CASCADE
Catastrophic shifts in drylands:
How can we prevent
ecosystem degradation?

CASCADE REPORT series

Report on threshold dynamics

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Deliverable 4.3

Dryland restoration dynamics and thresholds as a function of plant pattern and diversity

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June 2017

WP4: Manipulative field mesocosm experiments on ecosystem dynamics

Contents

Executive summary

The degree and extent of current dryland degradation as well as their impacts on economic and political stability are widely recognized. Accordingly, societal demand for ecosystem restoration is rapidly increasing and environmental policy is increasingly embracing restoration. Drylands may response in a gradual, continuous way to a gradual change in human-induced and/or climate pressures, but they may also exhibit non-linear dynamics and sudden shifts between alternative stable states, including shifts to degraded states in response to increasing pressure. The mere decrease or cessation of the degradation pressure may not result in the recovery of the degraded or undesired state, which could require much better initial conditions than those that resulted in the degradation of the system. Feedbacks between the degraded state and a variety of internal and external factors make the degraded state highly resilient, and act as potential barriers to restoration. Explicit consideration of these feedbacks in the design of restoration could help overcome these barriers and enhance restoration success.

The intrinsic spatial heterogeneity and patchiness of dryland vegetation are essential dryland features that control ecosystem functioning and dynamics. However, little previous research has focused on restoration of vegetation patches and investigated how diversity, size, and spatial arrangement of plant patches could affect dryland restoration success. Progressing in our capacity for reverting degradation and restoring degraded drylands requires a better understanding of the role played by the biotic and spatial structure of restored vegetation patches, as well as by the feedbacks that control the resilience of degraded drylands.

The general objective of the work reported in this Deliverable is to determine degradation reversal dynamics and thresholds as a function of plant colonization pattern and diversity. We have addressed this objective at two levels: at the plant patch scale and at the ecosystem scale. Main research questions at the patch scale pursue identifying the spatial and biotic structure of plant patches that would optimize the recovery of degraded drylands. At the ecosystem scale, we investigated the potential for degradation reversal and restoration of dryland ecosystems as a function of the initial plant cover and the strength of the ecohydrological feedbacks that control dryland dynamics.

We built two large, unique experimental stations of 24 (2 x 1 m) plots and 56 (8 x 5 m) plots, respectively, for the assessment of plant diversity and spatial pattern effects on dryland restoration by means of mesocosm experiments at the scale of the plant community. We conducted a variety of manipulative experiments on both stations, which focused on different aspects of the questions addressed in this work, and for which patch cover, pattern, size and diversity were independently manipulated in order to test their independent and combined effects on restoration potential for a variety of plant communities created ad hoc. To analyze the main basic effects of global and local feedbacks on the recovery potential of degraded drylands, we followed a modelling approach, extending a well-known spatially explicit dryland model that exhibits catastrophic transitions with the incorporation of global and local feedbacks.

The effect of patch diversity and size on plant performance depended on the plant functional types considered and the climatic conditions, yet some common pattern was found for a large variety of dryland species tested. Thus, at early stages of the restoration trajectory (first 1-2 years after planting), with all plant seedlings sharing similar rooting space, there was no evidence of complementarity between species that may have resulted in higher productivity in multispecies patches as compared with monospecific patches. However, there was no evidence either of detrimental effects of interspecific competition, as compared with intraspecific competition in monospecific patches. Big diverse patches benefited better from the higher capacity for trapping water and other resources from runoff than big monospecific patches. However, under stressful conditions, facing both intra-specific and interspecific competition within the plant patch is more challenging for the species than interacting only with conspecific individuals. Individual biomass was not significantly reduced by increasing the number of accompanying species in the same patch. Increasing patch size and diversity may reduce to some extent the probability of sapling survival in the restored patch. However, our results indicate a positive net outcome from the trade-off between a relatively low risk of decreasing survival and the potential benefits derived from increasing diversity.

At the community scale, low initial plant cover did not constrain the potential for restoration success, which could be explained by the positive effect of water and sediment transfer from large bare soil areas to few existent plant patches. Our findings have demonstrated that ecohydrological feedbacks between resource redistribution and vegetation dynamics that are mediated by bare-soil connectivity exert an important role in modulating the restoration potential of dryland ecosystems. Larger bare-soil connectivity implies larger water and sediment losses from semiarid slopes, but it also implies larger inter-patch areas and associated larger runon inputs to existent plant patches, which is beneficial for the performance of the vegetation in the patch. This local feedback, if enough strong, increases the range of conditions (external stress, minimum initial cover) that allow the recovery of the system.

From an applied perspective, in a context of dryland restoration, a number of recommendations can be derived from our results, including (1) using (creating) multispecies big patches, yet minimizing intraspecific competition by reducing the number of individuals per species within the same patch; (2) spatially arranging plant patches on slopes in a way that maximizes the capture of runoff water by plant patches; (3) combining species in the plant patches with plant traits that maximize the capture and deep infiltration of runoff water.

1 Introduction

Drylands, which are home to ~40% of the global population, are under threat from multiple stresses that result from the interplay of natural processes, such as recurrent droughts and low soil fertility, and unsustainable land use practices, jointly leading to land degradation and desertification (Millennium Ecosystem Assessment 2005). As an example, considering Africa alone, 320 million hectares – 25 per cent – of the continent's drylands are considered to be desertified (UNEP, 2006), with ongoing climate change and a rapidly growing population being expected to exacerbate the existing degradation problem and the vulnerability of the inhabitants of African drylands (UNCCD-UNDP-UNEP, 2009). Similar figures are estimated for other continents, including Europe (Gibbs and Salmon, 2015).

The Sustainable Development Goals (SDGs) include a target to "combat desertification, restore degraded land and soil, including land affected by desertification, drought and floods, and strive to achieve a land degradation-neutral world" by 2030 (Target 15.3; UNGA, 2015). In agreement with this target, the Parties within the United Nations Convention to Combat Desertification (UNCCD) decided to integrate Land Degradation Neutrality (LDN) into the implementation process of the UNCCD (UNCCD, 2015). Achieving global LDN, and dryland degradation neutrality in particular, requires sustainable land management that avoids or reduces degradation, but also efforts to reverse degradation through restoration or rehabilitation of land (Orr et al., 2017). In fact, given the degree and extent of current land degradation, societal demand for ecosystem restoration is rapidly increasing and, accordingly, environmental policy is increasingly embracing restoration (Suding, 2011).

Drylands may respond in a gradual, continuous way to a gradual increase in human-induced and/or climate pressures. However, some empirical evidence and modelling experiments suggest that drylands may also experience sudden shifts from functional to degraded states in response to increasing pressure (Rietkerk et al. 2004, Kéfi et al. 2007a). These critical transitions assume the occurrence of alternative stable states: different configurations of a system that are able to exist at the same set of external conditions, corresponding to a stable equilibrium or basin of attraction in nonlinear response to external conditions (Litzow and Hunsicker, 2016). It is widely accepted that the mere decrease or cessation of the degradation pressure may not result in the recovery of the healthy or desired state (Van Auken, 2000; Gao et al., 2011), which could require much better initial conditions than those that resulted in the degradation of the system. This fact implies that the trajectories of collapse and recovery differ (Fig. 1), which is known as hysteresis, a common feature in non-linear ecological systems that implies different critical transitions in response to increasing and decreasing external conditions (Litzow and Hunsicker, 2016).

Non-linear models such as the fold-bifurcation model represented in Figure 1 incorporate thresholds and positive feedbacks that explain both why small perturbations may propel the system to another stable state and why the degraded system is resilient to recovery.

These feedbacks often involve plant-plant interactions and water redistribution (Kéfi et al. 2007b; Mayor et al., 2013; Meron, 2016), yet less is known on how these mechanisms could enforce the resilience of degraded systems (Carpenter et al., 2001). Under the framework of alternative stable states, sudden shifts, and internally reinforced degraded or undesired states, restoration appears as the key management action that could reverse degradation. However, the feedbacks between the degraded state and a variety of internal and external factors that make the degraded state highly resilient, are also potential barriers to restoring degraded systems (Bakker and Berendse, 1999), and thereby should be taken into account when designing restoration approaches and actions.

CASCADE-WP4 has contributed to characterize key ecohydrological feedbacks between plant spatial pattern, water redistribution, and plant functioning that lead to sudden shifts in drylands, and how they may be modulated by plant diversity (D4.1). A decrease in the cover and size of vegetation patches would increase 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 global feedback towards degradation. In contrast, at the plant patch scale, increasing 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, completing a negative feedback that may prevent further degradation. The present Deliverable D4.3 reports on WP4 Task 3 results on the role played by these feedbacks in the recovery of degraded drylands.

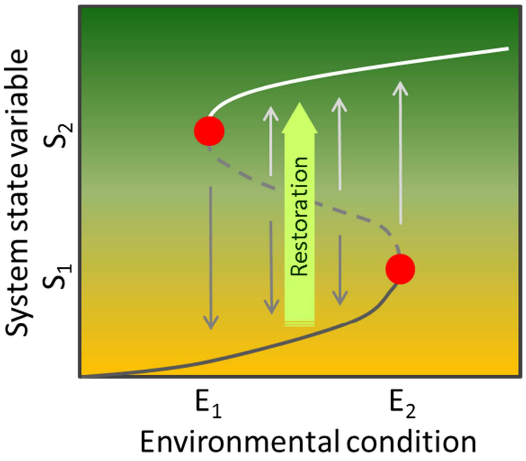

Figure 1. Alternative stable states model for ecosystem dynamics, with bifurcation points (red dots) representing critical transitions between states. At S_2, worsening environmental conditions below E_1 results in the collapse of the system to S_2 or below. Improving the conditions above E_2 returns the system to the healthy state S_2. At conditions between E_1 and E_2, the system could move to either the healthy S_2 or the degraded S_1 (bistability). Once the system has collapsed to S_1 or below, it will not return to S_2 unless conditions are improved to E_2. Restoration could help the system return to S_2 without the need to improve conditions above E_2 (adapted from Suding et al., 2004).

Dryland restoration faces important constraints and limitations, mostly derived from the limited and spatially and temporally heterogeneous resource availability (Whitford, 2002).

Restoration approaches developed for mesic areas are seldom suitable for drylands, as ignoring dryland heterogeneity, the typical patchy nature of dryland landscapes, and the critical role played by plant-plant interactions in dryland vegetation communities could easily result in restoration failures.

Research on dryland restoration has mostly focused on improving nursery and field treatments to increase seedling survival and optimize plant growth (e.g., Chirino et al. 2009; Valdecantos et al., 2014). In the last two decades, the role of positive plant-plant interactions is being increasingly considered in restoration ecology (e.g., Maestre et al., 2001; Gómez-Aparicio et al., 2004). However, progressing in our capacity for reverting degradation and restoring degraded drylands requires a better understanding of the role played by the biotic and spatial structure of restored vegetation patches, as well as by the feedbacks that control the resilience of degraded drylands.

Ecological approaches to restoration emphasize process repair (i.e., reestablish rates or regimes of key processes that sustain the target ecosystems, such as fire or flooding regimes, erosion and sediment transport, etc.) over structural replacement (such as the construction of particular habitat or landscapes structures or the introduction of particular species) (Falk, 2006; Beechie et al., 2010). However, drylands are mostly controlled by ecohydrological processes that are tightly coupled to the biotic and spatial structure of their ecosystems and landscapes. For example, the transfer of resources from bare-soil interpatches to downslope vegetation patches contribute to plant productivity and overall ecosystem productivity (Aguiar and Sala 1999, Yu et al. 2008, Turnbull et al. 2012), with this transfer being modulated by the spatial pattern of the vegetation and the size of the upslope bare-soil areas (Bautista et al., 2007; Urgeghe et al., 2010; Urgeghe and Bautista, 2015) and the species functional group in the plant patch (Bochet et al., 2006; Mayor et al., 2009). Despite the importance of the spatial pattern and the patchy structure of vegetation for the overall functioning and dynamics of dryland ecosystems, to our knowledge few previous research has investigated the restoration of patches (Ludwig and Tongway, 1996) and no previous work has addressed how features such as the diversity, size, and spatial arrangement of plant patches could affect dryland restoration success.

2 Objectives, research questions, and approach

The general objective of CASCADE-WP4 addressed in this Deliverable is to ***determine degradation reversal dynamics and thresholds as a function of plant colonization pattern and diversity.*** Assuming the patchy spatial structure of dryland vegetation, we have addressed this objective at two levels: at the plant patch scale and at the ecosystem scale.

Main research questions at the patch scale pursue identifying the spatial and biotic structure of plant patches that would optimize the recovery of degraded drylands. Specifically, under the framework of restoration actions applied to bare-soil dryland areas, we investigated if:

- Facilitation (individuals perform better when growing with other species) dominates in plant patches
- Diverse patches perform better than monospecific patches
- Bigger /denser patches perform better than small patches with few individuals, either from the same or different species
- Functional diversity is more relevant than species diversity for plant patch performance
- The role of patch diversity and size depends on the plant functional types considered.

At the ecosystem scale, we investigated the potential for degradation reversal and restoration of dryland ecosystems as a function of the initial plant cover and the strength of the ecohydrological feedbacks that control dryland dynamics. Specifically, we investigated if:

- For a given plant community, there is a minimum threshold for vegetation cover below which potential for recovery is negligible. From a restoration perspective, an alternative version of this question could be if, for a given plant community, there is a minimum vegetation cover value that triggers the recovery of the community.
- Higher strength of positive global ecohydrological feedbacks (decreasing vegetation cover → increasing global resource loss from the system → decreasing vegetation cover) would reduce the recovery potential of dryland ecosystems.
- Higher strength of negative local ecohydrological feedbacks (decreasing vegetation cover → increasing runon-driven inputs to plant patches → increasing vegetation growth and cover) would increase the recovery potential of dryland ecosystems.

In order to address these questions, CASCADE-WP4 has followed a fully manipulative experimental approach combined with modelling. 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 general models. Model development was carried out in collaboration with WP6, yet the modelling work performed was specific for WP4 research questions.

3 Methods

3.1 Manipulating dryland plant communities in mesocosms

Within CASCADE WP4, we built two large, unique experimental stations for the assessment of plant diversity and spatial pattern effects on dryland restoration by means of manipulative experiments at the scale of the plant community. Both the soil used (soil from old fields developed on limestone and marl substrates) and the plant species included in the cultures established (species from semiarid Mediterranean shrublands and steppes) are common in semiarid all across the Mediterranean Basin. For all the experiments conducted, climatic conditions were relatively dry (annual precipitation slightly lower than annual average).

The first station, ES24 (Fig. 2), includes a set of 24 closed (2 x 1 m) plots, which allow event-based monitoring of runoff and sediment yields, and are meant to be used for short-term (few years) experiments. The plots were filled with soil from nearby degraded abandoned field, creating a slope angle of 25%. The soil was previously homogenized, sieved through a 2 cm mesh (to remove stones), and kept exposed to very dry conditions for weeks in order to dry out existing seeds and most of the soil fauna. This treatment allowed establishing quite homogeneous and relatively inert initial conditions in all plots, minimizing the influence of uncontrolled factors in the plant communities created for the experiment.

Figure 2. Aerial view of the experimental station ES24 located at the University of Alicante (Spain), showing the 24 (2x1 m) closed plots of ES24, including runoff and sediment collectors, and the greenhouse facilities in the area. Photo by D. Fuentes.

The second station, ES56 (Fig. 3), consist of a large-scale set of 56 permanent (8 x 5 m) plots on an artificial slope built from aggregate mining overburden and soil from nearby abandoned degraded fields. This station aims to provide data on the role of species and functional diversity in dryland restoration success at the short-term, as well as a pioneer long-term experimental setting for the assessment of the interplay between biodiversity-function relationships and community-scale plant-plant interactions in shaping dryland vegetation dynamics.

Figure 3. General view of the experimental station ES56 in Alicante (Spain) on an artificial slope with degraded soils built *ad hoc* for experimental purposes. Photo by S. Bautista.

3.1.1. Short-term experiments on ES24

We sequentially conducted two manipulative experiments on the ES24 set of plots, which focused on different aspects of the questions addressed in D4.3, and where patch cover, pattern, size and internal diversity were independently manipulated in order to test their independent and combined effects on restoration potential for a variety of plant communities created *ad hoc*. Each experiment was conducted over a period of 1-1.5 years.

The first experiment (experiment #1) conducted on ES24 was also used for the assessment of the feedbacks between the effect of pattern on resource conservation and the effect of resource availability back to vegetation (See D4.1). Regarding D4.3, this experiment allowed investigating the role of patch size and diversity as well as the dominant plant-plant interactions within the plant patches for contrasting plant functional groups. We used 1-year-old plant seedlings of three different species to create artificial plant communities with contrasting patch size: big-patch pattern (6 big patches of 9 individual plants each), vs. small-patch pattern (18 small patches of 3 plants each), and contrasting diversity: mono-specific vs. diverse communities (Fig. 4). 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 (polycultures), all the plant patches include the three species used (3 plants/species in the big patches; 1 plant/species in the small patches). In the “monospecific” plots, all patches include the same single species. There were 3 plot replicates for each treatment combination (2 patterns X 4 plant communities). We monitored plant performance over a one-year period, a time window that allowed testing the factors that controlled the establishment of the communities, after which the experiment was dismantled and all plants were harvested for biomass estimation (See D4.1 for further details on this experiment).

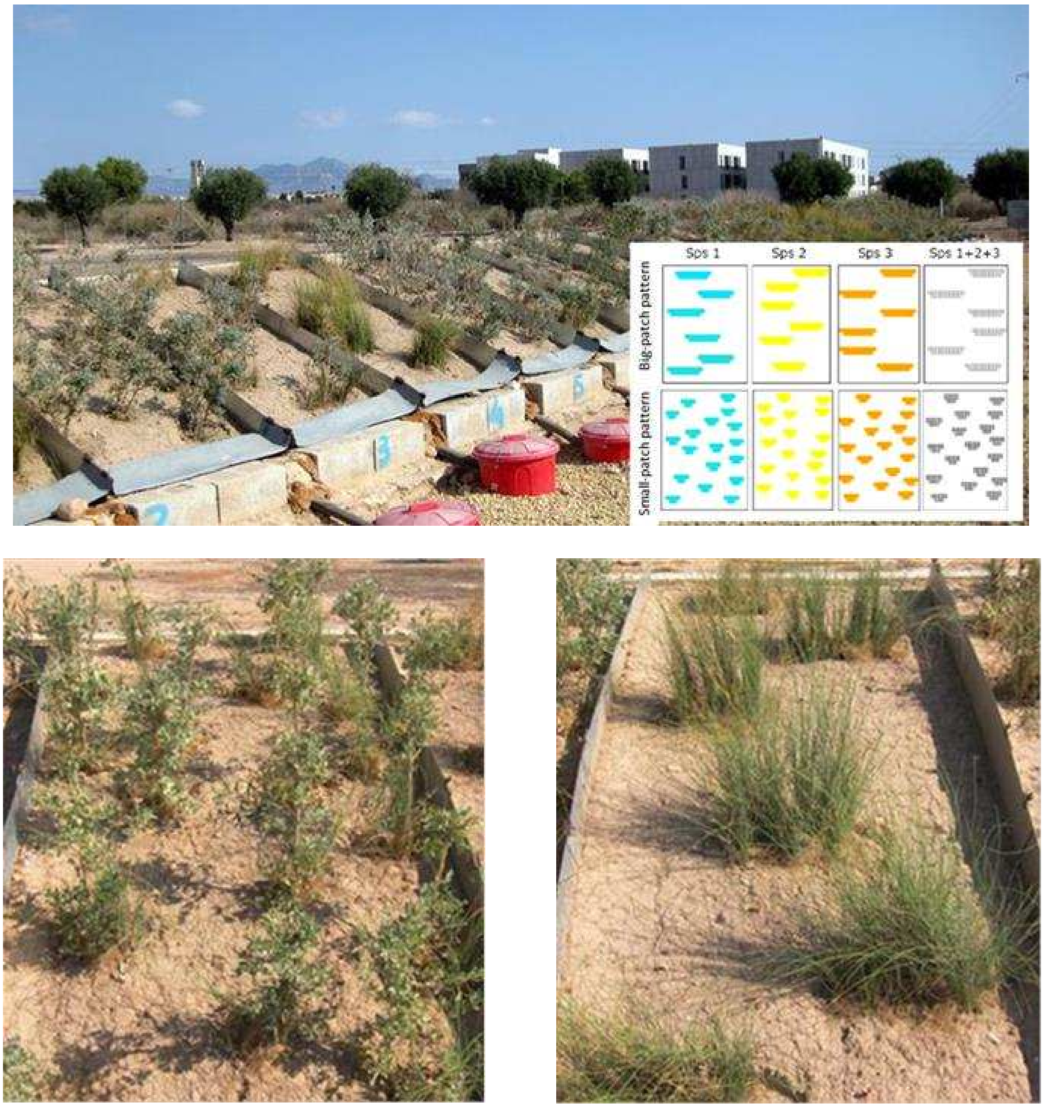

Figure 4. General view and outline of the experimental design of for experiment #1 in ES24 (top), and details of a fine-grained (18 mall patches) plot (bottom, left) with diverse (3 species) patches, and of a coarse-grained (6 big patches) *Lygeum spartum* plot (bottom right). Photos by S. Bautista.

In order to assess the effect of the initial plant cover in combination with patch size and diversity, and to further explore the interaction between grass and woody species, we conducted a second experiment (#2) on ES24 using the perennial grass *Brachypodium retusum* (Pers.) P.Beauv. and the late-successional, deep-rooting shrub *Rhamnus lycioides* L. as target species. These two species represent very contrasting features regarding water use and are very abundant in natural semiarid shrublands in the Mediterranean Basin region. An outline of the different plant communities established is depicted in Figure 5. We compared six initial levels of patch cover values (5, 10, 15, 20, 25 and 30%), establishing four replicated plot for each level that varied in their spatial arrangement. Plant patches consisted of either two or six individuals, and were either mono-cultures (only *B. retusum* or *R. lycioides* plants) or bi-cultures (with plants of both species in the same patch).

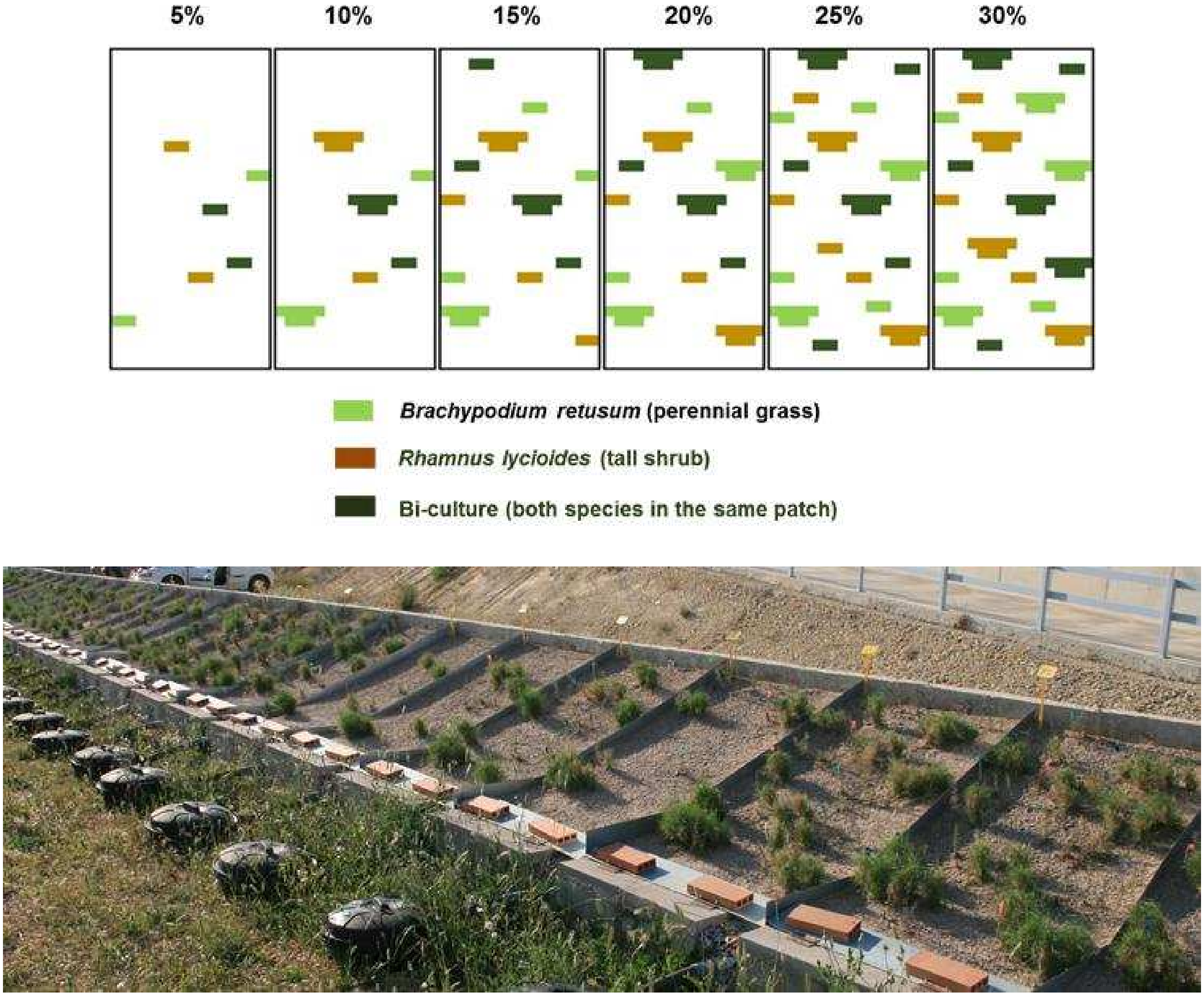

Figure 5. Outline of experimental design (top) and general view of the experiment #2 in ES24 (x 4 replicates for each level of cover). Photo by A. Fuster

3.1.2. Large-scale SE56 experiment

For this experiment, we created plant communities with varying levels of plant diversity and patch size by planting groups (patches) of varying diversity and number of young (6 months old) seedlings on bare-soil plots. The experimental design includes three factors: Species richness (S), with 4 levels (S1, S2, S4, and S8), corresponding with one, two, four and eight species respectively; functional diversity (F), with two levels (F1 and F4; one or four functional groups), and patch size (pz) with 4 levels (pz1, pz2, pz4 and pz8), corresponding with one, two, four and eight individuals per patch, respectively (Fig. 6). The eight target species were selected to represent contrasting functional group in terms of life form and successional dynamics, and included to tussock grasses (*Stipa tenacissima* and L. spartum), two sub-shrub legume species (*Anthyllis cytisoides* and *Dorycnium penthaphyllum*), two seeder shrubs (*Rosmarinus officinalis* and *Cistus clusii*), and two tall, resprouter shrubs (*Pistacia lenticus* and *P. angustifolia*).

Comparisons of subsets of plots allow assessing the independent role played by the various factors, thus comparison of S4(F4) and S8(F4) plots allows assessing the role of species diversity (4 versus 8 species) for a given level of functional diversity (4 functional groups) (Fig. 6).

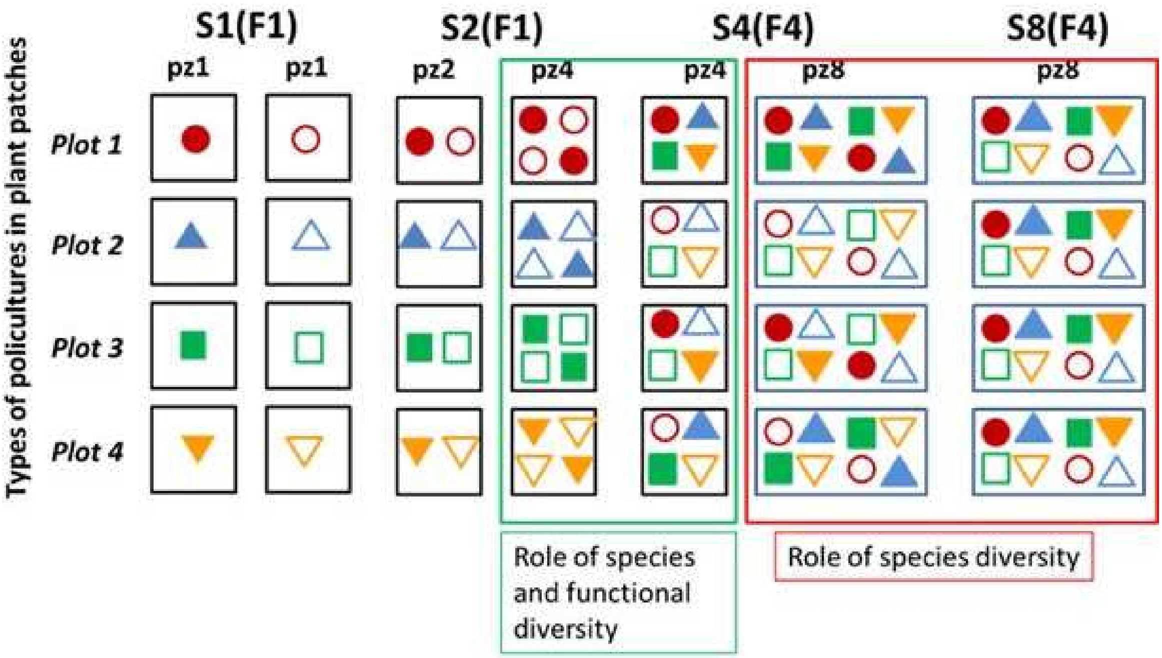

Figure 6. Outline of experimental design of the large-scale experiment in ES56. Treatments S and (F) represent number of species and functional groups, respectively; treatment pz# represents the number of individuals per patch. Different symbols represent different species; different symbol colors represent different functional group. Each plot (8x5 m) includes 12 patches with the same combination of treatments (8 plot replicates per treatment combination).

3.2 Modelling the role of ecohydrological feedbacks on degradation reversal

To analyze the main basic effects of global and local feedbacks on the recovery potential of degraded drylands, we used the mean field approximation (Morozov and Poggiale, 2012) to an extension of a well-known spatially explicit dryland model that exhibits catastrophic transitions (Kefi et al. 2007b; hereafter BCA model), with the incorporation of global and local feedbacks. The BCA model is a stochastic cellular automaton that represents a dryland ecosystem by a grid of vegetated, empty or degraded cells. Empty cells represent bare soil that is suitable for plant colonization, while degraded cells represent eroded soil that cannot be colonized by vegetation. The model represents local facilitation (i.e., the positive effect of vegetation on its local environment) as an increased regeneration rate of degraded cells when they are close to vegetated cells. The colonization rate of empty cells depends on a parameter (b) that reflects the external pressure on the system.

The incorporation of global feedbacks into the BCA model was carried out in Mayor et al. (2013) in the framework of CASCADE WP6, through the use of the hydrological connectivity index Flowlength (Mayor et al. 2008) as a proxy for the net loss of resources from the system, affecting the behaviour of the vegetated patches as:

$$b' = b \cdot \left(1 - \alpha \cdot \frac{FL}{FL_{\max}} \right)$$

where b' is the plant establishment as affected by the net loss of resources from the system; b is the potential plant establishment, which coincides with plant establishment in the original model of Kéfi et al. (2007b); α represents the strength of the feedback between plant functioning and vegetation pattern via the global loss of resources; FL is the global connectivity (measured as the Flowlength index); and FL_{max} is the maximum value of the global connectivity. The resulting model (hereafter GCA model) was also a cellular automata model, allowing investigating the effect of the global feedback by simulations for specific sets of parameters.

The incorporation of local feedbacks was carried out in the model ECOHYDRY (Mayor et al., in preparation), considering the redistribution of resources mediated by the hydrological connectivity, and using the Flowlength arriving to each cell of the grid as a proxy of the transfer of resources from bare to vegetated patches, affecting the behaviour of the vegetated patches as:

$$b'' = b' + \gamma \cdot (1 - b') \cdot \mathrm{H}\left(\frac{flveg}{flveg_{\max}} \right)$$

where b’’ is plant establishment as affected by both local and global feedbacks; γ represents the strength of the feedback between plant functioning and vegetation pattern via the local gain of resources; flveg is the local connectivity of neighbouring vegetated cells; flvegmax is the maximum value of the local connectivity of neighbouring vegetated cells; and H is a saturation function accounting for a nonlinear behavior of the local gains, attaining maximum effects from above a certain connectivity level.

To be able to derive mean field approximations for the GCA and the ECOHYDRY models it was necessary to have analytic expressions for the expectations of the global and local Flowlength values. As these expressions were not available, we carried out an instrumental work to derive them (Rodríguez et al., in review). In this work, we provided explicit theoretical expressions for the expected value and variance of the Flowlength index under random cover distribution and for a simple aggregated-pattern model; moreover, we illustrated the use of this kind of null model to disentangle the independent roles played by plant cover and pattern in dryland functioning, and we assessed the potential of using the deviation from the null model as indicator of ecosystem functional status and transitions. These analytic expressions were used to obtain and analyze the mean field approximation of the ECOHYDRY model, i.e., the BCA model of Kefi et al. (2007b) including the effects of both global and local feedbacks.

4 Results and discussion

4.1 The role of patch, size, diversity and spatial pattern in dryland restoration

Patch size and biotic structure (composition/diversity) modulated the functioning (productivity) of the dryland communities artificially established on bare degraded soils in the framework of the manipulative restoration experiments reported here.

For experiment #1 (Fig. 7), *Atriplex halimus* (a pioneer, fast-growth species that easily colonizes bare-soil areas) small-patch plots produced significantly higher biomass than plots with big patches. This result was partly unexpected, as previous WP4 work proved that big patches are more efficient in capturing water and other resources from runoff (D4.1), and probably reflects an adverse effect of the competition for space in big (dense) patches that counterbalanced and exceeded the positive effect of higher runon inputs. For the grass species *Lygeum spartum*, this effect of patch size was marginal. Biomass production for the tall-shrub, late-successional species *Phyllirea angustifolia* was very low and did not show any effect of patch size (Fig. 7, left). Biomass production in diverse patches (polycultures) did not significantly vary with patch size. Plot biomass from polycultures was marginally (no significant) higher than the average of the three monocultures (Fig. 7, right). However, this difference was only apparent for big-patch pattern and biomass production in polycultures was similar to plot biomass from the most productive monoculture (*A. halimus*), which indicates that enhanced production in polycultures was not due to any functional complementarity among the species but mostly to the presence of the most productive one in the mix (Loreau and Hector, 2001).

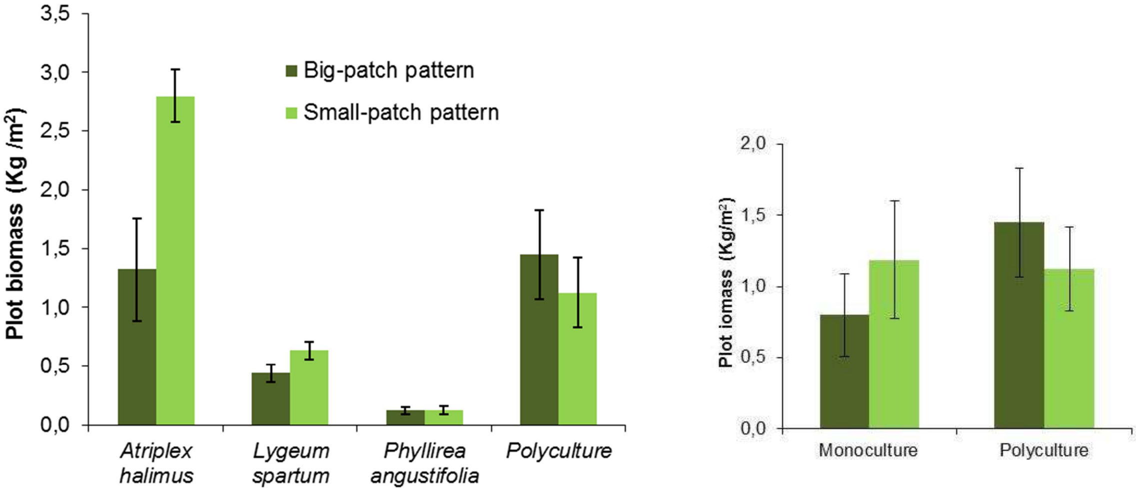

Figure 7. Plot biomass produced over a 1-year period as a function of the plant pattern and type of community (culture) of the experimental plot for all culture types (left) and for the aggregated (mean) values for all monocultures and polycultures (right).

In sum, at early stages after planting, with all plant seedlings sharing similar rooting space, there was no sign of complementarity between species that lead to higher productivity in diverse patches (polycultures). However, there was no sign of detrimental effects of interspecific competition either, as compared with intraspecific competition in monocultures. It seemed that big-patch polycultures benefited better from the higher capacity for trapping water and other resources from runoff (D4.1) than big-patch monocultures, which would explain that the slight positive effect of patch diversity on the overall patch productivity was only observed for big patches.

By looking at the individual plant response (individual plant growth rate) within the different types of patches, we found that the effect of patch size and diversity on plant growth largely varied as a function of the species considered and the environmental (climatic) conditions. Figure 8 shows the results for the most contrasting species *A. halimus* and *P. angustifolia*, with results or *L. spartum* (data not shown) being intermediate between those from these two species.

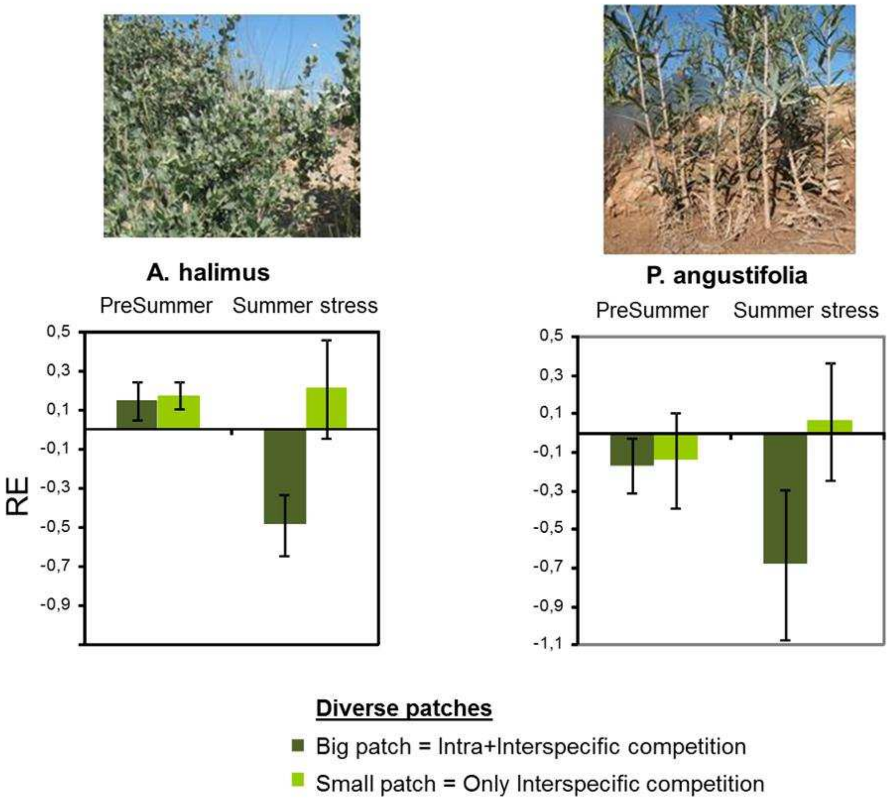

Figure 8. Relative effect (RE) of diversity: relative difference in growth rate between individuals growing in polycultures as compare with individuals of the same species growing in monocultures (sensu Loreau and Hector, 2001) for *A. halimus* (left) and *P. angustifolia* (right) growing either in big or small patches and for two contrasting periods: pre-summer (mild conditions) and summer stress (drought conditions). Standard growth rates were estimated for the change in basal diameter, BD (Ln BD final – Ln BD initial) for each monitored individual. Positive values for RE implies that individuals perform better in polycultures than in monocultures. Bars represent mean RE values and standard error.

Under good environmental conditions (pre-summer), the pioneer, fast colonizer *A. halimus* performed better in polycultures, indicating that intraspecific competition in monocultures was stronger than interspecific competition in polycultures. This response was similar for big and small patches. Conversely, the slow-growth, late-successional species *P. angustifolia* performed better in monocultures, particularly for big patches, reflecting the adverse effect of competition with the other two species. However, under stressful conditions (summer period) both species performed better in monocultures when growing in big patches, particularly *P. angustifolia*. Since big patches in polycultures included several individuals of each species, these results suggest that dealing with both intra-specific and interspecific competition under stressful condition is more challenging that interacting only with conspecific individuals. This kind of response has not been previously reported and has direct implications for restoration: in case of pursuing the restoration of multi-specific patches, it would be advisable to introduce only one individual per species, particularly if stressful conditions are expected to occur during the early stages of the restoration process.

Results from experiment#2 at the patch scale showed a significant effect of patch size for *B. retusum* growth rate, but not for *R. lycioides* growth rate. The effect of patch type (mono vs. bi-culture) was not significant in any case (Fig. 9). These results are consistent with those from experiment#1 in showing (1) similar performance of both species in polycultures and bi-cultures for small patches, (2) better performance of the fast-growing species (in this case: *B. retusum*) in small patches, and (3) a trend towards worse performance for the late successional species (*R. lycioides*) when coexisting with other species in big patches (Fig. 9).

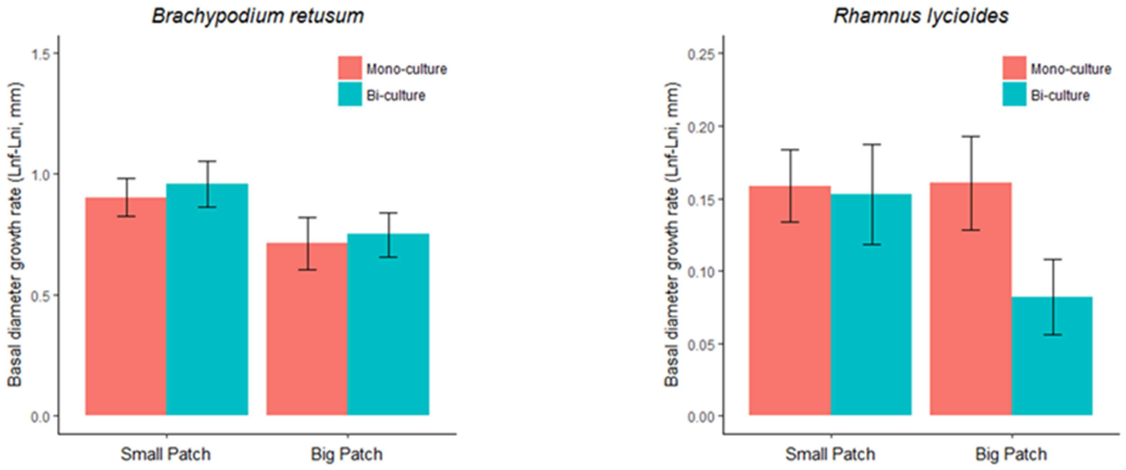

Figure 9. Variation in basal diameter, BD, growth rates (Ln BD final – Ln BD initial; 6-months period) for the grass species *B. retusum* and the shrub species *R. lycioides* as a function of patch size (big/small) and type (monoculture/biculture). Bars represent mean values and standard error.

It is generally assumed that grasses exert strong competition over seedlings and young saplings of woody species (Gómez-Aparicio, 2009), particularly if shrub seedlings grow within a matrix of grass cover and the associated dense belowground network of grass roots. However, our results highlight that under a context of dryland restoration of patchy landscapes, patches that include grasses and shrubs may not be that detrimental for the shrub species, particularly if enough bare-soil interpatch area is left around the patches.

Regarding the potential effect of initial cover on restoration success we did not identify any limitation to the restoration potential in the case of establishing plant communities with low, or very low, initial cover values (Fig. 10). In fact, initial plant cover hardly affected plant growth, with only *R. lycioides* in biculture patches showing a marginally significant decrease in growth rate with plant cover. These results challenge the conceptual framework provided by the fold-bifurcation type of models, which generally assume that dryland vegetation recovery would be very limited if starting with degraded low-cover, unless conditions largely improve. Restoration aims to act as a shortcut in the recovery dynamics of degraded drylands, facilitating the return to healthy states by manipulating either the environmental conditions or the initial state of the biotic community or both (Sudding et al., 2004). The fact that in restored patches, plants are introduced at the seedling stage may be an advantage –as compare with natural colonization from seeds– that contributes to overcome part of the limitations for recovery.

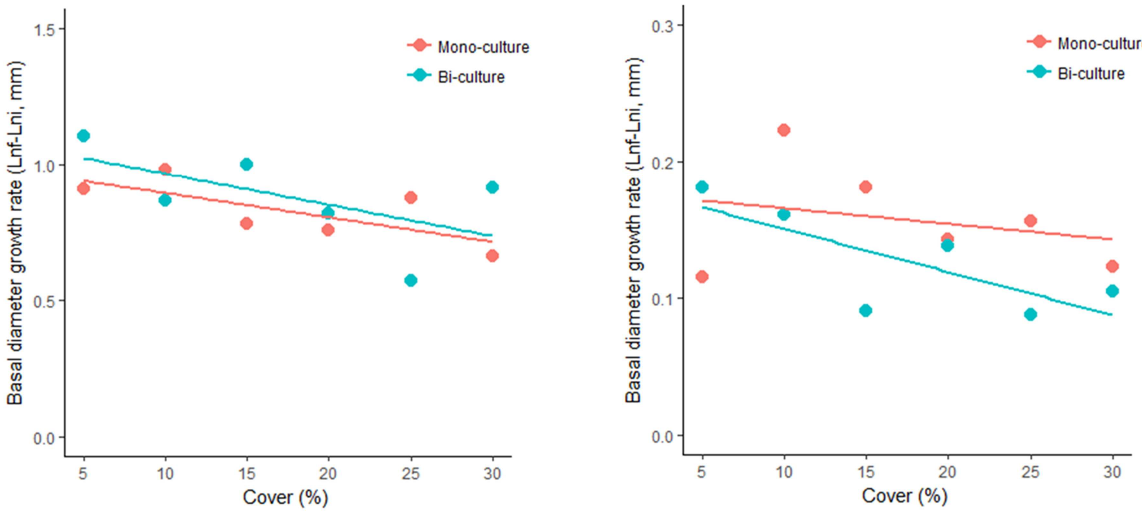

Figure 10. Variation in basal diameter, BD, growth rates (Ln BD final – Ln BD initial; 6-months period) for the grass species *B. retusum* and the shrub species *R. lycioides* as a function of initial patch cover (%) and patch type (monoculture/biculture). Lines are fitted regression lines.

Given the slow growth rate of most perennial species in dryland communities, the assessment of the recovery dynamics of experimental ecosystems is limited by the relatively short duration of any single research project. Therefore, in order to address WP4 questions on recovery dynamics, we relied on a modelling approach (See section

4.2 below). However, the results from the manipulative experiments described above suggest that a low initial plant cover does not constrain the potential for restoration success, which could be explained by the positive effect of water and sediment transfer from large bare soil areas to few existent plant patches (See 4.2).

Finally, the large-scale experiment conducted at ES56 followed a different approach to the ES24 experiments. Instead of comparing mono and polycultures, the experiment ES56 assessed the effect of increasing patch size (number of individuals) and diversity (number of species and/or functional groups), using the performance of patches with one individual and one species as reference. Figures 11 to 13 summarize the main results obtained at the early stages of the restoration trajectory.

We found that overall survival was not significantly hampered by increasing the number of individuals and/or species (up to 8 in both cases) in the restored vegetation patch (Fig. 11). However, not all plant functional groups responded in the same way to patch size and diversity (Fig. 12). Survival of grasses was hardly affected by including in the patch other species and/or individuals. Conversely, survival of woody species significantly varied between treatments, decreasing from patches with only one individual (treatment 1_1) to patches with two individuals (one per species) of two species from the same functional group (treatment 2_2); and further decreasing in patches with two individuals per species of two species of the same functional group (treatment 4_2). The exception to this trend was the group of resprouter phanerophytes (tall, late successional shrubs), which showed a very high survival for treatment 4_2, probably due to the influence of one of the experimental plots of this kind that was, incidentally, in particular good conditions. Further increase in number of species and functional groups per patch (treatments 4_4, 4_8, and 8_8) had a positive effect on woody species survival (Fig. 12).

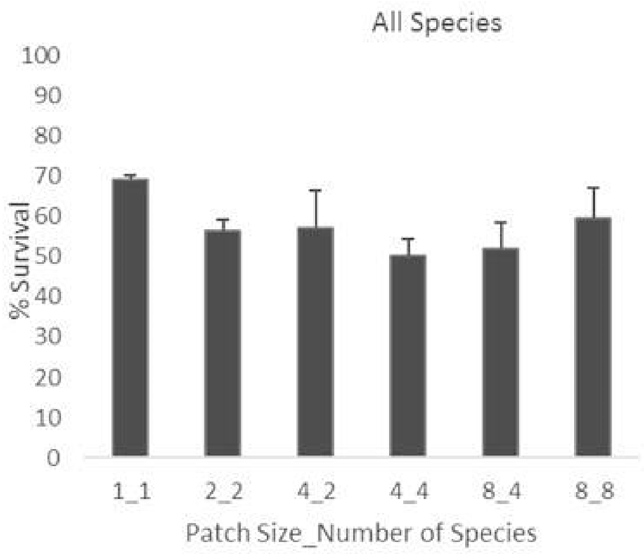

Figure 11. Global plant survival (all species together) in plant patches as a function of patch size (number of individuals in the patch; 1, 2, 4 or 8) and diversity (number of the species; 1, 2, 4 or 8). Labels in X axis represent the patch treatments, with first number representing the number of individuals and second number representing the number of species. Number of functional groups for treatments 1_1 and 2_2 is one, while for the rest of treatments number of functional groups is four. Bars represent mean values and standard error from replicated plots.

Overall, our results suggest that increasing patch size and diversity may reduce to some extent the probability of sapling survival in the restored patch, particularly if one single individual per patch is compared with two individuals –one per species– for two species that are functionally similar. However, in general, the reduction in survival with increasing diversity is minor for grasses and for seeder shrubs such as *Rosmarinus* and *Cistus* species, and relatively small for tall resprouter shrubs such as *P. lentiscus* or *P. angustifolia*. These results question traditional restoration approaches that assume that early colonists may inhibit the incorporation of new individuals, and promote the introduction of shrub and tree seedlings after the removal of neighbouring vegetation (Savill et al., 1997). Conversely, the results suggest a positive net outcome from the trade-off between a relatively low risk of decreasing survival and the unquestionable benefit of introducing high diversity patches in degraded drylands, which is expected to increase ecosystem functioning (Maestre et al. 2009), without significantly increasing restoration cost (James et al., 2013).

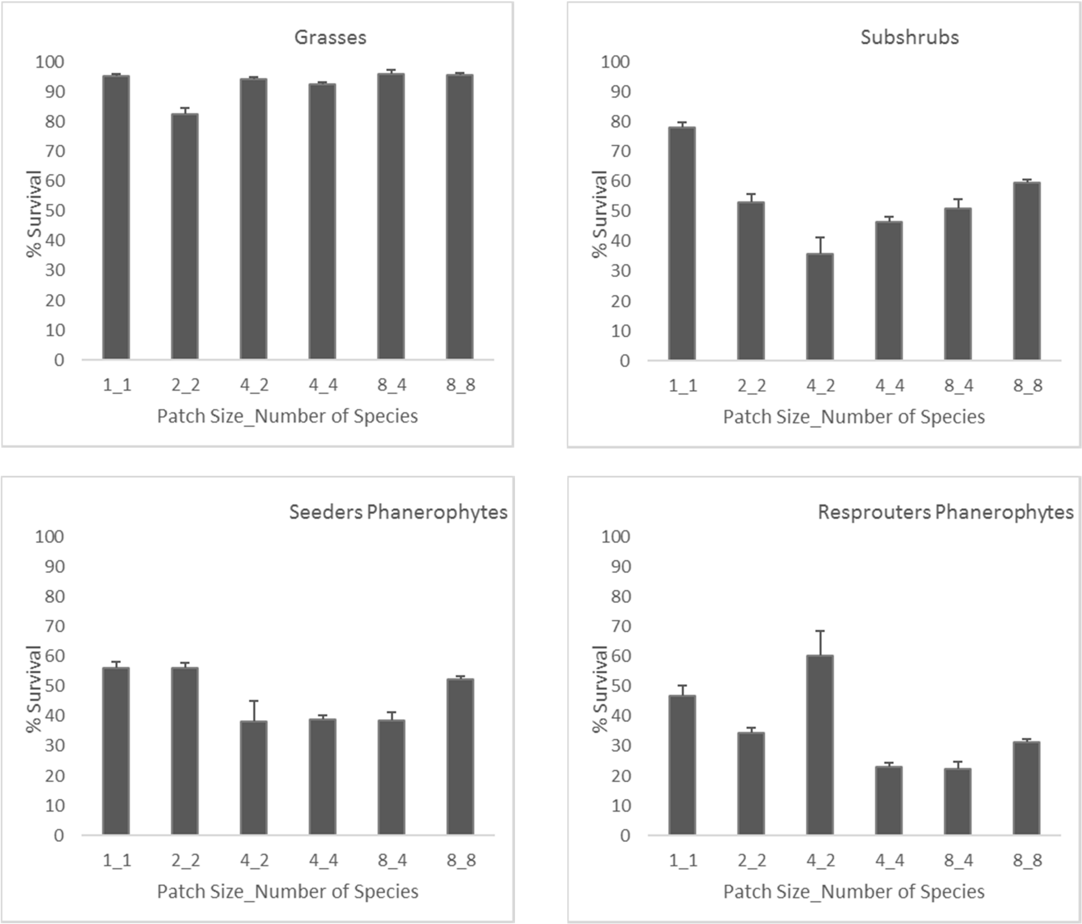

Figure 12. Plant survival by functional groups as a function of patch size (number of individuals in the patch; 1, 2, 4 or 8) and diversity (number of the species; 1, 2, 4 or 8). Labels in X axis as in previous graph. Bars represent mean values and standard error from replicated plots.

The variation in sapling biomass with increasing patch size and diversity was quite small (Fig. 13), i.e., individual biomass was not significantly reduced by increasing the number of accompanying species in the same patch. This result further supports the idea discussed above about a positive and cost-effective net outcome resulting from introducing several species with contrasting plant features in the same plant patch in the framework of dryland restoration.

It must be stressed that the results presented here correspond to early stages in the restoration trajectory (one year after planting), and thereby some degree of uncertainty exists about further development of the restored vegetation. However, it is worth noting that the earliest stages in restoration are the most critical ones, as survival typically decreases early after plantation (or seed germination), but then stabilizes after very few years (Chirino et al. 2009). Also, we could expect a larger niche differentiation and reduced competition between species with plant aging, as rooting depth and other critical plant traits differentiate according to the species functional group, provided these are contrasting groups.

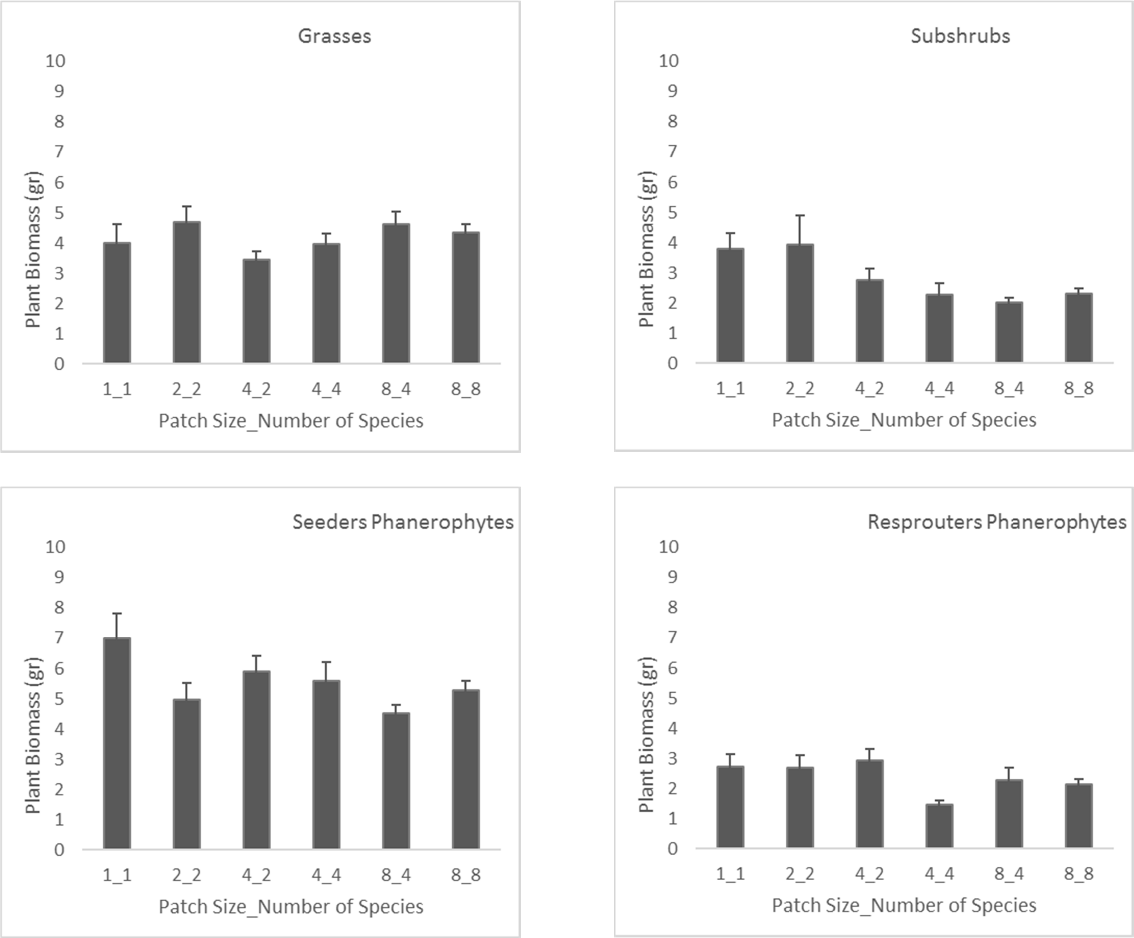

Figure 13. Plant biomass by functional groups as a function of patch size (number of individuals in the patch; 1, 2, 4 or 8) and diversity (number of the species; 1, 2, 4 or 8). Labels in X axis as in previous graph. Bars represent mean values and standard error from replicated plots; for each plot, a minimum set of four individuals for species were harvested for biomass estimation one year after planting.

Conversely to our expectations, functional diversity did not appear to be more relevant than species diversity for plant patch performance at this early stage of the restoration trajectory. For example, differences between treatments 4_2 and 4_4, which imply increasing both species and functional diversity from 2 to 4, were of the same order than differences between 8_4 and 8_8 that only had an increase in number of species (from 4 to 8) but shared the same number (4) of functional groups. However, as discussed above, it may occur that the contrasting features that distinguish the species from different functional groups fully develop with plant aging.

4.2 The role of ecohydrological feedbacks in dryland degradation reversal

Graphs representing equilibrium vegetation values in relation to the potential plant establishment (parameter b; see section 3.2), representing the external pressure on the system) allow analyzing the effects of the global and local feedbacks on the recovery potential of the system (Fig. 14). For fixed values of the rest of the parameters of the model (mortality, competition, etc.; see details in Kefi et al. 2007b), the light brown shaded area in the graph (nra) defines the region where no recovery is possible, so that ra=1-nra (green shaded region) is an integrated measure of the recovery potential of the system.

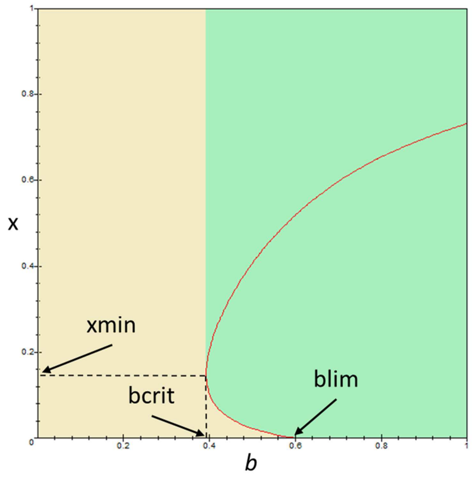

Figure 14. Model graph that represent equilibrium vegetation cover values (x) in relation to the potential plant establishment (b)

The minimum b value for which there is positive equilibrium vegetation (bcrit) informs about the harshest conditions that allow maintaining vegetation, while the value of vegetation cover for bcrit (xmin) indicates the minimum vegetation cover that can be in stable equilibrium in the system. The intersection of the graph with the horizontal axis (blim; blim=1 if there is no intersection) defines the upper limit of the range of external conditions that lead to bi-stability of the system (interval of b values from bcrit to blim). In this region, the system will end in the desert state when the initial cover is in the yellow shaded region, and it will recover to stable vegetated state if the initial cover is above the section of the graph separating the yellow and green areas (which constitutes an unstable equilibrium). In the cases where blim=1, the equilibrium cover value at this point indicates the minimum initial cover required for the system to recover under the best external conditions.

Figure 15 illustrates the effects of the global feedback (decreasing vegetation cover → increasing global resource loss from the system → decreasing vegetation cover) and the local feedback (decreasing vegetation cover → increasing runon-driven inputs to plant patches → increasing vegetation growth and cover) on the indicators of recovery of the system. In Figure 15 left, in the absence of local feedback (γ=0), the effect of different intensities of the global feedback is shown. When this intensity increases (increasing values of α), the regeneration capacity of the system worsens, with small increases of bcrit and xmin, and a decrease of ra. The most significant effect is the increase in the minimum vegetation cover needed to achieve regeneration in the bi-stability region, i.e., for conditions where the system can result in either a deserted or a vegetated stable state.

In Figure 15 right, the effect of different intensities of the local feedback, in the presence of a moderate global feedback (α=0.5), is illustrated. When the intensity of the local feedback increases (increasing values of γ), the general recovery potential of the system improves, but in this case the most significant effect is the possibility of stable vegetated states with much more harsher conditions (lower b values, with a significant reduction in bcrit) and with much lower vegetation cover values (with a significant reduction in xmin).

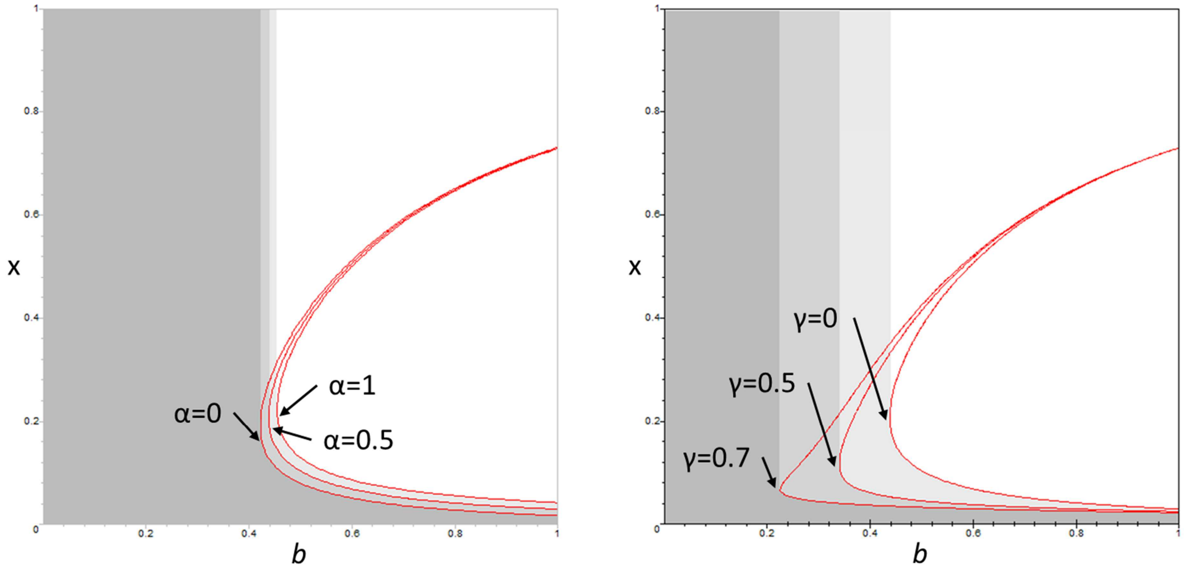

Figure 15. Equilibrium vegetation (x) in relation to the potential plant establishment (b) as a function of the strength of the global (α) feedback (left) and the local (γ) feedback (right) mediated by the bare-soil connectivity of the system.

As expected, higher strength of the positive global ecohydrological feedback reduces the recovery potential of dryland ecosystems. Conversely, higher strength of negative local ecohydrological feedback increases the recovery potential of dryland ecosystems.

However, the effect of both feedbacks is not symmetric. Variations in the negative local feedback have much larger influence in the recovery potential of the system than variations in the strength of the global feedback, being able to largely reduce the area (grey zone in Fig. 15) for which recovery is not possible, and allowing equilibrium vegetation with very low cover values. This result is in agreement with some of the results from the manipulative experiments reported above, which did not find any constraining effect of low initial plant cover on the dynamics of the experimental communities established.

Overall, the modelling results highlight the importance of the global and local ecohydrological feedbacks as modulators of the restoration potential of degraded drylands. According to these results, strengthening the local feedback (i.e., the positive response of the vegetation patches to increased upslope bare-soil connectivity) could largely enhance the recovery potential of the system. As both global feedback and local feedback depend on vegetation cover, the challenge would be to increase the local feedback while not increasing the global feedback The local feedback could be strengthened by creating plant patches with species or combination of species that combine deep rooting traits and a morphology that facilitates trapping runon water. This way, the capture and deep infiltration of the extra runoff water generated in large bare-soil areas is maximized (Mayor et al., 2009), which in turn would enhance plant growth.

5 Conclusions and recommendations

By performing a variety of manipulative experiments and modelling exercises, we have assessed the degradation reversal potential as a function of plant colonization pattern and diversity and the hypothesized ecohydrological feedbacks that modulate dryland dynamics. At the patch scale, we compared the performance of (1) multispecies versus monospecific patches, and (2) patches with single individuals versus patches with increasing number of individuals and or species.

At the patch scale, the effect of patch diversity and size on plant performance depended on the plant functional types considered and the environmental conditions, yet some common pattern was found for a large variety of dryland species tested.

At early stages of the restoration trajectory (first 1-2 years after planting), with all plant seedlings sharing similar rooting space, there was no evidence of complementarity between species that may have resulted in higher productivity in multispecies patches as compared with monospecific patches. However, there was no evidence either of detrimental effects of interspecific competition, as compared with intraspecific competition in monospecific patches. Big diverse patches benefited better from the higher capacity for trapping water and other resources from runoff than big monospecific patches. Under stressful conditions, facing both intra-specific and interspecific competition within the plant patch is more challenging for the species than interacting only with conspecific individuals.

Compared with patches with a single plant, individual biomass was not significantly reduced by increasing the number of accompanying species in the same patch. Increasing patch size and diversity may reduce to some extent the probability of sapling survival in the restored patch. However, in general, the reduction in survival with increasing diversity is minor suggesting a positive net outcome from the trade-off between a relatively low risk of decreasing survival and the benefits derived from increasing diversity. Functional diversity did not appear to be more relevant than species diversity for plant patch performance at early stages of the restoration trajectory.

At the community scale, low initial plant cover did not constrain the potential for restoration success, which could be explained by the positive effect of water and sediment transfer from large bare soil areas to few existent plant patches. Our findings have demonstrated that ecohydrological feedbacks between resource redistribution and vegetation dynamics that are mediated by bare-soil connectivity exert an important role in modulating the restoration potential of dryland ecosystems. Larger bare-soil connectivity implies larger water and sediment losses from semiarid slopes, but it also implies larger inter-patch areas and associated larger runon inputs to existent plant patches, which is beneficial for the performance of the vegetation in the patch. This local feedback, if enough strong, increases the range of conditions (external stress, minimum initial cover) that allow the recovery of the system.

From an applied perspective, in a context of dryland restoration, a number of recommendations can be derived from our results, including (1) using (creating) multispecies big patches, yet minimizing intraspecific competition by reducing the number of individuals per species within the same patch; (2) spatially arranging plant patches on slopes in a way that maximizes the capture of runoff water by plant patches; (3) combining species in the plant patches with plant traits that maximize the capture and deep infiltration of runoff water.

Overall, CASCADE WP4 has provided evidence (1) that supports the hypothesized role of ecohydrological processes and feedbacks as inside mechanisms underlying sudden shifts in drylands (D4.1); (2) on how increased pressure on dryland systems could trigger sudden shifts towards degraded states (D4.2), and (3) on how degradation reversal can be modulated by plant cover and diversity as well as by the ecohydrological feedbacks that connect plant pattern dynamics and resource redistribution (This Deliverable, D4.3).

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