

# Conservation genetics in a globally changing environment: present problems, paradoxes and future challenges

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**Abstract** Despite recent advances in conservation genetics and related disciplines and the growing impact that conservation genetics is having in conservation biology, our knowledge on several key issues in the field is still insufficient. Here we identify some of these issues together with addressing several paradoxes which have to be solved before conservation genetics can face new challenges that are appearing in the transitory phase from the population genetics into the population genomics era. Most of these issues, paradoxes and challenges, like the central dogma of conservation genetics, the computational, theoretical and laboratory experiment achievements and limitations in the conservation genetics field have been discussed. Further knowledge on the consequences of inbreeding and outbreeding depression in wild populations as well as the capacity of small populations to adapt to local environmental conditions is also urgently needed. The integration of experimental, theoretical and applied conservation genetics will contribute to improve our understanding of methodological and applied aspects of conservation genetics.

**Keywords** Biodiversity · Conservation genetics · Global change · Inbreeding depression · Outbreeding depression · Genetic markers · Genetic structure · Neutral vs selective variation · Adaptive variation

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## Introduction

Why is the interest for conservation genetics growing?

During the last two decades the role of genetics in conservation biology and in ecology in general, has been greatly emphasized (see for reviews: Frankham 1995; Hedrick 2001; Frankham et al. 2002; Frankham 2005). Important contributions to the understanding of the effects of habitat fragmentation and accompanying genetic erosion on extinction risk, the dynamics of adaptation of species to new environmental conditions have been added, forming an entire new scientific discipline: conservation genetics (Frankham et al. 2002; Ouborg et al. 2006). Moreover, while many conservation efforts are directed towards local or regional scales, they might deal with the biotic consequences of global processes, in particular recent climatic changes and their consequences on populations' extinction rate which is now believed to be above background levels (McLaughlin et al. 2002). The major consequences of climate-induced environmental changes for biodiversity at various scales are diverse, often complex and unpredictable and include: distributional range of species, phenology, community structure and species interactions (McCarty 2001; Walther et al. 2002). Even if variation in the environment does not always translate into variation in vital rates like for example growth rate, several studies have shown an interplay between environmental variation and population density in a broad range of species: large terrestrial herbivores (Coulson et al. 2005a, b), terrestrial birds (Saether et al. 2005), crabs and salmon (McCann et al. 2003), marine birds (Barbraud and Weimerskirch 2003) and small mammals (Stenseth et al. 2003). Of a total of 47 invertebrates, 10 mammals, 59 plants, 29 amphibians and reptiles and 388 birds species, ~80% of analysed species showed changes in the biological parameters measured in the manner expected with global warming. Not only increasing temperatures but also prolonged and more frequent extreme events are thought to affect biodiversity at various levels (IPCC; <http://www.ipcc.ch>).

The change of distributional range can produce fragmentations of the populations increasing the effects of random genetic processes which can lead to a reduction of the effective population size ( $N_e$ ), of the genetic variability and of the evolutionary potential (Bijlsma et al. 2000; Hedrick 2000; Spielman et al. 2004a, b). The change of distributional range becomes evident as recent findings suggest global warming to shift the species' spatial distributions on average 6.1 km per decade towards the poles (IPCC). The obvious example of a direct impact of increased average temperature is the summit trap phenomenon; species inhabiting mountain summits are forced to move to higher altitudes when temperatures increase. They have no escape route and may become locally extinct and even if the population does persist, the restriction of the suitable habitat reduces the carrying capacity and consequently the population size. Limited habitat ranges due to increased temperature are furthermore accelerated by human-induced habitat fragmentation, which may reduce the exchange of individuals (and consequently gene flow) between populations.

The change of distributional range can also have some apparently beneficial effects as it can bring previously isolated populations into contact, increasing gene-flow which typically increases the genetic variability of populations but can simultaneously impede their local adaptation (Holt and Gomulkiewicz 1997; Lenormand 2002). In a population, the actual degree of adaptation is the residual effect of the dynamic interaction between the selective pressure acting on the population and gene flow. Hence, high levels of gene flow can reduce or impede the capacity of adaptation to local conditions (Comins 1977; Taylor and Georgiou 1979) or may introduce essential new genes for future adaptation or increase the capacity to adapt (Slatkin 1987; Caprio and Tabashnik 1992; Orrock 2005;

Swindell and Bouzat 2006). Lastly it can also expose the populations to the risk of reduced fitness due to outbreeding depression (Marr et al. 2002; Vergeer et al. 2004; Sagvik et al. 2005).

## State of the art of conservation genetics

### *Genetic variation*

Heritable genetic variation is a prerequisite for evolution. Consequently, one central issue in conservation genetics is the amount of genetic variation present. Populations may only persist if the rate of adaptive evolution at least matches the rate of environmental change (Bürger and Lynch 1995). All the evolutionary response of quantitative traits (traits that are attributable to two or more genes) to selection requires the presence of heritable variation. The phenotypic response to selection is the product of additive genetic variance ( $\sigma_a^2$ ) times the selection differential or standardized intensity of selection coefficient (Lynch and Walsh 1998). The additive genetic variance effect describe the cumulative effect of the individual genes, while the dominance effect which is not heritable is the result of interactions between those genes (Lynch 1996). Generally, small fragmented populations are genetically depauperated (Palo et al. 2004; Kristensen 2005a). This loss of genetic variability has two potential consequences: (a) low genetic variability can be a threat in the long-term for adapting and evolving under changing environmental conditions and in disturbed habitats (Lande and Shannon 1996; Lynch 1996), and (b) small fragmented and isolated populations can suffer from inbreeding, i.e. relatedness between individuals as well as homozygosity, importantly autozygosity, is increased. This poses an immediate threat to such populations (Keller and Waller 2002). Inbreeding depression is expected to be particularly dangerous for species that normally outcross as they could have a genetic load, mostly due to mildly deleterious recessive alleles. The load becomes expressed when the population becomes small, resulting in sometimes severe fitness loss (Bijlsma et al. 1999; Crnokrak and Roff 1999; Hedrick 2000; Keller and Waller 2002; Spielman et al. 2004a), and increased probability of extinction (Bijlsma et al. 2000; Brito and Grelle 2004, 2006; Brito and Da Fonseca 2006). Information about the speed by which populations become inbred is an important prerequisite for the design of conservation strategies as the purging of mildly deleterious alleles only works when inbreeding occurs gradually and over several generations (Byers and Waller 1999; Reed et al. 2003). Hence, if inbreeding is sudden and extreme, drift becomes predominant relative to selection, resulting in more random fixations even for recessive mildly deleterious alleles (Day et al. 2003). The importance of gene flow as a force for the maintenance of genetic diversity and alleviating inbreeding depression is therefore quite evident and it is not surprising that one of the most common rescue-strategies adopted by conservation geneticists includes the increase of gene flow among populations (Gotelli 1991; Guillaume and Perrin 2006). However, as previously mentioned high levels of gene flow can reduce the capacity of populations to stay adapted to local conditions or introduce mal-adapted genes that can reduce viability of the population (outbreeding depression) (Templeton 1991; Andersen et al. 2002, for a review see Edmands 2007).

### *The dogma of conservation genetics*

The “central dogma of conservation genetics” is that genetic variability is beneficial, hence worth to be preserved as a primary concern. Evolutionary biologists and conservation geneticists often assume that increasing genetic variance always enhances the probability

of population survival (Frankham 2005). This perception of the advantages of genetic variation in a population stems from considering short- and long-term adaptability and evolution to a changing environment. An indication of the immediate evolutionary potential of the population, even if it has no necessary relationship to its future value, can be inferred from the estimate of the expected heterozygosity of the population, which is estimated from neutral markers and is considered as a surrogate of the additive genetic variance ( $\sigma_a^2$ ) which can provide an indication of the immediate evolutionary potential of the population (Nunney 1999). There is also a growing attention to the concept of effective population size ( $N_e$ ) which is considered as the most important and critical parameter for the prediction of a population's capacity to survive in a changing environment (Caballero 1994; Nunney 1999). Genetic variation can however be irrelevant when a population faces extinction due to demographic problems. The roles of genetics for extinction has been debated between conservation geneticists and ecologists (Gilpin 1987; Lande 1995; Spielman et al. 2004b). There is also a general consensus that conservation of biodiversity ultimately depends on the conservation of genetic diversity. Conservation genetics seems therefore to play a key role in developing a strategy for short- and long-term preservation of biodiversity. Recent studies and simulations in conservation genetics are beginning to broaden in scope and impact by attempting to correlate genetic, demographic and phenotypic properties of the same populations (Basset et al. 2001; Strand 2002).

#### *Inferring data on genetic structure by means of genetic markers*

Environmental factors and their changes are mirrored in the genetic composition of affected populations. Even small alterations of environmental conditions can affect the genetic composition of populations, both via demographic and selective responses (Schwartz et al. 2007). Understanding the consequences of demographic stochasticity in populations requires detailed knowledge of local fluctuations in population size, extinction probability and colonization potential as well as reproductive success, which can be gained from population dynamics analyses (Hanski and Gilpin 1997; Boyce et al. 2006). DNA analyses are increasingly used to estimate the extent and organization of genetic diversity in populations in order to infer the causes of spatio-temporal dynamics (see Luikart and England 1999; Pearse and Crandall 2004; Schwartz et al. 2007 for an extensive review). Such assessment of neutral genetic variation is informative for inferring both ancient or recent historical dynamics of populations as knowledge of the loss of variability that has actually taken place is often hampered by lack of information on the genetic composition of these populations, prior to the environmental perturbation event (Crandall and Dan Vasco 1999).

A useful tool to detect changes in  $N_e$  and changes in the genetic composition with time are the application of “so-called” ancient DNA techniques which utilize museum samples (Nielsen et al. 1997; Pertoldi et al. 2001, 2005, 2006a; Wisely et al. 2004; Garrigan and Hammer 2006 and for review see Paabo et al. 2004; Chelomina 2006). Several attempts to estimate  $N_e$  have focused on either genotypic information or allelic information. Commonly used methods include gametic disequilibrium, heterozygote excess and the so-called “temporal method” (Turner 2001; Pearse and Crandall 2004 for a review, Williamson-Natesan 2005). Changes in gene flow can be estimated by comparing “historical” estimates based on genetic differentiation ( $F_{ST}$ ), the so-called  $F_{ST}$  based approaches (Courtois et al. 2003) to current estimates based on assignment tests (Pritchard et al. 2000; Manel et al. 2002; Randi and Lucchini 2002). New statistical methods, which seek to identify the number of “populations” in a group of samples and/or assign individuals to population of origin, are also being widely applied (Bass et al. 2004, for a review see Pearse and Crandall 2004).

A further important issue in conservation genetics is the history and the current structure of a population or species, both in a demographic and phylogenetic sense. Also here genetic markers provide invaluable data for devising adequate management measures in conservation biology (Wang 2000; Beaumont and Rannala 2004). Neutral genetic markers are also widely used to assess inbreeding levels, genetic variation, population structure and phylogenetic or conservation units. For practical as well as biological reasons, “populations” are natural units for conservation and management. Therefore, the identification of population boundaries can have far-reaching management implications (Crandall et al. 2000). The identification of evolutionary significant units (ESU) (through the use of “neutral” molecular markers) and the preservation of genetic diversity, which should allow the evolutionary processes of natural selection and adaptation to continue in the future is one of the main goals in conservation genetics. However, the definition of ESU is only based on neutral genetic markers, and a broader definition including non-neutral markers would be more appropriate (Waples 1991; Crandall et al. 2000; Fabiani et al. 2003).

### *Computational, theoretical and laboratory experiment achievements*

Given the fact that most of the traits underlying fitness and adaptation to changing environmental conditions are generally of quantitative nature, a quantitative genetic approach is the most direct avenue towards a better understanding of the adaptive potential of populations and of the consequences of inbreeding and outbreeding depression (Edmands 2007). Quantitative genetic analysis is of paramount importance in the assessment of the extinction risk (Lynch 1996; Reed and Frankham 2001). Laboratory experiments have made an important contribution in dissecting fitness components in various genetic and environmental backgrounds, producing invaluable information on the fate of genetic diversity in small populations, the strength of selection and drift in bottlenecked populations, the importance of environmental stresses in the expression of functional genes, the recovery rates of neutral versus adaptive variability and the effects of inbreeding and outbreeding depression on survival (Andersen et al. 2002; Frankham et al. 2002; Edmands and Timmerman 2003; Gaggiotti 2003; Hoffmann et al. 2003; Edmands 2007).

The development of theoretical models and the use of computer simulations has also significantly contributed to conservation biology through, for example, the integration of genetics into metapopulation frameworks and the development of predictive models which incorporate both environmental and genetic data sets (Bouchy et al. 2005; Nomura 2005). Several stochastic models of ecology and population genetics have been developed (e.g. VORTEX and EASYPOP) (Balloux 1999; Basset et al. 2001). These models include stochastic environmental effects, allowing to make probabilistic predictions that can be quite precise when we consider averages over large scales (Boyce et al. 2006). Furthermore, although not completely solved, recent progress in biostatistics and bioinformatics (e.g. theory of coalescence, Bayesian statistics and algorithms for efficient simulation and sampling of complex processes), have elevated our potential to infer population genetic processes via the development of theoretical models. These models can for example allow the estimation of historical and current genetic  $N_e$ , degree of genetic isolation and rates of gene flow, past population expansion or declines and cryptic bottlenecks (Toro et al. 2002; Beaumont and Rannala 2004). Using a Bayesian approach, the integration of genetic and non-genetic data is also possible in order to go beyond the simple estimation of parameters and test hypotheses about the factors that control population dynamics and colonization processes (Manel et al. 2003).

## Unresolved questions and possible future directions in conservation genetics

### Problems affecting conservation genetics

#### *The lack of sufficient integration of the sub-disciplines of conservation genetics*

Despite the recent advances which are happening in the conservation genetics field, there is still a major problem which seems to lay in the fact that many of its sub-disciplines are quite isolated from each other and many of them have still quite evident limitations. As it often happens in disciplines where the advances have happened too quickly, some shortcomings regarding the robustness of the fundamentals on which this discipline has been built are getting more and more evident. Many of the fundamentals of conservation genetics are more or less postulates, which have rarely been demonstrated empirically and from which several corollaries have followed that also need validation. As a result, many of these sub-disciplines can still substantially benefit from a further development of their theoretical foundations and would vastly improve their effectiveness, should their potentials be combined in order to find solutions for the following problems.

#### *Inferring selection by means of neutral markers*

Neutral genetic markers are not necessarily relevant to understand the dynamics and effects of functional genes subject to selection which can be useful for assessing the potential adaptability of a population to environmental changes. Some controversies are surrounding the causal relationships between molecular genetic variation and phenotype-based measures of success. Part of this disagreement arises from a confusion of the different levels of organization at which genetic variation and phenotypic “success” has been conceptualized. This debate may be partially due to the fact that molecular markers cannot identify the likelihood of loss of genetic variance in traits of ecological significance, as the correlation between molecular diversity (e.g. heterozygosity) and quantitative genetic variation (e.g. heritability) is weak and becomes even weaker in expanding or declining populations (Hedrick 2001; Gilligan et al. 2005). The potential for evolutionary response in quantitative traits is not easily predicted by the use of neutral molecular markers, and a lack of molecular divergence among populations at neutral loci is potentially uninformative, as it cannot exclude local adaptations (Lynch 1996). Therefore, neutral molecular marker loci are not very useful for several purposes as they will provide little insight into adaptive variation, unless a large fraction of these markers are tightly linked to the relevant quantitative-trait loci. Neutral markers may however provide useful information in small populations where most of the fitness variation is neutral as genetic drift is predominant (Lynch 1996).

#### *Inferring population dynamics by means of neutral markers*

One of the main goals of conservation genetics studies is to use current patterns of genetic structure to elucidate underlying population processes, in particular, those dealing with migration dynamics. However, this approach has some serious limitations. Importantly, because many different population processes, such as population bottlenecks or local extinction lead to similar patterns of genetic structure, particular processes are difficult to infer from such patterns. In addition, the population genetic models most commonly applied to these systems are based on equilibrium conditions typically not found in nature, surely not in disturbed ecosystems, hence, influences of current and historical conditions are not easily separated. There is

therefore a need for a deeper understanding about how genetic measures can be used to identify causal processes and there is a need for a deeper knowledge about the genetic signature of a population declining due to habitat change or fragmentation. Also we need to find a common definition for the population concept, which in the literature represents inevitable variations of a common, standard definition, reflecting a fundamental diversity of views of what a population is (Crandall et al. 2000). One additional problem associated with the use of neutral markers lays in the fact that the two most commonly used markers, microsatellites and mitochondrial DNA sequences, are both fast evolving (high mutation rate), which provides high-information content. But at the same time, the high-mutation rate comes at a price called “homoplasy”, which together with other problems like for example the presence of null alleles and not well known mutation patterns, may render the interpretation of the results of the genetic investigations quite difficult (Kimberly et al. 2006).

#### *Lack of ecological relevance of computational and analytical models and laboratory experiments*

The complexity and the problems associated with the use of genetic investigations for conservation purposes may partly explain why several of these investigations have largely been confined to controlled laboratory conditions. There is however a rising discontent with the lack of ecological relevance of many laboratory experiments and an awareness of the fact that extrapolation from laboratory findings to real-world situations is often impractical (Harshman and Hoffmann 2000; Kristensen et al. 2007). Despite of the general understanding of the consequences of inbreeding and outbreeding depression under controlled conditions, evidence on the importance of inbreeding depression under natural conditions is still scarce (Walther et al. 2002). Only few well documented negative associations between inbreeding and fitness have been found in natural animal populations, as for example the study on the Gila topminnow *Poeciliopsis occidentalis* by Quattro and Vrijenhoek (1989) and the study on the white-footed mice *Peromyscus leucopus noveboracensis* (Jimenez et al. 1994; see Edmands 2007, for a review), whereas for plants in predominantly outcrossing species it is well known that inbreeding can cause a severe fitness reduction (Husband and Schemske 1996) Reports on populations which have suffered severe bottlenecks, but nevertheless prosper currently, challenge the assumption that inbreeding depression is a severe threat for the survival of natural populations (Hoelzel 1999). Evidently, this ambiguity could also arise from the difficulties of detecting inbreeding depression effects under natural conditions (Reed et al. 2003), as well as the fact that we are unable to monitor the fate of inbred populations on evolutionary time-scales.

Studies dealing with outbreeding depression in wild populations are even more scarce than those dealing with inbreeding depression. This can be partially due to the rarity of studies that extend beyond the first generation (see Edmands 2007, for a review). Even more challenging is a reliable assessment of the contribution of inbreeding and outbreeding depression to the risk of population extinction. Also the growing concern among conservation biologists that recovery plans for rare species will fail if individual fitness is reduced or local adaptations are lost via outbreeding needs more solid fundament (Templeton 1986; Lacy 1997). However, specific hypotheses for the effects of outbreeding in natural systems have escaped rigorous tests, because of the difficulty associated with the collection of empirical data. This difficulty is even more accentuated in studies dealing with outbreeding as compared to studies dealing with inbreeding, as outbreeding depression is often not expressed before the F2 (Dobzhansky 1970).

The central dogma of conservation genetics has also been recently the target of fierce criticism. The statement that genetic variability is beneficial, hence worth to be preserved



as a primary concern does not seem to be generally true. For example, in a constant environment genetic variance in a quantitative character creates in each generation a segregational load due to stabilizing selection against individuals that deviate from the optimum phenotype (Lande and Shannon 1996). Hence, genetic variability may be either beneficial or detrimental, depending on the pattern of environmental change (Bürger and Lynch 1995; Lande and Shannon 1996). Some studies suggest that only large populations experiencing relatively small environmental changes are likely to be rescued by evolution (Gomulkiewicz and Holt 1995), as in small populations, the selective pressures could be overwhelmed by genetic drift effects, rendering most traits and genes effectively selectively neutral. Then populations become unable to react in an adaptive way to selective pressures, despite the presence of genetic variability.

### *Genetic consequences of increased environmental variability*

The existing analytical models in population genetics do not directly include environmental and demographic stochasticity. This is a serious omission, because stochastic effects can even cause extinction of a population also if its mean intrinsic capacity for increase is positive (May 2001). Climate induced changes can increase the environmental variability ( $\sigma_e^2$ ). Increased  $\sigma_e^2$  corresponds most of the time to a reduction of the minimum population density, as fluctuations of the population density lead to a reduction of the population census size's harmonic mean, which is considered a proxy of  $N_e$  (Caballero 1994). In that way global scale environmental change may affect the local  $N_e$  and  $\sigma_e^2$  and may put its toll on genetic variance by lowering  $N_e$  through the population dynamic response to environmental fluctuations. The most known effect of a reduction of  $N_e$  is the acceleration of the process of loss of genetic variability ( $\sigma_a^2$ ). Increased  $\sigma_e^2$  can also produce a fluctuating selective regime and reduces also the evolutionary response which is directly correlated with its heritability ( $h^2$ ). Hence, both a decrease of  $\sigma_a^2$  and an increase of  $\sigma_e^2$  will decrease  $h^2$ , as  $h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_e^2)$ . Lastly, the stress experienced by a population can also contribute to a reduction of  $h^2$ . A number of investigations have shown that  $\sigma_p^2$  is positively associated with the level of genetic and environmental stresses that individuals experience (Kristensen et al. 2003; Kristensen et al. 2004).

The relationship between the  $\sigma_a^2$  of a trait and its  $h^2$  is not linear since increasing  $\sigma_a^2$  (numerator of the  $h^2$  equation) also implies a reduced  $\sigma_p^2$  (denominator) (Pertoldi et al. 2006b). Consequently, the concomitant increase of  $\sigma_a^2$  and the reduced  $\sigma_p^2$  are both contributing to an increased  $h^2$ . We should therefore also consider this additional premium due to a negative association between  $\sigma_a^2$  and  $\sigma_p^2$  that should be taken into account when making a cost benefit analysis of  $\sigma_a^2$  in changing environments. The scenario will become even more complicated if we consider that traits with different degrees of dominance and epistatic interactions have different degrees of susceptibility to the environment (Keller and Waller 2002; Marr et al. 2002). Long-term responses to selection in a finite population are also influenced by factors like gametic phase disequilibrium and mutational variance, which are dependent on the population structure and  $N_e$  (De Souza et al. 2000).

## **Challenges and paradoxes in conservation genetics**

### Integration of demographic and genetic data

An important challenge for conservation genetics is to introduce demographic considerations into studies of metapopulation genetics, rather than trying only to infer demographic



data from genetic data. Considerable progress has been achieved in incorporating age- or stage-structure into population genetic models, mostly in the context of life history evolution and estimation of  $N_e$  of large and stable populations (Basset et al. 2001). However, knowledge on the interaction between age- or stage-structure and other factors, such as variance in reproductive success, overexploitation, temporal fluctuations in population size, is still limited. This holds true even for the easy case of single panmictic populations. Future studies should take into account that moderate differences in life history between ecologically similar species can lead to substantial differences in  $N_e$ , and the effect of fluctuations in vital rate parameters induced by environmental change is dependent on the specific life history of each species.

In most studies, low genetic variability and low  $N_e$  are explained by population bottlenecks, founder effects or fluctuations in population sizes as the main determinants (Caballero 1994; Whitlock and Barton 1997), however, another important factor which should be more frequently considered is the variance in reproductive success (Nunney 1999). Very few studies consider the effect of life history (Gaggiotti and Vetter 1999; Gaggiotti 2003). Additional attention should also be paid on the ratio of  $N_e$  relative to census size ( $N$ ). There have been several recent studies showing very low  $N_e/N$  ratios of around 0.001 (Hauser et al. 2002; Turner et al. 2002; Waples 2002; Hedrick 2005). Species with large  $N_e/N$  ratios might be more strongly affected by environmental change than species with lower ratios (Hedrick 2005), even if demographic parameters as for example generation overlap seem to reduce such sensitivity (Frankham et al. 2002).

#### Effects of biodiversity on population stability

A long-standing debate in ecology has been the effect of biodiversity on the temporal stability of biological systems (Tilman 1996). The ecological consequences of biodiversity loss due to climatic changes and/or to human induced fragmentation, have gained increasing attention over the past decade (Bangert et al. 2005; Reusch et al. 2005). Current theory suggests that diversity has contrasting effects on the temporal stability of populations and communities (Tilman 1996). Theoretical work suggests a paradoxical effect of diversity on the temporal stability of ecological systems: increasing diversity should result in decreased stability of populations, while community stability is enhanced (Tilman 1996). While empirical work corroborates that community stability tends to increase with diversity, investigations of the effect of diversity on populations have not revealed clear patterns (Tilman 1996). Given that demographic instability in a population is translated into fluctuations of  $N$  and a reduced  $N_e$ , a management strategy with the goal of preserving biodiversity on the community level could theoretically lead to a reduction of  $N_e$  in single populations.

Changes in vital rates (i.e. age- or stage-specific fecundities and survivals) may sometimes have opposing effects on the growth rate and  $N_e$  (Gaggiotti 2003). Thus, changes in vital rates induced by environmental changes may for example facilitate range expansion in the short term by increasing population growth rate, but they may hamper expansion in the long term, if they lead to a decrease in  $N_e$ . All these considerations are of crucial importance, as they can produce disagreement about the optimal management strategies. Pertoldi et al. (2007a) showed that there is no unambiguous relationship between the arithmetic mean of  $N$  and the harmonic mean for populations fluctuating in size. As long as the variance of population size increases moderately with increasing arithmetic mean population size, the harmonic mean also increases, but if the variance of population size increases more rapidly, which existing data often suggest (Taylor 1961), then the harmonic mean may actually decrease with increasing arithmetic mean. Thus maximizing  $N$  may not

maximize  $N_e$ , but could instead lower the adaptive potential and hence limit the evolutionary response to environmental change. Large and relatively stable census size has the clear advantage of lowering demographic stochasticity, and hence extinction risk and under certain conditions large census size also minimizes the loss of genetic variation (Frankham 2005). Consequently, maximising census size of the species which are the target of conservation efforts has served as a useful dogma in ecology, genetics and conservation. Nonetheless, due to the intricate relationships among  $N_e$ , population viability and the properties of population fluctuations, we suggest that this dogma should be taken only as a rule of thumb as it could add an additional paradox in the conservation genetics field.

#### The use of non-neutral markers and microarray techniques in conservation genetics

Integrative studies which correlate the genetic variability using neutral molecular markers (e.g. microsatellites) and the genetic variability detected in quantitative and fitness-related traits could become quite useful for conservation geneticists but such correlations are difficult to study, especially in natural populations (Gilligan et al. 2005). However, the attempt to correlate neutral and non-neutral variability can be made by using a new and very promising tool in conservation genetics, the single nucleotide polymorphisms (SNPs), which are the most abundant polymorphic genetic marker in most genomes (Morin et al. 2004). SNPs hold the potential to significantly expand our ability to survey both neutral (non-coding region) variation as well as genes under selection (coding region) in natural populations, providing also broader genome coverage as compared to mitochondrial DNA or microsatellites (Vignal et al. 2002; Morin et al. 2004). An additional advantage of SNPs compared to microsatellites lays in the fact that the target DNA sequence in SNP-based genotyping is appreciably shorter (e.g. 50–70 bp) than that in microsatellite-based genotyping (80–300 bp), making also the investigations dealing with degraded DNA (scatology or ancient DNA) easier (Morin et al. 2004).

Conservation geneticists have generally focused on changes in amino acid sequences that alter the kinetic function of proteins, without considering other possible alterations of the DNA structure which can have evolutionary consequences (Stern 2000). The debate over the importance of structural genetic variation versus regulatory genetic variation is still open (Wang et al. 1996). The cDNA microarray technology has emerged as a powerful tool to monitor gene expression of thousands of genes simultaneously (Douglas 2006). Recent identification of functional genes and genes linked to quantitative traits are opening the way to the analysis of functional genes and components of genetic control on physiological processes. The technology has however been developed as a search tool for candidate genes (Townsend et al. 2003) rather than to investigate the evolutionary significance of gene expression diversity itself. The individual gene expression diversity has been so far considered as a nuisance parameter. However, any selection process acting on levels of gene expression is thus detectable by inter-individual differences in expression profiles, which are therefore a promising tool for studying local adaptation (Sørensen et al. 2007). Population genomics will very soon add important contributions to these issues, delivering large amounts of data on regulatory polymorphisms on a genomic scale, allowing to find answers to some crucial unanswered questions, like if the regulatory variation has a heritability and can alter life-time reproductive success (which both are necessary conditions for being evolutionary relevant). Also the impact on inbreeding and inbreeding by environment interactions on gene expression patterns have revealed insight into the genes whose regulation is affected by inbreeding (Kristensen et al. 2005b; 2006).

## Phenotypic plasticity

If populations encounter perturbations in their environment, they are left with few options. One strategy is to migrate, but if the landscape is fragmented, migration may not be possible. Two ways of adapting to environmental changes are therefore by evolutionary and/or by plastic responses, including maternal transmission. But, given the fact that many populations of conservation concern are too small to harbour enough genetic variability for an evolutionary responses their survival must rely on the capacity to react to environmental changes in a plastic way (Merila 1997; Pigliucci 2005). These plastic responses include changes in behaviour, physiology, morphology, growth, life history and demography, and can be expressed either within the lifespan of an individual or across generations (Merila 1997; Sheldon and West 2004; O'Regan and Kitchener 2005; Røgilds et al. 2005; Valladares et al. 2006). Phenotypic plasticity and maternal effect have the capacity to mask genetic differences among individuals, protecting the populations against fast potential changes of genetic structure under environmental changes (Ernande and Dieckmann 2004). At the same time, when the magnitude of genetic variation is insufficient to create a diversity of phenotypes that can be exposed to selection, phenotypic plasticity will enrich the evolutionary potential of a population. Phenotypic plasticity can also be considered adaptive if it allows a population to maintain a constant fitness despite environmental changes (Schlichting and Pigliucci 1998). When a species' range covers a heterogeneous environment, a single phenotype is unlikely to be associated with high fitness throughout the range (Ernande and Dieckmann 2004; Pertoldi et al. 2005). Phenotypic plasticity seems also to be influenced by climate induced changes as the regime of alternating selective pressures has been thought to select genes for plasticity in large populations (Schlichting and Pigliucci 1998). Niehaus et al. (2006) and references therein provided empirical evidence for increased phenotypic plasticity in populations living in fluctuating environments as compared to populations living in a stable environment. The importance of phenotypic plasticity and maternal effects are therefore quite obvious, especially in small populations (Pakkasmaa et al. 2003; Røgilds et al. 2005), and an urgent need for more detailed studies of phenotypic plasticity and genotype  $\times$  environment ( $G \times E$ ) interactions for specific traits and environmental gradients (e.g. life time reproductive effort in relation to human induced stress) is becoming evident. In particular, studies that quantify the extent of phenotypic plasticity and maternal effects for different phenotypic and life-history traits and the impact of environmental and genetic stressors (inbreeding and outbreeding) upon this are scarce (Pertoldi et al. 2007b).

## Stochastic models

Stochastic models are limited when considering specific predictions about particular systems. It would therefore be an advantage to have genetic models that integrate both spatial variability (e.g. heterogeneous landscapes) and temporal variability (e.g. metapopulation dynamics), to examine how these variations influence the genetic structure of populations and thereby our interpretations of genetic structure. Individual-based models would be quite useful for these purposes. The combination of individual-based models and genetics is just emerging, but it will soon be feasible to evaluate the impact of environmental changes on genetic composition of populations (Higgins and Lynch 2001; Strand 2002). Models should be developed to address several of the unresolved questions in conservation genetics. Assuming such models can be validated with respect to their predictive reliability, the future promise of the development of these theoretical models and the use of computer

simulations will support conservation genetics investigations through: (a) modelling alternative scenarios for the dynamics of genetic diversity within and among populations exposed to different environmental regimes and evaluation of short and long-term risks; (b) linking the genotype with phenotype, for example, modelling how a given trait (life-history or morphological trait) would develop in a given scenario. If the information obtained can be combined with empirical and molecular data, the model will be a powerful tool for understanding real-world dynamics. Once appropriate validation of both genetic and ecological components is carried out, genetic individual-based models ought to be an appropriate tool to simulate genetic and environmental interactions (e.g. in a climate change scenario), which cannot be predicted by analytical models.

#### Evolutionary significance of gene-flow

Gene flow among populations can be studied using an evolutionary time frame or as current gene flow. Evolutionary questions concerning the role of gene flow for genetic diversity, population differentiation, species identity and speciation, emphasize the evolutionary time scale. However, in conservation genetics, questions concerning the role of gene flow for future patterns must rely on estimates of current gene flow under current landscape conditions. Contemporary gene flow cannot be reliably estimated by conventional methods based on genetic structure especially in non-equilibrium situations due to population substructuring and/or to demographic fluctuations (Schwartz et al. 2007 and references therein). Evaluating the nature and magnitude of potential biases, has also several implications for the operational definition of a population. If the combination of spatially explicit genetic data and environmental data are available for the same landscape, we would be able to test hypotheses on the impact of “ecological distances” on gene flow (Manel et al. 2003). These are obvious opportunities for collaboration between geneticists measuring genetic parameters in the field and landscape ecologists, with the use of spatial dynamic models.

#### Possible benefits of a merging of different disciplines

Conservation genetics gives the impression to be at present an eclectic assemblage of several achievements in different fields. As a consequence, many of the works in conservation genetics trying to embrace several sub-disciplines simultaneously appear quite heterogeneous. Such heterogeneity of viewpoints when approaching a conservation-related problem can create severe difficulties in the interpretation of results. Therefore, there is need to increase the range of overlap among the different areas of the multidisciplinary field of conservation genetics.

To sum-up, further scientific progress will be achieved by merging and complementing current efforts in conservation genetics by: (a) collecting informative genetic and environmental data sets in natural populations and from preserved specimens, (b) merging taxonomic, ecological and genetic databases for the monitoring of natural populations for conservation, (c) using molecular data in synergy with quantitative traits and environmental data, (d) defining strategies to identify relevant functional genes in natural populations by assessing, e.g. the geographic distribution of genetic variability, (e) unravelling the distribution of variation at functional versus non-coding sequences in natural populations and (f) estimating fitness in changing environments. The main priority of conservation genetics should be the integration of several sub-disciplines with a first attempt that consists in answering and resolving some of the unanswered questions and problems accumulated

since the birth of the conservation genetics field. This goal can be achieved by multidisciplinary approaches and the integration of experimental, theoretical and applied conservation genetics will certainly have synergistic effects and contribute to improve our understanding of methodological and applied aspects of conservation genetics. The synergy resulting from such an integration of scientific knowledge, methodological toolboxes and data will not only lead to better insights into conservation genetic issues, but will also allow important steps towards the use of genetics in restoration projects, the restoration of connectivity between fragmented populations and—most importantly—will allow us to understand how and when a genetic rescue strategy is needed.

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