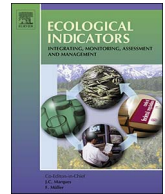




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A null model for assessing the cover-independent role of bare soil connectivity as indicator of dryland functioning and dynamics

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ABSTRACT

Recent research has identified the connectivity of the bare-soil interpatch areas as a key pattern attribute that controls resource conservation and structure-function feedbacks in dryland ecosystems, and several indices have been developed for this attribute. We aimed to characterize the dependence of bare-soil connectivity on vegetation cover and provide a null model that helps differentiate the independent roles of vegetation pattern and cover in hydrological connectivity and dryland functioning. Using a simple hydrological connectivity index, Flowlength, we developed explicit theoretical expressions for its expected value and variance under a null model of random vegetation cover distribution and constant slope. We also obtained the expected value of Flowlength for a model including an aggregation parameter. We found a non-linear inverse relationship between bare-soil connectivity and vegetation cover, which accounts for sharp increases in runoff and sediment yield for low cover values. The expressions for the mean values and standard errors for the random model allow the construction of confidence intervals, and thus testing for deviations from the null random model in experimental data. We found that positive deviations of Flowlength from the expected values, either under random or aggregated-pattern null models, sharply increase before transitions to a degraded state in a spatially-explicit dryland vegetation model, suggesting that an extraordinary increase in bare-soil connectivity may lead to unavoidable degradation. Our results show that increased deviation from the expected cover-dependent bare-soil connectivity may serve as indicator of ecosystem functional status and imminent transitions.

1. Introduction

Dryland vegetation is commonly structured in vegetation patches interspersed within a matrix of bare (or poorly vegetated) soil. The spatial pattern of vegetation patches and bare-soil interpatches is tightly linked to dryland ecosystem functioning (Ludwig and Tongway, 1995; Aguiar and Sala, 1999; Bautista et al., 2007; Moreno-de las Heras et al., 2012; Puttock et al., 2013; Mayor et al., 2016), and may undergo major changes in response to environmental variability (von Hardenberg et al., 2001; Rietkerk et al., 2004; Barbier et al., 2006; Meron, 2016). Accordingly, several spatial-pattern metrics have been proposed as indicators of dryland functioning (e.g., Tongway and Hindley, 2004; Ludwig et al., 2007a; Mayor et al., 2008), and as early warning signals of catastrophic shifts and desertification (e.g., Kéfi et al., 2007a, 2014; Guttal and Jayaprakash, 2009; Dakos et al., 2010; Corrado et al., 2014).

A number of theoretical and empirical works have pointed to the connectivity of the bare-soil interpatch areas as the key pattern attribute that drives the redistribution and conservation of resources in dryland ecosystems and landscapes (Ludwig and Tongway, 1995; Boer and Puigdefábregas, 2005; Ludwig et al., 2007b), influencing dryland vulnerability to environmental pressures (Mayor et al., 2013). Connectivity has been presented as an organizing concept (Okin et al., 2015) that relates to spatial interactions and feedbacks across scales and explains many patterns and processes observed in drylands. In particular, the connectivity and size of the bare-soil areas modulate the reallocation of water and other resources from source areas to vegetation patches (Espigares et al., 2013; Urgeghe and Bautista, 2015), which is considered to control the structure and function of drylands worldwide (Shachak et al., 1998; Ludwig et al., 2005; Yu et al., 2008). Moreover, changes in landscape-scale connectivity that increase ecosystem leakiness beyond critical thresholds are associated with dryland

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degradation and desertification (Ludwig et al., 2007b; Turnbull et al., 2008; Moreno-de las Heras et al., 2012), which suggests that changes in the structural connectivity of dryland landscapes could provide a good indicator of state transitions (Okin et al., 2009; Mayor et al., 2013; Zurlini et al., 2014).

Bare-soil connectivity is dependent on vegetation cover, as it is the case for many other pattern properties (Gardner et al., 1987). Vegetation cover is the most simple and widely used indicator of dryland ecosystem functioning (Elwell and Stocking, 1976; Herrick et al., 2005; Maestre and Escudero, 2009; De Keersmaecker et al., 2015), and has proven to be a good indicator of dryland resilience and potential for recovery after disturbances (Bestelmeyer et al., 2013). However, it has been shown that pattern-based metrics capture important additional information relative to vegetation cover measurements that could help to better define the ecosystem functional state and anticipate transitions. For example, for a given vegetation cover value, the larger and fewer the vegetation patches, the larger the interpatch bare-soil connectivity, and the larger the runoff and sediment yield (Bautista et al., 2007). For a large set of drylands sites across the globe, Berdugo et al. (2017) found that abrupt changes in ecosystem multifunctionality were best captured by the patch-size distribution of vegetation patches than by the total vegetation cover. The dependence of vegetation pattern on vegetation cover makes it difficult to disentangle their relative role in dryland functioning. Null models that represent the expected theoretical relationships between bare-soil connectivity and vegetation cover would allow assessing the independent effect of both properties on dryland functioning, providing a deeper understanding of the processes at work. This kind of null models could also be used to develop spatial metrics that provide early warning signals of desertification. Using a simple connectivity metric, here we aim to provide such theoretical relationships, illustrating their potential to assist in the assessment and analysis of dryland functioning and dynamics.

Existing metrics for bare-soil connectivity typically aim to capture the potential hydrological connectivity of bare-soil interpatches (Ludwig et al., 2002, 2007a; Mayor et al., 2008; Puttock et al., 2013). Mayor et al. (2008) developed Flowlength, a simple metric that specifically measures the accumulated length of the potential runoff pathways considering both vegetation pattern and topography. Flowlength is calculated as the average of the pathway lengths from all the pixels in a raster-based vegetation map of the area of interest. For each pixel in the map, the potential pathway for runoff is determined following the steepest descent direction until a runoff sink (i.e., vegetation pixel or topographic depression) or a boundary pixel is reached. Flowlength has been successfully tested against water and soil loss measurements at the slope and catchment scales, showing a positive linear relationship with runoff and sediment yield (Mayor et al., 2008). This metric has received much attention in both hydrological and ecological research (e.g., Cantón et al., 2011; Larsen et al., 2012; Moody et al., 2013; Puttock et al., 2013; Wu et al., 2016), and is being increasingly used to quantifying hydrological connectivity and estimating ecosystem functioning in dryland landscapes (Moreno-de las Heras et al., 2012; Muñoz-Robles et al., 2013; Liu et al., 2013; Mayor et al., 2013).

Here we aim to (1) provide explicit theoretical expressions for the expected value of the Flowlength index under a complete spatial random cover distribution and for a simple aggregated-pattern model, (2) illustrate the use of this kind of null models to disentangling the independent role played by plant cover and pattern in dryland functioning, and (3) assess the potential of using the deviation from the null model as indicator of ecosystem functional status and transitions.

2. Methods

2.1. Models

We develop explicit theoretical expressions for the expected value and variance of the Flowlength index under a null model of constant

slope and complete spatial random cover distribution (hereafter random model). To illustrate the effects of non-random patterns on bare-soil connectivity, we also obtain the expected value of the Flowlength index for a simple model including an aggregation parameter, which allows for local correlations that result from processes such as local facilitation of vegetation (Kéfi et al., 2007b). For details on the computation of the Flowlength index see Mayor et al. (2008). We consider a grid of cells or pixels of size ps in a planar slope with angle θ , so that the length of the flowpath (d_s) from a pixel to the neighboring downslope pixel is $d_s = ps/\cos(\theta)$. Since flow can only progress downslope, the analysis can be restricted to a column of 1-pixel width and L -pixels length along the slope. The strategy to derive the analytical expressions is to obtain recurrence relations for the expected values in terms of the length of the slope (L), which are solved and simplified (see Appendix A).

Using the theoretical expressions for the expected values provided in the next section (Eqs. (1)–(4)), estimations of the Flowlength index for real or simulated plots under the null models of random cover or locally aggregated cover are obtained (denoted eFLrdm and eFLagg, respectively). For a particular 2-dimensional plot with constant slope, consisting of M columns of length L , eFLrdm is calculated using Eq. (1), where the parameter p is estimated as the mean value of vegetation cover in the plot. The standard error for the estimation of eFLrdm can be calculated using Eqs. (1) and (2), and considering the plot as a sample of size M . To calculate eFLagg, Eq. (4) is used, where the aggregation parameter a_b (aggregation parameter for bare soil) is estimated from the frequency of pairs of contiguous bare pixels in the plot, computed column-wise, and the plot mean vegetation cover.

2.2. Null models versus observed connectivity and hydrological functioning

To illustrate deviations from the null model in real landscapes, we used images extracted from Google Earth imagery for two areas with contrasting vegetation patterns: banded patterns in Mulga landscapes, Northern Territory, Australia, and spotted patterns in Chihuahuan Desert shrublands and Semidesert grasslands, Southeastern Arizona, USA (Fig. S1, Supplementary material). Both areas have received attention in previous studies on pattern-function relationships and dryland degradation (e.g., Brown et al., 1997; Valone et al., 2002; Witford, 2002; Saco et al., 2007; Moreno-de las Heras et al., 2012). For each site, we extracted six square images (plots) that represented a gradient in vegetation cover. The plots from Arizona were $\sim 150\text{ m} \times 150\text{ m}$ in size, while the plots from the Mulga landscapes were of larger size ($\sim 800\text{ m} \times 800\text{ m}$) in order to capture the characteristic larger scale of the banded patterns. All plots had southern orientation, similar slope angles, and quite homogeneous topography. The plots were aligned with the maximum slope; the mean slope angle for each plot was also derived from Google Earth by considering the plot length and the elevation change along the plot. The extracted plot images were transformed into black (vegetation patches) and white (bare soil interpatches) binary maps through thresholding, using the graythresh function from Matlab (copyright *The Mathworks Inc.*), with similar dimensions in pixels ($\sim 800 \times 800$ pixels). From these maps, we estimated total vegetation cover and computed the observed Flowlength values for each plot and landscape type (Mayor et al., 2008), re-scaling them to unit length along the slope. We then assessed the deviations of the observed Flowlength values from the theoretical Flowlength-cover relationship estimated assuming a random distribution of vegetation patches on an idealized square plot of 800×800 pixels. We computed the expected value and also upper and lower limits (mean ± 10 times the standard error of the mean), providing a conservative 99% confidence interval under any distribution (Tschebyscheff's inequality, e.g., Rényi, 2007, p. 373).

To illustrate how the theoretical expressions for the expected values of Flowlength allow discriminating between cover and pattern effects on dryland functioning, we analyzed the covariation between available

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