Evolutionarily stable strategies of migration in heterogeneous environments

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Abstract. By means of a simulation model we are showing that the rates of migration can be related to avoidance of competition between relatives, especially in clonal organisms. This could result in a strong selective pressure for migration, even at a high cost. In addition, if the habitat is fragmented, migration can strongly affect local dynamics and result in a dramatic decrease of the densities in some places. In parthenogenetically reproducing organisms like aphids, the level of relatedness in local populations is expected to be very high and therefore they can serve as a good model group for testing these hypotheses.

Key words: aphids, dispersal, evolutionarily stable strategy, fragmented landscape

Nomenclature

Npatch	Total number of patches
N_{is}	Number of isolated patches
N_{cl}	Number of patches clumped in a 'forest'
$N_t(i,j)$	Number of individuals of clone i in patch j, at time t
λ	Finite rate of increase of the population
$Npatch_t(j)$	Total number of individuals in patch j, at time t
$Ntot_t(i)$	Total number of individuals of clone i, at time t
K	Carrying capacity of a patch
m	Proportion of migrants dying during migration (model A)
m_{is}	Proportion of migrants dying when they are outside the 'forest'
m_{cl}	Proportion of migrants dying when they are inside the 'forest'
P_l	Proportion of migrants leaving the 'forest'
$S_t(i)$	Proportion of individuals of clone i migrating at time t
Tfin	Number of time steps in a year
Ninit	Initial number of foundresses per patch

Introduction

Dispersal is common to all organisms yet there is little understanding of the relative benefits of investing in growth or dispersal. Authors who have considered the effect of the trade-offs between growth and reproduction on life history strategies did not take migration into account (Schaffer, 1974a, b; Sibly and Calow, 1986; Roff, 1992; Stearns, 1992). The models of migration, on the other hand, have tended to offer explanations framed in terms of spatial and/or temporal heterogeneity (Taylor and Taylor, 1978; McPeek and Holt, 1992; Krebs, 1994; Doebeli and Ruxton, 1997) or density dependence (Kidd, 1990). In a spatially and temporally constant environment, competitive interactions between related individuals are known to promote dispersal (Hamilton and May, 1977). However, the authors themselves acknowledge that their simple model probably has few close parallels in the real world. Moreover, in their model the cost of dispersal is constant, which is not the case in the real world.

The specific case we shall address in this paper is dispersal in clonal organisms, which can be regarded as an important component of the dynamics of each clone. This will be achieved by means of a simulation model that determines the evolutionarily stable strategy for dispersal in clonal organisms, taking into account avoidance of competition between relatives.

Aphids will serve as a model group here, as they reproduce parthenogenetically during most of the year and therefore the level of relatedness in a colony is expected to be very high. In most aphid species, an initial dramatic increase in population size in spring is typically followed by a steep decline in abundance caused by massive dispersal (Kindlmann and Dixon, 1996) during summer and sometimes a further increase in autumn. During spring and summer all the generations are parthenogenetic and short lived (2–4 weeks). In autumn, sexuals are also produced, which mate and lay the overwintering eggs that hatch the following spring and give rise to foundresses, the first parthenogenetic generation. The qualitative predictions of our model will be compared with the behaviour of species which do not obligatorily host alternate, as in host alternating species dispersal can clearly not be avoided, and offer an explanation for the variation in the incidence of dispersal observed between species.

Materials and methods

In our models, the landscape consisted of *Npatch* patches in which individuals reproduce parthenogenetically. Exchanges between local populations were achieved by migration from patch to patch. Local population dynamics were assumed to be logistic. Two scenarios were considered. In the first one (model A), all patches were assumed to be equivalent. In the second one (model B),

patches were split into two populations: isolated patches (whose number was N_{is}) and patches clumped in a 'forest' (whose number was N_{cl}). Isolated patches and 'forest' patches differed in the model by the likelihood for a migrant to survive migration. It was assumed to be high in the 'forest' and low for individuals originating from isolated patches. In both models, similarly to Doebeli and Ruxton (1997), population dynamics were described by discrete time equations. Each time step consisted of two phases: a phase of local increase followed by a migration phase. Although in reality, these two phases occur simultaneously, in computations they have to be separated. This, however, does not affect the outcome, provided the time step is very short.

Local population dynamics

The local population in each patch increased following logistic equation (Ricker, 1954):

$$N'_{t+1}(i,j) = N_t(i,j) \exp\left[\ln(\lambda)\left(1 - \frac{Npatch_t(j)}{K}\right)\right], \tag{1}$$

where $N_t(i,j)$ is the number of individuals of clone i in patch j, at time t, $N'_{t+1}(i,j)$ is the number of individuals of clone i in patch j, at time $t+1$, after population increase but before migration, λ is the finite rate of population increase, $Npatch_t(j)$ is the total number of individuals in patch j, at time t, $Npatch_t(j) = \sum_i N_t(i,j)$, K is the carrying capacity of the patch.

This phase was described in the same way in both models.

Migration

In each time step, a given proportion of the individuals was assumed to leave the patch and to migrate to another one. Not all the migrants succeeded in reaching a new suitable patch. The survivors were uniformly distributed among the patches.

In model A,

$$N_{t+1}(i,j) = N'_{t+1}(i,j)(1 - S_{t+1}(i)) + \frac{Ntot_{t+1}(i)(1 - m)S_{t+1}(i)}{Npatch}, \tag{2}$$

where $N_{t+1}(i,j)$ is the number of individuals of clone i in patch j remaining after migration, $S_t(i)$ is the proportion of individuals of clone i migrating at time t, $Ntot_t(i)$ is the total number of individuals of clone i, at time t, $Ntot_t(i) = \sum_j N'_t(i,j)$, m is the proportion of individuals dying during migration.

In model B, migrants were split into two groups: migrants inside the 'forest' and migrants outside the 'forest'. The first ones were those which left a 'forest'

patch but not the 'forest'. The second ones were those, which left an isolated patch plus those, which left the 'forest'.

The proportion of migrants leaving the 'forest' was equal to $P_1 = (1/\sqrt{N_{cl}})$. It means that this proportion can be estimated by the ratio of the perimeter of the 'forest' (proportional to $\sqrt{N_{cl}}$) to its surface (proportional to N_{cl}), because migrants are produced in the whole 'forest' but departure occurs through its edge. Migrants staying in the 'forest' were distributed equally in all its patches after having suffered a moderate death rate of m_{cl}. Migrants from the isolated patches were added to those who have left the 'forest' and distributed equally in all patches (isolated and 'forest') after having suffered a high death rate of m_{is} (Fig. 1).

The number of time steps in a year was set to *Tfin*.

Mechanism of evolution

Clones were defined by their migration strategies (the series $\{S_t\}$), all their other characteristics were assumed to be identical. At the beginning of each year, all the individuals but one (the mutant) were assumed to be of the same clone (the resident). Each local population of individuals was initiated with *Ninit* foundresses.

In model A, if the mutant has increased its relative frequency in the population at the end of the season, i.e., its relative rate of increase is higher than one,
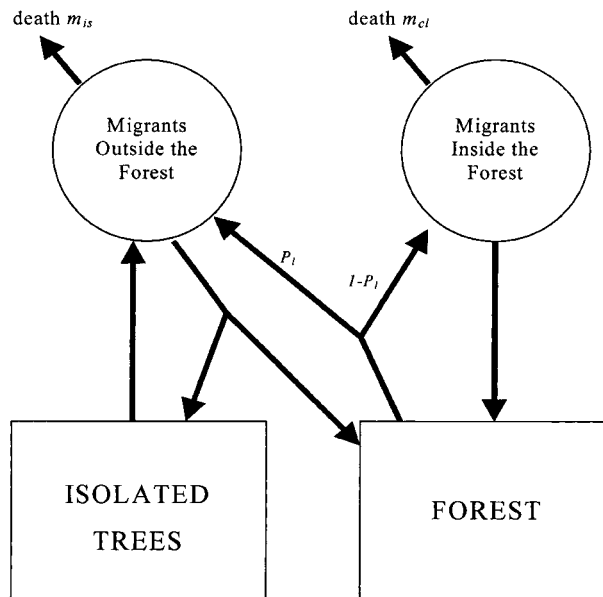

Figure 1. Schematic representation of model B.

$$\frac{Ntot_{Tfin}(\text{mutant})}{Ntot_{Tfin}(\text{resident})} \times (Npatch \times Ninit - 1) > 1, \tag{3}$$

then the strategy of the resident was considered not to be evolutionarily stable (Parker and Maynard Smith, 1990). The strategy of the resident was then eliminated and the mutant was chosen as the new resident.

In model B, the mutant could have appeared either in an isolated patch or in a patch in the 'forest'. Therefore, the criterion was the geometric mean of the relative rates of increase of the mutant (Bulmer, 1997), assuming that the probability of appearance of a mutant in each kind of patch was equal to the frequency of this kind of patch. If Ri is the relative rate of increase of a mutant that appeared in an isolated patch and Rc is the relative rate of increase of the same mutant if it appeared in the 'forest' (Equation (3)), then the mutant was chosen as the new resident if

$$\sqrt[Npatch]{Ri^{N_{is}} Rc^{N_{cl}}} > 1 \tag{4}$$

Mutation

Mutations were assumed to be of two possible types. Mutation could occur in the date of migration, the mutant differing from the current resident by the exchange of two randomly chosen values in the series $\{S_t\}$. Alternatively, it could occur in the intensity of migration, the mutant differing by a small modification of one or some randomly chosen values in the series $\{S_t\}$, where the magnitude of the mutation was chosen at random. At the beginning of each year a new mutant was created by a mutation of the strategy of the resident. The type of the mutation was taken at random with equal probabilities.

This procedure was run for thousands of years. Initial values of the series $\{S_t\}$ of the resident and of the mutant were chosen at random. The final strategy reached was assumed to be evolutionarily stable. To make certain that the final value was not a local optimum, the procedure was run five times with different initial values.

Winter

For simplicity, we assumed that a strong decrease in density occurred in winter leading to the same number of foundresses (*Ninit*) at the beginning of each season.

The criterion for the selection of a mutant was based on the ultimate density achieved at the end of the season (*Ntot_{Tfin}*). Therefore, it also implicitly assumed that frequency of a clone remained unchanged during winter.

Results and discussion

Non-structured population of patches (model A)

The simulations were run for a period of 10,000 years, it was set as $Tfin = 10$, $\lambda = 4$, $K = 100$ and $Npatch = 50$.

Single foundress per patch (Ninit = 1). In the first approach, patches were considered as being evenly colonised by a single aphid ('foundress') in order to investigate the effect of the highest intra-clonal competition within the local colonies. The evolutionarily stable strategy then consisted of a single migration event (all the migration rates but one equal to zero) whose magnitude depended only on the mortality rate during migration and not on the values of K or λ (Fig. 2). Migration rate quickly decreased from 1 to 0.5 as mortality
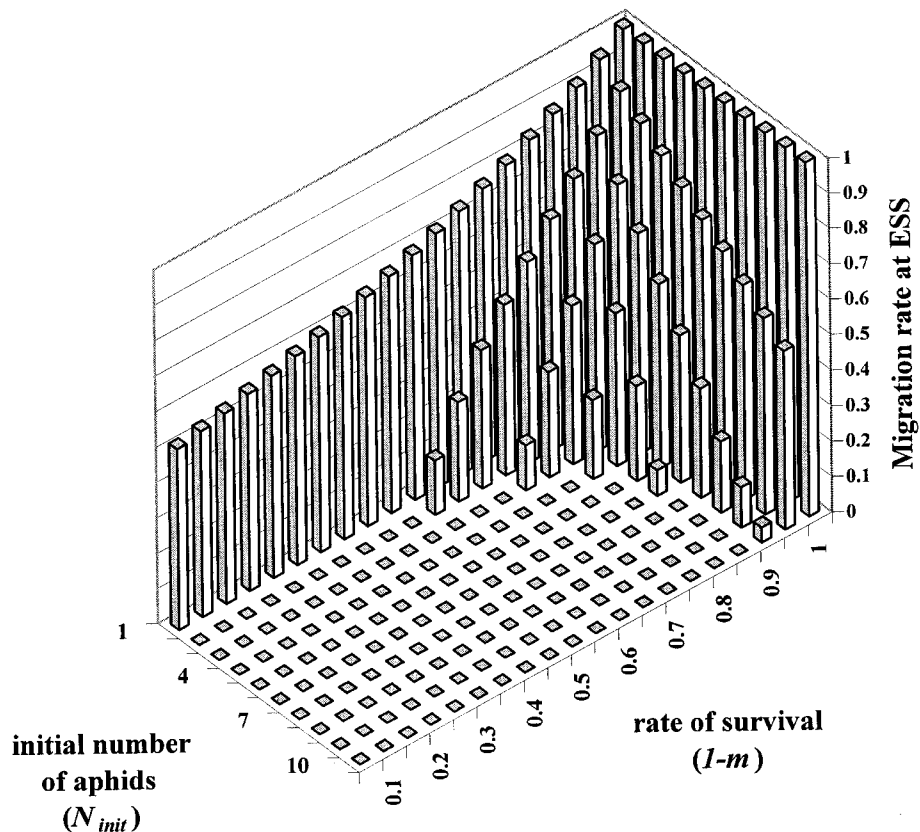

Figure 2. Influence of the number of foundresses on the relation between migration rate and survival rate at ESS (Model A).

increased from 0 to 1. Even if the proportion of survivors was very low, the number of migrants remained high. We interpret this result by the fact that leaving of one individual allowed survival of the related ones. It is important to bear in mind that due to identity of all patches, ESS migration rates should be zero in the absence of intra-clonal competition (Doebeli and Ruxton, 1997). Thus if intra-clonal competition is strong, clonal organisms should always evolve a high rate of migration.

More foundresses per patch (Ninit > 1). In the second approach, the number of foundresses was varied from 1 to 10. Results are presented in Figure 2. They show that migration rate decreased very quickly as the intra-clonal competition was relaxed, this decrease being more dramatic when the rate of survival was low. Interestingly, the simulation results presented in Figure 2 conform perfectly to the general equation first suggested by Hamilton and May (1977) and then generalized by Frank (1986) relating rate of migration (M) to level of relatedness (R) and to cost of migration (c):

$$M = \frac{R - c}{R - c^2}, \quad \text{if } R > c \tag{5}$$

and

$$M = 0, \quad \text{if not.}$$

In our case, $R = 1/Ninit$ and $c = m$. This result is of great interest because it suggests that Equation (5) is not sensitive to the particular dynamics of the population.

Date of migration. In this paper, we did not focus on the optimal date of migration. In the approach developed, competition between individuals was taken into account by describing local population dynamics by means of a classical logistic equation. This implies that competition arises as soon as more than one aphid is present in the patch. It leads to migration occurring as soon as possible in order to avoid any competition between relatives, namely, at the end of the first reproductive period. This is not in agreement with observations that show that migration occurs after some period of local population increase (Dixon, 1969). In real patches, no actual competition probably occurs before the population has reached a relatively high density. Moreover, various authors have shown that at small densities a kind of 'co-operation' occurs, probably mainly due to a decrease in the risk of predation and/or an increase in the efficiency in feeding (Ekbom *et al.*, 1992; Hales *et al.*, 1997; Prado and Tjallingii, 1997). To investigate whether our results would be the same if 'co-operation' were taken into account, the function $f(N)$ in the local population dynamics equation,

$$N_{t+1}(i,j) = N_t(i,j) \exp(\ln(\lambda)(1 - f(Npatch_t(j)))) \tag{6}$$

was assumed to be

$$f_2(N) = \frac{4}{K^3} \cdot N^3 - \frac{1}{K^2} \cdot N^2 - \frac{2}{K} \cdot N \tag{7}$$

instead of the logistic $f_1(N) = N/K$, as in the simulations above.

This function is phenomenological and was chosen because it had the required shape: $f(N)$ is negative at low densities ('co-operation'), $f(N) = 0$ when $N = 0$, $f(N)$ is minimal when $N = K/2$, $f(N) = 0$ when $N \approx 0.84 \cdot K$ and $f(N) = 1$ when $N = K$ (Fig. 3).

To avoid chaotic behaviour of the new model, R was decreased and set to 1.1 in the simulations. Accordingly, $Tfin$ was increased to 50. As expected, the introduction of 'co-operation' led to a delay in the date of migration. For example, with one single foundress per patch, migration occurs at a single event at the end of the 35th time step (the date at which population reaches $K/2$ or its maximal rate of increase in the absence of migration). The most important feature, however, was that the proportion of migrants remained unchanged when compared to the previous results. Results were the same when the number of foundresses was varied. The optimal date of migration was always at the instant when population reached $K/2$ and the proportion of migrants was unchanged. For example, with an initial value of 3 foundresses per patch, migration occurs at the end of the 23rd time step.
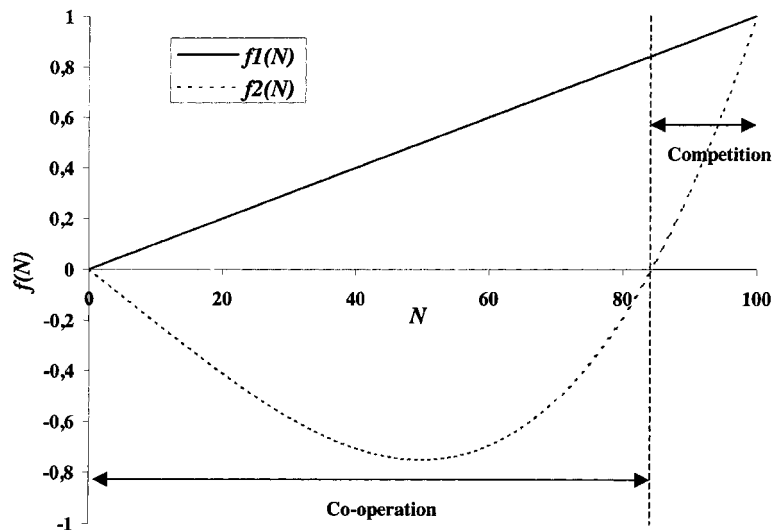

Figure 3. Compared shapes of the functions $f(.)$ introduced in the original model A ($f_1(.)$) and in the modified one ($f_2(.)$) to account for 'co-operation' between aphids at low densities ($K = 100$).

These results can also be compared with those obtained by Frank (1986). They have shown that despite an increase in complexity of population dynamics, Equation (5) was always satisfied. However, while ESS rate of migration was actually only determined by cost of migration and level of relatedness in the population, ESS timing of migration depended on the particular shape of population dynamics.

Other arguments could also account for observed delay in migration: decrease in the number of clones due to competition among them (De Barro *et al.*, 1995) or increase in survival of migration due to better weather conditions later in the season. In any case, our results have shown that the evolutionarily stable strategy in terms of proportion of migrants produced will remain unchanged.

Partitioning the patches into two populations:
isolated vs. 'forest' patches (model B)

The simple simulation model in the 'Non-structured population of patches' has demonstrated that competition between relatives could account for the high rate of migration observed in many aphid species if two conditions are satisfied: (i) the probability that they survive migration is not too low and (ii) the number of foundresses is low, leading to a high level of competition between identical phenotypes. The second condition is strongly supported by empirical data (Kindlmann and Dixon, 1996, 1998; Dixon *et al.*, 1996). The first condition, however, seems to be in disagreement with some observations (Ward *et al.*, 1998). One possible explanation can be that patches are non-uniformly distributed in space: some of them may be isolated and therefore survival of migration is low for individuals that leave such patches, while some of them may be aggregated in 'forests', in which probability of survival of migration from one patch to another is much higher.

Effect of the presence of a 'forest' and of its size on the ESS. Simulations were performed keeping all the parameters but the relative numbers of isolated and 'forest' patches constant. Survival of migrants in the 'forest' was assumed to be very high ($m_{cl} = 0.05$), while survival outside the 'forest' was set to a low value ($m_{is} = 0.99$), similarly to actual estimates (Ward *et al.*, 1998). It was set to $\lambda = 4$, $K = 100$, *Npatch* = 1000, *Ninit* = 1 and the proportion of isolated patches was varied from 0 to 1. Figure 4 shows that the presence of even a small 'forest' where the survival of migration is high makes the proportion of migrants higher than expected with no connection between populations in the 'forest' and in isolated patches. This leads to a strong decrease in the densities in isolated patches at the date of migration, similar to that often observed in the population dynamics of aphids (Fig. 5). In fact, the behaviour in isolated
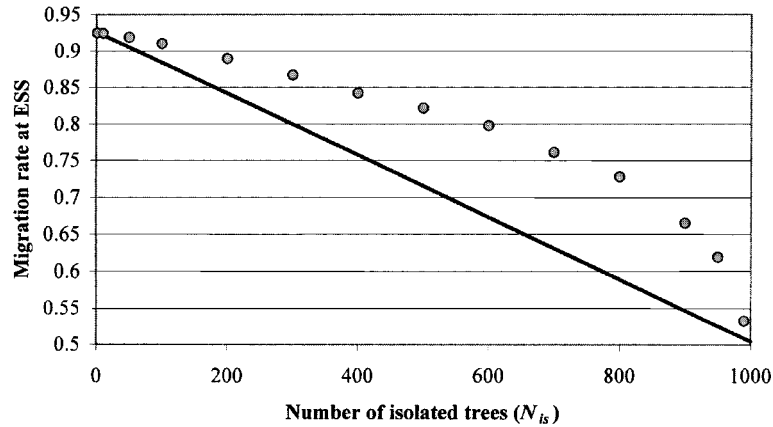
Figure 4. Proportion of migrants at ESS against number of isolated patches among the 1000 total number of patches (Model B). Straight line is average of local migration rates at ESS obtained if population would not exchange individuals.
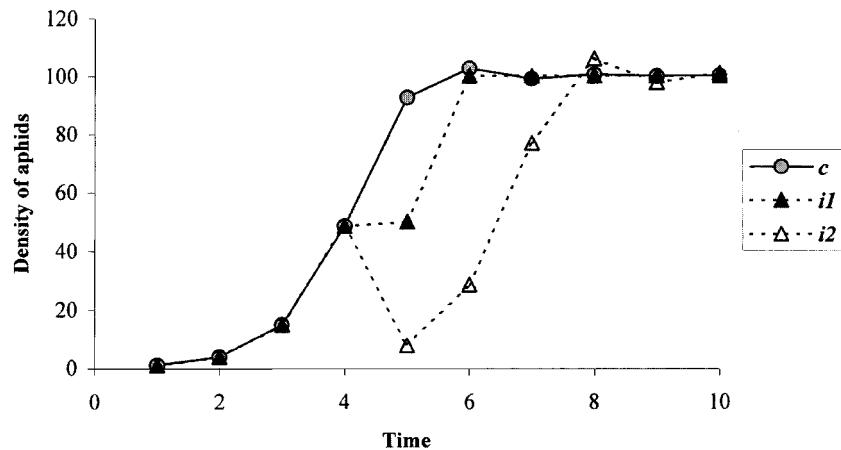

Figure 5. Population dynamics of aphids in isolated patches (i) and in the 'forest' (c) (number of isolated patches set to 50 among 1000, date of migration assumed to be 4). $i1$, dynamics expected when isolated patches do not exchange migrants with the 'forest' $i2$, when they do.

patches appears to be misadapted because it is driven out from the local ESS by the arrival of migrants from the 'forest'.

Effect of relative survivals of migrants inside and outside the 'forest'. Simulations were carried out with a constant number of patches isolated (100) and clumped in the 'forest' (900) but survival rates inside and outside the 'forest' were varied. The resulting ESS migration rates are presented in Figure 6. Migration rates are mainly dependent on what happens to migrants inside the 'forest'.
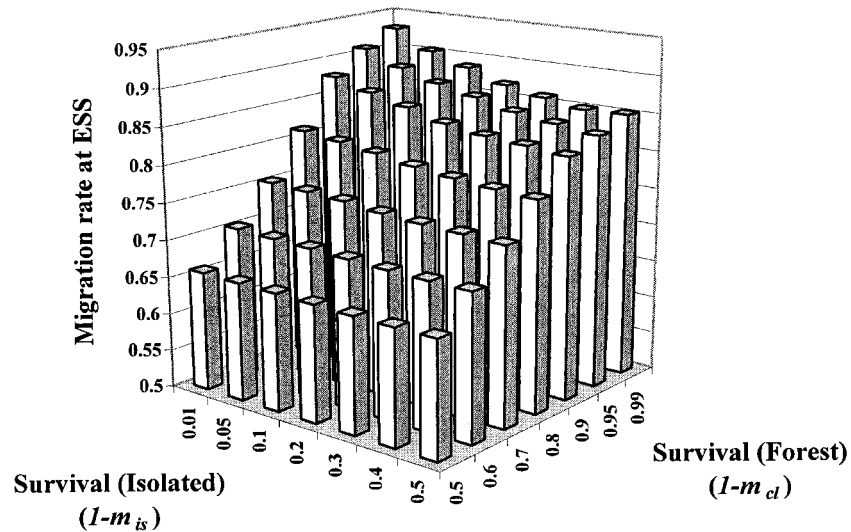
Figure 6. Migration rate ESS against survival inside $(1 - m_{is})$ and outside $(1 - m_{cl})$ the 'forest' for a number of isolated patches (N_{is}) set to 100 and a total number of patches (*Npatch*) set to 1000.

ESS rate is much more correlated with survival inside than with that outside the 'forest'. In isolated patches, ESS appeared to be mainly constrained by the presence of a 'forest'. The results in Figure 6 are partly due to the fact that the proportion of patches inside the 'forest' was very large. However, in all cases, the effect of isolated patches is lower than expected from their number. One counter-intuitive result was that the increase in survival outside the 'forest' led to a decrease in the tendency to migrate. In other words, a global increase in migration survival rate can result in a decrease of the production of migrants. This consequence of partitioning the landscape into two habitats is contrary to the results obtained with simple models (Taylor, 1988). Increase in survival outside the 'forest' for low values of this parameter leads to enhancing the relative importance of local ESS in isolated patches in the determination of the global ESS and therefore to a reduction of the tendency to migrate. The precise shape of the relation between migration rate at ESS and survival outside the 'forest' is dependent on the relative size of the two populations: in the 'forest' and in the isolated patches (Fig. 7). At low values of survival, the two populations are weakly connected. Then, isolated patches are mostly acting as sinks and ESS value depends on the size of the 'forest', which determines the number of migrants leaving it. As survival increases, populations in isolated patches and inside the 'forest' become more and more connected. It leads first to a decrease in migration rate as the local ESS in isolated patches, which is low, becomes more influent in the determination of the global ESS. When survival reaches a critical value, migration rate begins to increase again
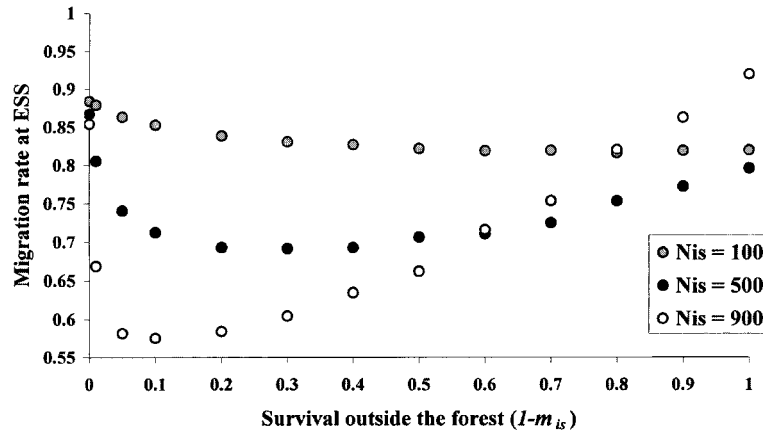
Figure 7. Relation between migration rate at ESS and rate of survival outside the 'forest' for three different sizes of population in isolated patch (survival inside the 'forest' and total number of patches set respectively to 0.9 and 1000).

as global functioning of the system tends to become that of a 'forest' (high level of connection between patches and high level of migration survival). Then the lowest rates of migration at ESS are achieved at intermediate values of survival.

Relevance to other models. We have shown that the results of Hamilton and May (1977) and Comins *et al.* (1980) hold even for much more realistic models than are the original ones. We extended Frank's (1986) results and showed that the relation he found between ESS rate of migration and cost of migration and level of relatedness is robust and holds for various population dynamics models. We have also shown that though the shape of the population dynamics curve has no effect on the proportion of migrants produced in the population, it determines the timing of migration. Frank's (1986) Equation (5) only describes a stationary phenomenon where a constant proportion of the offspring migrates. So, it would imply all the $\{S_t\}$ in our model are equal to this ESS value and not all but one equal to zero. The problem with Frank's (1986) model is that the coefficient of relatedness does in reality not remain constant during the season. The first event of migration leads to a decrease in this coefficient as the population is redistributed among patches. It can be easily demonstrated that relatedness after migration is necessarily less than m and approaches m^2 when population is close to the ESS (See Appendix 1). Therefore, no further migration can occur before an external event (winter in the aphid case) restores the initial high relatedness. Thus migration, when caused by relatedness, is very unlikely to appear as a stationary phenomenon, as Frank's (1986) equation would suggest, but occurs in

pulses whose frequency is determined by the mechanism that restores the initial relatedness.

Logistic population dynamics leads to selection of clones migrating as soon as possible because it assumes that competition occurs even at very low densities. If co-operation takes place in low densities or if the initial population age structure is highly synchronised (most of the individuals are of the same age), which is the case early in the spring in many aphid species, then the highest rate of increase is achieved at intermediate densities. This leads to a delay in the predicted optimal date of migration, which occurs when the rate of increase is maximal.

In patchy environments, the tendency to migrate from patches where survival of migration is very low is strongly influenced by the presence of a close patch ('forest') in which this survival is much higher. Migration then appears to be locally misadapted and we have demonstrated that it could have a strong negative influence on population dynamics in such patches: they are likely to be irregular with periods of very low densities, which, if some stochasticity is assumed, could result in frequent local extinctions. The ESS rate of migration does not then maximise the density of the metapopulation and it is not the 'best for the population' (Hamilton and May, 1977). Similar results were also obtained by other authors (Comins *et al.*, 1980; Olivieri *et al.*, 1995; Olivieri and Gouyon, 1997). Frequent extinctions may lead to a further increase in the ESS rate of migration and drive the population dynamics to an evolutionary spiral resulting in the maintenance of populations in isolated elements of the landscape being unlikely. This evolutionary spiral arises from the counter-intuitive negative relationship between cost of migration and tendency to leave the patch. A similar relationship has also been found by Gandon and Michalakis (pers. com.), but for different reasons.

Relevance to empirical data. Aphids are a very good biological model for the study of migration and relatedness because: (1) their population rates of increase are high and they reproduce parthenogenetically, and therefore they are likely to achieve very high levels of relatedness in local populations and (2) they are living and feeding on plants and their environment is therefore necessarily fragmented.

Our theoretical predictions are consistent with published empirical data on aphids. Avoidance of competition between relatives promotes the high migration rates observed in aphids. Moreover, if the local number of foundresses is low, avoidance of competition between relatives alone is sufficient to explain most of it. One of the reasons for the often observed strong decrease in aphid density caused by migration may be local misadaptation on isolated host plants. However, many other factors may account for the high migration rates

in aphids too: temporal or spatial heterogeneity, risk of local extinction, etc. The relative importance of all these factors remains to be explained.

Due to its general assumptions, our model is far from being restricted only to aphids. Avoidance of competition between related individuals may play an important role in the determination of migration behaviour in other species achieving high level of local relatedness, particularly clonal ones. It also provides an additional explanation for the inverse relationship between regional plant diversity and number of aphid species (Mackenzie *et al.*, 1994), as diversity is expected to be positively correlated with the mean level of isolation in plants and therefore with the frequency of local extinctions in aphids. Finally, one could expect applications of our results in conservation biology, when the effect of migration in fragmented habitats is considered.

Acknowledgements

Appendix

Assume that a mutant appeared with ESS migration rate S_1 in a population whose migration rate is S_2, then according to Equation (5)

$$S_1 = \frac{R - m}{R - m^2}$$

For simplification, we assumed that $R = 1$, but results are the same for any value of R. The situation just after migration is as following:

On the patch where the mutant is appeared, densities are

$$\text{for the mutant: } \lambda \cdot N - S_1 \cdot \lambda \cdot N + \frac{(1 - m) \cdot S_1 \cdot \lambda \cdot N}{Npatch}$$

$$\text{for the resident: } \frac{(1 - m) \cdot S_2 \cdot \lambda \cdot N \cdot (Npatch - 1)}{Npatch}$$

On the other ($Npatch - 1$) patches, densities are

$$\text{for the mutant: } \frac{(1 - m) \cdot S_1 \cdot \lambda \cdot N}{Npatch}$$

$$\text{for the resident: } \lambda \cdot N - S_2 \cdot \lambda \cdot N + \frac{(1 - m) \cdot S_2 \cdot \lambda \cdot N \cdot (Npatch - 1)}{Npatch}$$

For *Npatch* high enough, the level of relatedness in the mutant will be

on the original patch $\dfrac{\lambda \cdot N - S_1 \cdot \lambda \cdot N}{\lambda \cdot N - S_1 \cdot \lambda \cdot N + (1 - m) \cdot S_2 \cdot \lambda \cdot N}$

$$= \dfrac{1 - S_1}{1 - S_1 + (1 - m) \cdot S_2}$$

on another patch 0

Then, its average local relatedness will be $R' = \dfrac{(\lambda \cdot N - S_1 \cdot \lambda \cdot N) \cdot \left(\frac{1 - S_1}{1 - S_1 + (1 - m) \cdot S_2}\right)}{\lambda \cdot N - S_1 \cdot \lambda \cdot N + (1 - m) \cdot S_1 \cdot \lambda \cdot N}$

After replacing S_1 by $\frac{R - m}{R - m^2}$ and simplification, it leads to

$$R' = \dfrac{m^2 \cdot (1 - m)}{m \cdot (1 - m) + (1 - m) \cdot (1 - m^2) \cdot S_2}$$

This expression reaches its maximum for $S_2 = 0$ where $R' = m$. Therefore $R' \leq m$ and then below the threshold required by Frank's equation for a further migration be selected.

It can be noticed than when population is close to ESS rate, namely when $S_2 \approx \frac{1 - m}{1 - m^2}$, relatedness after migration will be set to $R' = m^2$.

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