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Evolution in structured populations

Texts edited by

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Résumé.–PERRIN N., KELLER L., GOUDET J., (dir.), 1994. Evolution en populations structurées. *Bull. Soc. vaud. Sc. nat. 83.2*: 153-174.

Cet article est un compte-rendu du colloque «Evolution in Structured Populations», tenu du 14 au 16 Septembre 1994 à l'Université de Lausanne. Consacré aux causes écologiques et conséquences évolutives de la structuration des populations naturelles, ce colloque a réuni des chercheurs d'horizons divers (zoologie, botanique, anthropologie, mathématiques), utilisant des approches variées, aussi bien empiriques que théoriques. Plusieurs exemples concrets de structurations génétiques de populations naturelles ont été documentés, et leurs causes analysées. Celles-ci sont variées, certaines étant extrinsèques à la biologie des espèces concernées (distance géographique, barrières écologiques, etc), d'autres intrinsèques (stratégies de reproduction, mutations chromosomiques).

Les outils quantitatifs les plus largement utilisés pour analyser ces structures restent les F-statistiques de Wright; elles ont néanmoins fait l'objet de plusieurs critiques. D'une part, elles n'exploitent pas toute l'information disponible (certains orateurs ont d'ailleurs proposé diverses améliorations dans ce sens); d'autre part, les hypothèses qui sous-tendent leur interprétation conventionelle (en particulier l'hypothèse de populations à l'équilibre) sont régulièrement violées. Plusieurs des travaux présentés se sont précisément intéressés aux situations de déséquilibre et à leurs conséquences sur la dynamique et l'évolution des populations. Parmi celles ci: l'effet d'extinctions démiques sur les stratégies de dispersion des organismes et la structure génétique de leurs métapopulations, l'inadéquation du modèle classique de métapopulation, dit modèle en île (les modèles de diffusion ou de «pas japonais» (*stepping stone*) semblent généralement préférables), et le rôle de la «viscosité» des populations, en particulier en relation avec la sélection de parentèle et l'évolution de structures sociales. Le rôle important d'événements historiques sur les structures actuelles a été souligné, notamment dans le cadre de contacts secondaires entre populations hautement différenciées, leur introgression possible et la biogéographie de taxons vicariants.

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Parmi les problèmes récurrents notés: l'identification de l'unité panmictique, l'échelle de mesure spatiale appropriée, et les difficultés d'estimation des taux de migration et de flux de gènes. Plusieurs auteurs ont relevé la nécessité d'études biologiques de détail: les structures génétiques n'ont d'intérêt que dans la mesure où elles peuvent être situées dans un contexte écologique et évolutif précis. Ce point a été largement illustré dans le cadre des relations entre structures génétiques et stratégies de reproduction/dispersion.

Summary.–PERRIN N., KELLER L., GOUDET J., (eds). 1994. Evolution in structured populations. *Bull. Soc. vaud. Sc. nat. 83.2*: 153-174.
This paper accounts for a meeting held at Lausanne University, 14-16 September 1994, and devoted to the ecological causes and evolutionary consequences of population structuration. Patterns of genetic structures were widely documented, both in plants and in animals. The causes to such patterns were diverse, some extrinsic (geographical distance, ecological barriers) but others intrinsic to the biology of concerned species. The F-statistics, which are the quantitative tools mostly used to make sense of genetic patterns, received some criticisms. A minor one was that they do not make full use of all available information; in this context, possible extensions were proposed. Major criticisms concerned the assumptions underlying conventional interpretations of F-statistics, in particular those of population equilibrium. The effects of disequilibrium on population dynamics and evolution were investigated, both theoretically and empirically. Among the main themes addressed were the effect of demic extinction on dispersal strategies and on the genetic structure of metapopulations, the use of alternative metapopulation models (diffusion, stepping stone), and the role of population viscosity, in particular with respect to kin selection and the evolution of social structures. The importance of historical events in molding present-day patterns (in particular secondary contacts, introgression, and biogeography) were also stressed. Among the recurrent problems discussed were: the identification of panmictic units, the appropriate spatial scale of measurement, and the difficulties in estimating migration rate and gene flow. Also stressed was the importance of detailed biological studies paralleling that of genetic structures, and the heuristic value genetic studies may get in this context.

INTRODUCTION

Evolution in structured populations: under this title we recently organized a meeting at the University of Lausanne, Switzerland (14-16 September, 1994). The present paper is aimed at providing an account of the meeting. We first shortly introduce the theme and reasons for choosing it, we then publish the abstracts of the papers presented, and finally propose a general discussion of the main topics of interests that emerged during these few days.

Natural populations of plants and animals are said panmictic when the gametes of constituting individuals fusion randomly. Panmixis is rare, and usually realized only at very local scales: individuals tend to mate with close neighbours; they do not move across the whole geographic range of species, spreading their genes around. Such patterns induce a genetic structuration of species, as exemplified, for instance, by marked differentiation among geographic areas: populations that are geographically close tend to be genetically similar. But geographic distance is not the only relevant factor: several kinds of local barriers may further prevent free spreading of individuals and genes. Some are linked to ecology (e.g. availability of suitable habitats) others to reproductive biology (e.g. mating and dispersal strategies).

As a consequence, natural populations are often more adequately described as metapopulations: that is, series of demes (panmictic units) interconnected by some level of migration (Fig. 1). This kind of structure has potentially very important consequences on the dynamics and evolution of populations. The size of a deme, for instance, affects its extinction probability, level of genetic drift, response to local selective pressure, etc. This is obviously important to applied ecology: the management of viable populations, both in terms of numbers and genetic diversity, must take account of population structure. But this issue is also crucially important to a more fundamental biology, in particular to evolutionary ecology.
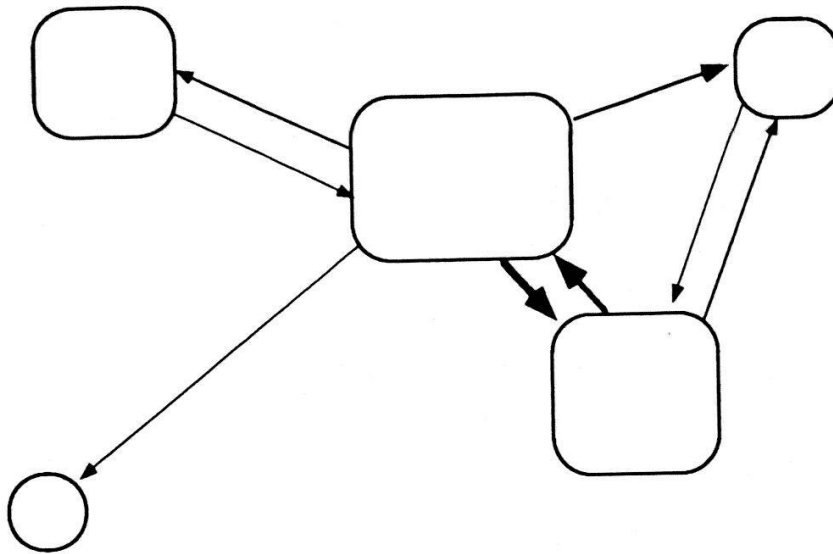

Figure 1.–A metapopulation, represented as a series of demes (panmictic units) interconnected by some level of migration (arrows). In this example, demes differ in sizes and migration rates.

Studying evolution in structured populations is complex. Such studies lie at the interface between distinct biological fields (ecology and evolution) and have to integrate their respective problematics. Different approaches are required: empirical-experimental, but also theoretical, with the needs of tools from statistics, mathematics, computer simulations, etc. Moreover, several disciplines are concerned, including botany, zoology, anthropology. The Lausanne meeting indeed aimed at interdisciplinarity. The twenty or so contributions pointed to the main ecological and evolutionary implications of population structuration. Their themes were interconnected as illustrated in Fig. 2. Some authors addressed the causes of structuration (1), focusing on barriers to exchange (habitat fragmentation, reproductive strategies, etc), while other pointed to consequences. The special dynamic properties of metapopulations (2), as well as the way such dynamics interact with microevolutionary processes (genetic drift, local selection, etc) to generate specific evolutionary mechanisms (3) were among the consequences investigated. The resulting genetic patterns (inbreeding, differentiation, etc) were analysed from statistical and empirical perspectives (4). Their relationships to kinship, and thereby to the evolution of sociality were also put under scrutiny (5), as well as the progressive differentiation of demes into races, sub-species, or species (6).
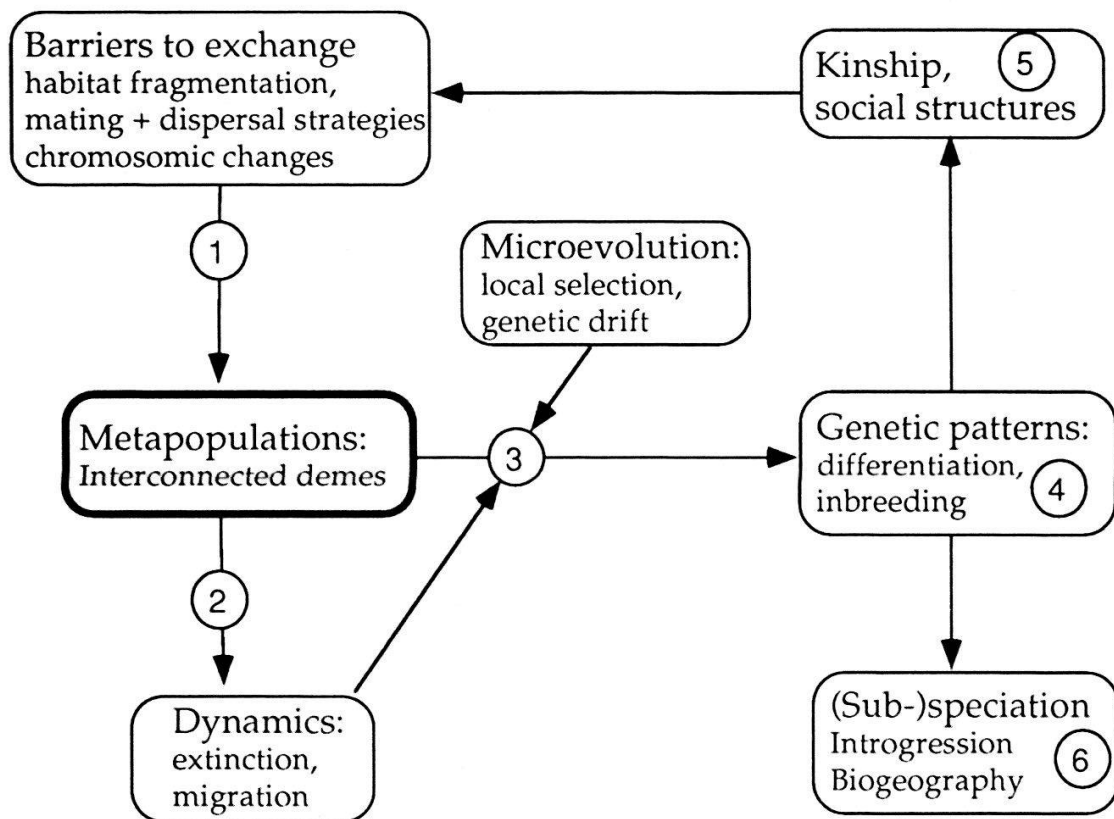
Figure 2.–Interconnections between the main themes addressed during the meeting. See text for further explanations.

As will clearly appear from the abstracts that follow, our main purpose was to bring together people from different horizons, with different backgrounds, and taking different approaches, as a way to get, as far as possible, a synthetic overview of the topics.

ABSTRACTS

Do we need any experiments to assess the effects of habitat fragmentation ?

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Understanding the consequences of the destruction and fragmentation of natural habitats is essential to predict the fate of populations of (endangered) species. The causes of local extinction may be deterministic (due to the removal of essential resources) or stochastic (chance variation in individual

birth and death rates, genetic effects, environmental variation and/or catastrophes). Effects of habitat fragmentation include a reduction of the area available for the organisms, a division of existing populations (resulting in subpopulations of small size), an isolation of fragments, and changes in habitat charateristics in the fragments (e.g. changes in (micro-)climate and edge effects).

Field surveys that record the number of species in fragments cannot explain the processes of extinction. Therefore experiments are needed. I present an experiment in which a dry grassland is artificially fragmented into patches of different sizes. We plan to follow the fate of populations of selected species (vascular plants, land snails) in the fragments by recording in detail demographic parameters and genetic variation. In several taxonomic groups we record changes in species diversity and analyse differences in vulnerability to extinction in relation to body size, life history, mating system, mode of reproduction and local population density. In a series of complementary experiments we examine effects of the edges of fragments on the spatial distribution and dispersal of animals and plants, their 'perception' of habitat heterogeneity, and their movement patterns in relation to fragment size.

Floral biology and the genetic structure of plant populations: an ecological approach to mating system evolution

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One of the most fascinating aspects of plant evolutionary biology concerns the study of the evolution and maintainance of the immense diversity of mating systems that can be observed in natural populations. In this context two evolutionary trends are of particular significance:
  1.–the evolution of floral polymorphisms that promote outcrossing,
  2.–the evolution of selfing from outcrossing ancestors.

The relative amount of selfing or outcrossing can critically affect the genetic variation in natural populations and the spatial structure of this variation. As regards pollen transport, for instance, genetic structuration (among-deme differentiation) is one order of magnitude more important in autogamous than in wind-pollinated species. The same is true of seed dispersal: structuration is maximal when gravity alone disperses seeds, and minimal when wind is responsible.

Floral polymorphisms or variation in quantitative floral traits interact with levels of inbreeding depression to influence the capacity of a plant to self or outcross. Inbreeding depression is a cost to selfing, but outbreeding also has genetic costs (e.g., disruption of coadapted genes). Ecological factors may also favour selfing over outcrossing (reproductive assurance, lower energetic costs to selfing, etc). Benefits may thus counterbalance costs, whith the result that intermediate selfing rates are often evolutionary stable.

Changes in mating and dispersing systems may strongly condition the fate and evolution of species. A detailed ecological understanding of plant mating systems is fundamental to the conservation of threatened plant species.

Migration strategy and metapopulation viability

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A model of a metapopulation is presented in which each subpopulation can exist in three possible states: 0 (extinct), 1 (close to the Allee threshold), and 2 (at carrying capacity). The dynamics is modelled in discrete time by a Markov chain. In addition to growth and death processes, migrations are included that can depend both on the state of the source subpopulation (e.g., inversely) and the state of the target habitat. Several migration strategies are considered: random migration, conspecific attraction (occupied patches receive a larger fraction of migrants), and conspecific repulsion (empty patches are preferred). Emigration events affect the density of the source habitat (transitions from 2 to 1 or from 1 to 0). Immigration causes either a recolonisation of an empty patch or a transition from 1 to 2 in the target habitat. With methods of queuing theory, it was possible to obtain analytical formulas for the extinction probability and the persistence time. The effect of several dispersal strategies was investigated. The direction of the influence of random dispersal and that of directional dispersal depends on intrinsic population parameters. It is shown that, while at high growth and mortality rates conspecific repulsion generates a higher metapopulation viability, there exists a threshold value for the growth rate below which it is aggregation that increases viability. A biological interpretation of these results is proposed in terms of the core-satellite hypothesis of Hanski, that suggests an association of between-population kinetic rates and the dispersal mode.

One- and two-patch populations in periodic environment

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I present a model for the dynamics of one- and two-patch populations in stable and periodic environments. Subpopulations are assumed to experience an Allee effect (fecundity drop at low density, e.g. due to inbreeding depression), which is incorporated by introducing a threshold density in the continuous logistic equation. The environmental effect is represented by a density-independent term, either constant or periodic. Migration rate is assumed proportional to the difference in subpopulation densities.

In constant environment, the one-patch population either goes to extinction or reaches its carrying capacity. A two-patch population can have up to three stable non-zero equilibria (i.e., with different relative abundances in the two subpopulations), depending on the combination of model parameters. Which one is reached depends on initial conditions.

Provided a stable steady-state equilibrium exists in the constant environment, periodicity causes stable population fluctuations around that equilibrium with a period identical to that of environment. Linear approximation can be used to obtain explicit formulas for the fluctuations, and to calculate their amplitude and lag behind the environmental changes.

Migration increases population viability in variable environments. This increase depends on the similarity between environments: when fluctuations are in contrasting phases, the two-patch population can persist as long as a single population with double carrying capacity. However such a perfect negative synchronicity is strongly unplausible in natural conditions; furthermore, stochasticity also plays an important role. In the general case, therefore, a single population with double capacity is more viable.

Evolution out of equilibria: Non-equilibrium and non-uniform population dynamics significantly affect evolution in structured populations.

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Metapopulations in nature are not like the island model most often assumed by population genetic models. Local populations go extinct, colonize, separate into two or more new populations, or change in size or migratory pressures. Moreover, local populations are not all the same: population sizes, migration rates, and extinction rates vary in space and time; sometimes some local populations are very stable and act as sources of migrants while others are likely to go extinct and act as migrant sinks.

It is possible to describe the effects of these demographic processes on the genetic variance among populations and the effective population size of a metapopulation using identity-by-descent measures. The usual effect of non-equilibrium or non-uniform population dynamics is to increase the amount of differentiation among populations while decreasing the effective population size of the metapopulation, relative to a similar island model. These non-equilibrium situations have strong consequences on the patterns of evolution. Fluctuating populations, for instance, are more likely to depart from local optima due to increased genetic drift, and thereby more likely to reach global optima of the fitness landscape.

This theoretical framework is exemplified by empirical work on the forked fungus beetle *Bolitotherus cornutus*. Ecological measurements of extinction and migration rates, probability of common origin of colonizers and population sizes were used to predict extent of genetic differentiation, which was otherwise assessed independently through protein gel electrophoresis. Direct and indirect measurements were highly corroborative. Population fissions were also measured, and shown to enhance the genetic differentiation of populations.

The statistical analysis of molecular data for inferring population genetic structure: The AMOVA framework

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Population genetic structure generally appears whenever genes are not free to move across the whole range of a given species. The consequence will be that populations or individuals sampled at different locations will present

differences in their genetic repertoire. These differences may either consist in variable gene frequencies or in variable arrays of molecular variants. It follows that population structure will be best estimated when taking into account both allele frequencies and molecular differences between alleles.

For this purpose, we have introduced a new methodology called AMOVA, based on an Analysis of MOlecular VAriance framework, to estimate molecular variance components due to differences in the genetic composition of several hierarchical evolutionary units (individuals, populations, groups of population, etc...) and their conventional associated F-statistics, here called Φ-statistics. Molecular information is introduced in the analysis under the form of squared Euclidian-distances between molecular haplotypes, wich may be simple counts of site differences. With such molecular distances, F-statistics are exactly equal to weighted averages of Φ-statistics over all molecular sites considered. Although this relationship does not strictly hold when non-Euclidian distances are used, alternative molecular distances do not markedly affect the outcome of the analysis. The significance of the different statistics are tested by non-parametric permutational tests, which do not require specific assumptions on the underlying evolutionary mechanisms.

The application of this methodology is straightforward for RFLP and DNA sequence polymorphisms. A program for computing and testing the different statistics is available under MS-Windows upon request.

Multigenic estimates of population structure

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Analyses of allelic frequencies at different levels, (within individuals, between populations, etc) provides information about the reproductive system of species, as well as the spatial and temporal structure of populations. F-statistics, that compute average kinship coefficients at these different levels (e.g. inbreeding coefficient for the within-individual level), provide a synthetic account of the distribution of genetic diversity (e.g. COCKERHAM and WEIR 1993, Evolution).

This approach can be generalized by measuring kinship coefficients between individuals I and J for n loci, where f^n_{IJ} can be defined as the probability that n randomly chosen genes from I and n homologous genes from J are identical by descent (the usual kinship coefficient corresponds to order n=1). There is a correspondence between linkage disequilibria and these multigenic descent measures. Partitioning the total linkage disequilibrium in a within-population- and a between-populations component (as done in the case of 2 loci; NEI and LI 1973, Genetics) is an alternative way to analyse genetic structures using multigenic information.

For the island model (infinite number of populations, all exchanging an equal number of migrants, so that genetic identity between populations is 0), one can get analytical formulae of the kinship coefficient for the different orders and different levels. These coefficients allow estimation of the model parameters (such as local population size N and migration rate m). They also allow testing some assumptions of the metapopulation model used (here the

island model), provided the number of measures exceed that of parameters. The assumption that population size has been constant through time, for instance, can be tested in this way (see Figure 3: lower curve refers to a decreasing population, upper curve to an expanding, and medium curve to a stable one).
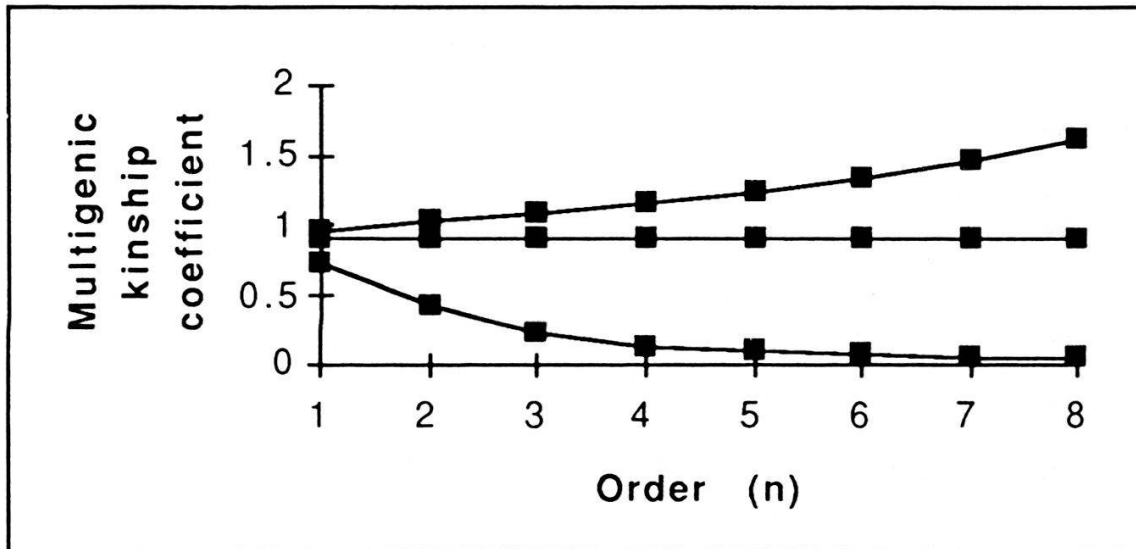

Figure 3.–Multigenic kinship coefficient as a function of order (number of loci) for a decreasing (lower curve), stable (medium curve) and expanding (upper curve) population.

Gene-for-gene coevolution in a metapopulation model

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In order to understand the influence of population structure on the coevolution between plants and their pathogens, we built a spatially structured metapopulation model. We simulated the evolution of a metapopulation made of 100 patches, with local density-dependent regulation of population sizes, and gene-for-gene interactions of hosts with pathogens (1 locus, 10 alleles, assuming a haploid asexual organism).

We measured Spearman rank correlation coefficient, ρ, between gene frequencies in the host and the matching gene frequencies in the pathogen. Averaged over 2000 generations, it was significantly negative, thus providing evidence for coevolution.

The absolute value of ρ was strongly affected by demographic parameters, as well as by migration and mutation rates. These rates have multiple effects: both increase variation, but migration has an homogeneizing effect, while mutation may disturb coevolution. These effects vary with the spatial scale of observation (regional versus local).

Estimation of gene differentiation in metapopulations: the example of the perennial dioecious plant, *Silene dioica*

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We investigated the genetic properties of a diploid, perennial, dioecious plant, *Silene dioica*. This plant is a member of the deciduous phase of primary succession of the studied area: Skeppvisk Archipelago, in the Gulf of Bothnia, Sweden. One very useful feature of this archipelago is that it has been submitted to land uplift for the past 7,700 years because of glacial recession. The rate of land uplift has been a constant 0.9cm/year since. The height of the islands are therefore a good indicator of their ages.

Colonisation by *S. dioica* occurs when islands are 70-150 years old. Populations expand rapidly and attain large sizes and high densities on islands 120-250 years old. On islands 200-400 years old, populations become increasingly restricted to the shores. On islands 250-500 years old, the later successional species have successfully occupied the islands, and *S. dioica* populations go extinct. Recolonisation of the same island does not occur.

Using electrophoretic loci, we showed that this system is a metapopulation (a system of semi isolated populations undergoing fluctuations in sizes, extinction and colonisation): genetic differentiation among young populations is larger than among populations of intermediate age. We also showed that Isolation By Distance occurs in this system, according to the direction of prevailing winds and currents. One of the important factors that explain levels of gene differentiation is the source of colonisers, and gene differentiation is increased when colonisers come from the same patch. Since we could not detect any correlation between the matrix of genetic distances and that of geographical distances among young populations, but a high correlation between the two matrices for populations of intermediate ages, we were able to conclude that colonisers are likely to come from many sources.

This work is important in that it brings together theory and field data. The analytical model helped us building hypotheses about observed patterns of genetic differentiation. We tested the hypotheses and could then point out where there were agreements and discrepancies between the model and the data, which will in turn help in incorporating new elements in the model.

Population structure of a herbivorous insect and its host plant

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Parasites typically live in a patchy environment. This environment is often heterogeneous, in the sense that parasites may encounter hosts with different degrees of suitability for the parasite's development and reproduction. Therefore, knowledge of the gene flow of both the parasite and the host would be valuable to infer the heterogeneity of the environment of the parasite (i.e.

the heterogeneity of the host populations) and the potential for parasites to become locally adapted.

We investigated the population structure of an insect herbivore, the weevil *Larinus cynarae*, and its host, the thistle *Onopordum illyricum*. We sampled populations of both weevils and thistles at different geographical scales ranging from 50 m to 100 km. We found that weevil populations show high levels of gene flow at all geographical scales, such that populations 100 km away are almost identical. On the contrary, thistle populations at the same geographical scales show significant levels of differentiation.

The high levels of gene flow between weevil populations can be explained by the ephemeral nature of thistle patches. Indeed, thistle populations go often extinct due to fire or human activities. These host-population extinctions cause massive migration movements of adult weevils, resulting in high levels of gene flow. Thus, selection for dispersal in weevils, due to the frequent extinctions of their host plant populations, could limit their potential for population differentiation and local adaptation.

Genetic structure of leaf beetle populations

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Herbivorous insects that use the same hosts as larvae and adults often live in subdivided populations that reflect the patchy distribution of their host plants. Host plant populations are also frequently separated by geographic barriers such as bodies of water or mountain ranges.

Genetic differentiation in the herbivores should reflect the effects of these barriers on individual dispersal. I used allozyme electrophoresis to study genetic differentiation of willow-feeding leaf beetles in the Sierra Nevada Mountains of California (*Chrysomela aeneicollis*), and the Valais Alps (*Phratora vitellinae*). I also sampled *Ph. vitellinae* populations on islands in the Saimaa Lake system in Eastern Finland (island size 0.1 - 3 km). Finally, I measured the genetic differentiation among lowland populations from Switzerland to northern Finland.

For *C. aeneicollis*, the F_{st} value (proportion of variance due to differentiation among demes) among three drainages spanning less than 40 km was 0.043. The values within the three drainages were lower, indicating that the mountain ridges constituted barriers to gene flow. The among-population differentiation in the middle drainage appeared to result from gene flow into it from the neighboring drainages. For Alpine *Ph. vitellinae*, the among-drainage F_{st} values were similar to those for *C. aeneicollis* (0.053). However, the differentiation across northern Europe was lower (0.021, excluding the Alps). There was no differentiation among islands in eastern Finland.

This suggests that geographic barriers do play an important role in determining the patterns of genetic variation. The differentiation within the Alps may also result from gene flow into them from northern and southern populations. Finally, the low differentiation at the allozyme loci corresponds to low among-population differentiation in host preference.

Chromosomes and genetic structuration of populations in the shrews of the *Sorex araneus* group

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Although extremely similar morphologically, the shrew species from the '*Sorex araneus* group' vary widely in their caryotypes. The same basic chromosomal elements can be identified in all species, but they are variously combined into acrocentric or metacentric chromosomes. The species *S. araneus* itself is highly polymorphic with this respect: 12 arms may be fused or not, defining several chromosome races. 27 such races have been described today.

A general examination of the data shows that:

1.–large-arms fusions are spread across broad areas, with no polymorphism.

2.–medium-sized arms are fused over large areas. The resulting metacentrics define groups of related chromosome races. Polymorphism is restricted to some marginal races.

3.–small-sized arms are often free. In *S. araneus*, fusions characterize local races, but polymorphism is frequent. Convergent fusions have occured independently in several populations.

Thus fusion –rather than fission– is the main mechanism for this chromosomal evolution. Furthermore, large arms appear to have fused earlier than small ones and/or the resulting metacentrics have spread quicker across populations. The spreading of a given metacentric is stopped only where it meets another, incompatible metacentric (i.e., with monobrachial homologies). The most plausible selective pressure for fusions seems a mechanic advantage during meiosis. The result is a 'boxes in boxes' geographical structuration of species and populations. Gene flow between populations vary with the level of karyotypic differentiation: it is completely cut between species, and almost so between the large groups of chromosome races of *S. araneus*. By contrast, some gene flow occurs between poorly differentiated local populations.

This chromosomal structuration shows clear discrepancies with the genetic structuration as recorded by mtDNA analysis. Since mtDNA clones are transmitted by females only, which presumably are highly philopatric, their distribution might reflect the past history of the populations. Metacentrics by contrast, transmitted by the less philopatric males as well, could apparently spread across mtDNA clonal groups. This suggests a recent origin for the observed chromosomal structuration.

Gene flow in a hybrid zone of the shrew *Sorex araneus*

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The chromosomal races «Vaud» and «Valais» are two karyotypically and genetically distinct forms of the common shrew *Sorex araneus*, that came into

contact in western Switzerland after the last glaciations. These two forms co-occur today in the Bernese Oberland (Haslital, Innertkirchen) in an hybrid zone over a distance of about 2 km.

Viable hybrids have been produced in laboratory. However, due to extensive monobrachial homologies, meiosis is extremely complicated in hybrids due to the formation of multivalent chains of 11 (!) elements. This should drastically reduce hybrid fertility.

To study the genetic structure of populations in contact, and estimate the gene flow, I examined the karyotypes, nuclear markers (albumin and urinary pepsin) and cytoplasmic markers (cytochrome b gene on the mtDNA) along a transect throughout the hybrid zone.

Only 4 hybrid karyotypes out of 33 have been found until now in the contact zone. This fact, together with a high heterozygote deficiency, indicate that F1-hybrids are rare in nature. Laboratory-produced hybrids provide no evidence for reduced viability, either before or after birth. Thus, a premating barrier is a more plausible explanation.

Cytonuclear disequilibria (calculated from the differential introgression of nuclear and cytoplasmic genes) indicate both an important reproductive isolation and an assymetrical gene flow: the Vaud-females tend to mate more easily with the Valais-males than vice versa. This might be due to differences in female choosiness. Experiments in mate choice are currently in progress to test this idea.

Introgressive hybridization between freshwater snail species

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Viviparus ater and *V. contectus* coexist in Lake Garda (Italy). Although they occupy different ecological niches, interspecific copulations commonly occur (10% of observed copulations). I examined six informative allozyme markers to check whether experimental crosses result in effective hybridisation, and to estimate gene flow in nature.

While experimental hybrids between male *ater* x female *contectus* revealed sterile, the reverse cross between female *ater* and male *contectus* produced fertile hybrids –with however a 50% reduced fecundity in females. F1 and backcross hybrids could be found in nature, but were rare (F1 frequency ranges 0.2-1.5%). Allele frequency distribution suggests some introgression for all markers, except at one pair of presumably linked loci.

Thus, *V. ater* and *V. contectus* apparently exchange genes through backcrosses. However, in spite of the high introgressive potential shown in laboratory, hybridization is rare in nature, so that species remain distinct at the morphological and biochemical levels.

Genetic structure of a hybrid zone between diploid and tetraploid *Anthoxanthum alpinum*

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Polyploidy is the presence, in genetically related taxa, of cytotypes with chromosome numbers that are multiples of each other. Polyploidy promotes genetic isolation between ploidy levels. Isolation is nevertheless not absolute and gene flow between diploids and tetraploids may occur either through triploids, or directly by the fusion of two 2n gametes or by the fusion of one 2n gamete produced by a diploid with a gamete produced by a tetraploid.

Hybrid zones between diploids and tetraploids are ideal sites for the evaluation of gene flow between cytotypes. *Anthoxanthum alpinum* Löve and Löve is a widespread grass species of the upper subalpine and alpine belts in Western Europe which has two ploidy levels with complementary ranges. In Switzerland, diploid *A. alpinum* (2n=10) grows in most of the Alps and in the Northern part of the Jura. Its autotetraploid, *A. alpinum* (2n=20), replaces the diploid in the Northwestern fringe of the Alps and in the Southern part of the Jura. Both cytotypes form a narrow hybrid zone between Vanil Carré and Pointe de Cray, located North-West of Chateau-d'Oex. No morphological difference exists between both cytotypes except the size of stomata and of pollen grains which are larger for the tetraploid. Evidence of gene flow was searched for by caryological analysis and allozyme study.

In the North-Eastern part of the hybrid zone, the limit between diploids and tetraploids is located on the ridge of the mountain and in its South-Western part, both cytotypes are growing on the South-Eastern versant. Triploid hybrids occurred exclusively when cytotypes grew on the same versant. Analysis of caryopses sampled from nature showed triploids in the offspring of both diploids and tetraploids. Tetraploids were found in the progeny of diploids. In that latter case, hybridization occurred mainly, but not exclusively, in the neighborhood of the limit of the taxa. Experimental hybridizations confirmed these results. Thus, gene flow from diploid to tetraploid occurred by triploid bridge or directly by the intermediary of 2n gametes. The caryological analysis showed no evidence of gene flow from tetraploids to diploids.

Allozyme study was based on a new sample of pure zones and of a zone of mixture in the hybrid zone. Moreover, 2 pure populations of each cytotype of the surrounding area were studied for comparison. Analysis was performed on 8 enzymatic systems totalizing 22 loci. No diagnostic alleles were found, confirming the autopolyploid origin of tetraploid *A. alpinum*. Preliminary analysis indicates that allele frequencies of a peroxydase locus did not differ between tetraploid pure populations and both cytotypes of the hybrid zone, but was lower in the diploid populations. Gene flow from tetraploids to diploids might have caused this difference in gene frequencies. Nevertheless, selection or historical event may not be excluded. Gene diversity tended to be lower in the hybrid zone than in surrounding pure populations.

Genetic structure of shrews on continental islands: historical effects of fragmentation

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Modern approaches in biogeography include the comparison of the paleogeographic history of a region with the phylogenetic evolution of organisms living in the same region. D.R. Brooks proposed a parsimony technique (BPA) for the study of macroevolutionary processes which govern patterns of species distribution. This method allows the reconstruction of a biological area cladogram, which represents the historical involvement of geographic areas in the evolution of the species. This reconstruction is based on the null hypothesis that all species have a common history with the areas under study (pure vicariance hypothesis); inconsistencies (homoplasies) are interpreted as episodes of colonisation and/or extinction.

The Malay Archipelago is an array of oceanic and continental islands inhabited by a great diversity of organisms. Most of these islands were connected to various degree during Pleistocene glaciations, when sea-level dropped as a consequence of ice-cap formation. Thus, it is easy to reconstruct a paleogeographic hypothesis of past vicariance events by recording the minimal sea depth separating the islands. This is the area cladogram. The next step is to reconstruct the phylogenetic history of a monophyletic clade, here the SE-Asian shrews of the genus *Crocidura*. Most species living in this region were examined for allozymic variation at 33 loci. Phenetic and cladistic analyses of these data yielded a consensus phylogeny which was submitted to the final step of BPA, the reconstruction of a biological area cladogram.

As expected, SE-Asian shrews do not have a single zoogeographic history and the initial hypothesis of pure vicariance evolution must be rejected. Careful analysis of both phylogenetic and geological data suggest that colonisation events better than vicariance events account for the zoogeographic history of SE-Asian shrews. This is probably related to recurrent effect of sea-level variations which produced several episodes of island fragmentation followed by connection. The vicariance model documents only one cycle and thus is a poor predictor of the whole geological phenomenon. This rises the problem of evaluating the proper time scale at which the biological phenomenon acts. Corroboration between several independent clades of different ages should therefore be considered before inferring conclusions of a general model of zoogeographic evolution in the Malay Archipelago.

Genetic structure and sociality

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According to Hamilton's inclusive fitness theory, genetic structure lies at the heart of the evolution of social interactions. Altruism can evolve only if the interactants are related. Theory shows that a simple definition of relatedness is widely applicable. Empirical evidence confirms that it is important.

Altruists are nearly always related to their beneficiaries. In addition, individuals make appropriate choices based on relatedness. This is best seen in the sex ratios of social insects. Recent work has shown that workers adaptively adjust sex ratio based on genetic-structure changes due to queen replacement, queen number, and the queen's mate number. The first two can be assessed by environmental cues, but the assessment of mate number implies that workers can assess genetic variability.

However, not all forms of genetic structure contribute to the evolution of altruism. First, the current evidence does not support the idea that social insects distinguish among the various matrilines or patrilines in their colony. Second, relatedness generated by population viscosity does not necessarily promote altruism. Viscosity increases relatedness to neighbors, but it also increases competition with neighbors, and in a variety of models these two factors exactly cancel.

Genetic relatedness and population viscosity in polygynous *Formica* ants

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Estimating genetic relatedness among nestmates is important to assess the role of kin selection in the evolution of social behaviour. In social insects, intranest genetic relatedness is shaped by the reproductive structure of the colony, particularly the number of reproductive individuals, and by the local population structure.

In the Swiss Jura mountains, the red wood ant *Formica lugubris* has from a few hundreds to a few thousands queens per nest, and therefore genetic relatedness is expected to decrease to virtually 0. But if the population is structured at a very local scale with new nests being founded by budding and restricted gene flow between nests this may boost relatedness estimates. I studied intranest genetic relatedness and local population genetic structure of *F. lugubris* with microsatellites, which are highly polymorphic DNA markers perfectly suited for this kind of detailed analysis.

Intranest genetic relatedness, as measured with 4 loci in a sample of 20 nests along a 1.2 km transect, was 0.17 ± 0.04. This is surprisingly high given the high number of queens per nest. But a positive inbreeding coefficient ($F_{is} = 0.07$) indicates that either associative matings between relatives occur or that there is a geographical differentiation at a very local scale. When corrected for this effect, the relatedness falls down to 0.05, a value compatible with a fairly high number of queens per nest. This result indicates that local population structure and/or inbreeding boost relatedness estimates, even when measured with respect to a local and relatively small population of reference.

The microgeographic population structure is viscous, as indicated by the progressive changes in allele frequencies along the transect. A Mantel test shows that there is a correlation between geographical distance and genetical differentiation between sites expressed as a paired F_{st} coefficient.

Dispersal tactics and genetic population structure in ants

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Ants have two main modes of colony founding: 1. Young winged queens participate in a nuptial flight and then establish new colonies independently, relying on the resources they have accumulated in the natal colony, or 2. Winged queens mate inside the natal colony, and remain there to reproduce. New colonies then arise through the formation of bud-nests. An intermediate form of colony-founding also occurs, where young queens depart on mating flights and then overtake heterospecific nests by killing the queen.

The present study analyses the genetic relatedness, mating system and population structure in the ant *Formica truncorum* where colony-founding occurs both through nuptial flights and intranidal mating. The results show clear differences between separate populations of this species, with some populations consisting exclusively of multi-queen colonies and others of single-queen colonies. Multiple-queening is associated with considerable genetic subdivision of populations, although effective population sizes are high, whereas no such differentiation was detectable in populations with single-queen colonies.

The mating system, as analysed both by behavioural studies and genetic analyses, also differs between the two population types. Multiple-queening is associated with matings between relatives, whereas outbreeding appears to be the rule in the single-queen societies. Although no significant inbreeding was detected in the multiple-queen population, the occurrence of diploid males suggest some loss of variation at the sex determining loci, possibly because of bottleneck effects when the populations were established.

An unusual case of gene flow opposing selection

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We present evidence that gene flow counteracts strong directional selection to maintain a high level of polymorphism at *Pgm-3*, a gene known to have a major effect on reproduction in the population of the ant *Solenopsis invicta* that we studied.

Reproductive queens in this population never possess the homozygous genotype *Pgm-3$^{a/a}$*, whereas pre-reproductive and non-reproductive females possess it at substantial frequencies. The loss of *Pgm-3$^{a/a}$* queens, which occurs because workers selectively destroy all such queens as they initiate reproductive development, constitutes a process of strong negative selection on the allele *Pgm-3^a*. This allele is maintained at high frequency in the study population in spite of such directional selection by means of continual gene flow from a population of a different social form, in which equivalent selection is not found and the allele *Pgm-3^a* is common.

Evidence for such gene flow comes from two sources. First, *Pgm-3^a* genotype and allele frequencies for parental and offspring generations suggest

that a large majority of matings at five of our six study sites, and half or more of the matings at the final site, are between resident females and immigrant males of the alternative social form. The exact proportions of matings attributable to immigrant males at each site vary predictably according to distance from an upwind source of such males. Second, the proportions of queens that are mated within the study population depend to a large extent on the proximity to an upwind source of immigrant males. This system represents a unique example of how the extent of genetic variation and its distribution within and between populations can be affected by gene flow occurring in the face of strong, locally restricted, selection.

Social structure and relatedness in the greater white-toothed shrew *Crocidura russula*

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While sympatric in western Switzerland, the two similarly-sized shrews *Sorex coronatus* and *Crocidura russula* differ markedly in their ecology and social behaviour: *C. russula*, that lives in more patchy and structured habitat, also displays a more social life, spending winter in communal nests. Did sociality evolve from the kinship structures stemming from habitat patchiness ? To address this question, I studied the patterns of juvenile dispersal in three *C. russula* metapopulations during two consecutive years.

These metapopulations consisted of series of demes, each made of several territories ('home ranges') inhabited by monogamous pairs. Each pair produced 3-4 litters per breeding season. The first-litter dispersal was biased towards females, who left their natal home range and occupied new territories two or more home ranges away from their birth site, but within their parental deme. All of these females were pregnant when recaptured 30 days after weaning.

Males were still more philopatric: the largest male from the first litter remained in its natal home range for the whole season, sharing parental nest with subsequent litters. These males did not reach maturity this same year, but inherited the parental territory the following one. The second largest male settled in a neighbouring territory, sharing it with a pregnant juvenile female from the same deme, and reached maturity the same year. The second and third litter showed no sex difference in dispersal: all juveniles remained in their natal home range.

These patterns clearly show that demes actually correspond to close familial groups. As a consequence, only kin coexist in winter, when animal share communal nests. I tried to corroborate these interpretations with genetic markers. However, multilocus DNA fingerprinting revealed unsuitable, due to the surprisingly low variance found, even among geographically distant populations. The possiblitity of using microsatellites loci is currently under investigation.

DISCUSSION

One of the striking features of the meeting was the impressive diversity of views from which metapopulations can be looked at. As put by one participant, there are plenty of good reasons to study metapopulations, not least because they are so ubiquitous.

The genetic patterns resulting from metapopulation structures were widely documented throughout the meeting, both in plants (THOMPSON, GOUDET & GILES, HUMBERT-DROZ & FELBER, MICHALAKIS *et al.*) and in animals (RANK, CHAPUISAT, SUNDSTRÖM, KELLER & ROSS). These patterns were stemming from a variety of causes, some of which purely environmental, e.g. geographical barriers (RANK) or simply distance (GOUDET & GILES, MICHALAKIS *et al.*). Distance effect can act at surprisingly small scale (CHAPUISAT), even in wind-pollinated herbs (HUMBERT-DROZ & FELBER). Mating and dispersal strategies play a crucial role as well. In plants, the ways pollen or seeds are dispersed have dramatic effects on the differentiation among populations (THOMPSON). In ants, similarly, differentiation strongly depends on whether sexuals exhibit mating flights or not (CHAPUISAT, SUNDSTRÖM, KELLER & ROSS). A third significant cause of population structuration, namely chromosomic mutations (robertsonian fusions or, more commonly in plants, polyploidisation), was also largely documented (HAUSSER, BRÜNNER, HUMBERT-DROZ & FELBER).

To make order from this diversity, one needs some unifying approaches and quantitative analytic tools. F-statistics, most widely used in this context, allow in principle to disentangle the effects of geography and mating systems by distinguishing several levels of analysis (COUVET): F_{st} accounts for the proportion of variance within metapopulations due to differentiation among demes, F_{is} for the proportion of variance within demes due to inbreeding, etc.

F-statistics, however, received several criticisms. A minor one addressed the fact that they do not make full use of all available information. In this context, EXCOFFIER proposed an extension to include molecular data: when measuring differentiation, it may be useful to know not only whether alleles differ between populations, but also of how much they differ (e.g. in terms of point mutations). Another kind of extension was proposed by COUVET to include information from multiple loci associations. One of the nice features of such multigenic estimates is that they also allow to test some assumptions of the underlying metapopulation model (here the island model), such as that of constant size through time.

These assumptions were precisely the focus of other, more fundamental criticisms to the use and misuse of F-statistics. The island model, on which conventional interpretations of F-statistics are based, relies on a series of strong assumptions about population structure, among which: demes are assumed similar in size and constant through time; all are interconnected by a similar and constant amount of migration; genetic drift and migration equilibrate (equilibrium condition), selection is absent, etc. The problem is that real populations do vary in size, some go extinct, they divide or fuse, gene exchange may depend on distance, etc. As convincingly advocated by WHITLOCK, real populations evolve out of equilibrium. This has strong consequences on the meaning and informative value of F_{st}. Effective population size, for instance, may be grossly over- or under-estimated by F-statistics in non-equilibrium populations. Non-equilibrium also has strong

evolutionary consequences: genetic drift induced by fluctuating population size, for instance, may increase the probability that a given deme eventually reaches global (as opposed to local) adaptive peak in a fitness landscape (WHITLOCK).

From the many empirical examples presented at the meeting, certainly none fitted all the assumptions of the island model. Several aspects of such non-equilibrium situations were investigated.

The problem of extinction and colonisation events was tackled both from an empirical (BAUR) and a theoretical (ARDITI, GRUNTFEST) perspective. Habitat fragmentation potentially has many distinct effects on populations (BAUR), all of which are likely to increase extinction probability. Experiments are needed to quantify and disentangle these potential effects. BAUR presented an on-going project, exemplifying the conceptual and practical difficulties in designing such experiments.

Theoretical approaches showed that, while extinction risk at the demic level mainly depends on deme size and environmental variablity, many factors interact at the metapopulation level, including the number of demes, the temporal correlation among their environments (GRUNTFEST), as well as the dispersal strategies of organisms (ARDITI). Complex systems with multiple equilibria result, where historical effects may play a significant role (GRUNTFEST). Metapopulations show emergent properties, in that their dynamics does not reduce to the sum of the dynamics of constituting demes.

Concerning dispersal strategies, of crucial importance is whether migrants are able to distinguish target populations according to state. Intuition suggests that migrants settling in an empty patch may hope a brighter future than those joining a saturated or declining population. But the reverse may actually occur, depending on the values of demographic parameters (ARDITI). This should obviously affect the evolution of dispersal strategies. There is indeed plenty of evidences that dispersal strategies are optimized by natural selection (THOMPSON). However, the point was also made that, unlike models of population management, natural selection does not necessarily minimize extinction risk of metapopulations: strategies may invade even though they are detrimental to metapopulation survival. For an evolutionary perspective, an ESS approach should be preferred over optimization techniques.

Dispersal strategies are also relevant to the genetic structure of metapopulations. The usual consequence of non-equilibrium dynamics is to increase population differentiation (WHITLOCK). However, in two-species interactions, like as host-pathogen systems, high extinction rates of hosts may actually homogoneize pathogen populations by selecting for high dispersal rates. This is indeed suggested by the results from MICHALAKIS *et al.* on phytophagous beetles, in which the high extinction rate of the host plant seems responsible for the low differentiation among insect demes. In this precise case, high extinction rates of hosts apparently prevented coevolution with associated pathogens. This however is certainly not a general situation in non-equilibrium metapopulations, as OLIVIERI and CAPOWIECZ showed by statistical analyses of computer simulations.

The question may be asked, conversely, how specific genetic structures, (e.g. low genetic diversity) may affect extinction rates. Inbreeding in small populations has often been assumed to enhance extinction risks, and this assumption is frequently built in theoretical models (e.g. the Allee effect,

GRUNTFEST), and advocated when designing experimental studies (BAUR) or management policies for endangered species (THOMPSON). But empirical evidence remains scarce.

Active dispersal strategies may strongly bias gene exchanges between demes, thereby falsifying assumptions of the island model. But passive dispersal may have the same effect, and unequal gene flow may result from still other processes. Consistent evidence was provided that gene flow between populations are often assymetrical (HUMBERT-DROZ & FELBER, KATOH, BRÜNNER), which may in some cases arise from behavioural differences among populations (e.g. in female choosiness; BRÜNNER).

Geographic distance may induce strong biases as well (GOUDET & GILES), sometimes on a very small scale (HUMBERT-DROZ & FELBER, CHAPUISAT). This argues for stepping-stone or diffusion models, much more than for the island model, which obviously affects the interpretation of F-statistics. Differential gene flow from unsampled neighbourgs, for instance, may strongly exaggerate the estimation of F_{st}. A good example was provided by RANK: the high differentiation among beetle populations from Alpine valleys was more likely due to gene flow from unsampled neighbouring populations than to a low migration rate.

Stepping-stone and diffusion models induce viscosity in populations; the genetic consequences of a given migration rate thus strongly depend on the distribution of migration distances. Do migrants join other demes independently of distance, or only immediate neighbours? The empirical results provided suggests that natural populations are often very viscous, sometimes extremely so (CHAPUISAT, FAVRE). This is also bound to affect the measurement and interpretation of relatedness (CHAPUISAT, SUNDSTRÖM). This issue is central to the evolution of social behaviour, since, while relatedness definitely affects the evolution towards sociality (QUELLER), viscosity does not necessarily so: the relatedness gradient induced by viscosity frequently correlates with competition gradients, with the result that their opposing effects on altruism cancel out (QUELLER).

The importance of historical patterns also advocates against the island model: metapopulations do not necessarily arise from the progressive subdivision of large panmictic populations. Buddings occur, as well as fusions and fissions (CHAPUISAT, WHITLOCK & ZEUS); geographic differentiation can be followed by secondary contacts; isolated historical events, such as chromosomic fusions or polyploidisation (HAUSSER, HUMBERT-DROZ & FELBER), may play a big role. Some historical knowledge is often necessary to interpret today's patterns. This is clearly evident at the biogeographical level where, even in environments that a priori most closely match the island model (like archipelagoes), simple covariance model of speciation can be definitely rejected (RUEDI). This is also nicely exemplified by studies of secondary contacts between subspecies (HAUSSER, BRÜNNER, HUMBERT-DROZ & FELBER) or species (KATOH): present-day barriers to gene flow have no ecological meaning, and clearly result from historical expansions of ranges. Studies of secondary contacts may provide surprising side results: different species may exchange genes but still remain distinct (KATOH), while different populations currently assigned to the same species may have no exchange, even in close contact (HAUSSER). This has interesting implications for the 'biological' definition of species.

A recurrent problem was the identification of panmictic units and appropriate scale of measurement. GOUDET and GILES gave strong indication that islands in their archipelago were not random breeding units. What about social insects? Should measurements be taken at the level of nest or of colony (CHAPUISAT, SUNDSTRÖM) ? As simulations show (OLIVIERI & CAPOWIESCZ), which patterns are observed depend on the scale of observations; patterns may emerge from noise as sampling area increases.

Another recurrent discussion topic was the difficulty in estimating migration rates and gene flow. Direct methods (marking and recapture of individuals) have weaknesses: how confident are we that migrant individuals do really contribute genes ? What happens with not-recaptured animals (FAVRE) ? But indirect methods (sharing of common alleles) also have problems: does a shared polymorphism indeed reflect gene flow, or was it inherited from a common ancestor (KATOH, BRÜNNER) ? Furthermore, indirect estimation of migration rate may depend on the genetic markers sampled: within a given contact zone, some markers may show introgression, while others don't (KATOH, BRÜNNER). Some peculiar situations do permit high confidence in gene flow estimates. KELLER & ROSS gave compelling evidence that gene flow alone was able to maintain in a population an allele otherwise strongly selected against. Such clear-cut situations are however rather uncommon. The best way in general to tackle such difficulties lies in combining measurements of allele frequencies, field studies of individual dispersal, and behavioural observations in the laboratory (WHITLOCK, KATOH, BRÜNNER, FAVRE).

As a matter of fact, many authors stressed the importance of detailed biological studies. Genetic patterns are not interesting per se; they gain value only insofar as they can be linked to biology, and put in a perspective involving ecological causes and evolutionary consequences. Clear examples were provided by connections between genetic patterns and mating systems or social structures (THOMPSON, QUELLER, SUNDSTRÖM, CHAPUISAT, KELLER & ROSS). In this context, the results of genetic studies may reveal highly heuristic: observed discrepancies between the introgression of nuclear vs mitochondrial markers (HAUSSER, BRÜNNER), for instance, have the potential to throw important light on sex-biased dispersal-strategies or mate-choice patterns.

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