

European Science Foundation
Standing Committee for Life, Earth and Environmental Sciences (LESC)

ESF LESC EXPLORATORY WORKSHOP

**Positive interactions, biodiversity
and invasibility in a changing world**

Scientific Report



Arcachon, France, 3 - 7 September 2006

Convened by:
Richard Michalet and Blaise Touzard



- Background Information

Workshop Summary:

The implications of facilitation for biodiversity and invasibility have to be explored. Facilitation appears particularly important in stressful environments (e.g. tundra and deserts), areas identified as sensitive to anthropogenic changes. Understanding the mechanisms that regulate biodiversity is vital for biodiversity management. We propose a workshop to utilize global expertise to explore the role of facilitation in regulating biodiversity and invasibility, integrating facilitation into mainstream theory, and developing novel field experiments.

Workshop Structure and Key Targets:

The workshop will be structured in order to encompass the following key aims:

1. Review the current state of facilitation research
2. Consider the implications of facilitation for existing ecological theory, with particular emphasis on the diversity and invasibility of ecosystems and environmental change
3. Develop a theoretical framework that will more closely incorporate facilitation into ecological theory and provide a predictive capacity with respect to biodiversity change in threatened ecosystems.
4. Design targeted experiments to specifically address novel predictions arising from the new theoretical framework.
5. Generate collaborative funding initiatives and proposals for respective participants that will fund global research encompassing biogeographical and large scale syntheses.

Innovative Character of the Project:

Although five ESF Exploratory Workshops have investigated drivers of biodiversity, only one of them has explored the relationship between biotic interactions and diversity, specifically for arthropods in tropical rain forests. Relationships between plant biodiversity and biotic interactions, in particular positive interactions, have never been addressed despite the potential important ramifications of positive interactions for ecological theory and biodiversity conservation. In fact biotic interactions have rarely been addressed, except for a particular focus on parasitism and mutualism. Furthermore, no workshop to date has incorporated consideration of diversity, invasibility, and biotic interactions within the same framework, despite the obvious clear links between these important subjects. The coverage of our proposed workshop clearly makes it an innovative, not only in the topics being addressed but also in their synthesis into an overarching ecological framework. These goals are tractable given the expertise and scope of the participants listed.



1 - Executive Summary

28 participants from 7 European and 3 North and South American countries + 2 Tunisian people + 1 Israeli people met from Monday 3th September to Thursday 6th September (15h30), at the Arcachon Marine Biological Station of the University Bordeaux 1 (France) to discuss central achievements and future perspectives of research on the role of facilitation for biodiversity and invasibility in a changing world. From the fifties onwards the individualistic nature of communities has been held as a fundamental ecological tenet by many plant ecologists; competition has been considered as *the* significant biotic filter structuring plant communities at local scale. Negative interactions are thus prominent in a number of key ecological theories, in particular those concerned with community richness and invasibility such as the hump-backed diversity model of Grime and the diversity-invasibility hypothesis of Elton. However, despite the historical dominance of competition, in the last fifteen years there has been considerable renewed academic interest in facilitation. Following an initial hypothesis that the role of positive interactions increases in stressful or highly disturbed communities numerous experimental studies have demonstrated that positive interactions indeed play a fundamental role in plant communities, especially in severe environments. However, the focus of plant community ecologists on the role of facilitation for biodiversity and invasibility is recent. Because positive interactions may affect community richness through an enlargement of species' realized niches, Michalet et al. (2006) proposed in a recent paper published in *Ecology Letters* a new interpretation of the humped-back model of Grime (1973), including facilitation. In this revised model, facilitation promotes diversity at medium to high environmental severity, by expanding the realized niche of stress-intolerant competitive species into harsh physical conditions. The decrease in species richness towards the severe end of the gradient is proposed to be driven by a collapse of facilitation due to increasing environmental severity. Biotic interactions are thus proposed to shape both sides of the humped-back model of Grime. They suggested that the collapse of facilitation probably occurs because nurse plants become less successful at ameliorating abiotic conditions and promoting the survival of beneficiary species in the most severe environments.

This theoretical model was based on the results of few experiments and the main aim of the workshop was to gather specialists who conducted facilitation or competition studies in various environments in order to analyse the relevance of the model in a set of constrained conditions and propose future experimental tests of the model. Furthermore, researches on facilitation had progressed very rapidly in 2006 and there is a hot debate about the place of facilitation in water-stressed environments. Recent meta-analyses have questioned the relevance of the single theoretical model of the literature for semi-arid and arid environments. We decided to enlarge the session scheduled on this topic by inviting young researchers who have recently produced significant results on the place of competition in arid environments.

During this workshop these topics were strongly discussed. The participants provided first their experience on these researches including reviews of the literature. Two field excursions were also organized to present the results of the Bordeaux team in coastal sand



dunes and salt marshes. Then we discussed in working groups on a collective paper and on grant applications.

2 - Scientific Content

From Monday 3th to Wednesday 5th September (15h30), after an introductory talk of Richard Michalet on the model to be discussed, four plenary sessions were organized to assess the knowledge on the role of facilitation for biodiversity and invasibility in a set of constrained environments. These plenary sessions included 3 to 8 talks and were followed or interrupted by 30 minutes-long discussions.

Session 1: Facilitation, biodiversity and invasibility in coastal sand dunes.

Session 2: Biotic interactions in water-stressed environments: implications for biodiversity.

Session 3: Modelling and evolution.

Session 4: Facilitation, biodiversity and invasibility in alpine ecosystems.

Concerning the first session the discussion emphasized the importance of the abiotic environment in this physically very severe system and in particular the role of disturbance due to sand deposition. The first speaker of the session proposed that disturbance due to sand deposition was the primary factor explaining the collapse of interactions and the decrease in biodiversity in coastal dunes from South-West France which appeared as a nice refinement of the proposed theoretical model. During the field excursion of Monday afternoon, the model system was presented and intense discussions aroused on the way to calculate community productivity in these very disturbed environments.

The second session was the longest with 8 talks. After a review of the results of the literature in water-stressed environments proposed by Richard Michalet, there were presentations on diverse arid or semi-arid systems (South-East Spain, the Sahara in Niger, the Negev desert in Israel, the Central Massif in France). Discussions were very active, in particular because the stress-gradient hypothesis which postulates that facilitation should increase with increasing stress was recently questioned by some scientists who were in Arcachon. The importance of the species and of the method used to quantify the interactions was in particular stressed by some participants. It was proposed to include all these topics in a review paper to be prepared at the end of the Arcachon meeting. It was also suggested that more precise ecophysiological and environmental measurements are needed if we want to improve our knowledge of the direct mechanisms of interactions in water-stressed conditions. The talk on the dead end of the gradient emphasized the need to distinguish direct positive and negative interactions to understand the net outcome of interactions. The afternoon of the second day began with a talk on invasive molluscs in the Arcachon Laguna and was followed by a boat excursion in the Laguna and the salt marshes. The field excursion in the salt marshes induced also nice discussions on the role of disturbance for interactions and biodiversity in this system which appeared as very similar to the dunes because disturbance and stress vary in a converse way along natural complex gradients.



The third session on modelling and evolution revealed our need to increase our research effort in those quite new directions in relationships with genetists. The last session focused on alpine, arctic environments in the global change context. This session was introduced by a review of Robin Brooker who recently published a Tansley review on this topic in *New Phytologist*. Experimental studies were presented from the Andes, the Caucasus the Alps and the arctic. Studies from the Chilean Andes stressed the particular adequacy of this system to analyse the role of facilitation for biodiversity and invasibility in a changing world. Finally Ragan M. Callaway synthesized most outstanding results of the talks in a conclusive talk on the future of facilitation studies.

From Wednesday 5th September (15h30) to Thursday 6th September we worked in small groups on two items:

1. A collective review paper.
2. Grant applications.

Discussions were very efficient and their results are summarized in the outcome of the meeting.

3 – Assessment of the results, contribution to the future direction of the field, outcome

1. Collective review paper:

The outline of the paper was prepared during the end of the workshop and we worked by E-mail from this date until now. The paper is almost finished and we have already the allowance of *Journal of Ecology* to submit it in their ideas and perspectives theme. This paper will be signed by all the participants to our workshop. Here are the aims and plan of the paper:

Facilitation in plant communities: the past, the present and the future

Aims of the paper

Plants interact in a vast range of different ways, both negative and positive. For example plants compete for light, nutrients, space, pollinators, and water, but at the same time may protect one another from the impacts of herbivores, potential competitors, or extremes of climate. There has been a recent resurgence in interest in positive, non-trophic interactions between plants. Substantial new research has addressed this field, exploring in detail the mechanisms and processes by which such interactions take place, the way in which they control the structure and function of communities, and the implications of positive interactions for classic ecological theory. Facilitation research is now starting to make links to some of the most important current ecological issues, for example climate and land use change. It is therefore perhaps a suitable time for reviewing the progress that research in this field has made and the current state-of-play. Has this substantial recent research effort taken



this field forward? Do we know enough about facilitative interactions to actually understand their role in mediating the impact of environmental change drivers? Given our current understanding, what gaps in our knowledge of facilitative interactions most urgently need to be addressed?

The aims of this paper are to attempt to address some of these questions. Firstly we discuss the historical context to recent developments in facilitation research – the historical context is important in understanding why some topics have been of particular interest to researchers working on plant facilitation. Secondly we review some of the recent studies that explore these key topics. Finally we suggest areas of the field of positive plant interactions where we consider that there are great opportunities for future research developments, and suggest some approaches that might be used to take this work forward.

The potential future research topics that we will consider are:

Facilitation, biodiversity and ecological processes

1. Facilitation and ecosystem restoration
2. Connecting facilitation to evolution
3. Facilitation and global change (including invasive)
4. Facilitation and biodiversity

Improving our understanding of facilitation processes

1. Indirect interactions
2. The importance of facilitation relative to other “filters” of community composition
3. Facilitation along gradients
4. Facilitation and modelling

2. Grant application:

We have prepared during the ESF workshop the draft of a proposal to be submitted either to EUROCORES or to the 7th European Framework in preparation. However, it seems that the 7 Eurocores calls recently published do not seem to be relevant for our proposal and we will have certainly to focus on the 7th European framework. Here is the draft of this proposal:

The role of facilitation for the invasibility of cold and arid ecosystems under a global change scenario.

Two main questions will be addressed in this proposal:

1. Does facilitation influence the recruitment of invasive species in cold and arid environments?
 2. Will facilitation vary in a converse way in both systems under global change and how this will affect the recruitment of invasive species?
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Following Petit et al. (2004) the term invasion refers in our project to all types of range expansion (including native species), because we focus on the first part of the invasion process, the recruitment of new species in a recipient community. Processes driving the recruitment of a species beyond its resident community in new environmental conditions are not expected to differ strongly for real exotics and native species. We propose to address these questions in two types of experiments, depending on the amount of money we can ask:

1. along natural gradients of increasing temperature or drought, to simulate global change effects in alpine-arctic or semiarid-arid ecosystems
2. along experimental gradients of increasing temperature (and decreasing wind) in alpine-arctic systems or drought in semiarid-arid systems.

Within both designs we will transplant both exotics and native species outside their native environmental conditions, either with or without local nurses from the recipient communities to address these two questions.

List of the partners and sites (two last lines concern non EU-partner which may design experiments with their own money, depending on the call):

PIs	Lab	Country	Sites	Gradients	Functional groups	Climate
Acosta	Univ. Roma	Italy	Coastal dunes	Latitude (water)	Graminoids Shrubs	Mediterranean
Anthelme	IRD Montpellier	France	Andean paramos	Elevation (temp., water)	Cushions Tussocks	Tropic Alpine
Brooker	MI Aberdeen	UK	Scotland Abisko	Elevation (temp.)	Dwarf shrubs Graminoids	Arctic
Coll	CTFC Barcelona	Spain	Pyrenees	Elevation (temp.)	Trees Shrubs	Temperate
Kunstler	CEMAGREF Grenoble	France	Alps	Elevation (temp.)	Trees Shrubs	Temperate
Maestre	Univ. Rey Juan Carlos	Spain	Steppes	Latitude (temp., water)	Tussocks Graminoids	Mediterranean
Michalet	Univ. Bordeaux 1	France	Pyrenees	Elevation (temp, water)	Graminoids	Temperate
Olofsson	Univ. Umea	Sweden	Scotland Abisko	Elevation (temp.)	Dwarf shrubs Graminoids	Arctic
Pugnaire Kikvidze	CSIC Almeria	Spain	South Spain	Elevation (temp., water)	Shrubs Tussocks	Mediterranean
Tielbörger	Univ. Tuebingen	Germany	Alps or Negev (Israël)	Elevation Latitude (water)	Graminoidss Annuals	Temperate Mediterranean
Callaway	Univ. Montana	USA	West USA	Rainshadow (water)	Graminoids	Semi-arid
Cavieres	Univ.	Chile	Central	Elevation	Cushion	Mediterranean



4 - Final Programme

Sunday 3 September 2006

Afternoon/Evening *Arrival*

Monday 4 September 2006

- 09:00-09:05 **Chardy**
Welcome talk of the head of the station
- 09:05-09h20 **Ceulemans**
Presentation of the European Science Foundation (ESF)
(Standing Committee for Life, Earth and Environmental Sciences)
- 09:20-09:45 **Michalet**
- **Introduction to the workshop**
- The role of facilitation for biodiversity and invasibility.
- 09:45-10:15 **Discussion**
Open discussion on the model to be tested
- 10:15-10:30 *Break*
- SESSION 1**
FACILITATION, BIODIVERSITY AND INVASIBILITY IN
COSTAL SAND DUNES
- 10:30-11:00 **Forey & Touzard**
Facilitation, biodiversity and invasibility in French coastal sand dunes
- 11:00-11:30 **Acosta & Izzi**
Biodiversity and invasibility in Italian coastal sand dunes
- 11:30-12:00 **Lortie**
Facilitation, biodiversity and invasibility in Californian coastal sand dunes
- 12:00-12:30 **Discussion**
- The relevance of the model in coastal sand dunes.
- Experimental approaches to be used to test the models in coastal sand dunes.
- 12:30-14:00 *Lunch*
- 14:00-19:00 **Field trip:**
Aquitaine coastal sand dunes.

Dinner
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Tuesday 5 September 2006

SESSION 2 BIOTIC INTERACTIONS IN WATER-STRESSED ENVIRONMENTS: IMPLICATIONS FOR BIODIVERSITY

- 08:30-09:00 **Michalet**
Introductory talk: Is facilitation in arid environments the result of direct or complex interactions?
- 09:00-09:30 **Maestre**
Competition-facilitation mediated through changes in water availability in semi-arid environments
- 09:30-10:00 **Coll**
Morphological and Physiological responses of tree seedlings to belowground competition
- 10:00-10:30 **Kunstler**
Indirect facilitation and competition in tree species colonization of sub-Mediterranean grasslands.
- 10:30-10:45 *Break*
- 10:45-11:15 **Seifan & Tielbörger**
Facilitation and biodiversity in arid and semi-arid Israeli ecosystems.
- 11:15-11:45 **Armas & Pugnaire**
Facilitation and biodiversity in arid Spanish ecosystem.
- 11:45-12:15 **Anthelme**
Respective influences of aridity and grazing on positive interactions (between *Acacia raddiana* and *Panicum turgidum*) in a saharian environment
- 12:15-12:45 **Discussion**
The relevance of the theoretical model in arid ecosystems
- 12:45-14:00 *Lunch*
- 14:00-14:30 **De Montaudouin**
Biotic interactions and invasion ecology in benthic ecosystems, a study case: the slipper limpet (*Crepidula fornicata*).
- 14:30-19:00 **Field trip:**
Salt marshes and benthic communities of the Arcachon Bay
Dinner

Wednesday 6 September 2006

SESSION 3 MODELING AND EVOLUTION

- 08:30-09:00 **Travis**
Null models and biodiversity-invasibility in community ecology
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- 09:00-09:30 **Schiffers**
Modeling the spatial component of plant interactions
- 09:30-10:00 **Liancourt**
Facilitation in ecological speciation: Disruptive or cohesive Force?
- 10:00-10:30 **Discussion**
Open discussion on modeling changes in biodiversity and invasibility
- 10:30-10:45 *Break*

**SESSION 4
FACILITATION, BIODIVERSITY AND INVASIBILITY IN
ALPINE ECOSYSTEMS**

- 10:45-11:15 **Brooker**
Plant interactions and conservation in a changing world
- 11:15-11:45 **Cavieres**
Nurse species in the Andes and their role in plant species diversity and invasibility
- 11:45-12:15 **Kikvidze**
Studies in the Caucasus
- 12:15-12:45 **Olofsson**
Effects of positive and negative plant-plant interactions for the invasibility and biodiversity of Swedish tundra ecosystems.
- 12:45-14:00 *Lunch*
- 14:00-14:30 **Callaway**
Future directions for community ecology in alpine environments
- 14:30-15:30 **Discussion**
The relevance of the model in Alpine and Arctic ecosystems
- 15:30-18:30 **Workgroups**
Experimental design and grant applications
- Dinner*

Thursday 7 September 2006

- 08:30-10:30 **Workgroups**
Experimental design and grant applications
- 10:30-10:45 *Break*
- 10:45-13:00 **Michalet**
Synthesis of ideas and discussion for preparing an application for funding under future European Calls
- 13:00-14:00 *Lunch* End of the meeting
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5 - Final list of participants

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6 – Statistical information on participants

Origin of participants:

France (8)

Germany (3)

United Kingdom (2)

Italy (2)

Spain (5)

Belgique (1)

Sweden (1)

Israel (1)

Tunisia (2)

Canada (1)

USA (1)

Chili (1)

Of these participants were 8 Female and 20 male.
