Meeting report

Integrating population genetics and conservation biology in the era of genomics

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As one of the final activities of the ESF-CONGEN Networking programme, a conference entitled 'Integrating Population Genetics and Conservation Biology' was held at Trondheim, Norway, from 23 to 26 May 2009. Conference speakers and poster presenters gave a display of the state-of-the-art developments in the field of conservation genetics. Over the five-year running period of the successful ESF-CONGEN Networking programme, much progress has been made in theoretical approaches, basic research on inbreeding depression and other genetic processes associated with habitat fragmentation and conservation issues, and with applying principles of conservation genetics in the conservation of many species. Future perspectives were also discussed in the conference, and it was concluded that conservation genetics is evolving into conservation genomics, while at the same time basic and applied research on threatened species and populations from a population genetic point of view continues to be emphasized.

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1. INTRODUCTION

> The one process now going on that will take millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly our descendants are least likely to forgive us.

This quote from Wilson (1984), in the preface of a recent textbook on conservation genetics (Allendorf & Luikart 2007), set the scene for the recent conference on conservation genetics, from 23 to 26 May 2009, in Trondheim, Norway, organized by the Norwegian Institute for Nature Research and Norwegian University of Science and Technology (NTNU), in cooperation with the ESF-CONGEN networking programme. The theme of the meeting: '*Integrating population genetics and conservation biology*', which is also the theme of the ESF-CONGEN networking programme, which has been running for almost five years, brought together around 150 researchers from all over Europe (with participants

from outside Europe). They gathered for three days to present an overview of the current developments in the field of conservation genetics and to discuss future directions.

In his starting lecture, giving an historic overview, John Avise (University of California Irvine) defined conservation genetics as an applied discipline that merges knowledge and approaches from population and molecular genetics with ecology and biodiversity sciences to create a foundation for the genetic conservation of populations and species. The birth of conservation genetics is generally attributed to the publication of books by Frankel & Soulé (1981) and Schonewald-Cox *et al.* (1983). These authors, for the first time, worked out in detail that the conservation of populations and species has clearly identifiable evolutionary and genetic components. However, the current popularity of conservation genetics is relatively recent and can perhaps be best marked by the publication of the first textbook on conservation genetics in 2002 (Frankham *et al.* 2002).

The ESF-CONGEN programme was intended to support the further development of conservation genetics, by bringing together conservation biology and population genetics. Now, as the end of this programme approaches, the Trondheim conference was the logical time to present and evaluate recent developments in the field of conservation genetics and to discuss its future direction.

2. CONSERVATION GENETIC THEORY

Conservation genetics has always been based upon—and stimulated by—predictions of population genetic models. The basic premise of conservation genetics—that small populations may be genetically threatened—is based on the population genetic prediction that random genetic drift and inbreeding will affect allelic and genotypic variation within populations as a function of the effective size of these populations.

In recent years two important developments have dominated conservation genetic theory. First, an increasing number of models have been developed, incorporating an increasing amount of life-history and landscape complexity, aiming to make more accurate predictions of the dynamics of genetic variation in time and space. The success of this development was illustrated by Armando Caballero (Universidad de Vigo, Spain) who incorporated the complexity of subdivided populations into his METAPOP model, and could show that this led to more accurate predictions of the effect of various migration scenarios on the distribution of genetic variation through space. Steinar Engen (NTNU, Norway) incorporated age structure and fluctuating environments into stochastic population growth models and estimates of effective population size, and demonstrated that this increased the accuracy of the predictions. These developments show two things: (i) it is clear that we can improve our understanding and prediction of the fate of populations and species by incorporating biological realism, and (ii) it also shows that we are increasingly in need of empirical data, necessary to include biologically realistic details.

A second important theoretical development in conservation genetics is the ongoing development of more

sophisticated methods for analysing genetic data. This development is strongly stimulated by new, higher resolution markers, each with their own genetic properties, becoming available, including the already routinely used microsatellite and amplified fragment length polymorphism markers, genome-wide single nucleotide polymorphism (SNP)-markers and increasingly expressed sequence tag (EST) based markers and genomic sequences of genes. The first step, applying these markers in empirical studies of threatened populations, is easy to make, but it is much harder to carry out the second step of extracting all information on past demography and population genetic processes that the observed marker patterns contain. Increasingly, Bayesian statistics, coalescence theory, maximum likelihood approaches and Markov Chain Monte Carlo techniques are being used. Joao Lopes (University of Reading, UK) demonstrated the superiority of the recently developed approximate Bayesian computation technique (Foll *et al.* 2008) for inferring the history of populations from marker data. Juan Robledo-Arnuncio (Departemento de Sistemas y Recursos Forestales, Spain) presented a maximum likelihood method for estimating real-time gametic immigration rates into a population from several source populations. Bayesian clustering techniques such as Structure (Pritchard *et al.* 2000) and BAPS (Corander 2003) have become a routine part of the analysis of empirical marker data, as was shown in many of the posters that were presented. Because of the complexity and quantity of data from the new genomic screening techniques, development of new techniques for analysing data is one of the more prominent achievements in the field of conservation genetics. Hence, further developments are to be expected in the near future, when other types of markers, associated with functional genes, will become available for routine use in population studies.

3. INBREEDING DEPRESSION

From the very beginning, inbreeding depression—the reduced fitness of inbred individuals—has been a central phenomenon in most conservation genetic studies. Over time, the conservation genetic image of inbreeding depression has developed into a dynamic concept, in which inbreeding depression may be enhanced by the random genetic processes that are associated with small population size, but may be reduced by selection, a process known as purging. Lukas Keller (University of Zurich, Switzerland) and Jane Reid (University of Aberdeen, UK) presented an overview of this development, illustrated by an analysis of the extensive pedigree data of the song sparrow *Melospiza melodia*. They demonstrated that purging is rarely efficient enough to remove inbreeding depression from a population, and argued that what we really need to know is under which conditions inbreeding depression will affect the population dynamics and under which conditions purging may be most effective. Therefore, while inbreeding depression is one of the best investigated conservation genetic phenomena, clear gaps in our knowledge still exist.

This was further emphasized by Isabelle Olivieri (Université Montpellier II, France), who presented the results of long-term studies of populations of threatened plant species in Southern France. She argued that it is not enough to detect individual inbreeding depression in nature, but that this has to be translated into its effects on population growth. This can be done by incorporating stage-specific inbreeding depression values in the population projection matrix models that are often used for demographic analysis. As some life stages contribute more to population growth than others, depending on the demographic structure of each particular population and species, inbreeding depression in these highly contributing stages is expected to have more impact on viability than inbreeding in other stages. Olivieri demonstrated that hardly any data exist that precisely do this, and thereby identified yet another gap in our knowledge.

The need to use stage- (in plants) or age- (in animals) specific inbreeding depression values was clearly demonstrated by Juan Bouzat (Bowling Green State University, USA), who deliberately inbred populations of *Drosophila melanogaster* to study the dynamics of inbreeding depression over time. Based on a series of experiments he concluded, in line with results presented by several others, that inbreeding depression is variable between populations, between genotypes and between life-history traits. Therefore, the impact of inbreeding depression on population growth and viability cannot be assessed based on a single inbreeding depression value per population.

4. OTHER CONSERVATION GENETIC PROCESSES

Although inbreeding depression does play an important role, the viability or genetic integrity of populations may be affected by other processes that are not related to inbreeding.

Xavier Vekemans (University of Lille, France) provided clear and convincing evidence that so-called Allee-effects, the problems of finding a suitable mate in a small population, affected reproductive output in populations of the self-incompatible plant species *Biscutella neustriaca*. Owing to loss of genetic variation, S-alleles at the incompatibility locus were lost, suitable mates were lacking and seed production dropped dramatically.

Increased isolation between populations owing to habitat fragmentation was identified as a genetic threat to the survival of populations in many presentations. Translocation of individuals, known as the genetic rescue strategy, has frequently been suggested as a solution. However, the genetic rescuer strategy is not undisputed, as this often involves the immigration of non-adapted individuals, which may cause outbreeding depression in offspring when immigrants mate with native individuals. During the conference the dispute continued and was not completely resolved. Richard Frankham (Macquarie University, Australia), based on long-term experimental work on *Drosophila*, argued that the risks of outbreeding depression, associated with genetic rescue, are

generally low. Indeed, monitoring of actual genetic rescue programmes in the Florida panther and the Mexican wolf provided no evidence of negative effects of genetic rescue, as was shown by Phil Hedrick (Arizona State University, USA). Nevertheless, Hedrick warned that a set of strict requirements are needed for making the decision to carry out individual translocations in order to minimize the risks of negative effects. The necessity of these requirements was demonstrated by the experiments of Kuke Bijlsma (University of Groningen, The Netherlands), who demonstrated the negative effects of genetic rescue when translocated *Drosophila* individuals carried 'hidden' recessive deleterious alleles. These negative effects became especially evident under changing and deteriorating environmental conditions.

5. APPLIED CONSERVATION GENETICS

The principles of conservation genetics play an important role in the conservation of many species. However, judging from the programme of the conference, the field seems to be dominated by mammalian and bird species. For instance, of the 41 oral presentations, only four dealt specifically with plants, and only 10 out of 64 poster presentations had plants as their object of study. Nevertheless, some of the better examples of genetic erosion have been found in plant studies. The overemphasis on big mammals and birds may reflect the societal demands to conservation genetics, rather than being a sign of these species groups being more threatened or better suited for conservation genetic research.

In animals, the principles of conservation genetics are applied to the management of wild populations, zoo populations, livestock breeds (Jack Windig; Animal Breeding and Genomic Centre Wageningen, The Netherlands), and salmon and trout hatcheries (Michael Hansen; Technical University of Denmark). Fred Allendorf (University of Montana, USA) emphasized that the principles of conservation genetics need to be applied to monitor the (genetic) effects of hunting and harvesting of animals. Besides illustrating the more obvious effects, in the form of selection against certain phenotypes, Allendorf also showed that many effects might be much more subtle. For instance, age and size at maturity, secondary sexual traits, and timing of reproduction are all traits under the influence of both sexual selection, hunting and harvesting. Hunting and harvesting may in turn disrupt sexual selective processes and might, therefore, have more long-term effects than is generally assumed.

Despite the many areas of potential application, conservation genetic arguments are still not used in all areas where they should be. Linda Laikre (Stockholm University, Sweden) pointed out that international biodiversity treaties still largely ignore genetics, and urged scientists to step up and ask for implementation of conservation genetic guidelines in international politics. Ingerid Hagen (Flinders University, Australia) warned that conservation genetics may become characterized as a purely academic exercise. In many Third World countries, often hotspots of biodiversity, management advice based on conservation genetic principles (and any other principle) is often not implemented for socio-economic reasons.

6. FUTURE DIRECTIONS

At the end of the conference John Avise, Phil Hedrick and Richard Frankham presented their views on which direction conservation genetics will or should take in the future. They agreed that, in the very near future, conservation genetics will evolve into conservation genomics. There are at least three reasons for this expectation. The first, very practical reason, is that technical developments in the field of genomics are progressing rapidly, so genomic resources, such as thousands of SNPs and EST-based microarrays, will soon become available—or in some cases are already available—for non-model species. Second, at several moments throughout the conference, the need was expressed to obtain more insight into the balance between genetic drift and selection, when affecting genetic variation and (lack of) adaptation. By using genomic techniques, markers will become available that are linked to functional, selectively important parts of the genome. The patterns observed in these markers can be compared to patterns in the supposedly neutral markers, which are now routinely used in conservation genetics, to obtain insight into the contribution of selection. Third, by adopting a functional genomics approach, for instance, by coupling the change in expression of genes or gene-pathways in response to inbreeding, detailed insight can be obtained into the mechanisms that lead to lower fitness in small, fragmented populations.

During the conference, the signs of this evolution towards conservation genomics appeared several times. Chris Wheat (Max Planck Institute for Chemical Ecology, Germany) and Joop Ouborg (Radboud University Nijmegen, The Netherlands) both demonstrated that for non-model species (the butterfly *Melitea cinxia* and the plant species *Scabiosa columbaria*) with high-throughput 454-pyrosequencing of mRNA-pools, tens of thousands of ESTs can be obtained within a relatively short time span and can be exploited in gene expression studies. Torsten Kristensen and Kamilla Pedersen (Aarhus University, Denmark) used microarray and proteomic techniques in a transcriptomic study of *Drosophila* inbred lines to identify genes that are over- or under-expressed in relation to inbreeding depression. Their results show that inbreeding, among other things, leads to upregulation of general stress genes, indicating that inbreeding and environmental stress have synergistic effects.

Although conservation genomics thus shows great promise, there were also cautionary words from Avise, Hedrick and Frankham. Conservation genomics will not solve all of conservation genetics' problems, nor will its application be as evident and easy as we perhaps hope it will be. Although genomic techniques are of invaluable help and genomic approaches are a very important addition to conservation genomics, it should add to, rather than replace, the current diversity of topics and approaches that were so well presented at this conference.

Allendorf, F. W. & Luikart, G. 2007 *Conservation and the genetics of populations*. London, UK: Blackwell.

Corander, J. 2003 Bayesian analysis of genetic differentiation between populations. *Genetics* **163**, 367–374.

Foll, M., Beaumont, M. A. & Gaggiotti, O. 2008 An approximate Bayesian computation approach to overcome biases when using amplified fragment length polymorphism markers to study population structure. *Genetics* **179**, 927–939. (doi:10.1534/genetics.107.084541)

Frankel, O. H. & Soulé, M. E. 1981 *Conservation and evolution*. Cambridge, UK: Cambridge University Press.

Frankham, R., Ballou, J. D. & Briscoe, D. A. 2002 *Introduction to conservation genetics*. Cambridge, UK: Cambridge University Press.

Pritchard, J. K., Stephens, M. & Donnelly, P. 2000 Inference of population structure using multilocus genotype data. *Genetics* **155**, 945–959.

Schonewald-Cox, C. S., Chambers, S. M., MacBryde, B. & Thomas, L. 1983 *Genetics and conservation: a reference for managing wild animal and plant populations*. London, UK: Benjamin-Cummings.

Wilson, E. O. 1984 *The Biophilia hypothesis*. New York, NY: Island Press.