



Report on the potential for sudden shifts

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1 Introduction

1.1 Sudden shifts in ecosystems

The field of sudden shifts in ecosystems is blooming and challenging the classical theory assumption that nature responds in a smooth way to gradual change. Theoretical developments and empirical analyses and observations have provided evidence that small increases in human and climatic pressure may trigger sudden shifts between healthy and degraded ecosystem states once a threshold has been surpassed (Scheffer et al. 2001, Rietkerk et al. 2004, Schröder et al. 2005, Bestelmeyer et al. 2011). This implies the possibility for rapid, large, and not easy to reverse ecological and economic losses and explains the effort that is being dedicated over the past few years to finding early warning signals (Dakos et al. 2012, Kéfi et al. 2014). Sudden shifts affect a wide range of aquatic and terrestrial ecosystems (Scheffer and Carpenter 2003, Rietkerk et al. 2004) but knowledge advance has been less developed for terrestrial systems, including drylands, where the factors and mechanisms, pressures, and interactions that control and drive sudden shifts remain largely unknown.

1.2 Potential for sudden shifts in drylands

Drylands cover 41% of the Earth's surface and provide ecosystem services to over 38% of the global population including some of the poorest and most vulnerable on the planet (Millennium Ecosystem Assessment 2005). Currently, 10% to 20% of the world drylands are already degraded, and ongoing population growth and climate change are expected to exacerbate desertification risk (Millennium Ecosystem Assessment 2005). Modelling experiments suggest that drylands may experience sudden shifts from functional to degraded states in response to smooth increases in human and climatic pressures in these areas such as grazing and drought (Rietkerk et al. 2004, Kéfi et al. 2007). These shifts are hypothesized to be governed by plant-plant interactions and (ecohydrological) feedbacks between vegetation and water redistribution, which despite being widely accepted are still poorly understood and quantified by empirical data. CASCADE-WP4 aims to empirically investigate the main mechanisms and processes involved in some of these ecohydrological feedbacks, specifically those between plant spatial pattern, water redistribution, and plant functioning, and how they may be modulated by plant diversity.

1.3 Ecohydrological feedbacks and sudden shifts in drylands

Ecohydrological observations in dryland communities have suggested that a decrease in the cover and size of vegetation patches increases the hydrological connectivity of bare-soil areas (i.e. runoff-source areas) and the global losses of water and nutrients from the system, which may in turn reduce plant productivity and further decrease plant cover, completing a positive degradation feedback (Bautista et al. 2007, Mayor et al. 2008, Turnbull et al. 2010, García-Fayos et al. 2010, Bestelmeyer et al. 2011) (left feedback loop in Fig. 1). In contrast, at the plant patch scale, the coarsening of plant pattern (i.e., increasing of bare-soil connectivity) would result in a relative increase in resource inputs to the individual patches, which may increase patch productivity and growth, which in turn increases plant cover and decreases bare-soil connectivity (Puigdefábregas and Sánchez 1996, Ludwig et al. 2005, Urgeghe et al. 2010) (right feedback loop in Fig. 1). Despite the interplay between these opposite feedbacks is increasingly recognized as a critical mechanism underlying dryland functioning and potential for sudden shifts (Ludwig et al. 2005, Turnbull et al. 2012, Mayor et al. 2013), the quantification of their relative strength and of their individual or combined impacts in dryland functioning is currently

lacking. Further, among a number of critical factors, plant diversity is expected to modulate these feedbacks (Bautista et al. 2007, D'Odorico et al. 2012), but this role is still largely unknown.

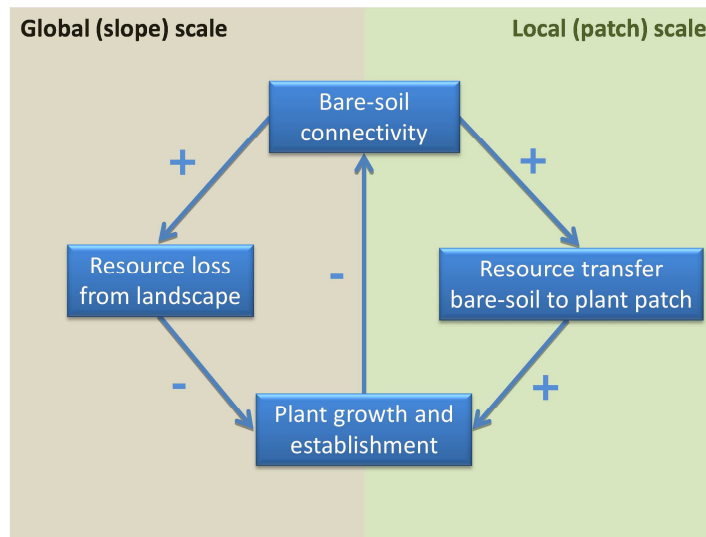


Figure 1. Global (left) and patch-scale (right) feedback loops connecting plant spatial pattern (and associated bare-soil connectivity) to plant growth and establishment through resource loss and transfer. Positive (+) and negative (-) signs represent positive and negative impacts, respectively.

1.4 Experimental approaches to the analysis sudden shifts

Although theoretical models predict that drylands can experience sudden shifts, empirical evidence on this topic is very scarce and shows contrasting results. For instance, while Gao et al. (2011) found a degradation threshold ($\approx 20\%$ vegetation cover) for natural restoration of overgrazed rangelands in a long-term (35-years) observational study in China, Bestelmeyer et al. (2013) found no critical thresholds, even at low plant cover values, in Chihuahuan Desert grasslands after a long term (13-year) pulse-perturbation experiment of heavy grazing and shrub removal. Different strengths and modulating factors of the ecohydrological feedbacks studied in CASCADE-WP4 could provide insights on these apparently contradictory results. Although observational field experiments are essential to illustrate sudden shifts in ecosystems, they are often unable to provide conclusive results, which is in part due to the background environmental heterogeneity of the landscape, particularly strong in drylands, but mostly to the complex interactions occurring between multiple control factors. Conversely, appropriate manipulative experiments allow disentangling the relative role of the factors involved, yet they may imply an over-simplification of real ecosystems. CASCADE-WP4 has adopted a combination of mesocosm and field manipulative experiments with field observations as the most promising approach for the study of the feedback mechanisms that may trigger sudden shifts in ecosystems. Deliverables from CASCADE-WP4 will sequentially report on WP4 experiments that address (1) ecohydrological feedbacks linking plant cover and pattern, resource conservation/redistribution and plant growth (this report D4.1); (2) the role of increasing pressure in triggering rapid changes in ecosystem status (D4.2); and (3) degradation reversal dynamics and thresholds as a function of plant colonization pattern and diversity.

2 Assessing dryland ecohydrological feedbacks

2.1 Approach and objectives

In order to disentangle the various components of the ecohydrological feedbacks that relate plant pattern, resource availability and productivity in drylands, as well as the independent role of critical factors that control these feedbacks, CASCADE has followed a fully manipulative experimental approach combined with field observations. Manipulative experiments allow the isolation of the processes and factors of interest, thereby facilitating the understanding of the underlying mechanisms and providing useful information for developing, parameterizing, calibrating and validating general models. Three interlinked experiments were used to determine:

- (1) The independent role of plant cover and plant pattern on resource (water, soil) conservation in drylands.
- (2) The two-way feedbacks between plant pattern and resource conservation, and the role played by plant diversity in modulating these feedbacks.
- (3) The relevance of local transfer of resources from bare-soil inter-patches to downslope plant patches for plant performance and patch productivity.

The first two experiments were conducted on a set of 24 closed (2 x 1 m) plots, which allowed event-based monitoring of runoff and sediment yields, and where patch cover and pattern were manipulated in order to create a variety of patch spatial patterns. The first experiment (see section 2.2) focused on assessing one side of the feedback process: pattern→resource conservation. By using inert materials, we mimicked the structural role of vegetation on resource conservation, but avoided the potential response of vegetation to the resulting changes in resource availability; this way the feedback loop was artificially broken, facilitating the independent assessment of one of the components. The second experiment (see section 2.3) used real plant communities, artificially arranged in patterns of interest; this way both sides of the feedback loop (the effect of pattern on resource conservation and the effect of resource availability back to vegetation) were assessed. The third experiment (see section 2.4) focused on further assessing the local (patch scale) aspect of pattern-resource feedbacks (i.e., the effect of local redistribution of resources, from inter-patches to downslope patches, on plant performance) in natural communities, and used natural slopes from a degraded semiarid area on which a variety of shrub seedlings were planted in 2004.

2.2 Spatial pattern and resource redistribution in drylands

2.2.1 Critical questions and experimental design

Contrasting water infiltration between bare-soil inter-patches and plant patches (Bochet et al. 2006, Mayor et al. 2009) combined with physical obstruction of water flow by plant patches (Ludwig and Tongway 1996) drive the redistribution of water and other resources in drylands: bare-soil areas act as sources of runoff water, sediment, seeds and nutrients that travel downslope and are captured by vegetation patches (Tongway and Ludwig 1997). These source–sink dynamics are considered to control soil and water conservation in dryland systems at multiple scales (Wilcox et al. 2003, Ludwig et al. 2005,

Yu et al. 2008). Although plant cover is considered to be the most critical vegetation property that control water and soil conservation in drylands, several works have pointed out that ecosystem efficiency in retaining water and sediments becomes higher as the density of plant patches increase and the grain size of the plant pattern decreases (Tongway and Ludwig 1997, Puigdefábregas 2005, Bautista et al. 2007). However, a decrease in the size of plant patches has been also considered a sign of land degradation (Kéfi et al. 2007). An ongoing debate exists on the relative importance of plant cover and plant pattern as indicators of ecosystem functioning (e.g., Kéfi et al. 2010, Maestre and Escudero 2010). It is worth noting that changes in plant cover and pattern are often linked, making difficult to disentangle and assess their relative ecohydrological roles. In order to do so, we independently manipulated patch cover and plant pattern and investigated their independent effect on runoff and sediment yield.

Using synthetic sponges (8 x 12.5 cm in size) placed on 2 x 1 m plots (Fig. 2), we created different spatial arrangement of mimicked plant patches that ranged in patch cover (from 5 % to 30%), patch density (from 10 to 60 sponges/plot), and patch size (from 100 cm² to 600 cm², which represent patches made of 1 up to 6 sponge units). In addition, plots for intermediate values of patch cover (40 sponges/plot) and the various spatial arrangements considered (10, 20, 30 and 40 patches of decreasing size), were replicated three times (hereafter, replicated *pattern* plots). Table 1 shows the whole set of cover and pattern combinations considered (24 plots in total). The sponges were fixed to the soil using pins (See details in Fig. 2).

Table 1. Patch size (cm²) for each combination of patch cover and patch number, and total number of plots per each cover value

Number of sponges (cover)	Number of patches						Total number of plots
	0	10	20	30	40	60	
0 (0%)	-						1
10 (5 %)		100					1
20 (10%)		200	100				2
30 (15%)		300	150	100			3
40 (20%)		400	200	133	100		4 x 3rep = 12
60 (30%)		600	300	200	150	100	5

In bold, Patch size in the replicated pattern plots: 3 replicates (rep) for each 20%-cover plot type (having 10, 20, 30 or 40 patches each).

We monitored runoff and sediment yield after each natural rainfall event during the experimental period (6 rainfall events totaling 79 mm). In addition, to further explore the effect of patch pattern, we artificially increased the capacity of the patches for trapping runoff from overland flow by installing two small metal sheets on the laterals of the upslope side of each sponge (enhanced-sink patches) in the replicated *pattern* plots (see details in Fig. 3) and conducted a set of high-intensity rainfall simulation experiments (Fig. 3) on these plots with and without the metal sheets. We used a large rainfall simulator, with two sprinklers that evenly distributed water over the entire surface of each 2 x 1 m plot, we applied a 65 mm h⁻¹ rainfall over a 30 minutes period on each replicated *pattern* plots (intermediate patch cover: 40 sponges/plot; four different patterns: 10, 20, 30 and 40 patches; 3 replicates per pattern type).

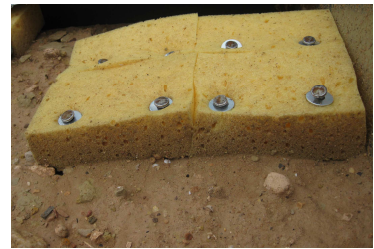


Figure 2. General view of the cover/pattern experiment using inert materials (sponges) to mimic vegetation patches (left) and detail of one large (400 cm²) patch (right).

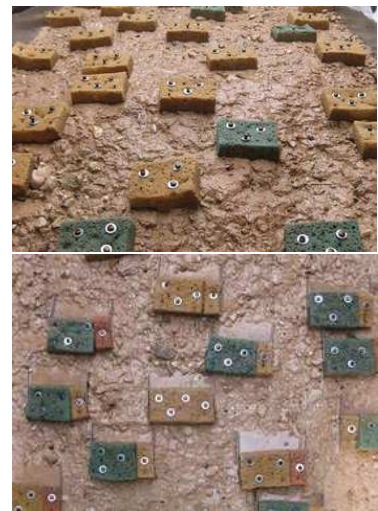


Figure 3. Rainfall simulation (left) and details of the plot surface at the end of rainfall simulation runs on plots with standard patches (right, top) and with enhanced-sink patches (right, bottom).

2.2.2 Results: Both plant cover and pattern matter

As expected, we found that increasing patch cover reduces the amount of runoff and sediments produced on our experimental plots, with runoff coefficient (percentage of rainfall that turns into runoff) and sediment yield being reduced by half on plots with 30% cover as compared with bare plots (Fig. 4, left). Unexpectedly, we did not find a significant effect of patch pattern (Fig. 4, right). However, under high-intensity rainfalls and particularly when the sink capacity of the vegetation patches was enhanced, the effect of patch pattern emerged (Fig. 5), with coarser patterns (lower patch density; higher patch size) producing more runoff than finer patterns, for the same patch cover values.

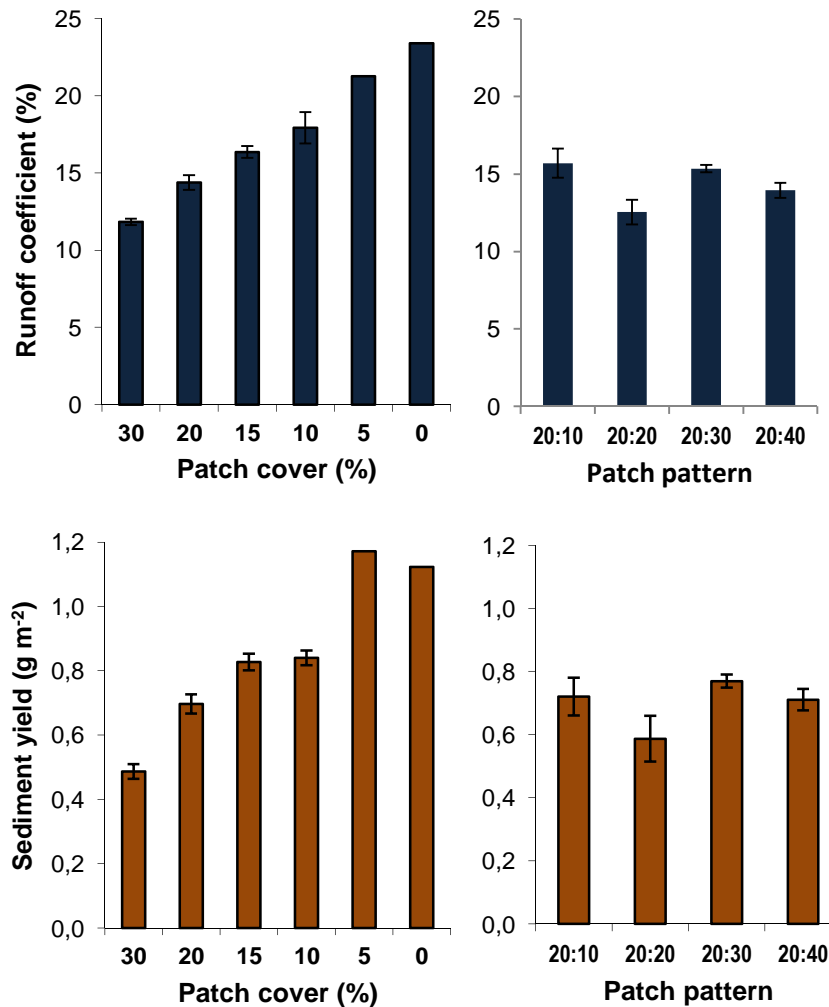


Figure 4. Runoff coefficient (top) and sediment yield (bottom) for a gradient of patch cover values (left) and of patch pattern (right). Data are mean values \pm 1 SE. Patch pattern classes represent 20% patch cover distributed in 10, 20, 30 or 40 patches, respectively.

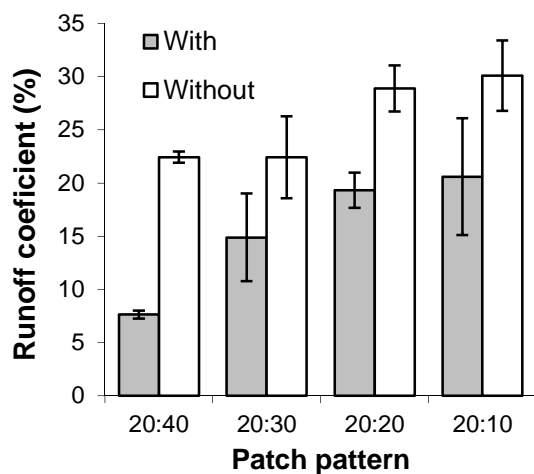


Figure 5. Runoff coefficient for a gradient of patch pattern in plots with enhanced-sink patches (With) and in plots with no-sink patches (Without). Pattern classes as in Figure 5.

The well-known role of plant cover as control factor of runoff and sediment yield relies on the combined effect of several processes including rainfall interception by the canopies, physical disruption of overland flow, which promotes opportunities for water infiltration and sediment retention, and increased infiltration capacity and hydraulic conductivity in the soil underneath vegetation patches (Ludwig and Tongway 1996, Mayor et al. 2009). Mimicking vegetation patches by placing sponges on the soil surface allowed assessing the role of the first two processes: rainfall interception and physical disruption of overland flow. The addition to the sponges of a structure that captured runoff water allowed also mimicking and independently assessing the role of increased infiltration (sink) capacity of the soil underneath the plant patches. Overall, our results suggest that the control of overland flow by patchy vegetation relies mainly on increased water infiltration capacity under the plant patches rather than on rainfall interception and surface flow disruption. Thus, only mimicking rainfall interception and flow disruption resulted in no effect of patch pattern and a relatively small effect of patch cover as compared with data reported in the literature (e.g., Elwell and Stocking 1976, Francis and Thornes 1990), while mimicking all three processes revealed the effect of patch pattern. According to these results, runoff and erosion control measures that base only on creating physical barriers to overland flow could be of little value as compared with measures based on the establishment of vegetation patches, which have the potential for increasing water infiltration under their canopies.

The results from this manipulative experiment are conclusive about the relevance of both patch cover and patch pattern as hydrological control factors in patchy landscapes. However, patch cover appeared to be a stronger control factor, with patch pattern playing a subsidiary role that mostly relies on the sink capacity of the patches and exhibits its full potential only when the amount and/or the intensity of the rainfall result in significant overland flow and subsequent runoff source-sink dynamics. It is worth noting though that plant communities with similar low plant cover values but different plant pattern are common in semiarid lands (e.g., Abrahams et al. 1995, Bartley et al. 2006, Bautista et al. 2007). This fact suggests that plant cover alone may be not sufficient to predict runoff and sediment yield variation in semiarid lands. Our results support combining plant cover with other indicators that also capture plant pattern properties.

2.3 Feedbacks between plant pattern and resource conservation: A mesocosm experiment

2.3.1 Critical questions and experimental design

The transfer of resources from bare-soil interpatches to downslope vegetation patches contribute to plant productivity and overall ecosystem productivity (Aguilar and Sala 1999, Yu et al. 2008, Turnbull et al. 2012). However, patch growth would contribute to reduce the size of the bare-soil areas, which in turn would reduce the amount of resources transferred to downslope patches. According to Puigdefábregas et al. (1999), in a functional ecosystem, the relative amount of source and sink areas remains within a certain range of variation around a hypothesized optimum source:sink ratio that maximizes both the availability of resources and the growth of vegetation patches. Using a spatially distributed model, Urgeghe et al. (2010) found that total amount of runoff water reaching herbaceous patches was maximum at intermediate values amount of bare-soil cover, which points to a tradeoff between the source area for generating runoff and the sink area for capturing runoff. Despite the increasing interest in the interactions between vegetation spatial pattern, productivity, and hydrological processes, there is still

very scarce experimental fieldwork testing the underlying assumptions and quantifying the feedbacks involved (Asbjornsen et al. 2011). Furthermore, the scarce experimental and modelling works conducted on this topic hardly consider multiple species at once, ignoring the potential role of plant diversity as modulator of the ecohydrological feedbacks operating in drylands. In the framework of CASCADE WP4, we designed a manipulative experiment that focused on the global feedback between plant pattern (and associated bare-soil connectivity) and resource conservation depicted in Fig. 1. The experiment specifically assessed (1) the role of plant pattern (patch density and size) on resource conservation for different plant species (2) the role of plant diversity in modulating pattern effect on resource conservation, and (3) the impact of resource conservation/loss on plant performance.

Using 1-year-old plant seedlings of three different species, we created artificial plant communities with contrasting plant pattern: coarse-grained pattern (6 large patches of 9 individual plants each), vs. fine-grained pattern (18 small patches of 3 plants each), and contrasting diversity: mono-specific vs. diverse communities (Fig. 6). Total number of plants per plot was the same (54 plants) for all plots, and initial cover values were very similar. The species used were one steppe grass (*Lygeum spartum* L.) and two shrubs (*Atriplex halimus* L., and *Phillyrea angustifolia* L.). In the “diverse” communities, all the plant patches include the three species used (3 plants/species in the patches of the coarse-pattern plots, 1 plant/species in the patches of the fine-pattern plots). In the “monospecific” plots, all patches include the same single species. The plant communities were established on 24 plots of 1x2-m, located on an artificially created slope (Fig. 7). There were 3 plot replicates for each treatment combination (2 spatial patterns X 4 plant communities). Over a one-year period, we monitored (1) Runoff and sediment yields from each plot, (2) Soil moisture in plant patches and bare-soil interpatches, (3) bare-soil connectivity, and (4) plant performance (survival, growth).

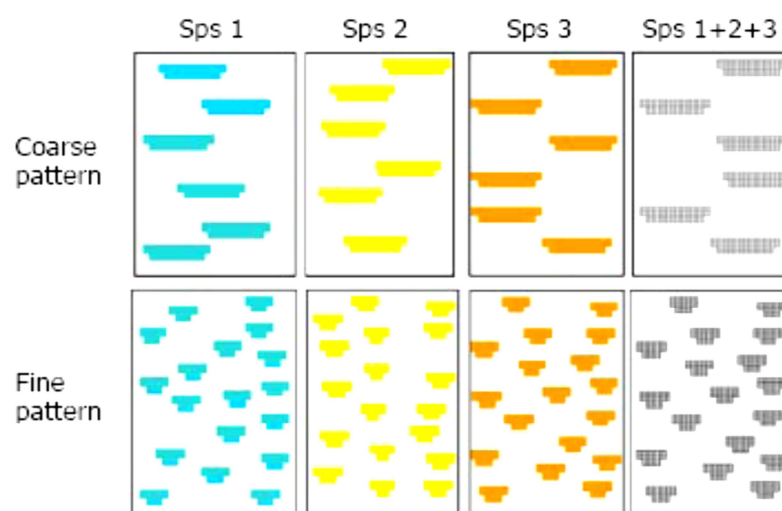


Figure 6. Outline of the experimental design of the plant-pattern experiment.
Each type of plot was replicated three times



Figure 7. General view of the experimental plots (top), and detail of a fine-grained diverse plot (bottom, left) and of a coarse-grained *Lygeum spartum* plot (bottom right).

2.3.2 Hydrological response to plant pattern and diversity

Overall, the two contrasting plant spatial patterns assessed in this experiment (coarse and fine) did not show significant differences in the hydrological response of the experimental plots (Fig. 8). This result is due to the fact that the differences in runoff and sediment yield between coarse pattern (i.e., few big patches) and fine pattern (i.e., many small patches) were not consistent across species (Fig. 9), with *Atriplex halimus* and *Lygeum spartum* being more productive in coarse patterns and *Phillyrea angustifolia* being more productive in fine patterns.

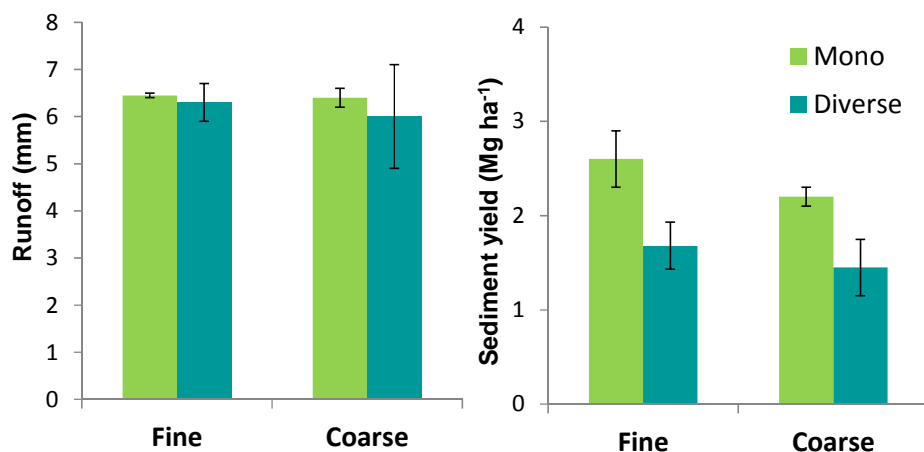


Figure 8. Average total runoff (left) and sediment yield (right) produced on plots with either fine-grained or coarse-grained patterns and monospecific or diverse plant assemblies.

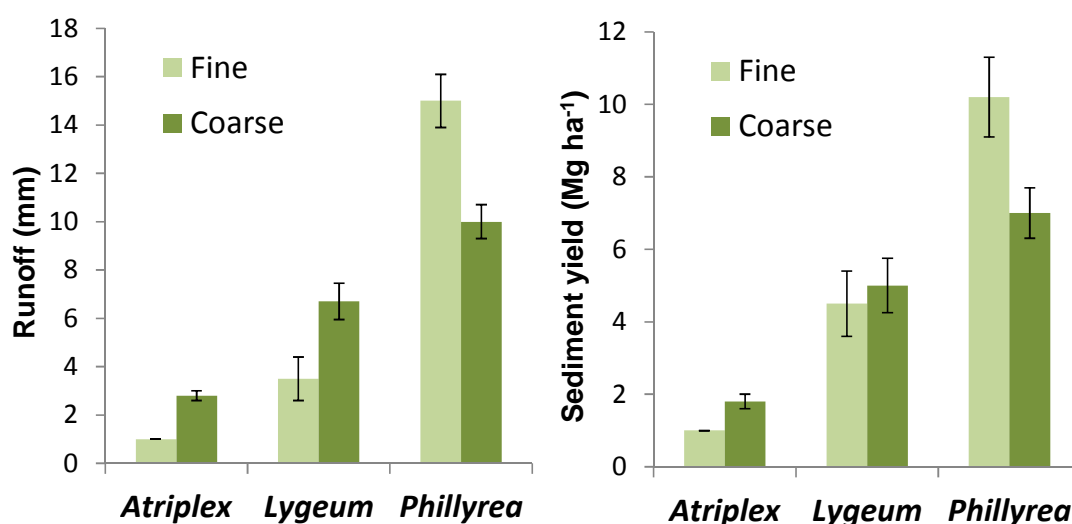


Figure 9. Average total runoff (left) and sediment yield (right) produced on fine-grained or coarse-grained pattern plots for monospecific assemblies of each of the three species assessed: *Atriplex halimus*, *Lygeum spartum*, and *Phillyrea angustifolia*.

Plant diversity did not show any significant effect on runoff production, but it significantly reduced sediment yield. Thus, diverse plots produced less than average than monospecific plots (Fig. 8), similar or even less than the least productive monospecific assembly (*Atriplex*; Fig. 9 right), which suggest some kind of complementary of plant traits regarding the control of soil loss and the capacity for trapping and storing sediments. For example, while the dense canopy of *A. halimus* plants may have protected the soil from detachment by raindrop impact, the dense ground cover of *L. spartum* may have been particularly effective in trapping sediments that were transported by overland flow.

Regardless the broad class of plant spatial pattern of each plot, total plot runoff (Fig. 10) and sediment yield (data not shown) were positively correlated to the connectivity of the bare soil areas (measured with the Flowlength index; Mayor et al. 2008), pointing to this property as a key factor driving runoff and sediment yield in drylands. Although our initial expectations were that bare-soil connectivity would be greater for coarse-grained patterns than for fine patterns, both patterns resulted in a similar and rather wide gradient of bare-soil connectivity. This fact revealed that only when coarser patterns imply more connected bare soil, a negative impact of this type of pattern on water and soil conservation could be expected (e.g., Bautista et al. 2007).

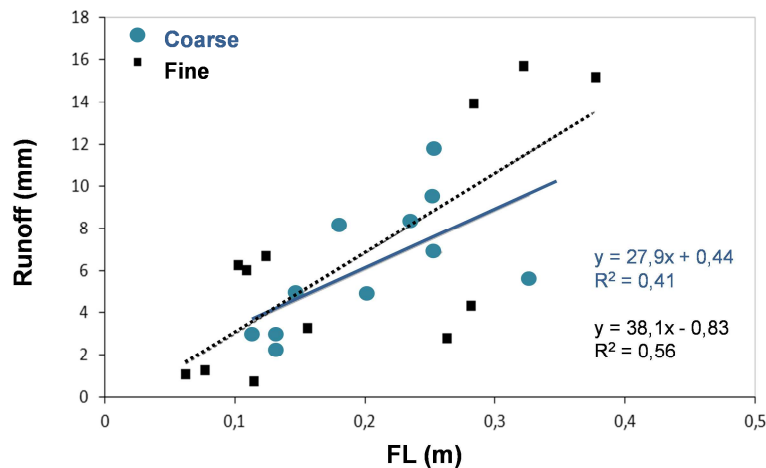


Figure 10. Relationships between total runoff and bare-soil connectivity (FL) for coarse-grained and fine-grained plant spatial patterns.

Finally, plot-averaged soil moisture was generally similar between coarse and fine patterns. However, at the patch scale, there was a consistent trend of higher water gains in the plant patches of the coarse pattern than in the patches of the fine pattern. One of the reasons to explain this behavior is higher runoff redistribution from inter-patches to patches in the coarse pattern due to larger runoff-contributing areas (i.e., bare soils) upslope the patches. This possibility is supported by the positive relationship between soil moisture increase after a large rainfall and the size of the upslope contributing area of the patches, only found in the coarse-pattern plots (Fig. 11).

Overall, our results show that the key pattern property driving runoff and sediment yield is the connectivity of the bare soil, regardless the grain size of the pattern: coarse (i.e. few big patches) or fine (many small patches). However, big patches, with big bare-soil inter-patch areas upslope receive more runoff water after major rainfall events. These results highlight the interplay of local (patch-scale) and global (plot scale) effects of bare soil connectivity, and can be used to feed and validate dryland models that consider these effects (e.g., Mayor et al. 2013).

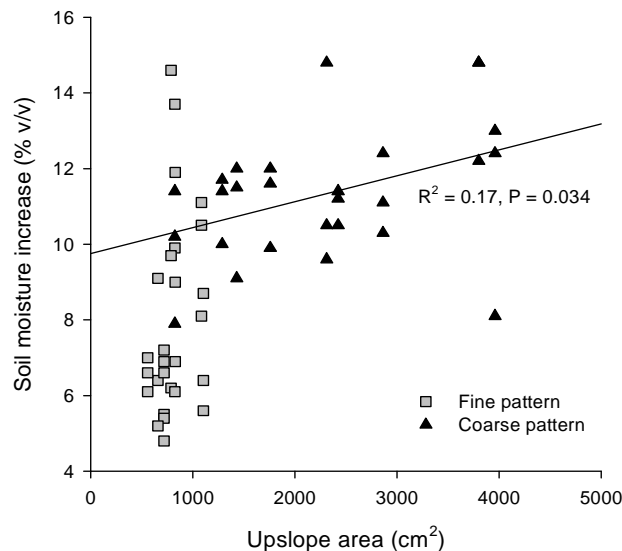


Figure 11. Relationships between soil moisture increase after a rainfall event and the size of upslope runoff-contributing area of plant patches for fine pattern and coarse pattern plots. Only significant regression line is showed.

2.3.3 Vegetation response to plant pattern

The results reported in previous sections consistently showed that both plant cover and pattern are critical for resource conservation in semiarid patchy landscapes, even within a relatively small range of variation in plant cover. A critical question that derives from these results is to what extent this pattern-driven variation in resource availability determines plant performance and contributes to further variations in plant cover and pattern.

To address this question, we assessed how individual plant growth depended on the variation in runoff (and so in water losses) driven by differences in plant pattern and cover. We monitored 27 individuals from each plot and estimated the average standardized relative growth rate per plot by (a) calculating the relative growth in basal diameter, BD ($\ln \text{BD final} - \ln \text{BD initial}$) for each monitored individual in a given plot, (b) standardizing the individual growth rates by making them relative to the average growth rate of the respective species, and (c) averaging the standardized individual values per plot. Figure 12 shows the relationship between average standardized growth rates and water losses from runoff for each experimental plot. Although the data seem to follow a decreasing trend, no significant relationship was found between these two variables. Several factors may have contributed to this result. On the one hand, the spatial (2-m² plots) and temporal (1 year) dimensions of the manipulative experiment reported here have resulted in only small differences in water losses between plots. Thus, the largest difference between plots (25 mm of total runoff) represents less than 10 % of the total rainfall input (335 mm) during the study period. These differences in resource availability appeared to be rather small to influence plant growth at the global (plot) scale. On the other hand, plant performance is expected to also respond to variations in water inputs at the patch scale (Fig. 1), and thus while larger bare-soil connectivity leads to larger runoff losses, it also implies larger water inputs at the patch scale (Fig. 11), which may have counterbalanced and masked the impact of small differences in global losses. Overall, these results point to the need of further investigating the interplay between global and patch scale feedbacks between plant pattern and resource availability, upscaling the spatial (see section 2.4) and temporal extent of the experimental settings. On-going

additional large-scale experiments in CASCADE WP4 address this need and investigate the long-term impact of vegetation removal (and associated changes in plant pattern and bare-soil connectivity) in plant pattern dynamics.

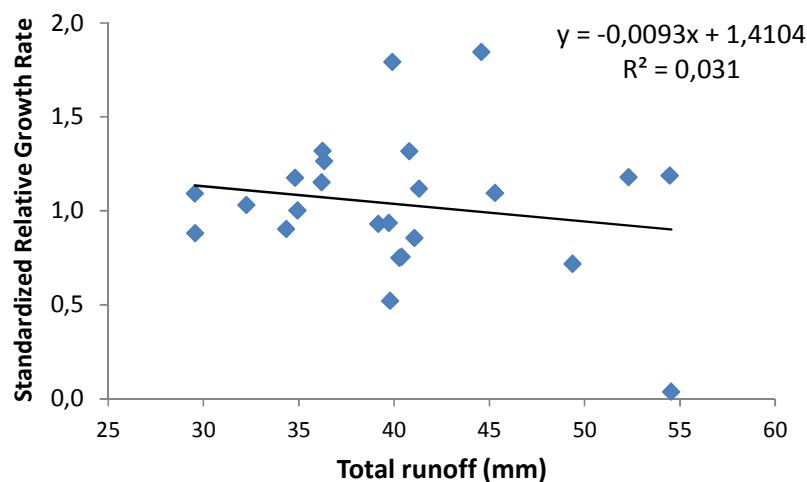


Figure 12. Standardized relative growth rate (plot average of standardized individual growth rates) as a function of total runoff losses in the experimental plots.

2.4 Patch-scale effect of resource redistribution on plant performance

2.4.1 Critical questions and experimental design

To improve our understanding of the role of source–sink dynamics in plant productivity in drylands, and thus to gain insights on the local (patch-scale) effect of pattern-driven resource redistribution in these ecosystems, critical information about the relationships between plant-patch performance and the size, connectivity, and conditions of the inter-patch areas is very much needed. Questions of particular interest include: (i) how does the size of the upslope runoff-source areas control soil water availability and plant performance in the respective downslope patch? (ii) What is the role of soil surface properties, connectivity and topographic features of the upslope runoff-source areas in modulating plant performance? To address these questions, we examined the relationships between the characteristics of the respective upslope runoff-source areas and the performance of planted Mediterranean woody species in Albaterra Long-term monitoring (LTEM) CASCADE site, in Southeast Spain. We hypothesized that the larger the upslope length and the larger and more runoff-prone the upslope inter-patch area (runoff-source area), the better the seedling performance.

Albaterra LTEM is a small catchment (24 ha) characterized by a semiarid Mediterranean climate with a very high interannual variability. Mean annual temperature is 18.7 °C and mean annual rainfall is 280mm. Monthly rainfall follows a bimodal distribution: two rainy seasons (spring and autumn) separated by a very dry summer. Soils are sandy-loam, shallow to moderately deep (20–60 cm), well drained, slightly basic, stony and with a very low nutrient content. Natural vegetation is composed mainly of sub-shrubs, such as *Globularia alypum* L., single or mixed patches of sod-forming short grasses, such as *Brachypodium retusum* (Pers) P. Beauv. and chamaephytes. Plant cover ranges from

34% to 48%. High cover of rock fragments and physical soil crusts are common on bare-soil surfaces, whereas biological soil crusts are almost absent.

Because of the degraded condition of the area, resulting from synergies between water scarcity and long-term resource exploitation, the Albaterra catchment was selected by the Spanish National Plan to Combat Desertification as a demonstration area to implement and monitor innovative restoration strategies to combat desertification (Vilagrosa et al. 2008). In 2004, seedlings pertaining to a variety of evergreen trees and native shrubs were planted on the catchment area. Since then, seedling growth and survival have been monitored on a number of permanent plots. We established our sampling area (3500m² in size) on one of these long-term monitoring plots (Fig. 13). Because of its south-facing aspect, this plot represents the most stressful condition in the catchment area. At the planting time (2004), plant density was 500 seedlings/ha, with planted seedlings distributed in a 4 × 5m regular pattern. We focused our study on two of the most widely planted species in Albaterra: *Pistacia lentiscus* and *Olea europaea* var. *sylvestris*. These species showed contrasting responses regarding seedling survival, with overall survival values of ~80% for *O. europaea* and ~50% for *P. lentiscus* at the beginning of our experiment (2010), 6 years after the implementation of the restoration project. At that time, there were 21 (20 alive and 1 dead) *O. europaea* individuals and 27 (11 alive and 16 dead) *P. lentiscus* individuals in our sampling plot.

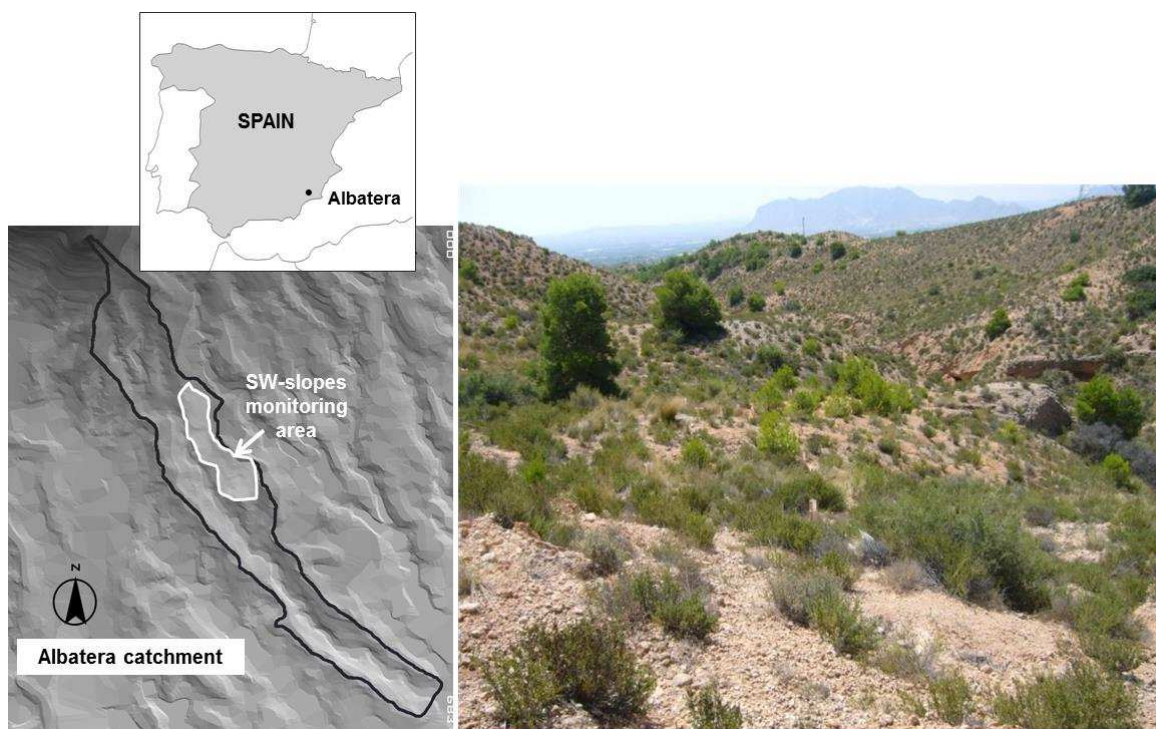


Figure 13. Location map of the study area

For each sampling plant, we assessed size, surface properties and topographic characteristics of its respective runoff-source area (hereafter, individual drainage microcatchment). For each alive seedling, we assessed a range of plant performance attributes related to plant growth (seedling growth rate over the first 6 years after planting, and final height and basal diameter 6 years after planting) and to plant water-stress level (relative leaf water content, specific leaf weight, and leaf and stem integrated water use efficiency, as estimated from $\delta^{13}\text{C}$ natural enrichment; Farquhar et al. 1989).

To characterize the runoff-source area of the target seedlings, the perimeter of each individual drainage microcatchment was delineated and marked in the field. We then geo-referenced every target plant, captured the projected area of the associated microcatchments using a GPS (Trimble, GeoExplorer XH) with submetric resolution, imported this information into a Geographical Information System (ArcGIS, Environmental Systems Research Institute Inc., California), and mapped the location of the target plants and their respective microcatchments (Fig. 14, left). From these maps, we calculated the distance between the target plants and the upslope hillslope boundary (upslope length). We outlined and mapped in the field the canopies of the plant patches located within each seedling microcatchment (Fig. 14, right). The field maps were scanned and digitalized and used for estimating the hydrological connectivity of each microcatchment through the Flowlength index, developed by Mayor et al. (2008). This connectivity metric is based on the assumption that bare soil performs as runoff sources whilst vegetation patches traps resources, behaving as runoff sinks (e.g. Puigdefábregas et al., 1999; Reid et al., 1999; Ludwig et al., 2005; Bochet et al., 2006): a higher value of the index indicates a higher hydrologic connectivity of runoff-source areas. We further characterized the microcatchment surface conditions by estimating stone and soil crust cover on three bare-soil squares (0.5×0.5 m) per microcatchment.

To assess the role of microcatchment area and upslope length in modulating the amount of water inputs to the planted seedlings, we measured soil moisture in the planting hole of each target seedling for three consecutive sampling dates after a run of rainy days in May 2010 (26.6mm of accumulated rainfall) that generated several runoff events. Soil moisture was measured using a TDR100 tester (Campbell Scientific, Inc., Logan, USA) on one 25-cm long TDR probe vertically installed in each seedling planting hole. These measurements provided an integration of the volumetric soil water content in the top 25 cm of the planting hole.

For each species, we computed PCA analyses to integrate the information on growth and water-stress variables into independent single variables (PCA axis). For *O. europea* individuals, the PCA on growth-related variables resulted in one axis (hereafter PCA1–Growth) explaining 71% of the total variance and being positively correlated to height growth rate, seedling height, and basal diameter. The PCA on water-stress related variables resulted in two axes: the first axis (PCA1–Water–stress) explained 60% of the total variance and was positively correlated to stem $\delta^{13}\text{C}$ and leaf $\delta^{13}\text{C}$, and negatively to RWC. This axis was interpreted as a proxy of the individual's water–stress level, with higher values of this axis representing higher water–stress experienced by the plants. Similarly, for *P. lentiscus* individuals, PCA analyses resulted in one axis explaining 81% of the total variance for the plant growth-related variables (PCA1–Growth) and two axes for the water–stress related variables, with the first axis, explaining 50% of the total variance (PCA1–Water–stress). Further analyses for each species were performed with the first axes (components) that resulted from each of the PCA analyses.

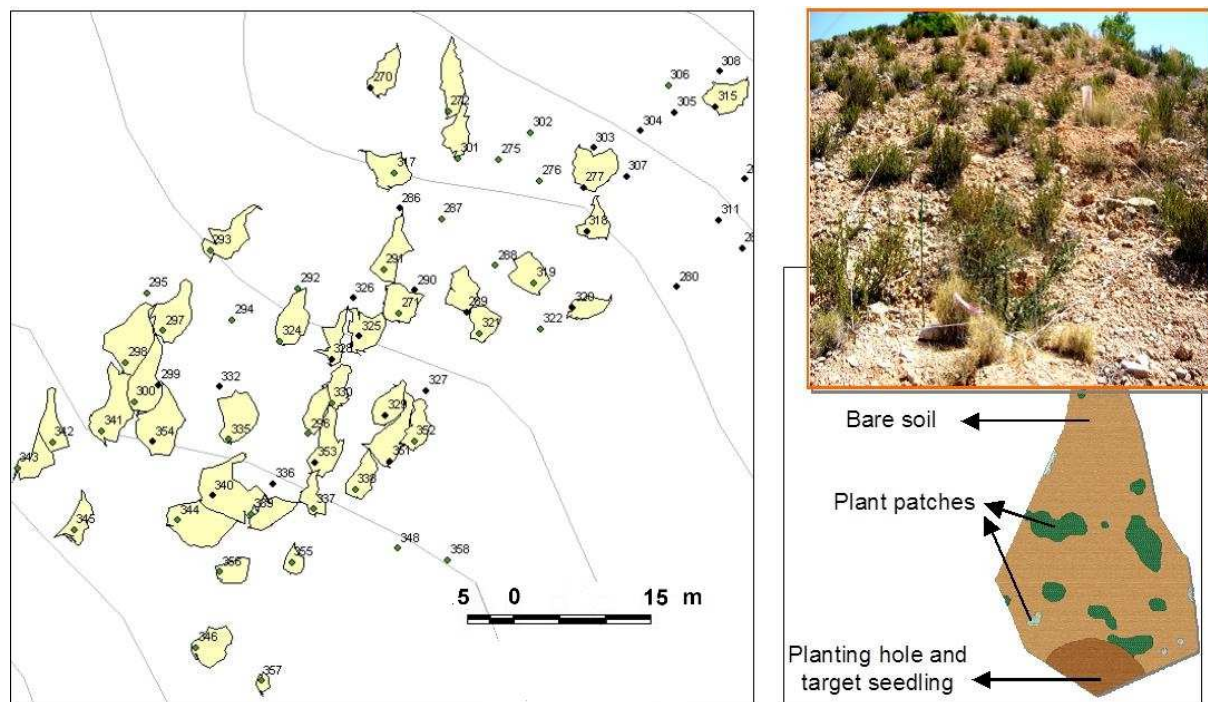


Figure 14. Map of target (*O. europaea* and *P. lentiscus*) seedlings and associated individual drainage microcatchments located on one of the slopes of the selected monitoring plot in Albaterra catchment (left) and one example of the microcatchments assessed and mapped (right).

2.4.2 Local effect of resource redistribution on plant performance

The hypothesis on the positive relationship between plant performance and the size of the associated upslope runoff-source area was supported by the observed growth response of *O. europaea* plants in our experiment. Thus, PCA1–Growth for *O. europaea* was positively related to the projected area of the individual drainage microcatchments (Fig. 15, top, left). The assumption that the mechanism behind this relationship is the transfer of water and other resources from upslope runoff-source areas to downslope plant patches is in agreement with our results on soil moisture variation: for several days after a number of consecutive rainfalls, soil moisture showed positive relationships with microcatchment projected area, which eventually vanished when the soil became drier (Fig. 16, left). This slow drying process suggests that increased soil water content due to runoff inputs was evapotranspired at a relatively low rate, which could be explained by the conservative water strategy attributed to *O. europaea* (Hernández et al. 2011).

Surprisingly, slope length (upslope the target plant) showed no relationship with plant growth (Fig. 15, top right), which is in agreement with the weak relationship found between soil moisture and slope length (Fig. 16 right). The general assumption of increased soil moisture in lower topographic positions has been often challenged in semiarid lands (e.g. Singh et al. 1998, Cantón et al. 2004). In our study site, topographic position barely controlled soil moisture, and certainly to a lesser extent than microcatchment size, which supports the contrasting response of plant growth to these two variables.

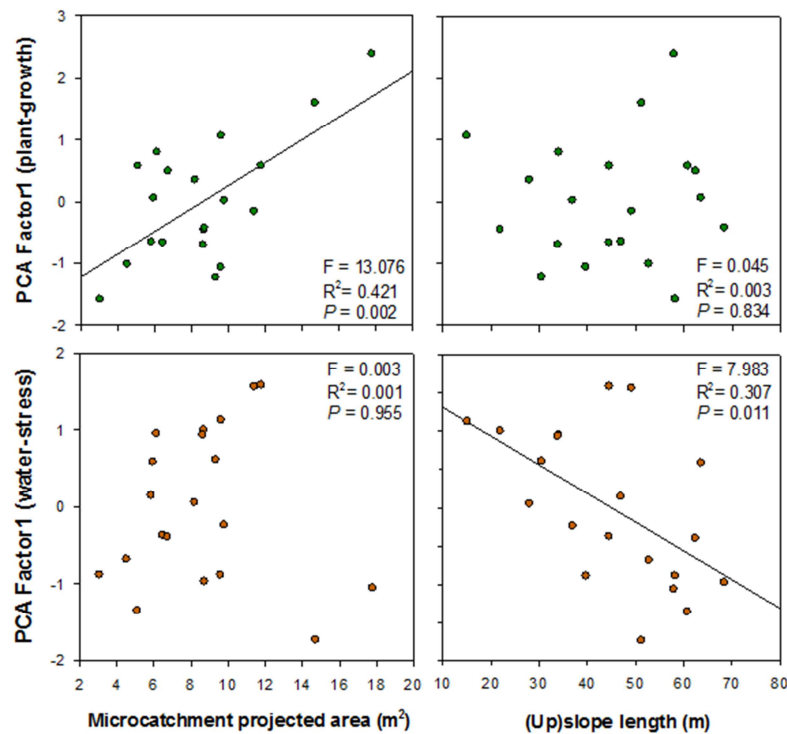


Figure 15. Relationships between the first component of the PCA on plant growth-related variables (top) and on water–stress related variables (bottom) as a function of the microcatchment projected area (left) and the length of the hillslope area upslope each target *O. europaea* seedling (right). Results from the respective regression analyses are included in each graph.

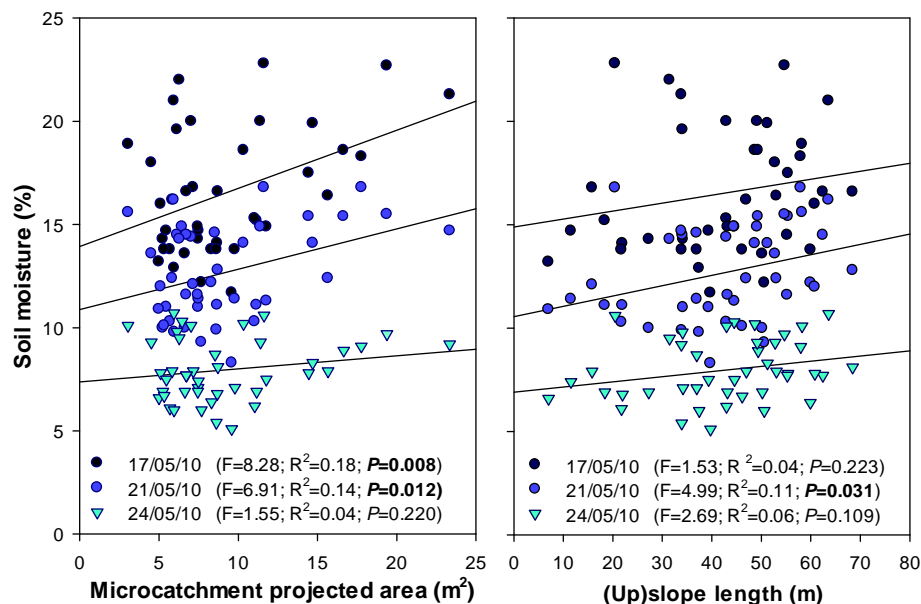


Figure 16. Relationships between volumetric soil moisture (0–25 cm depth) and the projected area of individual drainage microcatchments (left), and the length of the hillslope area upslope each target seedling (right) for three sampling dates after a run of rainfall events that produced 26.6mm of accumulated rainfall. Results from regression analyses are included in the graph.

Conversely to seedling growth, the combination of variables related to the water–stress level of *O. europaea* plants (PCA1–Water–stress) showed a significant negative correlation with slope length, but no relationship with microcatchment size (Fig. 15, bottom). These results suggest that factors associated to the topographic position, such as radiation load and evaporative demand for –more or less– exposed seedlings, could be more critical for seedling water–stress than factors such as microcatchment size that control extra surface water inputs during rainfall events.

Bare-soil connectivity (Flowlength) showed a negative (marginally significant) correlation with PCA1–Water–stress. This suggests that increased bare-soil connectivity within the drainage microcatchment could enable higher resource inputs to the vegetation downslope (Puigdefábregas 2005, Bautista et al. 2007, Mayor et al. 2008, Yu et al. 2008). However, the fact that Flowlength index showed a negative (though weak) correlation with seedling water–stress, but no correlation with plant growth suggests that connectivity-driven differences in runoff inputs were too small at this scale as per having affected plant growth, yet they could have influenced water–stress during critical dry periods. For example, high hydrological connectivity close to the target plant can be essential for generating runoff inputs after small rainfall events (Valdecantos et al. 2014), and this is crucial in Mediterranean drylands as most summer rainfalls are very small (Lázaro et al. 2001).

We found no relationship between plant performance and soil surface properties such as stone and crust cover. This result was unexpected, as the role of rock fragment cover and soil crusts in controlling water surface flows is well established (e.g. Poesen and Lavee, 1994; Belnap, 2001; Eldridge et al., 2010). However, at the spatial scale considered in our study, the potential effect of these surface features may result only in small changes in water inputs to downslope plants, insufficient to promote a relevant impact in plant survival and performance.

Survival of *P. lentiscus* seedlings was low. Alive seedlings of this species did not show any significant relationship between their growth or water–stress level and microcatchment characteristics, probably due to the low number of individuals available. However, the survival response of *P. lentiscus* was rather consistent with the response to stress of *O. europaea*. Thus, comparisons of microcatchment properties between dead and alive *P. lentiscus* individuals showed that survival of *P. lentiscus* did not show any significant effect of microcatchment size, whilst it significantly increased with slope length (Fig. 17), with no alive *P. lentiscus* seedling found at less than 30m from the top of the slope (Fig. 18). These results indicate that factors that control seedling water–stress rather than those that control seedling growth during favourable (rainy) periods seem to be the most critical for seedling survival in these environments.

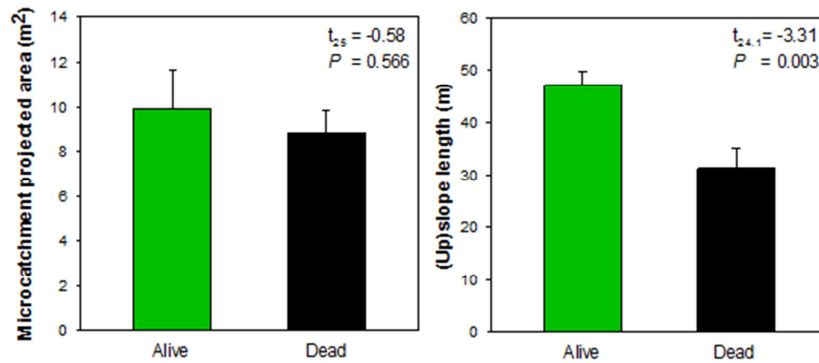


Figure 17. Average projected area (left) and average length of the hillslope area upslope the target seedlings (right) for alive and dead *P. lentiscus* planted seedlings. Error bars represent 1 standard error; results from t-tests are included in each graph.

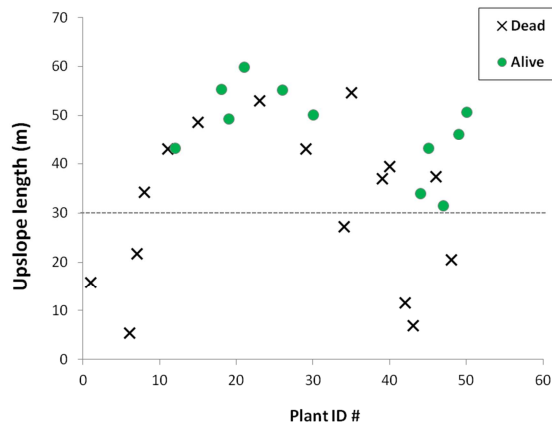


Figure 18. Upslope length for each alive and dead *P. lentiscus* seedling assessed in the study area. Dashed line represents the threshold below which no alive seedling was found.

In sum, the interplay between the size of the upslope inter-patch and the relative location on the hillslope, i.e. the upslope length, modulate the performance of plant patches in Mediterranean drylands, yet the strength of the effect and the relative role of each factor may vary with the species considered. Overall, our results prove that runoff inputs from upslope inter-patch areas control seedling growth, while seedling survival and water-stress level is mostly controlled by the position on the slope. Thus, the larger the upslope inter-patch size, the higher the plant growth; while the lower the relative location on the slope, the higher the survival probability. The implications of these results must be considered in combination with the potential counterbalancing effects of inter-patch size at the global (slope, catchment) scale, as higher inter-patch size also implies higher resource losses from the slopes and therefore lower global resource availability for the vegetation (see section 2.3). Further research is needed to better define this optimum source:sink ratio for semiarid plant communities.

Both, inter-patch size and relative upslope length, should (and can easily) be considered in spatially-explicit models that represent dryland dynamics, where the combined impact of the global (slope, catchment) and local (patch) implications of these ecohydrological feedbacks could be assessed for a large variety of scenarios.

Further details of the work summarized in this section 2.4 can be found in Urgeghe and Bautista (2014).

3 Synthesis and conclusions

By performing a variety of manipulative experiments and observations, we have tested the main ecohydrological mechanisms and processes underlying the hypothesized feedback loops that drive dryland dynamics, response to stress, and potential sudden shifts in drylands.

Our findings have demonstrated that both plant cover and plant pattern exert a critical role in controlling water and soil conservation in patchy ecosystems. This role mainly relies on the sink capacity of the soils underneath the plant patches, rather than on the capacity of the patches for rainfall interception and physical obstruction to overland flow. The connectivity of bare-soil emerged as the most critical pattern attribute for explaining the hydrological behavior of patchy ecosystems, as it reflects and depends on both cover and pattern. Larger bare-soil connectivity implies larger water and sediment losses from semiarid slopes, but it also implies larger inter-patch areas, which is beneficial for the performance of the downslope patch.

Our results provide critical insights on the control factors of source–sink dynamics in semiarid lands. Spatially explicit or mechanistic models that investigate the interactions between spatial vegetation pattern and resource redistribution (e.g. Urgeghe et al., 2010; Mayor et al. 2013), as well as ecogeomorphic evolution models (e.g. Saco and Moreno-de las Heras 2013) may greatly benefit from the empirical findings presented here.

Understanding the control factors that drive plant performance and ecosystem productivity in semiarid lands is critical to the conservation, management and restoration of these areas. The evidence for a positive relationship between seedling growth and the size of the upslope inter-patch area should be considered when designing conservation and restoration actions in semiarid lands. Along these lines, treatments that exploit and enhance source–sink dynamics on dryland slopes can improve the re-introduction of native shrubs into areas under strong water–stress conditions. Furthermore, with the aim of recovering previous landscape processes and minimizing resource leaks, the spatial pattern of the introduced seedlings should pursue a functional patchiness and source:sink area ratio, that maximizes both vegetation cover and the amount of water input that can be captured by the vegetation. Further research is needed to better define this optimum source:sink ratio for a number of plant communities and spatial scales.

Finally, although plant cover and biomass are the most common vegetation properties used for hydrological modeling, our results suggest that other patch metrics like patch number and/or size distribution could be better hydrological indicators than patch cover. Integrated indexes based on capturing the connectivity of the bare-soil matrix in patchy ecosystems, such as Flowlength index, have great potential as surrogates for the hydrologic functioning in semiarid landscapes. These indices can be easily obtained from aerial photographs and incorporated into hydrologic and erosion models at the hillslope and catchment scales.

Overall, the results reported here from a first set of WP4 experiments support the hypothesized role of ecohydrological processes and feedbacks as potential inside mechanisms underlying sudden shifts in drylands. New, on-going experiments within WP4 will test how increased pressure on dryland systems could trigger sudden shifts towards degraded states, and how this degradation can be reverted by manipulating plant cover and diversity.

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