Effects of fragmentation on pollen and gene flow in insect-pollinated plant populations
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Effects of pollination system and plant architecture on genetic erosion in fragmented habitats: a theoretical study

With F.J. Weissing

Summary

Fitness effects of genetic erosion were studied, with special attention to the interactions between plants and their animal pollinators. Pollinator behaviour is modeled as a ‘decision rule’, which determines gene flow patterns and hence the genetic structure of the plant population. Furthermore, pollinator behaviour induces adaptations of plant architecture, i.e. allocation of resources to survival, attractiveness to pollinators and investment in seeds, with obvious ecological implications for population persistence. To model genetic erosion, we concentrated on the accumulation of deleterious alleles due to mutation-selection balance, and used the frequency of deleterious mutations, mean population viability and mean vigor as indicators of population performance. Selection by the pollinators, via attractiveness and seed investment, resulted in a reduced mutation load in a large population, when compared to a pure viability selection model.

We considered three different pollinator decision rules, varying in their reaction to plant attractivity: highly selective Best-of-Two (BOT) strategy, non-selective Difference-of-Two (DOT) strategy and intermediate On-its-Own. After fragmentation, purging of the mutation load was more efficient with strong pollinator selection on attractiveness (BOT), reducing the impact of genetic erosion. Fragmentation might affect not only population size, but also the degree of isolation between remnant subpopulations. However, spatial population structure had only marginal effects on genetic erosion. In contrast, an increase in the selfing rate after fragmentation may substantially enhance genetic erosion. If habitat fragmentation is accompanied by a change in pollinator type, especially a switch from BOT to DOT pollinators may enhance the effects of genetic erosion. A high ecological vulnerability and a low genetic vulnerability, both induced by very selective pollinators (BOT), are two sides of the same coin.
1. Introduction

Habitat fragmentation threatens the persistence of many plant populations (Soulé 1986; Weeda et al. 1990; Caughey 1994). When natural habitats are fragmented, large, continuous plant populations are often divided into several smaller and relatively isolated patches. These small, remnant populations experience an enhanced risk of extinction due to factors as demographic and environmental stochasticity. These risks are especially important for specialized plant-pollinator systems, since the combination of two vulnerable partners will certainly increase the extinction risk of the whole system.

In addition to such ‘ecological’ risks, fragmented plant populations may be threatened by genetic risks as well. In small and isolated populations, allele frequencies change due to random genetic drift, allowing the spread of deleterious alleles. Moreover, homozygosity is expected to increase, giving inbreeding effects a more dominant role. How rapid such ‘genetic erosion’ (Bijlsma et al. 1991; Van Treuren et al. 1993a) occurs and to what extent it influences population fitness is still not well understood. The mating system of a plant species will certainly be of crucial importance, since the genetic structure of a population is strongly affected by selfing and restricted gene flow (e.g. Slatkin 1987; Hartl and Clark 1989).

In animal-pollinated plants, gene flow and hence genetic population structure is largely determined by the behaviour of their pollinators. It is therefore conceivable that the (genetic) risks of habitat fragmentation are different for insect-pollinated plants, as compared to plants that do not depend on pollinators for their reproduction. In fact, pollinator choosiness introduces an additional selective force, which might efficiently reduce the genetic load of a plant population, resulting in a reduced potential for genetic erosion. If plants carrying a larger number of deleterious mutations are not attractive to pollinators, they will rarely be visited, resulting in an efficient elimination of these deleterious alleles. As a consequence, by reducing the potential for genetic erosion, the pollinators might buffer a plant population against the extinction risk by genetic processes. By means of a suite of models, we want to investigate whether and under what circumstances, the pollination system affects the mutation load and ‘genetic vulnerability’ of plant populations to habitat fragmentation.

Models for genetic erosion are usually based on the idea that fragmentation allows the accumulation of deleterious, recessive mutations (e.g. Lande 1995). In most of these models, deleterious mutations have negative effects on population performance due to the reduced viability of individuals carrying many of these deleterious alleles. In this paper, we extend such viability selection models to include other selection pressures, in particular pollinator-induced selection via the mating system of the plant. In addition to viability, we consider other fitness
components like attractivity to pollinators, production of rewards and investment in seed development. To this end, we assume that the genetic constitution of a plant determines its ‘vigor’, i.e. its potential to acquire a certain amount of resources. The lower the number of deleterious mutation a plant harbours, the more resources it has available. We assume that vigor is positively related to three fitness components, namely viability, attractivity and seed production. Obviously, viability affects the survival of the plant itself. The attractivity of a plant to pollinators determines male fitness, i.e. the relative contribution of a plant to the pollen pool, which is thus crucially dependent on the behaviour of the pollinators. Seed production is related to successful fertilization by pollinators, but also includes all kinds of maternal effects, influencing the survival of the seeds.

The behaviour of the pollinators is a crucial aspect of our model. The model is individual-based from the plant perspective, but to keep it as simple as possible, the pollinators are indirectly represented by their ‘decision rule’. Mediated by the pollinators’ decision rule, the investment of a plant into attractivity is translated into its contribution to pollen export and pollen import. The impact of attractivity is studied for two different scenarios. In one of the scenarios, attractivity is important for both male and female function, as is the case for many monoecious plants. In the other scenario, attractivity effects on male and female reproductive contribution are relatively independent of each other, as may be found in some dioecious plants.

This study aims at investigating the effect of the pollinator decision rule and the relation between male and female function on genetic erosion. However, it does not make much sense to compare different pollination systems directly with another, because each plant species will be adapted to its specific set of pollinators. Since there will be a trade-off between the various fitness components, the allocation of resources to these components is expected to vary with the pollination system. In other words, the relative importance of fitness components, which are related to pollen export and pollen import, is strongly dependent on the type of pollinator.

Consequently, the decision rule of the main pollinator has important consequences for ‘plant architecture’, i.e. the amount of resources that a plant invests in its own survival compared to the amount invested in advertisement and seed production. For our study, this implies that we cannot assume that plants with very choosy pollinators have the same allocation pattern as plants with non-selective pollinators. In order to make a ‘fair’ comparison between pollination systems, we first derive the evolutionarily stable allocation pattern corresponding to the system under study. Afterwards, we use the adaptive allocation pattern to investigate the accumulation of deleterious mutations and the genetic consequences of habitat fragmentation. In particular, we want to know whether a switch in the prevailing pollinator, accompanying habitat fragmentation, makes a plant
more vulnerable with respect to genetic erosion.

The paper is structured as follows. As a reference system, we first consider mutation-selection equilibrium in a context of viability selection and the genetic consequences of fragmentation in this context. We then extend this model to include other fitness components, related to pollen export and pollen import. We consider several variants of the model, corresponding to different pollinator decision rules and different relations between male and female function. For each version of the model, the optimal resource allocation pattern is determined by an Evolutionarily Stable Strategy (ESS) analysis. Once the optimal plant architecture has been derived, the plant population is fragmented and the consequences of genetic erosion for plant population performance are studied. Our main focus is on the effects of pollinator decision rules and the dependence between male and female function for genetic erosion in a single small population. Additionally, we investigate the impact of pollinator-mediated gene flow between subpopulations, and of increased selfing rates after fragmentation. Finally, we study the consequences of changes in pollinator type after habitat fragmentation.

2. Deleterious mutations in small populations

One of the most plausible causes for genetic erosion is the accumulation of deleterious mutations in small, remnant populations. New, deleterious alleles are continuously created by mutation and usually disappear by selection. In large populations the selection pressures are sufficiently strong to keep the mutant alleles in a low frequency (mutation-selection balance). In smaller populations deleterious mutations are more exposed to selection, which gives the opportunity for purging of the mutation load. On the other hand, in small populations deleterious alleles become easily fixed due to random genetic drift. The net effect of these opposing forces is not always clear (Charlesworth et al. 1993; Gabriel et al. 1993; Lande 1995; Lynch et al. 1995). To analyse these processes we will study in a simulation model the effects of genetic erosion due to a large number of loci. We want to investigate to what extent the mutation load will increase after fragmentation of a large, continuous population into small and relatively isolated populations. In this section we first consider the deleterious effects of mutations on viability. Later this will be extended to other selection pressures, like attractiveness and seed production, which result from the interactions between plants and pollinators.
The Haldane-Muller principle

In a large population deleterious mutations are kept at low frequencies by mutation-selection balance. At a single locus the equilibrium frequency for completely recessive deleterious alleles is \( q^* = \sqrt{\mu / s} \), where \( \mu \) is the mutation rate to deleterious alleles. The selection coefficient \( s \) represents the reduction in fitness if an individual is homozygous for a deleterious allele. As a consequence the mean fitness (i.e. viability) of the population is given by \( \bar{F} = 1 - s \: q^2 \approx 1 - \mu \) (e.g. Hartl and Clark 1989). Interestingly, the mutation load of the population, i.e. the reduction in mean viability due to deleterious mutations, is independent of the selection coefficient \( s \) and depends only on the mutation rate \( \mu \). This independence of the mutation load from the selection coefficient is called the Haldane-Muller principle. For partially recessive deleterious alleles a similar principle holds. Here the equilibrium frequency is \( q^* = \mu / h \: s \), where \( h \) represents the degree of dominance. This results in a mean fitness (viability) of the population approximately equal to \( \bar{F} \approx 1 - 2 \: \mu \), which is again independent of the selection coefficients \( s \) and \( h \).

The Haldane-Muller principle in a multilocus context

While classical theory has focused on a single locus context, the mutation load in a real population is spread over many loci. To investigate whether the Haldane-Muller principle extends to the multilocus context we used a simulation model. To this end we used a large number of loci (say \( n=100 \)), which are unlinked. Each locus has a wildtype allele with maximal fitness and a number of deleterious alleles, which all reduce fitness to a certain extent. Mutations of the wildtype to deleterious alleles and backmutations to the wildtype allele occur with mutation rate \( \mu \), which was assumed to be equal for all loci. For simplicity we assume that all mutations are completely recessive, that means that loci have maximal fitness when deleterious alleles are in heterozygous condition and that fitness is reduced by an amount \( s \) when they are homozygous for deleterious alleles. The value of the selection coefficient \( s \) was taken the same for all loci. Therefore the fitness of an individual depends on \( H_d \) the number of loci for which it carries homozygous deleterious alleles. It is often assumed that loci interact multiplicatively (e.g. Lande 1995; Charlesworth and Charlesworth 1998; Lynch and Walsh 1998) and that individual fitness is given by \( (1 - s)^{H_d} \). In contrast, we make the simplifying assumption of an additive interaction between loci, leading to fitness \( F = 1 - H_d \cdot s \). (Since for the parameters considered have \( (1 - s)^{H_d} \approx 1 - H_d \cdot s \), the differences between these two types of models are of marginal importance.)
With additive interactions between unlinked loci, one might expect that the mean fitness of the population in mutation-selection equilibrium for completely recessive alleles were \( \overline{F} \approx 1 - \mu n \). In other words the mean viability of the population should only depend on the genome-wide mutation rate \( (2\mu n) \), and be independent of the selection coefficient \( s \). To investigate whether the mutation load in a multilocus context conforms to this prediction we ran a number of computer simulations. We kept the genomic mutation rate at a value of \( 2\mu n=1 \) and varied the number of loci \( (n) \), the mutation rate per allele per locus \( (\mu) \) and the selection coefficient \( (s) \). Figure 1 shows the results for six different parameter combinations. The first half of each panel \((-1000 < t < 0)\) shows that the mean fitness of the population (mean viability, \( \overline{F} \)) and the mean number of loci homozygous for deleterious alleles \( (\overline{H_d}) \) rapidly converge to an equilibrium value. The number loci which are homozygous for deleterious alleles clearly depends on the strength of selection \( s \), with lower values of \( \overline{H_d} \) for higher values of \( s \) (compare panels A to C). This is not unexpected since, according to the mutant allele frequency \( \hat{q} \approx \sqrt{\mu / s} \), the per locus homozygosity of deleterious alleles is inversely related to \( s \). In contrast, the mean fitness of the population, or more precisely its mean viability, is less dependent on the selection coefficient. In fact, with the product \( \mu n \) kept constant, the actual mutation rate \( \mu \), the number of loci \( n \) and the selection coefficient \( s \) seem to be of marginal importance for the mean population fitness (compare panels 1 and 2). In this sense the results are in line with the Haldane-Muller principle. However, the mean viability is \( \overline{F} \approx 0.65 \) and hence larger than the predicted value \( 1-\mu n = 0.5 \), which corresponds to a lower equilibrium frequency of deleterious alleles (not shown). The most probable explanation for this discrepancy is that the population is large \( (N=1024) \), but not infinite, giving rise to stochastic effects. In addition, it is conceivable that, even in the absence of linkage, associations between loci develop (e.g. Hartl and Clark 1989; Charlesworth et al. 1992; Charlesworth et al. 1993), violating the independence assumption on which the naive expectation \( \overline{F} = 1 - \mu n \) is based.
Figure 1. Mean fitness (bold) and mean number of loci with homozygous deleterious alleles (dashed) before \((-1000 < t < 0)\) and after \((0 < t < 50)\) fragmentation. In the first 1000 generations a single large population \((N=1024)\) evolved to mutation-selection equilibrium. At \(t=0\) this large population was fragmented into 64 small, completely isolated populations of \(N=16\) individuals each. In all cases the genomic mutation rate \(2\mu n\) was equal to 1. Panels differ in the values of \(\mu\) and \(n\) (panels 1 and 2). The selection coefficient \(s\) is increased from 0.05 to 0.5 (panels A to C).
Fragmentation

Figure 1 also illustrates the fate of a (relatively) large population in mutation-selection equilibrium that is fragmented into multiple small and completely isolated subpopulations (64 populations with N=16 each). The effects of fragmentation on the mean fitness of the population and on the accumulation of loci with homozygous deleterious alleles are shown in the second half of the panels (0 < t < 50). The severe reduction in population size results in a decline in mean viability of the population within a few generations. When many loci (n=250) are involved, the number of loci with homozygous deleterious alleles doubles after fragmentation and mean fitness is reduced to half the original value. With a lower number of loci (n=100) the effects of fragmentation are less severe and the reduction in mean fitness is only half as large compared to 250 loci, even when the genomic mutation rate is equal. The selection coefficient s had only a minor effect on the decline in fitness. Although the number of loci with homozygous deleterious alleles was much higher for low values of s, this low selective disadvantage resulted in a more or less similar reduction in fitness compared to high values of s.

After a few generations purging of the mutation load starts, due to selection against homozygous deleterious mutations. The frequency of loci which carry homozygous deleterious alleles declines and mean viability rises again (e.g. Charlesworth et al. 1993; Lynch et al. 1995). This decrease in mutation load and increase in mean fitness are slightly slower when a smaller number of loci are involved. In our simulations the original mean fitness was never fully restored nor exceeded. Especially with a relatively low number of loci the mean fitness at generation t=50 remained below the original fitness of the large population, probably because we prevented fixation of alleles in the small subpopulations by allowing continuous mutation and backmutation. With a high selection coefficient s the increase in fitness due to purging of the mutation load started earlier (t<10 if s≥0.25, but t>20 for s=0.05). Strong selection also induced more rapid purging, resulting in a much shorter time with very low population fitness (less than 50 generations for s≥0.25).

To summarize, the effects of fragmentation on population fitness are most severe and the time needed for subsequent recovery is longest in case of many loci with a low mutation rate and weak selection against individuals homozygous for deleterious alleles. Although this may be the most realistic scenario for natural populations, we will for the rest of this paper focus on the scenario n=100, μ=0.005 and s=0.25. In particular, we chose a relatively small number of loci, due to computational and time limitations. But we want to stress beforehand, that in view of Figure 1 our results might be too optimistic, concerning the impact of population fragmentation in natural systems.
3. Plant-pollinator interactions and their consequences

Most studies on the effects of genetic erosion were only concerned with viability selection. In a plant-pollinator system additional selection pressures arise, which might have important implications for the (genetic) vulnerability of the plant population. Attractivity of the plants has an important role for their pollination. Therefore a relatively large investment of resources into pollinator attraction is beneficial for the plant. These high investments in attractivity can have serious negative consequences for the fitness of the plants, as is well known from the theory of sexual selection (Andersson 1994). Pollinator selectivity, i.e. a preference for more attractive plants, corresponds to a selection pressure, which is potentially stronger than viability selection. Hence pollinator selectivity contributes to the reduction of the mutation load in plant populations.

The effect of attractivity on plant fitness is mediated via the number of visits a plant receives. The number of visits is obviously related to the export and import of pollen. How attractivity differences are translated into differences in pollinator visitation strongly depends on the selectivity of the pollinator decision rule. We will here consider three different decision rules and investigate their consequences for the number of visits and accordingly pollen export and pollen import.

Pollinator decision rules

A plant’s pollination depends on the number of visits it receives by the pollinators. The decision rule used by the pollinators to decide which plant to visit is therefore crucial for the distribution of visits over the plants. In our model, pollinators have a preference for more attractive plants. Plant attractiveness is at least partially determined by the genotype of the plant. Attractivity has a broad interpretation, which might include the number of simultaneously opened flowers, their arrangement in inflorescences, flower size, flower colour, production of odours, etc. The plants in the population vary in their attractivity value. We distinguish three types of pollinators, which differ in selectivity, i.e. the strength of their preference for more attractive plants.

The first decision rule is based on the idea that a pollinator samples plants sequentially and that it decides for each plant separately whether the plant will be visited or not. This decision rule will be called ‘On-its-Own’ (OIO), since the chance to be visited, once being (randomly) sampled, only depends on the plant’s own attractivity. Still, OIO results in frequency dependent selection if the total number of pollinator visits to the plant population as a whole is fixed. In that
case the actual number of visits to a given plant depends on its own probability to be visited (its own attractivity) relative to the visitation probability of the other plants (mean attractivity).

The other two decision rules are fundamentally different, since they are based on the direct comparison of different plants. The simplest of these rules is ‘Best-of-Two’ (BOT), where a pollinator compares two randomly sampled plants and visits the plant with the highest attractivity value. This decision rule is a special case of the more general Best-of-n strategy, where the best out of n sampled males is chosen (Janetos 1980). The Best-of-Two decision rule corresponds to highly selective pollinators, since any difference in attractivity value, however small it may be, results in large differences in the number of visits a plant will receive. We therefore included in our study a less selective, comparative decision rule which we call ‘Difference-of-Two’ (DOT). A pollinator applying the DOT decision rule randomly samples two plants. Its decision which plant will be visited is based on the difference in the attractivity values between the two sampled plants. If the difference in attractivity is small both plants have an almost equal probability to be visited, while a large difference in attractivity results in most pollinator visits being made to the more attractive plant. This DOT decision rule might thus represent the increase in ‘errors’ when a pollinator has to discriminate between plants with very similar attractivity values.

Plant visitation

Consider a population of plants, which vary in their attractivity value A, which varies from 0 to 1. If P(A) describes the distribution of attractivity values in the plant population, the mean attractivity in the population is given by \( \int_{0}^{1} P(A) \cdot A \, dA = \bar{A} \).

The plant population is visited by pollinators, which make on average \( \bar{\phi} \) visits per plant. These visits are distributed over plants with different attractivity values according to the visitation function \( \varphi(A) \), which reflects the decision rule of the pollinators. Pollen export is assumed to be directly dependent on the number of visits a plant receives and thus on the attractivity value of the plant.

For decision rule OIO, pollen export is directly proportional with the attractivity of a plant: \( \varphi(A) \propto A \). For decision rule BOT, the number of visits a given plant receives is proportional with the probability that the other plant sampled has a lower attractivity value:

\[
\phi(A) \propto \text{Prob}(\alpha < A) = \int_{0}^{A} P(\alpha) \, d\alpha.
\]
For decision rule DOT, a pollinator has to choose between two randomly sampled plants, with attractiveness values $A_1$ and $A_2$, respectively. If both plants have an equal attractiveness value, each has a chance of $\frac{1}{2}$ to be visited. This basic probability is modified according to the difference in attractiveness values, $A_1 - A_2$. For plant 1 the probability to be visited is increased if its own attractiveness is higher and decreased if its own attractiveness is lower than that of the other plant. The probability that plant 1 is visited is thus given by $\frac{1}{2} + \frac{1}{2} (A_1 - A_2)$. Hence, the number of visits a plant with attractiveness $A$ receives is proportional with $\frac{1}{2} + \frac{1}{2} (A - \bar{A})$:

$$\varphi(A) \propto \frac{1}{2} \left( I + A - \bar{A} \right).$$

For all three decision rules, the constant of proportionality is easily obtained from the consistency requirement $\bar{\phi} = \int_0^A \phi(A) \cdot P(A) \; dA$.

As a result, we obtain the following relation between plant attractiveness and the number of visits:

**On-its-Own**

$$\phi(A) = \frac{A}{\bar{A}} \cdot \bar{\phi} \quad (1a)$$

**Difference-of-Two**

$$\phi(A) = \left( I + A - \bar{A} \right)\bar{\phi} \quad (1b)$$

**Best-of-Two**

$$\phi(A) = 2 \int_0^A P(\alpha) \; d\alpha \cdot \bar{\phi} \quad (1c)$$

All three visitation functions are depicted graphically in Figure 2.
Figure 2. Relation between the number of visits a plant receives and its attractivity for different pollinator decision rules. For OIO (solid) and DOT (dotted), the number of visits is linearly related to the plant’s attractivity, while the relation for BOT (dashed-dotted) corresponds to the cumulative distribution of $A$. Notice that for OIO and DOT a plant with average attractivity receives the mean number of visits. For BOT, this is only the case when the distribution of attractivity values is symmetric, i.e. if the mean equals the median, as assumed in this figure.

Pollen exchange and seed production

Both export of pollen to other plants and deposition of pollen on stigmas, i.e. the contribution to the next generation via male and female function, depend on pollinator visitation. Pollen export is clearly dependent on the number of visits a plant receives. In fact, we assume that pollen export and hence male function is directly proportional with the number of visits:

$$\text{pollen export} \propto q(A)$$

One might expect that pollen import occurs in a similar way to pollen export and is determined by the number of visits. However, several other aspects are important for the deposition of pollen. A larger nectar production, for example, generally results in a longer duration of visits (Primack and Silander 1975; Thomson and Plowright 1980; Harder 1988),
probably leading to a larger amount of imported pollen. Additionally, maternal investment in the development of seeds (e.g. endosperm production) has a positive effect on seed quality. For simplicity, we combine nectar production and other maternal effects into a single allocation component, which we call seed investment, $I$. We assume that pollen import and seed production are proportional with this seed investment and with the attraction of pollinators: seed production $\propto I \cdot \psi(A)$. The influence of pollinator attraction on pollen import, $\psi(A)$, need not be the same as on pollen export, $\varphi(A)$. For example, in dioecious plants or in plants where male and female flowering are separated in time, these two functions can be quite different. For simplicity, we consider only two extreme scenarios. In the first scenario (‘type I plants’), seed production only depends on seed investment, i.e. $\psi(A)=1$. This is, for example, the case for wind-pollinated plants. In the second scenario (‘type II plants’), pollen export and pollen import are governed by the same principles, i.e. $\psi(A)\varphi(A)$. This scenario probably applies to most monoecious plants. In other words

\begin{align}
\text{type I:} & \quad \text{seed production } \propto I \quad (3a) \\
\text{type II:} & \quad \text{seed production } \propto I \cdot \varphi(A) \quad (3b)
\end{align}

**Allocation components**

Viability, attractiveness and seed investment are all important for the reproductive contribution of a plant to the next generation. However, plants have only a limited amount of resources to invest in these fitness components and the plant has to choose how many of its resources it will allocate to each component. We assume that a plant’s capacity to acquire resources depends on its genetic constitution, that means on the number of deleterious, recessive mutations it has accumulated. This genetically determined capacity to acquire resources will be called vigor ($F$). The vigor of a plant is given by

$$F = 1 - s \cdot H_d \quad (4)$$

where $H_d$ is again the number of loci which carry homozygous deleterious alleles and $s$ denotes the selection coefficient.
We assume that a plant has to divide its resources over three different fitness components: viability ($V$), affecting survival, advertisement ($A$), determining the number of visits, and seed investment ($I$), influencing pollen import and seed production. We suppose that the allocation of vigor is governed by three genetically determined allocation parameters: $v$ for viability, $a$ for advertisement and $i$ for seed investment, respectively. These allocation parameters represent the relative allocation and sum to unity, $v+a+i=1$. The resulting fitness components are

$$V= vF, \ A= aF, \ I=iF$$  \hspace{1cm} (5)$$

Thus the amount of resources allocated to each fitness component depends on the plant’s architecture (i.e. the combination of allocation parameters) and on the genetically determined vigor of the plant.

**Short-term versus long-term effects**

In principle, plant vigor ($F$) as well as plant architecture ($v, a, i$) both reflect the genetic constitution of a plant. It is important to realize, however, that changes in the allocation pattern will occur on a very different time scale than changes in plant vigor. In fact, changes in plant architecture will occur on a long-term, evolutionary time scale, reflecting the adaptation of a plant to its pollinators. In contrast, changes in plant vigor may occur much more rapidly (on an ecological time scale) in response to changes in the local environment, e.g. fragmentation. For this reason we will consider changes in allocation parameters separately from changes in plant vigor.

In a first step (section 4) we investigate the expected change of $v, a$ and $i$ in response to pollinator behaviour. We assume that the evolution of allocation parameters takes place under favourable and relatively constant environmental conditions. Accordingly, vigor ($F$) is assumed to have a more or less fixed value. Given this fixed value of $F$ we determined the evolutionarily stable allocation pattern $v^*, a^*$ and $i^*$. In a second step (section 5) we investigate short-term changes in plant vigor $F$ in response to environmental disturbance. Since on the corresponding short-term time scale the allocation pattern will hardly change, the allocation parameters will be kept fixed at their ESS values.
4. Optimal allocation patterns

Our main goal is to obtain insight into genetic erosion for various types of plant-pollinator interactions. We have to face the complication that the pollination system and plant architecture are not independent from one another. In fact, the allocation parameters of the plant will reflect the plant’s interactions with its pollinators. In other words, \( v, a \) and \( i \) should not be viewed as arbitrary parameters, but as the result of an evolutionary adaptation process.

We use an Evolutionarily Stable Strategy (ESS) approach (Maynard Smith 1982) to determine the allocation pattern \( v^*, a^*, i^* \), which is optimal for a given pollination system. To this end, we assume that the plant population is large and unfragmented. All plants have the same fixed vigor \( F \). Up to a normalization factor the absolute resource investments are equal to the allocation parameters: viability \( V = v \), advertisement \( A = a \) and seed investment \( I = i \), respectively.

**ESS analysis**

Quite generally, an evolutionarily stable strategy can be found as follows (Maynard Smith 1982). Consider a resident population with allocation pattern \( x^* \), which is invaded by a rare mutant with allocation pattern \( x \). The fitness of the mutant in such a resident population is denoted by \( W(x,x^*) \). The allocation strategy \( x^* \) is an ESS if the fitness of all possible mutants is lower than the fitness of the resident type. In other words, an ESS is given by

\[
W(x^*,x^*) = \max_x W(x,x^*)
\]

(6)

Technically an ESS can be determined on basis of the criterion

\[
\frac{\partial W}{\partial x} \Bigg|_x = 0, \quad \frac{\partial^2 W}{\partial x^2} \Bigg|_x < 0
\]

(7)

where the notation indicates that the partial derivatives are evaluated at \((x^*,x^*)\), i.e. for \( x = x^* \).

**The Shaw-Mohler equation**

In case of reproductive allocation, the fitness of an allocation strategy \( x \) in a resident population \( x^* \) is given by the Shaw-Mohler equation (Charnov 1982)

\[
W(x,x^*) = \frac{1}{2} \left[ \frac{m(x)}{m(x^*)} + \frac{f(x)}{f(x^*)} \right]
\]

(8)

In this equation \( m(x) \) and \( f(x) \) denote the reproductive contribution to the next generation via male and female function, respectively. In our case the variable \( x \) corresponds to an allocation pattern \((v, a, i)\) which, due to the constraint \( v+a+i=1 \), can be represented by the two variables \( v \) and \( a \). We assume that the reproductive contribution via pollen (male fitness) is proportional to
two factors: a plant’s viability \( v \) and the expected number of visits \( \varphi(a,a^*) \) that a plant with advertisement \( a \) receives in a resident population with advertisement level \( a^* \). Male contribution is thus given by \( m(v,a) = v \cdot \varphi(a,a^*) \). The reproductive contribution via seeds depends on the plant type. For plants of type I (see 3a) the production of surviving seeds (female fitness) is independent of the number of visits and depends only on viability and seed investment, \( f(v,i) = v \cdot i = v (1-v-a) \). For plants of type II (see 3b) the reproductive contribution via seeds depends also on the number of visits the plant receives, \( f(v,i,a) = v \cdot i \cdot \varphi(a,a^*) = v (1-v-a) \varphi(a,a^*) \). As a result we obtain two versions of the Shaw-Mohler equation, one for each plant type:

**Type I:**

\[
W = \frac{1}{2} v \left[ \frac{\varphi(a,a^*)}{\varphi(a^*,a)} + \frac{1-v-a}{1-v-a} \right]
\]  
(9a)

**Type II:**

\[
W = \frac{1}{2} v \cdot \varphi(a,a^*) \cdot \left[ 1 + \frac{1-v-a}{1-v-a} \right]
\]  
(9b)

**ESS allocation patterns**

In view of (9), the ESS values of the allocation parameters can be obtained from the criteria:

\[
\frac{\partial W}{\partial v} \bigg|_* = \frac{1}{v} - \frac{1}{2(1-v-a)} = 0
\]  
(10)

and

\[
\frac{\partial W}{\partial a} \bigg|_* = \frac{1}{2} \left[ \frac{1}{\varphi} \frac{\partial \varphi}{\partial a} \right]_* - \frac{1}{2(1-v-a)} = 0
\]  
(11a)

**Type II:**

\[
\frac{\partial W}{\partial a} \bigg|_* = \frac{1}{\varphi} \frac{\partial \varphi}{\partial a} \bigg|_* - \frac{1}{2(1-v-a)} = 0
\]  
(11b)

In other words, we obtain the ESS conditions:

\[
v^* = 2(1-a^*-v^*) = 2i^*
\]  
(12)

and

**Type I:**

\[
\frac{1}{\varphi} \frac{\partial \varphi}{\partial a} \bigg|_* = \frac{1}{v} \frac{1}{1-v-a} = \frac{1}{i^*}
\]  
(13a)

**Type II:**

\[
\frac{1}{\varphi} \frac{\partial \varphi}{\partial a} \bigg|_* = \frac{1}{2(1-v-a)} = \frac{1}{2i^*}
\]  
(13b)
If we call $\kappa = \frac{1}{\phi} \left. \frac{\partial \phi}{\partial a} \right|_{a}$, we arrive at the following ESS allocation pattern:

\[
\begin{align*}
\text{type I:} & \quad v^* = \frac{2}{\kappa}, \quad i^* = \frac{1}{\kappa}, \quad a^* = 1 - \frac{3}{\kappa} \quad (14a) \\
\text{type II:} & \quad v^* = \frac{1}{\kappa}, \quad i^* = \frac{1}{(2\kappa)}, \quad a^* = 1 - \frac{3}{(2\kappa)} \quad (14b)
\end{align*}
\]

or equivalently:

\[
\begin{align*}
\text{type I:} & \quad v^* : i^* : a^* = 2 : 1 : \kappa - 3 \quad (15a) \\
\text{type II:} & \quad v^* : i^* : a^* = 2 : 1 : 2\kappa - 3 \quad (15b)
\end{align*}
\]

**Dependence on pollinator decision rule**

Obviously, the quantity $\kappa = \frac{1}{\phi} \left. \frac{\partial \phi}{\partial a} \right|_{a}$, indicating the increase in the number of visits which a mutant with higher advertisement will receive, is of crucial importance for the optimal plant allocation pattern. In view of (1) and since $\bar{a} = a^*$, in the resident population, the expected number of visits depends in the following way on the decision rule of the pollinators (illustrated in Figure 3):

\[
\begin{align*}
\text{OIO:} \quad & \phi(a, a^*) = \frac{a}{a^*} \cdot \phi^* \quad \Rightarrow \quad \kappa = \frac{1}{a} \quad (16a) \\
\text{DOT:} \quad & \phi(a, a^*) = (1 + a - a^*) \phi^* \quad \Rightarrow \quad \kappa = 1 \quad (16b) \\
\text{BOT:} \quad & \phi(a, a^*) = \begin{cases} 0 & \text{if } a < a^* \\ \phi^* & \text{if } a = a^* \\ \phi_{\text{max}} & \text{if } a > a^* \end{cases} \quad \Rightarrow \quad \kappa = \infty \quad (16c)
\end{align*}
\]
Figure 3. Expected number of visits $\varphi(a,a^*)$ of a mutant with advertisement level $a$ in a resident population with advertisement level $a^*$ for various decision rules. In case of OIO (solid) and DOT (dotted), the number of visits increases linearly with $a$, while BOT (dashed-dotted) leads to a step-function. Less extreme choice functions will probably lead to an S-shaped function $\varphi(a,a^*)$ which is also indicated in the figure (dashed).

Inserting (16) into (14) yields the ESS allocation pattern for all three decision rules. Notice that in case of the very selective pollinator decision rule BOT, plants should invest all their resources into advertisement, since a minute increase in advertisement results in a much higher pollinator visitation ($\kappa=\infty$). Selection pressures by pollinators using the DOT decision rule are much lower. In fact the value of $\kappa$ is equal to 1, which would formerly result in a negative allocation in advertisement: $a^*<0$. Of course this is impossible, but at the ESS the allocation to advertisement will be minimal ($a^*=0$), resulting in $v^*=2/3$ and $i^*=1/3$. Although pollinators with choice rule DOT do select plants according to their advertisement, well-adapted plants should invest no resources into this fitness component. The benefit of additional resource allocation to advertisement is in equilibrium much lower than the benefit of investing these resources into viability or seed production. For the decision rule OIO we find the following optimal allocation patterns: $\kappa = 1/a^* = 4$ for type I and $\kappa = 1/a^* = 2.5$ for type II plants (Table 1).
Table 1 ESS allocations to viability (v*), advertisement (a*) and seed investment (i*). For plant type I male and female contribution are independent, whereas for plant type II female contribution depends also on the number of visits to the plant.

<table>
<thead>
<tr>
<th>Decision rule</th>
<th>plant type</th>
<th>viability, v*</th>
<th>seed investment, i*</th>
<th>advertisement, a*</th>
</tr>
</thead>
<tbody>
<tr>
<td>On-its-Own</td>
<td>I: f = iv</td>
<td>0.5</td>
<td>0.25</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>II: f = qiv</td>
<td>0.4</td>
<td>0.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Diff-of-Two</td>
<td></td>
<td>0.67</td>
<td>0.33</td>
<td>0</td>
</tr>
<tr>
<td>Best-of-Two</td>
<td></td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

ESS allocations for a partially selfing plant

Many hermaphrodite plants are self-compatible and undergo regular selfing (Charlesworth and Charlesworth 1987a). Selfing changes the relative importance of allocation to male and female reproductive structures. For a plant with a fixed selfing rate S, the fitness contribution of selfed seeds depends only on female reproductive effort, whereas the fitness of outcrossed seeds depends on both male and female reproductive allocation. This results in a modified version of the Shaw-Mohler equation:

\[
W(x, x^*) = S \frac{f(x)}{f(x^*)} + (1 - S) \frac{1}{2} \left[ \frac{m(x)}{m(x^*)} + \frac{f(x)}{f(x^*)} \right]
\]

(17)

Calculations analogous to those in the absence of selfing give the ESS allocation pattern for partially selfing plants:

type I: \( v^* : i^* : a^* = 2 : 1+S : \frac{16}{1+2S} - (3+S) \)  \( (18a) \)

(type II: \( v^* : i^* : a^* = 2 : 1+S : \frac{2}{1+2S} - (3+S) \)  \( (18b) \)

With help of (16) the ESS allocations can be solved for our decision rules (Table 2).

Table 2 ESS allocations to viability (v*), advertisement (a*) and seed investment (i*) for partially selfing plants with fixed selfing rate S. For plant type I male and female contribution are independent, whereas for plant type II female contribution depends also on the number of visits to the plant.

<table>
<thead>
<tr>
<th>decision rule</th>
<th>plant type</th>
<th>viability, v*</th>
<th>seed investment, i*</th>
<th>advertisement, a*</th>
</tr>
</thead>
<tbody>
<tr>
<td>On-its-Own</td>
<td>I: f = iv</td>
<td>( \frac{1}{2} )</td>
<td>( \frac{1+S}{4} )</td>
<td>( \frac{1-S}{4} )</td>
</tr>
<tr>
<td></td>
<td>II: f = qiv</td>
<td>( \frac{2}{5+S} )</td>
<td>( \frac{1+S}{5+S} )</td>
<td>( \frac{2}{5+S} )</td>
</tr>
<tr>
<td>Diff-of-Two</td>
<td></td>
<td>( \frac{2}{3+S} )</td>
<td>( \frac{1+S}{3+S} )</td>
<td>0</td>
</tr>
<tr>
<td>Best-of-Two</td>
<td></td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>
**Simulation approach**

A limitation of the ESS approach is that it assumes a monomorphic resident population, which is invaded by a single mutant. In contrast, natural populations are often highly polymorphic. We therefore ran a number of individual-based computer simulations in order to investigate the robustness of the ESS predictions (12) and (15). To this end, we consider a large population of diploid plants (N=1024), whose allocation patterns are determined by the alleles at three allocation loci. The population is potentially highly polymorphic, since at each locus a broad spectrum of alleles (with allelic values ranging from 0 to 1) is feasible. For each plant, the allocation to a given fitness component is proportional to the sum of the two allelic values at the corresponding allocation locus. Hence, for a plant with ‘allocation alleles’ \( v_1, v_2, a_1, a_2, i_1, i_2 \) the allocation to viability is given by \( (v_1 + v_2) / (v_1 + v_2 + a_1 + a_2 + i_1 + i_2) \). The resulting allocation pattern determines the plant’s expected viability, number of visits and seed production. Based on these expectations, the real values are determined by a chance process. In addition to selection, the population is affected by genetic drift and mutation. Mutation is modeled as follows: with probability \( \mu \) (\( \mu=0.0001 \)) per gamete and generation, a mutation is created which differs from the original allele by a value that is drawn at random from the interval \([-0.01, +0.01]\). Figure 4 shows that in all cases the population converged rapidly to an allocation pattern that closely resembles the ESS predictions (indicated by arrows). This shows that the ESS predictions are quite robust. The decision rule Best-of-Two led to rapid extinction of the population, because the investment in viability evolved to zero and no seeds survived to the next generation (not shown). Although it is theoretically possible that natural selection drives a population to extinction, we consider this not very likely for real populations. We therefore assume from now on, that none of the allocation parameters can be zero. More specifically, for the rest of the paper, we assume that the relative allocations cannot drop below 5% of the total available resources.
Figure 4. Comparison of ESS predictions (arrows) and the outcome of individual-based Monte Carlo simulations. For various pollination mechanisms the evolution of allocation parameters is shown for a large, unfragmented population (N=1024). Mutation rate $\mu$ was 0.0001 and the maximal mutation step size was 0.01. Means for 10 replicate simulation runs are given. Note that for BOT the time scale with plant type I ($f = iv$) is much longer than for the other simulations (panel C1). Viability: upward triangle; advertisement: open circle; seed investment: downward triangle.
Conclusions

Obviously, the pollination system is of crucial importance for plant architecture, i.e. for a plant's optimal allocation of resources to viability, advertisment and seed production. The pollinator's decision rule is more important than the plant type for the optimal allocation pattern. In fact, only for pollinators with decision rule OIO does the plant type matter at all. Not surprisingly, in this case allocation of resources to advertisment is lower in plants where seed production is independent of the number of visits (type I plants). However, the pollinator's decision rule is the dominant factor determining the ESS allocation pattern. The decision rules DOT and BOT induce relatively extreme plant allocation patterns, while decision rule OIO, which leads to intermediate selectivity (see Figure 3), induces a mixed allocation pattern. The extremely low allocation in viability, which is induced by decision rule BOT, results in an enhanced vulnerability of the plants. Notice that these specific adaptations to the pollinator can have implications for fragmentation, because habitat fragmentation can be accompanied by a shift in the main pollinator type.

5. Genetic erosion in a plant-pollinator system

Now that we have derived the optimal allocation pattern for a given pollination system, we can address the effects of habitat fragmentation on genetic erosion. From now on, we keep the allocation patterns fixed at their optimal values (with a minimal allocation of 0.05) and investigate whether and to what extent the mutation load is affected by fragmentation.

Simulation model

The simulation model is similar to the model for genetic erosion in a viability selection context (Figure 1). We now include allocation to viability $V$, advertisment $A$ and seed production $I$. For each pollination system the allocation parameters are fixed at their ESS values, with the proviso that at least 5% of the available resources should be allocated to each fitness component. According to the genetic constitution of the plant, its resulting vigor $F$ and the fixed allocation parameters $v^*$, $a^*$ and $i^*$ the plant allocates $V$, $A$ and $I$ (see eqn. 5) to the three fitness components. A population comprises a fixed number of $N$ positions. For each position male and female gametes are drawn repeatedly from a pollen pool and ovule pool, until a surviving seed results. The survival probability of a newly formed seed is given by $V=v^*F=v^*(1 - s \cdot H_d)$ and hence reflects the genetic constitution of the seedling. A surviving seedling has advertisment $A=a^*F$, which results in a number of visits $\varphi(A)$, depending on the decision rule of the pollinators (see eqn. 1). The contribution of a seedling to the pollen pool is proportional to $\varphi(A)$. The
contribution to the ovule pool depends on the seedling's investment $I = i * F$ and, in case of type II plants, on the number of visits received $\varphi(A)$ (see eqn. 3). As described above, plant vigor $F$ is determined by the number of loci carrying homozygous deleterious alleles, $F = 1 - s \cdot H_d$. In all cases, we use $n=100$ loci, a genome wide mutation rate of 1 and a selection coefficient $s=0.25$. As mentioned earlier, a lower mutation rate $\mu$ and weaker selection will result in more dramatic effects than the parameter combination used here.

To study the effects of genetic erosion we monitored the mean frequency of deleterious alleles, the average number of loci homozygous for these alleles ($H_d$) and the resulting mean vigor. Moreover, we observed changes in the mean population viability. This might in reality be an important indicator of the vulnerability of a plant population. To quantify population viability we kept track of the number of trials $M$, which are needed to fill the $N$ available positions, and defined population viability $V = N / M$. Notice that $V$ is roughly equivalent to $v * F$.

We start all simulation runs with a relatively large population ($N=1024$), which is allowed to evolve to mutation-selection equilibrium before fragmentation takes place. For all pollination systems 1000 generations were sufficient (Figure 5, $-1000 < t < 0$). After 1000 generations the population is fragmented into many small populations ($64$ with $N=16$ each). We study different degrees of isolation and self-pollination. Finally in some of the simulations fragmentation is associated with a switch of pollinator type.
Figure 5. Effect of pollination system on the mutation load and genetic erosion. Mean vigor (bold), population viability (solid) and mean number of loci with homozygous deleterious alleles (dashed) before (-1000 < t < 0) and after (0 < t < 50) fragmentation. The effects of different pollinator decision rules are compared (panels A to C). In the first 1000 generations a single large population (N=1024) evolved to mutation-selection equilibrium. At t=0 this large population was fragmented into 64 small, completely isolated populations of N=16 individuals each. In all cases n=100 loci were used, with mutation rate µ=0.005 and selection coefficient s=0.25. Panels 1 show the results for type I plants (f = iv), panels 2 for type II plants (f = φiv). Panel D (up to a change in scale the same as Figure 1 B2) gives the results for viability selection only.
**Mutation-selection equilibrium**

The first part (-1000 < t < 0) in the panels of Figure 5 shows how the mutation load depends on the pollination system. When compared with pure viability selection (Figure 5 D, which is equal to Figure 1 B2) the mutation load is lower when plant-pollinator interactions play a role. With respect to the number of loci with homozygous deleterious alleles, and hence also mean vigor, the most selective decision rule BOT prevented best the accumulation of deleterious mutations. It is followed by the less selective decision rules OIO and DOT and finally by pure viability selection. Accordingly, mean vigor is highest for Best-of-Two and lowest for viability selection. Interestingly, the opposite is the case for mean population viability. Since plants confronted with very selective pollinators have only few resources left to invest into viability, the mean viability of the population is highest for pure viability selection, followed by DOT, OIO and BOT. Compared to the effects of the pollinator decision rule the plant type is of minor importance. Only in case of BOT type II plants differ from type I plants: if seed production also depends on advertisement (type II) the mutation load is slightly lower and accordingly mean vigor higher.

**Complete fragmentation**

Figure 5 also shows the effects of population fragmentation (0< t<50). The fragments generated at t=0 were completely isolated from one another. Notice that fragmentation resulted in a rapid increase in $H_d$ and correspondingly a rapid decrease in mean vigor. After fragmentation mean vigor drops to approximately 3/4 of the value just before fragmentation. Since population viability is roughly proportional with mean vigor ($\bar{V} \approx v^* \bar{F}$) the same principle applied to population viability, be it at a smaller scale. Interestingly, the drop in vigor after fragmentation was most pronounced for those systems having the lowest initial level, due to non-selective pollination (pure viability selection and pollinator decision rule Diff-of-Two). In fact, the drop in vigor for these systems was to ±73% of the original value, compared to ≥80% for the more selective decision rules OIO and BOT. Qualitatively, however, the dynamics of genetic erosion after fragmentation was not much affected by plant type or pollinator decision rule. In all cases, vigor gradually increased again after the initial drop, due to purging of the mutation load. However, in none of the cases, 50 generations were enough to approach the value found before fragmentation.
Partial isolation between subpopulations

Obviously, the genetic consequences of fragmentation are most drastic in case of complete isolation. In natural systems, isolation will often be less complete than simulated in Figure 5. To simulate incomplete isolation, we modified our simulation model by allowing a certain fraction of between-population pollen flow. In the modified model female gametes are always drawn from the local ovule pool, while male gametes are drawn with probability $\lambda$ from the local pollen pool and with probability $1-\lambda$ from the pollen pool of another small population. Hence, $\lambda$ is a measure for the degree of isolation, $\lambda=1.0$ corresponding to complete isolation (as in the simulations of Figure 5). Concerning between-population pollen flow, we consider three scenarios for the choice of the pollen donor: ‘random’, ‘nearest neighbour’ and ‘attractivity-based’. For scenario ‘random’, the pollen donor is picked from the pollen pool of a randomly chosen subpopulation. With ‘nearest neighbour’, a linear arrangement of subpopulations is assumed and a foreign pollen donor is picked from one of the two adjacent subpopulations. The scenario ‘attractivity-based’ reflects the idea that the cumulative advertisement of all plants in a subpopulation determines the attractivity of the subpopulation to pollinators. In this scenario, the chance of a given subpopulation to contain a pollen donor depends on the mean advertisement of the plants in that subpopulation.

As illustrated by Figure 6 the three scenarios hardly differed in their effects on genetic erosion. For a given degree of isolation (Figure 6A), the dynamics of genetic erosion was qualitatively similar to that in case of complete isolation, but, not surprisingly, less pronounced for smaller values of $\lambda$. Figure 6B shows the mean vigor after 10 generations of fragmentation for the three scenarios and various values of the isolation parameter $\lambda$. Mean vigor $\bar{F}$ at $t=10$ decreased slowly from 96% of the original value for $\lambda=0$ to 77% for $\lambda=1$. This reduction in vigor occurred gradually with increasing isolation. Notice that for $\lambda<0.6$ mean vigor is hardly affected by fragmentation, but even for larger values of $\lambda$ the effects of fragmentation on vigor are limited.
Figure 6. Effect of different scenarios for the choice of the pollen donor with incomplete isolation between population fragments: ‘random’ (solid), ‘nearest neighbour’ (dashed) and ‘attractivity-based’ (dotted). (A) Changes in mean vigor over time with $\lambda=0.8$. (B) Relation between mean vigor after 10 generations of fragmentation and the degree of isolation, $\lambda$. Simulations were performed with plant type II ($f=\varphi iv$) and pollinator decision rule Diff-of-Two. A large population (N=1024) was fragmented into 64 subpopulations (N=16 each) and we used $\mu=0.005$, $n=100$, $s=0.25$.

Increased selfing

Thusfar, we have focused on the effects of fragmentation per se, without considering the possibility that fragmentation is associated with changes in the pollination system. For example, it is conceivable that the lower availability of plants for pollinators in small populations leads to an increase in the selfing rate. Such an increase in selfing will have a twofold effect. On the one hand, increased selfing will increase mean homozygosity, leading to a more pronounced drop in plant vigor and a more efficient purging of the mutation load. On the other hand, the plants are no longer optimally adapted to their pollinators, since the optimal allocation pattern critically depends on the selfing rate (see Table 2).

To study these combined effects we repeat our previous simulations, but now increase the selfing rate from $S=0$ before fragmentation ($-1000<t<0$) to $S=0.2$ and $S=0.5$ after fragmentation ($0<t<50$), respectively. Now, the drop in vigor, which was to 75% of the original value in the absence of selfing (Figure 7A), was more pronounced (63% resp. 51% of the original value, Figure 7B and 7C), when the selfing rate was increased. However, this drop in vigor was transient. Since the increased level of homozygosity, associated with selfing, leads to an enhanced exposure of deleterious alleles to selection, these deleterious mutations are relative efficiently purged from the population. As a result, after about 50 generations mean vigor reached almost the same level, independent of the selfing rate.
Figure 7. The effects of an increase in the selfing rate after fragmentation on plant vigor (bold), population viability (solid) and the number of loci with homozygous deleterious alleles (dashed). A large, non-selfing population (N=1024) was fragmented into 64 small (N=16 each), completely isolated subpopulations (S=0, panel A). The other panels show the results when, at the moment of fragmentation, also the selfing rate was increased from $S=0$ to $S=0.2$ (B) or $S=0.5$ (C) respectively. We used type II plants ($f=\varphi n$) with decision rule DOT and $\mu=0.005$, $n=100$, $s=0.25$. 
Change in pollinator type

Another factor, that will frequently be associated with fragmentation, is a change in the abundance of pollinator species. It is easily conceivable, that the original pollinator of a plant species is replaced by a new one. This might have implications for genetic erosion, since the plant’s allocation pattern will no longer be optimally adapted. To investigate the effects of a change in pollinator type we run the simulations anew, but switching the pollinator type at the moment of fragmentation (t=0). The results are illustrated in Figure 8.

In general, a switch in pollinator type had a relatively minor effect on the drop of vigor after fragmentation (although the drop was somewhat higher, when the switch was to the least selective pollinator, using decision rule DOT). However, the change in pollinator type had a marked effect on purging, that means the recovery of vigor after fragmentation. Generally, recovery was fastest for original pollinators of low selectivity and new pollinators of high selectivity. In fact, the most efficient purging occurred for a switch from DOT to BOT (Figure 8 B3), while vigor remained at a low value, when pollinator type BOT was replaced by DOT (Figure 8 C2). Obviously, the population viability was mainly affected by the allocation pattern, which, in turn, was adapted to the original pollinator type.
Figure 8. Effects of a switch in pollinator type after fragmentation on plant vigor (bold), population viability (solid) and the number of loci with homozygous deleterious alleles (dashed). A large population (N=1024) was fragmented into 64 small (N=16 each), completely isolated populations. At the moment of fragmentation also the pollinator decision rule was changed. Results are shown for all possible switches in decision rules (A, B, C: same original pollinator type; 1, 2, 3: same new pollinator type). We used plant type II (f = φ/ν) and μ=0.005, n=100, s=0.25.
6. Discussion

Genetic erosion and population persistence

With no doubt, ecological risks are of major importance for the persistence of plant-pollinator systems. In this paper, we did not address these ecological risks, but focused on the role of genetic erosion, which may also influence the extinction risk of animal-pollinated plants. The exact relation between genetic erosion and the probability of population extinction is still unknown. Therefore, we did not model the ecological consequences of genetic erosion explicitly. In fact, we kept population size constant, making extinction of the plant population impossible. We also neglected the possibility that habitat fragmentation may result in lower pollinator visitation rates and insufficient pollination. In natural populations, a reduction in vigor will often lead to a reduced seed production and a decline in population size. Pollen limitation of seed set is another plausible consequence of habitat fragmentation, although the degree to which plants suffer reduced seed set might vary (e.g. Byers 1995; Ramsey 1995; Le Corff et al. 1998; McCauley and Brock 1998; Totland et al. 1998). If we had allowed varying population sizes and a reduction in pollinator visitation after fragmentation, many of our populations would probably have gone extinct due to pollinator limitation. Instead, we used the frequency of deleterious mutations, mean population viability and mean vigor as indicators of population performance. However, at the moment the ‘ecological’ relevance of these indicators is unclear.

Fitness consequences of genetic erosion

To model genetic erosion, we concentrated on the accumulation of deleterious alleles due to mutation-selection balance. The genomic mutation rate, that means the total number of mutations per individual per generation, is of crucial importance. Estimates of the genomic mutation rate usually vary between 0.2 and 2.0 mutations per individual per generation (Lynch and Walsh 1998), but see Crow (1999). Here, we used a genomic mutation rate of U=1.0. In theory (see section 2) only the genomic mutation rate appears to matter for genetic erosion, rather than the per locus mutation rate \( \mu \). This allowed us to compensate for a relatively low number of loci \( n=100 \), speeding up the simulations) by a relatively high mutation rate per locus. However, the theoretical expectation that only \( \mu n \) matters, which was derived for infinite populations, seems to hold only approximately for the smaller populations considered here. In fact, for a given genomic mutation rate, the effects of genetic erosion seem to be more severe in case of a larger number of loci with a smaller mutation rate per locus (see Figure 1). By using a relatively small number of loci, we will thus have underestimated the consequences of genetic erosion in our simulations.
According to the Haldane-Muller principle (see section 2), the effect size of deleterious mutations (the selection coefficient $s$) does not affect genetic erosion, at least in an infinite population. Again, in the finite populations studied here, the Haldane-Muller principle only holds by a rough approximation. It was found that genetic erosion had the strongest effects for the smallest values of the selection coefficient $s$ (see Figure 1). Empirical estimates of the average effect size of deleterious mutations vary enormously, but they are usually considerably smaller than the selection coefficients chosen in our simulations ($s=0.25$) (Lynch and Walsh 1998). Hence, our simulations will probably underestimate the amount of genetic erosion.

To keep the genetic assumptions as simple as possible, we only considered recessive deleterious alleles. In natural populations, deleterious mutations will often be only partially recessive, but estimates of the fitness depression of heterozygotes, $1-hs$, vary considerably. Our choice of $h$ equal to zero will probably overestimate the effects of genetic erosion, since a small value of $h$ has similar effects as a small selection coefficient $s$ (e.g. Charlesworth et al. 1993). We did not study the possibility of overdominance in fitness, which might have a large impact on genetic erosion, but is generally considered a less important factor (Lynch 1991; Fu and Ritland 1994). However, even if the majority of loci correspond to the pattern of partial dominance, a small number of loci with overdominance may have a large effect, because genetic erosion due to overdominance cannot be purged.

In this paper, we kept the genetic assumptions as simple as possible, in order to focus on the fitness effects of genetic erosion that may be typical of plant-pollinator interactions. In particular, we addressed the extent to which it matters whether selection is only acting on viability (as is usually assumed in models of genetic erosion) or also on other fitness components. In our models, where also attractivity and seed investment played a role, the mutation load in a large population was reduced, when compared to a pure viability selection model (see Figure 5). Qualitatively, the system reacted in a similar way to habitat fragmentation as in the case of pure viability selection. Quantitatively, however, purging of the mutation load was more efficient with strong selection on attractivity, reducing the impact of genetic erosion.
Modeling pollinator behaviour

Pollinator behaviour (i.e. ‘decision rule’) is a central aspect of our model. On the one hand, the pollinator behaviour determines gene flow patterns and hence the genetic structure of the plant population. On the other hand, the pollinator behaviour has more long-lasting effects by inducing adaptations of plant architecture, with obvious ecological implications for population persistence.

To keep the model as simple as possible, individual pollinators were not modeled explicitly, but instead represented by their ‘decision rule’. Although pollinator behaviour is certainly much more complex, preferential visitation of certain flowers and plants is an important aspect of their foraging strategy. It is often found that plants with large floral displays (large flowers or inflorescences with many flowers) are visited more frequently than plants with a small floral display (Klinkhamer et al. 1989; Goulson et al. 1998; Le Corff et al. 1998; Krupnick et al. 1999). Soltz (1986) found that bumblebees visited mainly nearby inflorescences, but made occasional visits to plants farther away. She suggested that these plants are more attractive to pollinators.

An important aspect that is obviously missing in our model, is the individual behaviour of pollinators, which might have an important impact on the local genetic structure of plant populations. Mainly for simplicity, we focused on small, unstructured patches. However, we also considered pollinator-mediated gene flow between subpopulations, which can be viewed as spatial structure on a somewhat larger geographical scale. In general, we only found marginal effects of spatial population structure on genetic erosion, unless the degree of isolation between subpopulations was high ($\lambda>0.6$, Figure 6). The exact way in which the effects of spatial structure were modeled was not important. We studied three different scenarios for the choice between subpopulations, which were inspired by empirical observations that pollinators might follow different flight paths between patches of flowering plants: more or less random, area-restricted searching or traplining along fixed routes (e.g. Soltz 1986; Herrera 1987; Stacy et al. 1996; Thomson 1996; Velterop and Kwak 1997). All three scenarios for the choice between subpopulations gave similar results (Figure 6). Certainly, to really quantify the effects of spatial structure on genetic erosion, a more extensive study is required, based on a spatially more explicit model with individual pollinators.
Implications of pollinator behaviour

The importance of plant attractiveness for pollinator visitation differed between the pollinator decision rules. Differences between pollinator species were found empirically in studies to the reaction of insects on plant attractiveness, which is usually measured as floral display, i.e. the number of simultaneously opened flowers. For example, bumblebees reacted more strongly to differences in floral display of *Wurmbea dioica* than did flies (Vaughton and Ramsey 1998). Although they found butterflies to be more selective too, in other studies butterflies were more concerned with searching mates than with foraging for food, presumably resulting in non-selective flower visitation (Goulson 1997; pers. observ.).

In our model, we considered three different pollinator decision rules, which are perhaps not sufficiently realistic, but on the other hand, might reflect, at least qualitatively, different pollination systems. One might speculate that our highly selective Best-of-Two (BOT) strategy represents a specialist plant-pollinator interaction, while the non-selective Difference-of-Two (DOT) strategy corresponds to a generalist pollinator, which might be less ‘critical’ with respect to flower choice between and within plant species. In view of our result that genetic erosion is more severe in case of a non-selective pollinator (see Figure 5), one might therefore predict that, at least from a genetic point of view, specialized pollination systems are less vulnerable to fragmentation than plants with generalist pollinators.

In this paper, we have focused on the direct effects of fragmentation on the genetic composition of a plant population. However, habitat fragmentation will often be accompanied by changes in other factors, which are important for genetic erosion. It is conceivable that pollinators become less selective after fragmentation of a large population into small subpopulations, because fewer alternative plants are available for visitation in the vicinity. Other aspects of pollinator behaviour might also change. For example, Klinkhamer et al. (1994) found that bumblebee visitation sequences to isolated plants were longer as compared to large groups of plants, resulting in increased geitonogamy. As shown in Figure 7, such increased selfing rate after fragmentation may substantially enhance genetic erosion. As a consequence, self-compatible plant species might be genetically more vulnerable to habitat fragmentation, compared with self-incompatible plants.
Even more drastic than such changes in pollinator behaviour, are switches in the pollinator type, that might regularly accompany fragmentation of natural habitats (e.g. Olesen and Jain 1994; Allen-Wardell and al. 1998; Kearns et al. 1998). Our simulations showed that new, highly selective pollinators (BOT) were able to purge the genetic load quicker, and needed fewer generations to restore population viability to its original value (see Figure 8). One might expect that when switches in pollinator type occur, often (highly) selective pollinators will be replaced by less selective pollinators. As shown by our simulations (see Figure 8, panel C2), such a switch may enhance the effects of genetic erosion.

**Effect of evolutionary history on plant vulnerability**

By explicitly addressing the effect of the pollination system on plant architecture, we have stressed the importance of evolutionary history for the future prospects of a plant population. We are aware that our allocation model is rather simple and perhaps not sufficiently realistic. We assumed, for example, that the total amount of resources available had to be distributed over three non-overlapping compartments. This simplifies the analysis, and one should realize that a more mechanistic approach may lead to rather different evolutionary predictions (Pen and Weissing 1999). Our assumption that resource allocations translate linearly to the fitness components, was also made only for simplicity. More sophisticated models should include the possibility of condition-dependent allocation, where the allocation pattern depends on the amount of resources available (e.g. Klinkhamer et al. 1997). Even with these limitations, we are convinced that evolutionary considerations should not be neglected in the context of conservation genetics.

In our case, the combination of evolutionary arguments with an analysis of the short-term genetic consequences of fragmentation, illustrates the interplay between genetic and ecological vulnerability. On the one hand, the most selective pollinator leads to a reduced mutation load, resulting in less severe genetic erosion. On the other hand, the same very selective pollinators induce a low allocation of resources to viability. Consequently, plants with this type of pollinators will be more susceptible to seed failure, due to demographic and environmental stochasticity. Hence, a high ecological vulnerability and a low genetic vulnerability, both induced by very selective pollinators, are two sides of the same coin.
List of symbols

n  number of loci
q  frequency recessive deleterious allele
µ  mutation rate per allele per locus
s  selection coefficient
H_d  number of loci homozygous for deleterious mutations
h  degree of dominance
t  time in number of generations
F  vigor
V  total viability
A  attractiveness (total advertisement)
I  total seed investment
ν  allocation to viability
a  allocation to advertisement
i  allocation to seed production
φ(A)  number of visits a plant with attractiveness A receives
κ  steepness of φ(A) for plants with equilibrium attractiveness, i.e. the increase in number of visits which a mutant with higher advertisement will receive (eqn. 13 and 14)
ψ(A)  pollen import by a plant with attractiveness A
W(x,x*)  fitness of mutant with strategy x in resident population with strategy x*
m(x)  reproductive success via male function
f(x)  reproductive success via female function
N  number of individuals
V  population viability
M  number of trials needed to obtain a surviving seed
S  selfing rate
λ  degree of isolation

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