CASCADE

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

CASCADE REPORT series

Report on simulated pressures and ecosystem responses

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CASCADE
Catastropic shifts in drylands

Deliverable 6.1

Report on simulated pressures:
Response of Mediterranean drylands to increasing pressures

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Summary

The main goal of the European project CASCADE was to improve our understanding of the degradation of drylands which occupy 41% of the land area on Earth and support more than 38% of the human population. Such fundamental understanding is crucial to define strategies to *predict* and *prevent* dryland degradation. CASCADE focused particularly on the occurrence of catastrophic shifts, i.e. abrupt, unexpected and often irreversible degradation of dryland ecosystems. To achieve its goal, a key complement to CASCADE empirical studies was the development of mathematical models, informed and improved by the empirical studies, that allowed to further investigate how Mediterranean drylands cope with various levels of environmental stress.

This deliverable presents the models developed in WP6. WP6 models focused on two axes of improvement of current dryland models relevant to study dryland resilience (Task 1 of the DOW): i) the way external pressures are incorporated in dryland models; we focused on three types of external pressures: grazing, fire and drought; ii) the way vegetation (the 'biotic component') is modelled; we incorporated species, functional groups and species-species interactions in dryland vegetation models. We investigated how the additional ecological mechanisms included affected the response of the ecosystem to stress (Task 2 of the DOW). We especially looked for shift behaviors and identified the conditions that favored the emergence of catastrophic shifts at the ecosystem scale.

Grazing is one of the main causes of desertification of drylands worldwide and a possible cause of degradation in four of the CASCADE field sites. Understanding how and why different types of grazing and different levels of grazing pressures affect dryland resilience is of great importance to inform dryland management and help preventing desertification. We developed a model for vegetation dynamics in drylands, which incorporated an important aspect of grazing typically ignored in dryland models: its spatial component. Indeed, plant species adapted against grazing can provide refugia from large herbivores to neighboring plants (a phenomenon is known as associational resistance). We found that, along a drought gradient, dryland desertification (in this case, the loss of the vegetation) happened as a catastrophic shift. Moreover, spatially heterogeneous grazing increased the abruptness of the shift and decreased its reversibility.

Fire is the main driver of degradation in two of the CASCADE field sites. Because of the long history of fire in the Mediterranean basin, most Mediterranean plant species are well adapted to fire, but global changes have led to an intensification of the fire regime in the last decades. It is however unclear how these changes in fire regimes will affect dryland vegetation dynamics. We developed two different models, each mapped to one of the two Cascade field sites of Varzea (Portugal) and Ayora (Spain), to study the effect of fire on vegetation succession. The models include several functional groups, reflecting the different species strategies toward fire. The results suggest that oaks will eventually dominate the landscape, independent of the initial conditions or of the fire frequency. Those results are in agreement with paleobotanical records, which suggest that the prevailing vegetation in the Iberian Peninsula during the past centuries or millennia probably consisted of a mixed pine-oak woodland, with a relative dominance of oak. Moreover, one of the models suggests that the incorporation of a feedback between fire occurrence and species composition could lead to alternative stable states, and therefore catastrophic shifts between contrasting plant communities (an open shrubland instead of the expected late-successional oak forest) when fire is combined with droughts.

Besides grazing and fire, a common stressor in all drylands is drought. Global climate models project changes in rainfall intermittency in arid and semiarid regions with more confidence than possible changes in annual and seasonal rainfall volumes. For the semi-arid Mediterranean area, an increase in meteorological drought frequency is predicted (medium confidence), together with an increase in heavy precipitation events (high confidence). it is unknown if and exactly how these projected changes in rainfall intermittency are going to affect the productivity and functioning of semiarid ecosystems. We addressed the question of how rainfall intermittency influences drylands ecosystem dynamics with two separate studies. One of the study showed that an increase in mean rainfall intensity widens the rainfall range for which the ecosystem has alternative stable states. Another focused on the role of rainfall intermittency for the coexistence of plants with different strategies based on experimental measurement performed in the CASCADE site of Santomera. The study showed that realistic, intermittent, rainfall can lead to co-existence of the two species under one single resource, whereas constant rainfall lead to competitive exclusion of one of the species.

A number of model studies performed in WP6 aimed at better understanding the role of species interactions in drylands, in particular how different stressors (drought, grazing) affect plant-plant interactions and how that, in turn, affects species coexistence and ecosystem dynamics. Facilitation between plants is known to be an important mechanism driving vegetation dynamics in dryland, but we lack understanding of how interactions between plants change in response to combined effects of drought and consumer pressure. The models developed suggest that the relative importance of facilitative vs competitive plant-plant interactions varies along stress gradients, thereby driving the possibility for species coexistence. In particular, facilitation via associational resistance allows species coexistence under a range of environmental conditions. When space is explicitly taken into account, the ecosystem exhibits catastrophic shift to desertification once a threshold of aridity passed. With different plant functional groups (e.g. a nurse and a protégée), this catastrophic shift is more complex than usually found in models: before vegetation extinction, there is a zone of tristability between a desert state, coexistence between the two species and the nurse alone. This creates the possibility of different types of catastrophic shifts among these three states. Our models overall suggest the importance of facilitation for species coexistence and ecosystem resilience. The models, when extended to evolutionary dynamics, suggest that facilitation could also have played a role at evolutionary timescales by promoting spatial environmental heterogeneity and therefore acting as a selective pressure which favored non drought- or grazing-adapted phenotypes. Facilitation could therefore be key in explaining the coexistence of drought-tolerant and drought-sensitive traits observed today under dry environmental conditions in the Mediterranean region. Indeed, facilitation may have allowed the persistence of the Tertiary, drought-sensitive trait-syndrome in the Mediterranean basin after the climate shift from the wet Tertiary period to the dry Quaternary.

In sum, our results highlight the importance of the role of the spatial aspect of the external pressure, demographic stochasticity, rainfall intermittency and rate of environmental change, the way species interact with each other (facilitation/competition), and the relevance of different types of ecological feedbacks for our understanding of the species composition and the dynamics of dryland ecosystems. The deliverable concludes on the main results of these models and possible implications. Those model, combined with socio-economic analysis, could help build management strategies to help prevent dryland degradation. We provide the codes and information necessary to run these models to promote the dissemination of this work.

1. Introduction

Drylands occupy 41% of Earth's land surface and support more than 38% of its human population [1]. Severe ecosystem degradation has already occurred in about 10–20% of drylands, and its consequences affect ~250 million people [2]. These values are likely to increase with climate change and current rates of human population growth [1,3]. Understanding how drylands respond to these ongoing environmental changes is extremely important for global sustainability [4] but challenging owing to the complex, dynamic interactions that exist among multiple drivers and ecosystem processes.

A core aim of the European project CASCADE is to improve our understanding and thereby our ability to *predict* and *prevent* dryland degradation, and in particular catastrophic shifts, i.e. abrupt, unexpected and often irreversible degradation of dryland ecosystems. Therefore, a number of field sites have been chosen (see CASCADE Deliverable D2.2) in which a combination of field survey and experiments (see CASCADE Deliverables D3.1, D4.1, D4.2, D4.3, D5.1 and D5.2) aim at improving our understanding of the degradation process in Mediterranean drylands. A key complement to these empirical studies is the development of mathematical models, informed and improved by the empirical studies, that allow to further investigate how Mediterranean drylands are able to cope with various levels of environmental stress. The main objective of WP6 is therefore the development of new models, based on sound ecological mechanisms. This deliverable presents the main results achieved by the models of WP6 regarding the response of drylands to various pressures (Tasks 1 and 2 of the DOW, *Task 1: Improving the realism of dryland models, Task 2: Investigating the role of these detailed ecological mechanisms for system's behaviour*).

For over two decades, mathematical models have been used to understand vegetation dynamics in drylands and more precisely the emergence of spatial patterning in dryland vegetation [31–34] and its links with dryland functioning [9–12]. Some of the key limitations of current dryland models used to study catastrophic shifts are:
-   *the way external pressures are incorporated in dryland models.* We have made developments on two types of external pressures which are central in Mediterranean ecosystems in general and in CASCADE field sites: grazing and fire. Moreover, we have explored how change in rainfall intensity, as predicted by climate change models, affect dryland functioning.
-   *the way vegetation (the 'biotic component') is modelled.* Most dryland models typically include one vegetation type and do not take the variety of species and of their strategies into account (in particular species-species and species-abiotic environmental interactions). A number of models developed in CASCADE WP6 now take different plant functional groups into account.

Those two axes of improvement of current dryland models add a level of complexity which is relevant to study dryland resilience and investigate indicators of degradation (Task 1 of the DOW). The two major external stresses identified in addition to aridity, grazing and fire, led to two types of models developed within WP6 aiming at describing the grazed CASCADE sites in Randi forest, Cyprus and Santomera, Spain (mainly developed in CNRS Montpellier, France) and the fire-prone sites in Valencia, Spain and Aveiro, Portugal (mainly developed at Utrecht University in the Netherlands) (Fig. 1). Note that compared to what was announced in the DOW, biochemical processes were not included in any of the models developed. Note also that the spatially-explicit

models did not target the Italian CASCADE site, which is the only site which does not exhibit vegetation patchiness.

All the models developed in WP6 were investigated, analytically when possible, as well as numerically, in order to get insight into the role of the mechanisms included for species coexistence, ecosystem functioning and resilience (Task 2 of the DOW). An overall objective of the WP was to investigate the role of these detailed ecological mechanisms for ecosystem behavior. More particularly, we investigated how the additional ecological mechanisms included affected the response of the ecosystem to stress (Fig. 1). Ecosystem response is considered to be e.g. vegetation cover, total biomass, species diversity, species identity, spatial structure (size of vegetation patches in the system, maximum patch size, and patch size distribution), and dynamic changes in these. We especially looked for shift behaviors and identified the conditions that favor the emergence of catastrophic shifts (and of what type) at the ecosystem scale.
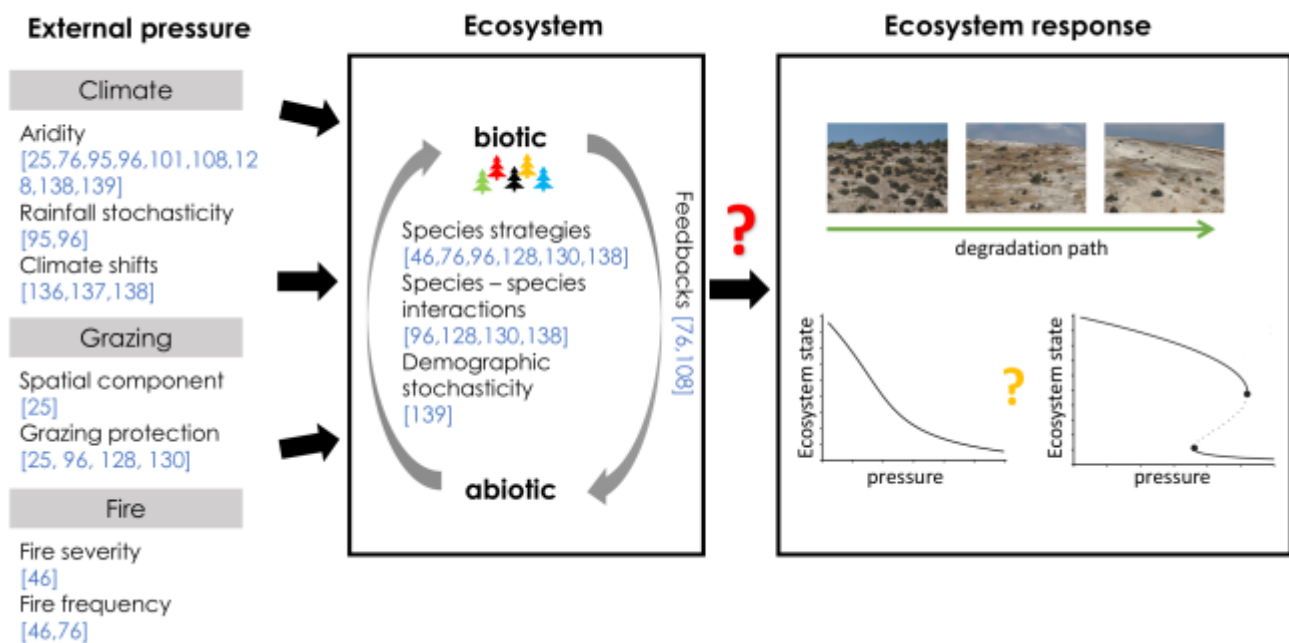
Figure 1: General figure illustrating the different studies made within CASCADE WP6. Numbers refer to the references in this document.

2. Dryland response to different pressure types and modalities

As mentioned in the introduction (§1), the first aspect that we will report on is how various external pressures were incorporated in dryland models to improve our understanding of their effect on dryland dynamics and resilience. Our work has focused on grazing, fire and drought (or rainfall modalities), the main stressors of Mediterranean drylands, and the CASCADE sites in particular.

## 2.1. Dryland response to grazing and droughts

Grazing is one of the main causes of desertification of drylands worldwide [1,13]. Understanding how and why different types of grazing and different levels of grazing pressures affect dryland resilience is therefore of great importance to inform dryland management and help preventing desertification. One of the objectives of WP6 was to develop and analyze models that help us investigate the role of grazing in dryland dynamics and resilience, by improving the realism with which grazing is classically incorporated in dryland vegetation models.

In a number of dryland models [8,11], plant mortality is taken as a proxy for grazing pressure. Grazing, in these models, simply increases plant mortality. Moreover grazing is typically considered to be homogeneous in space, meaning that it is affecting all individuals equally [7,8,11,14].

However, grazing can have a strong spatial component [15–18]. In arid shrublands that have historically been exposed to grazing by large herbivores, most plant species have developed mechanical defenses against large herbivores, such as fast regrowth from the root stock, indigestible tissue, the development of prostrate growth forms and the evolution of spines and thorns [19,20]. Thus, coinciding with the effects of abiotic facilitation, i.e. the amelioration of the local environmental conditions through shading or water retention by the presence of vegetation [21], the canopy of plants with defenses against large herbivores also provides refugia from large herbivores to neighboring plants [21–24].

This mechanism leads to low individual mortality in places where local plant cover is high. We refer to this feature of a spatially constrained negative density dependence of mortality as 'associational resistance' (see [21] for a discussion on the term). Vice versa, a low local plant cover will increase the risk of dying due to grazing for the remaining vegetation [21]. As a consequence, if the overall benefit of grazing protection outweighs the cost of competition for limiting resources, plants coincidentally team up with other plants [24], which contributes to the formation of patch pattern at the landscape scale [21]. In such case, the highest risk of being grazed is borne by plants that grow isolated from others, whereas plants that are growing at the border or in the center of a patch are less vulnerable to grazing or even entirely unaffected because they benefit from associational resistance [21,23].
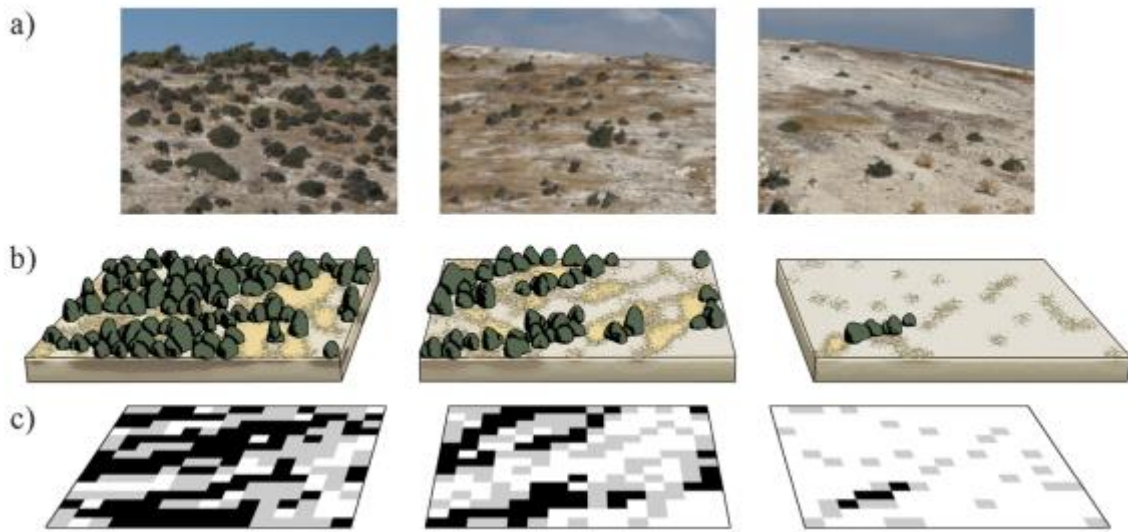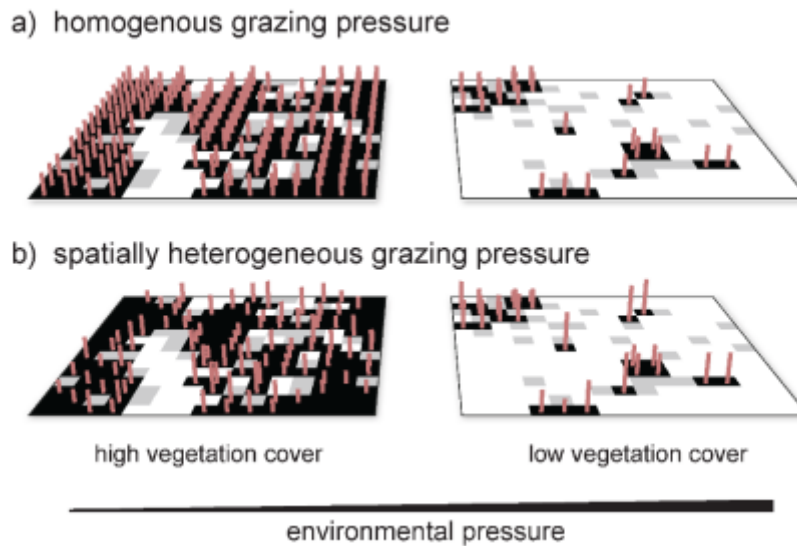
Figure 2: *schematic illustration of the abstraction process from a real landscape (a), to a simplified landscape with vegetation and bare soil, to a cellular automaton model such as the one used in this study.*

We introduced 'associational resistance' in a spatially explicit dryland vegetation model, i.e. the mutual reduction of grazing impact by sharing defensive traits [25]. This dryland vegetation model was used to investigate the interactive effects of grazing (now a spatially heterogeneous pressure) and aridity on the spatial vegetation patterns and on ecosystem resilience. The model was inspired by the Randi forest CASCADE site in Cyprus, but can be generally applied to grazed patchy drylands.

Model description

The model is an interaction particle system that describes the landscape as a grid of cells, each of which can be in one of three states: 'vegetated' cells are occupied by a plant (black cells in Fig. 2c); 'empty' cells do not contain adult plants but are suitable for seeds to germinate and establish (grey cells in Fig. 2c); 'degraded' cells represent bare ground which has been eroded, lacks organic matter, is characterized by bad water retention, and therefore cannot be colonized by arriving seeds (white cells in Fig. 2c). Transitions between cell states are only possible between vegetated and empty (by the processes of plant 'death' and 'recolonization') and between empty and degraded (by 'degradation' and 'regeneration'). In biological terms, a degraded site needs to be enriched first, before a plant can establish on it. Conversely, when a plant dies, it leaves the spot empty but still enriched, until it becomes degraded by erosion.

Associational resistance was introduced in the model as follows: we assume that plants in the center of a patch therefore bear a lower risk of being grazed by herbivores than plants growing isolated from others (Fig. 3). By including this mechanism, grazing becomes a spatially heterogeneous pressure. The probabilities for these transitions to occur on any cell currently at state might be constants or functions of the global vegetation cover or of the local vegetation cover in the neighborhood of the focal cell (equations can be found in [25]).

a) homogenous grazing pressure

b) spatially heterogeneous grazing pressure

high vegetation cover   low vegetation cover

environmental pressure

Figure 3: Individual plant risk of death due to grazing (red bars). (a) In most previous spatially-explicit models of dryland resilience, grazing was defined homogeneously, i.e. affected all plants likewise, regardless of local or global cover. (b) A more realistic approach to grazing assumes plant death to be reduced by the presence of other plants in the direct neighborhood, i.e. the mechanism of 'associational resistance', with implications for the total plant mortality at both high (left panels) and low (right panels) vegetation cover. Figure from Schneider & Kéfi [25].

Results

We found that spatially heterogeneous grazing altered ecosystem stability. Indeed, with associational resistance, plants' risk of being eaten depended on the local configuration. Therefore, grazing impact was minimized at high cover but became self-enhancing in more fragmented landscapes. This feedback on plant mortality disrupted patch growth and put even apparently 'healthy' drylands under high risk of catastrophic shifts (Fig. 4). More specifically, the range of pressure levels at which both desert and vegetated landscapes were simultaneously stable (i.e. the so-called bistability area) increased as spatially explicit grazing became more intense. This is consistent with previous modelling studies of spatially homogeneous grazing pressure [8,11,26]. Second, under high grazing pressure, state transitions from a vegetated to a bare landscape were more sudden and unexpected and the ecosystem shift to desert occurred at higher vegetation cover and connectivity, i.e. in apparently 'healthy' landscapes.

Conclusion

Our results indicate that when ignoring the interfering feedback mechanisms caused by the spatially explicit pressure (here grazing), we might over-estimate ecosystem resilience and impede the success of sustainable management practices.
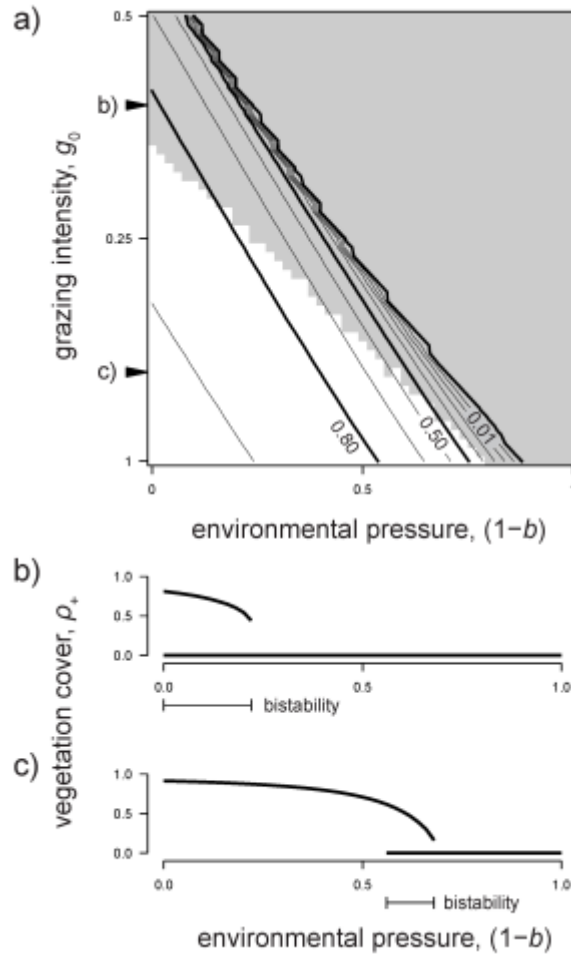
Figure 4: a. Changes in the vegetated (black contour lines: vegetation cover) and desert (i.e. no vegetation) states (grey zone) along gradients of environmental and grazing pressure; overlap of the grey zone and the contour lines correspond to the bistability area where both the vegetation and the desert states are stable. The tipping point, at which the ecosystem drops from vegetated to desert, is reached at the lowest contour line (vegetation cover < 0.01). (b, c) Cross sections of (a) at low (b; g0 = 0.1) and high (c; g0 = 0.4) grazing intensities showing the steady state vegetation cover. Figure from Schneider and Kéfi [25].

2.2. Dryland response to fire

In the Mediterranean basin, there is a long history of exploitation and deforestation, which resulted in the conversion of the natural landscapes to agriculture [27]. In the past decades, Mediterranean forests have experienced intense changes, which resulted in extensive afforestation using pine plantations, or in marginal cropland abandonment [28–30]. In turn, these changes have led to an intensification of the fire regime, with an increase in the amount of burnt area and in the frequency of wildfires [28,29].

Most Mediterranean plant species are well adapted to fire, commonly responding to it through different mechanisms. Their three main post-disturbance regeneration strategies consist of:
  i. plant survival through the resistance of below-ground buds to fire, followed by resprouting of the above-ground tissues (**obligate resprouters**, e.g. oaks),
  ii. plant mortality but survival of the seeds (**obligate seeders**, e.g. pines),
  iii. a combination of both these mechanisms (**facultative species**; [30,31]).

Studies of post-fire dynamics have shown that resprouter species (which are usually late successional) are more resilient to both short and long fire frequency intervals than seeder species [32]. Pine seeds are often enclosed in serotinous cones, which open right after the fire, allowing pine population recovery [33]. However, as most pine species do not resprout, the resilience of pines to frequent fires is limited by seed production. Thus, the occurrence of repeated fires in a short interval of time or of a single fire in a young pine forest can cause the local extinction of pines [33,34]. This eradication gives place to the dominance of other species, which could either be early or late successional species. Intensive use of the land and high wildfire frequency can favor the replacement of pine and oak forests by fire-prone shrublands [34,35]. Furthermore, the re-introduction of late successional species, such as oaks, in fire-prone shrublands can be limited by several factors related to seed dispersal and micro-climate conditions [36,37]. These recruitment limitations could arrest successional processes, locking the system in a shrubland state [35,36]. However, there is also evidence that oak species can become dominant in former pine forests that have been eradicated as a result of recurrent fires [32,38].

Species from various successional stages can co-occur after disturbance, and the time after disturbance at which they attain dominance depends on their growth rate and longevity [39]. High fire frequency could thereby either result in the dominance of seeder species with short life spans and persistent seed bank, or in the dominance of resprouter species with high growth rate, whereas fewer fires would favor the dominance of seeder species with longer life spans, such as pine species [40]. Even so, the abundance of obligate seeder species with short life spans can be compromised by recurrent fires, through the exhaustion of their soil seed bank [41,42]. Such circumstances could be advantageous for species with resprouting ability (facultative species and resprouter species).

We developed two different models to study the effect of fire on succession. We adapted the models to the conditions in the two Cascade field sites of Varzea (Portugal) and Ayora (Spain), where fire is the main driver of degradation. For the Portuguese site, we developed a cellular automaton model to study the effect of fire succession in pine stands, and we focused on the effect of fire severity and on the occurrence of safe germination microsites, connected to the existence of a litter layer (see upcoming section §2.2.1). For the Spanish site, we developed a spatially-implicit model for vegetation cover including six different vegetation functional, and we focused on the effect of the feedback between species composition and fire frequency, and on the combination of fire and drought effects (see upcoming section §2.2.2). This second model has been calibrated with data from WP5 (and from previous EU project EUFireLab and LUCIFER).

2.2.1.   Effect of repeated fire in pine plant communities (Portugal)

The conditions under which a given species composition is expected in Mediterranean areas with recurrent fires remains largely unknown. Besides what was already mentioned at the beginning of section §2.2, plant succession is expected to be also modulated by factors such as fire severity [43], seed sources and disperser preferences [37], and the occurrence of safe germination microsites. In particular, the existence of a layer of litter after a fire modifies the probability of plant colonization, and the characteristics of the pine litter layer after a fire are largely determined by fire severity [44,45]. Despite the important role of litter as a modulator of the composition and structure of plant communities, its effects have not been included so far in the analysis of the successional dynamics of pine stands under different fire regimes.

We developed a dynamic successional model of pine plant communities that i) explicitly takes the litter layer into account, and ii) simulates the population dynamics of three plant functional types: pines, oaks (late successional species) and obligate or facultative shrubs (early successional species) [46]. This model was used to investigate how the wildfire frequency conditions affect plant succession dynamics in pine forests.

Using this model, we studied the long-term vegetation dynamics of the ecosystem under different fire frequency conditions, and we analyzed the dynamics of the transient period (medium-term), by investigating how long it takes for the late successional species (oak) to attain relative dominance. Additionally, we studied how plant species composition, colonization capacity (represented by the arrival of acorns) and post-fire microsite conditions (represented by fire severity and litter depth) influence succession, measured by the time when oak attains relative dominance.

We hypothesized that, in the long term, pine forests would be replaced, through facilitation processes, by late successional species (*Quercus* spp.) in undisturbed regimes. Moreover, increased fire frequency in pine forests where facultative shrub species are abundant would enhance the dominance of this type of shrubs (because of their resprouting capacity) and delay succession towards mature forests.

Model description

The model is an interaction particle system, where each cell is dominated by one of three plant functional types: pine, oak or shrub [26,46]. Accumulation of litter is a spatial-explicit process, that takes place in the cells occupied by a mature pine tree as well as in their eight neighboring cells. The different functional groups have different colonization probabilities of empty sites, which depend on the number of seeds available in the cell for each of the functional groups, the establishment capacity of each functional group, and the microsite conditions, determined by litter depth. The accumulation of a litter layer in the absence of disturbance is expected to have a prominent role in successional processes [47]. The germination of small seeded species under thick litter layers may be prevented [48,49], whereas bigger seeds tend to remain over the soil surface and germinate easily in such conditions. This pattern is observed consistently in Mediterranean resprouter (late successional) and obligate seeder or facultative shrub species (early successional), with the former having often bigger seeds and, at the same time, exhibiting less persistence in the soil [50]. Moreover, in pine forests, litter acts as a function of canopy cover, which by shading and reducing climate extremes and increasing water availability in the summer, favors the establishment of late successional species over early successional species [51–53]. Therefore, the model assumes that a higher litter thickness favors the relative dominance of late successional species while, at the same time, inhibiting the colonization of early successional species.

Fire disturbance regime was defined stochastically, with the occurrence of fires defined by an exponential distribution of return times [54]. The simulation was first run for 100 years without fire. After that, we introduced fire with one of three different average return times: seven, fifteen and thirty years. We also kept a scenario without fire. These fire regimes were indicative of what was observed in the centre-north of Portugal, where the average fire frequency is 24 years, and where the regeneration of pines is threatened in 15% of the area [55]. When a fire occurs, the functional groups with resprouting ability (oaks or facultative shrubs) continue to occupy the same cell, whereas pines and obligate seeder shrubs die. In the high fire severity scenario, all the needles and litter are consumed, whereas in the low severity scenario, the needles of mature pines remain intact and fell on the soil surface, creating a litter layer.

Results

In the absence of fire, we found that the ecosystem reached a stable co-existence between the three functional types after about 1000 years, and this, independent of the initial conditions of the simulation. This steady state consisted in the dominance of oaks (~75%) with co-existing pines (~15%) and shrubs (<5%) (Fig. 5). The changes in plant species relative dominance over time were related to the life span of each species: during the first decades, the short lived species (i.e. shrubs) dominated (after ~100 years), then the intermediate lived species (i.e. pines) dominated, and finally the long lived species (i.e. oak) dominated (at ~250 years).

The relative dominance of oaks at steady state (i.e. cover values higher than 50%) was maintained under all fire frequency conditions (Fig. 5). The co-existence of all three functional types, however, was not observed under fire disturbance, since pines went extinct in all fire frequency conditions. In case of high fire frequency and severity, obligate seeder shrubs also went extinct. When facultative shrubs were included in the simulations, a long term co-existence of shrubs and oaks was reached under all the fire disturbance regimes (Fig. 5).
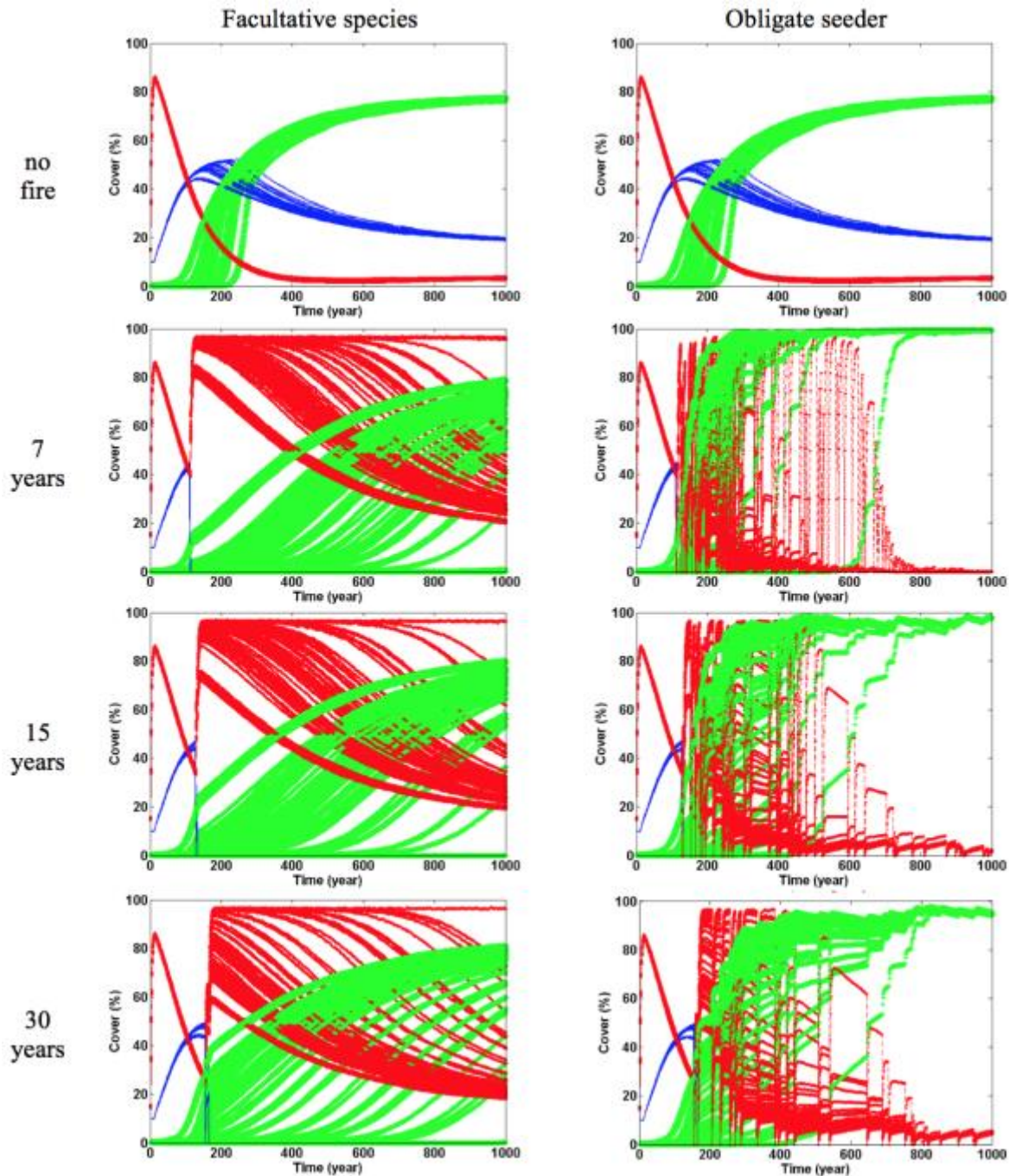
Figure 5: Plant species relative abundance (% cover) over time for different fire return intervals (no fire, 7, 15 and 30 years) in communities with a facultative shrub species (left) or obligate seeder shrub (right) for conditions of high fire severity. Pine is represented in blue, the shrub species (both facultative species and obligate seeder) is represented in red and oak is represented in green. Each line corresponds to a specific run, and a number of 20 runs was repeated for each value of oak seed input (1, 5, 20 and 200 per year per hectare). Figure from Vasques et al. [46].

The time at which pines went extinct depended exclusively on the recurrence interval of fire events (Fig. 5). However, the model results suggested that the time at which oak reached dominance depended mostly on the acorn yearly input, and thus on oak nearby populations. In particular, Oak dominance was delayed substantially (up to 800 years) when acorn influx rates were low. Moreover, high fire frequency accelerated oak dominance when coexisting with an obligate seeder shrub, but delayed it when coexisting with a facultative shrub species (i.e. with a resprouting ability). This result was observed for all influx rates of oak seeds and fire severity did not change this pattern considerably.

Conclusion

Our model results are in agreement with paleobotanical records, which suggest that the prevailing vegetation in the Iberian Peninsula during the past centuries or millennia probably consisted of a mixed pine-oak woodland, with a relative dominance of late successional species, such as *Quercus robur* [56]. The persistence of pines in the system has been linked to fire occurrence [57], which usually results in open areas that are favourable for pine colonization, but could also be explained by local less favourable environmental conditions for the regeneration of oak, such as steep slopes and cold or dry sites [58]. Furthermore, crop abandonment and the fact that very little artificial oak plantations have actually occurred limited oak seed sources, making acorn inputs close to inexistent in many instances, hence absolutely changing pine forest post-fire succession.

As expected, in the model, oak dominance under optimal conditions for oak establishment was accelerated by a higher yearly input of acorns. This could have important management implications since by understanding and manipulating the potential and effective dispersal of oak plants, we may be able to predict the time at which oaks would reach dominance. The main seed dispersals of oak species are jay (*Garrulus glandarius*) and mice, with the first having a much wider territory range (up to 100 ha) than the second (up to 1 ha; [59]). Furthermore, the species present in a given plant community can affect the colonization capacity of oaks, since, for example, pine stands foster seed arrival, whereas shrublands are usually avoided by jay, because of their higher exposure to predators in these open areas [60]. If seed arrival is inhibited by shrub dominance, the system can be locked in an early successional phase, especially when pines are eradicated from the system. This would agree well with the findings of Acacio et al. [36] who found seed arrival to be one of the limitations of oak establishment in shrublands.

2.2.2. Effect of recurrent fire and drought on vegetation succession in Mediterranean forest

We studied two more elements that are very important for Mediterranean forests. The first is the fact that some species are more prone to fires than others, as they have different e.g. flammability, heat and water content, standing dead biomass [61–64] (see Cascade WP5 Deliverables 5.1 and 5.2). This determines the possible existence of a feedback between fire occurrence and species composition, as the most fire prone plant types are early successional shrub seeders, or grass resprouters, that can regrow very fast after a fire, and thus maintain the system in a highly fire-prone condition, while the slow-growing late successional species (mainly oaks) are much less prone to fires. As it has been shown in other ecosystems, e.g. in savannas, such feedback between fire and vegetation can create

bistability in the system [65,66], and thus possibly determine the occurrence of catastrophic shifts in the vegetation composition.

The second element is drought and its interaction with fire, which is expected to increase the chances of a (possibly catastrophic) shift in species composition. For the Mediterranean area, an increase in temperature and in drought occurrence is expected [67]. Drought affects directly species composition, via the limitation of recruitment, growth and survival, to which the late-successional resprouter species are more subject than shrubs and pine seeders [68–73]. Drought also increases the probability of fire, thus also indirectly influencing species community composition. The combination of these direct and indirect effects can influence dramatically species composition and ecosystem functions [74,75].

> **We developed a model to explore the effect of fire feedbacks and drought, in shaping plant succession in abandoned fields, pine stands, and shrublands, which are the most common land use in our study area [76].** The model is inspired by the conditions in Easter Spain, represented mainly by the Ayora CASCADE site, although the model is applicable more generally to the Mediterranean area.

Under the current climatic conditions, we expected, as in the study by Vasques et al. (§2.2.1; [46]), that late successional species (*Quercus* spp.) would replace the other species, when given enough time. Moreover, we investigated the possible existence of alternative states between open shrubland and closed oak forest, due to the fire feedbacks, which are a necessary condition for catastrophic shifts to occur [77].

Model description

Inspired by the vegetation of the Ayora Cascade site (see also description in WP5 deliverables), the model represents six plant types, namely (in order from late to early successional, i=1...6 in Table 1): *Quercus* spp, *Pinus halepensis, Rosmarinus officinalis, Ulex parviflorus, Cistus* spp., and *Brachypodium retusum*. Oak (*Quercus*) and grass (*Brachypodium*) can resprout after fires, while the other four plant types (pines and three shrub seeders) regrow via seed germination after a fire.

The model represents the dynamics of the vegetation cover in a plot. We modified a model that was first introduced by Tilman [78] to study succession, in which we included specific terms to represent the responses of the different plant types to fire. The dynamical variables, b_i, represent the fraction of space ($0 \leq b_i < 1$) in the plot occupied by a certain vegetation type i. After a fire, resprouters keep most of their cover (to represent the fact that they resprout out of their roots). Seeders, however, burn down completely, meaning that the space they occupy is reduced to zero, but their germination ability in bare soil is high after a fire, because of the seed bank originated before the fire. For pines (i=2), the seed bank falls from the canopies to the ground at each fire, and the seeds are then available for approximately two years. The seed bank depends on the age of the pines before the last fire, because pines produce seeds only at mature age (around 10-12 years). For shrub seeders (i=3…5), the seed bank is re-calculated at each fire as a function of the seed bank produced since the last fire (which is a product of the average plant cover between the fires and the seed production), the seed durability in the soil and the seed survival rate to fire.

Fires are modeled as stochastic events with an average return time [54]. We perform two types of simulations. In the first ones, there is no dependence of fire return time on vegetation cover. These runs are thus called the "no feedback" runs (and are similar to Vasques et al. [46] model runs). The second type of runs includes the feedback between fire and vegetation composition (the "feedback" runs). We assume that fire return time depends on vegetation cover and composition (similarly to

e.g. [79,80]) such that a larger extent of more flammable species increases the average fire frequency.

Table 1 *List of vegetation types in their hierarchical order*

i	Vegetation type (genus or species)	Acronym	Fire strategy
1	*Quercus* (*ilex, coccifera*)	Q	Resprouter
2	*Pinus halepensis*	P	Seeder
3	*Rosmarinus officinalis*	R	Seeder
4	*Ulex parviflorus*	U	Seeder
5	*Cistus* (mostly *albidus,* but also some *monspeliensis*)	C	Seeder
6	*Brachypodium retusum*	B	Resprouter

The datasets
Succession
The model without fire was calibrated using data from different sites where vegetation cover had been previously recorded. Data were obtained in abandoned old fields ranging from 1 to 100 years since abandonment. A total of 75 sampling sites were used from previous studies on vegetation succession located in the Western Mediterranean Basin [35,81–84]. Data were a product in parts of CASCADE WP5 (Ayora site), and in other parts of the EU-project EUFireLab (FP4 EU project EVR1- 2001-00054 "Euro-Mediterranean wildland Fire Laboratory, a "wall-less" laboratory for wildland fire science and technologies in the Euro-Mediterranean region", 2002-2006).
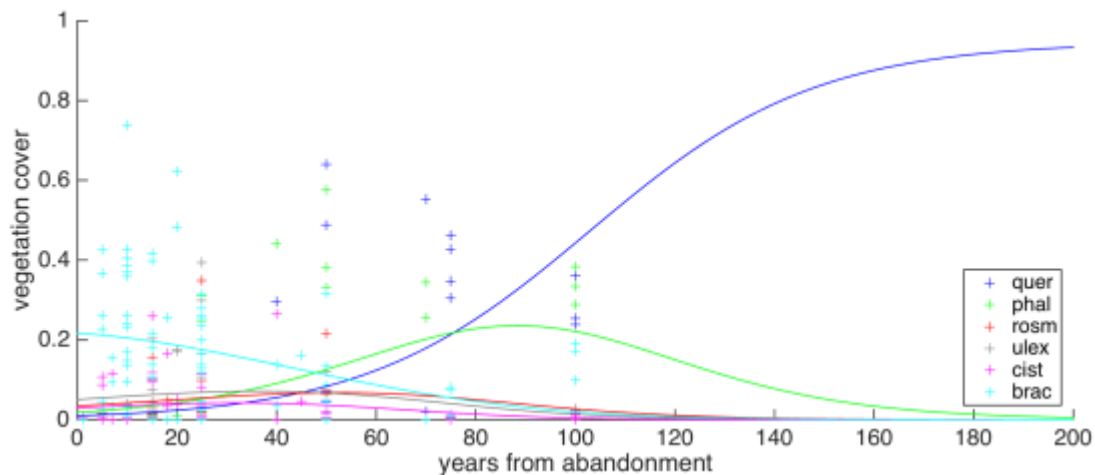
Fires
The data for calibrating the model including fires were obtained from a series of experimental sites located in SE Spain [85]. Data originated in parts from CASCADE WP5 (Ayora site), and in other parts from the EU-project LUCIFER (FP4 EU project DGXII ENV4-CT96-0320 "Land use change interactions with fire in Mediterranean Landscape", 1996-2000). We used data from four sites, namely Onil, Pardines, Ayora (Cascade site), and La Torre. These sites have experienced several wildfires during the last three decades, and within the same site we dispose of three neighboring plots with 1, 2 or 3 fires. These plots are part of a permanent long-term study established in 1994 and they keep being sampled approximately every six months the first two years after a fire, once a year until 5 years after fire, and afterwards every 5 years.

Model calibration
We performed a model calibration to find the optimal parameters by minimizing the residual sum of square of the model trajectories and data. More precisely, we minimized the mean square deviation between model and data, to the variance of the data, using the index H^2, that is zero for a theoretically perfect model, and is one when the variance of the data and the mean square deviation are equal [35,73–76]. The optimization was performed using the simulated annealing algorithm [87]. First, we calibrated the model using the successional data and without including fire in the simulations. We obtained an optimal value for the six colonization rates, and we also optimized the initial conditions for the six vegetation types (see model trajectories in Fig. 6). Second, we calibrated the full model using the fire data. For each site, we used the historical fire sequence to determine time of fires and time between fires. As initial conditions, we used the first data in the time series (i.e. the vegetation cover at the time the second fire occurred, for all cases but Ayora).

Results

Although coexistence is theoretically possible in the model adopted for succession [78], with the set of parameters obtained from the optimization procedures, there was no possibility of coexistence in the long term, in the model without fire: oaks became dominant (here defined as their cover is above 50%) after about 120 years from abandonment, and all the other species disappeared within the first 150-200 years (Fig. 6).

Figure 6: Data of fractional vegetation cover of sites without fires, for the six vegetation types (symbols, see legend for color code), as a function of the year from (estimated) land abandonment. Lines represent model trajectories with colonization parameters calibrated with the successional data shown ($H^2=0.70$). Figure from Baudena et al. [76].

When fires were included in the simulations, vegetation covers did not reach steady state, but kept varying as a consequence of the stochastic fires, with the resprouters decreasing only of a certain fraction and the seeders becoming nearly extinct at each fire. Despite the fire disturbances, oaks eventually dominated the system, independent of the initial conditions or of the fire frequency, given that they have enough time to establish (Fig. 7, 8 first column). The time at which oaks became relatively dominant depended, as expected, on the initial conditions of the oak itself (as in the model of Vasques et al. [46], see §1.2.1 above), but not on the initial conditions of the other vegetation types. More frequent fires could slightly delay the oak dominance (Fig. 7). The species composition in the initial part of the simulations, before the oaks became relatively dominant, varied largely depending on the initial conditions of the different vegetation types, and on the fire regimes. For example, pines disappeared as soon as two subsequent fires occur within about 12 years (i.e. pine maturity age).

To simulate what would be the effect of drought on the species composition a system subject to recurrent fires, we implemented drought effects on: i) oak reproduction and establishment, via lowering of the colonization ability parameter; ii) via lowering the oak resprouting ability parameter; iii) via fire recurrence, either directly by increasing the average return time (no feedback case, not shown), or indirectly by increasing the probability of fire in the presence of the different plant types (feedback case) (Fig. 8). For both fire dynamics, we observed that reduced resprouting ability and

lower oak colonization rates could lead to a very different community, namely composed of *Cistus* and *Brachypodium*, with more than 50% of the available space left empty. When including the fire feedback, an increased flammability of all species was necessary to obtain this different state (Fig. 8).

In some cases, the existence of these communities depended on the initial conditions: if the ecosystem was initially mainly composed of oaks, the forest remained and fires were relatively infrequent (~every 40 years), while if the initial abundance of seeders and/or *Brachypodium* were high, the system stayed locked in the shrubland/grassland state ("degraded"), with more frequent fires (~every 15 years). This is a so-called stochastic bistability (see Fig. 8 where the panels displaying bistability are marked with an asterisk). This bistability implies that catastrophic shifts may occur in the system under drier conditions than the current ones: a shrubland may then not evolve naturally into an oak forest anymore, as expected under the current climatic conditions, but it would stay locked in its (degraded) state. If the drought further increased the flammability, or decreased the oak resprouting ability, the system inevitably (i.e. for any initial conditions) developed into the degraded state, and it never reached the forest state. The no-feedback case (not shown) was similar, but it did not display any bistability, thus indicating that bistability was a consequence of the fire feedback itself. Also, for the system to evolve into a degraded state, increasing the fire frequency was not a strictly necessary condition: when oak recruitment and resprouting were limited, the degraded state was reached in conditions where fires were relatively rare (e.g. every 40 years). Finally, the degraded state could also be composed of *Cistus* alone or with a minor (<10%) fraction of oaks. This suggested that when the fire feedback was included, the grass survived because of it could withstand the highly recurrent fire that were generated by its high flammability thanks to its resprouting ability.

Conclusion

This second fire modeling effort suggests again that, under the current conditions, the successional process in the Mediterranean area generally leads to a dominance of the oaks. Also, pine forests disappear in all cases as a consequence of their highest vulnerability to fires (as in Vasques et al. [46]; see §2.2.1 above and [88]). However, this study also shows that drier conditions, expected as a consequence of climate change, can diverge the succession, leading to an open shrubland instead of the expected late-successional oak forests. This is due to drought reducing the resprouting capacity, the growth and seedling establishment of oaks, in combination with an enhanced flammability, which is expected based on current observations (see e.g. Deliverables D5.1 and D5.2). Within a certain range of drought intensity, and if the feedback between species community composition and fire is considered, shrubland is effectively an alternative (stochastically) stable state to the closed forests, implying that catastrophic shifts between these states are possible if drier conditions occur. The degraded shrubland is mainly composed of *Cistus* and *Brachipodium*. The dominance of rockrose (*Cistus* spp.) over the other shrub seeders is expected, as a consequence of the low regeneration rate of *Ulex parviflorus* and of the difference in plant longevity, combined with their flammability [89].
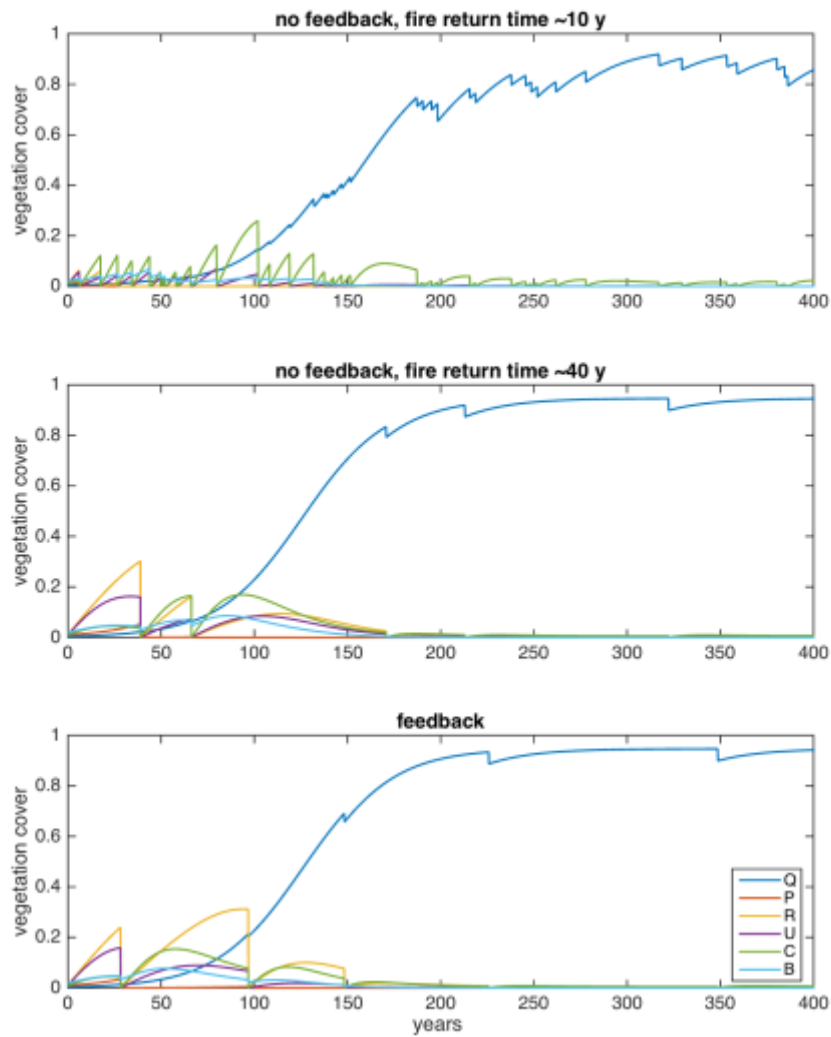
Figure 7: *Time series of vegetation cover as a function of time for the six vegetation types. After a transient period where all the species coexist, the system converges to an oak forest. Top and middle panels: fire return time is imposed (no feedback with vegetation composition) and is equal to 10 and 40 years, respectively. Bottom panel: average fire return times are determined by species composition (resulting in an average return time of ~66 years calculated between 200 and 400 years). Figure from Baudena et al. [76].*
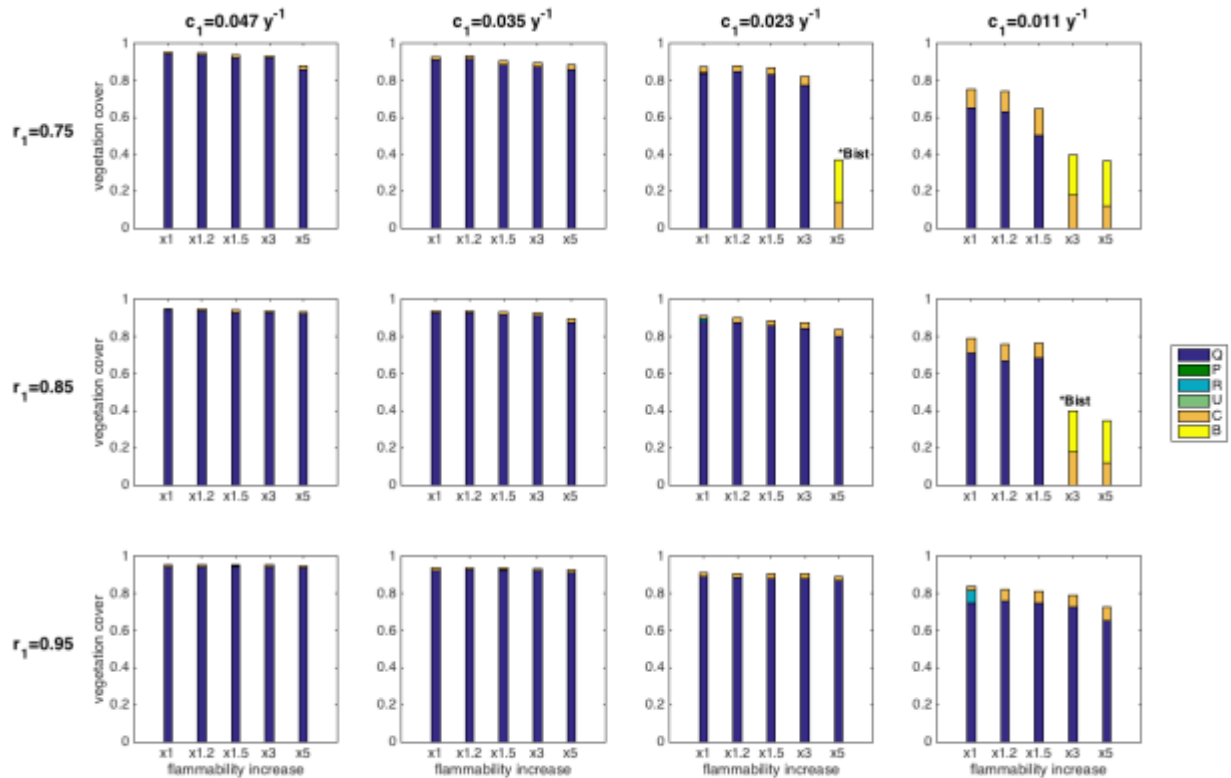
Figure 8: *Plant community composition for different drought scenarios, increasing plant flammability, and decreasing oak resprouting and colonization abilities. The bars represent average vegetation cover (calculated between 8000 and 10000 years from start of run) of each of the plant types for different values of: i) x-axis: flammability (multiplied by the factors indicated, i.e. between 1 and 5 times as much as the values of fire return time); ii) from left to right, decreasing values of oak colonization ability, c_1; iii) from top to bottom, increasing values of oak resprouting ability, r_1. The top-right panels, and the rightmost bars, represent the harshest drought conditions. Two bars are indicated as bistable ("*Bist"), since the same runs, started with high oak initial conditions, would result in Quercus and Cistus only. Figure from Baudena et al. [76].*

2.3. Dryland response to changes in rainfall intermittency

Global climate models consistently project upcoming changes in rainfall intensity in arid and semiarid regions [3,90]. These changes in rainfall intermittency are projected with more confidence than possible changes in annual and seasonal rainfall volumes. As mentioned above, for the semi-arid Mediterranean area, an increase in meteorological drought frequency is predicted (medium confidence), together with an increase in heavy precipitation events (high confidence) [3].

Although hydrological models suggest that rainfall intensity and frequency both play a role in rainwater partitioning and lateral surface water redistribution, it is unknown if and exactly how the projected changes in rainfall intermittency are going to affect the productivity and functioning of semiarid ecosystems. Modelling the effect of changes in rainfall intensity on these ecosystems requires the coupling of processes that act on the time scale of a single rain event, with processes that

act on much longer time scales, such as plant growth. Rainfall intermittency is fundamental to plant survival in drylands [91]. However, the current spatially explicit models, which capture vegetation self-organization in drylands, mostly represent rainfall as continuous in time, and thereby they do not explicitly deal with this issue ([92] but see [93,94]). Temporal stochasticity in rainfall pulses is also an important driver that has been suggested to explain the co-existence of plants competing for a single resource in drylands. However, no model study has explicitly investigated how competition for resources can lead to coexistence under realistic rainfall scenarios.

We addressed the question of how rainfall intermittency influences drylands ecosystem dynamics with two separate studies. Siteur et al. [95], addressed the role of changes in **rainfall intensity** for the response of self-organized vegetation spatial patterns in semiarid ecosystems (see upcoming §2.3.1). In Verwijmeren et al. [96], we studied the role of **rainfall intermittency** in the coexistence of plants with different strategies (see upcoming §2.3.2).

2.3.1. Effect of increases in rainfall intensity on semiarid ecosystems

Model description

We used a spatially explicit version of the water limitation model by Rietkerk et al. [97] that we coupled with a hydrological hillslope model that explicitly describes depth independent infiltration and infiltration excess (Hortonian) runoff generation on an event basis with simple conditional rules [95]. Rainwater partitioning and the runoff-runon processes are fast short-term processes that are modeled with event-based descriptions in the form of simple conditional rules. Temporal upscaling of the obtained infiltration rates yields a continuous formulation for infiltration, which is then used in the spatially extended version of the water-limitation model by Rietkerk and van de Koppel [98]. The full model acknowledges both processes that operate on short temporal scales, such as rainwater partitioning and redistribution, as well as processes that operate on longer temporal scales, such as plant growth.

Results

With the chosen parameter values, the model generates spatially periodic patterns in plant density along the hillslope. These so-called vegetation bands migrate in the uphill direction: colonization occurs directly uphill from the vegetation bands, while plant density slowly decays in the downhill part of the bands. This is in line with observations [99] and modeling studies [6], although fixed patterns have also been reported.

The model shows that an increase in mean rainfall intensity widens the rainfall range for which the ecosystem has alternative stable system states (Fig. 9). We conclude that projected increases in rainfall intensity can induce and enhance bistability in semiarid ecosystems.

Changes in mean rainfall intensity can also induce a critical transition to a desert state or cause a recovery from a desert state, even if aggregated rainfall rates remain unchanged (Fig. 9). Surprisingly, we found that, for a constant annual rainfall rate, both an increase and a decrease in mean rainfall intensity could trigger desertification. This finding was attributed to the fact that water can be lost from the system in two ways. During high intensity rain events, a fraction of the water flows through the vegetation bands and is lost as runoff, while during low intensity events a large portion of the water that precipitates over the bare interbands infiltrates locally, and gets lost due to soil evaporation and percolation without producing any run-off to the neighbouring vegetated bands

Conclusion

Our study suggests that changes in rainfall intensity may lead to increased resource losses, due to bare soil infiltration and runoff, and that these losses can potentially trigger desertification. This work suggests that in the future, field data could be used to assess the rainfall intensities that separate the different event types as identified in our model study. These values, combined with the frequency distribution of rainfall intensity, can be used to estimate the fractional loss of water from the system in current and future climates, and may thereby help in assessing the proximity of semiarid ecosystems to critical thresholds.
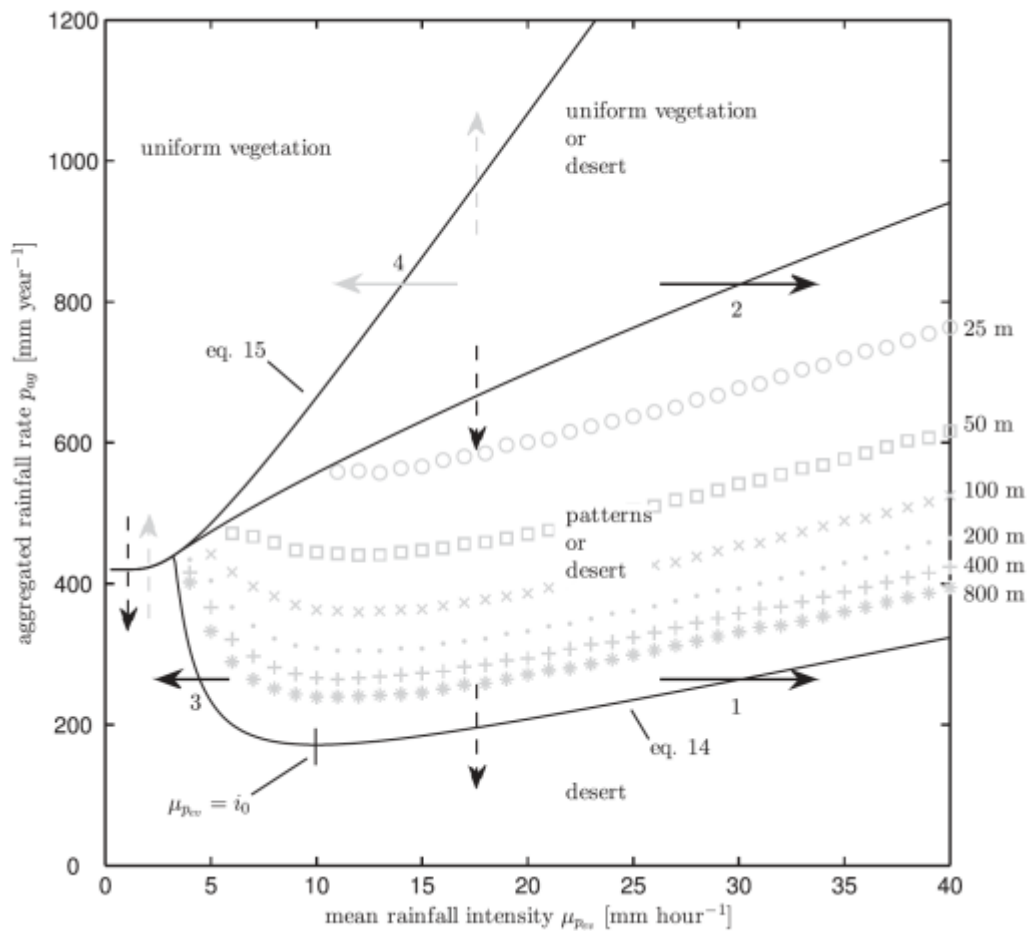
Figure 9: *Regions for which uniform vegetation, patterns, and/or desert states exist. The markers show the lower rainfall limits of patterned states with the indicated wavelengths and were obtained using the bisection method. The arrows indicate how changes in aggregated rainfall rate (dashed) and mean rainfall intensity (solid) can result in a transition to the desert state (black) or in recovery from a desert state (gray). If the system is in a patterned state, an increase in mean rainfall intensity can result in desertification (arrow 1). A transition to a bare desert state can also occur if the system is in a uniformly vegetated state (arrow 2). Less intuitive is the fact that a transition to a desert state can result from a decrease in mean rainfall intensity (arrow 3). If the system is in the desert state, decreasing rainfall intensity can also result in revegetation. Note that, since rainfall intensity can change while aggregated rainfall remains constant, the interarrival time and/or event duration change along the x axis, implying that on the left end of this figure the rainfall is characterized by continuous drizzle, whereas on the right-hand side rainfall consists of sporadic intense events. Figure from Siteur et al. [95].*

2.3.2.   Effect of rainfall intermittency on species coexistence

Model description

The model adopted here describes the coupled dynamics of vegetation and soil moisture, and it is a combination and extension of the models presented by Baudena et al. [91] and Díaz-Sierra et al. [100]. Model assumptions and parameter settings are based on the experimental measurement performed in the CASCADE site of Santomera in South-Eastern Spain [101]. The model is spatially implicit, and water input in the model consisted of stochastic rainfall events based on statistics of historical data for the yearly amount and timing of rainfall. The model includes two plants: a relatively drought resistant plant, and a plant with a higher optimal growth rate, similar to the woody perennial species in the CASCADE site *Artemisia herba-alba* and *Anthyllis cytisoides*, respectively [96]. We provide a more detailed description of the model later (in §3.2.1.); the version of the model used here does not include grazing or facilitation.

We modelled realistic (stochastic) rainfall scenarios to explore the effect of rainfall intermittency on the co-existence of these two species.

Results

Our study shows for the first time that realistic, intermittent, rainfall can lead to co-existence under one single resource due to the differences in their optimal growth rate and wilting points, i.e. so-called relative non-linearity in growth (Fig. 10). We showed that higher intermittency results in stable co-existence of the two species, whereas (nearly) constant rainfall leads to competitive exclusion of the species with higher growth rate by the more drought resistant species. With low intermittency, or nearly constant rainfall, the species with lower wilting point outcompetes the other species along the whole rainfall gradient, as the soil is never wet, whereas with increased intermittency the protégée can become dominant at nearly the whole rainfall gradient without outcompeting the nurse species.

Conclusion

This study shows that an increase in drought due to a changes in the temporal partitioning of rainfall (higher and less frequent events) can shift the competitive outcome of the two vegetation types, resulting in a shift in species composition from a drought resistant vegetation type to a coexistence of two vegetation types.
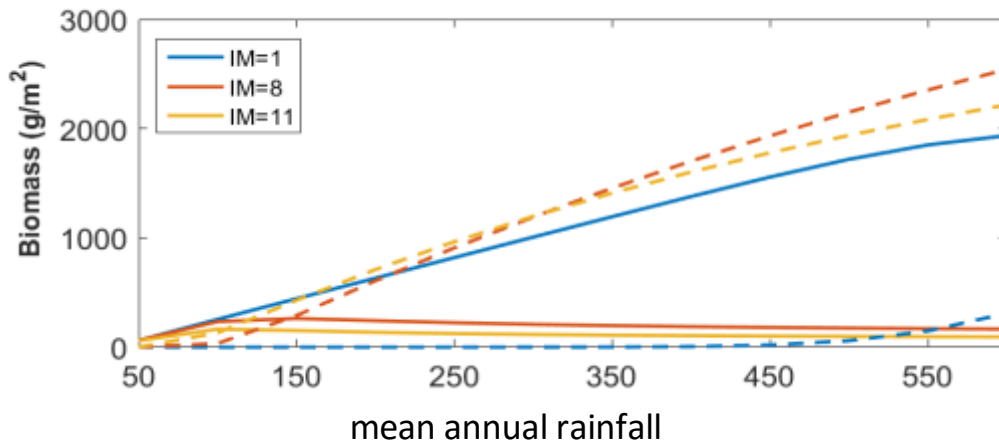
Figure 10: *Average equilibrium biomass (after 1000 years of run, average over the last 200 years) for drought resistant species (solid lines) and species with a higher optimal growth rate (dotted lines) for three intermittency scenarios (IM= 1 day, IM = 8 days, IM = 11 days). IM is the average number of days between rainfall events, thus low values are closer to constant rainfall. The value of IM for the CASCADE Santomera field site is currently ~ 8 days. The range of co-existence along the rainfall gradient increased with intermittency, as in the low intermittency scenario (IM=1 d) coexistence starts for rainfall larger than 450 mm y⁻¹, while for higher intermittency levels the two species coexist already around 100 mm y⁻¹. Figure from Verwijmeren et al. [96].*

3. Species interaction, feedbacks and dryland response to stress

The studies presented in §2 have investigated how taking into account the spatial component of grazing [25], the various plant strategies to cope with fire [46,76], the combined effects of fire and drought [76], the changes in rainfall intensity [95] and rainfall intermittency [96] as predicted by climate change affect dryland response to increasing stress, and more precisely the probability of catastrophic transition to an alternative, degraded ecosystem state [25,76,95], the vegetation succession [46,76], and the expected composition of the plant community with possible feedbacks on ecosystem functioning [46,76,96]. As mentioned in the introduction §1, most dryland models so far have typically included one vegetation type and have therefore not specifically investigated the relevance of species-species and species-abiotic environmental interactions for dryland dynamics and resilience. This is what we investigated in the studies presented in what follows.

3.1. Including ecohydrological feedbacks between vegetation pattern and resource redistribution

In drylands, the vegetation cover is typically composed of vegetation patches interspaced by bare ground [102]. Both the total amount of vegetation cover and vegetation pattern greatly impact the potential of the ecosystem to conserve key resources such as water, soil, and nutrients [103–106]. Despite the existing consensus on the crucial role of such connectivity-mediated feedbacks in the behavior of dryland ecosystems, their impact on dryland response to land degradation drivers has been barely tested and assessed in experimental or modelling studies (but see [107]).

We included, for the first time, feedbacks between vegetation pattern, and resource redistribution and productivity in a spatially-explicit model of dryland dynamics (Fig. 11) [108]. We studied how these feedbacks shape the ecosystem response to changing environmental and human pressures.

We extended the model of Kéfi *et al.* [11] by including a positive feedback between increased hydrological connectivity of bare-soil areas, global losses of water and nutrients from the system, and reduced plant productivity, which in turn then further increases hydrological connectivity (connectivity-mediated feedback, Fig. 11). The loss of water and nutrients was estimated with Flowlength [109], a spatial metric designed to be used as a surrogate for the loss of resources on hillslopes where runoff is the main agent of sediment transport and deposition. Flowlength is based on the assumption that bare soil (i.e., either empty or degraded cells in the model) and vegetated patches behave, respectively as sources and sinks of runoff and sediments. Flowlength measures the connectivity of bare-soil areas by calculating the average of the runoff pathway lengths from all the cells in the system, with higher values representing higher hydrological connectivity of bare-soil areas.
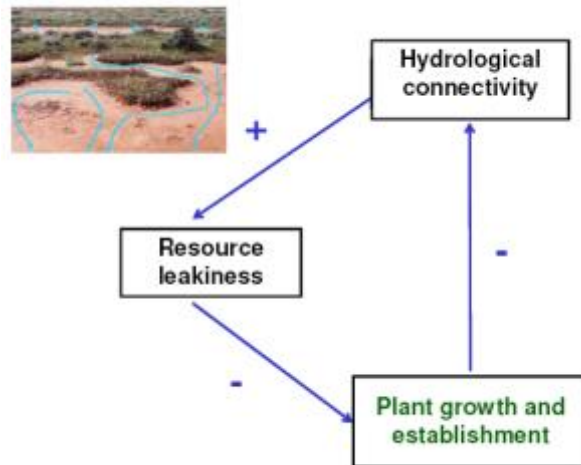
Figure 11: Connectivity-mediated feedbacks between plant patterns, resource redistribution and productivity [108].

The simulations suggested that the connectivity-mediated feedback decrease the amount of pressure required to cause a critical shift to a degraded state (ecosystem resilience). If environmental conditions improve, this feedback increases the pressure release needed to achieve the ecosystem recovery (restoration potential). Interestingly, the simulations also showed a higher sensitivity of the bare-soil connectivity index (Flowlength) to changes in the spatial organization of the vegetation during the transition to a degraded state, in comparison with bare-soil (or vegetation) cover, which shows a rather linear evolution during this transition.

Our results suggest that modelling studies on dryland vegetation dynamics not accounting for the connectivity-mediated feedbacks studied may overestimate the resistance, resilience and restoration potential of drylands in response to environmental and human pressures. Moreover, our results suggest that changes in both vegetation cover and pattern (and associated hydrological connectivity) along degradation trajectories may be more informative early-warning indicators of dryland degradation than changes in vegetation cover. Thus, the acceleration of bare-soil connectivity from spatially-explicit time-series data may provide an early warning of imminent shift. This bare-soil connectivity index could be of special interest for management, since it helps identifying the critical point at which measures should be adopted to prevent drastic changes in ecological conditions.

3.2. Including plant-plant interactions along drought and grazing gradients

Facilitation between plants is known to be an important mechanism driving vegetation patchiness [12,102,110], but we lack understanding of how interactions between plants change in response to combined effects of drought and consumer pressure – the main stressors in many arid ecosystems.

In semi-arid ecosystems, shrubs, trees and annual plant species compete for water, which is considered the main growth-limiting resource. Shrubs, however, often also provide positive (i.e. facilitative) effects by relieving drought stress for less drought-tolerant neighbouring plants, for

example by shading or by increasing water availability (via increased infiltration) within their direct vicinity [111]. Shrubs can also lower grazing pressure by protecting neighbouring individuals against herbivore damage, a process known as associational resistance [112]. The total net effect of one plant (nurse plant) on the other plant (protégée plant) is a trade-off between competitive and facilitative effects, and a crucial question to be answered is **how a combination of different stressors (e.g. drought and grazing) influences the direction and strength of plant-plant interactions in dryland ecosystems** [113] .

Early conceptual models of plant-plant interactions hypothesized that the net outcome of plant–plant interactions shifts from competition towards facilitation with increasing drought stress or grazing pressure [15,114]. Recent meta-analyses indeed showed that at the global scale a shift towards more facilitative plant–plant interactions is observed as stress levels increase [115,116]. However, recent studies question if positive species interactions can be expected under very severe drought stress [117], as competitive effects may become more intense during severe dry periods. In addition, studies from grazed ecosystems show that under severe grazing stress, plant-plant interaction wane from facilitation to neutral, as plants that provide benefits for neighbours lose their ability to do so under very high grazing pressure [118,119]. Very few studies have empirically tested the impact of combined effects of drought and grazing (but see [120,121]), and changes in plant-plant interactions along combined stress gradients are still not well understood [113].

Previous ecohydrological models investigated the balance between positive and negative interactions between two plant species [10,100], by modelling the competitive water uptake by plants in combination with an increased infiltration of water in the soil due to increased biomass. These studies assessed which factors tilt the balance between the facilitative and competitive effects along a drought gradient. However, it has not yet been studied with mechanistic models how the joint effects of grazing and drought - highly realistic in (semi-) arid ecosystems - shape the net interactions between plants.

We formulated a conceptual model describing the relationship between stress and facilitation intensity and how this determines the position of a critical threshold [122]. There, we propose that a decline in facilitation intensity at the severe end of a stress gradient may occur prior to a critical transition and that including grazing will speed up this process. Also we propose that seedling-facilitator associations and facilitator recruitment may provide additional early warning signals for imminent critical transition [122].

3.2.1. Effect of rainfall intermittency and grazing on plant coexistence

To study how the combination of drought and grazing gradients affects plant-plant interactions, and thus community composition and stability, we extended the model previously described in §2.3.2 [96], where two plant species differed in their water and drought functional traits. For the first time, a study of plant-plant interactions represented rainfall as highly intermittent, i.e. it catches the fact that rainfall in drylands occurs in pulses [123]. In this model, the drought resistant species was also an unpalatable nurse species, which protected the palatable protégée species from grazing damage (facilitation via grazing protection). The protégée species had a higher optimal growth rate when soil water content was higher. The two species compete for water, but also one species facilitates the other via grazing protection. This modelling work was based on the plant-plant dynamics studied within a field experiment, located in the UA CASCADE site of Santomera,

Spain [101] (in the same way as the study in §2.3.2). The experiment also provided part of the parameters for the model.

Model description

To study the interacting effects of annual rainfall amount, rainfall intermittency and grazing on plant coexistence and on the competitive or facilitative effects of a nurse species on a protégée species, we developed a mechanistic two-species-model coupled to a hydrological model of a single soil layer. The model describes the coupled dynamics of vegetation and soil moisture, and it is a combination and extension of the models presented by Baudena et al. (2007), Laio et al. (2001) and Díaz-Sierra et al. (2010) [91,100,124]. We used a one-layer bucket model, because in our field site we observed relatively shallow soil depths (20-30 cm) accessible for the root systems of both plant types (personal observation). The system dynamics was modelled by using three coupled ordinary differential equations (ODEs), for the soil water (s) dynamics, and for the nurse (N) and the protégée (P) plant growth dynamics.

Water input in the model consisted of stochastic rainfall events based on statistics of historical data for the yearly amount and timing of rainfall. Rainfall was modelled as stochastic Poisson events, with exponential distributions for inter-arrival time (i.e., time in between rainfall events), and for mean daily rainfall intensity (calculated from the mean annual rainfall) [124]. We also included a dry season without any rain, occurring once every year, to simulate the summer dry season that is characteristic for the climate of the field site. We calculated realistic values for mean annual rainfall, rainfall inter-arrival time and length of drought season, based on 72 years of rainfall records for the Alcantarilla weather station nearby our field site (Agencia Estatal de Meteorología, AEMET). We varied rainfall mean annual values and intermittency values in subsequent model runs, with a higher intermittency resulting in higher rainfall inter-arrival time and thus also increased mean daily rainfall intensity.

Based on previous models [97,100], plant growth was modelled as proportional to transpiration, a function of the soil water content, with a proportionality constant that would determine the maximum growth rate. The 'nurse' species (N) suffered a baseline mortality rate but did not suffer a grazing mortality. The second plant type, the 'protégée' species (P) also suffered a baseline mortality on top of which a grazing mortality was implemented. The biomass removal per year was proportional to its own biomass with grazing rate.

Grazing damage was reduced by a function depending on the ratio of nurse biomass over protégée biomass. The nurse species decreased the amount of grazing-induced mortality for the protégé species. We followed the approach by Gross [125], but while that model uses the grazing protection as a function of the neighboring species alone, we choose to model grazing protection as a function of the ratio of nurse biomass over protégé biomass to account for size dependence (a small nurse plant cannot protect a larger protégé plant). Grazing protection was modelled using a Holling type III function, where the ratio of the nurse biomass over the protégé biomass determined the amount of reduction in grazing mortality.

Our two distinct plant functional types, nurse (N) and protégée (P), are woody perennial species that were selected in a parallel experiment in which plant growth of protected and unprotected planted saplings of *Anthyllis cytisoides* was monitored [101]. In line with this experiment, performed in the CASCADE site of Santomera (Spain) we used *Artemisia herba-alba* as nurse plant in this study and modelled its growth. *Artemisia spp.* is not preferred by goats and has been found to be spatially associated with *A. cytisoides* in previous studies [121]. Also in line with field observations and parallel experiments, we used *Anthyllis cytisoides* as protégé species in our model. *A. cytisoides* is a

drought-deciduous shrub from the *Fabacaea* family, and it is highly palatable for both goat and rabbits. *A. cytisoides* has been found to constitute 41 % of livestock goat diet and is thus considered as highly preferred food source for goats [126].

In the default parameter setting, the two species are characterised by a trade-off: although *A. herba-alba* has the benefit of being able to grow under lower soil moisture levels because of its lower wilting point, *A. cytisoides* has a higher growth rate under more benign moist conditions. A similar trade-off between drought tolerance and optimal growth rate has been reported in several studies in dryland ecosystems and has been proposed as a possible mechanisms promoting plant coexistence [123].

Results

Biomass of nurse and protégée species and the competitive outcome were heavily dependent on the rainfall intermittency, annual rainfall amount and grazing rate variations (Fig. 12*)*. We did not find any effects of varying the initial conditions of nurse or protégée biomass on the final biomass values, implying that the modeled system did not display any multistability. In other words, there is no possible catastrophic shift in this model, probably as a consequence of the fact that the model does not represent the spatial dynamic of plant growth and of grazing (as opposed to the above described model of Schneider et al. [25] presented in §2.1).

We show that under increasing grazing pressure, species can coexist thanks to grazing protection under current rainfall amount and intermittency scenario. In the low intermittency scenario (Fig. 12, left panel), the nurse species biomass is constant over the grazing gradient, as grazing does not affect it and the protégée is fully outcompeted. The protégée without a nurse can persist when being grazed, but only for high rainfall values or low grazing rates (see Fig. 12, dashed line in the panels of the bottom row or the right end of each panel). The protégée without a nurse can only obtain biomass values higher than the nurse under ungrazed conditions. Under current rainfall conditions (300 mm/y and inter-arrival time between events IM=8, Fig. 12, central panel), high grazing would lead to protégée extinction, but the protection of the nurse allows for the protégée species to survive.

Moreover, we show that grazing results in increased facilitation of the nurse on the protégée, but only under current or higher intermittency conditions, and with an increasing relevance of facilitation with rainfall (Fig. 13). This means that an increase in rainfall intermittency (leading to longer drought periods) or in grazing pressure will result in more facilitative interactions between plants. We also found that competitive interactions may become prevalent with drought stress. To quantify plant interactions, and their positive and negative net effects, we use two new indices (NIntA and NImpA), which we mathematical formulated from the classical concept of intensity and importance, respectively [127] (see Table 2).

Table 2. *The new family of Neighbour effect Indices (NInd$_S$), with the formulas of the two intensity and the two importance indices, with additive or multiplicative symmetry, as defined in [127]. P$_{-N}$ (resp. P$_{+N}$) performance of the protégée without (resp. with) neighbours. ΔP = P$_{+N}$ - P$_{-N}$: total impact of neighbours. P$_{sum}$ = P$_{+N}$ + P$_{-N}$: sum of the performances of the target species with and without neighbours. MP$_{-N}$: The maximum value of target species without neighbours along the gradient. MP$_{sum}$: The maximum value of P$_{sum}$ along the gradient.*

NInd$_S$	ADDITIVE SYMMETRY	MULTIPLICATIVE SYMMETRY
INTENSITY	$NInt_A = 2\dfrac{\Delta P}{P_{-N} + |\Delta P|}$	$NInt_M = 2\dfrac{\Delta P}{P_{-N}+P_{+N} + |\Delta P|}$
IMPORTANCE	$NImp_A = 2\dfrac{\Delta P}{2\,MP_{-N} - P_{-N} + |\Delta P|}$	$NImp = 2\dfrac{\Delta P}{2\,MP_{sum} - P_{-N} - P_{+N} + |\Delta P|}$

Conclusion

This model suggests that the relative importance of facilitative vs competitive plant-plant interactions varies along stress gradients, thus determining the possibility for species coexistence and may affect ecosystem functioning. This information is crucial to obtain a better insight into the long-term co-existence of species in semi-arid ecosystems in response to future climate change.
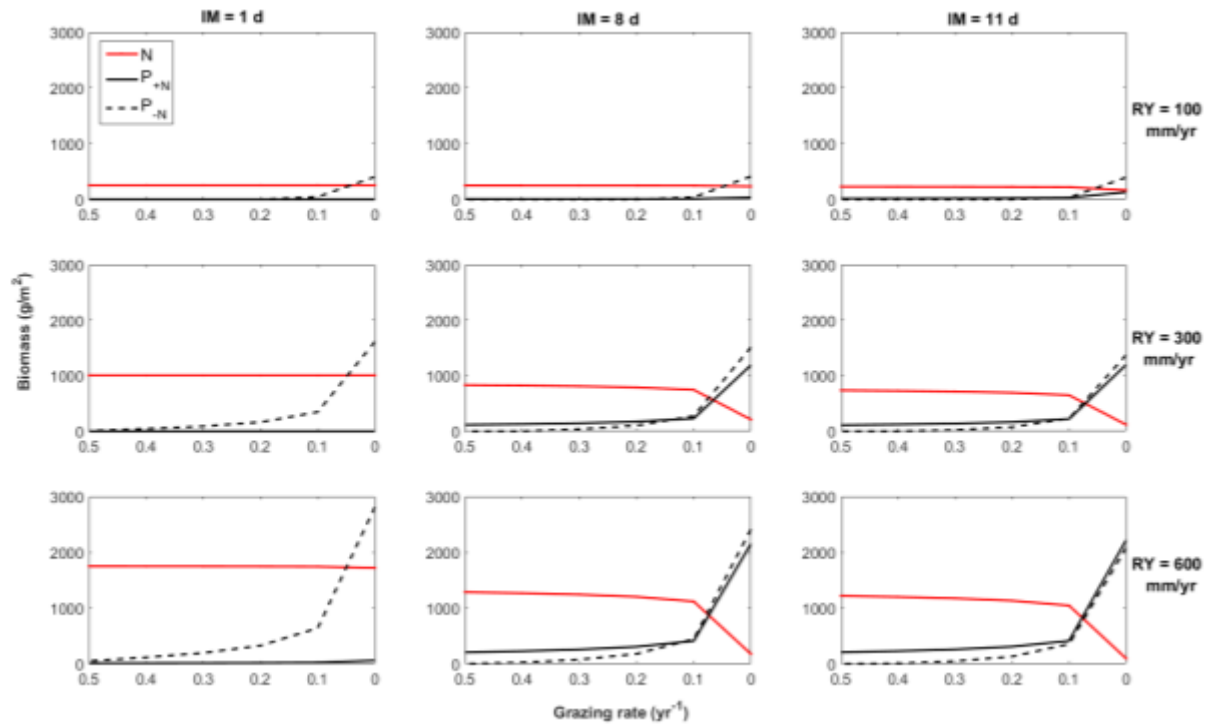
Figure 12: Average biomass for the nurse (N, red line), the protégée with a neighboring nurse (P_{+N}, solid black line) and the protégée without a neighboring nurse (P_{-N}, dashed black line). Columns represent different intermittency scenarios (IM=1, IM=,8, IM=11 days). Rows represent different annual rainfall (RY=100, 300, 500 mm yr^{-1} from top to bottom). For each parameter combination, the value displayed is the average of the final 200 years of 1000 year simulations. Figure from Verwijmeren et al. [96].
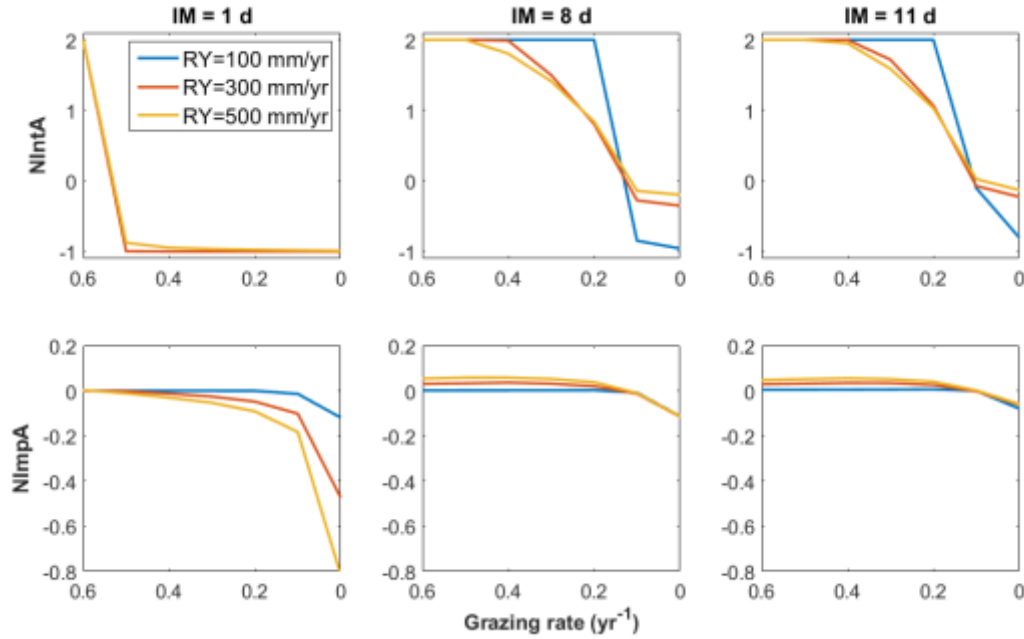
Figure 13: *The intensity (NInt$_A$) and the importance (NImp$_A$) of the nurse on the protégée biomass along a grazing gradient for three intermittency scenarios (IM=1, 8 or, 11 days) and three annual rainfall scenarios (RY=100, 300 or 500 mm yr^{-1}). See table 2 for the expressions of NInt$_A$ and NImp$_A$. Positive values represent facilitative net effects and negative values competitive effects. The two indices used to quantify intensity and importance have been newly defined in another CASCADE paper [127]. Figure from Verwijmeren et al. [96].*

3.2.2.   Effect of biotic and abiotic facilitation on plant coexistence along drought and grazing gradients

Following up on the results of §3.2.1., obtained for a specific system and a given set of species, we explored the generality of these results, and **included, besides grazing protection, facilitation due to the effect of plants on soil water content**, which is a very relevant mechanism in drylands [8,102]. We therefore developed a model to study theoretically the role of plant interactions along drought and grazing gradients for the resilience of dryland ecosystems [128].

Model description
We modified an existing model including two plants, light and soil moisture [100], in a similar way as in the above presented work (§3.2.1; [96]). In the present model, the nurse plant can have two separate positive effects on the protégée: i) increasing water infiltration (abiotic facilitation) and ii) protecting from grazing (biotic facilitation). Soil water and light availability are modelled explicitly, and so are water and light competition between the two plant types. In this model, the nurse species is not assumed to be limited by water, but instead we assume that it is limited by light availability [100], which provides a coexistence mechanism for the two species, and allows a simple comparison of the two positive effects. We also simplified the model of §3.2.1 [96] to assure analytical tractability in two main ways: a) the rainfall is modelled as constant; b) plant transpiration functions are modelled as differential functions of the soil moisture content and light availability, respectively. We also modified the model to fully analyze the effect of positive interactions of the nurse on the protégée. First, we considered that the protégée may not have any positive effect on the soil water, i.e. it did not increase infiltration. This assumption allows us to study separately the effects of the two different types of facilitation included in this model. Second, we introduced a limit to the

maximum grazing protection that the nurse can provide. In the previous model (§3.2.1, [96]), the nurse fully prevented grazing, when its biomass was a number of times higher than the one of the protégée. We decreased this values to simulate partial grazing protection even at large densities of the nurse.

For the parameters that are shared with the previous model (§3.2.1, [96]) we used the values previously deduced, except for the maximum water uptake of the nurse, which was cut by half to satisfy the classical criteria for nurse and protégé coexistence even for small positive interactions (the nurse species should consume less of the resource that limits the growth of the protégée, i.e. water, [100,129]). For the parameters involved in the nurse light absorption growth we proposed a set of tentative values, which allowed species coexistence and the analysis of net facilitative and competitive effects along the same environmental gradients.
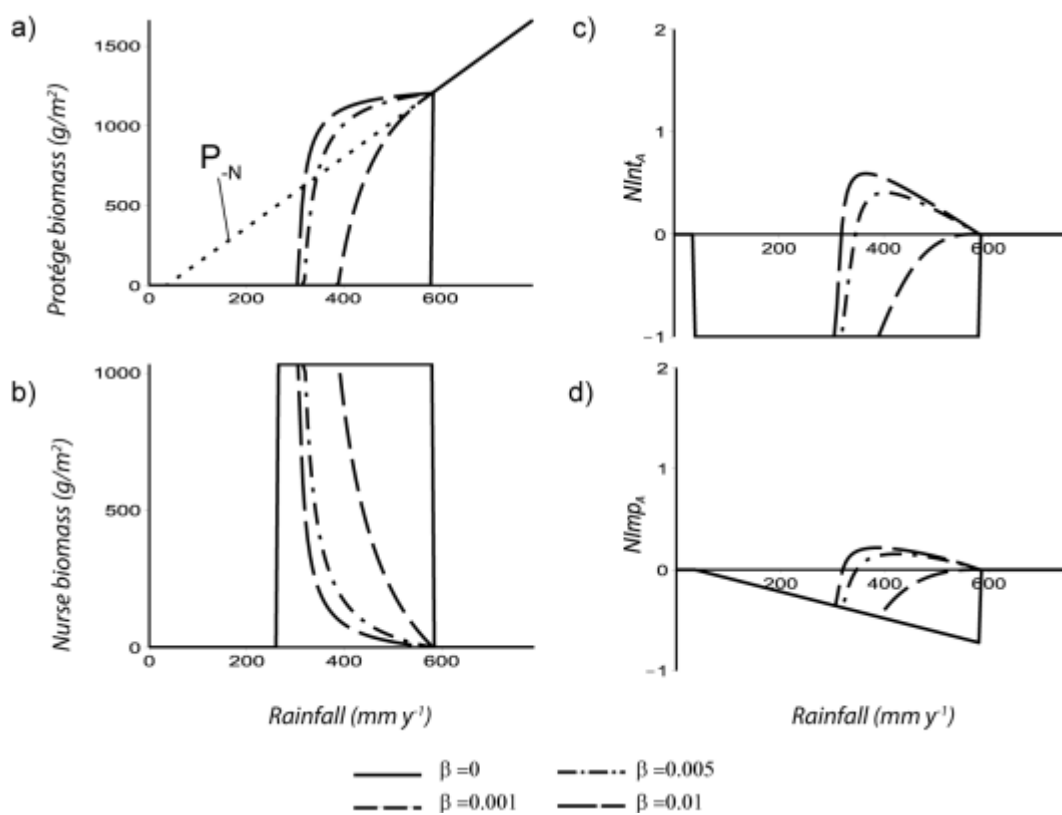
Figure 14: *(a-b) Equilibrium biomasses of protégée (a) and nurse (b) plants along a rainfall gradient for four different values of the parameter β, which represents the ability of the nurse species to increase soil water infiltration. (c-d) Intensity ($NInt_A$) and importance ($NImp_A$) of the nurse on the protégée biomass along a rainfall gradient (as calculated from panels a-b). Positive values represent facilitative net effects, and negative values represent competitive net effects. The two indices used to quantify intensity and importance have been newly defined in another CASCADE paper [127]; see §3.2.1 for an intuitive explanation of these metrics. Figure from Diaz-Sierra et al. [128].*

Results

Our analysis shows that facilitative mechanisms affect coexistence (Fig. 14-15 a, b). The more the nurse species either increases water infiltration (Fig. 14 a, b) or protects the protégée from grazing (Fig. 15 a, b), the larger the range of annual rainfall values or grazing pressure values, respectively,

where coexistence of the two species is observed. In details, when rainfall decreases, the protégée equilibrium biomass decreases, and a nurse species that increases soil water infiltration can invade while previously excluded. Because the nurse species is drought tolerant (and provided they satisfy a classical criteria of water to light consumption, [100,129]), the two species will coexist (Fig. 14 a,b). Along a grazing gradient, the less competitive nurse species can invade when grazing increases. Since the invading species can protect the established species from grazing, the two species coexist at equilibrium (Fig 15 a, b).

We also quantified the net effect of the facilitative and competitive interactions along the two stress gradients, showing that the type of shifts between competition and facilitation along a stress gradient depends on the specific interaction mechanisms and on their intensity (Fig. 14 c, d, 15 c, d).
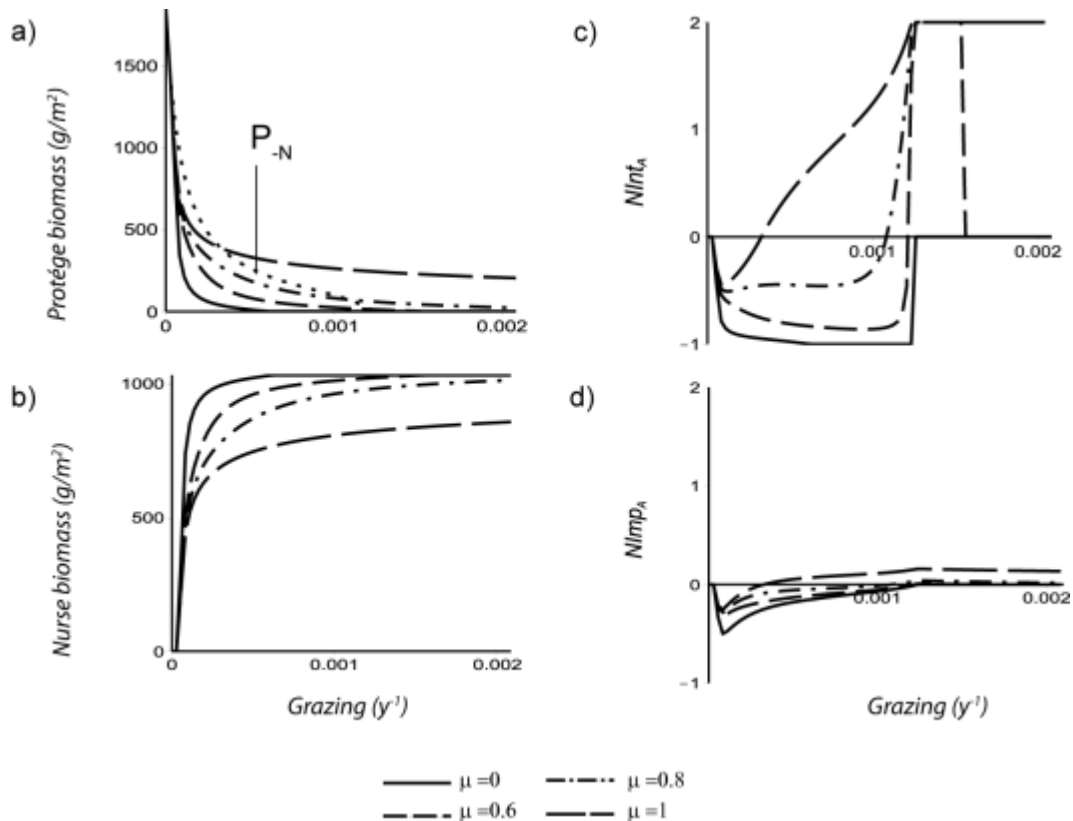
Figure 15: (a-b) Equilibrium biomasses of protégé (a) and nurse (b) plants along a grazing gradient (x-axis), for 4 different values of μ, which represents the ability of the nurse to protect the protégée from grazing. (c-d) Intensity ($NInt_A$) and importance ($NImp_A$) of the nurse on the protégée biomass along a grazing gradient (as calculated from panels a-b). Positive values represent facilitative net effects, and negative values represent competitive net effects. The two indices used to quantify intensity and importance have been newly defined in another CASCADE paper [127]; see §3.2.1 for an intuitive explanation of these metrics. Figure from Diaz-Sierra et al. [128].

Conclusion

We conclude from this model analysis that it is not possible to find a unique trend in the facilitation/competition curves, as expected from the stress-gradient hypothesis, in its original or revised forms, which postulated that facilitation would be most relevant at high or intermediate level

of stress. Our results show that the intensity and the net effect of the mechanisms leading to facilitation or competition can change depending on several factors.

3.2.3. Effect of biotic and abiotic facilitation on ecosystem resilience

The models presented in §3.2.1 and §3.2.2 studied the role of grazing protection from a nurse on species coexistence and on plant-plant interactions along stress gradients, but these models did not exhibit catastrophic shifts (in the parameter range analyzed). To follow up on these studies, we built on the model presented in §2.1 which includes both grazing protection (i.e. biotic facilitation) and abiotic facilitation, but also exhibits catastrophic transitions to desertification [25].

We extended this previous model with associational protection (§2.1, [25]) to two types of species: a nurse species (adapted against grazing) and a protégée species (without any adaptation against grazing but benefiting from the protection from nurse species when they grow next to them). **The model was used to investigate how the nurse and protégée may coexist along gradients of grazing or aridity and to evaluate ecosystem resilience to those stresses** [130].

Results
Along a gradient of grazing intensity, the model shows that at low grazing intensity, only the protégée maintains itself in the system because it is more competitive than the nurse (Fig. 16 left). Coexistence between both species is possible at intermediate grazing intensities. Above a threshold of grazing pressure, only the nurse can maintain itself because of its adaptation against grazing. This threshold of grazing pressure decreases as aridity increases, therefore favoring the nurse species at higher aridity levels. This succession of species along a grazing gradient matches field observations [131–133].

Moeover, studying the ecosystem response to increasing aridity shows that the system exhibits a high vegetation cover which decreases as aridity increases until a threshold is reaches at which the vegetation cover collapses to desert in catastrophic way (i.e. with hysteresis and bistability). Including the two species and the mechanism of indirect facilitation makes this schema more complex: before the extinction of the vegetation, there is a zone of coexistence which is tristable: desert is stable, the coexistence happens along a degradation path and the nurse alone maintains itself in case of regeneration.

Conclusion
This model with only two species shows how including different species and different strategies can affect the resilience of the ecosystems and more specifically transform the typical catastrophic shift curve into a more complex situation with practical implications of ecosystem restoration.
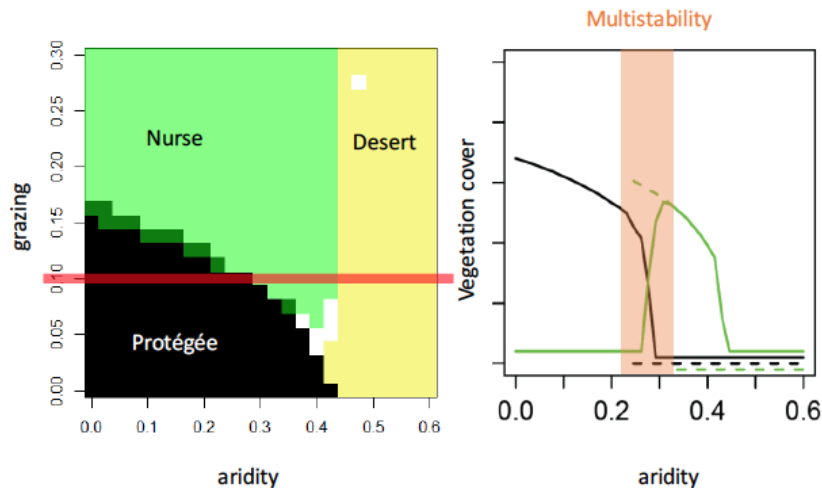
Figure 16: Outcome of a model of the dynamics of nurse and protégées along gradients of aridity and grazing. Left: state diagrams where colors correspond to different outcomes of the model, either the protégée only survives (black), or the nurse only survives (light green), or the two plant species coexist (dark green), or no plant survives in the ecosystem (yellow). White pixles are parameter combinations for which more simulations are needed. Right: cross section of the left diagram showing the vegetation cover of the protégée (black) or of the nurse (green) along an aridity gradient for a grazing level of 0.1. Solid lines are obtained when aridity is gradually increased starting from a low aridity level. Dashed lines are obtained starting from a high aridity level and gradually decreasing it. In the orange area, at intermediate level of aridity, the system exhibits multistability, meaning that its state depends on the initial condition (or the history) of the system. Figure from Danet [130].

3.2.4.   Effect of facilitation and climate shifts on plant coexistence

The previous sections (§3.2.1, §3.2.2 and §3.2.3) have investigated how plant-plant interactions could contribute to coexistence of different plant species and functional groups along stress gradients in drylands. The studies, however, did not address the question of the origin of the different species and functional groups currently present in drylands.

The present semi-arid Mediterranean climate arose about 3 Mya, when there was a climatic change from the wet Tertiary to the dry Quaternary period. Today, the Mediterranean basin vegetation can be grouped into two contrasting trait-syndromes, the old Tertiary trait-syndrome and the modern Quaternary trait-syndrome which have contrasting traits but coexist in the region [134]. The tertiary trait-syndrome appeared in the region before the establishment of the more arid Mediterranean climate (3 Mya) and is known to be less drought-tolerant than the Quaternary trait-syndrome. In spite of this climatic change, most Tertiary species did not disappear from the region, but remained relatively abundant, coexisting with the more drought-tolerant Quaternary species. Empirical studies have shown that the Quaternary plants often serve as nurse plants which provide a suitable local environment for the Tertiary plants allowing them to persist in such an environment [135]. A hypothesis is therefore that facilitation between plants can act as an evolutionary force, by creating dynamical spatial heterogeneity in the environment and therefore allowing divergent adaptation to happen.

Here, **we investigated whether facilitation was crucial for the persistence of the Tertiary trait-syndrome in the Mediterranean basin** after the climate shift (from wet to dry), while adaptation to the new semi-arid climate could evolve. We therefore developed a phenotypic model of evolution for dryland vegetation dynamics, which is individual-based and spatially-explicit [136–138]. We studied the response of drylands to abrupt climate shifts and investigated the potential of local facilitation to explain the existence of two distinct trait syndromes in the Mediterranean.

Model description

This model is an interaction particle system, which is an extension of previous models [11,25,130], including those presented in §2.1 and §3.2.3 of this document. In the model, individual plants improve their local neighboring environment, providing better conditions for seed germination and seedling survival (a.k.a. early survival) of other plants, thus mimicking the locally improved supply with water and organic matter observed in drylands (abiotic facilitation). We defined early survival of the plants as a function of local environmental quality, a simplified representation of soil quality and water availability at a particular location. Early survival here combines a number of morphological and physiological traits that lead to higher tolerance to drought and represents the different trait-syndromes. During a plant's reproduction in the landscape, the offspring will either inherit its parental early survival trait or undergo a mutation that results in a random displacement from the parental phenotype. This way, individuals could adapt to drier environmental conditions at the cost of a shorter lifespan.

We ran numerical simulations of the model following the fate of mutants with different early survival rates in the plant population. We investigated the environmental conditions (arid vs. humid) that resulted in the evolution of either of the trait syndromes [136,137]. Finally, we investigated under which conditions the facilitative effects of the Quaternary plants enable ecological coexistence of the two functional groups.

Results

We found that local facilitation increased the diversity of traits in the system along phenotypic evolution. It allowed the coexistence of drought-tolerant and drought-sensitive traits under dry environmental conditions such as the ones observed today in the Mediterranean region. This suggests that local facilitation can act as a selective pressure which favors non drought-adapted phenotypes, by promoting spatial environmental heterogeneity.

After a period of climatic change from wet to dry conditions, facilitation was responsible for the maintenance of the Tertiary-like trait in the lattice (Fig. 17); without facilitation only the Quaternary trait persisted, with no other coexisting ecotype. Thus facilitation could have been a mechanism by which the Tertiary plants persisted within the current Mediterranean climate, while adaptation to the semi-arid climate occurred.

Conclusion

Our work offers a new perspective on the importance of positive interactions for the maintenance of diversity through evolutionary time.
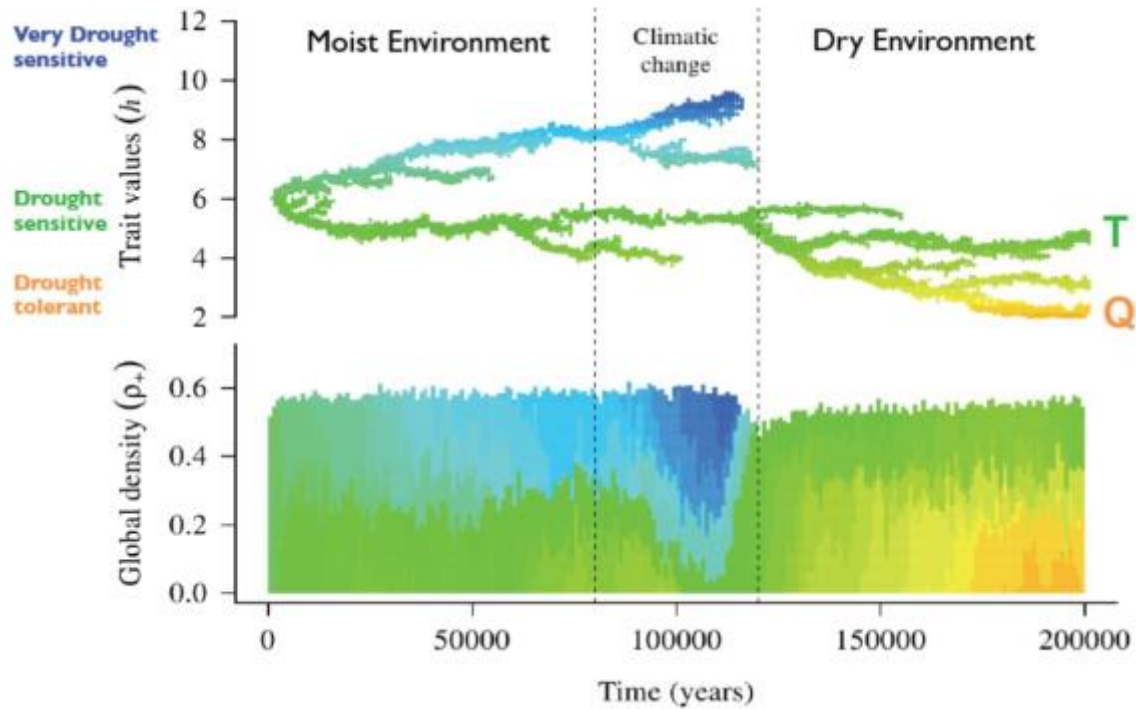
Figure 17: Simulations of an individual-based spatial-explicit model of phenotypic evolution for plants in Mediterranean drylands along a changing environment in the presence of facilitation. Top panel: changes of the trait value, h, in the plant population through time. The trait h reflects how tolerant a species is to harsh environmental conditions (i.e. how able a species is to reach adulthood at in harsh environments). Bottom panel: global vegetation cover through time. Climatic change occurred linearly between 80 000 and 120 000 years from a moist to a dry environment. The colors correspond to the different h-values (defined on the y-axis of the top panel). After the climatic change, most drought-sensitive ecotypes went extinct (blue). The Tertiary-like ecotype (green) persisted through the climatic change and adapted to the new dry condition (orange color). Facilitation was responsible for the maintenance of the Tertiary-like trait in the ecosystem after the climate change; indeed in other simulations without facilitation only the Quaternary trait persisted, with no other coexisting ecotype. Figure from[136,138].

3.2.5. Effect of demographic noise on dryland response to stress

Model description

Model studies of drylands ecosystems often discard the individual nature and stochastic behavior of plants. These may give rise to demographic noise, which in certain cases can influence the qualitative dynamics of ecosystem models, such as the stability and resilience of the final states. **To improve this aspect, we introduced a spatial stochastic hybrid model of a semi-arid ecosystem, in which plants are modeled as discrete entities subject to stochastic dynamical rules**, while the dynamics of surface and soil water are described by continuous variables [139].

Results

We show that demographic noise can have important effects on estimating the extinction and recovery dynamics of the ecosystem from models. In particular, **we find that including the individual dynamics and its stochasticity, vegetation escapes extinction under a wide range of conditions for which the corresponding deterministic model predicts desert as the stable system state** (See an example run in Fig. 18). This is an important observation, given that semi-arid ecosystems are characterized by a rather scarce number of plants, scattered across regions of empty land. Intuitively, the demographic stochasticity is expected to promote extinction when the number of plants is small. It is therefore remarkable that we observed a relevant regime of parameters in which including the stochastic individual nature of the plants actually increased the likelihood of vegetation pattern emergence, and of escaping the desert state.

Conclusion

This investigation indicated that, in certain regimes, including demographic noise, and thus the individual nature of plants, could lead to a better (and larger) estimate of the resilience of semi-arid ecosystems. The study of semi-arid ecosystems might therefore benefit from the use of individual based models.
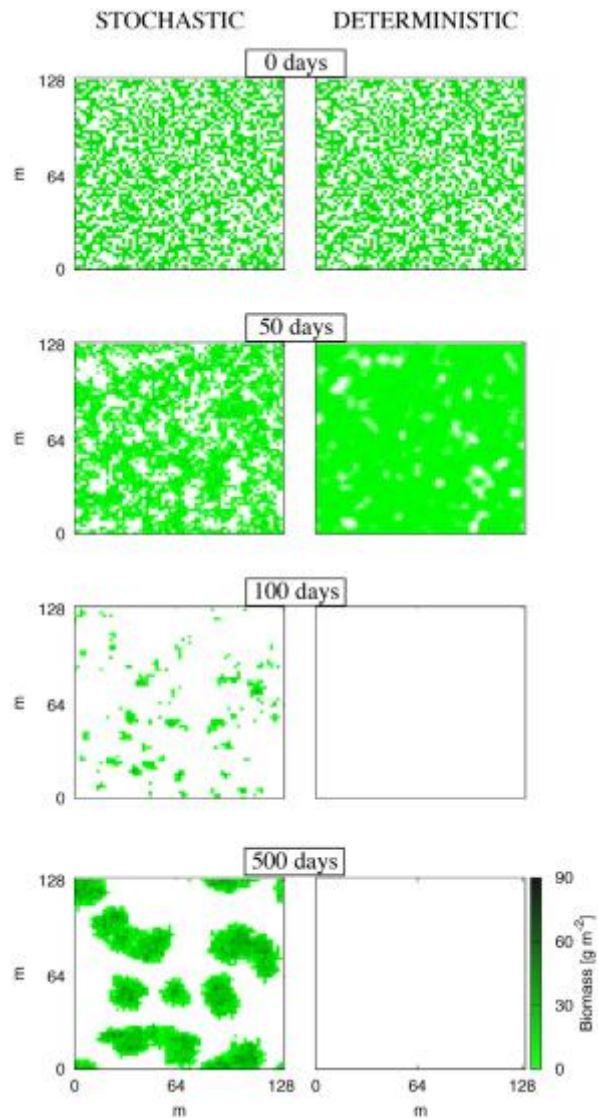
Figure 18: Comparison of the dynamics of the vegetation profile in the model including individual based dynamics (left) with that in the corresponding deterministic approximation (right); the axes correspond to the two spatial dimensions. While the deterministic approximation leads to extinction, in the full stochastic model the vegetation recovers, even though the only difference between the two simulations is the way the vegetation is modelled (i.e., either stochastically or deterministically). Both the stochastic model and its deterministic approximation were started with the same initial conditions. The deterministic approximation is fairly similar to e.g. [8,140]. See Realpe-Gomez et al. [139] for details of the simulations.

4. Conclusion

Within WP6, we developed a number of dryland vegetation models, starting from existing models and sequentially including additional ecological mechanisms thought to be relevant for drylands' ability to cope with increasing pressures. These mechanisms include:

i) modeling more realistic grazing pressures (§2.1; [25]),
ii) modeling the effect of fire on drylands (§2.2.1 and §2.2.2; [46,76]),
iii) taking the variability of the external pressure (rainfall) into account (§2.3.1, §2.3.2, §3.2.1; [95,96]),
iv) incorporating different types of feedbacks such as erosion feedbacks known to be important for dryland functioning (§2.2.2 for fire-vegetation feedback and §3.1 for vegetation pattern-resource loss feedback; [76,108]),
v) taking different plant functional groups into account as a first step into taking more species characteristics into account (§2.2.1, §2.2.2, §2.3.2, §3.2.1, §3.2.2, §3.2.3, §3.2.4; [46,76,96,128,130,136–138]).

Our results highlight the importance of the role of the spatial aspect of the external pressure (§2.1; [25]), demographic stochasticity (§3.2.5; [139]), rainfall intermittency and rate of environmental change (§2.2.1, §2.2.2, §3.2.4; [95,96,138]), the way species interact with each other (facilitation/competition) (§2.2.1, §2.2.2, §3.2.1, §3.2.2, §3.2.3, §3.2.4, §3.2.5; [46,76,96,128,130,138,139], and the relevance of different types of ecological feedbacks (§2.2.2, §3.1; [76,108]) for our understanding of the species composition and the dynamics of dryland ecosystems.

Mathematical modeling can be very insightful as experimental or observation studies are often not able to follow dryland ecosystem dynamics at relevant spatial and temporal scales along wide controlled gradients consisting of multiple stressors, or for extreme stress situations that are expected in the near future. In WP6, a number of key mechanisms currently lacking from available models were highlighted at the start of the project and incorporated in already existing models. Generally speaking, two 'lines' of models were developed within WP6, corresponding to two different types of mathematical formalism which each have advantages and disadvantages.

On the one hand, interaction particle systems were used for their relative mathematical simplicity and implementation [25,46,108,130,136–138]. They provide a very intuitive representation of space as a grid of cells, where each cell can be in a number of pre-defined states (e.g. occupied by a nurse, occupied by a protégée or empty). Within WP6, we developed a code to ease the use of such models (see §5.3).

On the other hand, differential equation models were used used for the possibility of representing explicitly ecological and physical mechanistic dynamics using continuous state variables [95,96,128,141], or for their (mathematical) tractability, which allowed for solving them analytically [76,128], and/or to include stochastic elements in the dynamics of the forcing stress (rain, [96]; or fires, [76].

Main results
All the models developed in CASCADE WP6 confirm the importance of positive feedbacks in driving the emergence of catastrophic responses at the ecosystem scale as a response to increasing stress. In §2.1, we showed that incorporating a realistic aspect of grazing, which is that grazers tend to eat more at the borders of vegetation patches in a patchy landscape, decreased dryland resilience

by increasing the size and the probability of catastrophic shifts under increasing stress (drought or grazing intensity). In §2.2.2, we found that incorporating a feedback between fire occurrence and vegetation composition promoted, in combination with drought, the emergence of alternative stable states and therefore of possible catastrophic transitions between those states. In §3.1, the connectivity-mediated feedback (i.e. the feedback between vegetation pattern, resource redistribution and productivity) decrease the amount of pressure required to cause a critical shift to a degraded state. Not including these feedbacks into dryland ecological models may lead to an overestimation of ecosystem resilience and therefore failures in the prediction of catastrophic shifts.

Furthermore, the model results suggest that the upcoming climate change predicted for Mediterranean drylands, and in particular the rainfall patterns, could induce and enhance the occurrence of catastrophic shifts in those ecosystems [95].

The models also highlight counterintuitive results. For example, in §2.3.1 [95], we found that, for a constant annual rainfall rate, both an increase and a decrease in mean rainfall intensity could trigger desertification. This finding was attributed to the fact that water can be lost from the system in two ways. During high intensity rain events, a fraction of the water flows through the vegetation bands and is lost as runoff, while during low intensity events a large portion of the water infiltrates in the bare interbands, where it is not available to plants and eventually lost due to soil evaporation and percolation.

The fire models suggest that the oak forests are very resilient and that in this case, catastrophic shifts may actually be less common than previously thought [46,76] (although alternative states emerge when a positive feedback between vegetation composition and fire occurrence is introduced in the model [76]).

Implications of the models for management

The model developed in WP6 contribute to the fundamental understanding of what determines the species composition of a given dryland and how that drivers the response of the ecosystem to increasing stress, in particular: why and how alternative stable states, and therefore catastrophic shifts, occur in drylands. This fundamental understanding provides some keys for 1) preventing dryland degradation and 2) restoring degraded ecosystems. Following the upcoming work of WP8 aiming at merging those ecological models with socio-economic models, those models could help suggest appropriate management measures.

The grazing model [25] suggests that vegetation patterns provide early warning signals of approaching desertification (i.e. the spatial structure itself). However, spatially heterogeneous grazing does not only altered ecosystem stability (by increasing the probability of catastrophic shift) but could also blur the early warning signals at high grazing pressure. This suggests that we need to be cautious regarding the use of early warning signals of ecosystem degradation when the pressure at play has a spatially-explicit component. It also suggests that additional indicators of degradation need to be developed taking into account the spatial component of the stressor.

Furthermore, model simulations suggest that using a bare-soil connectivity index (Flowlength [108]), in addition to vegetation cover and pattern, may provide more informative early-warning indicators of dryland degradation. Thus, the acceleration of bare-soil connectivity from spatially-explicit time-series data may provide an early warning of imminent shift.

Eventually, quantifying those indicators derived from model studies on field data may help identify field sites that are at the higher risk of irreversible degradation and prioritize those for conservation measures. More details regarding the indicators developed via the models will be exposed in the upcoming deliverable of WP: D6.2.

For a given ecosystem studied (e.g. Cascade field sites of Varzea (Portugal) in §2.2.1 and Ayora (Spain) in §2.2.2), the models developed allow reaching a better understanding of how different

interactions and drivers control the composition of dryland communities and their changes through time. Such a knowledge can be extremely useful in terms of management, e.g. to foster one given community over another (or to prevent being trapped in an undesired community). For example, the model results underline the importance of the practice of planting seedlings from late successional, resprouting species to increase the resistance and resilience to forest fires, which has been already proposed and put into practice by restoration ecologists from the CEAM Cascade unit [142] in the Cascade site of Ayora (see Deliverable 5.2). The modelling approach reinforces such practices as it underlines the importance and the resilience of late successional resprouter species on the time scale of a few generations of these plants, which is well beyond human observation.

Moreover, the essential role of facilitation for both species coexistence and ecosystem resilience highlighted by the models [25,130,138] suggests that it may provide a good opportunity for ecosystem restoration. In a degraded dryland, remaining adults individuals can be used as nurses to increase the recruitment probability of seedlings planted below or close to their canopies [143]. In degraded grazed drylands, the same strategy can be applied using preferentially nurse species adapted against grazing, to improve the early survival of the planted seedlings.

Outlook

The next step of this work could consist in investigating whether it would make sense to try to merge these two sets of approaches into a single framework, which would provide a single model including all the mechanisms investigated here in a single framework. The result of such an effort might very well be that the most adapted framework depends on the precise question asked, on the specific ecosystem studied and on the ecological mechanisms that are relevant for the ecosystem under study. In other words, merging the two approaches into a single one might bear the same types of drawbacks as the ones we are currently facing, which lead us to choose different mathematical formalisms for different questions.

To ease the transferability of the CASCADE WP6 work to other people, the codes underlying the models were made accessible online with some information. We present this in the next section (§5).

5. Communication of the results

5.1. Code and information sharing

To improve project documentation and quality standards for the work done in WP6, we proposed that all model development should use git as a version control system. We invited all model developers to join Github and opened a Github organisation account for WP6 that was meant to provide a hosting space for our projects. This facilitates internal pre-publication code review and portability of the projects to open source with the publication of articles.
Organization account for WP6 on Github: https://www.github.com/cascade-wp6

In particular, source code for simulation and analyses of the grazing model [25] is publicly available online at:
https://github.com/cascade-wp6/2015_schneider_kefi/

The code for the fire model for the CASCADE Portuguese site [46] is publicly available online at:
https://github.com/anavasques/ModelFirePT

We also gave workshop about Github to CASCADE members whose documentation is all online:
Presentation on git: https://fdschneider.github.io/git_intro/#/
Public repository of the git workshop : https://github.com/fdschneider/git_intro

5.2. Development of a visual, interactive version of the grazing model

For easier communication of cellular automata models, we implemented the spatially explicit models of grazing in dryland ecosystems in NetLogo. NetLogo is a user-friendly simulation environment which allows to transfer the model into an interactive 'game' that can be used to communicate the model's mechanisms and the emergent alternative stable states.
Link: https://github.com/cascade-wp6/netlogo_models

Netlogo can be used to communicate and explore the dynamics of the model, since the user can modify the parameter settings live and see directly how the model responds. Such interactive "games" allow to communicate the complexity of the dynamics in drylands under different sources of pressure (like drought, grazing, or fire) to stakeholders, to access their knowledge and to teach them about the nature of catastrophic shifts in drylands.

5.3. Development of a R package to run cellular automata models: caspr

As an end product of CASCADE WP6, Florian Schneider wrapped the R code that he developed for running cellular automata simulations of his grazing model into an R package. The package allows to run cellular automata with a spatially explicit pressure and apply spatial indicators (from 'spatial_warnings') on the temporal and spatial output.

Code available at: https://github.com/fdschneider/caspr

caspr allows to run cellular automata in R with a few lines of code. The speed is considerable fast, depending on the model implementation (C code can be used for better performance). The output can be a full timeseries, a timeseries of snapshots of the lattice, a gif-animation, an array of simulations along a parameter gradient, etc.

The package will contain functions to transfer the output of caspr into valid input objects for the spatial warnings package (see deliverable 6.2).

A direct installation from Github is possible via the devtools package

```
install.packages("devtools")
devtools::install_github("fdschneider/caspr")
library(caspr)
```

The package is capable of running a couple of different models, but most importantly the grazing model that was developed for CASCADE. It's parameters and specifications can be reviewed by typing `?grazing`.

To run a model simulation, an initial landscape object needs to be provided, i.e. a grid of cells that matches the specifications of the model.

```
l <- init_landscape(states = c("+","0", "-"), cover = c(0.7,0.15,0.15), width = 100)
par(mar = c(1,1,1,1))
plot(l)
```

Then, the simulation is started using the default parameters (returning a warning at the end of the simulation) by employing the function `ca()`:

```
run <- ca(l, model = grazing, t_max = 60, t_min = 60)
par(las = 1, bty = "n")
plot(run)
```

The `plot()` function plots the timeseries of the vegetation cover (cover of cell state "+") and the `summary()` function returns the mean cover of all potential cell states.

5.4. Socio-ecological models

In WP8 of CASCADE, different land use management practices are implemented and evaluated in a probabilistic manner over time. In contrast to the work described in this deliverable, WP8 is looking at transient dynamics rather than steady state situations, to answer the questions for the probability and quantitative improvement after application of management methods. A version of the livestock resilience model [25] for this kind of analysis is available at:

https://github.com/cascade-wp6/socialecological

The functions were wrapped into a small R package. It can be installed from Github from within R.
```
install.packages("devtools")
devtools::install_github("cascade-wp6/socialecological")
library("socialecological")
```

This makes all functions available in R. A package vignette with a full set of examples can be found here:
https://github.com/cascade-wp6/socialecological/raw/master/inst/doc/socialecological.pdf

Simulations by members of WP8 are currently ongoing, in collaboration with Florian Schneider and Sonia Kéfi.

Regarding the fire model of Vasques et al. [46], discussions were initiated with the members of WP8 in December 2015. The management options considered in Portugal are conservative and non-conservative logging and possibly mulching with pine needles. The effect of these management techniques under different fire severity scenarios and fire recurrence could be evaluated using the model developed with WP6 [46]. For the cost-benefit analysis of WP8 the most interesting variable is pine biomass as a proxy of timber production (although other variables such as pine cover and age could also be interesting). The current model output is focused on pine cover; pine biomass therefore has to be estimated from pine cover and age. Simulation scenarios were discussed regarding the resilience of pine stands to different management options. The version of the code allowing to simulate the version of the model currently available was shared with the members of WP8.

Appendix: List of products from WP6 D6.1

Models:

Reference	Pressure investigated	Mechanisms included	Link with CASCADE site (for model calibration/parameter estimation)
Verwijmeren et al., in prep [96]	Aridity, grazing	Species water functional traits, facilitation via associational protection, rainfall intermittency 2 species	Santomera Spain
Diaz-Sierra et al., in prep [128]	Aridity, grazing	Species water functional traits, facilitation (via infiltration or associational protection) 2 species	Santomera Spain
Baudena et al., in prep [76]	Fire, aridity	Species fire functional traits, fire feedback with species composition, hierarchical competition 6 functional groups	Ayora Spain
Vasques et al. in prep [46]	Fire	Species fire functional traits, litter 3 functional types	Varzea, Portugal
Benateau et al. in prep [138]	Abrupt climate change	Evolutionary dynamics/adaptation Possibly *n* species	(generic for Mediterranean drylands)
Danet [130]	Aridity, grazing	Associational protection 2 species	Randi forest, Cyprus, Snatomera, Spain
Schneider F. and S. Kéfi. 2016 [25]	Aridity, grazing	Associational protection (spatial component of grazing)	Randi forest, Cyprus Santomera, Spain
Siteur et al. 2014a [95]	Aridity	Rainfall intensity, infiltration facilitation	(generic for Mediterranean drylands)
Siteur et al. 2014b [141]	Aridity	Infiltration facilitation	(generic for Mediterranean drylands)
Mayor et al. 2013 [108]	Aridity	Ecohydrological feedbacks	(generic for Mediterranean drylands)
Realpe-Gomez et al. 2013 [139]	Aridity	Individual based plant model, infiltration facilitation	(generic for Mediterranean drylands)

Other (conceptual) papers:

Verwijmeren, M., **M. Rietkerk**, M.J. Wassen and C. Smit. 2013. Interspecific facilitation and critical transitions in arid ecosystems. Oikos 122: 341-347 [122].

Vasques, A., **Keizer, J.** 2014. Desenvolvimento de bases ecológicas para o uso de espécies vegetais em restauro ecológico após graves perturbações in: Planeamento e gestão dos recursos naturais. Homenagem Professora Doutora Celeste Coelho. António Ferreira, Fátima Alves e Jacob Keizer (eds.). Universidade de Aveiro, Portugal. ISBN 978 972 789 432

Kéfi, S., M. Holmgren, M. Scheffer. 2016. When can positive interactions cause alternative stable states in ecosystems? Functional Ecology. 30: 88-97. **[77]**

Maestre, F. T., D. J. Eldridge, S. Soliveres, **S. Kéfi**, M. Delgado-Baquerizo, M. A. Bowker, P. García-Palacios, J. Gaitán, A. Gallardo, R. Lázaro, M. Berdugo. 2016. Structure and Functioning of Dryland Ecosystems in a Changing World. Annual Review of Ecology, Evolution and Systematic. Vol. 47. In press. [4]

Student reports:

June 2014: Alain Danet, "Résistance à l'herbivorie et stabilité des milieux arides » (in French). BEE master, Montpellier. Supervision: Sonia Kéfi and Florian Schneider

February 2014: Marina Rillo, "Facilitation and the evolution of plant trait-syndromes in the Mediterranean basin". M2, MEME Eramus Mundus Master in Evolutionary Biology. Supervision: Sonia Kéfi and Florian Schneider

July 2013: Marina Rillo, "The emergence and coexistence of trait syndromes in Mediterranean vegetation". MEME Eramus Mundus Master in Evolutionary Biology. Supervision: Sonia Kéfi and Florian Schneider

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