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POPULATIONS: ECOLOGY AND GENETICS

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7.1   INTRODUCTION

A population is defined as a group of potentially inter-acting organisms of the same species occupying a given space at the same time. The physical environ-ment (the local sites) in which the populations of a species are found is termed the species' **habitat**. In restoration ecology, population processes should be approached in the context of processes taking place at the landscape scale (see Chapters 2 and 5). Therefore, in this chapter considering populations of both plants and animals, and also plant–animal interactions, we will focus in particular on the dynamics of spatially structured **metapopulations**, which are defined as assemblages of local populations connected by mutu-ally dispersing individuals in a network of habitat patches. Within their habitat patches, species interact with a subset of the entire **biotic community** in the ecosystem. Interacting species obviously perceive the spatial scale of discontinuities in the landscape differ-ently, depending on their trophic level, degree of habitat specialization, body size and dispersal ability, among other variable traits and factors. Habitat destruction and fragmentation, or other impacts on the spatial structure of habitats, can therefore alter the extent and outcome of interactions between popula-tions of different species in a community.

Population ecology and the ecology of metapopula-tions are somewhat different, and make different con-tributions to restoration ecology. Population ecology focuses on understanding local abundances and can, among other things, be used to predict population per-sistence over time. Metapopulation studies (see section 7.3, below) explicitly link population ecology to bioge-ography, link the regional occurrence of species and specifically contribute to restoration ecology in terms of optimizing among-population processes that are critical for species persistence; specific interventions may include determining the best ways of adding, rein-forcing, reintroducing and connecting populations. Both fields require detailed biological knowledge of a species and long-term data sets providing not only mean values but also spatio-temporal variances in demographic parameters (vital rates) at different life stages of populations under a range of relevant envi-ronmental conditions.

The fate of populations is not only determined by demographic and environmental parameters, but also by genetic factors. Populations that have become small and isolated due to habitat destruction and fragmenta-tion generally suffer increased extinction risk for several reasons, including demographic, environmental and genetic factors and their interactions, and often it is not easy to identify the primary cause. Population viability analyses (Menges 2000) and estimates of *minimum viable population* (MVP) size (Traill *et al*. 2007) – con-cepts that are being applied to conservation and resto-ration – depend on whether genetic variation is included or not. Yet, the role of genetic factors in the persistence or extinction of threatened species has been long debated. This debate has been inspired by the fact that in some species, populations that have gone through a bottleneck of even a single pair, resulting in high levels of inbreeding and low genetic variation, nonetheless are able to persist (Groombridge *et al*. 2000). Frankham (2005) considers it risky to use such examples to argue that genetic factors do not play a role in determining the fate of small isolated populations, as they in fact may represent exceptions: a much larger fraction of genetically impoverished populations might have gone extinct compared to similar-sized populations with higher levels of variation or lower levels of inbreeding, as indeed shown in experimental studies (Reed & Frankham 2003). For instance, genetic variation as measured by heterozygosity appears to be on average 35% lower in threatened (IUCN red list) plant and animal taxa than in related, nonthreatened, taxa (Spielman *et al*. 2004a). Low genetic variation also reduces opportunities for populations to tolerate chang-ing or fluctuating environmental regimes or the ability to evolve and adapt to them (Bijlsma & Loeschcke 2005; Bakker *et al*. 2010). Without considering genetic factors, extinction risks tend to be underestimated and restoration strategies may be inappropriate.

In this chapter we will first deal with local popula-tion ecological and genetic processes that are relevant for **restoration ecology** and show how knowledge of these processes can help in planning and managing succesful **ecological restoration** (section 7.2). We will then elaborate on these processes in the spatial context of metapopulations and discuss the challenges of restoration from a metapopulation perspective (section 7.3). Next, we will discuss the implications of changes in the spatial structure of the habitat for trophic interactions between populations that respond at different spatial scales and its relevance for restora-tion ecology (section 7.4). Finally, in section 7.5, we reflect on new challenges implied by restoration as compared to conservation of populations. In Box 7.1 we present commonly used measures of genetic varia-

Box 7.1 Estimating genetic diversity and its use in conservation and restoration

Measuring genetic diversity. A good quantification of genetic variation allows assessment of variables that are important for decision making in conservation and restoration, including within- and between-population divergence, local adaptation, inbreeding and gene flow. At the population level, genetic diversity is often measured as (1) P = proportion of loci that is polymorphic (the fraction of all loci for which two or more different alleles have been observed), (2) H = average heterozygosity (the proportion of loci at which individuals on average are heterozygous, i.e. have two different alleles) and (3) A = allelic diversity (the average number of alleles observed per locus). All of these parameters are generally positively related to fitness (Reed & Frankham 2003; Leimu *et al*. 2006).

Use of near-neutral genetic markers. Different types of genetic markers can be used as a basis for such estimates, from DNA or protein to phenotypic variants. DNA-based markers offer the advantage that they generally yield a large number of polymorphic loci. Some of these, like Amplified Fragment Length Polymorphism (AFLP), are relatively easy to develop, but lack the ability to discriminate between homozygotes and heterozygotes due to dominant inheritance. Others, like microsatellites (Simple Sequence Repeats, SSR), do not bear this disadvantage (co-dominant inheritance) but do take a bit more time to develop. With the rapidly declining cost of sequencing, sequence-based markers like Single Nucleotide Polymorhisms (SNP) are becoming more widely available, offering opportunities of genotyping vast numbers of polymorphic loci with co-dominant inheritance.

Estimating population genetic parameters. From the distribution of the observed neutral genetic variation between and within populations and individuals, a number of basic population genetic parameters can be assessed. Estimates are based on deviations of observed heterozygosity from expected heterozygosity. Any nonrandom mating amongst individuals included in the sampling results in a deviation (deficit) of heterozygotes compared to those expected in infinitely large, outbreeding, perfectly random mating populations without mutation, migration or selection (Hardy–Weinberg equilibrium). Deviations of subpopulations relative to the total population (F_{ST}) indicate population differentiation, while deviations of individuals relative to their subpopulation (F_{IS}) indicate inbreeding within populations. The degree of population differentiation (F_{ST}, or G_{ST}, the equivalent for multiple loci) is inversely related to effective population size N_e and the number of migrants (m) and hence can be used to infer gene flow, while F_{IS} can be used to infer the degree of inbreeding within populations.

Use of neutral versus quantitative genetic markers. Genetic diversity based on DNA markers predominantly assesses neutral molecular variation. Unfortunately, neutral molecular variation generally has poor predictive power for phenotypic and quantitative genetic variation on which natural selection acts, and that is important in local adaptation to the environment (Reed & Frankham 2001; McKay & Latta 2002, and references therein). Therefore, a combination of studies with neutral and quantitative markers is often advised in conservation and restoration (Kramer & Havens 2009). Neutral genetic studies are well suited for assessing gene flow to identify historical and current movement and mixing of populations, inbreeding and divergence within and between populations. Quantitative genetic trait studies such as common garden, reciprocal transplant and quantitative trait loci studies are better suited to estimate fitness costs associated with inbreeding, adaptive genetic diversity and adaptive population differentiation. Combining neutral genetic and quantitative genetic studies are especially useful to dissect adaptive versus random population genetic divergence. For instance, the ratio of Q_{ST} to F_{ST} (or G_{ST}) – where Q_{ST} is the equivalent of F_{ST} for quantitative trait loci – has been used to identify traits involved in adaptive differentiation, that is, traits that show larger population divergence (Q_{ST}) than that observed for neutral loci (F_{ST}).

tion and indicate the value of their use in conservation and restoration science.

7.2   LOCAL POPULATIONS

Destruction and fragmentation of habitat lead to a reduction in the population sizes of resident species, as well as increased isolation among populations, resulting in reduced migration and *gene flow*, that is, the movement of alleles between populations by migration, or transport of pollen and seeds. Reductions in population size are often the start of a self-reinforced negative spiral towards extinction that is known as the *extinction vortex* (Figure 7.1). Small, fragmented and isolated populations become inbred because of the higher proportion of matings that occur between relatives, often leading to lower ofspring fitness (*inbreeding depression*). Such populations are also more prone to a loss of genetic diversity because rare alleles are more easily lost from small than from large populations as a result of *random genetic drift*, as explained in section 7.2.3. The increased inbreeding and loss of genetic diversity lead to reduced fitness and potential for adaptation, further reducing population size and the susceptibility of populations to effects of demographic stochasticity, environmental variation and catastrophies, until extinction occurs (Frankham *et al.* 2005).

As far as the species level is concerned, ecological restoration programmes aim at restoring habitat conditions and/or **reintroducing** or **reinforcing** populations, thereby enhancing population size and promoting greater connectivity among populations (Montalvo *et al.* 1997; McKay *et al.* 2005). In this section we consider population ecological and genetic processes that are relevant in the context of ecological restoration. Restricted gene flow affects the performance of populations in various ways. On the one hand, it facilitates the process of local adaptation (section 7.2.1). On the other hand, it results in increased inbreeding and associated inbreeding depression within populations (section 7.2.2) and restricts the opportunities to restore genetic variation that is becoming depleted by random genetic drift (section 7.2.3); the strength and impact of these genetic processes stongly depend on population size. Finally we will
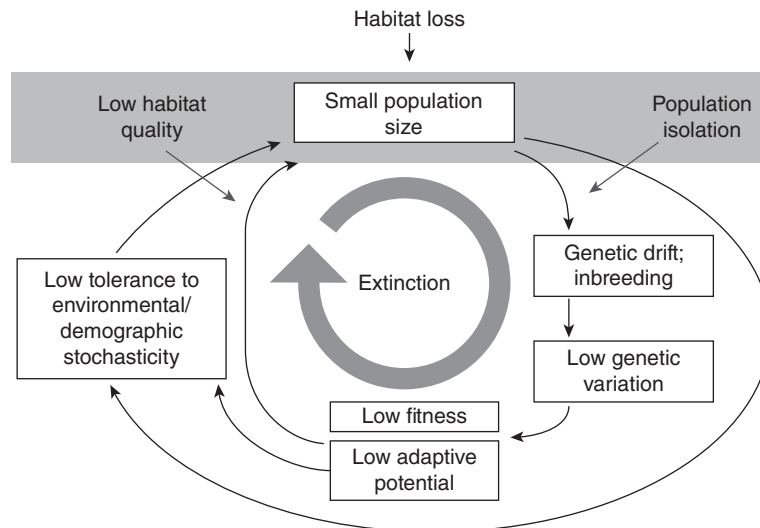

Figure 7.1 The extinction vortex. Habitat destruction leads to low quality of remaining habitat, isolation between remaining populations and small population size (grey bar). Reduction of population size leads to a progressive increase in inbreeding and genetic drift, loss of genetic variation and reduced fitness, further decreasing population size until extinction. Reduced population size also increases susceptibility to effects of environmental and demographic stochasticity and catastrophies, further enhancing extinction risk. Other effects of habitat destruction (increased isolation and low quality of remaining habitat) enhance the spiral to extinction through their negative effects on genetic variation and fitness. Ecological restoration aims to counteract these effects. (Modified from Frankham *et al.* 2005.)

discuss the consequences of inbreeding and genetic drift for population fitness and viability and the prospects of 'genetic restoration' (section 7.2.4) in order to counteract the negative effects of inbreeding and genetic drift.

7.2.1 Local adaptation

Local populations have two basic ways in which to adapt to their environment and changes therein. *Phenotypic plasticity* is the ability of an individual to produce different phenotypes or behaviours from the same genotype under different environmental conditions, a mechanism that is important for sessile organisms in particular. Although this might suggest that phenotypic plasticity is a nongenetic mechanism, the extent to which plants are able to show phenotypic plasticity in traits ususaly has a strong genetic basis and is, itself, subject to natural selection. The second mechanism is by *adaptive genetic differentiation* in response to selection pressures in the local environment. If the variation in the traits under selection has a genetic basis, selection may increase the frequency of alleles in a population that enhance local fitness. The latter process will result in **local adaptation**, the 'home advantage' of genotypes in their local environment, provided that gene flow between populations is restricted, so that the differentiation that evolves is not continuously swamped by import of alleles that have experienced different selection pressures (Kawecki & Ebert 2004). Local adaptation, being an adaptive response of populations, is of concern in reintroduction programmes, as translocation implies the risk of introducing individuals that are maladapted to the conditions in the restoration area (examples are given in Chapter 8).

There is ample evidence for local adaptation of plant populations to their respective environments (Hufford & Mazer 2003), but it may in fact be less prevalent than was previously thought. A meta-analysis of plant transplantation studies (Leimu & Fischer 2008) shows that in more than 70% of the studied cases local genotypes outperform foreign genotypes at their site of origin. However, when these analyses are restricted to reciprocal transplant studies only, it appears that in half of the studies in fact one of the two local populations performed best at both sites (outperforming the other population both at its local and nonlocal site). Only in 45% of the cases studied did both local popula-

tions perform best at their own home site, thus exhibiting local adaptation in the strict sense (Kawecki & Ebert 2004). Also, local adaptation of plants to the biotic component of their environment is much less evident than local adaptation to the abiotic environment. In fact, host–parasite studies, including those of plant–pathogen and plant–herbivore interactions, generally show parasite local adaptation (Greischar & Koskella 2007), indicating that host plants suffer more from their local than from nonlocal biotic threats. This is especially true for parasites that have higher migration rates and shorter generation times than their hosts (Gandon & Michalakis 2002). The relative importance of abiotic and beneficial or detrimental biotic factors as determinants of fitness may thus affect the extent of local adaptation (Cremieux *et al.* 2008).

Nonetheless, local adaptation of populations is, and should be, an important consideration in the choice of **provenances** used in reinforcement or reintroduction. For instance, local adaptation may be one of the main factors explaining why the establishment success of reintroduced populations of rare or extinct wetland plant species in Switzerland is best explained by ecological similarity between source and introduction sites (Noël *et al.* 2011; Figure 7.2). Consequently, the choice of provenances in plant reintroduction programmes is commonly based on considerations of minimizing geographical distance to the restoration site or, more
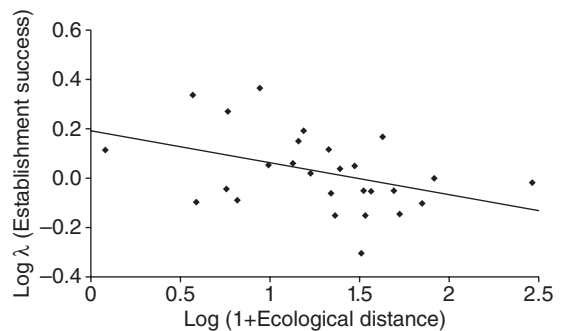
Figure 7.2 The relationship between establishment success of populations of 14 reintroduced wetland plant species in Switzerland (log λ, change in log population size per year) and the ecological distance between source and introduced site (based on PCA scores capturing differences in humidity, pH, nutrients, light, temperature and continentality). Life history traits and propagule pressure could not predict establishment success. (From Noël *et al.* 2011.)

importantly, matching habitat conditions (Vander Mijnsbrugge *et al*. 2010) in combination with genetic considerations explained in section 7.2.4.

7.2.2 Inbreeding

As a result of restricted gene flow between populations, individuals within a population become related over successive generations and mating will occur between individuals that are related by ancestry, a process called *inbreeding*. Inbreeding results in a redistribution of genetic variation. The fraction of individuals carrying two copies of the same allele at any particular locus (homozygotes) increases at the expense of individuals carrying two different alleles at a locus (heterozygotes). In other words, inbreeding leads to a loss of heterozygosity. The latter is generally accompanied by *inbreeding depression*, the lower reproductive fitness of progeny resulting from matings between relatives than of progeny resulting from mating between unrelated parents, for two reasons. First, populations accumulate recessive mutations that have slightly deleterious effects on fitness. In heterozygotes, their negative effects are masked by the presence of a dominant functional allele; loss of heterozygosity leads to increased expression of the recessive deleterious alleles in a homozygous state. Second, many beneficial traits show a *heterozygote advantage* (heterozygotes have trait values higher than either of the homozygotes, *overdominance*); loss of heterozygosity abolishes this advantage.

Inbreeding depression is common. Crnokrak and Roff (1999) show that inbreeding depression occurs in 90% of 157 examined data sets from natural populations, including many plants. Inbreeding depression is not only associated with reduced offspring fitness but also with increased population extinction rate, as for example shown for the annual evening primrose relative, *Clarkia pulchella* (Newman & Pilson 1997), and for the shore campion, *Silene littorea* (Vilas *et al*. 2006) (Figure 7.3). These studies corroborate results from stochastic computer simulations showing that inclusion of realistic levels of inbreeding depression significantly increases extinction risk (O'Grady *et al*. 2006). Inbreeding depression is especially a problem in small populations as the extent of inbreeding is inversely related to N_e, the *effective population size*, defined as the number of breeding individuals that would result in the same rate of inbreeding as observed in the census population if that population had been 'ideal' (a popu-
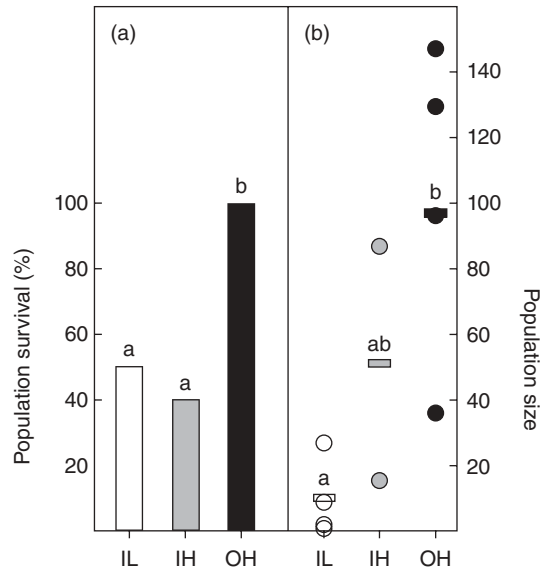

Figure 7.3 Effects of inbreeding and genetic variation on population extinction risk and population size of surviving populations in a reintroduction experiment of shore campion (*Silene littorea*) in Spain. (a) Experimental populations initiated with inbred plants and low genetic diversity (IL, white bars) or inbred plants with enhanced genetic diversity (IH, grey bars) had lower survival probability than populations initiated from outcrossed plants (OH, black bars). (b) Surviving populations initiated from inbred plants with low genetic diversity (white dots) also had lower population sizes in their second year than populations initiated from outbred plants (black dots). Symbols indicate different populations; vertical bars indicate population means and different letters indicate significant population type differences. (Adapted from Vilas *et al*. 2006.)

lation with random mating, constant population sizes etc.). N_e is often roughly an order of magnitude smaller than the actual census population size, for instance due to fluctuations in population size. This is because the years with small population sizes disproportionally contribute to an increase in the extent of inbreeding in a population.

7.2.3 Genetic drift

Transmission of alleles from parents to their offspring is essentially a random sampling process. Allele frequencies will therefore fluctuate from one generation

to the next, a process called *genetic drift*. In small populations, the consequences of such random sampling are much more pronounced than in large populations. First, in small populations rare alleles are more easily lost and common alleles are more easily fixed by chance than in larger populations, resulting in a loss of genetic variation. Second, in small populations, random changes in allele frequences due to genetic drift easily override changes in allele frequences due to natural selection, making the process of natural selection less effective. Third, when a large population becomes fragmented into smaller populations, different alleles may get lost or fixed in different population fragments, resulting in random genetic differentiation between habitat fragments. This contrasts with adaptive genetic differentiation as a result of a response to natural selection imposed by local selection pressures that underlies local adaptation (section 7.2.1). This may be one of the reasons that local adaptation is much more commonly observed in large than in small populations (Leimu & Fischer 2008), suggesting a lower ability to respond to environmental variation and change through adaptive genetic differentiation in small than in large populations.

Loss of heterozygosity and genetic diversity due to inbreeding and genetic drift in small populations generally results in a reduction of average fitness in the population (Reed & Frankham 2003). For instance, in the rare marsh gentian (*Gentiana pneumonanthe*), size and reproduction of plants strongly increases with the number of loci at which they are heterozygous (Oostermeijer *et al.* 1995). A meta-analysis of plant studies by Leimu *et al.* (2006) shows that genetic variation – measured as expected heterozygosity, number of alleles or proportion of polymorphic loci (see Box 7.1) – increases with population size and is significantly and positively related to fitness. Since molecular variation at neutral loci will generally not be strongly related to the quantitative variation that is important for adaptation and the ability to evolve (Reed & Frankham 2001), one might expect that measures of genetic variation based on near-neutral DNA markers are less strongly related to fitness than measures based on protein or phenotypic markers. This is not born out by data; according to the meta-analysis by Leimu and coworkers the associations are at least as strong for DNA as for allozyme data. Of course, associations between population size and fitness not only are mediated by genetic factors, but also may in part be due to nongenetic causes such as reduced quality of small habitat frag-

ments, and these factors may interact in their effects on population fitness.

7.2.4 Genetic rescue and genetic restoration

Due to inbreeding and genetic drift, alleles with slightly detrimental effects accumulate in small populations (called the 'genetic load' of a population), causing low mean population fitness. **Genetic rescue** is the intended introduction of (unrelated) individuals from other populations to reduce the genetic load, that has been advocated as a new management strategy to help avoid extinctions of such low-fitness populations (Tallmon *et al.* 2004; Edmands 2007). Even if one had wished to do so, restoration programmes that involve reinforcement or reintroduction of populations often cannot use source material from the exact local populations. Hence it introduces 'foreign' material, resulting in outcrossing with plants from different, genetically diverged populations, a process called *admixture*. Genetic rescue can be viewed as finding a balance between the positive effects of admixture (heterosis and increased genetic variation) and its negative effects (outbreeding depression).

Heterosis (or hybrid vigour) is the increased reproductive fitness of offspring resulting from admixture. In section 7.2.2 we have seen that this can be based either on dominance or overdominance of favourable alleles. Most of the experimental studies in plants indeed show increased fitness of interpopulation crosses, indicating potential for genetic rescue, including the rare yellow pitcher plant (*Sarracenia flava*) (Sheridan & Karowe 2000), the field mustard (*Brassica campestris*) (Newman & Tallmon 2001) and the rare Bavarian scurvy-grass (*Cochlearia bavarica*) (Paschke *et al.* 2002). The second potential advantage of admixture is increased genetic variation and the production of novel genotypes, increasing the adaptive potential of populations and their ability to cope with future environmental change. Conversely, there are risks of admixture if populations are locally adapted. The first risk is that it will dilute the locally adapted gene pool (i.e. reduce the pool of local alleles whose additive effects increase fitness); this process is called *extrinsic outbreeding depression*. The second risk is that admixture may lead to the breakdown of co-adapted gene complexes (positive interactions between alleles at different loci) that may have evolved in the local population;

this is called *intrinsic outbreeding depression*. For instance, in crosses between individuals from different North American populations of partridge pea (*Chamaecrista fasciculata*) which have differentiated via co-adapted gene complexes, the positive effects of heterosis are progressively counteracted by the negative effects of intrinsic outbreeding (Fenster & Galloway 2000). In contrast, in many species such as the rare whorled sunflower (*Helianthus verticillatus*), the positive effects of heterosis continue in subsequent generations without any sign of outbreeding depression. The importance of outbreeding depression is still much debated and is currently on the top priority list for conservation genetics research (Frankham 2010).

Genetic rescue has been extremely successful in a number of animals (Hedrick & Frederickson 2010), including adders (*Vipera berus*), greater prairie chickens (*Tympanuchus cupido pinnatus*), Mexican wolf (*Canis lupus baileyi*) and Florida panther (*Puma concolor coryi*), as well as in plants (Tallmon *et al.* 2004). Hedrick (2005) emphasizes, however, that genetic restoration involves more than just genetic rescue. Genetic rescue focuses on removing detrimental variants that increase in frequency in small isolated populations due to genetic drift, whereas the more comprehensive process of *genetic restoration* should not only focus on removing detrimental variation, but also consider how increased gene flow affects the other two types of variation: neutral variation and adaptive variation. Firstly, migrants may quickly spread in the population, increasing their representation in the gene pool and reducing the amount of neutral genetic variation that might be adaptive in future environments. Secondly, a few successful migrants may overwhelm selection that would otherwise maintain adaptive variants, reducing their frequency, a process called *genetic swamping*. For instance, in experimental populations of the field mustard (*Brassica campestris*), one immigrant per population increased fitness compared to no-immigrant controls (Newman & Tallmon 2001). Higher levels of immigration also increased fitness but led to less phenotypic divergence than with one migrant per generation, suggesting that lower immigration is sufficient to increase fitness without impeding the facilitation of local adaptation. An example of genetic restoration in animals is that of the Florida panther (Hedrick & Fredrickson 2010), the last surviving puma subspecies in eastern North America, that had in recent times nearly gone extinct in the state of Florida. Genetic restoration guidelines were to introduce eight pumas from a population in Texas that formerly had been connected to the Florida population by gene flow, to achieve an initial circa 20% ancestry from introduced Texas panthers, followed by one migrant per subsequent generation to eliminate detrimental variants while preventing the elimination of adaptive variants and increase the levels of neutral variation. Even though eventually no subsequent migrants were introduced, the admixture resulted in increased fitness, a doubling of heterozygosity, a decline in inbreeding correlates and a threefold increase in population size (Johnson *et al.* 2010).

7.2.5 Corollaries and consequences

The success of genetic restoration programmes in the past two decades has shifted our view regarding the risk of introducing foreign genetic material for restoration. Although outbreeding depression is a real phenomenon, its negative effects often do not outweigh the positive effects of heterosis, not only in first-generation hybrids, but also far beyond that. This has sparked renewed attention for the positive effects of low levels of gene flow for fitness and adaptive evolution and has provided faith in genetic restoration as a management tool if properly applied. Hedrick and Fredrickson (2010) recently devised 10 guidelines for successful implementation of genetic restoration, four of which specifically aim at minimizing the risks associated with admixture by continued management schemes that adjust the extent and number of repeated introductions. It is also worth taking a step back and asking whether the risk that intentional admixture will reduce population fitness is always the most relevant question to consider in an ecological restoration programme. After all, preserving or reintroducing populations with suboptimal fitness may in many cases be preferred over the final absence of populations that would result if no restoration at all is undertaken (cf. van Andel 1998; Kiehl 2010).

7.3 METAPOPULATIONS

Population processes take place in landscapes consisting of networks of habitat patches and, therefore, disciplines that explicitly link local abundance to regional occurrence are necessary to understand species abundance patterns at larger scales and how to restore them. Metapopulation ecology and genetics

approaches have been developed to deal specifically with consequences in sets of local populations whose dynamics are characterized by frequent extinction and recolonization. We start this section by presenting the scientific approach of metapopulation ecology and genetics (section 7.3.1), and then illustrate how they contribute to restoration ecology, focusing on the 'rescue' of metapopulations (section 7.3.2), in analogy to the rescue of populations.

7.3.1   Metapopulation ecology and genetics

Metapopulation approaches are useful in the context of restoration as they can provide guidance as to how to optimize not only within-population, but also among-population, processes that are critical for species persistence across their respective ranges, including patch connectivity and migration rates. Theoretical models can be classified according to the type of spatial organization of suitable habitat patches in the landscape matrix that they assume. Two extremes are (1) the mainland–island models derived from island biogeography (MacArthur & Wilson 1967) and (2) Levins's models (Levins 1969) described below. Most mainland–island models assume that there is one large source patch (mainland) and numerous smaller habitat patches (islands) that can go extinct and be recolonized from the mainland patch. In contrast, Levins's model assumes more evenly sized patches, any one of which can go extinct and then be recolonized from nearby patches. The spatial organization of most natural metapopulations will share characteristics of both and can be classified in more detail. Not all sets of populations are characterized by frequent extinctions and recolonizations, a key feature of metapopulation dynamics in the strict sense (Hanski 1999). Also, large patches do not necessarily act as sources. If their intrinsic growth rates are low, for instance due to low patch quality, they can act as sinks rather than sources within the metapopulation. In that case, restoration efforts that focus on large patches may in fact endanger the metapopulation as immigrant sources are neglected. Such knowledge is thus of vital importance when deciding which patches are important to focus on in restoration projects and programmes.

Migration rates play an important role in metapopulation persistence. On the one hand, migration rates should be large enough to ensure that recolonization rates exceed extinction rates, key to metapopulation persistence. On the other hand, migration rates should be small enough to allow demographics of patches within the metapopulation to proceed independently. Spatiotemporal variation in demographics among patches in a metapopulation is essential for species persistence as it ensures the presence of source patches at all times.

The structure of metapopulations may suggest that they should be well buffered against loss of genetic variation, better than single local populations. Indeed, compared to an unfragmented population of the same total size, structures with several small fragments that are ill connected (low levels of gene flow) initially retain higher genetic variation (Frankham *et al.* 2005). This is because different alleles will be fixed and lost in different fragments; the chance that they are lost from all fragments is therefore smaller than in a single large population. However, due to the low effective population sizes of the constituent fragments, all metapopulation structures are likely to suffer higher levels of inbreeding than a single large population. Due to the larger extinction probability of smaller fragments, any subdivided population structure will therefore eventually have lower total genetic diversity than a single large population. The role of genetic rescue in restoration of metapopulations could therefore be at least as important as in restoration of unfragmented populations.

7.3.2   Rescue of metapopulations

Similar to what we have seen for single populations (section 7.2.4), metapopulation persistence is enhanced by ecological and genetic rescue. The metapopulation rescue effect refers to the positive effect of the number of immigrants on occupancy of suitable patches, reducing extinction risk. Practices that enhance dispersal (reinforcement, stepping stones and corridors) therefore generally contribute to metapopulation rescue, as they increase the proportion of suitable habitat that is occupied and the successful colonization rate (establishment effect). Even a very limited amount of migration can have a profound effect upon the recipient population. We illustrate this with some examples given by Stacey *et al.* (1997). White-footed mice (*Peromyscus leucopus*) have persisted in a remnant network of woodlot patches in North America, connected by migration routes. Populations linked by these high levels of migration have higher growth rates than populations linked by lower levels of migration and

there is clear evidence for a similar rescue effect in several other small mammal species. Pool frogs (*Rana lessonae*) that occur in natural metapopulations along the Baltic coast of Sweden reproduce only in distinct water bodies. Over a 6-year period, populations isolated by greater than 1 km became extinct, whereas less isolated populations tended to persist.

In the aforementioned examples of metapopulation ecology, genetic aspects have not been considered. We now refer to a number of studies on the genetic rescue of metapopulations. Populations of blacktail prairie dog (*Cynomis ludovicianus*), which appeared to consist of several family groups called 'coteries', remain spatially distinct from each other because of a rigid social structure. Regular influx of male immigrants reduces inbreeding within local populations and elevates levels of heterozygosity, potentially 'rescuing' populations from inbreeding depression and possible extinction (Stacey *et al.* 1997). Also, for small mammals such as pikas (*Ochotona princeps*) migration among habitat fragments appears to be important in maintaining genetic variation within the metapopulation and preventing the loss of heterozygosity in component populations. In metapopulations of the checkerspot butterfly *Melitaea cinxia*, many local populations are small and inbred. Inbreeding depression is strong, especially under less favourable environmental conditions, and inbred populations suffer increased extinction risk (Nieminen *et al.* 2001). Since most populations within the metapopulation are small, the total number of migrants and thus the potential number of recolonizers within the metapopulation is low, increasing metapopulation extinction risk and calling for enhanced migration and metapopulations rescue. Similar observations have been made for plants. For example, in metapopulations of the white campion (*Silene latifolia*) effects of inbreeding are mitigated by higher gene flow into patches with genetically related than into patches with genetically unrelated individuals (Richards 2000). The effect is probably due to the higher success of outcross pollen in patches with genetically interrelated individuals than in patches consisting of unrelated individuals, pointing at a role of connectivity through pollen-mediated gene flow on persistence of isolated patches. In 27 populations of the marsh grass *Parnassia palustris*, distributed over three metapopulations, between-metapopulation crossings result in higher seed production than within-metapopulation crossings, especially for smaller populations. This *genetic rescue* is probably due to alleviation of the low pollen compatibility within metapopulations due to low genetic diversity (Bossuyt 2007).

7.3.3   Corollaries and consequences

Several generalities arise from metapopulation theory (cf. Maschinski 2006). Persistence is enhanced by higher numbers of suitable patches, larger average patch size, larger fraction of large patches at the interior, higher within-patch reproductive rates, enhanced patch connectivity, higher immigration rates and lower emigration rates. Metapopulation models help to predict the fate of a metapopulation as a whole, to assess the value of individual patches for species' persistence, and to manage migration by stepping stones, corridors and repeated introductions. They can also serve to estimate minimum viable metapopulation sizes (MVM), which is the minimum number of interacting local populations necessary for long-term persistence of a metapopulation. The MVM is thought to be governed by an equilibrium between the rates of extinction and of recolonization of suitable habitat patches. Metapopulations that are not at extinction–recolonization equilibrium are heading for extinction.

Even though most relevant models suggest that the largest patch in the metapopulation is the most important determinant of overall persistence, in any particular restoration programme it is often difficult to judge the relative benefits of enhancing size per patch (decreasing local extinction probability of subpopulations) versus constructing more patches (increasing metapopulation viability). Nicol and Possingham (2010) point out that the optimal metapopulation structure strongly depends on the specific metapopulation parameters and suggest stochastic dynamic programming as a tool to design optimal restoration strategies.

7.4   SPECIES INTERACTIONS AFFECTED BY HABITAT FRAGMENTATION

Habitat fragmentation of plant populations not only affects individual plant species themselves, but also their interactions with potential mutualists such as mycorrhizae and pollinators, as well as antagonists such as herbivores and pathogens (see also Chapter 6). This is because the spatial scale of population processes

and species–area relationships depend on trophic rank (Holt *et al.* 1999). Reductions in size and increased isolation among habitat fragments of different species can therefore disrupt trophic interactions. We distinguish between ecological and evolutionary genetic consequences of fragmentation for such interactions. The former reflects alterations in distribution, abundance and dynamics of potentially interacting species, affecting their encounter rate or interaction frequency. The latter, amongst other factors, reflects alterations in the genetic constitution of the potentially interacting species that affects the outcome of their interactions. Moreover, ecological and genetic consequences interact, that is, changes in encounter rate can drive life history evolution of organisms involved. In this section, we discuss some of the ecological consequences (section 7.4.1), and then, in section 7.4.2, some of the genetic and evolutionary consequences of habitat fragmentation for species interactions.

7.4.1   Ecological consequences

The spatial scale at which population processes operate differs among species, depending on their trophic rank, degree of habitat specialization, body size and dispersal ability, among other things. Consequences of alterations in spatial habitat structure such as fragmentation therefore differ between species, and consequently change or disrupt interactions such as pollination, parasitism or predation, and interspecific competition. Habitat fragmentation is most strongly felt by species if they have larger body size, lower dispersal capacity, are habitat specialists and are positioned at higher trophic levels (Tscharntke & Brandl 2004). The presumed increase in sensitivity to fragmentation with trophic rank indicates that fragmentation has important consequences for the outcome of multitrophic interactions. An example is the work of Elzinga *et al.* (2005, 2007). They performed a three-year study in a series of fragmented populations of the white campion (*Silene latifolia*) along the river Waal (Netherlands), to assess the effects of plant population size and isolation on trophic interactions between the plant, one of its specialist herbivores, the fruit-predating moth *Hadena bicruris*, and a range of hymenopteran insects that parasitize the herbivore (Figure 7.4). These studies have shown that the herbivore is present in virtually all plant patches, even the smallest and most isolated ones. However, the incidence of the most common

parasitoid, *Microplitis tristis*, strongly declines with plant population size (Figure 7.4a). The same is true for the parasitoid *Eurylabus tristis*, especially in isolated patches; in order to have a 50% probability of occurrence, a plant population size of 10 appears to be required for closely connected patches but a population size of more than 700 is required if the nearest neighbouring patch is two kilometers away (Figure 7.4b). Accordingly, parasitism rates of the herbivore are lower in smaller and more isolated plant patches (Figure 7.4c). Presence of the herbivore is thus not affected at the current scale of fragmentation of the plant's habitat, but that of the parasitoids is, corroborating the idea that higher trophic levels are more sensitive to fragmentation. Release of herbivores from parasitism in small isolated patches could result in increased herbivory. Indeed, the proportion of predated fruits on plants is much higher in small than in large populations (Figure 7.4d), but this may also be due to behavioural responses of the herbivore to host density.

Fragmentation not only alters interactions of plants with their herbivores and associated parasitoids, but also with diseases. Most airborne diseases have a threshold host population size below which they cannot persist; this threshold is higher for pathogens with low transmission efficiency. Both small host-population size and low connectivity may thus decrease the probability of host populations to be infected, as shown in several natural systems (Antonovics *et al.* 1997, and references therein). One of the ecological consequences of corridors designed to increase **connectivity** of target species is that they may also, inadvertently, facilitate the spread of herbivores and diseases (Hess 1996). Thus, whereas fragmentation may be detrimental for pollination service, it may reduce the contact rate with diseases. Since diseases can severely impact natural populations (McCallum & Dobson 2002), it should be ascertained whether the benefits of *corridors* outweigh their risks.

7.4.2   Evolutionary genetic consequences

As mentioned, **habitat fragmentation** results in loss of genetic variation, and increased levels of genetic drift and inbreeding. The genetic consequences of fragmentation for species interactions can be profound. A classic example of the effect of low levels of genetic variation and heterozygosity on resistance is the African cheetah, *Acinonyx jubatus* (O'Brien & Evermann 1988).
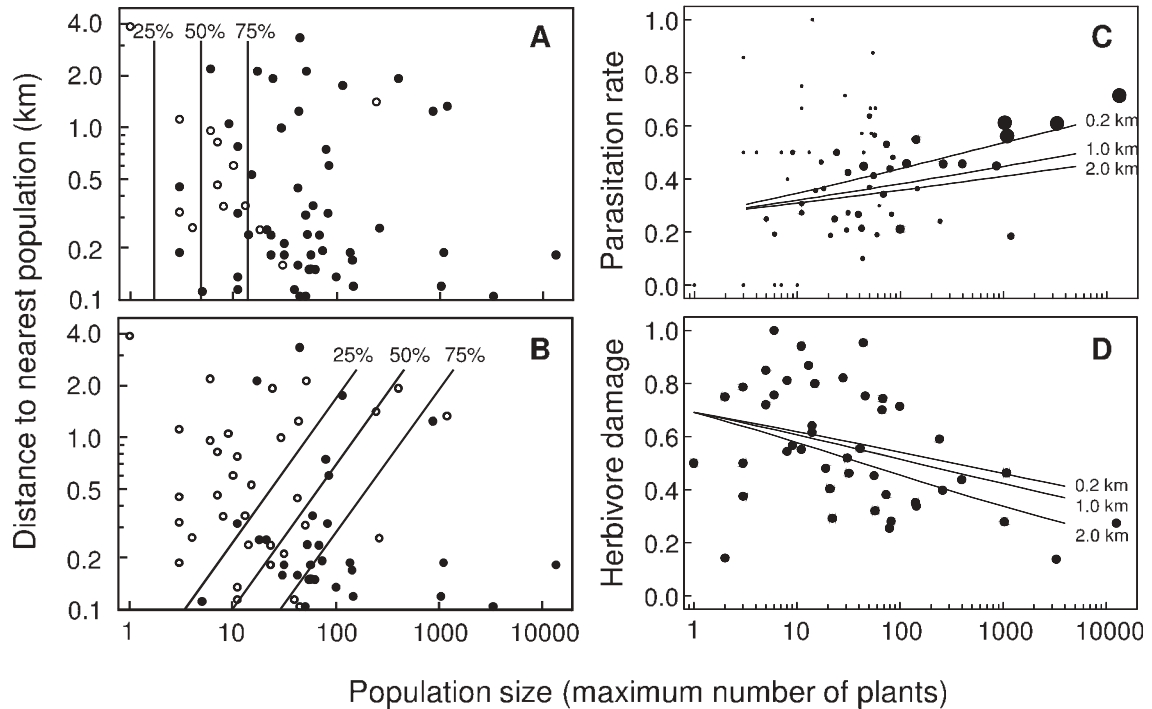
Figure 7.4 Mismatches between the effects of decreased population size of white campion (*Silene latifolia*) on its fruit herbivore *Hadena bicruris* and on the hebivore's parasitoids *Microplitis tristis* and *Eurylabus tristis*. (a) Presence (closed dots) and absence (open dots) of *M. tristis* as a function of plant population size and connectivity. Lines indicate population sizes required for 25%, 50% and 75% presence. (b) Same for *E. tristis*. (c) Effect of plant population size on the proportion of herbivores that is parasitized. (d) Effect of plant population size on the proportion of fruits predated by the herbivore. Lines indicate estimates for three levels of connectivity (distance to nearest population 0.2–2.0 km). (Modified from Elzinga *et al*. 2005, 2007.)

Populations with low levels of genetic variation at both neutral markers and functional genes of the immune system show high incidence of the parasite-induced disease 'feline peritonitis', although causal relationships have yet to be proven. Another way in which inbreeding affects the outcome of species interactions is through effects on the extent of adaptive plasticity. The fresh-water tadpole snail (*Physa acuta*) shows adaptive morphological and behavioural responses in the presence of predatory fish that contribute to predator avoidance. Inbreeding reduces the extent of these responses by half (Auld & Relyea 2010) thereby impeding its induced defense responses. But not only animals experience genetic consequences of fragmentation that impact their interactions with pests and predators. Also in plant populations, low levels of genetic variation and inbreeding (resulting in loss of heterozygosity) can

decrease their resistance to herbivores and pathogens (Spielman *et al.* 2004b). For instance, inbred plants of monkey flower (*Mimulus guttatus*) show increased suceptibility to spittlebugs (*Philaenus spumarius*) (Carr & Eubanks 2002). However, the magnitude and even the direction of the effect of inbreeding on resistance commonly vary among and even within populations. An illustrative example is the study of effects of experimental inbreeding in white campion, *Silene latifolia* (Ouborg *et al.* 2000), using a large number of inbred lines created by brother–sister matings for four generations, resulting in a range of inbreeding levels within each line. Contrary to expectation, experimental inbreeding on average slightly increases resistance of *S. latifolia* to one of its common pathogens, the anther smut fungus *Microbotryum violaceum*. But most strikingly, the effect of inbreeding is inconsistent among

lines, with some showing a strong increase while in others a strong decrease in resistance with inbreeding coefficient is observed. The inbreeding lines of *S. latifolia* also show varying levels of inbreeding depression in traits involved in the attraction of vectors of the disease, that is transmitted by pollinating insects, such as flower size and nectar production. Inbreeding depression in resistance and attraction traits even appear to be uncorrelated (Ouborg & Biere 2003), further hampering predictions of the overall effect of inbreeding on the probability of becoming diseased.

7.4.3   Corollaries and consequences

Habitat fragmentation has ecological consequences (changes in encounter rates among species) and genetic consequences (changes in the outcome of interactions) for species interactions that cannot be viewed in separation. Dynamics of host and pathogen population sizes feed back on the dynamics of frequencies of resistance and avirulence alleles and vice versa. For instance, changes in encounter rates with mutualists or antagonists can induce changes in selection pressures on resistance, avoidance and life-history traits (Hochberg & Moller 2001). Moreover, rapid evolution can take place if species interactions are changed, as in climate change-induced shifts and species invasions (Chapters 20 and 21). For instance, habitat fragmentation can select for traits related to dispersal (Olivieri *et al.* 1995). Likewise, loss of interactions with pollinators may select for traits related to reproductive assurance. These examples make it clear that to be effective, restoration efforts must incorporate considerations of the likely, multiple effects of interventions, manipulations and management on species interactions. This suggests the need to preserve or enhance pollinator interactions, genetic variation for defense-related traits, and minimize risks of connectivity on disease transmission, as many restoration programmes indeed already do.

7.5   FROM CONSERVATION TO RESTORATION: PERSPECTIVES

Conservation science and restoration ecology are complementary disciplines. Restoration may become essential if conservation efforts have failed to preserve local populations. Genetic aspects of restoration are challenging because in the case of both population reinforcement and species reintroductions the question has to be answered: from which external sources will provenances be taken? The knowledge that plant populations are often adapted to local site conditions implies that external seed sources may not match the conditions of the target site (McKay *et al.* 2005). Indeed, research-based 'seed transfer zones' have to be delineated, defined as the geographical regions within which individuals (seeds, seedlings, or adults) of native species can be transferred with no detrimental effects on population mean fitness (Hufford & Mazer 2003). Ecological similarity (matching habitat conditions) between source and introduction site may be at least as important as small geographic distance (Vander Mijnsbrugge *et al.* 2010; Noël *et al.* 2011).

Another important challenge for restoration ecologists is that conservation efforts may no longer be sufficient to ensure that populations can stand impending future unfavourable change due to the rapidly increasing habitat degradation and fragmentation, globalization of pests and diseases and climate change. Indeed, understanding the response of populations and communities to climate change, and their genetic consequences, is one of the most pressing research questions for the near future (Kramer & Havens 2009). As climate change is far beyond the control of organizations in charge of nature management, this is a most challenging argument to move from conservation to restoration, indeed (see also Chapter 21). Seed sourcing for restoration may therefore shift from a purely local provenancing strategy to a strategy based on careful admixture with seeds from more distant sources to maximize evolutionary potential (Broadhurst *et al.* 2008) or even from sources that better match the future local climate predicted by climate models (Crowe & Parker 2008). There is an increasing body of literature about mismatches between interacting populations of different species as a result of changing temperature regimes. For example, reduced spatial variability in plant phenology as a result of experimental and observed warming in the growing season resulted in a decline in the offspring production by female caribou, *Rangifer tarandus*, in Greenland (Post *et al.* 2008). Similarly, Visser *et al.* (2006) show from their analysis of a 20-year data set in a Natural Park in the Netherlands that the synchrony between offspring needs of the insectivorous great tit (*Parus major*), and the caterpillar biomass of this bird's main food species, have been disrupted

during the recent, unusually warm, decades and are not likely to be repaired in the decades to come.

These examples show that the recognition of interactions between populations of species that meet in a community is crucial in any restoration programme. Therefore, we conclude this chapter by referring to 'community genetics', a new field of science focused on the evolutionary genetic processes that occur among interacting populations in biotic communities. Heritable genetic variation within species, especially dominant or **keystone species**, can have effects beyond the population level, a phenomenon referred to as the *extended phenotype effect* (Whitham *et al*. 2003). For example, distinct genotypes of narrowleaf cottonwood (*Populus angustifolia*) support unique arthropod communities that remain consistent over many years. This is an example of so-called *community heritability* (Keith *et al*. 2010). There is increasing evidence that the extended phenotype effect can affect ecosystem processes ranging from nitrogen mineralization and litter decomposition to community structure of the insect species associated with a particular species of plant. For instance, differences in resistance among Pinyon pines to a keystone herbivore have community-level consequences for bird, mammal and rhizosphere microbe communities (Whitham *et al*. 2003). Genotypic diversity in a dominant old-field plant species, late goldenrod (*Solidago altissima*), affects arthropod diversity and community structure as well as net annual primary productivity. The magnitude of this effect can be as large as the effects generally observed for between-species diversity (Crutsinger *et al*. 2006).

One of the consequences of the extended phenotype effect of genes is that we have to reconsider how we should estimate minimum viable population (MVP) size. Whitham *et al*. (2003) defined MVIP as the minimum viable interacting population size, the size of a population needed to maintain genetic diversity at levels required for other interacting species in the community as well. No empirical estimates have been made to date, but clearly these will be larger than MVP. These observations emphasize the cascading effects of the impact of human activities on the evolution of species and communities.

In Chapter 21, the authors address how restoration ecologists and practitioners can apply theories on evolutionary and community dynamics to anticipate and incorporate future – and largely uncertain – environmental changes. In the present chapter, we have explored the foundations of the mechanisms of selection and evolution, knowledge that is indispensable for estimating whether the current *evolutionary potential* of species is a sufficiently sound ecological basis to 'restore to the future'. A bit more than 40 years after the pivotal work of Heslop-Harrison (1964), entitled 'Forty years of genecology', we can now state that the interface between population ecology and populations genetics has come of age.