



Habitat fragmentation effects on fitness of plant populations – a review

Judit Lienert*

Institut für Umweltwissenschaften Universität Zürich, Winterthurerstrasse 190, CH-8057 Zuerich, Switzerland

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Summary

Habitat fragmentation threatens the survival of many species and local populations. Habitat fragmentation has two major consequences: populations become more isolated and are reduced in size. Small compared with large populations have increased extinction risks because of different types of stochasticity (e.g. genetic drift) and inbreeding, which can negatively affect the fitness of individuals or populations. Habitat fragmentation may also change the abiotic conditions of the surrounding landscape, which influences biotic interactions. This review gives an introduction to the theory of the effects of habitat fragmentation on mean fitness of plant populations. It intends to help bridge the gap between conservation biologists and conservation practitioners. The paper shortly introduces basic concepts of population biology, demography and genetics and cites relevant and new literature. Special attention is given to more common plant species, which have attracted far less conservation attention than rare species.

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Habitat fragmentation

Human activities have changed between one-third and one-half of the earth's land surface and are leading to substantial and growing modification of the earth's biological resources (Vitousek, Mooney, Lubchenco, & Melillo, 1997). Among others, habitat destruction and habitat fragmentation are ongoing major anthropogenic impacts on landscapes, which

can strongly affect ecosystems, populations and species (Young, Boyle, & Brown, 1996; Young & Clarke, 2000). Plants and animals may live in naturally fragmented habitats and can be well capable of coping with the special conditions associated with habitat fragmentation. However, the extent of anthropogenic fragmentation during the last decades and centuries far exceeds natural fragmentation rates and is operating at a much

*Present address: Swiss Federal Institute for Environmental Science and Technology (EAWAG), Ueberlandstrasse 133 P.O. Box 611 CH-8600 Dübendorf, Switzerland. Tel.: +41-1-823-55-74; fax: +41-1-823-53-89.

E-mail address: judit.lienert@eawag.ch (J. Lienert).

faster time-scale than many populations can adapt to. For instance, in Switzerland practically all ecosystems that need large time ranges to evolve (e.g. wetlands and primeval forests) have disappeared from 90% of the landscape (Broggi & Schlegel, 1989). In the Brazilian Amazon basin, the mean rate of deforestation and fragmentation increased from 78,000 km² in 1978 to 230,000 km² in 1988 (Skole & Tucker, 1993). Such numbers illustrate that the preservation of many plants and animals in relatively intact habitats is no longer an option. In the introduction to their book on habitat fragmentation Young and Clarke (2000) state that there is an immediate practical need in biological conservation to understand the effects of fragmentation on population processes and viability, if informed management decisions are to be made for their long-term conservation. This paper is intended as an introduction to the theory of the effects of habitat fragmentation on mean fitness of plant populations for conservation practitioners. Hopefully, it will help to bridge the gap between conservation biologists and conservation practitioners. The paper shortly introduces basic concepts of population biology, demography and genetics, and cites relevant and new literature.

What is the main effect of habitat fragmentation? Habitat fragmentation divides once continuous, large populations into many smaller ones. These small remnants can be more or less isolated, depending on the structure of the intervening landscape and on the distance between them (Saunders, Hobbs, & Margules, 1991; Young, Brown, Murray, Thrall, & Miller, 1996; Wiens, 1997). Unfortunately, small population size and strong isolation of populations is associated with various negative consequences, which have been suggested and verified in several theoretical and empirical studies.

Metapopulations

What is a metapopulation?

Scattered populations of a species in a landscape, which are in contact via migration and which are characterised by local population extinction and by colonisation of unoccupied sites constitute a metapopulation (Levins, 1969; Hanski & Gilpin, 1991, 1997). Especially in the light of habitat fragmentation, the metapopulation concept has received increasing interest, and it has been widely discussed and expanded (e.g. Gotelli, 1991; Hanski & Gilpin, 1991, 1997; Ouborg, 1993; Harrison &

Hastings, 1996; Lopez & Pfister, 2001). Fragmented populations may be seen as a kind of metapopulation. However, fragmented populations are often only insufficiently connected through dispersal and may form a non-equilibrium metapopulation with higher rates of local population extinction than of colonisation (Harrison, 1991).

The difference between animals and plants

Important earlier work on metapopulations was conducted with animals (for references see Hanski & Gilpin, 1991, 1997). Since plants have many specialised features that differ strongly from those of animals, the application of metapopulation models for plants may not be fully adequate (see Eriksson, 1996; Freckleton & Watkinson, 2002). Classical metapopulation characters such as colonisation and extinction may be difficult to measure for many plant populations. Other specialised plant features include the sessile habitat, the sometimes extreme longevity (trees and clonal plants can become hundreds of years old), the often sporadic recruitment of new individuals, the possibility to reproduce asexually and the capacity to survive long periods of unfavourable conditions (Eriksson, 1996; Husband & Barrett, 1996). However, precisely these special features may in fact render plants extremely suitable for metapopulation studies. For instance, true extinction of local populations may be very rare for animals, since they can move to more suitable sites, whereas local population extinction does indeed occur in species with sessile adult stages, and especially in plant populations (Olivieri, 2000). Nevertheless, to date there are still contrasting views on the applicability of the metapopulation theory to the regional dynamics of plants. In particular, the distinction between local and regional dynamics needs to be carefully addressed in ongoing studies (Freckleton & Watkinson, 2002).

Evolutionary aspects

Habitat fragmentation may influence plant evolution by forcing once continuous populations into a metapopulation structure. Various plant characteristics could evolve differently than before, e.g. by altering the evolution of mating systems, life-histories or co-evolutionary interactions such as plant–pathogen relationships (Olivieri, 2000). For instance, population subdivision and metapopulation dynamics may affect the evolution of sex ratios in gynodioecious plants (e.g. Olivieri, Couvet, & Gouyon, 1990; Couvet, Ronce, & Gliddon, 1998;

McCauley, Olson, & Taylor, 2000). Gynodioecious plants have a mating system with both females and hermaphrodites co-occurring; sex expression is controlled by complicated genetic mechanisms, which can in turn be influenced by evolutionary forces. Similarly, in dioecious (all female or all male) bryophyte species, capable of asexual and sexual reproduction, metapopulation dynamics can influence sex ratios (McLetchie, Garcia-Ramos, & Crowley, 2001). Metapopulation processes could further influence the age of maturity and thus the life-history of plants (de Jong, Klinkhamer, & de Heiden, 2000). Another well-studied life-history trait affected by metapopulation dynamics is the dispersal strategy of plants (e.g. Olivieri, Michalakis, & Gouyon, 1995; Gandon & Michalakis, 1999; Ronce, Perret, & Olivieri, 2000). Finally, metapopulation dynamics such as local population extinctions and colonisations and a varying spatial structure could influence the co-evolution of plants and pathogens (e.g. Burdon & Thrall, 2000; Carlsson-Graner & Thrall, 2002).

Experimental and real-world approaches

To date, only a limited number of studies were conducted with plant metapopulations in the field or common garden. Partly, this may be because the study of local population extinction and recolonisation involves following many populations over an extended period of time. Giles and Goudet (1997) have elegantly overcome this problem by using a plant metapopulation system on islands, which are subject to a rapid, constant rate of land uplift. Hence, new land at the seashore is continuously available to colonisation. The study compared the degree of genetic differentiation among island populations of *Silene dioica* (L.) Clairv. with theoretical predictions. Isolation by distance occurred, and the authors found that colonisers were likely to come from several sources.

Quite a different approach was used in an experimental study with the short-lived *Arabidopsis thaliana* (L.) Heynh. (Lavigne et al., 2001). Here, 18 metapopulations, each consisting of 20 populations of the same initial genetic composition, were potted in a common garden. The experiment tested for effects of different population sizes, selection regime and extinction/colonisation regime and compared results with theoretical predictions. The advantage of this kind of experiment is that it allows for precise testing of hypotheses. However, the disadvantage is that drawing some general conclusions can be difficult. For instance, populations here consisted of 10, 25

or 100 individuals. In many real populations, 100 individuals would constitute a very small rather than a large population (see below), hence general conclusions regarding population sizes should be drawn with caution, especially for long-lived or clonal plants. At the moment, both field and experimental studies with plant metapopulations are needed to establish a more general picture.

The focus of this review

Theoretical and empirical metapopulation studies with plants have been conducted since the 1980s and have often focused on more long-term aspects such as evolutionary ecology (for references, see Husband & Barrett, 1996; Olivieri, 2000). In contrast, studies directly addressing habitat fragmentation focused on the more short-term impacts on mean fitness of populations. Most of these studies investigated consequences of the two major effects of fragmentation – reduced population size and increased isolation – without explicitly applying the metapopulation model or incorporating long-term evolutionary aspects. This is also the approach subsequently adopted in this paper. Fig. 1 gives an overview of the main potential effects of habitat fragmentation on plants, which will now be discussed in more detail.

Stochasticity

Natural catastrophes and environmental stochasticity

Habitat fragmentation creates small and/or isolated populations. Such populations have increased extinction risks by pure chance, compared with larger populations. Four types of stochasticity affecting populations are recognised: natural catastrophes, environmental stochasticity, demographic stochasticity and genetic drift (Shaffer, 1987). Natural catastrophes such as floods, fires or droughts can, of course, also drive large populations or even species to extinction in short time. However, large populations have a smaller probability of going extinct altogether than small ones. Likewise, adverse environmental conditions such as unpredictable changes in weather, food supply or pathogen infection will more likely drive an entire small population to extinction. I observed such a phenomenon in one relatively small population of the perennial *Primula farinosa* L. (ca. 1800 flowering individuals) when a strong local hail storm destroyed nearly all fruit capsules (Lienert &

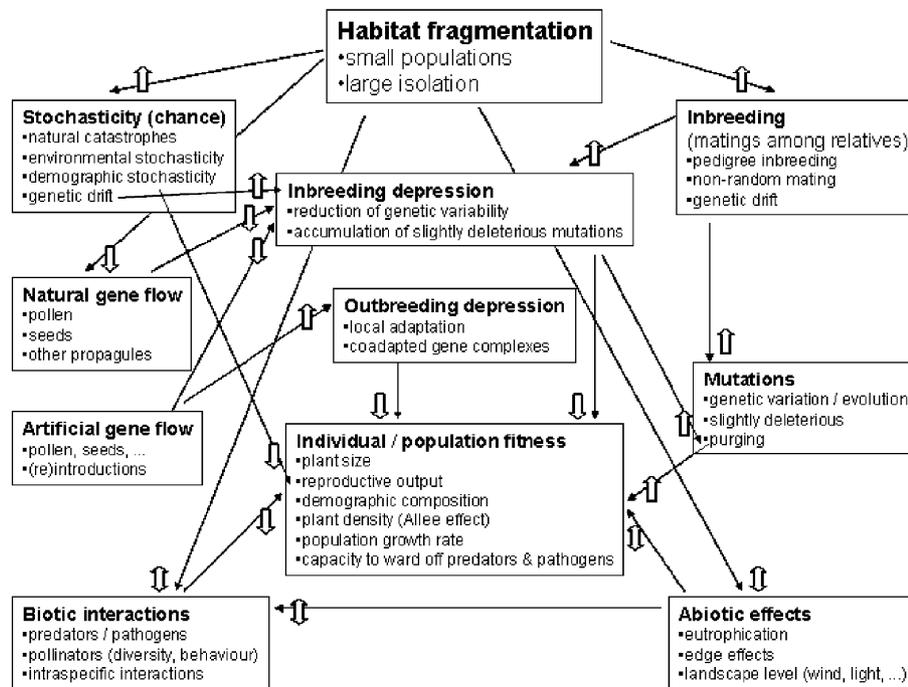


Fig. 1. Overview of the potential effects of habitat fragmentation on plants. This scheme represents a simplification and does not include various interdependencies between individual factors due to ease of comprehension (for details see text). Symbols: ↑ mainly positive/increasing effect; ↓ mainly negative/decreasing effect; ↓↑ both positive or negative effects. For example, habitat fragmentation creates small populations and increases isolation between populations. In small, isolated populations, chances of inbreeding increase ↑, which can increase inbreeding depression ↑. This in turn can lower individual or population fitness ↓.

Fischer, 2003). Although the hail storm did not immediately threaten the persistence of this population, its reproductive fitness was strongly reduced. In a larger population of, for example, 10,000 individuals, the actual amount of surviving capsules would have been far larger, even if the proportion of destroyed capsules were the same as in this small population.

Demographic stochasticity

Demographic stochasticity means fluctuations in population size and fitness traits due to random variation among individuals and can result in chance extinction of small populations. In small compared with large populations, the fluctuations in survival and reproduction of individuals can have very different outcomes (Shaffer, 1987; Lande, 1998). For instance, in dioecious species (species consisting of separate male and female individuals) the female–male ratio can deviate from a 50:50 distribution. This will not have severe consequences in large populations, because there will be still enough individuals of one sex to guarantee reproduction. However, in small populations the actual number of individuals of one sex may be

much smaller by chance, even if the expected sex-ratio stays the same. Hence, mating opportunities may become limited, which can eventually drive a population to extinction. A rather good example for demographic stochasticity in plant populations is provided by heterostyly. Flowers of heterostylous plants have two or three genetically determined morphs, which fit together like a key and a lock. In the primrose *Primula*, one morph (called pin) has a long receptive style protruding out of the flower, whereas the pollen-carrying anthers are positioned at the base of the flower. The other morph (called thrum) has a short style, which disappears in the throat of the flower, whereas the anthers carrying pollen protrude out of the flower. This guarantees that thrum flowers are pollinated only by pin flowers (and vice versa). Heterostylous flowers also have a biochemical self-incompatibility system, which ensures cross-pollination at a biochemical level. Heterostyly is inherited by the next generation like human sex chromosomes. Presumably, heterostyly evolved as a mechanism to protect plants from the negative effects of selfing and inbreeding and to ensure effective pollen exchange (Barrett, 1992; see below: inbreeding depression). Several studies confirmed that morph-ratios deviate more strongly from the expected 50:50

distribution in small populations (e.g. Barrett, Morgan, & Husband, 1989; Eckert & Barrett, 1992; Ågren & Ericson, 1996; Baker, Thompson, & Barrett, 2000).

Models incorporating demographic stochasticity mostly assumed identical expected survival and fecundity rates of all individuals. However, this is rarely – if ever – the case in real populations (Kendall & Fox, 2001; Fox & Kendall, 2002). For instance, in long-lived species traits affecting survival and fecundity of individuals in a certain year will also be influenced by conditions in the previous year. Similarly, survival probabilities of an individual may depend on the quality of the specific territory an individual plant is growing on, or on the fate of other individuals (e.g. because of competition; this is termed demographic co-variance). Recent research indicates that incorporation of differences of survival among individuals will lower predicted population extinction probabilities due to demographic stochasticity. In other words: conventional so-called population viability analyses may have overestimated demographic stochasticity (Kendall & Fox, 2001; Fox & Kendall, 2002).

Genetic drift

Genetic drift is closely linked to demographic stochasticity and means the change of allele frequencies in populations by chance from one generation to the next (Lacy, 1987; Shaffer, 1987; Hartl & Clark, 1989; Ellstrand & Elam, 1993). Alleles are variants at a particular gene locus. A population contains a certain variety of alleles at each locus. However, a given individual only carries a subset of all alleles present in the population and can therefore only pass on this subset to the next generation. Again, genetic drift affects both large and small populations, but the effects are much more severe in small populations. I will illustrate this with a simple calculation: imagine that a rare allele occurs with a probability of 1/100. If a population consists of 100,000 individuals, 1000 individuals will carry this allele. Presumably, at least some of these 1000 individuals will be able to pass on the allele to the next generation. However, if a population consists of only 100 individuals, only one single individual carries the rare allele and obviously, chances are high that it will not be passed on. Therefore, genetic drift randomly reduces genetic variability (as measured by expected heterozygosity under random mating) within a population. Heterozygosity means that a diploid individual carries two different copies of an allele at the same gene locus. In contrast,

homozygosity means that the two copies of the allele are identical. Moreover, through genetic drift the frequency of slightly deleterious recessive mutations might increase within each population. These mutations can accumulate, because natural selection is less effective in small populations (Lynch, Conery, & Bürger, 1995). The slightly deleterious mutations can become fixed, which leads to an ongoing fitness reduction of the population.

Hence, genetic drift has two main consequences: (a) in the short term, the random fixation of increased frequency of slightly deleterious mutations cause a fitness reduction of populations (Barrett & Kohn, 1991; Ellstrand & Elam, 1993; Young et al., 1996). (b) In the long term (of hundreds and thousands of years) neutral genetic diversity is lost. This means that the evolutionary capacity of populations to adapt to changing environments is reduced (Lande, 1988; Frankham, 1996). However, this expectation has rarely been studied, particularly in the context of conservation. Because of the random loss of genetic diversity, populations will also be increasingly different from each other as time goes on (Levin, 1988; Ellstrand & Elam, 1993). A third effect (c) of genetic drift is that the fixation of the genetic load in different populations can result in increased among-population heterosis (Keller & Waller, 2002). Heterosis is a term used for significantly increased fitness of offspring from crosses among populations, whereas progeny of inbred and outbred matings show few or no differences, because they reflect the effects of population inbreeding (also see below).

Methods to assess genetic drift

Different methods are used to assess the genetic variability of populations – a popular one being isozyme analysis (Soltis & Soltis, 1989). Isozymes are proteins coded for by alleles, which can be visualised with special laboratory techniques. Since populations can differ in the amount of alleles (i.e. variants at a gene locus), it is possible to assess the genetic variation of populations. Decreased isozyme variability in smaller populations has been reported in a number of studies, especially when species have become increasingly rare because of habitat fragmentation and destruction (e.g. van Treuren, Bijlsma, van Delden, & Ouborg, 1991; Ellstrand & Elam, 1993; Raijmann et al., 1994; Frankham, 1996; Young, Brown, & Zich, 1999; Lienert, Fischer, Schneller, & Diemer, 2002c). Moreover, so-called *F*-statistics (Hartl & Clark,

1989) offer the possibility to specify fragmentation effects. Habitat fragmentation can result in increased genetic differentiation of populations, when they are isolated and when they lose alleles due to genetic drift. This can be measured as F_{ST} , which can help to estimate the amount of gene flow among populations (see below). More precisely, F_{ST} is a measure of the amount of inbreeding because of population subdivision and can be viewed as the proportion of the total genetic variance among populations. A second measure, F_{IS} , refers to the amount of within-population inbreeding (see below). Hence, F_{IS} estimates the degree of relatedness between two mates compared with the relatedness of two randomly chosen mates. Increased levels of non-random inbreeding within a population (F_{IS}) can be caused by increased matings between relatives (selfing) or because of structuring within sample units (Wahlund effect). The total inbreeding, F_{IT} , is a function of both within-population (F_{IS}) and among-population (F_{ST}) inbreeding (for detailed explanations see e.g. Hartl & Clark, 1989; Keller & Waller, 2002).

F -statistic measures are dependent on the life-history of a plant species. For instance, F_{ST} values of fragmented plant species were 0.156 (*Salvia pratensis* L.), 0.175 (*Scabiosa columbaria* L.; van Treuren, et al., 1991) and 0.128 (*Swertia perennis* L.; Lienert et al., 2002c). These values are relatively high for dioecious, long-lived, outcrossing species and indicate the occurrence of genetic drift in smaller populations: a literature review showed that mean F_{ST} for predominantly outcrossing species was 0.118; of dioecious species it was 0.109 and of long-lived perennials it was 0.077 (Loveless & Hamrick, 1984). On the other hand, plants with other life-history traits can have very much higher F_{ST} levels. High F_{ST} values are characteristic for selfing ($F_{ST} = 0.523$), annual (0.430) or early successional species (0.411), and for species with gravity – (0.446) or animal-dispersed seeds (0.398; Loveless & Hamrick, 1984). Moreover, endemic species have mean F_{ST} values of 0.227, while widespread ones have much higher values (0.407). However, the values of any individual species can differ strongly from means. For instance, the narrow endemic species *Centaurea corymbosa* Pourret, known from only six populations in France, has $F_{ST} = 0.35$ (Freville, Justy, & Olivieri, 2001).

Recently, several types of molecular marker techniques to measure genetic differentiation and gene flow among populations have been developed (RAPD, RFLP, AFLP, microsatellites; see Ouborg et al., 1999 for references). The markers differ in the type and amount of variability they express,

and may sometimes be superior to isozyme analysis, because they offer a direct genetic approach to measuring gene flow, whereas the indirect approach via F_{ST} is based on a number of assumptions that are not valid for situations with frequent extinction and colonisation (Ouborg, Piquot, & Van Groenendael, 1999). For example, the variation of random amplified polymorphic DNA (RAPD variation) in relation to population size has been successfully used in the context of habitat fragmentation (e.g. Fischer & Matthies, 1998a; Fischer et al., 2000). Other investigations directly compared isozyme analysis with microsatellites, which have higher levels of variability (e.g. Freville et al., 2001). The results indicate that the appropriate markers and loci to measure gene flow can strongly depend on the type of species investigated (i.e. on the amount of its genetic variability) and on the given scale of the investigation.

Fitness reductions through inbreeding depression

Genetic mechanisms and inbreeding depression

The term 'inbreeding' is used to describe various related phenomena; all of them refer to matings among relatives, which increases homozygosity, and all of them are relative measures (see Keller & Waller, 2002). (a) 'Pedigree inbreeding' means that an individual is inbred if parents share ancestors; or in other words that two genes in different individuals are derived from the same gene in a common ancestor. (b) Inbreeding can be a result of non-random mating, meaning that the parents of an individual are more closely related than two randomly chosen individuals in the population. This can be estimated with F_{IS} . (c) As explained above, subdivision of populations can result in inbreeding because genetic drift reduces local diversity (F_{ST}). Whenever matings are non-random, the second effect (b) becomes important. However, if populations are small and alleles are lost by drift, the third effect (c) becomes important, independently of whether local mating is random or not.

All forms of inbreeding increase the frequency of individuals that are homozygous at gene loci. Increased homozygosity in an individual plant often leads to inbreeding depression or in other words to reduced fitness of individuals and to reduced viability of the entire population (Charlesworth & Charlesworth, 1987; Barrett & Kohn, 1991;

Ellstrand & Elam, 1993; Keller & Waller, 2002). Two proposed mechanisms may lead to inbreeding depression: overdominance and partial dominance (Charlesworth & Charlesworth, 1987; Barrett & Charlesworth, 1991; Byers & Waller, 1999). The overdominance hypothesis postulates that heterozygosity is superior to homozygosity. This means that the individuals carrying two different copies of an allele are 'fitter' than those that carry two identical copies of the same allele. The partial dominance hypothesis postulates that inbreeding increases the chances that two diploid individuals carrying recessive detrimental mutations mate with each other. Only in this case will the slightly negative effects of mildly deleterious mutations become evident (i.e. express themselves in homozygous offspring; Lande, 1995; Lynch et al., 1995). There seems to be evidence supporting both mechanisms, but recently the partial dominance hypothesis has been found to explain most inbreeding depression occurring in higher plants (see Keller & Waller, 2002).

Fitness reduction: demography of populations

Above, I wrote that inbreeding can result in reduced fitness of the following generations. But what is 'fitness'? By definition, the fittest individuals in a population are those that are expected (based on their genotypes) to leave the greatest number of descendants (Begon, Harper, & Townsend, 1990). Fitness is a relative term: the fittest individuals produce the most descendants *relative* to the other, less fit, individuals. Hence, the fitter individuals will more strongly determine the characteristics of future generations.

Direct measurements of the 'fitness' of individual plants are impossible. Components of fitness used to estimate fitness of individuals are, for example, the number of seeds and offspring, or the size of offspring. Estimating the viability of entire populations is even more difficult. One approximation used by plant population biologists is population turnover. If a population is to survive over many generations, the offspring must replace the dying parent generation, so that population growth rates (r) remain stable or positive ($r \geq 0$; Menges, 1990; Boyce, 1992; Oostermeijer, 2000). If population turnover is negative ($r < 0$), i.e. if fewer seedlings survive than are necessary to replace the dead plants, a population will eventually go extinct. In practice, it is often not possible to study demographic turnover rates – especially of long-lived plants – because one does not have the time to

follow populations over several years or decades. Hence, only few demographic studies have followed populations over an extended period of time (e.g. Menges & Dolan, 1998; Rose, Clarke, & Chapman, 1998). However, the density of seedlings, juvenile and mature plants in large and in small populations can be compared. If demographic turnover is disturbed, densities and proportions of age-size states (Gatsuk, Smirnova, Vorontzova, Zaugolnova, & Zhukova, 1980; Rabotnov, 1985) will also be changed, which can be detected by statistical analysis (e.g. Oostermeijer, 't Veer, & den Nijs, 1994a; Jules, 1998; Menges & Dolan, 1998; Hoofman & Diemer, 2002; Lienert, Diemer, & Schmid, 2002b). However, altered population structure can have genetic causes (inbreeding), but also non-genetic causes (e.g. Menges & Dolan, 1998).

The negative effects associated with reduced densities of populations are called Allee effects. The term describes an "inverse density dependence", meaning that small populations are affected by a positive relationship between population growth rate and density, which increases their extinction probability (Allee, Emerson, Park, Park, & Schmidt, 1949). Originally, the term was mainly used for problems of reproduction in small and sparse animal populations. Today, it also incorporates the negative effects resulting from low density in plant populations, and is sometimes even used as a more general label for any negative effect associated with small population size (Courchamp, Clutton-Brock, & Grenfell, 1999; Stephens & Sutherland, 1999).

Fitness reduction: reduced reproductive success

Small populations can have higher inbreeding levels because the chances of matings between close relatives increase, simply because there are fewer partners to choose from. Moreover, the likelihood of self-pollination within flowers and self-pollination among neighbouring flowers within the same plant (geitonogamy) can increase in small populations (de Jong, Waser, & Klinkhamer, 1993; Ellstrand & Elam, 1993; Rathcke & Jules, 1993). Many studies have shown that inbred plants produce fewer flowers and seeds, smaller seeds and seeds that germinate less well (e.g. Levin, 1984; Aizen & Feinsinger, 1994; Ouborg & van Treuren, 1994; Fischer & Matthies, 1997; Paschke, Abs, & Schmid, 2002). Inbreeding depression could further express itself in smaller plant height, smaller leaf-size or generally reduced plant

biomass (Hauser & Loeschcke, 1996; Kéry, Matthies, & Spillman, 2000; Hoofman, van Kleunen, & Diemer, 2003; Lienert et al., 2002b, c). This can in turn reduce the reproductive success, since sometimes only plants of a certain size are capable of producing flowers (e.g. Schmid & Weiner, 1993; Schmid, Polasek, Weiner, Krause, & Stoll, 1994; Wesselingh, Klinkhamer, de Jong, & Boorman, 1997) and since larger plants may produce more flowers than smaller ones (Calvo, 1990).

Fitness reduction: predators and pathogens

Inbreeding depression may reduce the capacity to ward off predators and pathogens. Plants can be attacked by herbivores, which consume leaves or flowers, frugivores, which consume fruits and seeds, or pathogens, which are causative agents of disease. For instance, pathogenic fungi can infect a plant systemically and reduce its viability. Reduced genetic variability due to inbreeding can increase the susceptibility to fungal infection (Schmid, 1994; Ouborg, Biere, & Mudde, 2000), and reduced genetic variability may increase the susceptibility to herbivore damage (e.g. Lienert et al., 2002c). Some plants can be infected by a smut fungus, which produces its spores in the capsules and inhibits seed production (Vánky, 1994). Hence, increased smut infection in small populations, could be indicative of inbreeding depression and a reduced capacity of warding off pathogen infection. However, in many plant populations, decreased rather than increased infection by smut fungi in smaller or less dense populations was observed (Jennersten, Nilsson, & Wästljung, 1983; Carlsson, Elmqvist, Wennström, & Ericson, 1990; Antonovics, Thrall, Jarosz, & Stratton, 1994; Burdon, Ericson, & Müller, 1995; Ericson, Burdon, & Müller, 1999; Groppe, Steinger, Schmid, Baur, & Boller, 2001; Lienert & Fischer, 2003). An alternative explanation to inbreeding depression is that in larger patches pollinators are more effective in distributing pollen, but also smut fungus spores (Jennersten & Nilsson, 1993; see below: plant–pollinator interactions). Moreover, fungal populations can fluctuate strongly, which increases extinction rates of small fungal populations by chance (Ericson et al., 1999). Increased isolation of sites may result in decreased pathogen incidence, because herbivores or fungus spores no longer reach a distant site (Kruess & Tschardtke, 2000; Groom, 2001). Finally, small plant populations can have reduced pathogen incidence because they harbour less dense or less diverse insect populations than large ones (e.g. Price, Bouton, Gross,

McPheron, Thompson, & Weis, 1980; Bach, 1988; Jennersten & Nilsson, 1993; Kruess & Tschardtke, 2000; Kéry, Matthies, & Fischer, 2001). This could be caused by inbreeding depression in the insect populations, which eventually leads to their extinction (Saccheri et al., 1998). However, this could also be an environmental effect, for instance, because small sites suffer from increased fertilisation from surrounding agricultural land, which can strongly affect herbivores (Mattson, 1980; Kytö, Niemelä, & Larsson, 1996).

Mutations and purging

Mutations occur randomly in any individual. Often mutations have no consequences, because they occur in unimportant regions in the genome (e.g. in spacer regions, which are not translated into proteins and are not expressed). If mutations do have consequences, they are mostly negative and can be mildly deleterious to lethal. But mutations are also the source of genetic variation, and theoretically balance the loss of genetic variability through genetic drift (Lande, 1995). Moreover, mutations are a driving force of evolution: if selection favours individuals with a mutation, the frequency of the mutation in the population increases over time. This can lead to the evolution of new traits or species.

Populations with a long history of inbreeding (i.e. that were small and isolated for many generations) may get rid of the mildly deleterious recessive mutations. In populations with strong compared to little inbreeding, mutations will first express themselves and negatively affect population viability. However, as time goes on, selection helps to eliminate the mutations from the population, because carriers of the mutation are a little less capable of surviving and reproducing. This mechanism is called purging of the genetic load (Barrett & Charlesworth, 1991; Lynch et al., 1995) and is based on the partial dominance hypothesis of inbreeding depression (see above). Recent simulations indicate that mildly deleterious mutations are purged from large populations, but can accumulate in very small populations, where drift is more dominant than natural selection (Bataillon & Kirkpatrick, 2000). Hence, here drift dominates over the effect of inbreeding so that mutations are not being purged.

Because populations that were only recently fragmented did not have the time to purge their genetic load, it is expected that they are most susceptible to inbreeding depression (Barrett &

Kohn, 1991; Ellstrand & Elam, 1993; Byers & Waller, 1999). Inbreeding depression can be expressed at different stages of a plant's life cycle, and its strength at different stages depends on the mating system (Husband & Schemske, 1996). Outcrossing species may be very susceptible to early acting inbreeding depression (i.e. inbreeding depression that expresses itself in the early life cycle stages such as seed production). In contrast, self-fertilising plants should be less affected by early acting inbreeding depression, because they may have purged some of their genetic load, whereas it seems as if most later-acting inbreeding depression (i.e. at the stage of growth and reproduction) cannot be purged (Husband & Schemske, 1996). However, a recent meta-analysis showed that purging is inconsistent and varies largely among different populations, species and breeding systems (Byers & Waller, 1999). Finally, even if purging does occur, migration can bring back mutations that have been purged from a certain population. Hence, to find out what is happening in the real world, it is important to further investigate these theoretical predictions, both experimentally and in real populations in the field.

Gene flow

Number of migrants

The negative effects of small population size on genetic mechanisms described above (i.e. the effects of genetic drift on neutral and non-neutral genetic diversity) can be alleviated if the populations are not completely isolated and receive additional 'genetic material' from other populations. This is called gene flow (Levin & Kerster, 1974; Slatkin, 1985; Levin, 1988; Ellstrand, 1992a, b; Ellstrand & Elam, 1993). The importance and magnitude of gene flow has been widely discussed. Earlier theories postulated that one migrant per generation is sufficient to compensate for the loss of genetic diversity through drift and to keep neutral alleles from fixation (Wright's island model; Wright, 1943; Allendorf, 1983; Lande, 1992; Ellstrand & Elam, 1993). This theory is based on a number of assumptions. For instance, it assumes that each of an infinite number of populations gives and receives migrants from the other populations, these migrants should be drawn at random and be unrelated, migration rates should be constant and there should be no selection or mutation. However, in reality migration rates vary in time because they depend on many factors such as pollinators, seed

dispersers and flowering phenology, and migration is not random, but is correlated with the distance between populations (Levin, 1988; Whitlock & McCauley, 1999). Hence, stochasticity influences the migration process, especially in plants, where migration is for instance often kin-structured (i.e. seeds of one plant cling together during dispersal) and where immigrants often originate from one or few neighbouring populations (Levin, 1988). Computer modelling confirmed that even five to 20 migrants per generation may not prevent loss of genetic diversity within and differentiation between populations (Lacy, 1987).

Magnitude of gene flow

In mobile animals, gene flow can occur over extremely long distances. In plants, gene flow occurs via migration of vegetative propagules, seeds or pollen and often depends on the foraging distances of pollinators. These differ from species to species: large bats can fly 100 km a night, honeybees 20 km, but many other pollinators never travel farther than 100–1000 m (Rathcke & Jules, 1993). Hence, different authors have very different ideas about the magnitude of gene flow in plants. Some say that it is very restricted and rarely occurs over distances larger than 1000–2000 m (Levin & Kerster, 1974; Levin, 1988). Others disagree, because the distribution of seeds and pollen in plants usually follows a leptokurtic curve: most seeds or pollen grains stay near the mother plant, but occasionally some may travel much farther (Levin & Kerster, 1974). These rare events may play a very important role (Silvertown, 1991; Ellstrand, 1992a, b), since they allow for gene flow among far-away plant populations and for colonisation of remote sites. Recent modelling indicates that even a small proportion (0.1%) of seeds that move long distances (1–10 km) can lead to an order of magnitude increase in the predicted spread rate (Higgins & Richardson, 1999). Some models are now taking such long-distance events in account, which are, for instance, strongly influenced by wind updrafts (Bullock & Clarke, 2000; Nathan et al., 2002). Perhaps the most realistic view is that gene flow is highly variable, both in space and time, and differs between species, breeding systems and landscape types (Slatkin, 1985; Ellstrand, 1992a, b; Nathan & Muller-Landau, 2000). Since dispersal interacts strongly with the life history of plants, with disturbance and with habitat loss, such factors need to be incorporated in models of plant migration (Higgins & Richardson, 1999).

Estimation of gene flow

How can migration rates be estimated? One possibility of estimating pollen flow is to use powdered dye as a pollen mimic in field experiments (e.g. Campbell, 1985), but this can only be done on a very small scale. Dispersal distances of seeds can be estimated by trapping seeds at various distances from the source or by recapturing marked seeds (see Ouborg et al., 1999; Nathan & Muller-Landau, 2000). A third (but laborious) possibility is to set up experiments. Bullock and Clarke (2000), for instance, isolated study plants from conspecifics by transplanting them into a grassland and placing seed traps along transects. Similarly, the movement of pollinators can be estimated by placing potted plants at various distances from natural 'source' populations in the field (Schulke & Waser, 2001). Like genetic drift and inbreeding, overall gene flow between populations via seed and pollen can be estimated by *F*-statistics (as N_{em} ; Hartl & Clark, 1989). This indirect method is risky for fragmented populations, because the underlying mathematical model is based on a number of assumptions that are very rarely met (Whitlock & McCauley, 1999). More recent molecular methods with microsatellites offer the possibility for a direct genetic measurement of gene flow (Ouborg et al., 1999).

Plant–pollinator interactions

Apart from the genetic effects described above, different reactions of pollinators in small compared with large populations may also reduce population viability. In small plant patches and in patches with reduced plant densities, pollinator diversity is often reduced (Rathcke & Jules, 1993). Often, pollinators are only attracted to large patches of the one same species or to large patches with many different flowers growing on them (facilitation effect; Sih & Baltus, 1987; Olesen & Jain, 1994). One explanation is that pollinating insects stay away because the offered reward (nectar or pollen) is not abundant enough. Altered pollinator efficiency with reduced plant densities is a typical example of Allee effects (Allee et al., 1949) and was found in different plant species (Kunin, 1993; Widén, 1993; Groom, 1998). The consequences of reduced pollinator visits can be dramatic, especially if plant–pollinator relationships are highly evolved. Good examples are certain orchids, which can only be pollinated by highly specialised bees (Rathcke & Jules, 1993). Deceptive species, which do not offer an award, are also a highly specialised

case (Ferdy, Austerlitz, Moret, Gouyon, & Godelle, 1999). Pollinators may actually avoid visiting cheating plants after experiencing an absence of award for several times. Here, the plants reproductive success can be dramatically influenced – negatively or positively – by competition among species or different patches (i.e. after fragmentation). Simulations suggest that at low plant density pollinator behaviour induces an Allee effect (Ferdy et al., 1999). Finally, plants that attract a wide array of pollinator species can also suffer from reduced reproductive output if pollinator diversity or efficiency is reduced. Pollination experiments help to determine, whether plants in small, isolated populations indeed suffer from pollinator limitation and inbreeding depression (e.g. Paschke et al., 2002).

Differential reactions to fragmentation; rarity

Rare plants

Through habitat fragmentation, plants (and animals) can be forced to live in small populations. This may make them rarer than they were before and can eventually lead to local population or even species extinction (Young et al., 1996; Young & Clarke, 2000). On the other hand, many plant species have evolved over long time ranges in naturally small, isolated populations and are well adapted to surviving under these special conditions. Several types of rarity are acknowledged in plant ecology: (1) rare species may be confined to a geographically narrow range, such as alpine plants, (2) they may occur only in a narrow and very specific habitat range, such as wetlands or (3) species may occur in small numbers and densities, which means that local population sizes are always small (Rabinowitz, 1981; see Begon et al., 1990). Different species can be classified into any combination of these categories. Whether a rare species also becomes endangered, depends on various attributes such as mode of reproduction, dispersal ability or habitat specificity. Moreover, survival can also largely depend upon the structure of the intervening landscape or habitat (Wiens, 1997).

An example for an endangered species could be a rare orchid that occurs at low population densities, in a very specific, geographically restricted habitat. Such a species can quickly become extinct, when the habitat is increasingly destroyed. On the other hand, many plants are adapted to surviving in small populations; they are capable of vegetative

(clonal) reproduction, or of self-fertilisation, and are not at all dependent on pollinating insects for reproduction. Some plants persist for long periods of unfavourable conditions and fluctuations in the environment with resistant underground organs or extensive seed banks, others can be very effective in colonising new sites, when their old habitat is destroyed. Dispersal ability for gene exchange can be crucial for long-term population persistence. However, depending on the landscape structure between habitat fragments, effective gene exchange may no longer be possible. Corridors may enable gene exchange between far-away populations, especially in mobile animals. Plants with their sessile habit are much more constrained. However, plants can also reach distant habitat remnants (Eriksson, 1996): plant propagules, pollen grains or seeds can be dispersed via wind, water, pollinating insects, adhesion to larger animals (e.g. seeds clinging to the wool of a sheep) or even via tractor tyres. Considering these large differences among species, it is important to study different categories of plants.

In the last decade, studies concerning the effects of habitat fragmentation and small population size have largely focused on once widespread or abundant species, which naturally constituted fairly large populations. These species are increasingly endangered, because their habitat is reduced in size and number and because habitats were increasingly isolated from each other. Many of the studied plants were already classified as rare, endangered or threatened in their study regions (e.g. Oostermeijer et al., 1994a; Oostermeijer, van Eijck, & den Nijs, 1994b; Ouborg & van Treuren, 1994; Fischer & Matthies, 1998a, b; Menges & Dolan, 1998). The general consensus for such rare and endangered plant species is that small population size and large isolation negatively affects mean population fitness. The effect of habitat fragmentation on species that are still quite common and that still exist in very large population sizes has so far received less attention.

Common or locally abundant plants

Locally abundant plant species may in fact play a very important role in their habitat. For instance, abundant species can be indicators, which means that their presence and fluctuations reflects the presence and fluctuations of other species in the community (Simberloff, 1998). Abundant plants can be of overriding importance for an ecosystem by forming the matrix of the community (e.g. a grass

in a prairie or a beech tree in a Central European forest). An abundant plant may offer shelter and food to many other species. Keystone species play an equally important role in ecosystems. They are defined as species “whose effect is large and disproportionately large relative to their abundance” (Power et al., 1996; Simberloff, 1998). Keystones can for instance be plants that offer resources for insects if they flower in times of scarcity, or large animal predators that occur at low densities but have large effects on the community (Power et al. 1996). Hence, studying habitat fragmentation effects on still abundant plant species is of equal scientific and conservation interest as are studies of increasingly rare plants. This reasoning was adopted by a large study with fragmented populations of abundant fen plants in Switzerland (Hooftman, Diemer, Lienert, & Schmid, 1999). The typical fen plant species *Succisa pratensis* Moench., *Carex davalliana* SM. (Hooftman & Diemer, 2002; Hooftman et al., 2003), *S. perennis* (Lienert, Fischer, & Diemer, 2002a; Lienert, Fischer, & Diemer, 2002b, c) and *P. farinosa* (Lienert & Fischer, 2003) are indeed affected by habitat fragmentation. All of these species can still occur in very large numbers (i.e. over 100,000 flowering adults) on individual sites. For these species ‘small populations’ may consist of over 1000 flowering adults—a large number, compared with the species of the above-mentioned studies on already regionally endangered plants (*Gentiana pneumonanthe* L., Oostermeijer et al., 1994a, b; *S. pratensis*; Ouborg & van Treuren, 1994; *Gentianella germanica* (Willdenow) Börner, Fischer & Matthies, 1998a, b; *Silene regia* Sims, Menges & Dolan, 1998). Since habitat fragmentation is threatening not only the rarest plants, but also fairly common habitat specialists, both rare and more common plants should be considered when studying habitat fragmentation effects.

Altered landscape structure and edge effects

Habitat fragmentation may not only have a direct impact on populations, by dividing and isolating them, but it can also change abiotic conditions of the surrounding landscape and of the habitat itself (Saunders et al., 1991). This will inevitably influence biotic interactions in the habitat remnant. For instance, if a certain habitat was formerly surrounded by woodland, wind flux across the landscape may be altered after destruction of the woodland. Such an effect was found in the maple

Acer saccharum Marsh., where pollen dispersal was increased after fragmentation, presumably because of increased wind flux after forest clearing (Foré, Hickey, Vankat, Guttman, & Schaefer, 1992; Young, Merriam, & Warwick, 1993). Similarly, solar radiation may increase in a habitat – and especially at the edges – if the habitat remnant is no longer overshadowed by the native vegetation such as forest (Saunders et al., 1991). Increased radiation can alter growing conditions, e.g. for shade tolerant plants. Animals can also be affected by increased solar radiation. For instance, the extinction of the bird species Carnaby's cockatoo (*Calyptorhynchus funereus latirostris*) was partially attributed to elevated temperatures (see Saunders et al., 1991, for examples). Another example is the water level of a wetland, which may be lower after fragmentation, because the intervening land was drained and is now agriculturally used. This could seriously affect the remaining wetland patches, because growth conditions may now be favourable to more generalist plants, which could eventually displace the original wetland species.

The larger perimeter-to-area ratio of small compared to large patches can also seriously affect remnant populations (Saunders et al., 1991). For instance, nutrient influx from surrounding agricultural land can impair a major proportion of a small patch, whereas in a large habitat patch it affects only the edges, but not the centre. If nutrient influx increases, the productivity of a site also increases (i.e. plants have larger leaves and are taller, thus total vegetative biomass increases). This is especially important in nutrient-poor habitats such as fens, which are often very species-rich. Here, increased productivity can decrease species richness or change community structure (e.g. Wheeler & Giller, 1982; Willems & Nieuwstadt, 1996; Pauli, Peintinger, & Schmid, 2002). One explanation is that typical plants of low-productivity sites with low growth rates are outcompeted (e.g. overshadowed) by faster growing generalist plants (Grime, 1973; Tilman, 1997). If this happens, the density of a single typical species is expected to be reduced at the edges, because conditions are less favourable than in the centre. Such an edge effect was observed in the wetland specialist *P. farinosa* (Lienert & Fischer, 2003). Finally, herbivore incidence could be increased at the edges, because herbivores such as snails or grasshoppers are attracted by the larger plants, because general conditions are favourable for herbivores or because the overlap of two different habitats harbours a larger diversity of species than only one of the habitats alone.

Minimum viable population sizes

For practicing conservation managers in particular, an important question arising from the above-described negative effects of small population size is how large a viable population would have to be. Much scientific effort has been placed into determining minimum viable population sizes (MVP). Widely accepted mathematical models showed that populations with less than 100–500 reproductive individuals will not be able to survive in medium time ranges (say around 100 years), because of chance fluctuations and inbreeding (Shaffer, 1987; Simberloff, 1988; Menges, 1991; Boyce, 1992). These theoretical predictions are strongly supported by the few existing plant studies relating documented population extinction to original population size (Matthies, 1991) or those modelling real-world data (Eriksson & Eriksson, 2000; Oostermeijer, 2000; Young et al., 2000), as well as by an extensive experiment with the fruitfly *Drosophila melanogaster* (Montgomery et al., 2000). Since population persistence depends upon a complex mixture of effects described above, as well as plant-specific traits, it is very difficult, if not impossible, to define a minimum number of individuals needed for population viability, and real-world situations should be carefully assessed. A more promising approach than using absolute numbers for a certain species or group is to monitor changes in population size (Booy, Hendriks, Smulders, Van Groenendael, & Vosman, 2000). However, here long-term data, possibly over many years, are necessary for valid predictions. A faster, but equally effective method is to assess changes in the demographic composition of populations (e.g. Oostermeijer et al., 1994a; Jules, 1998; Menges & Dolan, 1998; Hooftman & Diemer, 2002; Lienert et al., 2002b; Lienert & Fischer, 2003), in conjunction with a monitoring scheme.

Such a relative approach allows the integration of very diverse plant species, since minimum viable population sizes can for instance differ strongly for rare species compared with abundant species. Because abundant plant species usually occur at much higher densities than rare ones, population sizes may also be much higher, even on a very small site. For example, a small wetland remnant of a few hundred square meters may contain only few individuals of a rare orchid, but a few thousand individuals of an abundant grass species. Nevertheless, for the grass species this may be a small, isolated population, and inbreeding or genetic drift can affect it just as negatively as it would affect the orchid population. This reasoning is not yet well accepted. When I told people that I was going to

study the extinction of *S. perennis* populations, an overall rare but locally abundant species restricted to calcareous fens (*Caricion davallianae*; [Ellenberg, 1996](#)), I received quite a few astonished reactions from conservation biologists. However, my study with up to 127-year old herbarium records of 63 sites in NE Switzerland that had once hosted *S. perennis* populations revealed that 24% of the populations had indeed gone extinct during the 20th century ([Lienert et al., 2002a](#)). Local population extinction was attributed to both habitat fragmentation and intensified agricultural practices.

Possible conservation measures

Artificial gene flow and outbreeding depression

Since gene flow can alleviate the problems associated with isolation of small populations, it has been suggested to use artificial gene flow as a conservation measure. For instance, seeds from one large and vigorous population could be brought to a small and endangered population, hereby increasing its genetic diversity. However, gene flow is not necessarily only beneficial. Gene flow can also reduce fitness, because sessile plants with restricted dispersal capacities may be highly adapted to their local environment on a small spatial scale. Imagine two parent plants, each originating from two different populations. If each parent is highly adapted to the local environment, transplanting one parent into the others' habitat would result in reduced fitness. Additionally, the hybrid offspring of the two differently adapted plants could also show reduced fitness in each of the original habitats of the parents. This fitness reduction of hybrid offspring is termed outbreeding depression, and was shown to occur in a number of species ([Templeton, 1986](#); [Waser & Price, 1989](#); [Ellstrand, 1992a](#); [Waser, 1993](#); [Fischer & Matthies, 1997](#); [Lynch & Walsh, 1998](#); [Dudash & Fenster, 2000](#)).

What causes outbreeding depression? Two mechanisms are recognised: (1) Plants can carry alleles that are associated with local adaptation to a certain environmental condition. If these plants (parent A from environment A) mate with plants that carry another variant of this gene locus (parent B from environment B), the offspring will only carry half of the alleles of each parent. This can result in fitness reduction of the offspring in each of the environments A or B, because it only carries 50% of alleles associated with environment

A, and only 50% associated with environment B. In contrast, offspring of two parent plants from environment A will carry 100% of alleles necessary for adaptation to environment A. (2) Moreover, co-adapted gene complexes may become disrupted in the hybrid offspring. This means that individuals may carry an allele that depends on the presence of other alleles at a certain locus. These fine-tuned interactions among loci (termed gene complex) may be responsible for enhanced fitness of the individual. Hybridisation among parent plants can lead to disruption of the complex and will lead to fitness reduction of the hybrid offspring (see [Dudash & Fenster, 2000](#)).

In reality, a small population receiving additional genetic material will presumably be subject to a complex mixture of the beneficial effects associated with gene flow and the negative effects arising from outbreeding depression. So far, various studies have found indications for the occurrence of outbreeding depression (see above). However, the long-term consequences of artificial gene flow on hybrid offspring over several generations have so far not been comprehensively studied. Questions concerning the optimal spatial scale for hybridisation and the relative magnitudes of beneficial and detrimental effects remain unanswered ([Dudash & Fenster, 2000](#)). To be able to assess the long-term effects of habitat fragmentation on population persistence, these authors recommend integration of varying natural systems and the joint study of inbreeding and outbreeding depression.

(Re)Introduction of species

A second conservation measure to alleviate the negative effects of habitat fragmentation is to reintroduce species that have disappeared (restorations, translocations), to introduce typical but absent species or to restock populations with plants from other populations (augmentation). However, as for the use of artificial gene flow, the deliberate movement of individuals must be carefully assessed ([Primack, 1998](#)). Questions arising concern the appropriate species and sites for introduction, the appropriate source material and the number of individuals ([Booy et al., 2000](#)). Scientifically documented reintroduction of species has only rarely been done with plants, and the demographic viability of translocated populations has not been explored adequately ([Moritz, 1999](#)). Often, plant translocations were undertaken by conservation organisations, botanical gardens or amateurs, without scientific backup. Moreover, many of these experiments were unsuccessful

(see Given 1994; Moritz, 1999; Primack, 1998), especially when seeds rather than seedlings were used (e.g. Primack, 1998).

However, reintroduction of endangered species could reduce the risk of extinction and is therefore receiving increased attention. In Britain, *Filago gallica* L., which was extinct in 1955, was successfully re-established, albeit only in small numbers on one site (Rich, Gibson, & Marsden, 1999). A large re-establishment program in Australia with 151 plant populations and 48 species proved successful for 32% of the populations, 40% of the species and 12% of the plants (Morgan, 1999). Success or failure of establishment could not be explained by single plant or site attributes. Seedling recruitment was extremely rare, indicating that the long-term viability even of initially well-established populations is highly critical. To support seedling recruitment processes and population persistence, long-term commitment to management is essential (Primack, 1998; Morgan, 1999). In a recent experiment with *Arnica montana* L., which is strongly endangered in The Netherlands, short-term introduction to an experimental garden was successful, and no indications for outbreeding depression were found (Luijten, Kéry, Oostermeijer, & den Nijs, 2002). However, a breakdown of co-adapted gene complexes in the long term is still possible. In summary, before actually recommending this costly and laborious conservation measure, more empirical studies on the population genetic consequences and the long-term success are needed.

Summary and conclusions

Habitat fragmentation threatens the survival of many species and can cause the extinction of local populations (Ehrlich & Wilson, 1991; Young et al., 1996; Young & Clarke, 2000). Habitat fragmentation has two major consequences: populations become more isolated and are reduced in size. Small compared with large populations have increased extinction risks because of natural catastrophes and environmental, demographic or genetic stochasticity (drift). Genetic drift reduces the genetic variability of isolated populations and can result in strong genetic differentiation between populations. Moreover, genetic drift might randomly increase the frequency of slightly deleterious mutations in a population. In the short term, this can reduce mean population fitness. In the long term, the evolutionary capacity of populations to adapt to changing environments is reduced. Habitat fragmentation can further negatively affect popu-

lations via inbreeding, a term used for related phenomena, which all increase homozygosity and may lead to inbreeding depression, which means reduced fitness of individuals or entire populations. Fitness reduction can be estimated by comparing the demographic composition of populations, and fitness traits of individuals such as plant size, reproductive output and susceptibility to pathogen damage. However, the reactions to habitat fragmentation can differ strongly between species. The severity of effects depends on many factors such as a species' breeding system, capacity of survival, migration and colonisation, dependency on pollinators and on the time since fragmentation. Finally, habitat fragmentation not only affects populations directly via genetic effects, but can also change the abiotic conditions of the surrounding landscape, which in turn influences biotic interactions in the habitat fragment.

Most previous habitat fragmentation studies focussed on rare and endangered species, which often consisted of only a few hundred reproductive individuals. Mathematical models predict that such small populations will not be able to survive in medium time scales. However, also far larger populations with negative or variable long-term growth rates may ultimately face extinction (Holsinger, 2000). So far, formerly common habitat specialists that still grow abundantly on many sites have attracted far less conservation attention than rare species. A recent series of investigations on habitat fragmentation effects on abundant wetland species in NE Switzerland demonstrated that habitat fragmentation is threatening not only the rarest plants, but also fairly common habitat specialists (Hooftman & Diemer, 2002; Hooftman et al., 2003; Lienert et al., 2002a, b, c; Lienert & Fischer, 2003). Therefore, I recommend that future investigations and conservation activities also include more common plant species.

Recommendations for the minimum viable population sizes necessary for the persistence of a species are difficult, if not impossible to give. A more promising approach to using absolute numbers is to monitor population sizes or demographic changes. The negative effects of small population size and isolation could be alleviated with artificial gene flow between populations. However, the magnitude of gene flow actually occurring in plants differs strongly among species. Moreover, opinions differ on the magnitude of gene flow necessary to avoid negative effects of small population size and isolation. Because of outbreeding depression, the use of artificial gene flow for conservation purposes must be evaluated carefully beforehand, and comprehensive monitoring studies are needed.

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