

Landscape ecology: Population genetics at the metapopulation level

Domenica Manicacci¹, Isabelle Olivieri², Vtronique Perrot^{2,4}, Anne Atlan¹, Pierre-Henri Gouyon³, Jean-Marie Prossperi² and Denis Couvet¹

¹Centre Emberger, CNRS, Route de Mende, BP 5051, 34033 Montpellier Cedex, France; ²Station de génétique et amélioration des plantes, INRA Montpellier, Domaine de Melgueil, 34130 Mauguio, France; ³ESV, Batiment 362, Université Paris XI, 91405 Orsay Cedex, France; ⁴(Present address) Zoologisches Institut der Universität, Rheinsprung 9, CH-4051, Basel, Switzerland

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Abstract

Distribution of genetic diversity in a landscape depends on both within and among population processes. Selective pressures within populations have traditionally been studied by population genetics, which usually assumes that populations are at equilibrium. However, when selection pressures within and among populations are different, landscape processes are required to define an equilibrium (landscape being defined as the habitat of a set of populations called a metapopulation, and populations will differ depending on their situation in the landscape, *i.e.* their age and the state of neighboring populations). We examine reproduction systems and life history traits, for which variation depends on landscape processes. Predictions of their states in a metapopulation are drawn from theoretical models, and confronted to observations collected in natural populations.

Introduction

One of the goals of population biology is to explain how polymorphisms are maintained in natural populations. To achieve this goal, both the distribution of diversity and the outcomes of selection are usually studied at the population level. However processes occurring within population do not appear to explain the maintenance of some traits. Diversity is also known to be present among populations, and studies at larger scale, a set of populations, need to be developed. Distribution of genetic variability at such a larger scale has been less studied, in part because it involves larger temporal and spatial dimensions. Its study should be considered as a part of landscape ecology, since the distribution of diversity depends on the spatial and temporal dynamics of populations within the landscape. Indeed, distribution of genetic diversity de-

pends on parameters such as frequency and intensity of perturbations, migration rate between populations and the reproductive system of the species. Any change in landscape processes, due to natural disturbances or landscape management can involve modifications of selection pressures (which can act among species, leading to extinctions or invasions of species, as well as within species, by the evolution of the species which persist) and could then have predictable influences on the evolution of the biological diversity. How landscape dynamics influences biodiversity may be useful to the population biologist concerned by the evolution of such characters, and to the landscape ecologist concerned by the impact of environment on biodiversity.

Some characters, concerning reproductive biology (inbreeding, sexual forms and sex allocation) and life history traits (iteroparity and dispersal), are

specially relevant to study landscape properties because:

- they are responsible for the distribution of genetic diversity in space and time since reproductive traits determine mating choices, and life history traits determine the distribution of offsprings,
- they are genetically variable. This variability may be found within and among populations.
- they are sensitive to selective processes that depend on spatial and temporal dynamics of populations.

From a population genetics standpoint, a landscape can be defined as a set of sites, each site holding an ensemble of individuals called a population. The set of individuals that inhabit a landscape has been called a metapopulation, defined as a set of populations that communicate between each other (Levins 1970; Wilson 1973; Couvet *et al.* 1985; Olivieri *et al.* 1990). Migration between populations of the same metapopulation is more effective when populations are just founded, since their density is lower and a migrant can easily be recruited. A metapopulation being defined for one species, several metapopulations may coexist in the same landscape. The metapopulation has a dynamic component due to localised extinctions and recolonisations, which are determined by factors such as the life-span of a population (the time a population occupies a site), initial population size, the migration rate between populations. Some conditions are required for processes in a metapopulation to differ from processes within populations, and for landscape processes to influence the distribution of genetic diversity:

- a difference of selective pressures, in the same site, depending on the age of a population. Nevertheless we make the simplifying assumption that there is no correlation between the age of a population and the environmental characteristics of its site. This means that the evolution of the selective pressures only depends on the biological characteristics of the population, and/or
- founder effects (defined as a reduced variability in the origin of founders so that founders of two populations will differ) influencing the outcome of selection in a population (Olivieri *et al.* 1990). Each of these points is developed later.

In this paper we discuss which characters depend on landscape processes, which characteristics of the landscape will determine the outcome of natural selection, and what kind of relationship can be drawn between the state of these characters and the dynamic of the landscape.

Materials and methods

In this paper, theoretical predictions are presented, and, when possible, compared with data collected in natural populations.

Theoretical predictions are derived from population genetics models where selection operates in a landscape, *i.e.* on several sites of different ages, with migration between the different sites. Every site has a probability to be disturbed (and then the population disappears) which depends only on its age. Different genotypes are introduced, and computer simulations are used to determine which genotype would be favored.

Data are collected in the Languedoc region of southern France, most of the sites being located in the basin of Saint-Martin-de-Londres, 25 km north of Montpellier, France. A site is defined as an homogenous entity. Its area can vary from 20 m² (*Carduus* and *Thymus*) to 10000 m² (*Medicago*), depending on the dispersal rate (low dispersal rate implying genetic differentiation within a large site) and the density of the species considered.

1. Reproductive systems

When individuals often occur at low density (*e.g.* because disturbances are frequent and/or demographical increase is low) and when populations are structured (*i.e.* migration rate between populations is low), recruitment will be often density independent and preferential effort into female function (reproduction by seeds) will be favored (Hamilton 1967; Carothers 1980). We now develop two points in the case of gynodioecy: maintenance of female frequency, and sex allocation in hermaphrodites.

1.1. Gynodioecy

1.1.1. Theoretical background

We will deal more specifically in this section with gynodioecy in higher plants, *i.e.* in species where females (or male-steriles) and hermaphrodites coexist. Genetic determinism of gynodioecy usually involves nuclear and cytoplasmic genes (Lewis 1941; Cosmides and Tooby 1981; Gouyon and Couvet 1985). Under nuclear determinism, females (which do not produce pollen) must produce at least twice as many seeds as hermaphrodites to be maintained within a population, and, in populations at equilibrium, the frequency of females is positively correlated with the advantage of female fecundity and varies from 0 to 50% (Lewis 1941; Gouyon and Couvet 1985).

Founder effects, through the reduction of genetic variability within a population, may influence both nuclear and cytoplasmic gene frequencies. The absence of nuclear restorer gene (*i.e.* genes that determine the hermaphrodite sex) generally occurs in young populations and results in high female frequency in such populations. When restorer genes arrive in a population, by migration or eventually mutation, the frequency of females decreases. Consequently we can observe a negative correlation between the frequency of females and the age of populations.

The frequency of females observed in the landscape will then depend primarily on the dispersal rates of female and male gametes, the life-span of populations and the number of founders; *i.e.* variables that are determined by landscape dynamics. When gene flow is low, the number of founders is high and the life-span of populations is low, male-sterility may disappear, but may be maintained at a noticeable frequency when the number of founders is low and/or the life-span of populations is long (Gouyon and Couvet 1985; Frank 1989).

In this case the reproductive system of a species, hermaphroditic or gynodioecious, will depend on the internal dynamics of the species in a landscape.

1.1.2. Observations

In *Thymus vulgaris*, two different studies have concluded that the frequency of females first increases

in new populations, and then decreases (Dommée *et al.* 1983; Belhassen *et al.* 1989). However, populations in post-cultural successions show a higher overall female frequency than populations in post-fire successions (Dommée *et al.* 1983). Founders in the post-fire successions might be issued from the seed bank that has not been completely destroyed by the fire. In that case, founders may be more genetically related one to one another than those in a post-cultural succession, which originate from other sites. As a result the absence of the restorer gene of a cytoplasm is less likely to happen, and the expected frequency of females will be lower (Belhassen *et al.* 1990; Couvet and Gliddon, in prep.). The way founders originate in a landscape is then very important.

The frequency of females of *Thymus vulgaris* was measured in 1976 and 1988 (Fig. 2), in 57 populations grouped in 4 transects each considered as a different landscape (Fig. 1), while the average distance between two populations of the same transect is 0.15 km and the average distance between transects is 2.80 km. Average frequency of females does not differ in 1976 and 1988 (59.0% in 1976 and 58.8% in 1988, $p > 10\%$). We observed, in 1976, similar female frequencies in the four transects (58.3, 59.1, 59.1 and 61.5, $p > 0.92$), but different evolution of the frequency of females in the four transects (female frequency did not vary significantly for transects 1 to 3 but decreased highly in transect 4). In 1988, the frequency of females is significantly different among the 4 transects (63.2, 55.4, 58.0, 52.1, $p < 0.07$). The proportion of populations in which female frequency increased (or decreased) was significantly different in the 4 transects ($X^2(3) = 10.6$, $p < 0.05$). The evolution of female frequency was different in the 4 transects. Then landscape scale remains particularly relevant to study male-sterility dynamics since each landscape exhibits a different dynamics.

1.2. Sex allocation in hermaphrodites

1.2.1. Predictions

Hermaphrodite individuals bear both male and female reproductive functions. As long as a trade-off between these two sexual functions exists, alloca-

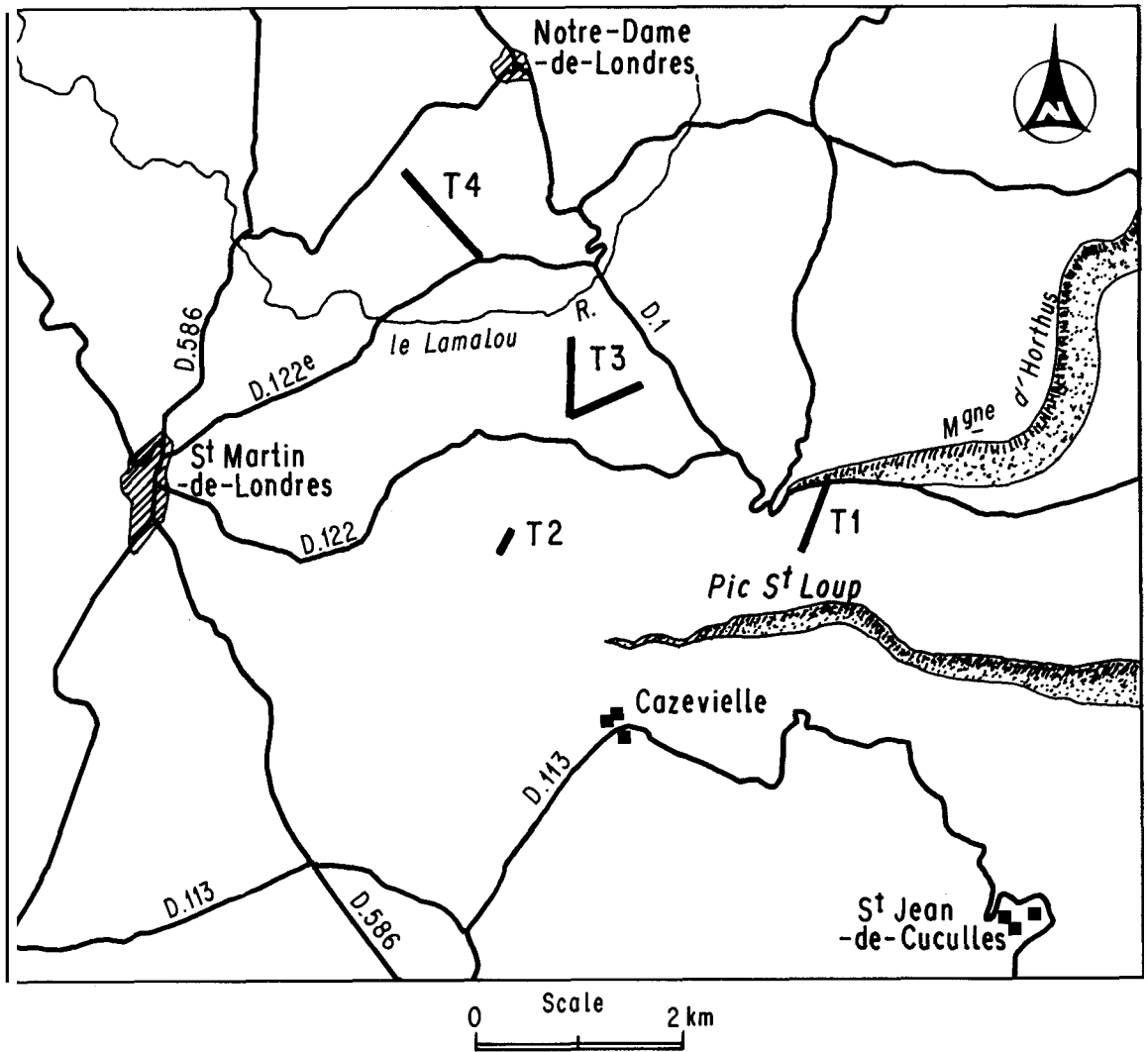


Fig. 1. Map of the basin of Saint-Martin-de-Londres (Languedoc, South France), where 4 transects of populations of *Thymus vulgaris* (T1 to T4) are located. Each transect bears 12 to 17 populations. The distance between populations within a set is less than 2 kms apart, the distance between sets is less than 10 kms.

tion to each function in hermaphrodites should respond to natural selection (Darwin 1877; Charnov *et al.* 1976). Increased allocation to female function, at the expense of male function, will occur as long as dispersal of female gametes is higher than that of male gametes (Bulmer and Taylor 1980). This will be the case when, for example, pollinators remain within a site, but migration between sites occurs only through seeds. Sex allocation should be more biased towards female function in newly colonized sites, so that the more disturbed a

landscape is, the more the hermaphrodites will invest into female function. The most critical variable influencing this process, will be the number of founders (Bulmer and Taylor 1980). In species where male-sterility is present, the frequency of females is expected to be related to sex allocation of hermaphrodites: the less hermaphrodites invest in female function, the more frequent male-steriles should be (Charnov *et al.* 1976; Lloyd 1976).

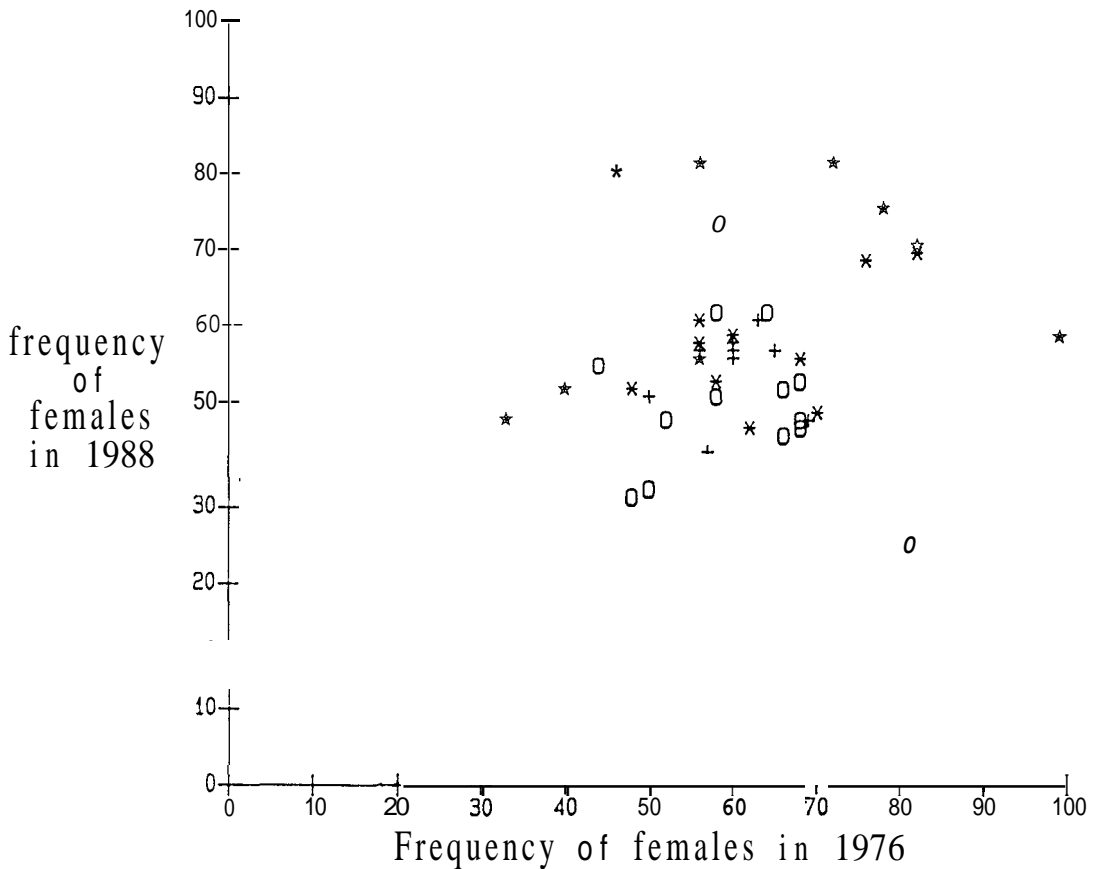


Fig. 2. Frequency of females in 57 natural populations of *Thymus vulgaris* in the basin of Saint-Martin-de-Londres on 1976 and 1988. These populations were grouped in 4 transects (see Fig. 1): * = T1, + = T2, ⋆ = T3, ○ = T4.

1.2.2. Observations

Observations tend to support such a correlation (Delph 1990). High variations of female frequency observed in the landscapes occupied by *Thymus vulgaris* (10 to 90% (Dommée *et al.* 1983), 48 to 83% (Belhassen *et al.* 1989)) should be accompanied by variations in the sex allocation of hermaphrodites. Measures of sex allocation in thyme, based on the number of pollen grains and seeds produced per flower for individuals collected from 10 populations, show a correlation, but the inverse of what was predicted: as frequency of females increases, hermaphrodites allocate less to male function. However, this result only appears when related populations, less than one kilometer apart, are compared. The result holds whatever the disturbance that originated the population: post-fire or

post-cultural succession. But for distant populations, sex allocation of hermaphrodites is more dependent on their geographic origin than on their age.

2. Allocation to survival and reproduction

2.1. Predictions

Allocation of sexual resources represents a trade-off between allocation to male and female reproductive functions. Likewise, longevity of individuals results from a compromise between survival and reproduction. In new populations, where density is low and recruitment is density-independent, high fecundity, even at the expense of survival, *i.e.* semelparity, will be favored (Lewontin 1965). At

Table 1. Age class and survival rate of 16 natural populations of *Medicago lupulina*.

Population	Age	Survival rate
BIR1	New	0.034
MAS	New	0.789
GAB1	Inter	0.000
GAB4	Inter	0.000
GAB3	Inter	0.000
BIR2	Inter	0.000
SMDL2	Inter	0.158
BOR4	Inter	0.158
BOR2	Inter	0.200
VIV5	Inter	0.281
MAT2	Old	0.000
BIR3	Old	0.000
PDR2	Old	0.029
BIR4	Old	0.031
BIR1B	Old	0.311
SMDL1	Old	0.400

the opposite, in populations where density is high and density-dependent selection occurs, higher survival, *i.e.* iteroparity, will be favoured. Vegetation succession, where semelparous colonizing species are often replaced by iteroparous species (Lepart and Escarré 1983; Walker and Stuart Chapin 1987) shows that such selective processes operate among species. The same process could operate within species, as long as variability for allocation to survival versus fecundity is present. Olivieri (1987) has shown that, for certain sets of landscape parameters, it is possible to maintain a polymorphism between annual and perennial genotypes in a metapopulation. In this case, the frequency of the annual genotype decreases with increasing age of the populations.

2.2. Observations

In *Medicago lupulina*, survival from year to year can vary between 0 and 80% of individuals within a population. The survival rates of individuals at a site were measured as the survival in fall, after the dry season, in 1988. Sixteen sites with *M. lupulina* were classified as new, intermediate or old, depending on apparent date of the last disturbance. Presence of straws from cereals was taken as in-

dicating recent cultivation. These sites were considered to be occupied by new populations. Abandoned vineyards were classified as new to intermediate, while garrigue sites, with native plants, were considered as old. Survival rate varied from 0 to 40% but no correlation was observed between population age and survival rate (Table 1).

3. Dispersal

Dispersal may occur i) in space (through seed movements by wind or animals, or flights for insects) and ii) in time (through seed dormancy or diapause). Selection on these characters will be highly dependent on spatial and temporal dynamics of landscapes.

3.1. Dispersal in space: migration

3.1.1. Predictions

As long as founders are migrants from other sites, one would expect a higher rate of migration in new populations – there has been selection in favour of migration abilities – and a lower rate in old populations: the higher the rate of migration of a genotype, the more likely it is to disappear from the site considered (Olivieri and Gouyon 1985). The migration rate favored within a metapopulation will depend on the number of generations populations last, as well as the likelihood for migrants to found new populations (Olivieri *et al.*, in review).

On the other hand, the distribution of individuals present in a landscape will depend on the migration rate. When migration is low, some new sites may be left unoccupied, although a high migration rate might decrease the probability of maintenance of a population in a given metapopulation (Olivieri 1987). The migration rate between populations that maximizes the number of individuals within a landscape is always greater than the migration rate that is selected for (Olivieri *et al.*, in review).

3.1.2. Observations

Loss of ability to migrate for insects and plants present on islands (MacArthur and Wilson 1967; Carlquist 1974) can be considered as support in favour of this hypothesis, the probability of

Table 2. Age class and migration rate of 15 natural populations of *Carduus pycnocephalus*.

Population	Age	Migration rate
JAS	New	0.786
DL2	New	0.782
QH7	New	0.799
IJ5	New	0.901
DL3	Inter	0.809
GAB	Inter	0.789
DL5	Inter	0.720
MOG	Inter	0.783
DL6	Inter	0.752
ATV	Inter	0.817
GAL	Inter	0.893
DL4	Old	0.665
QH2	Old	0.735
AT1	Old	0.883
AT2	Old	0.932

colonizing new sites being very low when individuals are on small islands because of the very low frequency of favorable sites.

Previous observations in Californian populations of *Carduus tenuiflorus* and *Carduus pycnocephalus* (Asteraceae with seed dimorphism for dispersal) have shown that the older the site, the lower the migration rate (Olivieri and Gouyon 1985). More observations were collected on fifteen populations of *Carduus pycnocephalus* in Languedoc region (Table 2). Migration rate was estimated by the proportion of migrant seeds (seeds with pappus) by plant. These observations did not confirm the correlation expected.

3.2. Dispersal in time: dormancy

3.2.1. Predictions

Dormancy will be higher in new populations when individuals are regenerated from the seed bank, and as long as there is genetic variability for that character. Neglecting population bottle-necks within a site, one expects a lower dormancy in older sites.

3.2.2. Observations

Dormancy was measured in three species belonging to the genus *Medicago*, *M. orbicularis*, *M. rigidula*, and *M. lupulina*. Rate of dormancy was estimated

Table 3. Age class and dormancy rate of natural populations of *Medicago*.

Population	Age	Dormancy rate
<i>a</i>		
VAL2	New	0.991
PUE	New	0.960
LEM2	New	0.897
SMDL2	Inter	0.975
MATV	Inter	0.960
BOR4	Inter	0.950
VIV6	Inter	0.942
MAT1	Old	0.962
LEM3	Old	0.954
SMDL1	Old	0.906
MAT2	Old	0.878
<i>b</i>		
MAS	New	0.984
BIR1	New	0.937
GAB2	Inter	0.983
GAB3	Inter	0.974
GAB1	Inter	0.964
BIR2	Inter	0.955
GAB4	Inter	0.907
BIR4	Old	0.990
BIR3	Old	0.990
BIR1B	Old	0.962
PDR2	Old	0.947
<i>c</i>		
LEM	New	0.995
VAL2	New	0.995
VIV8	New	0.990
LEM1	New	0.985
PUE	New	0.984
VAL3	New	0.960
BOR1	New	0.942
SMDL2	Inter	0.995
MATV	Inter	0.995
GAB1	Inter	0.990
VIV6	Inter	0.985
VIV5	Inter	0.985
GRA	Inter	0.975
GAB2	Inter	0.975
VAL	Inter	0.973
BOR4	Inter	0.943
LEM3	Old	0.995
MAT1	Old	0.993
VIV1	Old	0.990
SMDL1	Old	0.990
VIV4	Old	0.987
VIV2	Old	0.982
MAT2	Old	0.980

a: 11 natural populations of *Medicago rigidula*.

b: 11 natural populations of *Medicago lupulina*.

c: 23 natural populations of *Medicago orbicularis*.

as the rate of viable seeds that did not germinate immediately after harvesting (Table 3). Although variations of rate of dormancy were low (from 94 to 98% of seeds were dormant), significant differences existed among populations. However there was no correlation with the estimated age class of these populations.

4. The extent of inbreeding

4.1. Predictions

As a landscape may determine the distribution of individuals, it may determine relatedness of mating individuals and thus the extent of inbreeding. Depending on the reproductive system, inbreeding can result from selfing (*e.g.* self-compatible hermaphrodites, in plants and many invertebrates with the exception of insects) or from mating between close relatives (as in many plants, vertebrates, insects . . .). In both cases, the theory of population genetics predicts that inbreeding will be favored as soon as inbreeding depression (the decrease of fitness due to inbreeding) is lower than a critical value, which depends on the relatedness between mating individuals (May 1979), this value being two (*i.e.* outbred individuals are twice as fit as inbred individuals) in the case of selfing (Fisher 1941). The hypothesis that inbreeding depression is constant predicts that species should either be complete outcrossers or complete inbreeders, and that intermediate levels of inbreeding should disappear (Lande and Schemske 1985). However, for example in insect-pollinated plant species, intermediate selfing rates have been observed (Aide 1986; Valero *et al.* 1986), for which several hypotheses have been proposed to explain how an equilibrium level can be attained within a population (*e.g.* Maynard-Smith 1978).

One explanation of intermediate selfing rates, at the landscape level, could be that selection on avoidance of inbreeding might differ depending on the age of a population, so that an intermediate selfing rate could be selected within a metapopulation. Inbreeding depression might increase with the age of the population. One reason may be that inbreeding depression increases with competition be-

tween individuals, *i.e.* with the density of the site. Another reason may be sib competition, *i.e.* competition among the progeny of a single maternal parent, which may be higher in dense populations. In such a case outcrossing can be favored in old populations, even in the absence of any inbreeding depression, due to the advantages of genetic variability within each progeny (Williams 1975). However, variation of inbreeding depression depending on environmental conditions can also lead to the reverse prediction. Migration of a seed to a new environment, *i.e.* different from the environment present in the site of its parents, will favour new genetic combinations as well as heterozygosity, *i.e.* will favour outbreeding. As a result, a lower rate of inbreeding will occur in new populations and adapted inbred genotypes will be found in old populations (Holsinger 1986).

Whatever the trends of variation of inbreeding depression, which can be assumed to increase (Holsinger 1986) or decrease with the age of a population, and as long as genetic variability for inbreeding rate exists within a landscape, one can predict that the inbreeding rate will depend on the age of a population, and then that there will exist in the landscape an intermediate selfing rate which is the result of an equilibrium between antagonistic selective pressures.

4.2. Observations

Weeds (*i.e.*, plant species that are colonizers) are usually inbreeders (Baker 1965). Compared to non-weeds, weedy species will be mostly found in young populations, so that the present correlation can be considered as support for the idea that inbreeding rate should decrease with population age.

Within *Carduus pycnocephalus* as well as *Carduus tenuiflorus*, Olivieri *et al.* (1983) have shown that non-dispersed seeds (without a pappus) were more likely to be selfed than dispersed seeds (with a pappus) due to flowering biology. Selection for non-dispersing genotypes within populations suggests that inbreeding rate increases with population age.

Dommeé and Jacqard (1984) studied a set of 7 populations from 9 to 60 years old. In each popula-

tion they estimated inbreeding depression as the height of the females' offsprings (obviously produced by outcrossing) compared with the height of the hermaphrodites' ones (which may arise from inbreeding). Heterozygosity was measured with electrophoretic markers. They show a decrease of inbreeding depression and heterozygosity, suggesting an increase of inbreeding rate, when the age of the populations increases.

Discussion

We will first discuss processes, functioning within and among metapopulations, that are relevant for the interpretation of some traits. In a second part we will discuss the methodological difficulties that can obscure our interpretations for some characters.

Metapopulation functioning

Theoretical results support the idea that the state of some traits depends on the age of a population, and that equilibrium stages and/or maintenance of polymorphism are possible in a metapopulation, but not within a population. The characters concerned are dispersal in time and space, allocation to survival, as well as some reproductive characters. Different processes are responsible for their dependence on the age of a population.

– It can be due to the antagonism of selective pressures on colonizing and persistent genotypes in a given site. This involves dispersal and longevity (annual vs perennial). Higher dispersal and/or higher reproductive effort increase the likelihood of colonizing a new site, but may decrease the likelihood to persist in a site if there is a trade-off between dispersed and non dispersed seeds produced by a same plant and/or between reproductive effort and adult survival rate.

– It can be due to founder effects. This concerns traits for which the extent of genetic variability determines the course of selection. Theoretical models predict that fragmentation of the landscape increases the frequency of Robertsonian fusions in mice (Michalakakis and Olivieri, in review) and of nucleocytoplasmic male-sterility in plants (Couv

and Gliddon, in prep.). Restricted genetic variability may also be responsible for the fact that hermaphrodites in new populations of *Thymus vulgaris* allocate a greater proportion of resources to the female function. Lack of coadaptation between cytoplasmic and nuclear genomes (*i.e.* lack of nuclear restorer genes corresponding to present cytoplasmic genes of male-sterility), due to founder effects, simultaneously involve high female frequency and hermaphrodites with partial restoration of their male function. Restricted genetic variability in new populations can in general have a wide impact on a species reproductive system. It has been proposed to explain i) unequal frequencies of morphs in tristylous species, ii) the break-down of the tristylous reproductive system (Morgan and Barrett 1988) and iii) the higher incidence of dioecy on islands (Baker 1967). Landscape fragmentation, which influences genetic variability within populations through the size of breeding units in a landscape, will thus influence reproductive systems. However, founder effects do not last for ever, and although they may explain patterns of differentiation in young populations, it is likely that other processes will be involved in older populations (Gouyon *et al.* 1990).

Differentiation among landscapes

Distance between sites has been revealed as an important factor determining landscape patterns (indeed results on sex allocation show that correlation between a character and the age of a population is only true for neighboring populations). For distant populations other factors that differentiate landscapes will obscure this relationship. This is the case for female frequency in thyme (where patterns of variation differ from one metapopulation to another, *i.e.* from one landscape to another – Fig. 1) and for sex allocation in hermaphrodites (where the expected correlation is only observed within a landscape).

We will now discuss hypothesis for the lack of expected correlation between the age of populations and survival rate (in *Medicago lupulina*), migration rate (in *Carduus pycnocephalus*) or dormancy rate (in the genus *Medicago*).

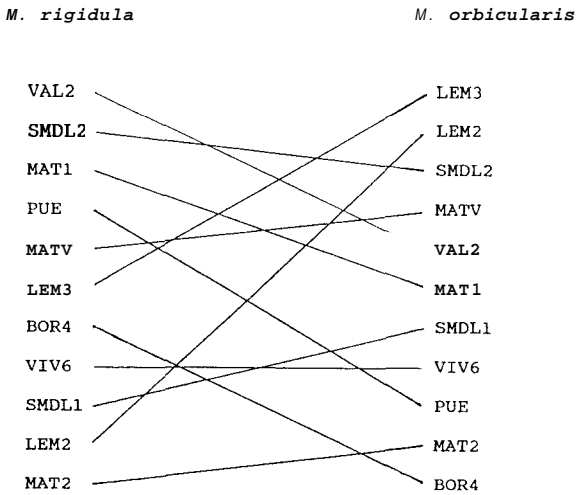


Fig. 3. Compared classifications of *Medicago rigidula* and *Medicago orbicularis* for germination rates. This scheme only concerns populations where both species were found. Rank correlation is not significant: $r = 0.25$, $p = 0.44$.

Determination of landscape scale

Observations on survival and dispersal were performed on sites that occupy the same sort of environment, the mediterranean garrigue, but which can be more than 20 km apart, and thus probably belong to a genetically differentiated landscape (this means that a change in one of the landscapes would not influence what happens in the others). This might explain why the expected correlation between the population age and the measured character was not observed. Such results emphasize the importance of the landscape unit: to interpret what happens within a population requires the knowledge of the landscape it belongs to (for example which genotypes are more probable in migrants and founders).

Estimation of the age of populations

The estimation of the age of a population as the time since the last disturbance could be a biased estimator for certain characters measured in the present study. The estimate was based on observations of the vegetation present as well as on remnants of previous site use. The older the last disturbance, the less precise the estimate was. However, even if estimations were wrong, a correlation between the different characters that are sensitive to

the age of a population should still exist. Such a correlation is not observed for example for the rate of dormancy between *Medicago rigidula* and *Medicago orbicularis* (Fig. 3). In the eleven sites where both species were present, the rank correlation between dormancy rates for each species is not significant ($r = 0.25$, $p = 0.44$). The lack of correlation could indicate:

- that the age of a population is species-dependent, because species do not occupy a site at the same stage and/or do not colonize each site in the same order, due to variations in efficiency of the migration rate and the ecological conditions necessary for successful establishment.

- that local disturbance induce spatial heterogeneity within a site, some parts of the population being younger than others (see Linhart *et al.* 1987; Feinsinger *et al.* 1988). Diachronic studies might be especially useful to avoid the difficulty to estimate the age of a population.

The amount of genetic variability

The rate of response to selection depends on the extent of genetic variability (Fisher 1941). Stochastic events during population lifetime (*e.g.* population bottlenecks, genetic drift ...) decrease the genetic variability (in a sense making the population genetically younger). The expected correlation between traits and age of the population will then disappear.

Between sites variability must be large to observe the proposed landscape processes. In the three studies where the age of a population was related to the frequency of male-sterility on thyme, variability is large enough (10 to 99% (Dommée *et al.* 1983), 48 to 83% (Belhassen *et al.* 1989)). On the other hand, the dormancy rate in the three species of *Medicago* studied was less variable (from 90.7 to 99% in *M. lupulina*, from 87.8 to 99.2% in *M. rigidula*, from 94.2 to 99.5% in *M. orbicularis*, Table 3) so that differences between populations are only significant for the first two species. Correlations are difficult to establish when variability is so low, and studies of larger sets of populations are necessary. Rate of survival in populations of *Medicago lupulina* varied between 0 and 80% (Table 1). However part of this variability was largely environment-dependent, since a single genotype of

this species can be annual in some environmental conditions and perennial in others (Hébert, Fauré and Olivieri, unpublished). In this case, observed variations will reflect environmental variability rather than landscape processes.

Correlations between characters

Correlation between different characters simultaneously selected might obscure the correlation observed. For example, seed dimorphism in thistles is related to both dispersal in time and space. Seeds that disperse in space have no dormancy, and dormant seeds do not migrate (Olivieri *et al.* 1983). In this case predictions depend on selective pressures on both characters, as well as on the genetic correlation between them, *i.e.* how much selection on one character will affect the other one.

In *Carduus pycnocephalus* and *C. tenuiflorus*, correlation between migration and selfing rate is used to deduce the evolution of inbreeding rate within populations. Direct observations on selfing rate would be more conclusive, although methodologically more difficult.

The origin of founders

Another cause of discrepancy is the origin of founders, depending on the kind of the succession. Founders might originate either from the seed bank, and in this case the dormancy rate will be higher for the original individuals, or from migration, and then the dormancy rate might be lower for original individuals if there is a negative genetic correlation between migration and dispersal as is generally observed in species with a seed dimorphism, (Venable and Lawlor 1980; Olivieri and Berger 1985). To understand the importance of the origin of founders it will be necessary to observe a series of populations that differ in regards to their origin. For example, a relationship between the frequency of male-sterility and the age of a population was observed in a post-cultural succession (Domée *et al.* 1983), and in post-fire successions (Belhassen *et al.* 1989). The female frequency was lower in the second kind of succession. As a result, mixing of the three data sets would obscure the effects observed. Founders can all originate from the same population, which should be a neighboring popula-

tion, or they can be a random sample from all the populations that occupy the landscape. In the first case, there can be a large population differentiation and thus a higher heterogeneity within a landscape (Slatkin and Wade 1978).

Conclusion

A population genetics approach to landscape ecology can have several purposes. One of them is to explain the mechanisms for the maintenance of different traits concerned by the shape of the landscape. These are the traits that determine landscape functioning: ability to colonise new sites (dispersal rates), growth rate and persistence of a population (allocation to survival and reproduction). For landscape ecology itself, such an approach can give indications for landscape management. It can show which amount of variability can be found in different sort of sites as well as in different sort of landscapes. It can also predict the difficulties a species is dealing with, depending on the part of the landscape it inhabits. For example, considering the selection on inbreeding rate, different predictions can be derived regarding the deleterious effects of consanguinity. Inbreeding rate can be higher in old established sites, or, alternatively, in recent populations. In regards to species management, it is important to know, for a given species, if the import of genetic diversity is more critical in old or new sites, and if lack of genetic diversity is more crucial in more fragmented or homogeneous landscapes.

Theoretical studies of migration show that the migration rate selected in a metapopulation differs from the migration rate that maximizes the number of individuals in the metapopulation. This discrepancy exemplifies the antagonism between selection within a species and selection among species. If one assumes that the extinction probability of a metapopulation is negatively correlated with the number of individuals, then selection on migration rate within a metapopulation will not maximize its likelihood to persist. Sex-ratio studies show that the higher the number of founders that establish in a site, the higher this discrepancy (Taylor and Bulmer 1980), as long as founders are not genetically relat-

ed (Herre 1985). In this paper, we have discussed the processes that determine the outcome of selection in a metapopulation and the extent of diversity within a landscape for a given species. For instance increased female reproductive effort will be found in very fragmented landscapes, where migration between sites is restricted, and the rate of disturbance is high.

Given the methodological difficulties involved in such an approach, the use of experimental metapopulations may provide explanation of which characters are susceptible or not to landscape processes.

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