 2 is located on the fold of the cusp, a reversal back to

13   grassland from the shrub-dominated state will exhibit hysteretic properties, and thus

14   experience a catastrophic jump. In order to shift the ecosystem to a point at which a

15   jump back to the former grass-dominated state can occur, a greater energy input to the

16   ecosystem is required than that which caused the grass-shrub catastrophic jump, in

17   order to surpass the positive feedbacks between biotic and abiotic entities that

18   reinforce the shrub-dominated landscape.

19   Hypotheses of environmental behaviour described by the cusp-catastrophe

20   model have a tendency to go untested. Since it has been established that both biotic

21   and abiotic factors determine ecosystem response, it is thus proposed that a process-

22   based ecohydrological model to simulate grass-shrub transition dynamics accounting

23   for the interactions between ecosystem structure and function, and interactions

24   between biotic and abiotic factors, can be used to test the hypothesis. If simulations of

25   grass-shrub transitions exhibit a similar underlying structure to that hypothesised by

26   the cusp-catastrophe model, this would suggest that the hypothesis is broadly correct

27   (Jones, 1977).

28   Conclusion

29   A framework has been outlined to provide a new direction for the study of semi-arid

30   grass-shrub transitions. Unlike other frameworks that draw upon hierarchy theory to

31   provide a broad, non-explicit conceptual framework, this new framework is based

32   upon the explicit linkage of processes operating over the continuum of temporal and

33   spatial scales by perceiving the ecosystem as a series of structural and functional

1 connections, within which interactions between biotic and abiotic components of the
2 landscape occur. The perception of the ecosystem as a series of structural and
3 functional connections and as an interactive biotic-abiotic entity facilitates the
4 emergence of non-linear dynamics.

5   Existing understanding of semi-arid grass-shrub transitions is limited, due to
6 previous attempts to understand ecosystem dynamics being carried out within the
7 disparate disciplines of ecology and hydrology. The recent recognition of the
8 importance of biotic and abiotic interactions in water-limited semi-arid ecosystems
9 requires a more integrated type of ecohydrological research which seeks to unite
10 ecology and hydrology, and consider ecosystems as an interactive biotic-abiotic
11 entity. Research carried out within ecology and hydrology has independently drawn
12 upon the notion of connectivity, to explore how linkages in landscape structure affect
13 the connectivity of landscape function. Hydrological studies have already started to
14 address the role of plant distribution and feedbacks between plants and soil on
15 modifying hydrological structure and function. Ecological studies have started to
16 recognise the rôle of geomorphological processes on structuring plant-soil
17 interactions, but these have not yet been adequately addressed.

18   The development of a new ecohydrological framework has led to the
19 hypothesised dynamics of semi-arid land-degradation that explicitly take into
20 consideration the key factors outlined in the ecohydrological framework –
21 biotic/abiotic and structural/functional connectivity over space and time. In order to
22 test the hypothesis that semi-arid land degradation conforms to the outlined cusp-
23 catastrophe model, further experimental research needs to be carried out, within an
24 ecohydrological context, to address the feedbacks between structure and function and
25 abiotic and biotic components of the ecosystem over grass-shrub transitions. Future
26 research should therefore (1) evaluate how abiotic and biotic function (i.e. water,
27 sediment and nutrient loss/redistribution) vary over grass-shrub transitions and (2)
28 quantify the biotic/abiotic structure over grass-shrub transitions, to (3) determine the
29 interactions between ecosystem structure and function, and interactions/feedbacks
30 between biotic and abiotic components of the ecosystem.

31

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1   **Table 1.** Ecosystem components which are classified as structural/functional and
2   biotic/abiotic.

		Structure	Function
Biotic		Vegetation: type and distribution	Ecological response: Growth, recruitment, establishment, mortality
Abiotic		Soil resource distribution	Hydrological response: Water, nutrient and sediment fluxes/redistribution
		Topography	

3

4

5   **List of figures**