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From structure to function: Understanding shrub encroachment in drylands using hydrological and sediment connectivity

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ABSTRACT

Hydrological and sediment connectivity can help us to understand better how physical and process-based linkages govern ecogeomorphic feedbacks and identify locations where degradation is likely to be pronounced. In this study we investigate how hydrological and sediment connectivity affect ecogeomorphic feedbacks in transitional landscapes. We propose a novel approach, the *Relative Connectivity Index* (*RCI*), to quantify landscape connectivity which explicitly integrates structural measures of landscape connectivity (*SC*) with functional measures of hydrological and sediment connectivity (*FC*) that are derived from runoff and sediment-transport modelling. We use the *RCI* calculated for runoff (RCI_H) and sediment (RCI_S) to identify locations and times when functional connectivity exceeds structural connectivity thresholds – where land degradation is likely to be pronounced – and explore how these thresholds are affected by rainfall-event size and antecedent soil-moisture content. We find that there are non-linear increases in RCI_H values with an increase in shrub cover, which suggest that ecogeomorphic feedbacks become more important in modifying system structure and function during late stages of shrub encroachment. Thresholds of sediment connectivity appear to be directly related to thresholds of hydrological connectivity, although rainsplash appears to be an important mechanism in creating connected sediment transport where there is no connected runoff. High RCI_H values are most widely distributed for the largest (45 mm) rainfall event, whilst high RCI_S values are observed to some extent across all stages of the grass to shrub transition for rainfall events as small as 10 mm. Whilst particularly large events have a low return period, they appear to be particularly instrumental in shaping ecogeomorphic feedbacks that are likely to drive catastrophic shifts in ecosystem state. The strength of the indicator approach used here is that it enables identification of regions with pronounced ecogeomorphic feedbacks, which act as potential trigger points for catastrophic shifts in ecosystem state, and thus, we demonstrate how the static limitations of existing approaches to developing connectivity indices may be overcome. The dynamic *RCI* allows the evaluation of the vulnerability or resilience of a particular system to variable driving mechanisms. The *RCI* can therefore be used to guide management interventions aimed at reducing or mitigating undesirable ecosystem state change, by focussing on specific locations/regions with high *RCI* values, to prevent further chances in system structure and function and to maximise the provision of ecosystem services.

1. Introduction

In this study we use the concepts of hydrological and sediment connectivity to gain insight into the location and timing of pronounced ecogeomorphic feedbacks operating in semi-arid grassland and shrubland environments. Ecogeomorphic feedbacks have been identified as being important dynamics that regulate the susceptibility of these systems to degradation (Turnbull et al., 2012). Evidence suggests that as shrubs invade grasslands, runoff-generating areas become more highly connected due to changes in soil-surface roughness and soil characteristics that reduce infiltration rates (Mueller et al., 2007; Turnbull et al., 2010a,b; Wainwright et al., 2000). The length of connected pathways is increasingly being recognised as being an important driver of changes in system state, potentially leading to desertification (e.g. Okin et al., 2009). As shrubs encroach into desert grassland, the change in connectivity of flow pathways and consequential redistribution of materials – which in turn alter soil characteristics and the availability of soil resources – is an important feedback mechanism by which continued shrub invasion ensues (Stewart et al., 2014). These feedback processes govern the coupling between structural elements of the landscape and their spatial connectivity (Wainwright et al., 2011), and as the length of connected pathways increase, so does the scale of

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structural heterogeneity (e.g. Schlesinger and Pilmanis, 1998; Ludwig et al., 2007). The onset and strength of these feedbacks between the connectivity of flow pathways and soil properties via the redistribution of materials is likely to be a critical element controlling the rate of shrub encroachment and the resilience of the shrub-invaded state.

Field-based experimentation has demonstrated that runoff-generating areas in grassland can generate highly connected flow, but only during the most extreme rainfall events that occur infrequently (e.g. Turnbull et al., 2010a,b). In contrast, in shrubland, it has been observed that runoff-generating areas become highly connected, even under relatively small rainfall events. The extent to which runoff-generating areas become connected determines the distance that water will flow over the land surface. This flow distance in turn determines the distance over which other plant-essential resources – soil and nutrients – will be redistributed (e.g. Stieglitz et al., 2003).

Little is still known on the specific locations and timing of ecogeomorphic feedbacks within these landscapes, which is important in terms of identifying locations most susceptible to degradation. These are locations where management approaches (such as modifying the structural or functional connectivity of the landscape) could be targeted most effectively. Here, using the concepts of hydrological and sediment connectivity, we present a novel approach for the quantification of hydrological connectivity and sediment connectivity that is dynamic and spatially explicit, enabling identification of locations and times when feedbacks between landscape form and function (runoff and erosion) are particularly pronounced.

Hydrological connectivity refers to connected pathways of water transfer though a system and is therefore dependent on runoff generation dynamics, the configuration of runoff-generating patches, the routing of flow through a catchment and the [lack of] opportunity for runoff to re-infiltrate. Sediment connectivity refers to connected pathways of sediment transfers though a system and is therefore dependent on sediment detachment, entrainment and connected transport through a system via wind or water. Hydrological connectivity and sediment connectivity are concepts that are increasingly being referred to in the fields of hydrology and geomorphology (e.g. Baartman et al., 2013; Bracken and Croke, 2007; Bracken et al., 2015; Turnbull et al., 2008; Wainwright et al., 2011). However, application of these concepts to improve our understanding of the form and function of the land surface tends to be either qualitative, or be based on runoff or erosion measurements at catchments outlets. While measurements at catchment outlets are useful as they enable assessment of the magnitude and duration of runoff and erosion processes, they are effectively 'black box' as they yield no information on regions of sediment source and patterns of sediment transport through the catchment. The key point to note here is that hydrological connectivity and sediment connectivity metrics are only useful concepts if they allow insight into land-surface processes and dynamics that measurements of landscape structure, runoff or sediment flux alone cannot yield.

In this study, we propose a novel approach to quantifying landscape connectivity which explicitly integrates structural measures of landscape connectivity with functional measures. Structural measures of landscape connectivity are by definition static; they can be quantified using information on the structure of the landscape surface in accordance with topography or other structural features and do not account dynamically for process-form linkages. Functional measures of landscape connectivity on the other hand are dynamic, and vary in accordance with, for example, drivers of runoff generation such as rainfall amount and antecedent soil-moisture content. These drivers of runoff in turn drive spatial and temporal dynamics of erosion. The functional connectivity of a landscape will vary over very short time scales, while structural connectivity is considerably less dynamic, and will change in response to functional connectivity feedbacks, predominantly in response to high intensity runoff events. Where the length scale of resource (water, sediment, nutrients and propagules) redistribution (functional connectivity) exceeds the scale of vegetation patches (structural connectivity) there is likely to be a net export of resources, and the landscape will become increasingly vulnerable to change. Where the length of functional connectivity is shorter than structural connectivity, resources will be retained within the landscape.

Our aim is to investigate where and when hydrological and sediment connectivity affect ecogeomorphic feedbacks in transitional landscapes. We evaluate how dominant hydrological parameters control ecogeomorphic feedbacks through changes in locations of resources in the landscape, and evaluate how these can be used to develop early-warning indicators for landscapes that are considered to be at risk of shrub encroachment. A classic example of such a landscape is in the deserts of the US Southwest. Here, we will use data collected from the Sevilleta LTER site, New Mexico, to apply the approach.

2. Methods

Previous approaches to quantifying landscape connectivity have focused on either the structural connectivity of the landscape such as the connectivity of topographically lined areas, or connectivity of vegetation patches (e.g. Antoine et al., 2011; Ludwig et al., 2007; Mayor et al., 2008), or its functional connectivity (i.e. connectivity of the runoff response and resulting flow) (e.g. Gomi et al., 2008; Jencso et al., 2009; Ocampo et al., 2006). However, a more meaningful approach to quantify landscape connectivity should focus on the linkages and feedbacks between the structural and functional connectivity of a landscape (Turnbull et al., 2008). Here, to address feedbacks between landscape structure and function within the context of connectivity, we compare functional connectivity (length of dynamic [i.e. event-based] runoff and sediment transport pathways modelled using MAHLERAN) with structural connectivity (estimated using field observations of vegetation cover and topography). We define a dimensionless, relative connectivity index (*RCI*) as:

$$RCI = \frac{FC}{SC} \tag{1}$$

where *FC* is a measure of functional connectivity [m] in relation to a specific process, and *SC* is the corresponding measure of structural connectivity [m]. *RCI* values < 1 indicate that the length of functionally connected pathways is shorter than the length of structurally connected pathways. *RCI* values > 1 indicate that functional connectivity exceeds structural connectivity. Locations and times where the $RCI > 1$ indicate when/where structural thresholds are exceeded, which is important as it represents key hot spots and hot moments within the landscape when structural re-organization and ecogeomorphic feedbacks are likely to occur.

We define *SC* as the way in which surface characteristics (i.e. morphology, vegetation and soil characteristics) are structured in a hydrologically and geomorphologically relevant way, so as to facilitate the potential connected transfer of water and sediment over the landscape. Two key determinants of *SC* (in this context) are topography, which determines the direction of water flow and water-driven sediment transport, and vegetation distribution as vegetation may act as a sink to which runoff from upslope areas may infiltrate, unless a vegetated patch has elevated topography in which case water may be diverted around vegetated patches. In arid landscapes, hydrology is one of the primary drivers of erosion, and thus topography and vegetation-patch distribution are also relevant variables for defining the *SC* of erosional processes. Thus, *SC* for both hydrology and erosion are conceptually and quantitatively the same. Structural connectivity for each point within the landscape is thus defined as the length of potentially connected flow pathways leading to that point. Using the approach of Mayor et al. (2008), for each cell within a domain, the maximum length of connected cells to a particular location within the landscape that does not encounter a vegetation sink is calculated, thus yielding spatial estimates of structural connectivity (Fig. 1).

Our method differs in two ways. First, we apply the D4, rather than

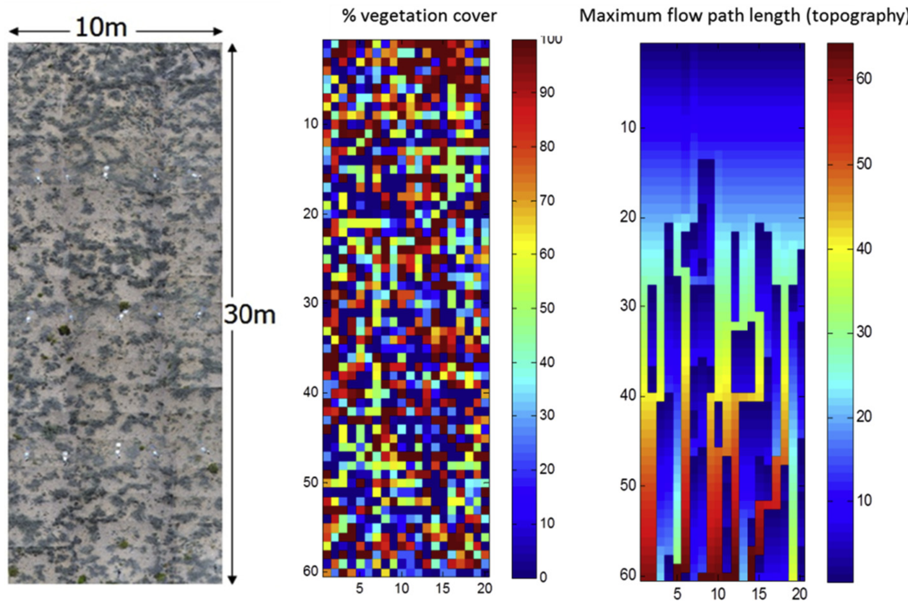

Fig. 1. Aerial imagery used to calculated % vegetation cover (left); resulting % vegetation cover map (centre); and topographically defined maximum flow path length (no. cells; right).

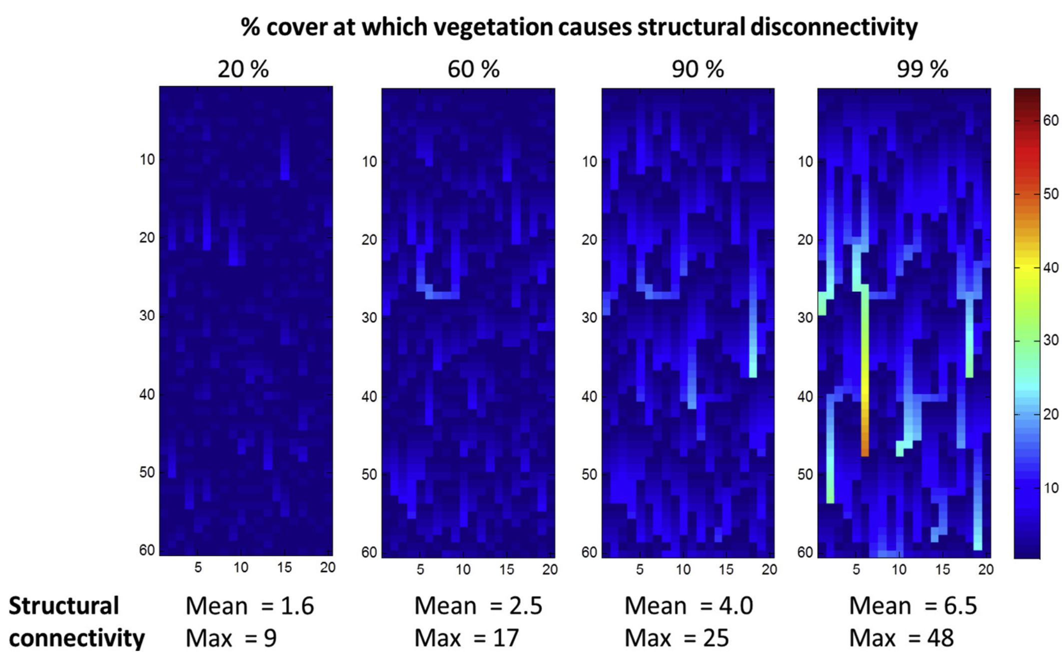

Fig. 2. Sensitivity of structural connectivity metric (showing length of connected pathways (no. cells)) to vegetation cover thresholds used to define runoff sink cells.

the D8, steepest descent flow-routing algorithm to a high-resolution (0.5 m) digital terrain model to count the maximum length of topographically connected cells. This distinction is a result of the structure of the model used to calculate the functional connectivity. Secondly, we used millimetre-resolution aerial photography to estimate presence or absence of vegetation, which was then converted to the same 0.5-m grid as the topographic data. The topographic data were derived from EDM survey of the elevation of the ground surface, so do not contain artefacts from the location of vegetation. Consequently, it was necessary to use a threshold to define individual pixels where the vegetation cover would be significant enough to act as sinks, and thus create the binary map as required by this approach. We use a threshold of 60% cover, which is the mid-point in the range of observed percolation thresholds for finite lattices with 4-coordination (Harel and Mouche, 2014) (Fig. 2).

Functional connectivity (*FC*) in hydrological and sediment-transport contexts depends not only on spatial variability of surface conditions but also on rainfall characteristics and antecedent conditions. Functional connectivity can be defined for water and sediment transport, based on runoff generation and flow characteristics, and sediment detachment and transport processes respectively. The key point to note here is that *FC* will vary over space and time, depending on the net interplay between antecedent conditions, rainfall event characteristics and the structure of the landscape. Here, for a specific rainfall-runoff event, functional hydrological connectivity and functional sediment connectivity are quantified based on calculating the length of connected pathways of runoff and sediment transport to each location within the study domain. These spatial measurements are seldom possible to obtain through empirical observations, and thus we use spatially explicit model outputs of runoff discharge and sediment transport for discrete rainfall-runoff events. The calculation takes the same flow paths as defined above and follows them downslope, incrementing the *FC* measure by the cell size for each additional cell where there continues to be flow above a specified threshold. Any point where the flow drops below that threshold results in setting *FC* to zero for that cell and restarting the increment process. For the *FC* of water flows (FC_H), the threshold is defined as 0.249 l over an event, which equates to a 0.8 mm flow depth across the 0.5-m cell, which is less than measurable in a field context; for sediment flows (FC_S) a value of 0.001 kg is used, based on the lowest steady-state values for splash erosion measured on a similar grassland by Parsons et al. (1994). We use an event-based runoff and erosion model (MAHLERAN; Wainwright et al., 2008a) to provide spatially explicit flow and sediment-transport data to calculate FC_H and FC_S. MAHLERAN has been extensively tested for these and similar sites for a wide range of rainfall events and antecedent conditions, and shown to produce realistic patterns as well as volumetric outputs (Turnbull et al., 2010c, Wainwright et al., 2008b,c). Because MAHLERAN explicitly represents runon infiltration and uses a transport-distance approach to sediment (and adsorbed nutrient) transport, it can more clearly represent the different functional dynamics that emerge in all aspects of the system under variable rainfall and initial conditions than any static representation can.

Scenario-based analysis is carried out for four sites that are representative of different stages of shrub encroachment into native desert grassland (grass, G [45% grass]; grass-shrub, G/S [39% grass, 4% shrub]; shrub-grass, S/G [14% grass, 12% shrub]; shrub, S [23% shrub]), at the Sevilleta Long Term Ecological Research site in central New Mexico USA (34°19′ N, 106°42 W; see Turnbull et al., 2010a for a full site description). Simulations are carried out for four sites over a shrub-encroachment gradient that have already been extensively measured and parameterized, and for which MAHLERAN has already been evaluated providing confidence that it captures the dynamics of the processes at the site (see Turnbull et al., 2010c). The *RCI* is calculated for hydrological (RCI_H) and sediment connectivity (RCI_S), for different antecedent soil-moisture contents (low, 3.8%; medium, 10.5%; high, 21.1%) and for different rainfall event characteristics (Table 1) which were selected based on analysis of the long-term rainfall record at the SNWR.

To analyse the effect of rainfall characteristics and antecedent soil-moisture content on the *RCI*, we (i) investigate the spatial maps of connectivity metrics; (ii) explore the empirical cumulative distributions (ecdf) of spatial RCI_H and RCI_S values for the four sites, and then (iii) use the percentile (*P*) value where RCI_H or RCI_S is ≥ 1 as an overall indicator of connectivity at each site. A lower *P* value will therefore indicate an overall higher level of relative connectivity.

3. Results

The length of structurally connected flow paths increases over the transition from grassland to shrubland (Fig. 3). Locations where $RCI_H \geq 1$ are most widely distributed for the largest (45 mm) rainfall event and to a lesser extent for the 24 mm rainfall event across all plots and all antecedent soil-moisture contents (Fig. 4). For the smaller rainfall events, locations where the length of functionally connected hydrological pathways exceed the length of structurally connected pathways are only found at the shrub (S) study site – closer to the downslope boundary of this site. The ecdfs show that distribution of RCI_H values fairly similar for the grass (G) and grass/shrub (G/S) site, with the G/S site showing a slightly higher proportion of cells with higher RCI_H values. At the shrub/grass (S/G) site, for the 45 mm rainfall event RCI_H values are much higher than for the other sites, indicating that here, the length of hydrologically connected pathways greatly exceeds the length of structurally connected pathways. For the 45 mm rainfall event RCI_H values are lowest at the shrub (S) site, indicating that locations where functional hydrological connectivity exceeds structural connectivity are less widespread than at the other sites. For the smaller rainfall events (15 mm, 10 mm and 5 mm), it is predominantly the shrubland site where locations with $RCI_H \geq 1$ are experienced.

The spatial patterns of RCI_S are much more pronounced across all sites than RCI_H (Fig. 5). Whilst the general spatial patterns of pronounced RCI_H and RCI_S are the same for the 45 mm rainfall event, the strength of connectivity is much higher for sediment connectivity, as indicated by the distribution of RCI_S values. The RCI_S values are also relatively high for the 15 mm and 24 mm rainfall event across all plots. However, the predominance of higher RCI_S values is less over the shrubland site than the others sites. For the two largest rain events, overall, the grassland site has highest RCI_S values, indicating that here, the length of connected sediment transport pathways is greater than the length of structurally connected pathways. The RCI_S values for the shrub/grass site are similar to the grassland site. For the 10 mm rainfall event, RCI_S values are still relatively high at the grassland/shrubland site, but comparatively lower across the other sites. For the 5 mm rainfall event RCI_S values are zero in most locations indicating a lack of connected sediment transport.

A comparison of RCI_H and RCI_S values for the 45 mm rainfall event with high antecedent soil-moisture content (Fig. 6) shows that whilst there is an overall positive relation between the two, there is reasonable scatter (G: $R^2 = 0.74$, $p < 0.001$; G/S: $R^2 = 0.86$, $p < 0.001$; S/G: $R^2 = 0.61$, $p < 0.001$; S: $R^2 = 0.89$, $p < 0.001$). Across all sites there are numerous locations where RCI_H is zero and RCI_S is greater than zero. High RCI_H coupled with high RCI_S values tend to occur with increasing proximity to the lower boundary of the study domain, especially at the grass-dominated sites. Lower values of the RCI_H and RCI_S (RCI_H and $RCI_S \sim 30$) persist at both long and short distances from the lower boundary of the study domain.

The cumulative percentile (*P*) value where RCI_H or RCI_S is ≥ 1 is used as an indicator of overall connectivity at each site. With an increase in event rainfall, $P(RCI_H)$ and $P(RCI_S) \geq 1$ decreases, indicting an overall increase in hydrological connectivity. For the grass, grass/shrub and shrub/grass sites, increases in event rainfall up to 15 mm yield no changes in RCI_H, followed by marginal increases in RCI_H at 24 mm and a great decrease in RCI_H at 45 mm event rainfall, indicating a great increase in connectivity, especially at the shrub/grass site. At the shrubland site, decreases in RCI_H with an increase in event rainfall are much more gradual, and less pronounced for the 45 mm rainfall event (Fig. 7a). There appears to be a threshold change in RCI_S between 10 and 24 mm event rainfall across low, medium and high antecedent soil-moisture contents, indicating a dramatic increase in sediment connectivity between these values. This threshold change is most pronounced for the sites with grass cover. Similar patterns are observed when RCI_H and RCI_S are plotted against event total discharge (Fig. 7b).

Table 1
Rainfall event characteristics for which RCI_H and RCI_S are calculated.

Event rainfall total (mm)	Rainfall intensity (mm hr^{-1})
5	48
10	61
15	76
24	91
45	211

4. Discussion

The observed non-linear increases in RCI_H values with an increase in shrub cover, most likely as a function of the more constrained and convergent flow pathways that emerge, suggest that ecogeomorphic feedbacks are more important with increases in shrub cover typical of the later stages of shrub encroachment. These results are in line with observations from Mulga landscapes in Australia where strong non-linear behaviour of degradation processes has also been observed, whereby a small shift in landscape structure can trigger a large shift in

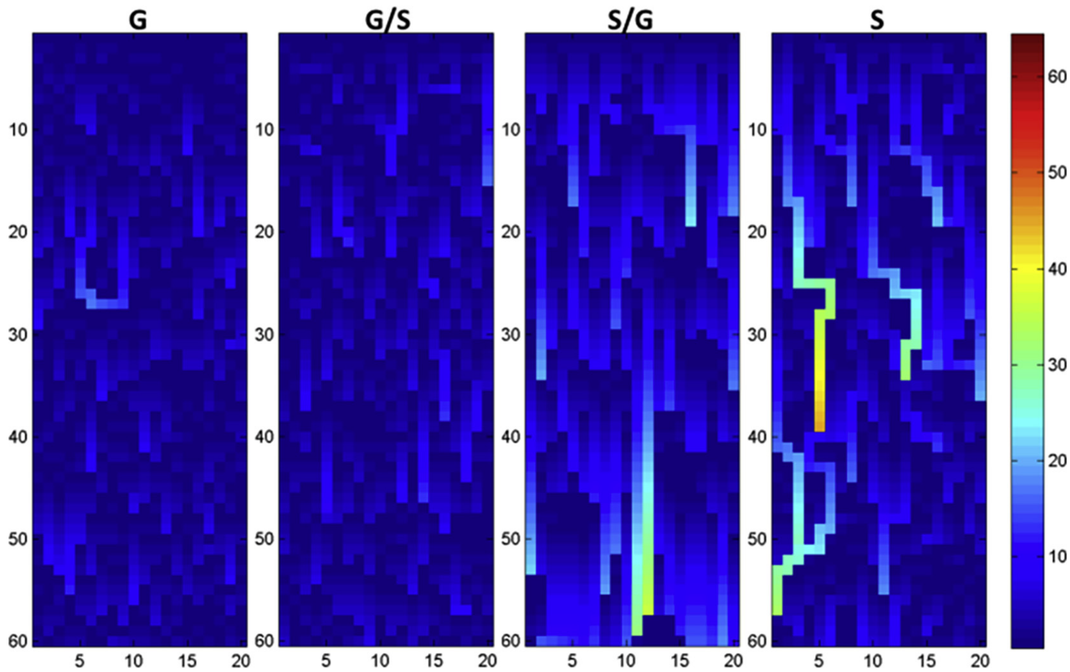

Fig. 3. Spatial plots of SC, based on the topographically defined maximum flow path length and structural disconnectivity where vegetation cover ≥60%.

ecosystem function (Moreno de las Heras et al., 2012). The widespread distribution of high RCI_H values indicates high levels of functional hydrological connectivity that exceed the length of structurally connected pathways. These high levels of hydrological connectivity, in combination with high levels of sediment connectivity (similarly observed by the widespread distribution of high RCI_S values) will drive changes in the structural connectivity of the landscape, by altering the distribution and redistribution of plant-essential resources (Schlesinger et al., 1996; Turnbull et al., 2010a). These structural connectivity changes also alter the hydrological characteristics of the soil which will in turn affect the future hydrological response of these locations to rainfall, and directly alter the structure of vegetation via the erosive energy of the connected water and sediment flows (Puigdefabregas, 2005). A surprising observation is that values of RCI_H are lower at the shrub-dominated site (which delimits the end point of the transition from grassland to shrubland) for the largest rainfall event, and lower values of RCI_S for all but the smallest rainfall events. The explanation for this is the level of structural connectivity is already very high, as shrublands have a shrub-associated microtopography with water naturally routed over the landscape in inter-shrub areas that are mostly devoid of vegetation. Therefore, high levels of hydrological and sediment connectivity do not result in high RCI_H and RCI_S values. For the purpose of using the *RCI* to identify locations where ecogeomorphic feedbacks occur, this results is important, since shrublands that represent the final stage of grassland to shrubland transitions are the manifestation of ecogeomorphic feedbacks that have already taken place. Therefore, although there are high levels of functional hydrological and sediment connectivity, this connectivity does not result in further pronounced changes to ecosystem structure. Moreover, it simply maintains the current state of the landscape which is in contrast with earlier stages of the grassland to shrubland transition where high levels of functional hydrological and sediment connectivity progressively yield changes in landscape structure. The *RCI* consequently provides a way to assess the prevalence of cross-scale interactions, which are often an important determinant of catastrophic transitions (Peters et al., 2004). *RCI* values > 1 indicate that coarse-scale runoff/sediment transport overrides the smaller scale structural connectivity of flow paths, thus exceeding the capacity of system to buffer against such extreme events. In the case of the shrubland site, the scales of runoff/sediment redistribution and structural connectivity of the landscape are well matched, and no threshold is exceeded.

Thresholds of sediment connectivity appear to be directly related to thresholds of hydrological connectivity, which is not surprising considering that runoff is one of the main drivers of sediment detachment and transport in this environment. The exception to this is locations within each site where values of the RCI_S are greater than zero and where values of the RCI_H are zero. The only plausible explanation for this observation is the role of rainsplash in creating connected sediment flow and in some cases exceeds structural connectivity, even where no runoff is generated.

An important distinction to make between the observed RCI_H and RCI_S values is that high RCI_H values are most widely distributed for the largest 45 mm rainfall event, and much less so for the smaller rainfall events, whilst high RCI_S values are observed to some extent across all stages of the grass to shrub transition for rainfall events as small as 10 mm. Large (> 10 mm) rainfall events account for as few as 20% of the total number of rainfall events at the SNWR, but contribute the majority of monsoonal precipitation – up to 66% in wet years (Petrie et al., 2014). Thus, whilst particularly large events (~45 mm, maximum intensity 211 mm h^{-1}) have a low return period (~50 years) (Bonnin et al., 2011), they are particularly instrumental in driving ecogeomorphic feedbacks that are likely to drive catastrophic shifts in ecosystem state. The smaller rainfall events have lower return periods (~5 years for the 24-mm rainfall event, ~2 years for the 15-mm rainfall event and < 1 year for the 10-mm rainfall event) (Bonnin et al., 2011). Thus, even though it is the most extreme events that usually cause the most erosion in drylands (e.g. 5% of the rain storms cause > 50 or sometimes 75% of total erosion; e.g. Gonzalez-Hidalgo et al., 2007), smaller events (that still have significant levels of RCI_S) are responsible for driving sediment-related ecogeomorphic feedbacks due to their high frequency of occurrence. These smaller events therefore do much of the ongoing 'work' in driving and maintaining functional-structural changes to the system that move a system closer to the point of experiencing a catastrophic shift in ecosystem state, without necessarily causing the system to 'tip' into a new and degraded shrubland state. These dynamics occur at discrete locations in the landscape, as indicated by the locations of high RCI_H and RCI_S values (Figs. 4 and 5). Whilst the initial effects are localised, the longer term implications

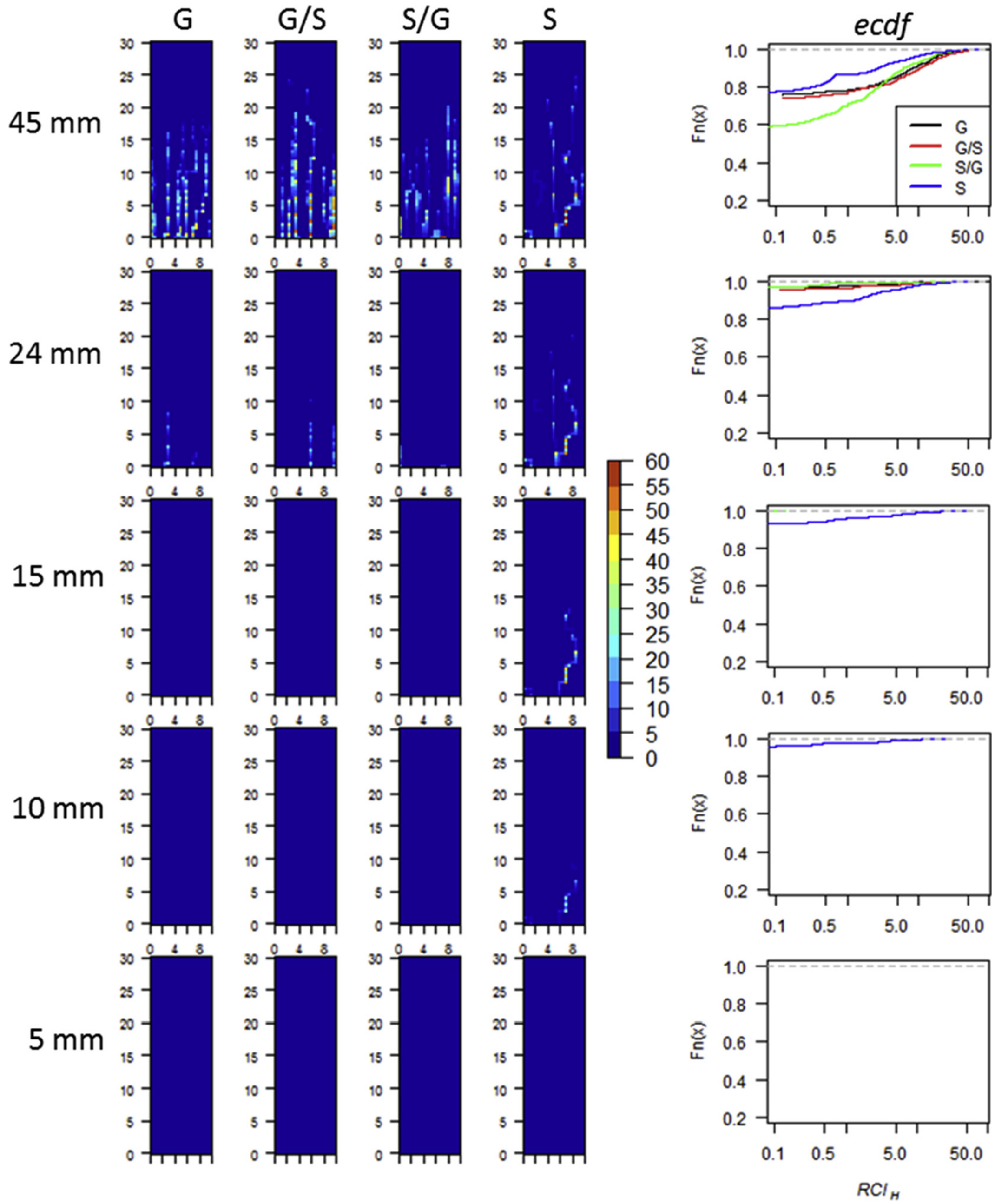

Fig. 4. Spatial plots of RCI_H for different total rainfall event size (45 mm, 24 mm, 15 mm, 10 mm and 5 mm), for high soil-moisture content (left) and associated empirical cumulative distribution function of spatial RCI_H values (right).

of these changes will be more widespread. High levels of RCI_H and RCI_S will result in localised increases in the structural connectivity of the landscape. For instance, pronounced step and riser topography in grassland impedes flow connectivity (Parsons et al., 1997), but under extreme conditions, concentrated runoff can cut through these structural microtopographic barriers and modify the structural connectivity of the landscape. These increases in structural connectivity will in turn facilitate future increases in the functional hydrological and sediment connectivity which impact the structural connectivity in downslope/adjacent locations causing further increases in RCI_H and RCI_S elsewhere within the landscape. Hence, the effects of increases in ecogeomorphic feedbacks at specific points within the landscape will eventually spread across the entire landscape driving widespread change.

The observation that some of the higher values of the RCI_H and RCI_S are located nearer to lower boundary of the study site indicates the partial significance of landscape position in controlling locations where ecogeomorphic thresholds might be exceeded. With an increase in contributing area, it becomes more likely for the length of hydrologically connected flow pathways to exceed the length of structurally connected pathways, therefore increasing RCI_H. These increases in RCI_H drive increases in the sediment detachment and transport capacity of the flow, therefore increasing the propensity for the length of pathways of connected sediment transport to exceed the length of structurally connected pathways. Nevertheless, results do indicate that there are locations, irrespective of distance to the lower boundary of the study domain, where the RCI_H and RCI_S are high, indicating the additional importance of local ecogeomorphic characteristics, including vegetation cover, local topography, and soil hydrological and erosion characteristics.

In landscape connectivity studies, connectivity analysis often forms the basis for management actions (Rudnick et al., 2012), and similarly, in the context of shrub encroachment into grasslands, quantifying

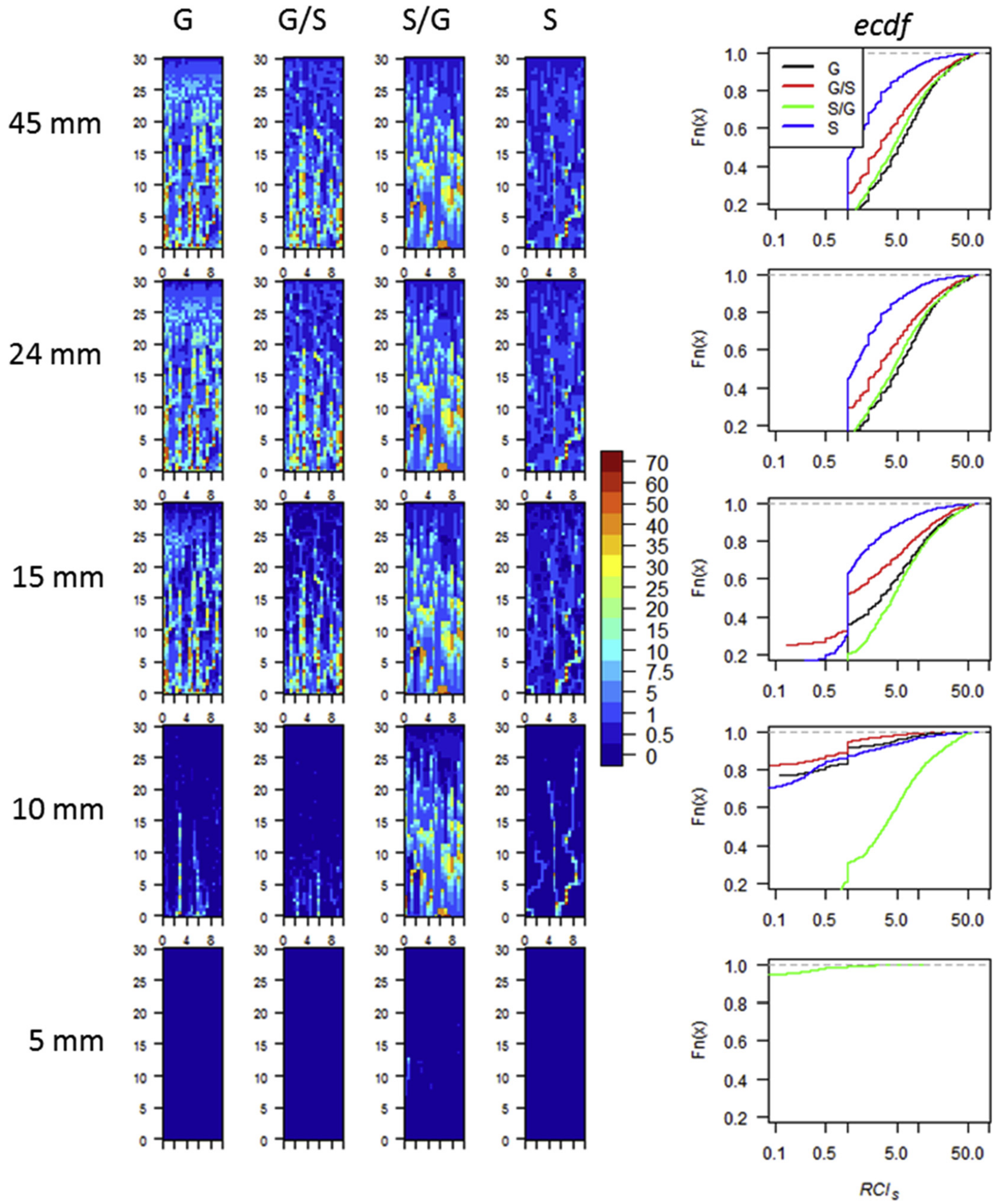

Fig. 5. Spatial plots of RCI_S for different total rainfall event size (45 mm, 24 mm, 15 mm, 10 mm and 5 mm), for high antecedent soil-moisture content (left) and associated empirical cumulative distribution function of spatial RCI_S values (right).

changes in connectivity can not only help us understand key processes and feedbacks, but can also provide a framework to evaluate strategies for mitigating undesirable changes in system state (Okin et al., 2009). The indicator approach used in this study similarly enables us identify regions with pronounced ecogeomorphic feedbacks which act as potential trigger points for catastrophic shifts in ecosystem state (Fig. 8). The large patches shown in Fig. 9 are where shrubs are located, and these will be more resilient to high connectivity than smaller patches. Over time, these locations will continue to evolve, in line with the ecogeomorphic structural-functional evolution of the system (Fig. 9). Management interventions aimed at reducing or mitigating undesirable ecosystem state change should thus be focussed on these specific locations as a starting point, to prevent further changes in system structure and function and to maximise the provision of ecosystem services. In rangelands, for example, the *RCI* might be used to identify regions where grazing should be excluded, or where vegetation restoration measures should be focussed restore a system to a less vulnerable state. What is clear from this approach is that to usefully identify and manage undesirable changes in ecosystem state, the evolution of system structure and function must be accounted for, and strategies be updated/located accordingly.

The magnitude of the *RCI* (i.e. the extent to which functional connectivity exceeds structural connectivity) is an important consideration in designing suitable interventions/remediation strategies. For instance, areas where the length of functionally connected pathways greatly exceeds the length of structurally connected pathways may require larger-scale interventions because of inertia that a small-scale manipulation is less likely to overcome, and thus, the scale of the potential remediation should match scale of connectivity (Okin et al., 2009), or the extent to which functional connectivity exceeds structural connectivity.

We have demonstrated the potential utility of this approach at the

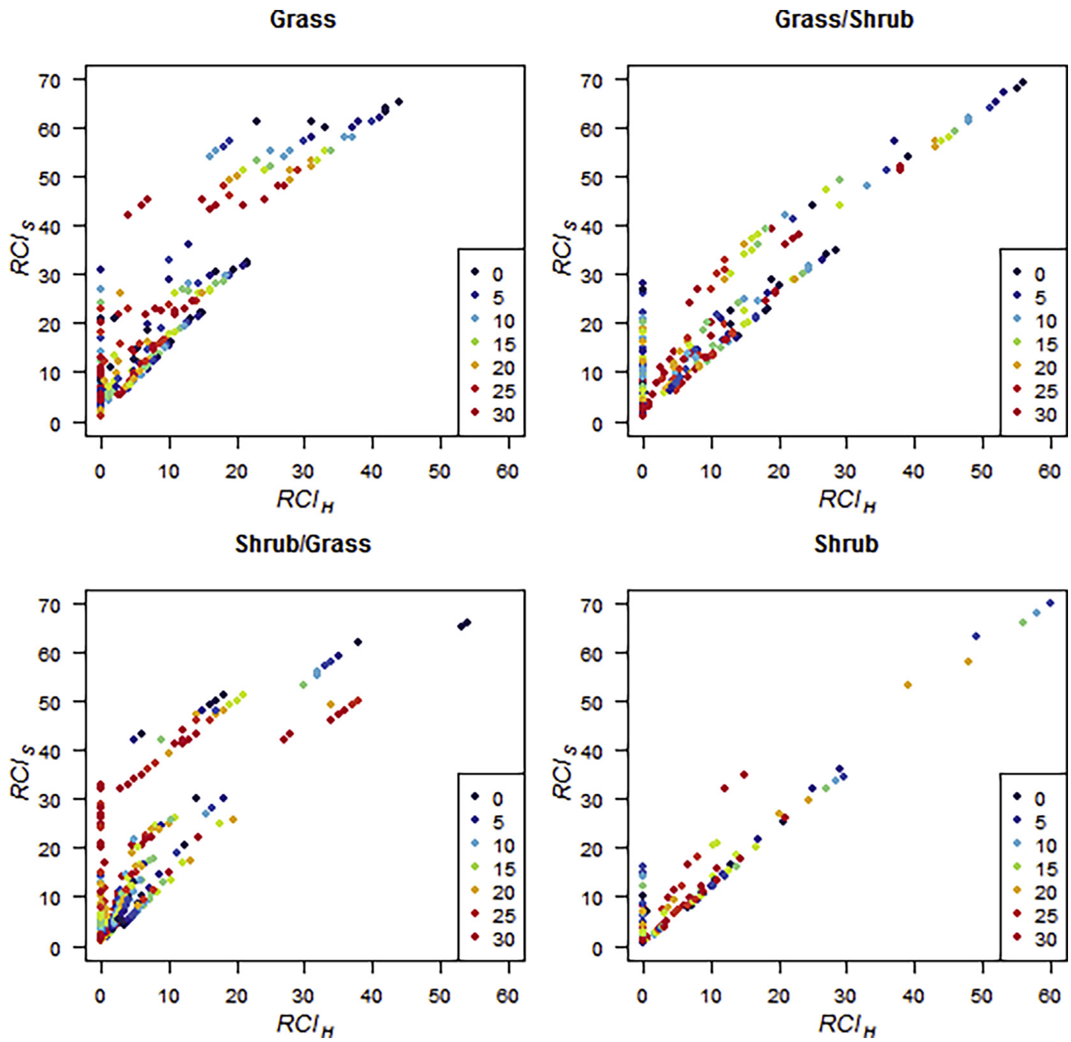

Fig. 6. Relation between RCI_H and RCI_S for the 45 mm rainfall event for high antecedent soil-moisture content. Points are shaded according to distance (m) from the lower boundary of the study domain.

hillslope scale. It could also, however, be applied at larger and coarser spatial scales, with the approach being used to identify key regions within a watershed where the $RCI > 1$. In this context, rather than using the approach to identify specific points, it could be used to identify key regions where management interventions should be focussed. For using connectivity indicators to inform management actions, the approach presented here is advantageous over other approaches in hydrology and geomorphology that tend to be focussed on quantifying the connectivity of flows to the catchment outlet (e.g. Antoine et al., 2009) which do not allow specific locations for management interventions to be identified.

5. Conclusions

To move from conceptual approaches of the links between structural and functional connectivity and how they drive ecogeomorphic processes (Bracken et al., 2015; Lexartza-Artza and Wainwright, 2009; Turnbull et al., 2008; Wainwright et al., 2011) to a practical application, we have produced an indicator accounting for both aspects of connectivity. By quantifying functional connectivity via modelling, we have been able to account for the dynamically changing conditions of connectivity that are very difficult to capture using monitoring approaches. In so doing, we demonstrate how the static limitations of existing approaches to developing connectivity indices may be overcome. Furthermore, the dynamic index allows the evaluation of the vulnerability or resilience of a particular system to variable driving mechanisms. Dryland environments are inherently characterized by climate variability, and therefore it is particularly relevant that our indicator approach enables the evaluation of system resilience to internal variations. Both climate change and increasing human pressure are also significant sources of external variation in these environments, and these may be accounted for explicitly in our indicator approach, through the direct effect of human pressures on modifying structural connectivity, or by climate-change effects on both functional connectivity and structural connectivity.

Using the different behaviours of the RCI_H and RCI_S, we demonstrate that water and sediment connectivity have different thresholds. To date, there has been a focus on hydrological connectivity in studies of dryland dynamics, as it is easier to measure. The different thresholds imply that there are different timescales of response of water and sediment, as well as different spatial scales. By focussing on only one type of connectivity, the detail of catastrophic shifts may be missed, given that other feedbacks are inherent in dryland degradation, such as nutrient and seed-bank depletion (Stewart et al., 2014; Moreno de las Heras, 2016), which are also driven in non-linear ways by water and sediment fluxes.

Mitigating undesirable changes in landscape structure and function must be underpinned by an understanding of the system complexities and their spatial and temporal scales using broader concepts of connectivity studies. This study has demonstrated how a connectivity

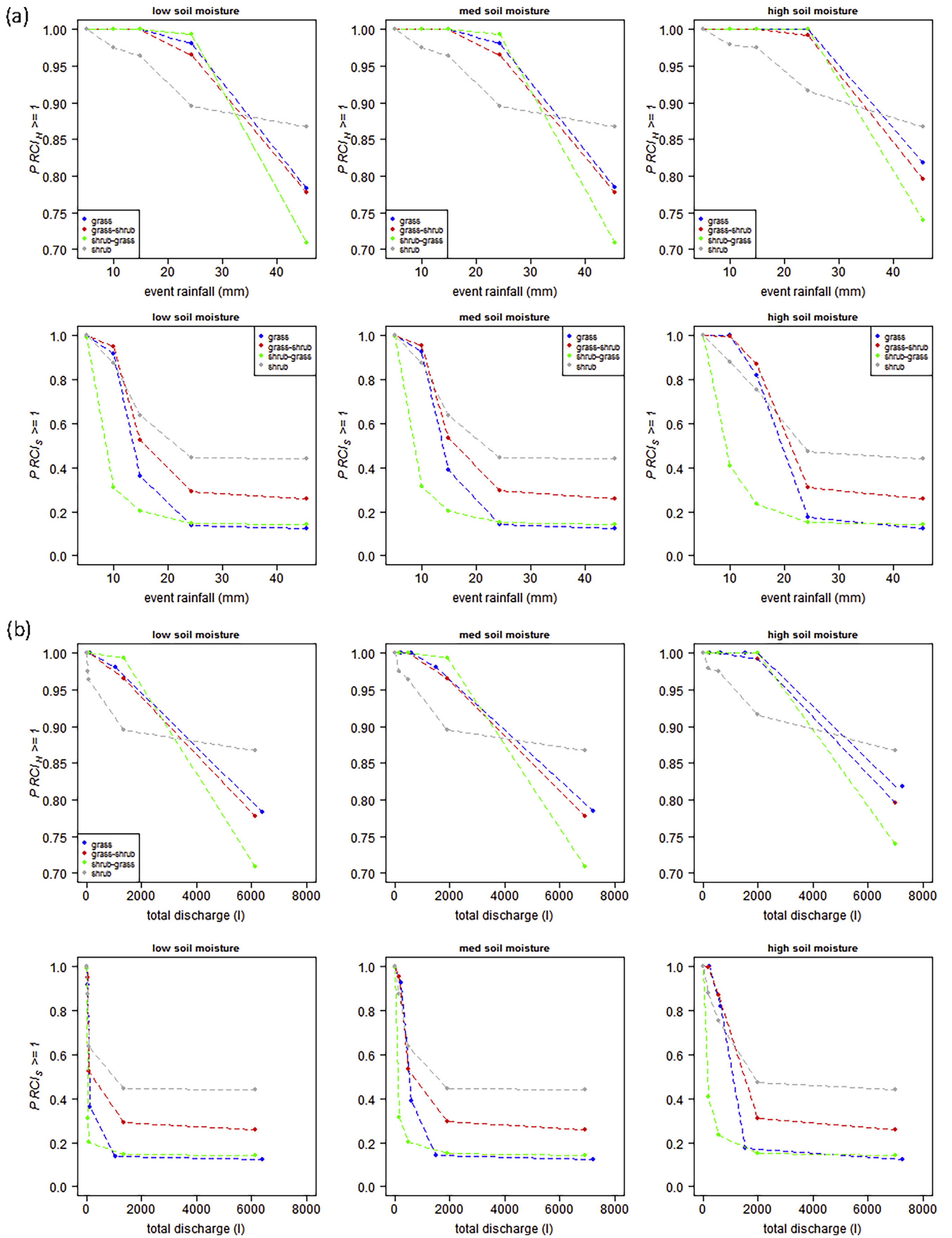

Fig. 7. Percentile value (*P*) at which RCI_H and RCI_S are ≥1 (i.e. connected) for (a) the different sized rainfall events and (b) the associated total discharge generated at the lower boundary of the study domain, plotted for low, medium and high soil-moisture content.

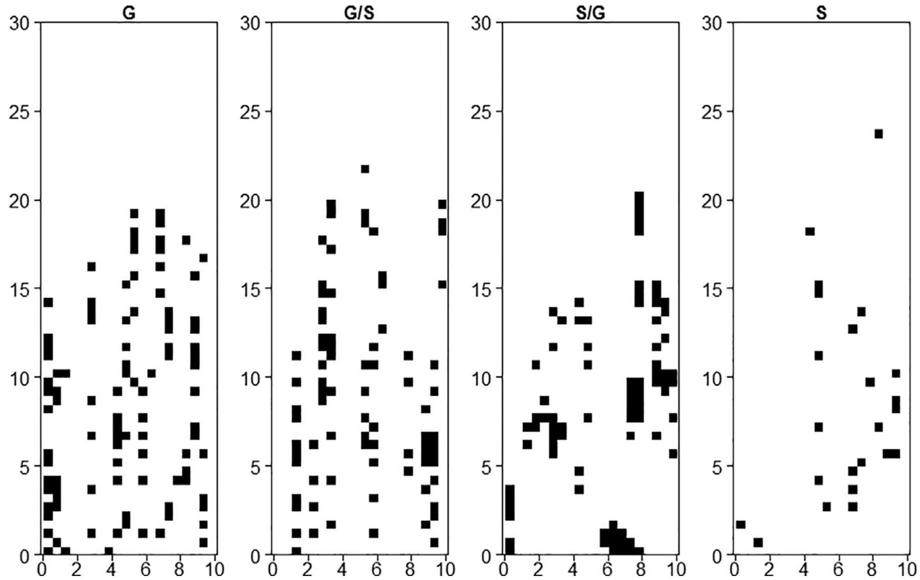

Fig. 8. Locations at each of the study sites where $RCI_H \geq 1$ overlap with locations where vegetation cover $\geq$60% cover causing structural disconnectivity (for the 45 mm rainfall event with high antecedent soil-moisture content). These are the locations where pronounced ecogeomorphic feedbacks will occur.

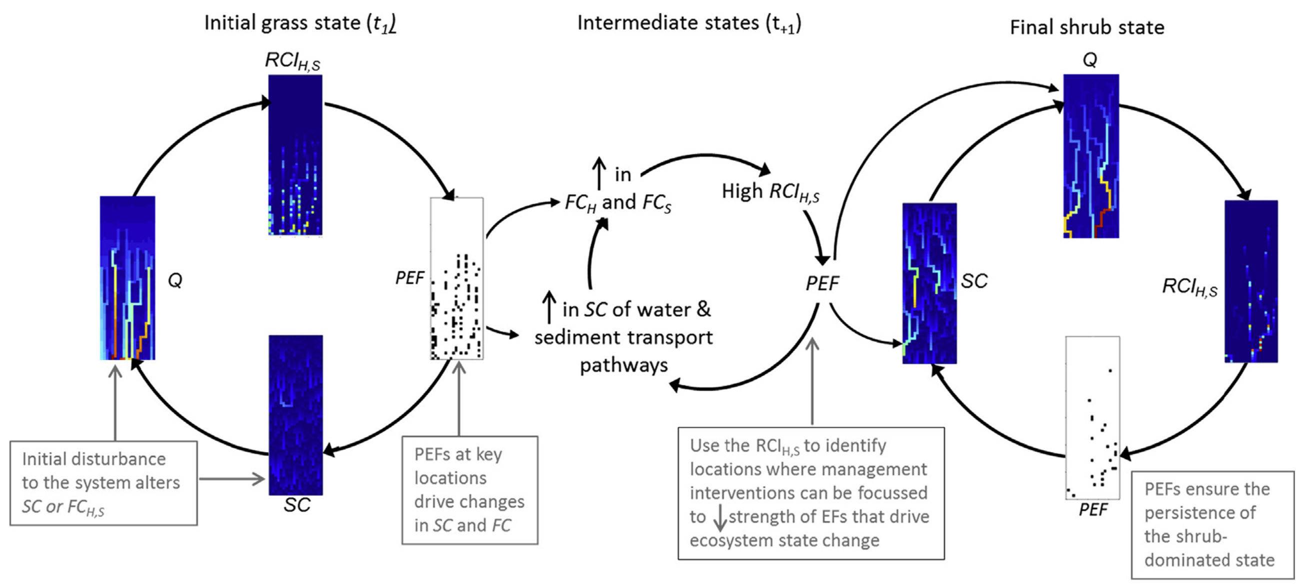

Fig. 9. Conceptual model showing how structural-functional feedbacks drive changes in ecosystem state following an initial disturbance, due to pronounced ecogeomorphic feedbacks (*PEF*) occurring at specific locations within the landscape that can be identified using the $RCI_{H,S}$. Ecogeomorphic feedbacks occurring at these locations will drive changes in system structure and function with effects cascading to adjacent/downslope locations. Interventions targeted at these locations with *PEF* may provide an opportunity to halt further ecogeomorphic feedbacks and prevent a catastrophic transition to a final shrub-dominated state.

indicator can be used to understand these complexities and identify critical locations where management interventions or restoration efforts should be focussed to mitigate undesirable changes that lead to catastrophic vegetation transitions.

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