University of Montpellier

THESIS PROPOSAL

Stress Gradient Hypothesis: insights from a functional and manipulative approach at the community level

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Introduction

General context

In the context of global change, the ecosystems are susceptible to be modified by the pressure change. Ecosystems can response in different ways to a pressure change. Some of them respond gradually to a increase of pressure, others respond in a abrupt way and finally some of them respond by a catastrophic shift. In the arid ecosystem, which covers 40% of the world land surface, are susceptible to respond by a catastrophic shift (Kéfi et al., 2007). Several hypothesis have been suggested and previous works shows that the interactions between plants play a key role in the catastrophic shifts (Rietkerk et al., 2004; Kéfi et al., 2007). In particular, the positive interactions between plants seem to be responsible for positive feedback between water and vegetation which cause the catastrophic shifts (Walker et al., 1981). By improving local conditions , the adult plants allow the recruitment of new individuals under their canopy. The question of how the interactions between plants would be affected by the climate change is thus crucial. Furthermore, the inclusion of the positive interactions in the ecological framework is fundamental (Bruno et al., 2003).

Positive interactions

Positive interactions between plants have been studied a lot since the very influential paper of (Bertness and Callaway, 1994), followed-up by (Bruno et al., 2003). In particular, Bertness and Callaway (1994) proposed the Stress Gradient Hypothesis (called hereafter SGH), which postulates that species interactions shift from competition to facilitation when the environment becomes harsher. Facilitation, or positive interaction, was originally defined as a situation where one organism benefits from another without causing harm to neither (Bruno et al., 2003). However, this definition has changed slowly since Schöb et al. (2014) who showed that there can be a cost of facilitation for the benefactor. By modifying the local environment, a plant benefactor can improve the establishment of individuals under its canopy by, for example, decreasing wind, buffering extreme temperatures and increasing water infiltration (Rietkerk et al., 1997).

Traditionally, studies have examined plant interaction outcome by comparing the performance of a facilitated species (often a sapling) in a open site and under a nurse (usually an adult) along a stress gradient, natural (e.g. altitude, grazers density) or manipulated (e.g. roofs or irrigation for water stress, controlled number of grazer and grazing duration for disturbance). We use sapling beacause early stages survival are considered the most critical stage of the plant. Using this approach, one concludes that positive interactions are dominant if the performance of the sapling is higher under a nurse than alone. Results showed that net interactions between pairs of plants become often positive for survival of saplings when the environment is harsh, but not for growth and reproduction (He et al., 2013). Those studies were successful in highlighting that positive interactions between pairs of species may be more common than previously thought. However, until now, no manipulative experimental study, as far as we know, has investigated facilitation at the community level.

Community level

Recently, observational studies at the community level have become more important in the literature (Soliveres et al., 2012; Gross et al., 2013; Soliveres et al., 2014; Cavieres et al., 2014). Soliveres and Maestre (2014) argue that we "*need more community-level studies and approaches assessing interactions among multiple species to understand better the consequences of facilitative interactions for the structure of whole communities*". While I agree with this statement, I think that we might miss an important step if we move directly from experiments investigating pairs of species to observations of species co-occurrences. By studying pairs experimentally, we can access the mechanisms underlying the interaction outcome. To access the mechanisms at community level, I propose to experimentally manipulate communities of saplings under a water and grazing treatment. One can imagine that when a seed pool arrives in a site, some will germinate (of several species) and several saplings of different species will experiment competition with each other. Only few of these saplings will become an adult. Previous experiments have only considered the case where one seed germinates under a patch (pair experiments). Here, we want to be more realistic by investigating competition between several saplings until their establishment. So, the first objective of this study is to add a step between pair experiments and observational studies by working at the community level. As discussed in the previous section, in the dry environments, the saplings often etablished under a patch. While we know a lot about interactions between one sapling species and an adult, it is not yet know how a community of saplings can react.

Functional approach

SGH investigations have produced contrasting results (Maestre et al., 2009). Several studies used Grime's functional types to explain post-hoc general patterns of interaction outcome (Maestre et al., 2009; Butterfield and Callaway, 2013; Michalet, 2006). This is a simple and practical way to consider plant strategies. By classifying species as competitive, stress tolerant or ruderal (CSR), we can better understand succession processes (**?**) and vegetation turnover under stress and disturbance. "Competitive" plants (C) are able to dominate when stress and disturbance are low, "stress tolerant" (S) when stress is high and disturbance is low and "ruderal" ones (R) when stress is low and disturbance high.Functional ecology focuses on connecting plant traits to plant functions. For example, the Specific Leaf Area (SLA) is related to plant resource management (**?**), a low SLA indicating an individual which quickly acquires resource and vice et versa. Plant height is related to competitive ability for light. So S-plants are characterised by a high SLA and a low growth-rate. On the contrary, C-plants and R-plants are characterised by a low SLA and a high growth rate. R-plants are distinguished by the fact they invest more in seeds while C-plants invest more in height growth. Although this classification was originaly designed on the herbaceous plants of Great Britain (**?**), Frenette-Dussault et al. (2012) succesufully described those syndromes in the arid ecosystems of Morocco.

It has been argued in the literature that the interaction outcome along a stress gradient will differ depending on the species that compose the sapling/adult pair (e.g. C-plant/C-plant, C-plant/S-plant or S-plant/S-plant) (Maestre et al., 2009) based on analysis of previous results.

However no study, as far we know, has explicitly taken in account the species traits to explain species response in an experimental design. As Butterfield and Callaway (2013) suggested, taking a functional approach of facilitation will allow us to better understand the context-dependence of facilitation. The second objective of this studies is to disentangle individual species responses by focusing on their traits and relating them to the community response.

Phenology

Plant phenology describes the timing of periodic events in the life cycle (growing period, flowering, fructification) but is rarely brought forward in ecology. However, phenology could be affected by climate change (**?**) because it varies depending numerous factors, mainly seasonal temperature and precipitation variations. By modifying the local environment, facilitation could therefore affect the phenology. Moreover, by modifying the phenology differently in open and in patch areas, facilitation could result in a genetic differentiation between open and patch sub-populations. As far we know, only the study of **?** examined the impact of facilitation on phenology. They found that facilitation affects the flowering timing at the start and at the end of the season but they did not find genetic differentiation. Here, we want to test the effect of facilitation on phenology along a stress gradient. Are different species impacted in the same way ?

We also know that variations in the flowering timing is an important way to promote coexistence by limiting competition on shared-pollinators (**?**). Here we want to ask how facilitation modulates phenology inside a community. If facilitation promotes a phenology homogenization, it could paradoxically increase competition.

In sum, this project aims at addressing the following research questions:

- Can we predict the species responses to facilitation based on its functional group?
- How do the species response to facilitation can be affected by the interspecific competition ?
- Can we infer the interaction strength from co-occurrence observations ?

Methods

Site

The experiment will take place near Alicante (South-East of Spain). Climate is semi-arid[...climate, soil, vegetation stuff]

Benefaciary species

Plant species were chosen based on Spanish literature reviews (McCluney et al., 2012; Navarro et al., 2006; Jauffret and Lavorel, 2003). According to those studies, we identified species which could be considered as competitive or stress-tolerator. For the pilot, we will use *Pistacia lentiscus* (competitive), *Atriplex glauca* (ruderal) and *Anthyllis citoides* (stress tolerant). We are going to use *Artemisia herba-alba* adults as patch plants. For the real experiment, we will replace *A.glauca* by *(Monicambia?)*. Saplings were grown in controlled conditions in a nursery (Viveros Muzalé S.L.) located in Abanilla (South-East of Spain, Province of Murcia).

Design

We set up a block randomized design. It consists in 4 crossed variables repeated in 4 terraces. The microsite variable allows us to estimate the relative importance of the interactions between the beneciary and the benefactor. It has 2 modalities: "open" or "patch" (i.e. below an adult *A.herba-alba*). We will use same *A.herba-alba* microsites than in a previous experiment in which microsites were randomly chosen (Verwijmeren, in prep). Open sites are placed at 1 meter from their associated *A.herba-alba* sites. The water stress variable has 2 treatments: "control" and "watering". The grazing variable has also 2 treatments: "control" and "grazing". The community variable has 4 treatments: species 1, species 2, species 3 or mixture of the 3 species. All those treatments are crossed in each terrace (Schematic representation Figure 1). We are going to plant 3 saplings of the same species in the monoculture treatment and 1 sapling of each species in the mixture one (i.e. 3 saplings in each case).

Planting will be done in March 2015. We are going to dig holes of 25*25*25 cm to plant the saplings which will be watered. The 3 saplings will be put in the same hole to insure that they will be in interaction and so, constitute a community. Furthermore, we will place the saplings in triangular way. Thus, the 3 saplings will be at the same distance from each other. For the patch sites, the holes were oriented to the north. In this way, saplings will receive most shading from *A.herba-alba*.

To summarize, there will be:

- 2 microsites [open/patch] * 2 disturbance level [grazing/no] * 2 water stress level [watered/no] * 4 types of community [3 mono/mixture] = 32 treatments

- 32 treatments * 4 terraces * 8 replicates per terrace = 1024 microsites
- 1024 microsites * 3 saplings per microsites = 3072 saplings

Notes to discuss:

- Number of saplings seems too large.
- Why not focus on one stress ? Discuss possible collaboration with Susana student.
- How to simulate grazing if we keep the grazing gradient ?

Measurements

Exploratory variables

Measurement
Survival
Biomass
Phenology
Reproductive output

Explicative variables (environment)

Measurement	Device	Biological relevance
Temperature	Temperature coin battery	Variation nurse/open
LAI	Plant Canopy Analyser	Light transmittance
LDMC	Furnace	CSR placement - Growth rate
Soil moisture	TDR/FD/Neutron probe	Variation nurse/open
Water potential	Pressure chamber	Stress of the plant

Table 1: LAI: Leaf area Index, LDMC: Leaf Dry Matter Content. We have to note that LAI is correlated to soil moisture and temperature, so we may not have to measure those 3 variables.

Analysis

Analysis will be performed using (**?**).

Interaction indices

[...] Detail available indices (Seifan et al., 2010).

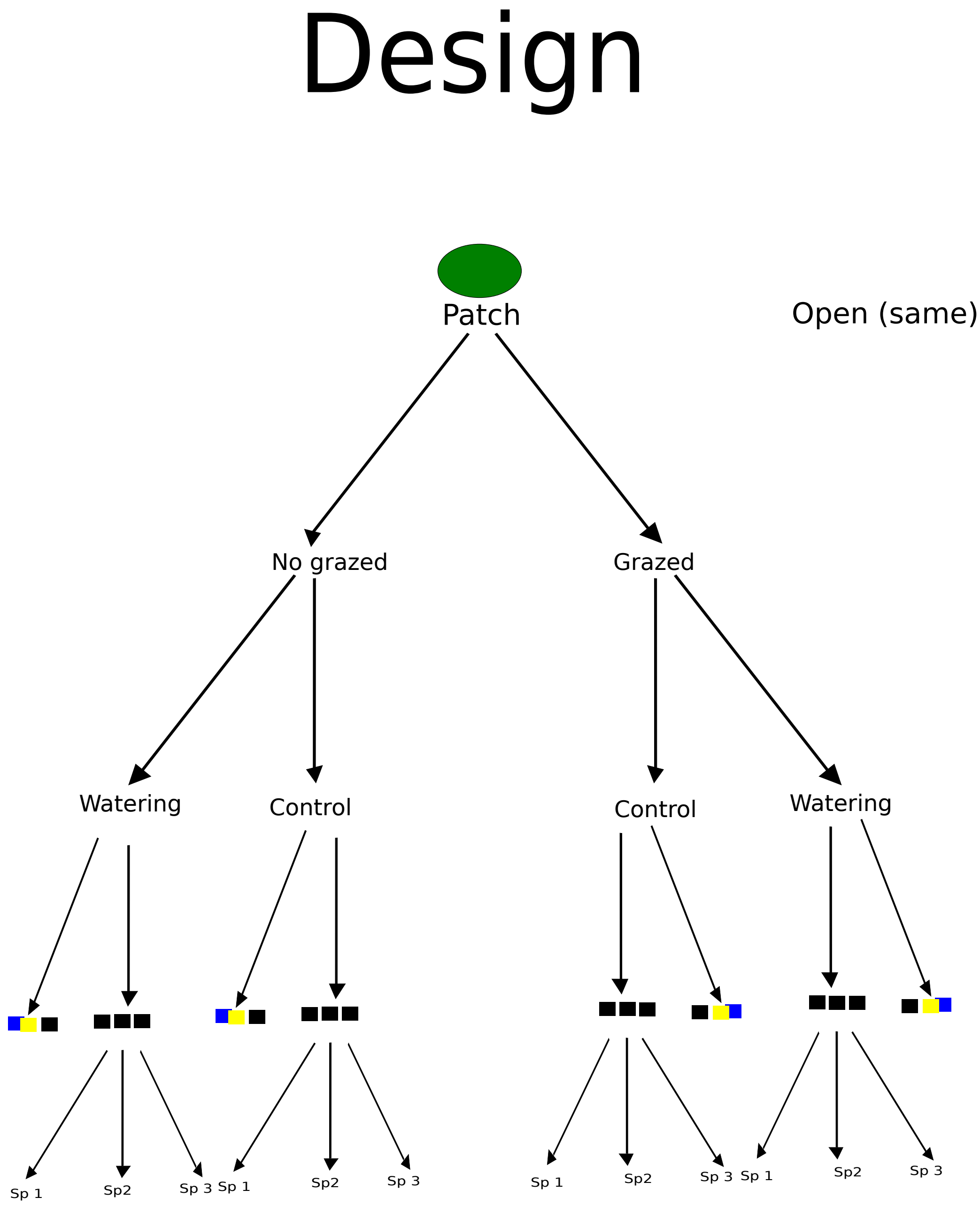

Figure 1: Experimental design.

Indice	Signification
I	Interaction indices
C	Community treatment
W	Water stress treatment
G	Grazing treatment
SM	Soil moisture
DSM	Soil moisture difference between open and patch
T	Temperature
DT	Temperature difference between open and patch
Sp	Species

Table 2: •

Species responses to stress: determinate the place of the species in the CSR diagram

We will analyse the species response in the monoculture/open combination of treatments. Compare to control, the C-plants should answer (in term of growth) the most to the watering treatment and S-plants the least. R-plants should be the least impacted by the grazing treatment and the C-plants should be the most impacted. The response of the R-plants should be the most important in the combination of watering and grazing treatment and the S-plant should response the least. All those predictions can be resumed in figure 2A.

Do facilitation modulate those responses ?

As mentioned in the literature, we can make the hypothesis that the species, representing each one functional type, will show different responses following to which distance to their ecological optimum the stress or/and disturbance led them. As we show in the figure 2B, the C-plants would be the most facilitated species since they will be the farthest of their ecological optimum and the S-plants would be the less facilitated species because on the contrary, because the control will represent the treatment the nearest of ecological optimum of S-plants. In the watered treatment, the R- and C-plants would be negatively affected by the presence of *A.herba-alba* of shading. Still in the watered treatment, the outcome of interaction could be null between the S-plants and *A.herba-alba* because they would be have enough resources for both of them and in the same time, adaptations to stress are often correlated to shade-tolerance (**?**). In the grazing treatment, the C-plants could be the most facilitated by *A.herba-alba* since they will profit of micro-habitat amelioration and protection from grazing. The S-plants would be less facilitated since they will only profit from grazing protection (see the prediction for the previous treatment). The outcome of interaction between the R-plants and *A.herba-alba* is excepted to null because they will profit of micro-habitat amelioration but will be affected by shading for growth whereas in open site, they would be affected by water restriction but they can grow after grazing event. In the combined treatment of watering and grazing, the R-plants could experiment competition in the presence of *A.herba-alba* because they will be near of their ecological optimum. On the contrary, the S- and C-plants could experiment facilitation because they will be protected from grazing.

Diversity effect on interaction along water stress

Test if interaction outcome along stress gradient is different between monocultures and mixtures.

$$I = C + W + C : W + Environment + random(Replicates, Terraces)$$

Plant strategy effect on interactions

Monoculture Test interaction modulation between species in monocultures across stress gradient. Can differences be explained by functional traits ?

$$I = Sp + W + Sp : W + Environment + random(Replicates, Terraces)$$

Mixture Same as previous. Test interaction modulation between species in mixture across stress gradient. Can differences be explained by functional traits ?

$$I = Sp + W + Sp : W + Environment + random(Replicates, Terraces)$$

Phenology

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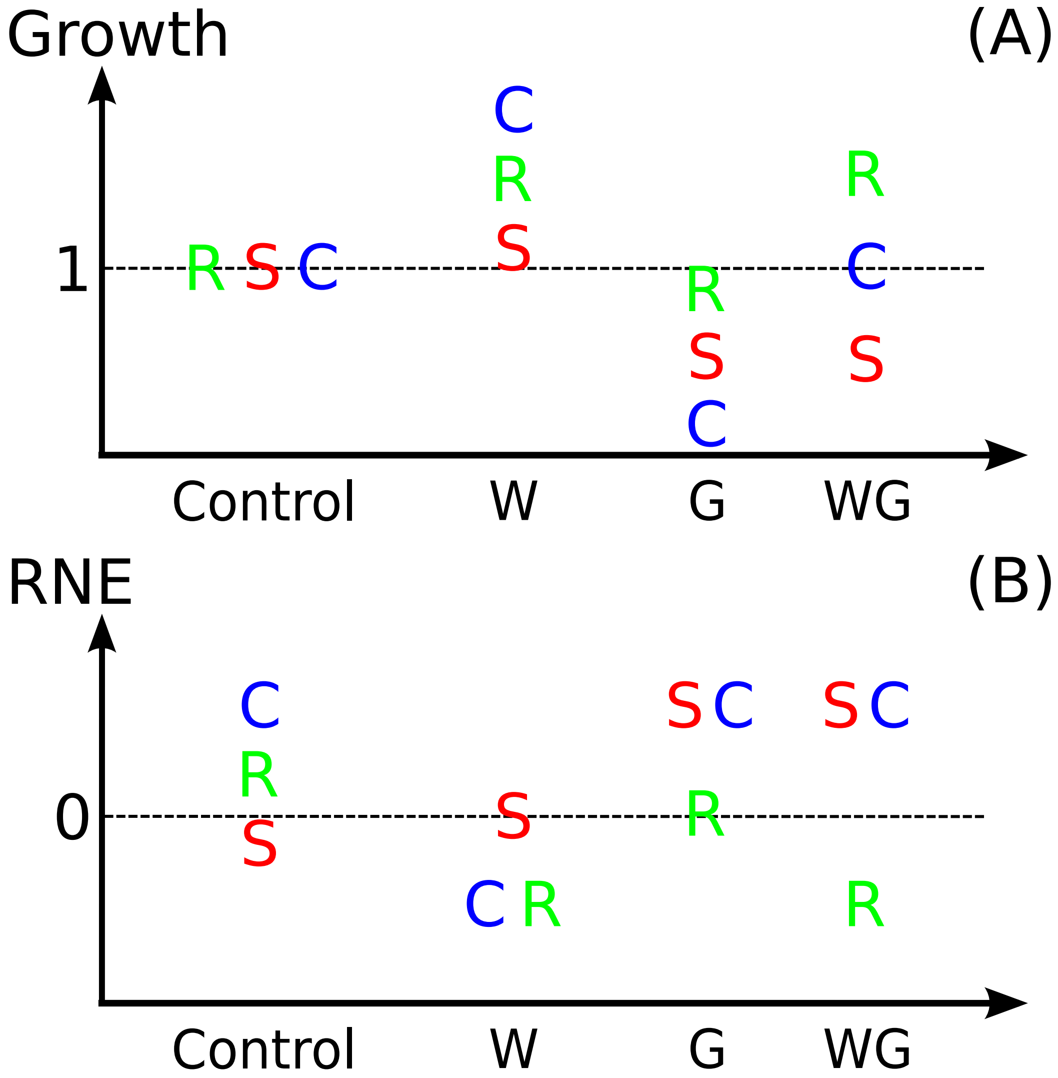

Figure 2: Predication about species behaviour in the monoculture treatment. W:watered, G:grazed, WG:watered and grazed. R:ruderal, S: stress tolerant, C: Competitor. (A): Relative mean growth of species in the monoculture treatment. (B) Relative Neibourgh Effect (RNE) of *A.herba-alba* on saplings in the monoculture treatment. The values which are superior to 0 mean that the most important interaction is the facilitation. On the contrary, the values below 0 indicates that the most important interaction is the competition.

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Annexes