



# ESF - Science Meeting - Final Report

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## APPLICATION DATA

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### SCIENCE MEETING

Reference Number : **1093**  
Report submitted : **11/10/2007 16:12:06**

### ESF ACTIVITY

Unit(s) : **LESC**  
Activity Title : **Integrating population genetics and conservation biology: Merging theoretical, experimental and applied approaches**  
Activity Acronym : **CONGEN**

### PROJECT

Science Meeting : **Workshop**  
Title of Science Meeting : **Experimental metapopulations in evolutionary biology**  
Location : **Montpellier**  
Date of Science Meeting : **06/12/2006 - 10/12/2006**  
Convenor Name : **Dr. Isabelle Olivieri, Montpellier cedex 05, France**

### BUDGET

Total estimated Expenditure : **25000 €**  
ESF Grant requested : **0 €**  
Co-sponsorship Income : **0 €**

### BUDGET GRANTED

ESF Grant FUNDING : **25000 €**

### ACTUAL EXPENDITURE

Travel : **6645,76 €**  
Accommodation : **9199,75 €**  
Meals (lunch and dinner) : **5544,18 €**  
Local administrative costs \* : **0 €**  
**TOTAL EXPENDITURE : 21389,69 €**

\* includes: administrative and technical assistance, printing, photocopying, telephone, fax, email, etc. Additional support for schools may be considered

## Results of ESF-ConGen workshop on “Experimental Metapopulations”

**Main questions.** Most species live in fragmented habitats, and many are threatened by fragmentation. General questions addressed during this workshop were: i) can manipulation of migration among fragments of habitat help to mitigate the negative consequences (such as high extinction risk, inbreeding depression or reduced evolvability) of small population size due to habitat loss?, ii) what is the optimal level of connectivity that maximizes the conservation of genetic diversity at a larger scale? What is the importance of local adaptation patterns (including to the biotic environment) and how does migration affect their evolution?, iii) how may habitat loss, changes in habitat heterogeneity and landscape features affect patterns of gene flow, in particular through either plastic or genetic changes in dispersal behaviours?

**Why do we need experimental metapopulations?** The ecological and evolutionary consequences of fragmentation have motivated the flourishing of metapopulation theoretical studies, with little empirical testing, partly because of the difficulty of manipulating metapopulations in nature. Artificial or semi-natural metapopulations may help overcome some of these difficulties and may provide powerful tools to evaluate our understanding of evolutionary and ecological processes in spatially structured systems, to improve conservation practices in fragmented landscapes. More specifically, experiments manipulating metapopulation parameters such as migration, extinction or habitat fragment size, either in semi-natural systems or in highly simplified artificial environments, should allow: 1) increasing the range of situations or parameters explored in comparison with empirical studies, which rely on pre-existing variability for such parameters, 2) better disentangling the effect of different sources of variation in metapopulation dynamics, and, by that, gaining a better understanding of the ecological, behavioural or evolutionary mechanisms responsible for the observed patterns, 3) quantifying the relative effects of different processes, 4) designing better theory by pointing at the oversimplifications that cause predictive models to fail. The aim of the workshop was to review existing experimental approaches in the field of metapopulation biology, to evaluate their strengths and weaknesses and to suggest potential avenues of development for this field. We will discuss the inputs of the different studies presented during the workshop in the light of the four previous points (exploration, access to mechanisms, quantification, stimulating the formulation of better models).

Given the diversity of organisms used in the experiments and despite the strong unifying questions addressed, a synthesis of the results presented during the workshop is not straightforward. However, most presentations dealt, either explicitly or implicitly, with dispersal, its expression, its evolution, its consequences both on demography and adaptation of populations.

**Complex expression of dispersal.** As in theoretical models, dispersal is often manipulated in artificial metapopulations by moving around a constant fraction of each local population. Patterns of dispersal, and thus of gene flow, may be strikingly different in nature as revealed by several studies examining the movements of individuals among patches of habitat when such movements are not imposed by the experimenter. Even organisms with limited cognitive abilities (such as *C. elegans*, Nicholas Friedenber), or protists such as *Paramecium caudatum* (Oliver Kaltz, Thibault Nidelet) express complex habitat selection strategies, with migration behaviour dependant both on their genotype (different mutant strains), their condition (e.g. infected or not) and on the quality of patches in the metapopulation (e.g. resources).

Contrary to classical expectations that migration should increase with density, manipulation of population size shows that the smallest population in *Daphnia magna* have a disproportionate impact on migrant production (Florian Altermatt). Not only the number of migrants but also the nature of migrants may vary with experimental conditions. In the common lizard *Lacerta vivipara*, the size of migrants varied depending on whether maternal presence triggered the dispersal behaviour of young (Jean Clobert). Consequences of dispersal for both gene flow and population dynamics can depend critically on details of who disperses and why, a fact that has been largely overlooked by theoretical studies. For instance, the dispersal of mated females does not have the same impact on genetic differentiation as male dispersal (Kuke Bijlsma) and conditional dispersal of different sexes at different stages may not respond to the same environmental cues. Probability of successful colonization of empty patches is higher when dispersal is triggered by mother-offspring competition in the common lizard than when juveniles respond to competition with unrelated adults (Jean Clobert). Several artificial metapopulation set-ups in which individuals are free to move from one microcosm to another rather than being manually displaced were presented during the meeting. How such set-ups change our conclusions about the evolutionary or ecological consequences of fragmentation has still to be explored. Finally, the existence of genetic variation for dispersal propensity raises the question of the evolution of dispersal strategies in fragmented landscapes, with potential consequences for persistence and genetic diversity in such metapopulations. During the workshop, first attempts to witness evolutionary changes in dispersal behaviours in artificial settings were presented (N. Friedenber, L. Turnbull), with promising perspectives.

**Gene swamping versus heterosis.** Two conflicting predictions can be made about the impact of gene flow on adaptation in a fragmented landscape. Migration may alleviate the effect of drift by replenishing genetic variance, avoiding inbreeding depression, and helping spread beneficial mutations. Conversely, if selection intensity or direction varies through space, migration may counteract the action of local natural selection and reduce both global diversity and local adaptation. When selection varies through time (as in arm-races in host-pathogen coevolution), theory predicts that increased migration may however help local adaptation. Furthermore by affecting the distribution of genetic diversity through space and the ecological interactions between individuals, migration may also change the type (e.g. frequency-dependant) and direction of selection on several traits (e.g. evolution of cooperation in yeast, Craig MacLean) and the way in which possible evolutionary pathways are sampled (e.g. evolution of diversity of carbon use in *E.coli*, Arjan De Visser). Different experiments illustrated these antagonistic effects of dispersal, confirming model predictions. For instance, ability to adapt to new types of stress was reduced in fragmented populations of *Drosophila* (Kuke Bijlsma). In artificial populations of wheat in absence of migration, genetic diversity for pathogen resistance and precocity was redistributed among populations without any loss at the global scale (Isabelle Goldringer, Bénédicte Rhôné). Large migration rates prevented local adaptation in metapopulation of *Drosophila* with artificial heterogeneous selection (Willemien Smith) and made specialisation on different host tissues more difficult in viruses promoting the evolution of generalist populations (Santiago Elena). Yet moderate amounts of gene flow did not prevent population divergence either in *Drosophila* metapopulations (Willemien Smith) or in metapopulations of *Arabidopsis thaliana* (Claire Lavigne) with heterogeneous selection regimes. Increased dispersal of parasites relative to hosts increased their degree of local adaptation as predicted by theory (Angus Bucking, Laura Lopez-Pascua) and more generally migration improved local adaptation of the antagonist actor most limited by mutational input (Mike

Brockhurst). Given the antagonistic effects of dispersal and the combined existence of variable selection pressures both in time and space in nature, theory still has little to say about the net effect of migration when the action of both inbreeding and local adaptation combine to determine fitness. Analysis of crosses between and within populations in two plant species growing in naturally highly fragmented landscapes (Markus Fisher) revealed significant heterosis (i.e. greater fitness of hybrids between populations) despite the presence of local adaptation patterns. Interestingly, the same study showed that local adaptation was a concern only for large populations, not for small ones. It would be interesting to witness the effect of migration in the longer term in such systems. Quite intriguingly, response to selection in small populations of *Arabidopsis thaliana* (Claire Lavigne) was higher in heterogeneous metapopulations than in homogeneous ones, suggesting that in the latter case migration might replenish lost genetic variation in very small populations.

Experimental studies also suggest new routes of development for theory. In particular, a consistent conclusion of experimental work about coevolution between host and parasites presented during the workshop was that the combined effects of abiotic environmental heterogeneity and heterogeneity mediated by antagonistic interactions may deeply affect patterns of local adaptation. This occurs because of genotype by environment interactions (Ana-lisa Laine), because migration of both host and parasite may vary with resource gradients (Oliver Kaltz, Thibaut Nidelet), because migration of the host might be manipulated by another organism (phage and nematodes, N. Friedenberg), because resource levels change the cost of resistance (Angus Buckling, Samantha Forde) or more generally the contribution of antagonistic interactions to fitness. This work also raised important methodological issues about how to measure local adaptation, which were discussed during the workshop: reciprocal transplant and cross-infections in the lab may show widely different patterns, measuring probability of infection or reproduction of host and pathogens may also reveal different sides of local adaptation (Ana-lisa Laine), as well as patterns of relative versus absolute fitness.

**Quantitative predictions** Some experimental studies presented during the meeting went beyond testing qualitative predictions of theoretical models, by assessing the quantitative fit between experimental results and those of simulations describing the systems studied. This was done when examining the relationship between population extinction and isolation in *Cardamine pensylvanica* (Jane Molofsky, see also project in development in aphid metapopulations Wolfgang Weisser), when measuring effective population size in *Drosophila melanogaster* (Kuke Bijlsma) or when comparing measures of differentiation in neutral markers and selected traits in *Arabidopsis thaliana* (Claire Lavigne). Quantitative comparisons extract more information from experiments by identifying the parts of the ecological or evolutionary processes that we fail to model correctly, even if the qualitative pattern is consistent with model predictions.

**Experimental metapopulations between theory and nature.** Some part of the discussion during the workshop was concerned with the general pitfalls and benefits of the experimental approaches in artificial settings, and we will first attempt to summarize this general discussion. Experimental approaches constitute a conceptual bridge between theory and a more descriptive empirical study of natural systems. Yet, as such, they have two potential pitfalls. One is that, by increasing artificiality, extreme ecological simplicity and use of model organisms highly adapted to lab conditions, their relevance to phenomena taking place in natural systems may be questionable. In that respect, one may wonder about the merits of such experiments compared to the simulation of a theoretical model. At the other extreme, even simple systems

may exhibit complex and poorly understood ecology, which may compromise inferences from patterns to mechanisms, just as descriptive studies of empirical patterns in nature might. To significantly improve our understanding of ecological and evolutionary processes, optimal experiments should: (i) either include sufficient complexity in the experimental system to test whether simplified models have correctly described and encapsulated the main driving factors of the system studied, (ii) or, conversely, test model predictions in situations simple enough to identify the source of discrepancy between models and experiments and improve future theoretical studies. Alternatively, manipulative experiments may inform the theory, without constituting proper tests of the theory, by revealing important features of biological systems (for instance the existence of conditional dispersal strategies) which may have been neglected by modellers. In that respect, experiments may be ahead of theory. The studies presented during the workshop provided many examples of the last type of input. In particular, such experimental studies inform us on aspects of evolution in fragmented landscapes on which models have little to say a priori: which genes are involved in local adaptation, what is the specificity of interaction between pathogens and host, what is the level of repeatability of evolutionary pathways, are similar phenotypic changes underlined by similar molecular genetic changes, what is the importance of genotype by environment interactions, etc.

Experimental studies must therefore achieve a delicate balance between complexity and simplification, between relevance to natural system and ease of manipulation and investigation. The studies presented during the workshop represent well the diversity of approaches along such a gradient. At one extreme, artificial populations of wheat of initial known composition set up since 1984 in different localities across France have provided the fascinating opportunity to witness evolution in natural conditions, with, within a few generations, consistent changes in genes involved in competition, precocity and pathogen resistance along natural climate gradients and naturally occurring disease outbreaks (Isabelle Golringer, Bénédicte Rhôné). At the other extreme, artificial populations of very short-lived organisms such as bacteria (Arjan De Visser, Angus Buckling, Mike Brockhurst) and viruses (Santiago Elena, Samantha Forde) in chemostats allow the manipulation of both environmental gradients and dispersal in a very flexible manner and the investigation of long-term evolutionary consequences in these artificial settings.

### **Perspectives for the future development of the field**

**Diversity of biological models: an advantage or a handicap?** The diversity of organisms used in experimental metapopulations presented during the workshop was also very high, including HIV virus, model systems such as *E. coli*, *C. elegans*, *Drosophila sp.*, and *A. thaliana*, but also endangered plant species, lizards and butterflies among others. Whether such diversity of systems is desirable or not was briefly discussed. Focusing on model organisms whose biology (genetics, development, sequence data) is well-known is indeed an advantage when evolutionary changes in phenotypes can be tracked back to changes in DNA sequences. Note that such model systems are not restricted to organisms with very short generation time, as illustrated by genomic data on wheat. The diversity of model organisms may also make the development of collaborative projects more difficult. The consensus during the meeting was however that the diversity of system was of scientific value because it may help mitigate the tension between complexity and artificiality in the experimental approach evoked above. Tentative feed-backs between empirical study systems in nature and artificial settings, where the relevance of processes analysed in controlled condition is assessed in nature, were particularly appreciated, as in the example of the evolution of cooperative behaviours of yeasts (Craig

MacLean), or the dispersal behaviour of daphnia in small populations (Florian Altermatt). Different organisms and different time-scale of analysis may also help us determine the domain of applicability of various patterns. For instance, the short-term consequences of population subdivision in homogenous environments was observed to be detrimental for artificial populations of *Drosophila* (Kuke Bijlsma), while population subdivision was found to ameliorate diversity and the rate of long-term adaptation of *E. coli* in complex environments (Arjan de Visser). Such different patterns may emerge because epistasis limits adaptation in the long-term in asexual organisms with large population size in the latter case, while drift and standing genetic variation limit the process of short-term adaptation in the former.

**Recommendation for conservation genetics.** Conservation genetics are primarily concerned with small populations, but not exclusively, as illustrated by the conservation of genetic resources in crop species, or the management of resistance genes in large-sized populations of pathogens or pests. Moreover, conservation of genetic diversity and adaptation in common keystone species is increasingly recognized as an important goal of conservation biology because of the multiple consequences of such genetic diversity on community organisation and ecosystem functioning. Different biological models are necessary because of the diverse conservation questions that we have to deal with. Fundamentally, however, the results of this workshop have repeatedly shown that evolutionary processes taking place in small populations can widely differ from those in large populations. Thus, caution should be used in extrapolating conclusions from large experimental populations to small endangered populations. In that respect, the development artificial metapopulations projects with small sub-population size (such as the *Arabidopsis* or the *Drosophila* metapopulations) should be further encouraged to better understand the role of drift in adaptation. The development of artificial metapopulations and large-scale experiments in nature (such as the wheat metapopulation project) also constitutes a very promising avenue of research, still underdeveloped, to witness evolutionary changes in the face of present environmental changes.

Definitive answers to the questions raised during this workshop are still forthcoming. Yet, the emergent conclusion from this diverse array of experimental results might suggest that: (1) a better understanding of the flexibility and determinants of dispersal seems necessary to predict the short-term and long-term consequences of habitat fragmentation; experimental studies of dispersal aimed at understanding its mechanisms (and not simple attempts to measure its importance) are still too rare; (2) moderate amounts of gene flow seem optimal in that they do not prevent the evolution of local adaptation (and can even stimulate it, in particular in the case of resistance to pathogens) while fixing other genetic or demographic problems that small isolated populations face. The existence of genetic differentiation for quantitative traits between populations should not be used as the sole argument to reject the possibility of reinforcement of such populations by migration from other populations. The experiments presented during this workshop also point at several methodological difficulties when inferring conservation measures from measures of neutral or selected genetic diversity, such as effective sizes order-of-magnitude smaller than demographic size due to selection, and QST-FST comparison being biased by linkage disequilibrium in case of inbred matings.

## Final programme

### DECEMBER 7 : METAPOPOPULATION DYNAMICS AND LIFE HISTORY EVOLUTION

**9h30 Jane Molofsky** "Extinction dynamics in experimental metapopulations"

**10h10 Lindsay Trunbull and Sima Fakheran.** "Evolution of seed size as a function of fragmentation in an experimental Arabidopsis metapopulation."

**11h05 Nicholas Friedenber**g "Habitat instability and the evolution of dispersal in experimental metapopulations of *C. elegans*"

**11h45 Henrique Teotonio** "*C. elegans* as a model system for experimental evolution of life-histories."

**13h40 POSTER PART 1**

**14h40 Jean Clobert**" Towards a new meta-population functioning ? Experimental two-patch system reveals the prominent role of information."

**15h20 Florian Altermatt** "Wind of change in metapopulations"

**16h15 Craig McLean** "Cooperation in experimental metapopulations of yeast"

### DECEMBER 8 : GENETIC DIVERSITY AND ADAPTATION IN METAPOPOPULATIONS

**9h15 Isabelle Goldringer** "Evolution of experimental wheat populations under dynamic management"

**9h55 Claire Lavigne** "Evolution of neutral genetic diversity, flowering time and frequencies of associated candidate genes in experimental metapopulations of *Arabidopsis thaliana*."

**11h05 Kuke Bijlsma** "Dynamics and significance of genetic variation in experimental *Drosophila* metapopulations"

**11h45 Willemien Smith** "The effect of population dynamics on neutral and selective traits in a metapopulation context"

**13h40 POSTER PART 2**

**14h40 Markus Fisher** "Consequences of inter-population crosses between genetically differentiated plant populations"

**15h20 Luisa Orsini** "Metapopulation genetic structure of the Glanville fritillary butterfly"

**16h15 Arjan de Visser** "Role of spatial structure in adapting populations of *E. coli*"

**16h55 Elena Santiago** "RNA virus replicate in an always fluctuating world: organ-specific adaptation, gene flow and metapopulation structure."

### DECEMBER 9 : EVOLUTION OF INTERACTIONS IN METAPOPOPULATIONS

**9h15 Andy Buckling** "Local adaptation of phages to bacteria"


**9h55 Mike Brockhurst** "Coevolutionary dynamics in host parasite metapopulations"

**10h50 Anna Lisa Laine** "Detecting local adaptation in parasite metapopulations – incorporating spatial and environmental reality"

**11h15 Oliver Kaltz** "Hosts and parasites and geographical range limits: Experimental epidemiology and coevolution -along a productivity gradient"

**11h40 Samantha Forde** "Gene flow reverses an adaptive cline in a coevolving host-parasitoid interaction."

**12h05 Wolfgang Weisser** "Local and spatial dynamics of a host-parasitoid system"

  
C. RONCE

  
I. OLIVIERI