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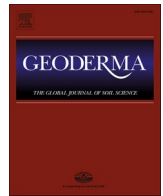
Biocrusts and catchment asymmetry in Tabernas Desert (Almeria, Spain)

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ABSTRACT

Catchment asymmetry is a fairly frequent phenomenon on a global scale but the main causes leading to its formation are still not well understood. Where the intervention of structural or tectonic causes is not relevant, asymmetry seems to result from differential erosion between opposite slopes that flow into the same channel, which is frequently associated with contrasted biocrust and/or vegetation covers. Biocrusts are known to be important surface stabilizing agents. However, their geomorphological consequences at the landscape scale are little known. In this study we combined field measurements with digital elevation models and image analysis to determine whether catchment asymmetry in the Tabernas Desert (semi-arid SE of Spain) is a local or general phenomenon, and to explore the main factors determining asymmetry occurrence, magnitude and direction. We pay special attention to the role of biocrusts. We found that catchment asymmetry is a very common phenomenon in the area; only 25% of the catchments are symmetrical, while approximately 40% present asymmetry with the relatively shady hillslope having a lower gradient, and 35% with that hillslope being the steeper. Solar radiation reaching the soil, surface area and channel gradient in the considered catchment stretch, as well as the total catchment area upstream from the lower point of the considered stretch were the main abiotic factors controlling the formation of the asymmetry. Microclimatic differentiation due to differences in radiation input caused by the uneven topography favoured the relative stabilization of the shadier hillslope and its colonization by biocrusts and later by plants. The effect of the biocrusts and vegetation protection against water erosion on shadier hillslopes is often stronger than that of the set of abiotic factors and gives rise to asymmetries with lower gradients in the shady hillslope by promoting lateral displacement of the channel. We hypothesised that the opposite pattern, with the sunnier hillslope having a lower gradient, occurs when abiotic factors control the development of asymmetry formation. In these conditions, the effect of biocrusts and plants would act in the opposite direction. We propose a conceptual model of feedbacks generating catchment asymmetry, with biocrust playing a crucial role.

1. Introduction

Catchment asymmetry occurs when the talweg is not in the geometric central line of a drainage area because of the differential steepness and length of the hillslope pairs dropping to the same talweg. Catchment asymmetry is a relatively frequent phenomenon that occurs worldwide (Poulos et al., 2012; Yetemen et al., 2015a), and has even been noted on Mars (Kreslavsky and Head, 2003), associated with insolation-related erosion and north–south hillslope aspects. Catchment asymmetry may be a result of several causes, differential processes or process interactions.

Among the major drivers of catchment asymmetry are structural or tectonic features (Bishop, 2007; He et al., 2019) as well as combinations of both. For example, in areas where the strata are dipping and the

channel reaches a harder stratum, it migrates laterally in the dipping direction, being the cuesta front affected by lateral erosion, while the reverse remains protected. Another important process frequently associated with catchment asymmetry formation is contrasted erosion between opposite hillslopes. Differences in erosion between opposite hillslopes occur as a result of differences in radiation and/or vegetation spatial pattern (Churchill, 1981; Kirkby et al., 1990; McGuire et al., 2014; Richardson et al., 2020). According Richardson et al. (2020), in the simplest scenario, insolation-driven microclimatic differences lead to different erosion rates on opposing slopes and topographic asymmetry develops. Lateral channel migration and the corresponding steepening of undercut slopes have also been suggested (Istanbulluoglu et al., 2008; Richardson, 2015) as an alternative dominant cause of topographic asymmetry. According to Langston and Tucker (2018), understanding how a bedrock river erodes its banks laterally is a frontier in geomorphology; in general, existing models do not seek to implement the lateral migration of bedrock channel walls.

Often, the complex interplay of biological, physical, and chemical processes in pedogenesis and hillslope evolution (Roering et al., 2010) limits our ability to predict and interpret landscape dynamics. Catchment asymmetry is a phenomenon that can contain information about ecological, geomorphological and hydrological processes, and thus its study can help us to understand ecosystem dynamics.

Drylands, except for the most arid ones, seem to be the best places to find catchment asymmetry because the discontinuous vegetation tends to concentrate in the better habitats (those relatively shaded, to minimize evapotranspiration), whereas erosion progresses in the worse ones (Monger and Bestelmeyer, 2006; Peters and Havstad, 2006). A clear example of this is semiarid badlands, where the formation of rills and other severe erosive forms can easily occur on bare hillslopes over Miocene sedimentary rocks (marls-mudstones), leading to very high denudation rates (Calvo-Cases et al., 1991; Harvey and Calvo-Cases, 1991; Nadal-Romero and García-Ruiz, 2018; Nadal-Romero et al., 2021). Badlands are regarded as excellent natural laboratories for geomorphological purposes (see, among others, Yair et al., 2013), being one of the best landscapes to deeply analyse asymmetry formation for several reasons: (i) catchment formation processes are often faster than in other regions having harder lithology, due to the soft materials. (ii) This leads to a very dissected landscape including a large number of catchments, or "hydrological units", in a relatively small area. (iii) Scarped topography also has an important effect on microclimate, which, in its turn, affects the spatial distribution of the different surface components. Thus, vegetation often tends to occupy more favourable positions within the landscape whereas in relatively less favourable areas, in which soil depth and/or water and nutrient constraints limit plant growth, other permanent life forms, such as biological soil crusts (biocrusts) dominate. Biocrusts are communities constituted by poikilohydric microorganisms, both microscopic (cyanobacteria, bacteria, algae, fungi) and macroscopic (mainly lichens and bryophytes), which inhabit the soil surface or the upper few centimetres of soil (Weber et al., 2016). They include autotrophs, heterotrophs and saprophytic life forms, as well as symbionts and parasites and provide habitats for small animals. Biocrusts are very frequent worldwide where vascular plants cannot form a continuous cover for climatic or pedological reasons (Rodríguez-Caballero et al., 2018a). By covering the soil surface, biocrusts affect soil biogeochemical cycles (Delgado-Baquerizo et al., 2015; Miralles et al., 2012) and water balance (Chamizo et al., 2016; Eldridge et al., 2020). In addition they bind the soil surface, preventing water erosion and controlling surface and subsurface transport processes, mainly in their advanced successional stages (Belnap et al., 2014; Belnap and Büdel, 2016; Bu et al., 2013; Chamizo et al., 2012b; Lázaro and Mora, 2014). For general biocrust features and functions see, for example, Belnap and Lange (2003) and Weber et al. (2016). Contrasted microhabitat formation, heterogeneous spatial distribution of soils, vegetation, biocrusts and bare areas and the precipitation regime of a semiarid climate allow erosion while still accommodating stabilizing

soils, biocrusts and vegetation in favourable microhabitats. This leads to a large contrast between opposite hillslopes dropping to the same channel.

El Cautivo, is an experimental field site used by the Department of Desertification and Geo-ecology of the Estación Experimental de Zonas Áridas (CSIC) located within the Tabernas Desert, in Spain. Catchment asymmetry is a particular feature of the landscape, and its spatial distribution seems far from random. Field observation over 25 years suggests that it is associated with (i) soil type and depth (Solé-Benet et al, 1997; Cantón et al, 2001a,b); (ii) the spatial patterns of erosion, and soil surface components, particularly biocrusts and vascular vegetation (Arnau-Rosalén et al., 2008; Cantón et al., 2002; Lázaro and Mora, 2014; Solé-Benet et al., 1997); (iii) slope orientations (Cantón et al., 2004); and, (iv) the relative age of the gullies or catchments and, probably, the order number of the channel (Lázaro et al., 2000). Vegetation pattern is often strong, associated with microclimates generated by the uneven topography, and every dominant biotype, from biocrusts to grasses, through annuals and shrubs, shows geomorphological preferences (Calvo-Cases et al., 2014; Cantón et al., 2004; Lázaro et al., 2000; Rodríguez-Caballero et al., 2019). Apparently, no asymmetric gully exists without a clear pattern of vascular vegetation and/or biocrusts. This suggests a probable significant effect of biocrusts, since they are primary colonizers (Lázaro et al., 2008), and vascular plants on the evolution of the landforms.

By determining the spatial structure, this asymmetry has functional consequences at the ecosystem scale, and its apparent frequency shows that the processes involved are key, as they are quite generalized. Therefore, knowledge of these processes is critical to understanding this ecosystem. In addition, this asymmetry feeds back into the generation of different microclimates and habitats (Calvo Cases et al., 2009; Lázaro et al., 2008; Rodríguez-Caballero et al., 2019), leading to a complex, ecohydrologically coupled system and providing structure and resilience to the ecosystem. As Suggitt et al. (2018) said, where precipitation is not sufficient to maintain a continuous vegetation cover, the spatial diversification of the habitats allows biodiversity to be maintained within the best habitats and reduces extinction risk by microclimatic buffering.

We framed our initial hypothesis based on all previous knowledge acquired during >25 years of active research in the area, as follows: Biotic components of the ecosystem, starting with biocrusts, which are the first colonizers (Belnap et al., 2003; Lázaro et al., 2008), contribute to the catchment asymmetry because they protect against erosion and feedback aggradation on a shadier hillslope, whereas the opposite sunnier hillslope, practically void of vegetation, remains more erodible. Biocrusts need a certain surface stability to successfully develop (Lázaro et al., 2000). However, at the beginning of the catchment development, topographically-driven differences in incoming radiation generate larger surface instability in the sunnier hillslope, hindering its colonization, while colonization is easier in the shadier hillslope. After biocrust development, and further soil evolution, vascular vegetation reinforces the stabilization process. Efficiency of the stabilizing effect of biocrust plus vegetation will depend on the intensity of abiotic factors controlling slope processes. Thus, at least solar radiation, contributing area and channel gradient, widely considered main drivers in slope processes (see, among others, Poulos et al., 2012; Richardson, 2015; Richardson et al., 2020), along with biocrusts and vascular vegetation (hereafter, vegetation) (Lázaro et al., 2008; Roering et al., 2010; Yetemen et al., 2015b) should be considered as important drivers explaining asymmetry.

The objectives of this work were:

1. To describe catchment asymmetry at El Cautivo field site and to verify the relative importance of different factors generating asymmetry by using structural equation modelling (SEM), in order to test our initial hypothesis at that field site.

2. To explore and describe catchment asymmetry in the Tabernas Desert, using the El Cautivo SEM model to test the factors generating asymmetry.
3. To develop a full conceptual model inserting the biocrust-driven-stabilization within the processes generating asymmetry, which can be used to frame future studies aimed at analysing the influence of biocrusts in landscape evolution.

2. Methods

While objectives 1 and 2 are based on new data and analyses, accounting for most of the results, objective 3 is based on establishing relationships between those results and previous research.

2.1. The study area

Tabernas Desert, in the Almeria province (Spain), at the southeast corner of the Iberian Peninsula, is the place name of the central part of a tectonic basin filled during the Upper Miocene by marine marls (or calcareous-gypsiferous mudstones) and turbidites, with occasional interbedded calcareous sandstones in peripheral situations corresponding to the continental talus of the Miocene sea. It is mostly a badlands landscape, and one of the driest areas in Europe. The basin is bounded by faults that delimit four important Betic mountain ranges: Sierra de Gádor, Sierra Nevada, Sierra de los Filabres, and Sierra Alhamilla, the first three higher than 2000 m a.s.l. Most of the rainy fronts come from the Atlantic Ocean, and the area is downwind of the Sierras de Gador and Nevada. Sierra de los Filabres intercepts the north winds, and Sierra Alhamilla intercepts the occasional rainfall coming from the Mediterranean Sea. Thus, Tabernas Desert is a rain-shadow area, receiving between 200 and 250 mm per year with some spatial variation and strong inter and intra-annual variation. The vast majority of events are a few mm (Lázaro et al., 2001). Heavy torrential rains, although they exist, are clearly less frequent than in other less arid Mediterranean areas. The dissection of the Upper Miocene sedimentary, mostly detrital, rocks, mainly since the Pliocene period, by a dense drainage net has created a singular erosional landscape including extensive badlands, but with a wide variety of landforms resulting from the sequence of dissection and stability phases controlled by environmental changes and pulses of uplift and tectonic deformation (Calvo-Cases et al., 2014). The area receives >3000 h of sunshine per year. Mean annual temperature oscillates spatially between 17 and 19 °C. Average of monthly temperature oscillation is 14 °C. Frosts show low frequency every year, although they can occur from November to March. Average relative humidity ranges between 52% in summer and 66% in winter, but its oscillation in periods of one to a few days is much larger than the seasonal oscillation. Annual potential evapotranspiration is 1666 mm on average (Lázaro et al., 2004). Where parent material outcrops, the predominant lithologies are marine marls, while at depth it is a moderately consolidated calcareous-gypsiferous mudstone, with an average organic matter (OM) of 0.5%). At El Cautivo experimental field site, this parent material is mainly composed of silt-size (>70%, mostly fine silt) siliceous, calcareous and gypsum particles; fine sand ranges from 5 to 20%, and clay ranges from 5% to 10% (recent unpublished data). The average mineralogy is muscovite 35%, calcite 20%, gypsum 20%, paragonite 10%, quartz 10%, chlorite + smectite 3%, and dolomite 2% (Cantón et al., 2001a). The geomorphological history of El Cautivo is described in Alexander et al. (1994) and Alexander et al. (2008). Soils are very thin (<10 cm) on S to W oriented slopes and defined as *Epileptic Regosols*, and moderately deep (from 0.2 m up to >1 m) on N to E oriented slopes and classified as *Endoleptic Regosols* at the upper slopes but *Calcaric Regosol* or *Haplic Calcisol* in downslope positions (Cantón et al., 2003). Eroded landforms occupy a third of the territory, another third is covered by short vascular vegetation with biocrusts in the interspaces, and the rest is covered by biocrusts (Calvo Cases et al., 2009; Cantón et al., 2004; Lázaro et al., 2000; Rodríguez-Caballero et al., 2014). Vegetation pattern is an

obvious feature of these badlands: S to W facing slopes are the sunnier and normally bare and eroded, while N to E facing slopes, relatively shadier, almost always have an important biocrust cover (including many species of terricolous lichens within an almost continuous matrix constituted by cyanobacterial biocrust), and often some vegetation formed by grasses, dwarf shrubs and annuals, along with a more or less developed soil. Between some catchments there are more or less flat areas, corresponding to old residual hanging pediments, which receive intense insolation, and have mainly cyanobacteria-dominated biocrust.

There are two main general biocrust types: (i) The primo-colonizer cyanobacterial biocrust, which often includes a diversity of small pioneer lichens such as *Endocarpon pusillum*, *Fulgensia desertorum* and *F. poelti*. This type is widespread, appearing in any orientation, although it dominates sun-exposed areas because it produces sunscreen pigments (Miralles et al., 2017). (ii) Lichen-dominated biocrust, which is thicker and rougher, develops mainly in the shadier slopes and includes an important diversity of lichens such as *Squamarina lentigera*, *Diploschistes diacapsis*, *D. ocellatus*, *Buellia zoharyi*, *Lepraria isidiata*, *Squamarina cartilaginea*, *Fulgensia fulgida*, and others (Lázaro et al., 2008). These biocrust types widely overlap in intermediate orientations (East and West) but they are spatially discriminated in the sunniest orientations and the shadiest. Biocrust, often lichenic, is the main cover in stable upper hillslope sectors, where soil water storage is low because runoff exceeds run-on, and biocrust can out-compete vascular plants. No biocrust develops in the slopes undergoing erosion (Lázaro et al., 2000; Cantón et al., 2004).

Except for some small isolated cultivated fields in terraces close to channels, the main uses of the site are to serve as a natural setting for movies and advertisements, hunting, hiking and scientific research. Fig. 1 shows the location of the study area, as well as several asymmetric catchments with biocrust and vegetation pattern.

2.2. Asymmetry analysis at El Cautivo field site

To explore the catchment asymmetry phenomenon at El Cautivo site, we used a 1 m resolution digital elevation model (DEM) built from elevation points acquired from an airborne LiDAR survey, with a resolution of 4 points per m² (see Rodríguez-Caballero et al., 2015a for further details). The DEM was used to extract the main channel network within the area and from this we identified different units containing paired hillslopes by selecting transversal areas including both opposite hillslopes every 50 m of channel. In addition, total covers of cyanobacteria-dominated biocrusts, lichen-dominated biocrusts and vegetation were obtained from the surface cover quantification performed by Rodríguez-Caballero et al. (2014). In this study we used a hyperspectral CASI image acquired in 2014 to calculate the subpixel cover of lichens, cyanobacteria, bare soil and vegetation by combining a support vector machine classification with linear mixture analysis, and the results were further validated by comparison with coverage values measured in 60 (4.5 × 4.5 m) field plots. The CASI image was also used to calculate the normalized difference vegetation index according to Eq. (1) (NDVI, Tucker, 1979), and the potential incoming solar radiation was calculated using the DEM and a geometric solar radiation model implemented in ArcGIS Solar Analyst by assuming a constant transmissivity of 0.5 (Fu and Rich, 2002). It has been demonstrated that the accuracy of incoming solar radiation estimates can be improved by applying empirical methods such as those described by Srivastava et al., (2021). However, our objective was to calculate a proxy of thermal and soil moisture microclimate between opposite hillslopes (Durham et al., 2018; Suggitt et al., 2018), and not to perform an exhaustive evaluation of the solar resource. For this reason and because atmospheric transmissivity varied at coarser spatial scales than the scale of our comparison, we decided to use a constant parameter of 0.5 to simplify the estimation of this parameter.

$$NDVI = (R_{850} - R_{670})/(R_{850} + R_{670}) \qquad (1)$$
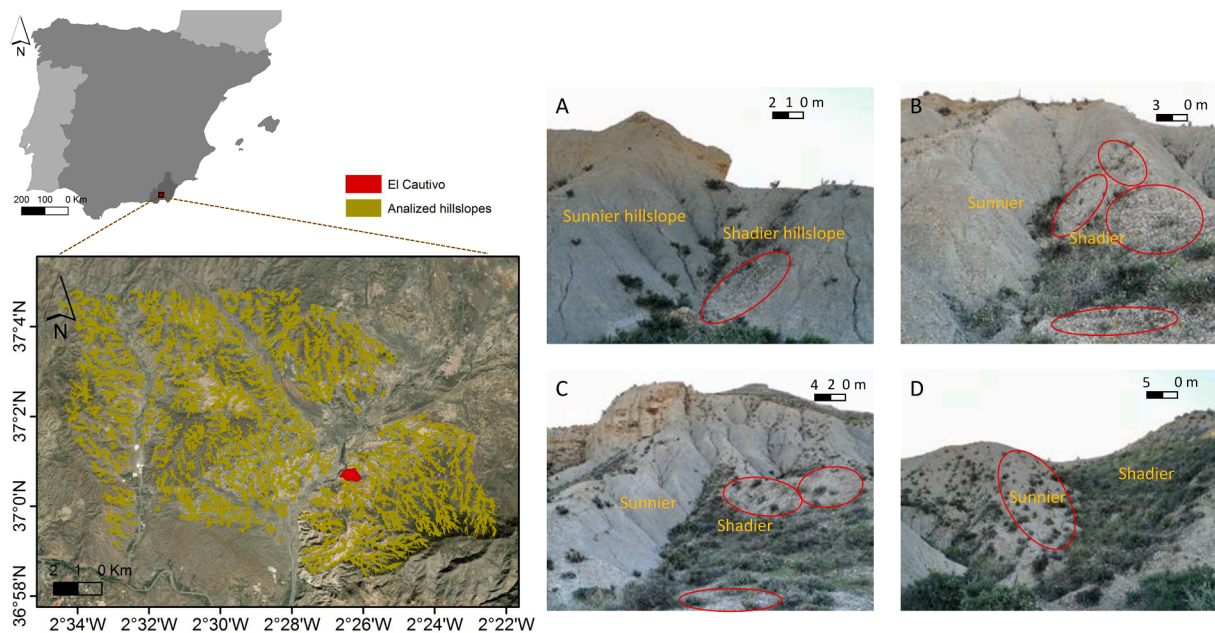
Fig. 1. In the upper-left corner, situation in Spain of the Almeria province and the study area (red rectangle). In the lower-left corner precise location of the study area, showing both the analysed catchments, in the core Tabernas Desert, and the El Cautivo field site (in red). Photos A and B are catchments showing progressively increased biocrust and negative asymmetry. In A, the plants in the slopes are *Salsola genistoides*, almost the only species growing in the eroded habitats of this region. In B, some other plant species appear on the shadier hillslope stabilized by biocrust. C shows a mature negative asymmetry with the shadier (NE oriented) hillslope gentler and vegetated. D shows a mature positive asymmetry with the shadier hillslope full of vegetation but steeper, because the sunnier is part of an area whose relief has been lowered by being between two channels. Red ellipses highlight biocrusts, checked in field, since distance does not allow distinguishing lichens independently from resolution. Since the photos have perspective, their scales are indicative.

where NDVI is the normalized difference vegetation index, and R_{850} and R_{670} are reflectance values at 850 (near infrared) and 670 (red) nm wavelet.

Using these layers, we calculated, for each single hillslope, the mean value of slope gradient, the mean annual potential incoming solar radiation considering topographical shadows, the mean coverage of biocrusts and vegetation and the NDVI which has been described as an indicator of both vegetation and biocrusts coverage and biomass (Rodríguez-Caballero et al., 2015b). We also estimated the channel slope of the section corresponding to each single couple of hillslopes (hereafter "sub-catchment") and the sub-catchment area, as the sum of the area of both hillslopes.

Sub-catchment asymmetry was quantified by using a Normalized Difference Asymmetry Index (NDAI) defined as the normalized ratio of the slope gradient between the hillslope with lower incoming solar radiation and the sunnier hillslope (Eq. (2)).

$$NDAI = (Slope_{shadow} - Slope_{sun})/(Slope_{shadow} + Slope_{sun}) \qquad (2)$$

where $Slope_{shadow}$ and $Slope_{sun}$ are the slope angle of the shadier and the sunnier hillslopes, respectively.

This index ranges from −1 to +1. Catchment asymmetry having a steeper sunnier slope has negative values for the index, whereas positive values indicate a steeper shadier slope. The larger the absolute value of the index, the stronger the asymmetry. Normalized difference ratios for vegetation cover (ND-Veg), biocrusts cover (ND-BSC), total biotic cover (summation of biocrusts and vegetation; ND-biotic), NDVI (ND-NDVI) and potential incoming solar radiation (ND-Sol) were also calculated as the normalized ratio of each variable between its value in the hillslope with lower incoming solar radiation and that in the sunnier hillslope. Thus, they represent the contrast in these parameters between hillslopes with lower and higher potential incoming solar radiation, with negative values indicating lower cover and NDVI on sunnier slopes and positive values indicating the opposite pattern. The cover data were obtained from Rodríguez-Caballero et al. (2014).

This asymmetry index is similar to that used by Poulos et al. (2012) and several other authors but we find it advantageous to normalize the index rather than use its logarithm, as in this way we can compare not only the direction but also the magnitude of the index between different pairs of hillslopes. After calculating the NDAI for every sub-catchment, we generated an asymmetry map of El Cautivo by overlapping the sub-catchment datasets into a 10 cm orthoimage of the area acquired in 2014. We also explored the frequency distribution of the NDAI values over the area, and how it varies depending on the catchment order.

Finally, we built a structural equation model (SEM) to analyse indirect effects of biotic and geomorphological features on catchment asymmetry. The proposed model was based on our initial hypothesis that considered, channel slope, ND-Sol, ND-biotic (including both vegetation and biocrusts) and their interrelationships as potential factors describing NDAI (Fig. 2).

As runoff often shows fairly limited routes in this area (Lázaro et al., 2015), we included in the model the sub-catchment area; but also the catchment area, defined as the area of the catchment upstream of every considered point, since it is expected to have both direct and indirect influence. Finally, we included the ND-NDVI as a factor controlled by biotic components (total cover of both vegetation and biocrusts), as demonstrated by Rodríguez-Caballero et al. (2015b) that we hypothesise as having an effect on NDAI. This gives us the possibility to use this index to explain the joint effect of the biotic components (vegetation and biocrusts) and to extrapolate it to the entire Tabernas Desert, where information about cover distribution is not available. Since most vascular plants develop where biocrusts had previously occurred (Lázaro et al., 2008; Rodríguez-Caballero et al., 2019), we can assume that biocrusts have an effect on asymmetry development at least where NDVI has an effect (see Discussion). Goodness of fit of observed to expected covariance structures was assessed by χ^2 and, because this test is prone to some statistical problems, two alternative indexes were used to provide an accurate fit to the data: the Non-Normed Fit Index (NNFI) (Bentler and Bonett, 1980), and the root mean square error of approximation (RMSEA) (Browne and Cudeck, 1992). Significant χ^2 results
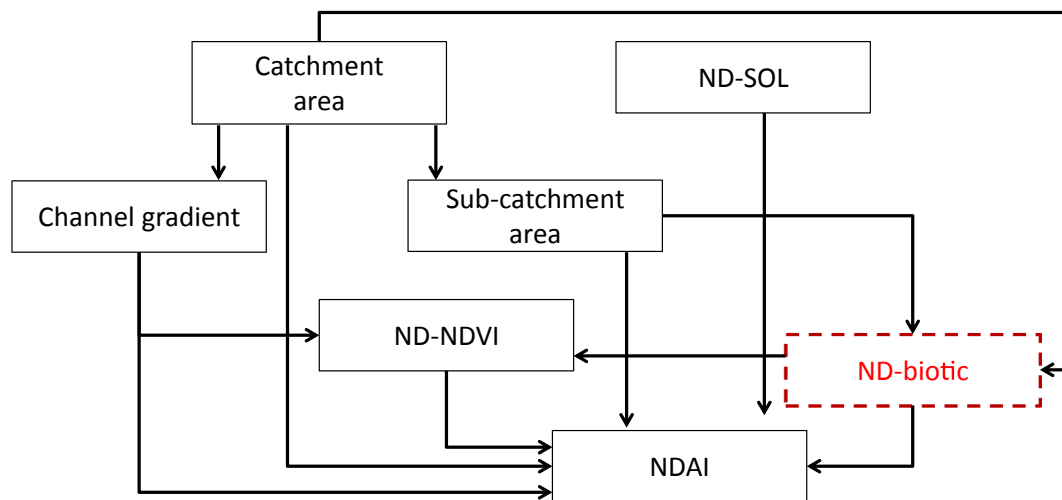
Fig. 2. Hypothetical meta-model showing causal relationships among the main factors affecting the Normalized Difference Asymmetry Index (NDAI) and the NDAI based on our initial hypothesis. Individual factors considered and the inter-relationships among them are defined in Section 2.2 of the main text. Factors included within the dashed red box are only considered for the El Cautivo area, as they are not available for the entire Tabernas desert.

indicated that the model did not fit the data, whereas, values over 0.9 NFI and below 0.05 for the RMSEA indicated that the model was good. SEM was developed and tested with SPSS AMOS 18 software (AMOS Development Corp., Mount Pleasant, South Carolina, USA).

We used cover data of bare (eroded) soil, cyanobacterial biocrusts, lichenic biocrusts and vascular vegetation obtained from Rodríguez-Caballero et al. (2014) to explore the relationships between covers and different hillslope aspects. We then checked the association between the covers of biocrust and vegetation and the catchment asymmetry as measured by the NDAI by examining the regression between ND-NDVI and ND-BSC and NDAI.

2.3. Empirical data on differential surface stability

To verify if an initial abiotic surface stabilization occurs, we performed a field campaign to check whether slope differentiation starts before biocrust colonization by taking field data of surface temperatures and firmness. These features were selected because high temperature values are expected to represent more intense desiccation cycles, and firmness is a good surrogate of stability. To do this, we identified 12 underdeveloped catchments (incisions of decimetres to approximately one metre deep); three for every aspect West, East, South and North. In each slope of the different underdeveloped catchments we performed six measurements using a Taylor Instant-Read Digital Pocket Thermometer and six measurements with a Bertuzzi Pocket Penetrometer for fruits. All measurements were made on dry soil conditions and during the first hours of the afternoon, within a period of a few days. We used ANOVA to test for differences between the shadier and the sunnier incipient hill-slopes with regard to the surface temperature and surface firmness, within every orientation as well as with the entire dataset together. Since biocrust grows better in east than in west aspects (due to two causes: (i) east has lower temperatures and evaporation; and (ii) east receives light during the early morning when temperatures are lower and some nocturnal moisture or dew still remains), in the rills having south and north direction we considered the east-facing incipient hill-slope to be the shadier.

2.4. Asymmetry analysis on the entire Tabernas Desert

To explore whether our hypothesis is a local phenomenon or affects the entire Tabernas Desert, we analyzed catchment asymmetry in the core Tabernas Desert, an area of approximately 17 km (longitude) $\times$ 13 km (latitude), which included 23 different basins. Detailed topography

for the Tabernas Desert was obtained from LiDAR data available in www.cnig.es, dating from 2014. All the points corresponding to ground surface were selected to build a DEM, 1 m resolution, by interpolating the elevation data by means of the IWD algorithm available in ArcMap. For this spatial scale, 'sub-catchment' was each transversal area between junctions including both opposite hillslopes. Headwaters cannot be included because they are a concave form, and do not include a pair of opposite slopes and a channel. Large used or disturbed areas (gas station, dual carriageway, parking…), as well as the main Rambla of Tabernas bed and disturbed surroundings, have been erased to avoid including non-natural topography. From the DEM we calculated the NDAI and all related variables, following the same process described in Section 2.2. Detailed information of biocrust and vegetation coverage is not available for the entire Tabernas Desert; thus we only considered the NDVI as a proxy of surface biotic cover.

This information was used to verify if the asymmetry pattern observed at El Cautivo predominates in the entire region and to explore the frequency distribution and spatial pattern of asymmetry by constructing an asymmetry map and calculating how frequent are the different NDAI values within each catchment order.

In addition, we tested our SEM model with the entire dataset based in the same model of Fig. 2, but not considering vegetation and biocrust coverage. The SEM analyses did not include sub-catchments located in the headwater of any catchment, nor those located in clearly disturbed or artificial areas. In addition, those with no information for any of the variables or with sub-catchment or hillslope size smaller than three pixels were removed. This led to a final dataset of 1701 sub-catchments widespread across the entire study area. This dataset was divided in two different sub-datasets: sub-catchments with steeper sunnier hillslope (negative NDAI values) and sub-catchments having steeper shadier hillslope (positive NDAI values). The SEM model was tested in each individual basin (with $n > 7$) and sub-dataset separately (23 basins $\times$ 2 sub-datasets). This gave us the possibility to analyse our hypothesis in both types of asymmetry and in basins of different size and complexity while avoiding the effect on catchment asymmetry of another important factor, lithology, since it is quite homogeneous throughout the study area.

2.5. Visual verifications

Because our initial hypothesis only explained the negative asymmetry, in a second phase we examined, in the field and/or by Google Earth, (which enables observation at different resolutions and from

different direction), all of the positive asymmetries at El Cautivo, and in the 66 subcatchments across the Tabernas Desert having the largest positive NDAI. We distinguished five categories of positive asymmetries: (i) Artefacts, due to the automatic nature of the procedure used to map the asymmetries (i.e., in some places the sunnier hillslope, although steeper, is very short and may not have been taken into account; or there is a pediment over it that can have decreased the overall slope; or the shadier hillslope has been paired with a tilted valley bottom). (ii) Human activities. (iii) Asymmetry cannot be seen with certainty with the naked eye. (iv) A meander undermines the base of the shadier hillslope. (v) The rest of the cases: mainly topography or a style of eroded hillslope evolution other than parallel retreat.

3. Results

3.1. Asymmetry analysis at El Cautivo field site

Fig. 3 shows asymmetry distribution within the El Cautivo area. As observed, most of the sub-catchments within El Cautivo are asymmetric, with dominance of negative asymmetries (68% of analysed sub-catchments), while positive asymmetries (red) are fairly infrequent, although covering a relatively wide range of NDAI.

Fig. 4 provides evidence of the large dominance of negative asymmetries at El Cautivo, because it shows that the steepest slopes are clearly concentrated in the south orientations. Fig. 4 also evidences that, while biocrusts (including all types) can be found in any orientation, the cyanobacterial ones are particularly able to dominate the sunny surfaces (if they are stable enough), whereas the late-successional lichenic biocrusts, having the larger protective effects, are more abundant in shadier aspects, following a pattern similar to that of the vascular vegetation,
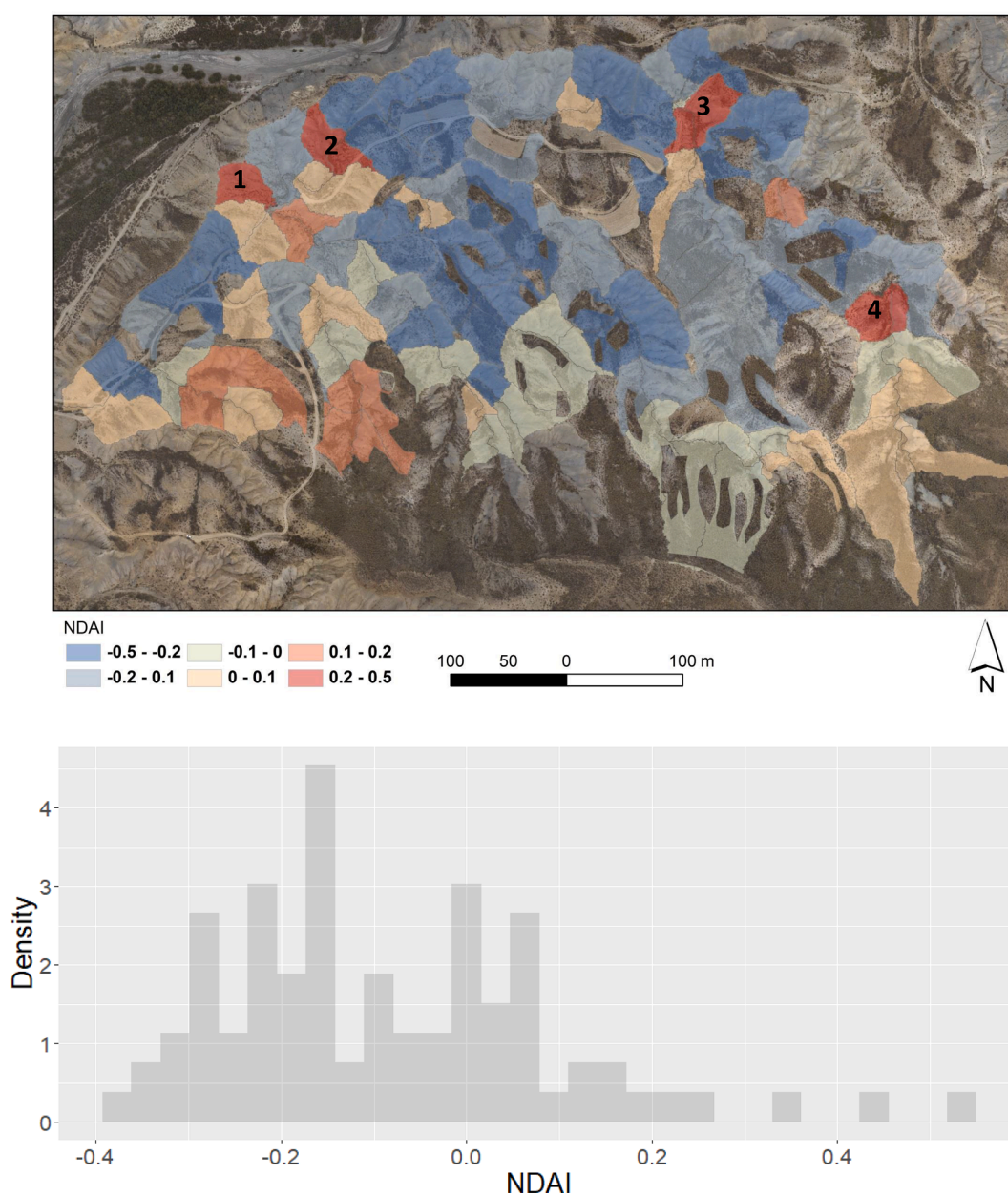

Fig. 3. Catchment asymmetry map of El Cautivo field site (upper part) along with frequency and distribution of every level of asymmetry (lower part). Most of the asymmetries were negative, but we found four positive cases (in red in the map), which are numbered because their causes are commented on later.
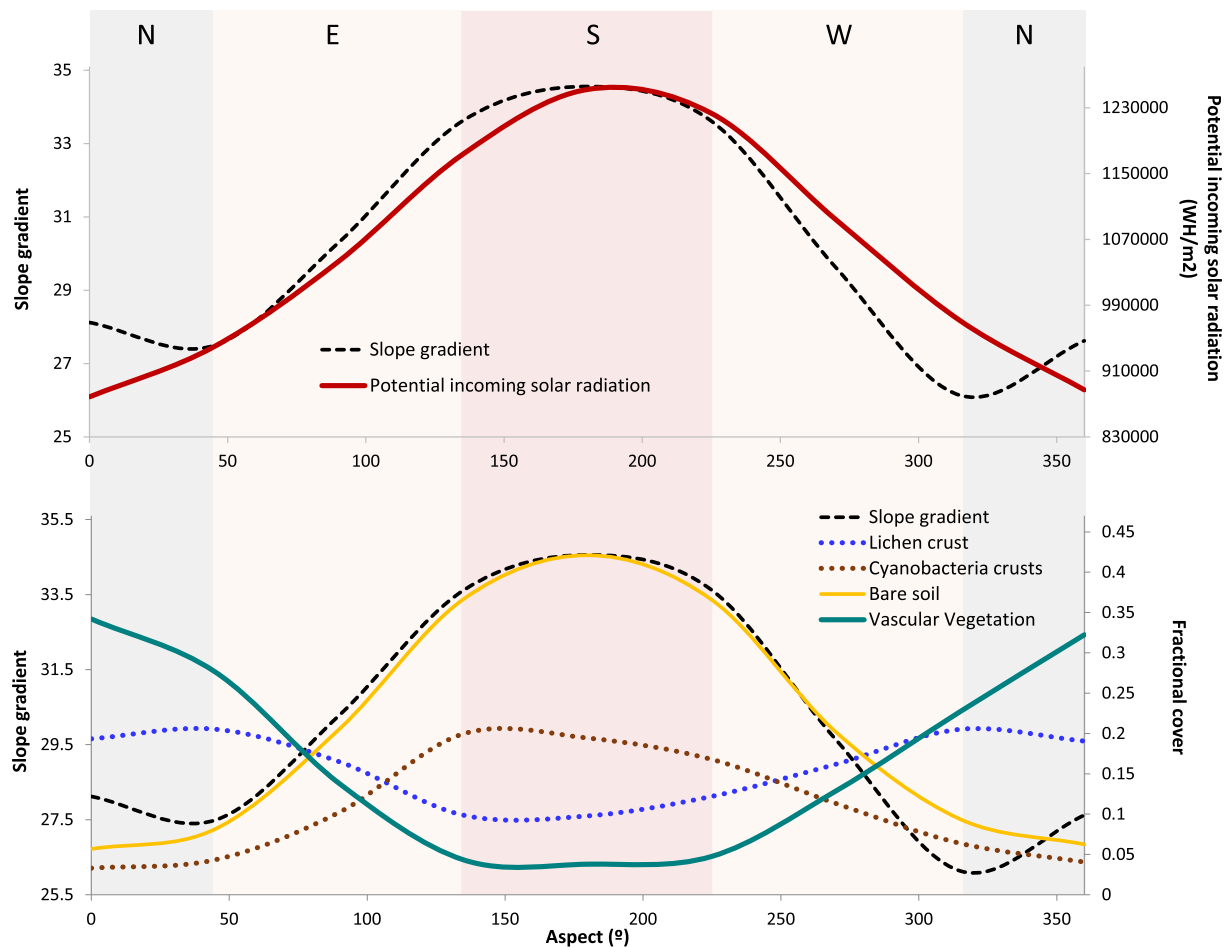
Fig. 4. Average values of slope angle and potential incoming solar radiation for different hillslope aspects (N = 0 and 360, E = 90°, S = 180° and W = 270°) (upper graph), and variations in covers of bare (eroded) soil, cyanobacteria-dominated biocrusts, lichen-dominated biocrusts and vascular vegetation for different hillslope aspects (lower graph). Covers were obtained from Rodríguez-Caballero et al. (2014).

although attenuated. Fig. 4 could give the false impression that cyanobacteria are in steeper places than lichens; in fact, the mean slope of the lichen biocrust is higher. What happens is that cyanobacteria dominate in stable and fairly flat areas such as the pediments between ravines receiving strong insolation, which appear in the same region of the graph as the eroded south facing slopes.

We found four positive asymmetries at El Cautivo (red patches in the map, Fig. 3; named 1–4 from west to east). At 3, positive asymmetry was caused by humans: the sunnier slope is mostly an old track. The rest of the cases belonged to the category 'v': At 1 and 4, the sunnier hillslope is a reduced area between two channels, where relief decreases as it is eroded on both sides. At 2, the sunnier hillslope had not suffered a parallel retreat but became gentler due to a larger and deeper development of its drainage net.

The SEM with all the sub-catchments of El Cautivo (n = 84; Fig. 5) explained 59% of the NDAI variance. As observed, catchment asymmetry is strongly influenced by biotic components, this effect being mainly explained by the spectral index NDVI. The higher the contrast in NDVI (ND-NDVI) and biotic components coverage (ND-Biotic) the more negative the NDAI. Abiotic factors, such as sub-catchment area, catchment area and channel slope, also have negative total effects on catchment asymmetry. However, this is less relevant than the influence of the biotic components (Fig. 5b), due to the opposite sign of the direct and indirect (through their influence on the distribution of the biotic components) effects of the abiotic variables on NDAI. For example, sub-catchment area and channel gradient have a direct positive effect on NDAI and an indirect negative effect through biotic components,

whereas catchment area and ND-SOL showed the opposite pattern: a direct negative effect and an indirect positive effect (Fig. 5b). It is also worth mentioning that most of the effect exerted by the biotic components on NDAI can be explained by their influence on ND-NDVI. Thus, we can consider NDVI as a good proxy of the influence of vegetation and biocrusts on NDAI.

Fig. 6 helps to understand the features of the association between differential covers of biotic components of the system and asymmetry. We used normalized difference of NDVI to represent the distribution of all biotic components between opposite hillslopes (graph on left), as well as the relationship between the normalized difference of biocrust cover between opposite hillslopes and asymmetry (graph on right). Taking into account the definition in Eq. (2), negative values of the Asymmetry Index correspond with positive ND-NDVI or ND-lichen cover, since NDVI and lichen cover are larger in shadier hillslopes in this region. However, ND-cyanobacterial cover shows the opposite pattern. The biocrust-cover difference occupies a wide range of the asymmetry index due to the complementary role of the lichenic and cyanobacterial biocrusts: Regression of lichen-dominated biocrusts cover is more associated with negative asymmetries, has negative slope with regard to the NDAI and approaches the form of vascular vegetation and general NDVI. Whereas the regression of cyanobacterial biocrust has a positive slope, being the main biocrust associated with positive NDAI, and having a distribution which is intermediate between that of lichens and that of bare soil (see Fig. 4). Due to that complementarity, if we carry out the regression with the normalized difference of total biocrust cover (lichens plus cyanobacteria) the cloud of points ranges from −0.2 to 0.4 NDAI, and the
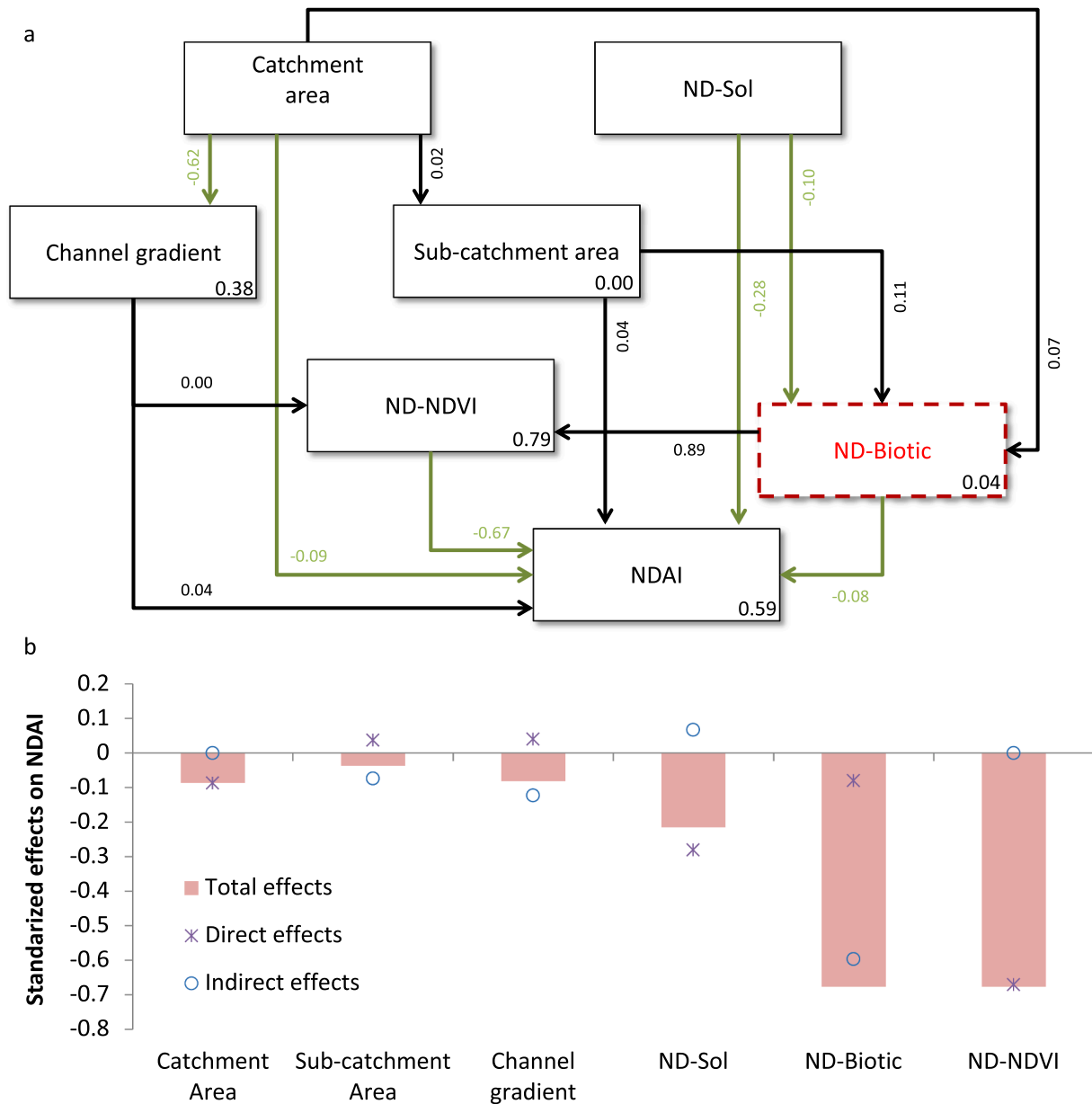
Fig. 5. Final SEM for the total dataset of 84 subcatchments within El Cautivo area. Graph a: Green and Black lines represent negative and positive effects, respectively. Graph b: bar plot showing total (bar), direct (small circle) and indirect (small 'x') standardized effects of different biotic and abiotic factors on the normalized difference asymmetry index (NDAI).

regression line is very slightly positive (y = 0.0696 × + 0.0156).

3.2. Differential surface stability

The analysis of surface stability in underdeveloped catchments reveals larger values of temperature and lower surface firmness in sunnier than in the corresponding shadier slopes (Table 1). According to the ANOVAS, differences between sunnier and shadier were significant in all the cases for both temperature and firmness. As these opposite hillslopes were incipient, the actual difference in orientation between them was not very large and the general orientation of the hillslope in which the rill was growing also had an influence (see the channel with south direction in Table 1). Thus, the differences according to channel direction were moderate. When all the data were analysed together, differences between sunnier and shadier for both variables were highly significant.

3.3. Asymmetry analysis on the entire Tabernas Desert

The spatial distribution of asymmetry through the 23 analysed basins in the Tabernas Desert, as measured by the NDAI for every sub-catchment, gave rise to the map with 6418 sub-catchments shown in Fig. 7 A. This result shows that catchment asymmetry is a general phenomenon in this area, occurring frequently in a range of stream orders, catchment sizes, and drainage directions, consistently with that suggested by field observation. While at El Cautivo, most of the asymmetries had negative NDAI (the steeper slope being the sunnier), at the entire Tabernas Desert scale we found that steeper sunnier and shadier slopes occurred with comparable frequency. In fact, approximately 25% of the sub-catchments were symmetrical, 40% demonstrated negative asymmetry, the steeper hillslope being the sunnier (equator-oriented) and, about 35% of the sub-catchments were found to have positive NDAI, the steeper hillslope being the shadier (pole-oriented). All asymmetry types were distributed all over the area and, for both
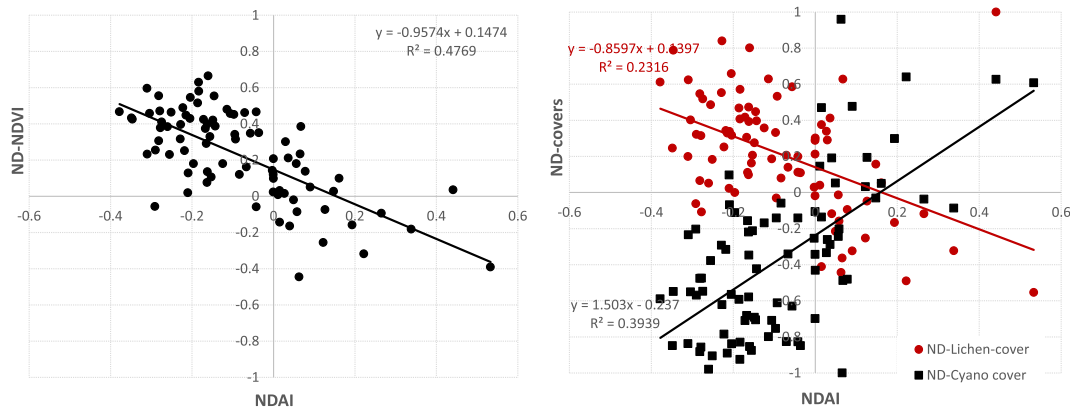
Fig. 6. Regressions of biotic factors *versus* asymmetry index (NDAI) at El Cautivo. The graph on left shows the normalized difference in NDVI between opposite hillslopes (ND-NDVI). The graph on right shows the normalized differences between opposite hillslopes in cover of lichen-dominated biocrust (red) and cyano-bacterial biocrust (black).

Table 1
Surface temperature and firmness in opposite incipient hillslopes of rills developing with different orientations.

Channel direction	Temperature °C			Firmness kg/cm^2		
	Shadier	Sunnier	p	Shadier	Sunnier	p
West	19.53	28.75	0.0111	6.69	4.84	0.0343
East	11.83	30.99	0.0000	7.33	4.85	0.0031
South	26.83	34.65	0.0005	7.20	4.86	0.0114
North	17.77	31.28	0.0000	9.00	4.33	0.0000
All data together	18.99	31.42	0.0000	7.56	4.72	0.0000

For both variables, the "p" values are the significance of the ANOVAS comparing shadier *vs* sunnier incipient hillslopes.

negative and positive asymmetries, the frequency of sub-catchments that present it decreases as the intensity of the asymmetry increases. We also found that asymmetry is clearly dependent on the order of the catchment, being much more frequent in those of low order (Fig. 7B). Furthermore, the relationship between slope angle and aspect strongly depended on the basin size. At all the small basins (numbered 2, 4, 5, 14, 16, 17, 18, 20 and 21 in Fig. 7) and half of the medium-size basins (7, 10, 15) slope clearly varies with orientation. However, at the larger basins it hardly varies (11, 13, 22, 23) or not at all (6, 8, 9, 12).

The three catchments types (no asymmetry, positive and negative) coexist in the Tabernas Desert. Of the 66 positive asymmetries examined across the Tabernas Desert, 26.66% were artefacts, and in 13.33%, the asymmetry was too weak to be clearly appreciated by the naked eye. Human activities (earth movements) explained 16.66%, and a meander undermining the base of the shadier hillslope explained 8.33%. The remainder (35%) were due to topographic reasons or to different styles of eroded hillslope evolution.

The detailed analysis of the main drivers of hillslope asymmetry in the entire Tabernas Desert area shows differences in comparison with the detailed analysis of El Cautivo. The results of the SEMs carried out separately for the sub-catchments with negative and positive asymmetry within every basin are summarized in Fig. 8. This figure shows several important results: (i) The Standardized Total Effect of channel slope was negative for both types of asymmetry, thus the relationship between the channel slope and the asymmetry is negative indicating that steeper channel slopes produce less asymmetry. This occurs because steeper channels increase erosion in the whole catchment, decreasing the ability of biocrusts and vascular vegetation to develop cover and neutralize erosive forces. (ii) Catchment area and sub-catchment area have opposite effects on asymmetry, positive in the case of the former and negative in the case of the latter. (iii) Small differences in solar radiation have

important consequences for NDVI, which shows larger differences, suggesting biotic-driven feedbacks producing divergence between opposite hillslopes; and (iv) NDVI is the only factor that behaves differently in each class of asymmetry. In negative asymmetries, the more NDVI, the greater asymmetry. However, in positive cases, vegetation slows down asymmetry development, as it goes against the preferences of the vegetation; thus, the relationship is negative.

4. Discussion

Catchment asymmetry is a global geomorphological phenomenon that can occur due to several causes. It includes information about ecohydrogeomorphological processes (McGuire et al., 2014), and is in the cutting edge of geomorphological knowledge (Langston and Tucker, 2018). Although catchment asymmetry is more frequent in temperate drylands, where biocrust can be the main soil cover, very little is known about the effect of biocrusts on these processes. Hereafter we provide evidence that the asymmetry is a general phenomenon in the Tabernas Desert (semiarid SE Spain), being able to be 'negative' (the sunnier hillslope being the steeper) or 'positive' (the shadier hillslope being the steeper), and that biocrusts are among the main drivers generating it. At El Cautivo, asymmetries were mainly negative but the frequency of positive asymmetries in the rest of Tabernas Desert allowed us to propose a conceptual model that improves our initial hypothesis and the hypotheses of Richardson et al. (2020) and by Istanbulluoglu et al. (2008).

4.1. Factors controlling catchment asymmetry distribution

Since most lichens in the region are light in colour, if not white, the contribution of biocrusts to the NDVI is relatively poor, but not zero (Rodríguez-Caballero et al., 2015b; Román et al., 2019), therefore the NDVI is probably an underestimate of the total cover of vegetation plus biocrusts. On the one hand, field observation often shows asymmetry associated with high biocrust cover, and that biocrusts are primo-colonizers (Lázaro et al., 2008). Also, while very few plant species present a resistance strategy that allows them to grow in eroded regolith, where they have limited effect on the substrate, most of them do improve their habitat (for example by contributing organic matter and enhancing soil aggregation, and by smoothing out fluctuations in soil temperature and moisture), but require a minimum of soil development and stability in order to establish (Gallart et al., 2002), and these minimums are usually provided by biocrust (see in the Section 4.2). Thus, we can assume that biocrust has an effect on asymmetry at least where NDVI is shown to have an effect on it according to our Structural Equation Models.
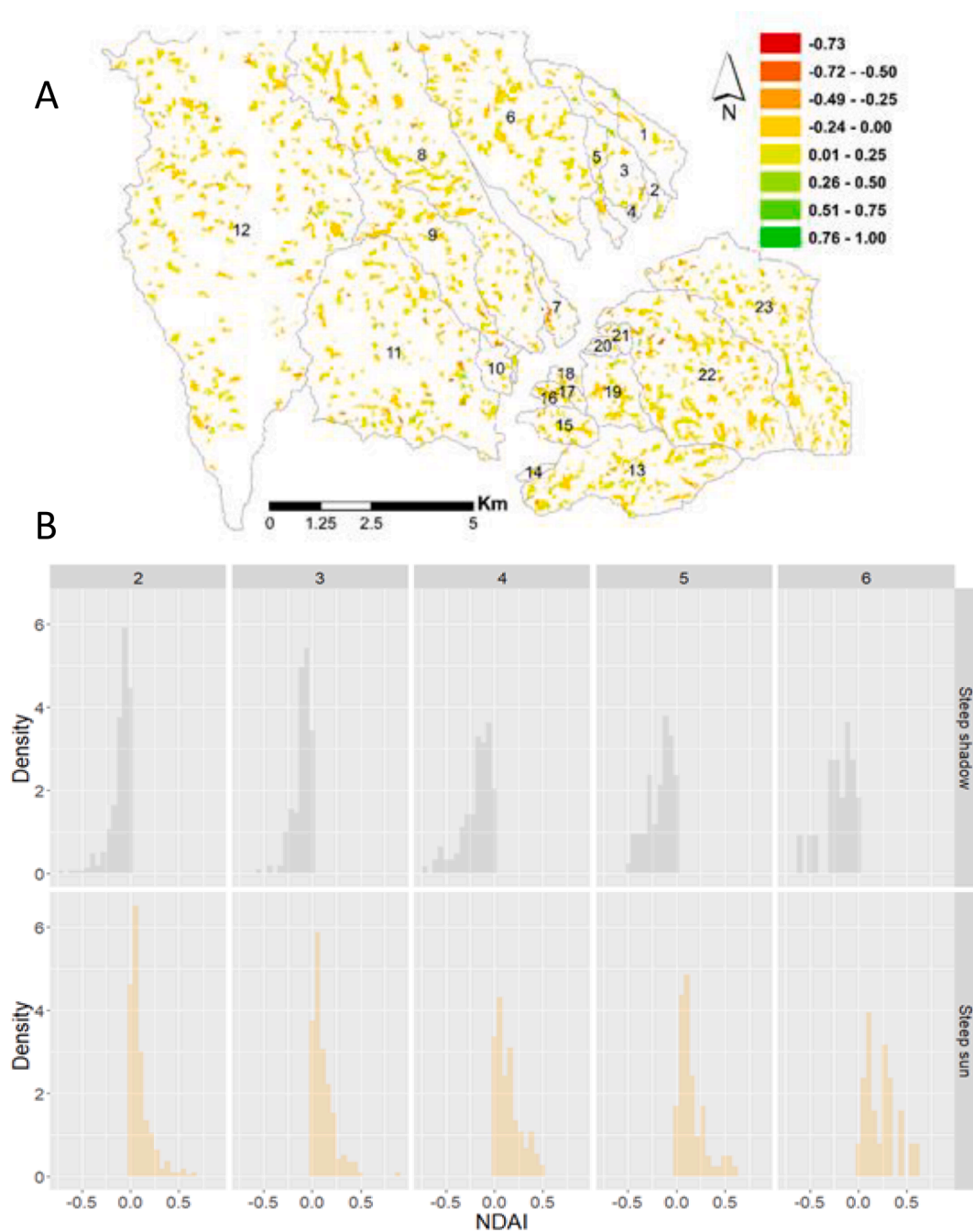
Fig. 7. A. Map of degrees and directions of asymmetry in sub-catchments within every basin of the entire study area, the core Tabernas Desert, semiarid SE Spain. Numbers on the map identify the different basins; basin 20 correspond with El Cautivo field site. B. Frequencies, expressed as probability density, of the different degrees of asymmetry according to the catchment order, for every asymmetry type (negative and positive).

Data from El Cautivo demonstrated that biotic components are the main factor controlling NDAI and that NDVI is a good proxy accounting for most of the biotic effects, to be used at a general scale. A seasonal reversal of the aspect-driven NDVI values has also been described as a result of the transition from water-limited to energy limited conditions during wet winters (Kumari et al., 2020). However, our study area is a badlands where sunnier hillslopes are almost always eroded and seasonal variation of NDVI (mainly due to the leaf fall during the dry season of many of the dwarf shrubs) never implies alternation of greenness between opposite hillslopes. At El Cautivo, solar radiation, contributing area, and channel slope were also important factors for NDAI. Except for biocrusts, all these factors are known to be main drivers affecting hillslope processes (Lázaro et al., 2008; Poulos et al., 2012; Richardson,

2015; Richardson et al., 2020; Roering et al., 2010; Yetemen et al., 2015b). The findings presented here agree with Melton (1960) as asymmetries occurred at intermediate values of channel gradient, as well as with low order channels (as stated by Johnstone et al., 2017). Our results strongly suggest the relevant role of sediment transport (West et al., 2014; Yetemen et al., 2015a), as differential transport controls the decoupling of one of the hillslopes generating the asymmetry. Although a soft lithology strongly favours asymmetry formation (Johnstone et al., 2017; Poulos et al., 2012), we have not explicitly included lithology because its hardness is low throughout our study area.

At global scale, where structural or tectonic factors are not important, catchment asymmetries are common, but the steeper hillslope is
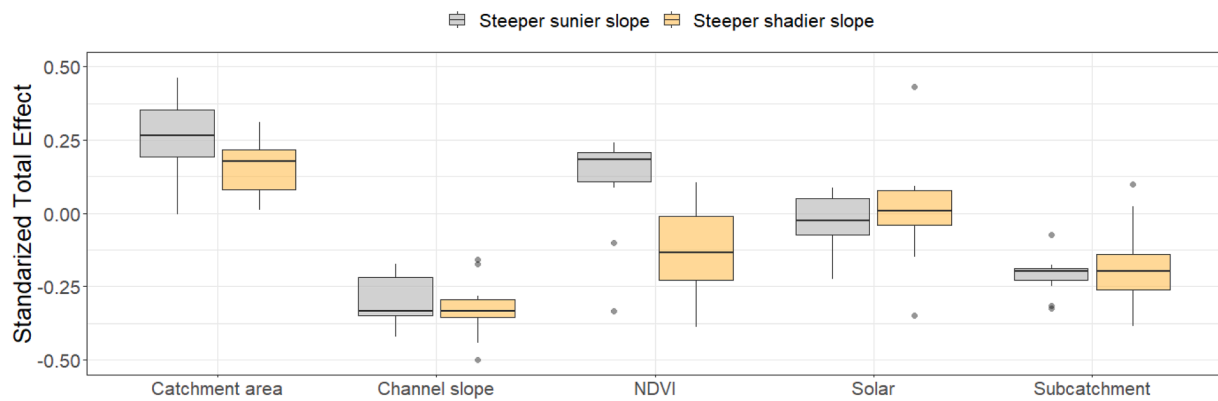
Fig. 8. Standardized total effects of the main factors describing asymmetry according to our hypothetical causal model (Fig. 2). Boxplots represent 25–75% intervals of standardised total effects obtained by the application of the model to the 23 different basins, whereas bars represent the 5–95% interval. Sub-catchments with negative asymmetry are represented in grey while positive asymmetry is in yellow.

sometimes the pole-facing, and sometimes the equator-facing one. In some cases, its aspect is due to the location, for example, the north-facing slope being the steepest in Alaska (Currey, 1964). But catchment asymmetries seem to occur mainly in drylands from 45°S to 45°N (Yetemen et al., 2015a). In this context, the pole-oriented hillslope has the best microclimate for vegetation (Rodríguez-Caballero et al., 2019). However, that vegetation preference does not always determine the direction of the asymmetry. In South Dakota (Badlands National Park, USA), Churchill (1981) found steeper, rectilinear, often shorter south-facing slopes due to high efficiency of material removal on the basal pediment. In semiarid north-eastern Arizona, the asymmetric catchments also have the south-facing hillslopes steeper (Burnett et al., 2008). Del-Toro-Guerrero et al. (2016), in Mexico, have found that polar-oriented slopes show higher NDVI values than equator-oriented slopes, and they have also noted that the equator-oriented slopes are more dependent on precipitation (Del-Toro-Guerrero et al., 2019). However, In New Mexico (USA), the xeric south-faced slopes show lower vegetation cover and undergo greater erosion, which produces shallower slope angles and pushes the channel laterally to the south, making the mesic north-facing slope steeper (Istanbulluoglu et al., 2008). Johnstone et al. (2017) also found equator-facing hillslopes being gentler, due to the elongation of low-order channels and increased drainage density on them; and the same had been found by Wende (1995) in Germany. Yet, Smith (1978), in western Algeria, found the east-northeast and southwest-west facing slopes much steeper than any others. Thus, to date, the relationships between asymmetry and aspect, as well as between slope and vegetation remain unclear. It seems that there are larger amounts of positive than of negative asymmetries, but the steeper polar-oriented slopes seem to have been found in relatively mesic places (Churchill, 1981). On the other hand, Melton (1960) reported that vegetation and erosion do not produce asymmetry; it is produced by lateral migration of the stream. Richardson (2015) also mentioned lateral channel migration. However, such lateral migration involves lateral erosion, which is necessarily caused by differential erodibility, which is hardly independent from vegetation and soil type.

In the Tabernas Desert, 35% of the positive asymmetries identified belonged to the category 'v'. Initially, we supposed that the retreat style of eroded hillslopes would be always more or less parallel and without sediment accumulation at the footslope, as it is at El Cautivo. Nevertheless, according to the literature, there are at least three mechanisms producing a gentler sunny hillslope despite it being the more eroded and much less vegetated: (i) that the upper part of the slope suffers high weathering because it receives runoff and its texture favours infiltration, exporting sediments, for example due to piping collapses, causing the retreat of the watershed; (ii) the sunnier hillslope became gentler due to a larger and deeper development of its drainage net (Wende, 1995; Johnstone et al., 2017), as occurred with positive asymmetry 2 of El

Cautivo; (iii) the sunny slope is part of a reduced area between two channels; its relief decreasing as it is eroded on both sides, as in cases 1 and 4 of El Cautivo (photo 4 of Fig. 1). Additionally, there is at least one further mechanism producing a similar final result: that the channel describes a curve and its direction moves away sufficiently from the slope line to cause, from the outset, one of the hillslopes to become steeper. Understanding this allowed us to complete our hypothesis.

4.2. The role of biocrust

The geomorphological effect of vascular vegetation, particularly trees (for example, Roering et al., 2010), is well known. However, there is less evidence on the long-term effect of biocrusts on landscape evolution. Biocrusts have been reported to perform multiple functions and processes within the ecosystem (Belnap, 2006; Berdugo et al., 2014; Cantón et al., 2020; Maestre et al., 2011). Some of them are important at the ecosystem scale, in particular that of protecting against erosion (Bu et al., 2013; Chamizo et al., 2012b; Lázaro and Mora, 2014) and those initiating pedogenesis (quotations below in this paragraph). Thus, biocrust can modify landform evolution by: (i) providing soil surface stability, decreasing erosion in two ways: enhancing particle cohesion by living structures and exopolysaccharides (so increasing the number and stability of aggregates) (Chamizo et al., 2012a; Miralles et al., 2017; Rossi and de Philippis, 2015), and by changing the albedo and diminishing temperature (Couradeau et al., 2016; Rutherford et al., 2017) and controlling moisture oscillations (Chamizo et al., 2013). (ii) triggering pedogenesis: changing the physical and chemical soil properties (Belnap and Gardner, 1993; Cantón et al., 2003; Castillo-Monroy et al., 2010; Miralles et al., 2012) and increasing porosity, aeration and infiltration (Miralles-Mellado et al., 2011), increasing soil organic matter (Chamizo et al., 2012a), nitrogen and nutrients (Castillo-Monroy et al., 2010; Delgado-Baquerizo et al., 2013). (iii) by improving soil conditions and facilitating plant recruitment (Escudero et al., 2007; Havrilla et al., 2019; Pendleton et al., 2003), the plants tending to concentrate in the lower part of the hillslopes using extra runoff water from biocrusted surfaces as water supply (Rodríguez-Caballero et al., 2013; Rodríguez-Caballero et al., 2018b).

As Fig. 4 shows, the ability of cyanobacteria to resist high levels of solar radiation (Lázaro et al., 2008; Miralles et al., 2017), allows biocrusts to colonize any aspect. Even, to stabilize the sunnier slope when it decouples from the channel, contributing to slow down the process generating positive asymmetry led by abiotic factors, which allows the biocenosis to occupy a larger space. The geomorphic processes generating negative asymmetry imply ecosystem maturation, because they produce an increase in extension of the vegetated patches, approaching them to their maximum limits imposed by the climate. However, positive asymmetry tends to reduce the vegetated areas.

The biocrusts are primo-colonizers, and their distribution is associated with the development of the negative asymmetry at El Cautivo as we have shown in Figs. 1, 4–6, 8, and 9. Churchill (1981) found in the USA Badlands National Park catchments such as those with negative asymmetry of Tabernas Desert; although he does not explicitly mention the asymmetry, it should exist according to his description of the hillslope morphologies. Also, the photographs in Fig. 4 of that work suggest that the northern slopes have biocrusts in the upper half, while the southern slopes do not.

The results of our SEMs for the entire study area provide evidence of the feedbacks started by biocrusts and reinforced by vegetation and soil development, because very small differences in solar radiation are largely magnified by the NDVI. This agrees with McGuire et al. (2014). NDVI is the only factor having an effect with different sign in negative and positive asymmetries, indicating that, in the positive ones, the asymmetry goes against the preferences of the vegetation.

4.3. The stabilization-colonization hypothesis conceptual model

We have synthesized our completed hypothesis in the flowchart of Fig. 9

Since biocrusts require a minimal soil surface stability to develop (Lázaro et al., 2000; Lázaro et al., 2008; Yair and Lavee, 1985), they often cannot trigger the hillslope differentiation. Thus, our stabilization-colonization hypothesis proposes as first step a divergence in surface stability of the opposite hillslopes due to abiotic causes. This is consistent with previous knowledge: Burnett et al. (2008) found that south-facing slopes were 1.4–5.6 °C warmer and soil moisture tension at 10-cm-depth averages at least 78 kPa lower (drier) than on north-facing. Churchill (1981) found, also in a badlands area, microclimates associated with differential topography-driven incoming radiation leading to hillslope differentiation through differences in weathering or soil stability between opposite slopes. Istanbulluoglu et al. (2008) also revealed larger erodibility in south-facing slopes caused by topoclimate. Our field data confirmed differences in surface temperature and firmness. Thus, radiation-generated microclimatic divergence is a driver of the spatial organization of ecohydrologic fluxes, soil and vegetation patterns and dynamics, and landscape morphology in semiarid ecosystems (Rodríguez-Caballero et al., 2019; Yetemen et al., 2015b).

While the sunnier incipient hillslope has lower stability due to larger temperature and moisture oscillations, hindering colonization, the shadier incipient hillslope allows colonization. Biocrusts are the primo-colonizers (Belnap et al., 2003; Lázaro et al., 2008) and feedback toward negative asymmetry because they largely reduce erosion (up to 10-fold hydric erosion according to Chamizo et al., 2012b; up to 40-fold wind erosion according to Bu et al., 2013). Next, plants establish; they tend to concentrate in the lower part of the hillslope, using runoff from biocrusted surfaces above as extra water supply (Rodríguez-Caballero et al., 2018b), and progressively retain water and sediments that accumulate at the bottom of this incipient hillslope, favouring vegetation and soil development, a process with positive feedback. These feedbacks lead to lateral channel migration towards the sunnier, barely-vegetated and easily erodible slope, developing negative asymmetry. The sunnier hillslope is progressively steep and undergoes a parallel retreat due to a frequent removal of material at the foot slope. Thus, this hillslope, almost void of vegetation, becomes mainly controlled by weathering (Cantón et al., 2001b). Whereas, in the shadier one, the erosion rate is lower, and the retreat process is mainly controlled by transport, which decreases because vegetation causes infiltration to be much higher. Then the slope angle decreases, as an active pediment-like landform progressively develops at the foot-slope. This crucial role of the transport agrees with Yetemen et al. (2015a) and West et al. (2014).

Where channel gradient is strong, the catchment is very active (Melton, 1960) and results in a symmetric form. When channel gradient decreases, biocrusts and vegetation can develop, and the backward movement of the sunny hillslope could produce a concave shady

hillslope independently from the mass movements in that shady slope. This concave form, in its turn, feeds back toward lower erosion (Istanbulluoglu et al., 2008). Besides, this form is reinforced because the shady hillslope undergoes erosive processes too, mainly associated with unusually heavy rains, but the sediments do not always reach the channel (although see Rodríguez-Caballero et al., 2021). When the pediment-like form of the shadier hillslope grows sufficiently, this hillslope becomes practically uncoupled from the channel (Rodríguez-Caballero et al., 2014. This decoupling is crucial. In fact, asymmetry could be defined as the morphologic consequence of the decoupling between the channel and one of the hillslopes whereas the opposite continues coupled. When both hillslopes are coupled, the catchment is symmetric and, when both are uncoupled (when channel gradient approximates to equilibrium and the valley widens in the oldest part of some catchments), asymmetry development ceases, although its shape can remain as relict (Smith, 1978). Thus, asymmetry appears within a certain time–space interval, and depends on the channel gradient, the catchment area and catchment order (as the three are related with the age; Fig. 7). In the Tabernas Desert it is often possible to find this entire sequence within the same catchment.

When local abiotic factors cause a steeper gradient in the shadier hillslope (for example, the basal undermining of a meander, or a change in channel direction to run obliquely across the slope), or a lower gradient in the sunnier hillslope (for example, a non-parallel style in its retreat, often with greater development of the drainage net), a positive asymmetry develops, with biocrusts and vegetation generally acting in the opposite direction to abiotic drivers, and the asymmetry becoming weaker or stronger depending on the ratio between biotic and abiotic forces. Positive asymmetry is evidence that local abiotic factors are more powerful than the biotic ones because vegetation always prefers the shadier habitats (Rodríguez-Caballero et al., 2019) in this region. However, while the development of biocrusts, vegetation and soils feeds back towards the decoupling of the greenest hillslope, a decoupling can also occur for other reasons; thus, the sunnier slope can become disconnected from the channel initiating a positive asymmetry. There would be two kinds of positive asymmetries: those with the shadier hillslope eroded and those not so. The former (8%) occurs when a meander strongly erodes the base of the shadier hillslope. Lateral movement of the channel is probable and, when the sunnier slope becomes gentle enough, and the erosion slows down, it can be colonized by a cyanobacterial biocrust that withstands high insolation (Miralles et al., 2017), and then by some lichens and plants, which could provide some positive feedback to this asymmetry. In the second kind (35–48%), lateral movement of the channel would not necessarily be involved as the sunnier hillslope could lose gradient due to a watershed retreat caused by the development of its drainage network, which, according Shelef and Hilley (2014), has a direct impact decreasing elevation. This asymmetry could be also caused because the shadier hillslope becomes steeper for topographical reasons due to a change in channel direction to run obliquely across the slope. Biocrusts, vegetation and soil development always counteract the abiotic forces that drive towards positive asymmetries but their effects are not always sufficient to overcome the abiotic forces.

5. Conclusion

Our results demonstrated that catchment asymmetry is a very common phenomenon throughout the Tabernas Desert. Three different types of catchment (or, more precisely, stretches of catchments, here named 'sub-catchments') are described based on their asymmetry: symmetric sub-catchments, sub-catchments with asymmetry produced by a gentler shadier hillslope (here named 'negative asymmetry') and sub-catchments with asymmetry produced by the shadier hillslope being steeper ('positive asymmetry'). The occurrence, direction and magnitude of asymmetry are driven by a series of biotic and abiotic factors. Among the abiotic are the solar radiation that reaches the soil, the area
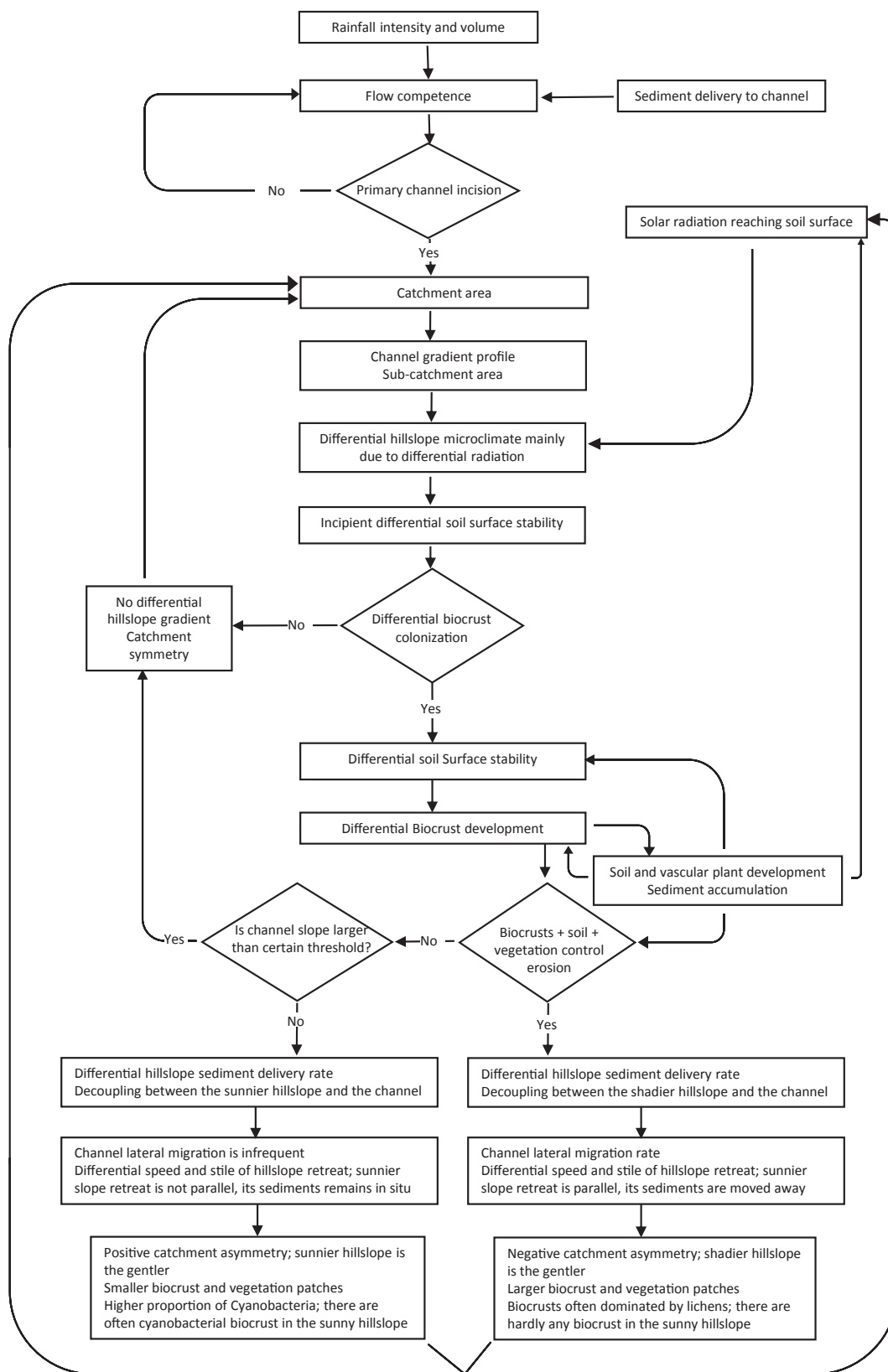
Fig. 9. Conceptual model proposed to explain the sequence of processes developing catchment asymmetry of any sign, explicitly including the role played by biocrusts.

and the channel gradient in the considered sub-catchment, and the total catchment area. Among the biotic factors, biocrusts were found to play an important role by triggering a feedback mechanism consisting of two main processes: (i) control of sediment transport in the shadier hillslope where the greater biomass gives rise to increased infiltration and sediment deposition, developing a pediment-like form that pushes the channel; and (ii) the greater erodibility of the sunnier hillslope, with minimal vegetation cover and sediment deposits at its base being ephemeral. Both processes together drive lateral movement of the channel, causing the formation of a negative asymmetry pattern as observed at El Cautivo experimental field site. However, we found an unexpected proportion of positive asymmetries when examining the entire Tabernas Desert. We hypothesize that positive asymmetries occur against the effects of biotic factors when, for local reasons, abiotic factors are more powerful. A small group of these asymmetries (where the shadier hillslope becomes steeper and fairly eroded because a meander undermines it) could include lateral movement of the channel; while the others do not necessarily require such movement; the sunnier hillslope becoming gentler due to the retreat of the watershed caused by the development of its drainage net. We propose a conceptual model of feedback processes that generate both negative and positive catchment asymmetries, with biocrust playing a crucial role in most of the cases.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Alexander, R.W., Calvo-Cases, A., Arnau-Rosalén, E., Mather, A.E., Lázaro-Suau, R., 2008. Erosion and stabilisation sequences in relation to base level changes in the El Cautivo badlands, SE Spain. Geomorphology 100 (1–2), 83–90.

Alexander, R.W., Harvey, A.M., Calvo, A., James, P.A., Cerda, A., 1994. Natural stabilisation mechanisms on badland slopes: Tabernas, Almeria, Spain, in: Pye, K., Millington, A.C. (Eds.), Environmental change in drylands. Biogeographical and geomorphological perspectives / edited by Andrew C. Millington and Ken Pye. British Geomorphological Research Group symposia series. Wiley, Chichester.

Arnau-Rosalén, E., Calvo-Cases, A., Boix-Fayos, C., Lavee, H., Sarah, P., 2008. Analysis of soil surface component patterns affecting runoff generation. An example of methods applied to Mediterranean hillslopes in Alicante (Spain). Geomorphology 101 (4), 595–606.

Belnap, J., 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. Hydrol. Process. 20 (15), 3159–3178.

Belnap, J., Büdel, B., 2016. Biological Soil Crusts as Soil Stabilizers, in: Weber, B., Büdel, B., Belnap, J. (Eds.), Biological soil crusts: An organizing principle in drylands. Springer, Cham, pp. 305–320.

Belnap, J., Büdel, B., Lange, O.L., 2003. Biological Soil Crusts: Characteristics and Distribution, in: Belnap, J., Lange, O.L. (Eds.), Biological soil crust: Structure, Function and Management, 1st ed., rev. 2nd printing ed. Ecological studies 150. Springer, Berlin.

Belnap, J., Gardner, J.S., 1993. Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. Great Basin Naturalist 53 (1), 40–47UR-.

Belnap, J., Lange, O.L. (Eds.), 2003. Biological soil crust: Structure, Function and Management, 1st ed., rev. 2nd printing ed. Ecological studies 150. Springer, Berlin, 503 pp.

Belnap, J., Walker, B.J., Munson, S.M., Gill, R.A., 2014. Controls on sediment production in two U.S. deserts. Aeolian Res. 14, 15–24.

Bentler, P.M., Bonett, D.G., 1980. Significance tests and goodness of fit in the analysis of covariance structures. Psychol. Bull. 88 (3), 588–606.

Berdugo, M., Soliveres, S., Maestre, F.T., 2014. Vascular plants and biocrusts modulate how abiotic factors affect wetting and drying events in drylands. Ecosystems 17 (7), 1242–1256.

Bishop, P., 2007. Long-term landscape evolution: linking tectonics and surface processes. Earth Surf. Process. Landforms 32 (3), 329–365.

Browne, M.W., Cudeck, R., 1992. Alternative ways of assessing model fit. Sociol. Methods Res. 21 (2), 230–258.

Bu, C., Wu, S., Xie, Y., Zhang, X., 2013. The study of biological soil crusts: hotspots and prospects. Clean: Soil, Air, Water 41 (9), 899–906.

Burnett, B.N., Meyer, G.A., McFadden, L.D., 2008. Aspect-related microclimatic influences on slope forms and processes, northeastern Arizona. J. Geophys. Res. 113 (F3).

Calvo Cases, A., Alexander, R.W., Arnau-Rosalén, E., Bevan, J., Cantón, Y., Lázaro, R., Puigdefábregas, J., Solé-Benet, A., 2009. Interactions of geomorphic processes and components distribution in the soil surface in relation to evolution of badlands in Tabernas (Almería). Cuadernos de Investigación Geográfica 35 (1), 43–62.

Calvo-Cases, A., Harvey, A., Serrano, A., 1991. Process interactions and badland development in SE Spain. M.Sala, J.L. Rubio & JM. García-Ruiz (Eds.), Soil Erosion Studies in Spain. Geoforma Ediciones. Logroño.

Calvo-Cases, A., Harvey, A.M., Alexander, R.W., Cantón, Y., Lázaro, R., Solé-Benet, A., Puigdefábregas, J., 2014. Badlands in the Tabernas Basin, Betic Chain. In: Gutiérrez, F., Gutiérrez, M. (Eds.), Landscapes and landforms of Spain. World geomorphological landscapes, Springer, Dordrecht, pp. 197–211.

Cantón, Y., Chamizo, S., Rodriguez-Caballero, E., Lázaro, R., Roncero-Ramos, B., Román, J.R., Solé-Benet, A., 2020. Water regulation in cyanobacterial biocrusts from drylands: negative impacts of anthropogenic disturbance. Water 12 (3), 720.

Cantón, Y., Del Barrio, G., Solé-Benet, A., Lázaro, R., 2004. Topographic controls on the spatial distribution of ground cover in the Tabernas badlands of SE Spain. Catena 55 (3), 341–365.

Cantón, Y., Domingo, F., Solé-Benet, A., Puigdefábregas, J., 2001a. Hydrological and erosion response of a badlands system in semiarid SE Spain. J. Hydrol. 252 (1–4), 65–84.

Cantón, Y., Domingo, F., Solé-Benet, A., Puigdefábregas, J., 2002. Influence of soil-surface types on the overall runoff of the Tabernas badlands (south-east Spain): field data and model approaches. Hydrol. Process. 16 (13), 2621–2643.

Cantón, Y., Solé-Benet, A., Queralt, I., Pini, R., 2001b. Weathering of a gypsum-calcareous mudstone under semi-arid environment in SE Spain. Laboratory and field-based experimental approaches. Catena 44 (2), 111–132.

Cantón, Y., Solé-Benet, A., Lázaro, R., 2003. Soil–geomorphology relations in gypsiferous materials of the Tabernas Desert (Almería, SE Spain). Geoderma 115 (3–4), 193–222.

Castillo-Monroy, A.P., Maestre, F.T., Delgado-Baquerizo, M., Gallardo, A., 2010. Biological soil crusts modulate nitrogen availability in semi-arid ecosystems: insights from a Mediterranean grassland. Plant Soil 333 (1–2), 21–34.

Chamizo, S., Cantón, Y., Lázaro, R., Domingo, F., 2013. The role of biological soil crusts in soil moisture dynamics in two semiarid ecosystems with contrasting soil textures. J. Hydrol. 489, 74–84.

Chamizo, S., Cantón, Y., Miralles, I., Domingo, F., 2012a. Biological soil crust development affects physicochemical characteristics of soil surface in semiarid ecosystems. Soil Biol. Biochem. 49, 96–105.

Chamizo, S., Cantón, Y., Lázaro, R., Solé-Benet, A., Domingo, F., 2012b. Crust composition and disturbance drive infiltration through biological soil crusts in semiarid ecosystems. Ecosystems 15 (1), 148–161.

Chamizo, S., Cantón, Y., Rodríguez-Caballero, E., Domingo, F., 2016. Biocrusts positively affect the soil water balance in semiarid ecosystems. Ecohydrol. 9 (7), 1208–1221.

Churchill, R.R., 1981. Aspect-Related Differences in Badlands Slope Morphology. Ann. Assoc. Am. Geogr. 71 (3), 374–388.

Couradeau, E., Karaoz, U., Lim, H.C., Da Nunes Rocha, U., Northen, T., Brodie, E., Garcia-Pichel, F., 2016. Bacteria increase arid-land soil surface temperature through the production of sunscreens. Nat. Commun. 7, 10373.

Currey, D.R., 1964. A preliminary study of valley asymmetry in the Ogotoruk Creek Area. Northwestern Alaska 17 (12), 84–98.

Del Toro-Guerrero, F.J., Hinojosa-Corona, A., Kretzschmar, T.G., 2016. A comparative study of NDVI values between north- and south-facing slopes in a semiarid mountainous region. IEEE J. Sel. Top. Appl. Earth Obs. Remote Sens. 9 (12), 5350–5356.

Del-Toro-Guerrero, F.J., Kretzschmar, T., Bullock, S.H., 2019. Precipitation and topography modulate vegetation greenness in the mountains of Baja California, México. Int. J. Biometeorol. 63 (10), 1425–1435.

Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., Bowker, M.A., Wallenstein, M.D., Quero, J.L., Ochoa, V., Gozalo, B., García-Gómez, M., Soliveres, S., García-Palacios, P., Berdugo, M., Valencia, E., Escolar, C., Arredondo, T., Barraza-Zepeda, C., Bran, D., Carreira, J.A., Chaieb, M., Conceição, A.A., Derak, M., Eldridge, D.J., Escudero, A., Espinosa, C.I., Gaitán, J., Gatica, M.G., Gómez-González, S., Guzman, E., Gutiérrez, J.R., Florentino, A., Hepper, E., Hernández, R. M., Huber-Sannwald, E., Jankju, M., Liu, J., Mau, R.L., Miriti, M., Monerris, J., Naseri, K., Noumi, Z., Polo, V., Prina, A., Pucheta, E., Ramírez, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres, D., Torres-Díaz, C., Ungar, E.D., Val, J., Wamiti, W., Wang, D., Zaady, E., 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. Nature 502 (7473), 672–676.

Delgado-Baquerizo, M., Gallardo, A., Covelo, F., Prado-Comesaña, A., Ochoa, V., Maestre, F.T., 2015. Differences in thallus chemistry are related to species-specific effects of biocrust-forming lichens on soil nutrients and microbial communities. Funct. Ecol. 29 (8), 1087–1098.

Durham, R.A., Doherty, K.D., Antoninka, A.J., Ramsey, P.W., Bowker, M.A., 2018. Insolation and disturbance history drive biocrust biodiversity in Western Montana rangelands. Plant Soil 430 (1–2), 151–169.

Eldridge, D.J., Reed, S., Travers, S.K., Bowker, M.A., Maestre, F.T., Ding, J., Havrilla, C., Rodriguez-Caballero, E., Barger, N., Weber, B., Antoninka, A., Belnap, J., Chaudhary, B., Faist, A., Ferrenberg, S., Huber-Sannwald, E., Malam Issa, O., Zhao, Y., 2020. The pervasive and multifaceted influence of biocrusts on water in the world's drylands. Glob. Change Biol. 26 (10), 6003–6014.

Escudero, A., Martínez, I., de La Cruz, A., Otálora, M., Maestre, F.T., 2007. Soil lichens have species-specific effects on the seedling emergence of three gypsophile plant species. J. Arid Environ. 70 (1), 18–28.

Fu, P., Rich, P.M., 2002. A geometric solar radiation model with applications in agriculture and forestry. Comput. Electron. Agric. 37 (1–3), 25–35.

Gallart, F., Solé, A., Puigdefàbregas, J., Lázaro, R., 2002. Badland systems in the Mediterranean. In: Bull, N.L.J., Kirkby, M.J. (Eds.), Dryland Rivers: Hydrology and Geomorphology of Semi-Arid Channels. John Wiley & Sons, Chichester, pp. 299–326.

Harvey, A.M., Calvo-Cases, A., 1991. Process interactions and rill development on badland and gully slopes. Z. Geomorphol. Suppl. 83, 175–194.

Havrilla, C.A., Chaudhary, V.B., Ferrenberg, S., Antoninka, A.J., Belnap, J., Bowker, M. A., Eldridge, D.J., Faist, A.M., Huber-Sannwald, E., Leslie, A.D., Rodriguez-Caballero, E., Zhang, Y., Barger, N.N., 2019. Towards a predictive framework for biocrust mediation of plant performance: A meta-analysis. J. Ecol. 107 (6), 2789–2807.

He, C., Rao, G., Yang, R., Hu, J., Yao, Q., Yang, C.-J., 2019. Divide migration in response to asymmetric uplift: Insights from the Wula Shan horst, North China. Geomorphology 339, 44–57.

Istanbulluoglu, E., Yetemen, O., Vivoni, E.R., Gutiérrez-Jurado, H.A., Bras, R.L., 2008. Eco-geomorphic implications of hillslope aspect: Inferences from analysis of landscape morphology in central New Mexico. Geophys. Res. Lett. 35 (14).

Johnstone, S.A., Finnegan, N.J., Hilley, G.E., 2017. Weak bedrock allows north-south elongation of channels in semi-arid landscapes. Earth Planet. Sci. Lett. 478, 150–158.

Kirkby, M.J., Atkinson, K., Lockwood, J., 1990. Aspect, vegetation cover and erosion on semi-arid hillslopes. In: Thornes, J.B. (Ed.), Vegetation and Erosion. Wiley, Chichester, pp. 25–39.

Kreslavsky, M.A., Head, J.W., 2003. North-south topographic slope asymmetry on Mars: Evidence for insolation-related erosion at high obliquity. Geophys. Res. Lett. 30 (15).

Kumari, N., Saco, P.M., Rodriguez, J.F., Johnstone, S.A., Srivastava, A., Chun, K.P., Yetemen, O., 2020. The grass is not always greener on the other side: seasonal reversal of vegetation greenness in aspect-driven semiarid ecosystems. Geophys. Res. Lett. 47 e2020GL088918.

Langston, A.L., Tucker, G.E., 2018. Developing and exploring a theory for the lateral erosion of bedrock channels for use in landscape evolution models. Earth Surf. Dynam. 6 (1), 1–27.

Lázaro, R., Alexander, R.W., Puigdefábregas, J., 2000. Cover distribution patterns of lichens, annuals and shrubs in the Tabernas Desert, Almería, Spain. In: Alexander, R. W., Millington, A.C. (Eds.), Vegetation mapping: From patch to planet. Biogeography Research Group symposia series. Wiley, Chichester.

Lázaro, R., Calvo-Cases, A., Lázaro, A., Molina, I., 2015. Effective run-off flow length over biological soil crusts on silty loam soils in drylands. Hydrol. Process. 29 (11), 2534–2544.

Lázaro, R., Cantón, Y., Solé-Benet, A., Bevan, J., Alexander, R., Sancho, L.G., Puigdefàbregas, J., 2008. The influence of competition between lichen colonization and erosion on the evolution of soil surfaces in the Tabernas badlands (SE Spain) and its landscape effects. Geomorphology 102 (2), 252–266.

Lázaro, R., Mora, J.L., 2014. Sediment content and chemical properties of water runoff on biocrusts in drylands. Biologia 69 (11), 1539–1554.

Lázaro, R., Rodríguez Tamayo, M.L., Ordiales, R., Tomás, J.P., 2004. El clima, in: Mota Poveda, J.F. (Ed.), Subdesiertos de Almería. Naturaleza de cine. Consejería de Medio Ambiente, [Sevilla], pp. 63–79.

Lázaro, R., Rodrigo, F.S., Gutiérrez, L., Domingo, F., Puigdefàbregas, J., 2001. Analysis of a 30-year rainfall record (1967–1997) in semi-arid SE Spain for implications on vegetation. J. Arid Environ. 48, 373–395.

Maestre, F.T., Bowker, M.A., Cantón, Y., Castillo-Monroy, A.P., Cortina, J., Escolar, C., Escudero, A., Lázaro, R., Martínez, I., 2011. Ecology and functional roles of biological soil crusts in semi-arid ecosystems of Spain. J. Arid Environ. 75 (12), 1282–1291.

McGuire, L.A., Pelletier, J.D., Roering, J.J., 2014. Development of topographic asymmetry: Insights from dated cinder cones in the western United States. J. Geophys. Res. Earth Surf. 119 (8), 1725–1750.

Melton, M.A., 1960. Intravalley variation in slope angles related to microclimates and erosional environment. GSA Bull. 71 (2), 133.

Miralles, I., Domingo, F., Cantón, Y., Trasar-Cepeda, C., Leirós, M.C., Gil-Sotres, F., 2012. Hydrolase enzyme activities in a successional gradient of biological soil crusts in arid and semi-arid zones. Soil Biol. Biochem. 53, 124–132.

Miralles, I., Jorge-Villar, S.E., van Wesemael, B., Lázaro, R., 2017. Raman spectroscopy detection of biomolecules in biocrusts from differing environmental conditions. Spectrochim. Acta Part A, Mol. Biomol. Spectroscopy 171, 40–51.

Miralles-Mellado, I., Cantón, Y., Solé-Benet, A., 2011. Two-dimensional porosity of crusted silty soils: indicators of soil quality in semiarid rangelands? Soil Sci. Soc. Am. J. 75 (4), 1330–1342.

Monger, H.C., Bestelmeyer, B.T., 2006. The soil-geomorphic template and biotic change in arid and semi-arid ecosystems. J. Arid Environ. 65 (2), 207–218.

Nadal-Romero, E., García-Ruiz, J.M., 2018. Chapter 7 - Rethinking spatial and temporal variability of erosion in badlands. In: Nadal-Romero, E., Murillo, J.F.M., Kuhn, N.J. (Eds.), Badlands Dynamics in a Context of Global Change. Elsevier, Amsterdam, pp. 217–253.

Nadal-Romero, E., Rodríguez-Caballero, E., Chamizo, S., Juez, C., Cantón, Y., García-Ruiz, J.M., 2021. Mediterranean badlands: Their driving processes and climate change futures. Earth Surface Processes and Landforms.

Pendleton, R.L., Pendleton, B.K., Howard, G.L., Warren, S.D., 2003. Growth and nutrient content of herbaceous seedlings associated with biological soil crusts. Arid Land Res. Manage. 17 (3), 271–281.

Peters, D., Havstad, K.M., 2006. Nonlinear dynamics in arid and semi-arid systems: interactions among drivers and processes across scales. J. Arid Environ. 65 (2), 196–206.

Poulos, M.J., Pierce, J.L., Flores, A.N., Benner, S.G., 2012. Hillslope asymmetry maps reveal widespread, multi-scale organization. Geophys. Res. Lett. 39 (6), n/a-n/a.

Richardson, P.W., 2015. Topographic asymmetry and climate controls on landscape evolution.

Richardson, P.W., Perron, J.T., Miller, S.R., Kirchner, J.W., 2020. Modeling the formation of topographic asymmetry by aspect-dependent erosional processes and lateral channel migration. J. Geophys. Res. Earth Surf. 125 (7) e2019JF005377.

Rodríguez-Caballero, E., Belnap, J., Büdel, B., Crutzen, P.J., Andreae, M.O., Pöschl, U., Weber, B., 2018a. Dryland photoautotrophic soil surface communities endangered by global change. Nat. Geosci 11 (3), 185–189.

Rodríguez-Caballero, E., Cantón, Y., Chamizo, S., Lázaro, R., Escudero, A., 2013. Soil loss and runoff in semiarid ecosystems: A complex interaction between biological soil crusts, micro-topography, and hydrological drivers. Ecosystems 16 (4), 529–546.

Rodríguez-Caballero, E., Cantón, Y., Jetten, V., 2015a. Biological soil crust effects must be included to accurately model infiltration and erosion in drylands: An example from Tabernas Badlands. Geomorphology 241, 331–342.

Rodríguez-Caballero, E., Chamizo, S., Roncero-Ramos, B., Román, R., Cantón, Y., 2018b. Runoff from biocrust: A vital resource for vegetation performance on Mediterranean steppes. Ecohydrol. 11 (6), e1977.

Rodríguez-Caballero, E., Escribano, P., Cantón, Y., 2014. Advanced image processing methods as a tool to map and quantify different types of biological soil crust. ISPRS J. Photogramm. Remote Sens. 90, 59–67.

Rodríguez-Caballero, E., Knerr, T., Weber, B., 2015b. Importance of biocrusts in dryland monitoring using spectral indices. Remote Sens. Environ. 170, 32–39.

Rodríguez-Caballero, E., Rodriguez-Lozano, B., Segura-Tejada, R., Blanco-Sacristán, J., Cantón, Y., 2021. Landslides on dry badlands: UAV images to identify the drivers controlling their unexpected occurrence on vegetated hillslopes. J. Arid Environ. 187, 104434.

Rodríguez-Caballero, E., Román, J.R., Chamizo, S., Roncero Ramos, B., Cantón, Y., 2019. Biocrust landscape-scale spatial distribution is strongly controlled by terrain attributes: Topographic thresholds for colonization in a semiarid badland system. Earth Surf. Proc. Land. 44 (14), 2771–2779.

Roering, J.J., Marshall, J., Booth, A.M., Mort, M., Jin, Q., 2010. Evidence for biotic controls on topography and soil production. Earth Planet. Sci. Lett. 298 (1–2), 183–190.

Román, J.R., Rodríguez-Caballero, E., Rodríguez-Lozano, B., Roncero-Ramos, B., Chamizo, S., Águila-Carricondo, P., Cantón, Y., 2019. Spectral response analysis: an indirect and non-destructive methodology for the chlorophyll quantification of biocrusts. Remote Sensing 11 (11), 1350.

Rossi, F., de Philippis, R., 2015. Role of cyanobacterial exopolysaccharides in phototrophic biofilms and in complex microbial mats. Life 5 (2), 1218–1238.

Rutherford, W.A., Painter, T.H., Ferrenberg, S., Belnap, J., Okin, G.S., Flagg, C., Reed, S. C., 2017. Albedo feedbacks to future climate via climate change impacts on dryland biocrusts. Sci. Rep. 7 (1), 44188.

Shelef, E., Hilley, G.E., 2014. Symmetry, randomness, and process in the structure of branched channel networks. Geophys. Res. Lett. 41 (10), 3485–3493.

Smith, B.J., 1978. Aspect-related variations in slope angle Near Béni Abbès, Western Algeria. Geografiska Annaler: Series A, Phys. Geogr. 60 (3–4), 175–180.

Solé-Benet, A., Calvo, A., Cerdà, A., Lázaro, R., Pini, R., Barbero, J., 1997. Influences of micro-relief patterns and plant cover on runoff related processes in badlands from Tabernas (SE Spain). CATENA 31 (1–2), 23–38.

Srivastava, A., Rodriguez, J.F., Saco, P.M., Kumari, N., Yetemen, O., 2021. Global analysis of atmospheric transmissivity using remote sensing and flux network datasets across different climatic zones. Remote SENSING 13 (9), 1716.

Suggitt, A.J., Wilson, R.J., Isaac, N.J.B., Beale, C.M., Auffret, A.G., August, T., Bennie, J. J., Crick, H.Q.P., Duffield, S., Fox, R., Hopkins, J.J., Macgregor, N.A., Morecroft, M. D., Walker, K.J., Maclean, I.M.D., 2018. Extinction risk from climate change is reduced by microclimatic buffering. Nat. Clim. Change 8 (8), 713–717.

Tucker, C.J., 1979. Red and photographic infrared linear combinations for monitoring vegetation. Remote Sens. Environ. 8 (2), 127–150.

Weber, B., Büdel, B., Belnap, J. (Eds.), 2016. Biological soil crusts: An organizing principle in drylands. Springer, Cham, 1 online resource.

Wende, R., 1995. Drainage and valley asymmetry in the Tertiary Hills of Lower Bavaria, Germany. Geomorphology 14 (3), 255–265.

West, N., Kirby, E., Bierman, P., Clarke, B.A., 2014. Aspect-dependent variations in regolith creep revealed by meteoric 10Be. Geology 42 (6), 507–510.

Yair, A., Bryan, R.B., Lavee, H., Schwanghart, W., Kuhn, N.J., 2013. The resilience of a badland area to climate change in an arid environment. CATENA 106, 12–21.

Yair, A., Lavee, H., 1985. Runoff generation in arid and semiarid zones. In: Anderson, M. G., Burt, T.P. (Eds.), Hydrological Forecasting. Wiley, Chichester, pp. 183–220.

Yetemen, O., Istanbulluoglu, E., Duvall, A.R., 2015a. Solar radiation as a global driver of hillslope asymmetry: insights from an ecogeomorphic landscape evolution model. Water Resour. Res. 51 (12), 9843–9861.

Yetemen, O., Istanbulluoglu, E., Flores-Cervantes, J.H., Vivoni, E.R., Bras, R.L., 2015b. Ecohydrologic role of solar radiation on landscape evolution. Water Resour. Res. 51 (2), 1127–1157.