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The conservation of genetic diversity: Science and policy needs in a changing world

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Executive Summary

A UKPopNet workshop on *The conservation of genetic diversity: science and policy needs in a changing world* was held at Losehill Hall from 19–21 October 2005. The workshop brought together researchers, policymakers and conservation practitioners to promote discussion on the future scientific, policy and practical needs for the conservation of genetic diversity in the UK.

Representatives of each of the stakeholder groups shared their views of the current situation in the UK, and more detailed presentations helped to inform the breakout group discussions that formed the main focus of the workshop. The breakout groups addressed the following questions:

- What is conservation seeking to achieve from a genetic standpoint?
- Can molecular markers be used to determine which of a species' populations are conservation priorities?
- Do we really need to know about genetic variation?
- What strategies do we need to adopt to conserve the processes that sustain diversity?
- How should we strike a balance between conserving local adaptation, avoiding inbreeding depression and promoting future adaptability?
- Protected areas or landscapes: a simple choice?
- Where are the key gaps in our knowledge, and what action or research is needed to address these?

Principles of genetic conservation

There was a broad consensus on some of the principles of genetic conservation that can be communicated to policy-makers and practitioners with a high degree of confidence. These include the following generalisations:

- high levels of genetic diversity within populations are almost always desirable to ensure that they are genetically sustainable;
- adaptability is correlated with diversity and should be an important driver for conservation in response to environmental change;
- genetic diversity is broadly correlated with population size, hence conservation should seek to maintain or create large populations;
- low levels of genetic diversity are detrimental to populations when they lead to inbreeding depression but can be of special scientific interest and may indicate ongoing evolution and speciation;
- gene flow between populations is desirable but care may be required where small populations have been isolated for a long period and local adaptation may be swamped;
- action to increase landscape permeability for one species may be bad for another but what is good for most species should take precedence.

Synthesis

Section 9.0 summarises the key knowledge gaps research questions and recommendations from each of the breakout groups. These lists have not been prioritised, as this was not within the scope of the workshop. Recommendations are:

General conclusions and knowledge gaps

Defining populations

- apply genetic approaches that define populations or identify migrant individuals, e.g. assignment tests or measurements of contemporary gene flow based on genetic markers;
- improve our understanding of the scale of populations, to determine at what scale species should be managed;
- synthesise existing evidence on what constitutes an 'effective population size' and its relevance to conservation, and initiate further research to support the development of new recommendations.

Defining units of conservation

- undertake comparative studies of the genetic composition of populations in protected areas versus the wider landscape;
- investigate the potential application of selectivity measures and conservation of management units;
- undertake the meta-analysis of existing research to establish relationships between life history/demographic information and genetic diversity;
- develop and test models based on life history/demographic information to assess genetic risks and, in partnership with practitioners and policymakers, apply this knowledge to issues of practical conservation.

Conserving evolutionary processes that generate and sustain genetic and taxonomic diversity

- conservation actions should take into account the evolutionary processes generating and sustaining diversity as well as named taxa and units of biodiversity themselves;
- research projects should aim to analyse evolutionary processes as well as simply describing the extent and distribution of neutral genetic diversity.

Hybridisation

- undertake a meta-analysis of existing data to establish past hybridisation rates;
- assess the frequencies of negative outcomes of hybridisation, including laboratory and field based approaches;
- undertake cost-benefit analysis of the possible outcomes of hybridisation and their value to biodiversity and conservation.

Understanding and managing gene flow in the context of adaptation and species' adaptability

- the effects of different levels of gene flow should be investigated in species with a range of effective population sizes and varying longevity and with different dispersal rates/mechanisms;
- undertake a review of existing landscape metrics to assess reliability and any possible need for new measures;
- undertake studies of dispersal in key taxa in a range of landscape types;
- synthesise existing research on species dispersal and colonisation abilities and the relative permeability of different habitats;
- undertake a meta-analysis of historical data to gain an understanding of any relationship between historical events and genetic composition of current populations;
- Study inbreeding and outbreeding in a range of taxa and populations, including those undergoing environmental fluctuation and/or change;

• initiate comparative studies on invasive species to establish whether genetic factors play a role in their invasiveness.

Understanding adaptation

- review existing data to establish current knowledge and, where necessary, initiate research to assess local adaptation in terms of community interactions;
- compare habitat type and distance in driving the differentiation of ecotypes;
- investigate the use of reciprocal transplant experiments to identify adaptive diversity;
- undertake further studies on quantitative traits and local adaptation in wild populations, and compare results with those from common garden and reciprocal transplant experiments;
- undertake studies on quantitative traits and adaptation in small populations;
- review existing research on the extent and distribution of adaptive diversity and initiate further studies for key taxa;
- study inbreeding and outbreeding in a range of taxa and populations and examine how they affect genetic composition and fitness of populations;
- review existing research on how populations with different levels of neutral and adaptive genetic diversity respond to change, and initiate studies of populations subject to environmental fluctuations and/or change;
- review existing research on the relative contribution of phenotypic plasticity and microevolution on adaptation to changing environments and, if necessary, instigate new research on whether plasticity itself evolves with changing environments.

Management of species, populations, habitats and landscapes

Conservation of species and populations

- undertake a review and meta-analysis of methods (including cost-benefit analysis) of setting conservation priorities across species with different breeding systems and population characteristics, by relating to genetic data;
- undertake studies to document genetic diversity in invertebrates, including key functional or indicator groups;
- construct and pilot a conservation management decision tool to facilitate the use of genetic information on a species-specific basis;
- synthesise and disseminate costs and benefits of the existing molecular marker systems;
- review existing research on the significance of genetic diversity for community species diversity and ecosystem function, and facilitate closer working between these research communities.

Conservation of habitats and landscapes

- undertake a review of the existing landscape matrix to assess permeability and the possible need for new agri-environment measures;
- assess the impacts of fragmentation on different scales;
- initiate landscape-scale field studies in near-natural systems and compare genetic impacts across a range of taxa;
- compare genetic parameters in UK and other populations and review the existing DNA literature on the genetic distinctiveness of UK populations;
- the use of selectivity measures and management units should be considered when conserving genetic diversity and evolutionary processes in the wider landscape;
- review existing research and promote discussion between policymakers and practitioners on the management of the landscape between and within protected areas to encourage gene flow;

• studies on the dynamics of gene flow between protected and unprotected areas are needed, as well as a better understanding of the process of colonisation.

Policy limitations and responses

- given the current state of our knowledge regarding the role of genetic diversity in biodiversity, conservation policies need to be set within a longer timescale than at present;
- a flexible interpretation of the precautionary principle is needed, in which adaptability is accepted as an important conservation objective;
- the precautionary principle may be too conservative, and actually be detrimental to the long-term sustainability of declining populations that have experienced some genetic depletion;
- there is a need to develop strategies that permit adaptation to environmental change.

Knowledge transfer activities

A list of collective actions was drawn up to indicate the steps which need to be taken to improve communications and the effectiveness of knowledge transfer between stakeholder groups:

- a UK conservation genetics forum needs to be established, to steer research, target funding, improve science communication, and aid research implementation;
- a conservation genetics handbook is required for conservation practitioners, to define important concepts and support informed communication with researchers;
- support needs to be provided to review management plans from a genetic perspective and to encourage consultation between practitioners and researchers.

More detail is provided in Section 9.3 Follow-up.

To maximise take-up of the research actions proposed in this report, it is important that readers:

- use this report to inform thinking in their own organisations, identify research falling within their remit and promote this actively among appropriate partners;
- communicate any actions taken to advance this research via the UK Biodiversity Research Advisory Group via Richard.Ferris@jncc.gov.uk

1. Background to the workshop

Introduction

There is an increasing awareness that the quantity and quality of genetic diversity possessed by populations might influence their sustainability (Frankham *et al.* 2002; Reed & Frankham 2003 and Saccheri 1998). However, such effects may be restricted in extremely small populations whose persistence is already severely threatened for demographic reasons. It therefore remains an open question as to how important genetic factors might be in species conservation (e.g. Caro & Laurenson 1994), especially at broader spatial scales. Further uncertainty revolves around the ability of molecular marker data to provide 'conservation shortcuts' (Pearman 2001), and the relative importance of inbreeding depression and the disruption of local adaptation when populations or individuals are translocated between sites (Vergeer *et al.* 2004).

Against this scientific backdrop, UK conservation organisations must provide guidance to research funding bodies and implement practical conservation management in support of UK Biodiversity Action Plan (UKBAP) objectives and international commitments. Thus far in the UK, the emphasis of conservation policy has been on maintaining the genetic distinctiveness of different species, sub-species or populations due to concerns that we need to maintain existing phenotypes, genetic integrity and local adaptations. However, faced with environmental change, the conservation of species adaptability and the processes sustaining and providing diversity might be of greater general importance than conserving specific local adaptations. This suggests that conservation should be promoting gene flow, rather than preventing it, in order to increase the range of genotypes subject to selection pressures and thereby enhancing the prospects for species survival.

This raises questions about how we manage not only species' populations, but also habitats and ecosystems at an increasing spatial scale. Consideration of the entire genetic footprint of species will include the need to understand the role of gene flow across species boundaries and the significance of protected areas and the wider landscape, how their resilience can be enhanced, and new strategies to allow greater adaptation to change. At landscape scales, an understanding of the permeability of habitats to migration between populations, and the appropriate time and source populations from which to supplement such gene flow, will be of importance in the effective management of genetic resources (Hufford & Mazer 2003).

Aims of the workshop

This workshop sought to:

- bring together leading conservation genetics research scientists and representatives of organisations shaping and delivering the UKBAP. In particular, to target those who are already attempting to integrate research and applied conservation;
- discuss currently controversial issues in both the research and applied spheres of the conservation of genetic diversity. Discuss the best approaches to the *in situ* management of genetic resources in native UK species and, where appropriate, draw up policy recommendations;
- identify existing data and critical gaps in knowledge that would be of relevance to current research, inform future policy recommendations, and guide future research in the area.

Acknowledgements

In 2005 UKPopNet granted funding for a collaborative workshop to assess the future scientific and policy needs of the conservation of genetic diversity in the UK. This came about by combining two independent, coincident proposals made on the topic by the UK Biodiversity Research Advisory Group (UK BRAG) in collaboration with the Woodland Trust, and by the Department of Animal and Plant Sciences, University of Sheffield.

We wish to thank UKPopNet (funded by the Natural Environment Research Council) for facilitating this workshop and providing the much-needed opportunity for discussion of the conservation of genetic diversity amongst diverse stakeholder groups, which has culminated in the publication of these proceedings. The workshop was organised by the JNCC (on behalf of UK BRAG), the University of Sheffield and the Woodland Trust, and took place in October 2005. Additional thanks go to Sara Holland (University of Sheffield) for helping to organise the meeting.

A full delegate list can be found at Annex A.

A number of key background documents were issued to delegates, in advance of the workshop. A list of these references is provided at Annex B.

Further information on UKPopNet and UK BRAG is provided at Annex C.

2. Brief viewpoints on the conservation of genetic diversity

A range of stakeholders and research scientists were invited to make short presentations on the need to incorporate genetic thinking into conservation management, and to outline the key issues from their own perspective. These presentations were intended to provide a broad context to the workshop, and to stimulate discussion at the meeting and during the breakout groups. The salient points of each presentation are summarised as 2.1–2.6 below.

2.1. Conserving the future

Dr H John Harvey, former Head of Nature Conservation, The National Trust, UK

Many nature conservation activities and conservation policy are predicated on an implicit assumption that the biological components of systems change little over time. There is increasing awareness that some external factors, such as climate change, can, and will, have dramatic impacts on the abundance and distribution of many species, but many conservation practitioners and policymakers are still not aware of the massive potential for genetic changes within populations. There is an urgent need both to increase awareness of genetic factors amongst the nature conservation community and for members of that community to build these issues into their plans and actions.

Examples such as recent studies of Darwin's finches on the Galapagos or of strains of *Agrostis* tolerant of the high levels of heavy metals in mine spoils in North Wales (Jowlett 1964) demonstrate the rapidity with which the genetic composition of populations can change. The former case also indicates the inadequacy of the common assumption that there are strong barriers preventing hybridisation between species and provides interesting insight into the issue of the genetic adaptation of local forms to local environments. The potential value of detailed genetic investigations is well exemplified by the recent demonstration that the apparent morphological variation between local populations of rock sea–lavender *Limonium binervosum* in the UK is not accompanied by detectable genetic differentiation, with implications for national conservation policy for this species (Leach & Pearman 2006).

A possible consequence of a more genetically based approach to conservation is that less attention may need to be paid to ensuring that revegetation schemes are based on the use of 'local' genotypes. This may particularly be the case for long-lived species, which may encounter very different environmental conditions in future years. An unresolved issue here is the role of phenotypic plasticity in enabling species to cope with environmental variation.

At a broader level, it must be asked whether the present nature conservation emphasis on seeking to retain the existing patterns of species distribution and abundance, together with the genes that determine these and the extent and composition of the communities that result from them, is either intellectually sound or sufficiently robust to cope with predicted future environmental change. From a genetic viewpoint, as illustrated by Darwin's finches, it may be more important for the survival of systems to ensure that processes such as reproduction, recombination of genes and selection continue than to seek to maintain the status quo. Similarly, the conservation of the much wider range of biological and ecological processes that occur in biological systems may be more effective in ensuring the survival of biodiversity than the present focus on the products of those processes. The outcome of such processes is likely to be beyond human control and society will need to become more willing to accept change in the nation's wildlife, such as the loss of valued icons and the development of new combinations of species in new locations.

2.2 We want to stick with what we've always had...

Grant Luscombe, Landlife, National Wildflower Centre, UK

...those evocative meadows, those beautiful maps and wonderful records. The fantastic work that tells us where each plant belongs, how it differs from its neighbour right down to its genes; and we can put them back just where they belong. Yes, I too would love to preserve that historic genetic integrity and cultural diversity of the natural landscape. It's how we see these islands, it's part of our heritage, and it's ingrained into our psyche.

The trouble is...CLIMATE IS CHANGING

Just how severe can these changes be? By 2050, we're looking at a 20% increase in winter rainfall and 20% decrease in summer rainfall, giving Devon a climate similar to the south of France and by 2100, North Africa! The recent realisation that global dimming (a 1–2% global decline in sunlight between 1950–1990) has been masking the underlying rate of global warming, means impacts are likely to be greater than previously forecast. At current rates of rising CO_2 emission (2 ppm per annum), a 2°C rise tipping point will be reached by 2015. Maybe the thermo-haline current will close down and Britain will cool, maybe it won't, either way we are in for some dramatic changes.

The trouble is...PLANTS ARE ON THE MOVE

The *New Atlas of British & Irish Flora* (2002) (Preston *et al.* 2002) analysed 9 million records over 40 years; one of its conclusions was that plants are as mobile as birds and butterflies! Just think about it. The impacts of climate change suggest that habitats are moving northwards at the rate of 50 to 80 kilometres per decade, demonstrated by the increased frequency of Mediterranean species in the south of England. We can't manage what's not there!

The trouble is...START POINTS MATTER MORE THAN END POINTS

Which end point do we select? The meadows of 1926? Just before the ice age, or yesterday? What about environmental justice? The North West of England, for example, where 92% of the land has little biodiversity value; do we deny people who have the most urgent environmental needs access to nature? Professor John Rodwell, who devised the *National Vegetation Classification* (Rodwell *et al.* 1991a, 1991b, 1992, 1995 and 2000), has called for there to be some "liberty in the system" (pers comm.).

The trouble is...NATURE IS DYNAMIC

Evolution is happening all the time. Is it survival of the fittest or survival of the luckiest? Darwin said, "It is not the strongest of species that survive, nor the most intelligent but *the ones most responsive to change*". We can already see the distribution and composition of species changing all around us.

The trouble is...THOSE BEAUTIFUL MAPS AND WONDERFUL RECORDS

We just don't want to lose them, do we? So we'll carry on as we always have... the trouble is ... THE EMPEROR IS STARK NAKED!

2.3 Genetics and conservation management: issues from an academic perspective (or never mind the science, where's the interaction!)

Mike Bruford, School of Biosciences, Cardiff University, UK

Although the application of molecular tools has proven to be a major new element in species recovery during the last ten years, real concerns remain as to how the data produced in such studies are applied. For example, conservation genetics projects in the UK are often carried out on a somewhat piecemeal basis, comprising small projects involving partnerships between research institutions, governmental and non-governmental organisations and often carried out with inadequate funding over an unrealistically short timescale.

When such studies have been completed, it is sometimes unclear how the data have been applied, or whether geneticists will feed into this process. To compound this problem, data are often not peer-reviewed unless they are published in journals, a process often compromised by the parochial and limited nature of solely UK-based studies. Finally, even when genetic data are incorporated into specific conservation measures, they are applied within the context of a 'policy vacuum' that exists in UK and EU legislation.

For molecular genetics to make a bigger impact in UK conservation it needs to be processdriven, involve explicit prioritisation mechanisms, receive adequate funding, be subject to peer review and be both an interactive and policy-relevant exercise. I argue that in the UK there is currently little evidence for joined-up thinking in conservation genetics in comparison to other sub-disciplines of conservation biology in species recovery. Future initiatives should attempt to address both the science and conservation needs of partners so that the best science and conservation can be applied within the context of a clear policy framework.

2.4 Genetics and the role of Flora locale

Donald MacIntyre, Flora locale, UK

The charity Flora locale exists to promote the restoration of wild plants, acting as a link between research and practice, and this it does by assimilating best knowledge and providing access to experts, web based data, printed literature and on-site training.

Local native origin

Flora locale has recommended "local native origin" when sourcing material for restoration. This ecologically based advice, with the aim of maintaining current native plant community structure, and restoring past structures, as a rough guide, has served us well. However, we are aware that it is appropriate to move towards a genetically based approach, promoting the restoration of processes rather than plants.

The generalisations, native good/alien bad and local good/non-local bad, no longer stand scrutiny, as either an appropriate message or as having a basis in genetics. Rather, advice on restoration needs to be based less on ecology and more on best current genetic knowledge. For many populations, species, communities and landscapes there are some genetic data, but not enough. Further research needs to focus on some of the following questions:

Questions

• What is the comparative importance of ecological distance, genetic distance and geographic distance in driving ecotypic differentiation?

- How important is ecotype preference among plant-specific fauna?
- Is non-adaptive genetic variation really non-adaptive?
- Are molecular measures of genetic variation better than measures obtained from garden experiments?
- Is there a standard working measure of genetic variation that will allow proper quantitative and qualitative comparisons to be made within and between disciplines?
- What has been the utility of gene banks and what has been their contribution to biodiversity?
- Are native species more invasive than alien species?
- Should our response to climate change be to facilitate the evolution of natives, or encourage the invasion of aliens?
- How important is the co-evolution of species pairs and species complexes within communities?
- What is a "genetics based" approach to restoration?

2.5 All for one and one for all: Integrating effort for more efficient and effective conservation

Rus Hoelzel, University of Durham, UK

Identifying priorities

Genetic studies, while more cost effective every year, remain relatively expensive and time consuming. For example, a study involving 1–4 species may take 2–3 years and cost £150–250k. Furthermore, the full process from identifying a problem to funding the work, publishing the results and generating a conservation strategy can take many years. Therefore, establishing priorities is essential, and there are various factors involved. These include: the urgency of the threat, the potential for effective mitigation, and the breadth of conservation impact (e.g. will conserving the target species have a positive indirect effect for other species at risk or critical habitat?). The integration of effort among disciplines (including ecologists, geneticists, managers, etc) can help identify these priorities.

Sharing effort from the start

There is considerable potential for facilitation in all directions when studies incorporate multidisciplinary cooperation from the start:

- the effective design of genetic studies and the interpretation of resulting data depend on integration with ecological/ observational/ political information;
- the coordination of effort in the field and in the lab can facilitate the objectives of both types of analyses;
- genetic studies require biological material that has been collected in an appropriate way.

Making full use of the potential of molecular methods

The World Conservation Union (IUCN) recognise the need to conserve genetic diversity, and while the application of genetic markers to the identification of diversity levels within and among populations is well known, genetic methods have a much broader potential application. For example:

Individual and species identification



Mark/ recapture for population size estimation through individual identification using genetic markers, e.g. Palsbøll *et al.* (1989).



Assignment of individuals to population and identification of sex, e.g. to aid enforcement of hunting regulations, e.g. Spong *et al.* (2000).



Identification of species in trade from their products (facilitated by recent initiatives in DNA barcoding and 'ancient' DNA technologies), e.g. Hoelzel (2001).

Conservation at, and beyond, the species level

- quantifying demographic dynamics and levels of gene flow using coalescent methods;
- understanding the relationship between genotype and phenotype, and the role of local adaptation (in a changing environment);
- identification of hybrids and assessing the rate of hybridisation;
- identifying phylogenetic uniqueness and lineage diversity.

Final thoughts

Every year numerous conservation genetic studies are published in journals such as *Molecular Ecology, Conservation Genetics, Journal of Heredity, Conservation Biology, Animal Conservation*, etc. Better integration is needed to facilitate efficient interactions between researchers and policymakers to translate results into conservation strategy and governmental policy, and to facilitate the use of the full potential of genetic methods.

2.6. Genetic resources and conservation

Richard Smithers, The Woodland Trust, UK

Conservation thinking in the UK has developed in the context of a largely static view of the natural world. This has led to a focus on site-centred protection and management of existing semi-natural habitats and species populations. It seems to me that the limitations of such an approach from a genetic standpoint are increasingly appreciated. For example, habitat fragmentation means that wildlife sites are, in ecological terms, often very small and isolated populations of species that may be vulnerable to random loss of genetic variation and impaired reproduction. The failure of active woodland management designed to save remnant butterfly populations from local extinction is often ascribed to such genetic problems (Martin Warren, pers. comm.).

However, it is apparent that some conservationists are concerned that the growing emphasis on habitat restoration and creation may lead to greater loss of genetic variation through hybridisation between introduced species or races and natural relatives, and the loss of long-

established patterns of genetic variation between and within populations. These concerns seem to stem from a desire to maintain the genetic distinctiveness of different species, sub-species or populations and thereby conserve the existing phenotypes, their genetic integrity and local adaptations.

For an increasing number of conservationists, climate change is bringing into sharp relief the fact that nature is dynamic and that conservation needs to look to the future and find sustainable solutions. From a genetic standpoint, I'd suggest this paradigm shift in conservation thinking is bringing into question the importance of conserving local adaptations, at the expense of promoting genetic diversity at a local level and thereby adaptability. However, there is a wide range of opinion as reflected, for example, by:

- discussion over whether an appropriate response to climate change is to promote the use of trees of local provenance, ensure wider genetic diversity of planting stock or introduce novel tree species from bioclimatic zones that are projected to shift here over the course of this century;
- Plantlife's recent drive to connect the general public with the perceived threat posed by the Spanish bluebell *Hyacinthoides hispanica* to our bluebell *H. non-scripta* woods, or Flora locale's wish to see strict adherence to the use of local provenance in relation to all habitat creation, as compared to Landlife's rather more pragmatic approach;
- the disquiet expressed by some conservationists to Defra's ongoing £3.4-million programme to eradicate the ruddy duck *Oxyura jamaicensis*, an introduction from North America, which is hybridising with the white-headed duck *O. leucocephala* in Spain, which is an endangered species.

It seems to me that amongst conservationists there may be many widely held misconceptions when it comes to genetics. For example:

- natural selection is often perceived as an optimising force. However, as Stephen Jay Gould (2002) argues, I'd suggest that it simply results in the survival of individuals that are better adapted to changing local environments. Thus many native plants fare poorly against introduced species. This would not be the case if natural selection produced local adaptations that were optimal, as native forms would always out-compete individuals from elsewhere;
- some people fear that the mixing of divergent gene pools leads to exclusion of rarer alleles. However, I gather from some studies of human genetics that this is not the case and that unusual variants may actually become more common when isolated populations merge (Chakraborty *et al.* 1988 and Neel *et al.* 1988);
- whilst we may lose species, this does not mean that all of the genetic variation amongst them is also lost, as many gene combinations and segments of chromosomes are common to different species.

Many conservationists have come to accept the rhetoric associated with developing ecologically functioning landscapes, but behind that acceptance there seems to be a reluctance to embrace the underlying paradigm shift. For the Woodland Trust it's not simply about developing big nature reserves surrounded by intensively managed land. At its most fundamental, I would argue that landscape-scale action needs to give as free a rein as possible to the processes that support evolution by ensuring that the whole landscape is managed with wildlife in mind. For example,

landscape-scale action will increase the variety of genotypes of a species subject to selection pressures at any given location, by promoting dispersal and gene flow between isolated patches of habitat. This in turn will enhance the prospects for survival of a diverse gene pool and enable the widest biodiversity to continue to evolve.

As a result, in the context of climate change, it seems to me that there is a need to reconsider the following questions:

- What priority should be given to use of local provenance?
- How strictly should conservation continue to focus on native species?
- How great a threat are invasive species?
- What should be our attitude towards the deliberate introduction of non-native species?

3. Session 1: Where are we now?

3.1. Introduction: conservation genetics – a maturing discipline

Terry Burke, Department of Animal and Plant Sciences, University of Sheffield, UK

The concept of 'conservation genetics' is relatively new, but is becoming well-established, with a number of academic workshops, edited volumes, text books (e.g. Frankham *et al.* 2002) and a journal (*Conservation Genetics*) entirely devoted to the field. This workshop is perhaps the first to bring together in a very deliberate way both academic researchers and representatives of the policy-making and stakeholder communities. It is the aim of my contribution to introduce some of the concepts of conservation genetics, especially to the non-academic community, and to provide a flavour of what this area of science potentially offers to wildlife conservation.

In the most extensive review of the field to date, Frankham *et al.* (2002) provide a list of what they consider to be the major genetic concerns in conservation biology, i.e. inbreeding depression, the loss of genetic diversity, genetic drift overriding natural selection, population fragmentation, taxonomic uncertainties and genetic adaptation in captivity. All except the latter (which applies particularly to the issue of zoo populations being used as conservation reservoirs) are of potential concern to the participants at this workshop. Although there has been research on these issues in many British taxa, on the whole, conservation policy has been devised without specific genetic data. On the other hand, much conservation practice is implicitly informed by an awareness of these genetic issues, such as the recognised need to maximise population size to minimise the effects of inbreeding and genetic drift and the desirability of maintaining habitat corridors to connect populations and minimise fragmentation, again to maximise population size.

The conservation geneticist's 'toolbox' currently combines an ability to detect variation in DNA sequences at marker loci in the laboratory with population genetic analytical methods that allow inferences to be made from such marker data. The most informative and commonly used genetic markers for deriving population parameters at the present time are microsatellites and amplified fragment length polymorphisms (AFLPs). Both exploit the polymerase chain reaction (PCR), which means that very little tissue has to be sampled from each individual to enable the analyses, making it possible to obtain genotypes with minimal or zero harm. Taxonomic questions are often best-resolved using sequence data, and organelle DNA sequences (chloroplast – cpDNA – and mitochondrial – mtDNA) have been especially useful in both phylogenetic (systematic) and population studies.

Robotics and high-throughput methods are making it possible to analyse thousands of samples within months or weeks. It is inevitable that, as technology improves and costs come down, the methods will become more DNA sequence-based in the future. For example, parallel pyrosequencing was recently used to sequence an entire bacterial genome in less than a day (Margulies *et al.* 2005), and to obtain 28 million base-pairs of sequence from a frozen mammoth corpse frozen for 28 thousand years (Poinar *et al.* 2006), and even newer methods on the horizon will reduce the costs of sequencing by further orders of magnitude. We are becoming less limited by technical and cost considerations in the laboratory, but the work remains far from routine, and for the moment we have to be selective about which problems should be tackled.

To date, most studies in the field have focused on *neutral* genetic variation and markers (including those just mentioned) that are expected to evolve in a predominantly neutral manner. These markers do not tell us anything about adaptation (with exceptions discussed below), but are being exploited increasingly to make inferences about relationships among individuals (whether identifying clones, family members, phylogeography or phylogeny) and about population dynamics (such as inbreeding and migration) and history (such as whether the

population has experienced a bottleneck). Neutral markers can therefore help us to detect and quantify the first five of the six above-mentioned processes listed as concerns by Frankham *et al.* (2002). The most powerful studies combine information on individuals in a population with information on markers.

For example, microsatellite markers have been used to compare the genetic variability of natterjack toad *Bufo calamita* populations in Britain (Rowe *et al.* 1999). The populations with least mean heterozygosity (a measure of the level of genetic diversity) were also those with the slowest tadpole growth rates – a trait known to be associated with fitness – indicating that they were experiencing inbreeding depression (Figure 1). The genetic variability in a population was also found to correlate with population size. The authors concluded that some populations had been bottlenecked to the point where they had become significantly inbred and their fitness had been reduced. In this case, therefore, it is now possible to make a decision from the variability at defined neutral genetic markers about whether a population size has at some point become too small and whether individuals need to be imported from other populations to boost the local genetic diversity.



Figure 1. Relationship between larval growth and expected heterozygosity in the natterjack toad *Bufo calamita* (means \pm SD). [From Rowe *et al.* (1999), with permission of Blackwell Publishing.]

In general, we cannot simply measure genetic diversity and conclude if a population is suffering the ill effects of inbreeding. There is much natural variation in the degree of variability among populations. For example, in a phylogeographic study, Petit *et al.* (2003) showed that populations of European trees become less genetically diverse at higher latitudes. This pattern is thought to reflect the history of these populations: as with many European organisms, the forests were limited to southern refugia during the last ice-age. Then, during the rapid expansion north there would have been a multiply-repeated chain of founder effect events at the leading edge. This reduction in neutral genetic diversity would not necessarily have had any deleterious effect on fitness, as genes with adaptive value would be expected to have been maintained in the populations by selection.

The pattern of genetic variation in a population results from a combination of the historical colonisation process and gene flow due to successful dispersal since colonisation. Consequently, most populations show a genetic pattern of isolation-by-distance. If the organism is continuously distributed in the landscape then such a pattern will result in a lack of distinct boundaries between populations, although comparisons between samples collected sufficiently far apart will be statistically significant (Figure 2). One of the consequences of this process is that populations that are now disjunct but were previously connected may be found to be

genetically different, although they are in fact the relicts of a single large, previously continuously distributed population. This means that populations that show a difference in their frequencies of neutral genetic markers should not *a priori* be regarded as units of conservation significance.



Figure 2. British populations of the badger *Meles meles* form a continuum of populations that are primarily isolated by distance (p < 0.0001)(a). This restricted gene flow leads to all populations such as those sampled within the discs in (b) being genetically distinct, although no specific population can be regarded to be an evolutionary significant unit (ESU) or of conservation genetic concern (based on Pope *et al.* 2006). Figures courtesy of L. Pope.

Conservation practitioners inevitably have to make decisions using limited information, particularly about what constitutes a potentially self-sustaining population. It is in this area that the modern conservation genetics toolbox has much to offer. For example, it is now possible to make inferences about both the effective size of populations and gene flow among populations – and sometimes both parameters simultaneously. For example, in a study of the great crested newt *Triturus cristatus*, Jehle *et al.* (2005) were able to apply a novel Bayesian analytical method to deduce which populations were contributing recruits to other populations in the subsequent generation (Figure 3). Related methods are making it possible to identify coherent groups of populations that are more genetically related to one another. For example, Wasser *et al.* (2004) used Bayesian methods to define elephant *Loxodonta africana* populations in Africa. The latter paper also nicely illustrates the potential of genetic methods in wildlife forensics, as the authors show that it is possible to determine the regional origin of elephant ivory using genetic markers. Wildlife forensics is likely to make an increasing contribution in helping to prevent the illegal exploitation of endangered species, and represents an additional valuable development in conservation genetics.



Figure 3. Contemporary gene flow among interbreeding great crested newts *Triturus cristatus* and marbled newts *T. marmoratus* in western France. Contemporary gene flow is quantified from Bayesian assignment tests that identify admixed genotypes (Wilson & Rannala 2003). Pairwise immigration rates between ponds of >0.1 are plotted as arrows. The sizes of the circles = breeding ponds and their sizes correspond to their census size (data not available for the ponds represented by hollow circles). See Jehle *et al.* (2005). Figure courtesy of R. Jehle.

Other recent advances in population genetics raise the prospect that the study of neutral markers may allow us to study adaptation. For example, in principle, it is possible to quantify the additive genetic adaptive variation held by a natural population by using genetic markers to deduce a matrix of relatedness between pairs of individuals in a population for comparison with corresponding measurements of trait similarity (Ritland 1996). This approach avoids the need to undertake time-consuming breeding experiments, which have in the past been the only route to assessing levels of quantitative genetic variation. In an alternative population genomics approach, a study of winkles *Littorina* spp identified specific AFLP markers that are located in genomic regions subject to differential selection in relation to the specific intertidal location that a winkle occupies (Wilding *et al.* 2001). This study was therefore able to use molecular evidence to deduce that winkles at different intertidal levels are subject to differential natural selection, and that similar selection acts on the same regions of the genome in disjunct populations.

In conclusion, the pace of technical and theoretical development in molecular population genetics provides the potential to provide an increasingly accessible and relevant contribution to conservation biology.

3.2. Recent developments in conservation genetics

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In recent decades, there has been increasing endangerment of many species and an increased rate of extinction throughout the world. As a result of this crisis, the discipline of conservation biology, and related areas of research such as conservation genetics, have become essential for understanding the scientific basis of these trends. Researchers have utilised three major approaches in conservation genetics: empirical, experimental, and theoretical. Empirical approaches have primarily been used to document information about threatened and endangered

species and to develop hypotheses about the causes of their endangerment. Experimental approaches have been used to support or falsify these hypotheses with consequent refinement of the hypotheses. Finally, theoretical approaches have been used to put empirical and experimental data in a general framework and to allow the prediction of future changes in specific situations.

The types of genetic variation can be divided into three general categories: neutral, detrimental, and adaptive (Hedrick, 2001). Neutral variation is defined as that genetic variation in which the impact of selection changing the variation is less than the impact of genetic drift causing chance genetic changes due to small population size. Neutral variants can be used in conservation genetics in a number of ways. First, they can be used for the identification of individuals, populations, species, Evolutionarily Significant Units (ESUs), or Management Units (MUs). Secondly, they can be used to estimate various non-selective population parameters, such as effective population size, past population bottlenecks, amount of gene flow, relationships between groups, or individual inbreeding level. Finally, neutral variants can be used as an indicator of the extent and pattern of detrimental and/or adaptive variation.

If the impact of selection is greater than that of genetic drift, then either the variants can have a negative (detrimental) influence on fitness or the variants can have a positive (adaptive) influence on fitness. Examples of detrimental variants are disease genes, lethals, or genes that reduce some aspect of fitness. A common way in which the impact of detrimentals is measured is from inbreeding depression, i.e., the lower fitness (survival or reproduction) of inbred individuals than non-inbred individuals (Hedrick and Kalinowski, 2000). In addition, the fitness of all the individuals in a population may be lowered compared to another population due to genetic load, i.e. the fixation or high frequency of deleterious genes in the population of interest.

A number of populations of endangered species appear to be suffering from genetic load. One way to document the presence of genetic load, and to eliminate it, is by the introduction of wild-type variants that lead to a reduction in the frequency of detrimental genetic variants causing the genetic load. This is called genetic rescue. For example, the Florida panther *Puma concolor coryi*, which exists only in a single disjunct population of around 80 individuals in southern Florida, suffered from genetic load with 68% of the males having only one descended testicle and very poor sperm quality, while 88% of the animals had a kinked tail (Figure 4) and very poor sperm quality (Roelke *et al.* 1993). To reduce this genetic load, in 1995 eight females were introduced from Texas (five produced offspring). Males with ancestry from Texas all had two descended testicles and only 7% of the Texas-ancestry animals had the kinked tail, this being a clear demonstration of genetic rescue (Land 2001).



Figure 4. An X-ray of the tail of a Florida panther showing the last five vertebrae fused at a right angle (Roelke *et al.* 1993).

There are a number of examples of adaptive variants, such as defensive or immune genes (major histocompatibility complex or MHC) (Garrigan and Hedrick 2003), and sperm or egg proteins. A population may be fixed, or nearly so, for an adaptive variant, from a past selective sweep, or a population may be polymorphic for adaptive variants. A number of approaches have been used to detect adaptive variation and these can be categorized by the time in which the selection is thought to have acted (Garrigan and Hedrick 2003). First, selection in the current generation can cause deviations from Mendelian proportions, Hardy-Weinberg genotype proportions, or association of particular alleles with a disease or environment. Secondly, selection may have acted over the history of populations, and this can be detected using tests detecting extreme linkage disequilibrium, population structure, or distribution of allele frequencies. Finally, selection may act over the history of species and this can be detected using tests based on DNA sequence information.

A study of a MHC gene in the red wolf *Canis rufus* provides a good example of adaptive variation (Hedrick *et al.* 2002). First, there was an excess of heterozygotes for the MHC gene while, for a sample of 18 neutral microsatellite loci in the same individuals, the genotypes were in the expected Hardy–Weinberg proportions, indicating selection in the current generation. Secondly, the four alleles found for this MHC gene were quite divergent and on average differed by 15.5 amino acids. A phylogenetic tree in which these alleles are indicated by closed circles, together with other alleles from coyotes *C. latrans* and grey wolves *C. lupus*, shows the extreme divergence of these four alleles (Figure 5). The closest sequences were from coyotes, which are thought to have had a recent common ancestry with red wolves. However, even grey wolves had sequences closer to a given red wolf sequence, suggesting that selection is maintaining MHC variation even over the formation of species.



Figure 5. A phylogenetic tree for an MHC gene where the sequences indicated with closed circles, squares, and triangles are from red wolves (Caru), coyotes (Cala), and grey wolves (Calu) respectively (Hedrick *et al.* 2002).

Neutral variation can be used to estimate effective population size (N_e) (i.e. the size of an ideal population that results in the same amount of genetic drift as that observed in a particular population) in winter–run Chinook salmon *Oncorhynchus tshawytscha* and Florida panthers. The winter–run Chinook salmon exist only in one population in the Sacramento River,

California. In the 1960s, there were nearly 100,000 spawners per year, but in 1991 the number of spawners was less than 200. As a result, a supplementation programme was initiated to increase the size of the run. The logic of supportive breeding is generally to increase survival through breeding in a protected captive environment. There may be a gain in the total production of offspring, but there may be a simultaneous reduction in the effective size of the total population that results in excess loss of genetic variability (Ryman and Laikre 1991). The releases from 1991 showed this type of problem, with 41% descended from one female and 61% descended from one male (Hedrick *et al.* 1995). As a result, a protocol to equalise the spawner contributions was developed, and the parents of returning spawners from the 1994 and 1995 matings were identified using microsatellite loci to examine the success of this approach (Hedrick *et al.* 2000). For example, the proportion of 93 returning spawners originating from each of the 1994 releases from the 16 female parents of the 1994 releases varied only from 0.022 to 0.108. In other words, the protocol equalised the contributions, and survival from different parents in the ocean appeared to be random. For 1994, the observed effective population size (31.5) was very close to that predicted (34.8) before the releases three years earlier.

As mentioned above, the Florida panther exists as a small population in southern Florida and was thought to be extinct in the 1960s. There is little information about population numbers over the past century but, by comparing genetic variation in museum samples before the numbers were reduced to that in the contemporary population, we could obtain an estimate of the size and extent of the genetic bottleneck. From a sample from museum specimens from the 1890s, the estimated heterozygosity for microsatellite loci was 0.311 and the diversity for mtDNA was 0.600. From a contemporary sample from the 1980s, the microsatellite estimate was 0.101 and the mtDNA estimate was 0.000, both much lower. With these numbers, what bottleneck combination is necessary to result in this loss of variation over 90 years (about 16 generations)? Figure 6 illustrates three scenarios that can result in the loss of microsatellite variation: a constant population size of about 7.5 the whole time, a bottleneck of two generations of two animals (with the rest of the generations higher), or a bottleneck of four for four successive generations.



Figure 6. Three scenarios that can explain the loss of variation between museum and contemporary samples in the Florida panther (Culver *et al.* 2006).

Using an N_e/N ratio of 0.32, where N is the census number, then a census number of 41 and a bottleneck census number of 6 for two generations could result in the observed loss of genetic variation. This low effective size may be the cause of the high frequency of deleterious traits in the Florida panther.

Overall, it is important to consider different types of genetic variation –neutral, detrimental, and adaptive. In particular, management can contribute to keeping N_e and N_e/N from being low (winter-run chinook salmon) and historical samples can be used to estimate past low N_e and bottlenecks (Florida panthers).

3.3. The dynamic nature of plant species distributions and adaptation

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Although plants are sessile organisms during the most evident (vegetative) phase of their life cycle, their geographic distributions are the result of the dynamic processes of dispersal, the ecological assembly of communities on the basis of abiotic and biotic interactions, and adaptation through natural selection on populations. Thus, while plants stand still, as with animals their genes do not.

The geographic distribution patterns of all plants are dynamic, including long-lived trees. Indeed, the current distribution of trees in Britain, and almost all other plants and animals, is the result of a history of colonisation of these latitudes from southern shores following the last ice age, i.e., following climate change after the Pleistocene glaciations. With the Earth's climate expected to change substantially in the coming decades and centuries, we therefore increasingly need to see the distribution of all plant and animal populations as dynamic and subject to change. Because change can mean extinction for those species unable to move or adapt to new environmental conditions, we urgently need to understand the processes by which organisms move and/or adapt, particularly plants whose dispersal prospects are perhaps more limited than those of animals. To this end, much can be learnt from plant species whose biology and distribution patterns are well known.

We are beginning to learn about these issues from studies of two weeds that are common in Britain, Oxford ragwort *Senecio squalidus* and annual mercury *Mercurialis annua*, an annual relative of the familiar dog's mercury *M. perennis* (Figure 7). Both species grow in humandisturbed habitats such as roadsides, railway sidings and wasteland, and both have revealing stories to tell about the dynamic nature of plant species distributions and evolution in Europe.

Senecio squalidus

S. squalidus found its way to Britain during the late eighteenth century in a sequence of introductions to private gardens and, ultimately, to the Oxford Botanic Garden, where it later 'jumped the wall' and began to spread across the country. It is now a familiar sight in towns and along railways throughout southern Britain, and it has made substantial inroads into Scotland, where it has been common since about 1950 (Harris, 2002; Figure 8). We recently asked whether *S. squalidus* has become genetically differentiated across Britain since its introduction as a result of natural selection under the different environments it now faces, particularly between northern and southern Britain. Using so-called 'reciprocal transplant' experiments, where individuals collected in the north and south were grown both 'at home' and 'away' in a reciprocal manner, we found that British populations have diverged in several traits affecting growth rate and tolerance to drought stress and to different temperature regimes. Northern 'genotypes', or genetic variants, grew better in the north, and were generally less tolerant to drought stress, than their southern counterparts, and vice versa (E. Allan, R. Andrerson & J.R. Pannell, unpubl. MS).





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Figure 7. Oxford ragwort *Senecio squalidus* and annual mercury *Mercurialis annua* (Euphorbiaceae) A – male, B – female and C – hermaphrodite.



Figure 8. Spread of *Senecio squalidus* across the UK, 1799–1999. Derived from Eastwood and Harris, unpublished.

These results confirm the notion that natural selection can operate remarkably rapidly, leading to genetically divergent populations that are locally adapted across the new range of a species. They also sound a cautionary note: populations of a species across its range are not interchangeable. Nonetheless, the results also highlight the fact that the movement of genetic material between localities can elicit rapid change, so that introduced populations, which might initially show lower survival and reproductive potential than local types, can quickly become locally adapted if they are sufficiently diverse genetically. *S. squalidus* is in fact a hybrid between two species that occur on the slopes of Mt. Etna in Sicily (James & Abbott, 2005), and we might thus expect it to possess particularly high genetic diversity. This case, therefore, also illustrates the idea that the adaptive potential of a species can be enhanced by allowing genetically divergent populations to interbreed. This potential can be beneficial for the conservation of species, but it is also well known that hybrid species can pose severe threats to biodiversity if they evolve invasive tendencies.

Mercurialis annua

M. annua is an uncommon weed in southern Britain, but it is widespread and abundant on the European continent, particularly in the western Mediterranean. Here, it displays extraordinary diversity in its sexual and genetic systems: not only do we find populations, as in Britain, that consist of male and female individuals, but there are also populations of hermaphrodites and others of hermaphrodites mixed with males, a rare situation found in only a handful of plants and animals worldwide. Iberian and Moroccan populations of *M. annua* also vary in the number of their chromosomes, in a way that is loosely related to sexual-system variation (Durand & Durand, 1992; Pannell *et al.* 2004). Where has all this variation come from, and how is it maintained?

The answers to these questions again illustrate the very dynamic nature of plant species evolution and biogeography. Genetic analysis in our lab indicates that the diversity found in Spain and Morocco is the result of dispersal and natural selection occurring at a range of spatial scales (Obbard *et al.* 2006). Populations with different numbers of chromosomes expanded their range into Iberia from quite distinct 'refugia' following the last Pleistocene glaciation. Those with 16 chromosomes (the 'diploids') spent the ice age in the eastern Mediterranean and expanded into Iberia from the east and north, while those with 48 chromosomes (the 'hexaploids') expanded into Spain and Portugal from Morocco. Interestingly, it appears that the hexaploids originated from hybridisation between two genetically distinct, but related, lineages, either prior to or during the Pleistocene (Obbard *et al.* 2006). Now these lineages, kept separate for thousands of years, have met at two zones of contact in northern Spain, where we can currently witness a clash of both genetic and sexual systems. Because the diploid males produce much more pollen than the hexaploid hermaphrodites, in recent years the diploids have been displacing the hexaploids, and pushing south, at a remarkable rate of up to 5 km per annum (Buggs & Pannell, 2006).

The case of *M. annua* illustrates clearly that populations that appear to be morphologically identical in the field can have very different evolutionary histories and might consequently possess very different and incompatible genetic systems. When such lineages are brought together, one can quickly replace the other as a result of contaminating gene flow, and irrespective of physiological adaptive differences. *M. annua* offers a rather extreme example of this, where natural patterns of dispersal and range expansion have led to different lineages coming to genetic blows. However, there are many similar examples of introduced species that have hybridised with local relatives (e.g., Rhymer & Simberloff, 1996); these also illustrate the potentially creative role of gene flow between genetically divergent populations, as well as its dangers.

Conclusions

Studies of *S. squalidus* and *M. annua* exemplify the contrasting effects of gene flow between divergent populations. Mixing genes can be both destructive, with one population or species contaminating another and potentially driving it to extinction, as well as creative, by allowing the rapid selection from a broad genetic base of locally adapted genotypes. (It is important also to emphasise the fact that hybrids can have drastically destructive effects on other species and communities if they become invasive.) The history of *S. squalidus* and *M. annua* in Europe highlights the dynamic nature of plant distributions, the rapidity at which local adaptation can evolve to new environments when compatible genetic variation is abundant, and the pace at which species can be driven to extinction when incompatible genomes are brought together.

4. Discussion

Three key questions relating to the papers presented in *Session 1: Where are we now? The conservation utility of neutral and adaptive genetic variation*, were addressed in parallel breakout groups, as follows:

- 1. What is conservation seeking to achieve from a genetic standpoint?
- 2. Can molecular markers be used to determine which of a species' populations are conservation priorities?
- 3. Do we really need to know about genetic variation?

The outputs from these groups are given below. A synthesis of the main points is provided in the final section of this report, which identifies knowledge gaps and the research needed to fill these.

4.1. Breakout group 1: What is conservation seeking to achieve from a genetic standpoint?

- To what extent is genetic sustainability an implicit goal in current conservation strategies?
- What is conservation seeking to achieve genetically?
- Do conservation objectives need to be broadened to incorporate genetic considerations?

Discussion Notes

Geneticists identified three areas where conservation is motivated by genetic aims:

- Maintenance of adaptive potential;
- Avoidance of inbreeding depression and loss of heterozygosity;
- Avoidance of outbreeding depression.

Priorities for conservationists were somewhat different. Their overriding interest is to avoid species' immediate extinction, taking account of genetics wherever feasible or necessary. Key issues were:

- Identifying situations where genetics limits population viability;
- Determining whether it is possible to group species usefully in the context of genetic risks.

Current evidence from meta-analyses indicates that extinction risk correlates inversely with heterozygosity at neutral genetic loci in a wide range of taxa (Reed & Frankham 2001). This strengthens the case for taking genetics seriously in conservation. However, before population genetics principles can be more fully incorporated into conservation, some significant communication gaps between geneticists and conservationists must be overcome. There are, in addition, non-trivial intellectual challenges to the development of such an approach, which must be addressed by further research.

Common terminology

Some terms, such as 'local', mean different things to different people (e.g. geographic *cf.* genetic locality). Common definitions are also crucial for concepts such as Evolutionary Significant Units (ESUs). Are ESUs populations rather than species? How do we define the level of genetic differentiation that is really important?

Definition of a population

It is also essential to consider how populations can be defined. Genetic approaches can help with this, e.g. by using clustering methods based on neutral markers that measure gene flow over time and geographic space.

Process conservation

Conservation of evolutionary processes rather than just of 'status quo' taxonomic units needs to be considered, and has genetic implications. Populations feed processes and vice versa. Future conservation strategies require a combined approach that can maintain existing species and populations but also allow for demographic dynamism and future environmental changes, e.g. those expected due to the climate. The current legal framework and obligations emphasise the importance of current taxonomy. Policy needs reconsidering in this context to include processes that generate novel taxa and diversity as well.

Gene flow, genetic differentiation and adaptation

Understanding and managing gene flow is central to the application of genetics in conservation. There is an inherent tension between (a) an emphasis on conserving potentially well-adapted local ecotypes, and (b) general maximisation of genetic diversity in every location to promote future adaptability. The issue of how to maintain both 'within' and 'among' population diversity is very important. Any future policy relating to gene flow (i.e. how much it should be promoted) should be flexible to account for variation in species' life history characteristics and whether populations are at centre or edge of their species' range. Conservation interventions that involve translocations should also be based on evidence (e.g. of population decline or inbreeding) wherever possible. Population size should not be used as the sole factor in deciding whether to mix genotypes from different populations to enhance their viability (i.e. to engage in genetic rescue).

Feasibility of facilitating gene flow

Human activities, such as changes in farming practices, have led (for many species) to range fragmentation, population isolation and decline. For such species, this raises the question of how far we can restore the natural processes that maintain gene flow, or whether we need to engage in active translocation to manage the genetic resources of wild species.

Key knowledge gaps

- conservation organisations need to incorporate genetic concepts and information into management strategies via improved communication with geneticists;
- how can critical units of conservation such as ESUs and MUs be defined? Selectivity measures and 'designated population segments' have all been suggested, and need discussion;
- more detailed evidence of population declines must be gathered so that genetic risks may be assessed for these populations, in order to determine the general prevalence of such risks;
- the legislative framework and current taxonomy limit the use of genetics in conservation and requires a rethink;
- what is the scale of local adaptation in different types of organisms, and how serious an issue is it? This might affect gene flow management significantly;
- how serious a risk is outbreeding depression? This might affect policy on gene flow and genetic rescue.

High priorities for future research

- guidelines for assessing gene flow; where and when to try and manage it, and
- relationships with landscape permeability.

4.2. Breakout group 2: Can molecular markers be used to determine which of a species' populations are conservation priorities?

- How much genetic diversity do we need to conserve?
- Do genetic methods (such as estimating population size or differentiation) provide a useful tool for managing populations?
- Where do we need to conserve diversity, and how?

Discussion Notes

Within the UK, sites are currently designated to protect wildlife on the basis of community type, habitat diversity, extent and health, presence of rare species and their population sizes. However, in order to conserve a genetically sustainable sample of any species' populations, conservation strategies must ensure the protection of sufficient genetic diversity to:

- Minimise population extinction risk associated with inbreeding;
- Conserve the range of current environmental adaptation;
- Protect the potential for future adaptability to environmental changes.

This raises the question of whether we can prioritise the conservation of populations of threatened species to maximise the genetic potential of those that are protected. For any given target species, several elements of biodiversity and biogeography might be important in deciding upon the prioritisation of population-level conservation from a genetic standpoint:

- Level of genetic diversity;
- Population fitness;
- Population differentiation;
- Historical distribution of populations;
- Level of ongoing gene flow.

Here we consider the utility of measures of neutral and adaptive genetic diversity in the context of demography for prioritising the conservation of populations.

Should we conserve the populations that harbour the most genetic diversity?

In naturally outbreeding species low levels of genetic diversity do correspond with low population fitness in many cases. But lack of diversity is a symptom, and not a cause of low population fitness. Little is known about this relationship in naturally inbreeding species. In addition, we need to consider a species' breeding system and also to understand the demographic history of populations (via coalescent approaches) to interpret the patterns of genetic diversity we observe. Populations that have always been large in size are those most likely to possess higher levels of standing genetic variation.

Measurement of mean expected heterozygosity (H_e) across genetic loci, appropriately standardised (Hedrick 2005), would provide a means to compare genetic diversity among populations and species. However, we suggest that there are no absolutes or instant comparability among different species cases that can be obtained using genetic information alone. There is also an inherent risk to gathering and relying solely upon genetic information, in that it can result in a reduced management impetus in the event that little diversity is present within a population.

Conservation prioritisation of adaptive diversity

The protection of current adaptations and of species' potential to adapt to changing environments is likely to be of high importance to the long-term success of species conservation programmes, but these attributes are rarely taken into account explicitly. We propose that there is a case for assessing the degree of adaptation harboured within British populations and using this as a basis for conservation prioritisation. This approach also necessitates the investigation of the most appropriate source populations for population translocations and reinforcement, rather than applying ad hoc rules of thumb. The aim of such a strategy would be to identify and conserve the adaptive potential of species of conservation concern, in order to maximise the species' long-term persistence.

Measurement of adaptive diversity

Adaptive diversity (the potential to evolve) is frequently measured using experimental quantitative genetics approaches that compare the similarity in phenotype of related individuals, or by candidate gene approaches. Despite the potential conservation benefits these approaches could bring to bear, their development times are too long to be of practical value for most organisms of conservation concern. Several potentially useful surrogates exist for assessing the extent of adaptive diversity within species:

• Single gene phylogenies

Phylogenetics can identify genetic differentiation at a very coarse scale and could be useful in clarifying taxonomy and identifying putative management units, which may show differences in adaptation to the environment. However, they do not tell us much about the potential for adaptation;

• Measurement of traits

Trait measurement can also contribute to taxonomic interpretation, but its use in diagnosing adaptation is obscured by variation in traits caused by the environment rather than by genes;

• Measurement of traits in 'common gardens' and via reciprocal transplant experiments

Common garden experiments provide a means to assess whether observed trait variation has a genetic basis by observing the phenotype of individuals within a single environment;

• Measurement of genetic diversity at neutral molecular marker loci

Neutral markers can give a quick and clear impression of population structure. There is, however, a danger of there being only a weak correlation between neutral diversity and adaptive variation, because neutral markers may show different patterns of distribution to adaptive genetic loci that are subject to the influence of selection. The absence of molecular differentiation does not imply the absence of adaptive differentiation;

• **Comparison of marker differentiation with trait differentiation** (see Session 2, Conservation of adaptive genetic variability - Insights from comparative studies of marker gene and quantitative trait differentiation).

A decision tree for assigning conservation priority to populations

Given the differences in distribution (past and present), demographics, mating system and the wide range of methods available for assessing genetic parameters, we suggest a hierarchical approach to incorporating information on intraspecific diversity and adaptation in practical conservation prioritisation.

Assessment of the species context

1. Past management history of populations:

- i. Do the populations occur on differing habitats with different management requirements? This may indicate the presence of possible differential adaptation amongst environments;
- ii. Does the low success of management implicate a possible role for genetic factors in limiting the fitness of some populations?
- 2. Historical context population size and connectivity:
 - iii. Was the species once widespread with well-connected populations? If so, a policy of encouraging connectivity may be more appropriate than conserving populations *in situ*.
- 3. Breeding system:
 - iv. Is the species naturally inbreeding or outbreeding?

Assessment of diversity

- 4. Determine phylogeny within the species (using neutral e.g. mitochondrial markers). Elucidate or clarify taxonomy, identify 'unique' variability.
 - This approach can be risky and complex; there can be a lack of congruence between phylogeny and geography.
- 5. Reciprocal transplant and common garden experiments can be carried out where appropriate to the species in question (e.g. most plant species), in order to identify potentially adaptive trait variation that has a genetic basis.
- 6. Investigate genetic structure amongst populations and determine levels of variability.

Conservation actions

- 7. Prioritise the conservation of populations that have had a continuously large size and so are likely to harbour greater amounts of genetic variation.
- 8. Conserve *in situ* populations for which there is evidence of adaptation to their habitat.
- 9. In the event of evidence of reduced adaptation, aim to conserve populations that represent, as nearly as possible, the full range of neutral genetic diversity present within species.
- 10. Encourage population connectivity where historical evidence or current genetic differentiation indicates past gene flow amongst populations.

Key knowledge gaps

- is it possible to generalise methods of conservation prioritisation for species with certain breeding systems and historical demography?
- are these factors a reliable indicator of the genetic structure of species ranges or the potential for adaptation?
- how much adaptive diversity can we expect to encounter within natural populations in the UK and elsewhere?
- are conservation actions encouraging connectivity or the maintenance of genetic diversity meaningful in the political context of the UK; do we need to consider wider geographic species ranges including those occurring on the European continent?
- will knowledge of genetic factors be important for managing invasive species and understanding their adaptation to habitats within the UK?

How can knowledge gaps be addressed?

- basic research is needed into the extent and distribution of adaptive genetic diversity within species having a range of breeding systems;
- simple experimental approaches should be adopted amongst conservation practitioners to identify adaptive diversity through, for example, reciprocal transplant experiments and common garden experiments;

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• conservation might benefit from a more holistic approach to identifying populations of conservation priority and in identifying appropriate sources for translocations and population reinforcements. This approach would involve a more explicit consideration of species mating systems and demographic history.

4.3. Breakout group 3: Do we really need to know about genetic variation?

- For the conservation of which taxa is genetic information important?
- Is rarity important in deciding when we need genetic information?
- When can alternative approaches be used or other measures be utilised?

Discussion Notes

Is species conservation a genetic problem?

Whilst species conservation may not be exclusively a genetic problem, the whole premise of the workshop has been that we do need to take genetic variation into consideration when setting priorities and agreeing actions. There is a need for a set of clear principles, to ensure best use of valuable resources. We must be clear about what and how genetic information is expected to contribute to policy and practice and how far conservation genetics can inform management decisions on the ground, and help to refine policies for the conservation of biodiversity.

Once general principles are established, what strategic work still needs to be done?

Such a strategic approach needs to be informed by what we already know. Specific taxa are more important than others, and we can transfer knowledge from some taxa and apply it to others. The same principles may be applied from studies carried out elsewhere. However, we need to take care not to miss those special cases, e.g. aspen *Populus tremula*.

There is an equal responsibility for researchers, policymakers and practitioners to formulate questions better in order to improve understanding. For example, the research community requires a clear statement about what the practitioners want to know. We need a change in culture, whereby these different communities operate in a more integrated manner.

The Convention on Biological Diversity and the need for flexibility

Conservation programmes do not allow the level of investment that agricultural practices can involve (e.g. animal husbandry). As a consequence, any mistakes can be costly. This tends to direct us towards taking a broad approach, including incorporating the precautionary principle. However, the focus of the Convention on Biological Diversity (CBD) is considered restrictive from a genetic standpoint, as it focuses on maintaining biodiversity and patterns of distribution when there is a need for greater flexibility in the face of environmental change. For example, we need to manage our response to climate change and, given the uncertainties surrounding this, need to keep our options open.

Indeed, there is a whole range of options that need to be explored. Clarity is needed when formulating these ideas, as they step outside of the CBD framework. In particular, there is a danger of confusing the practitioner community with advice that appears to contradict conventional policy approaches.

Focusing our efforts

As a general issue, it is essential that genetic variability in common species is understood and that these species are not overlooked as they provide the basis for biodiversity recovery. There is a need for comparative studies using rare **and** common species. However, it is important not to

overlook the cultural significance of rare or local species. The CBD can lead to the adoption of a 'stamp collecting' approach, where we worry about keeping everything. There are strong arguments in favour of concerning ourselves more with maintaining ecosystem function, since it may already be too late for the former approach. This would lead us towards a focus on functionally critical species.

Different approaches may be necessary for different taxonomic groups. For example, species definitions within invertebrate groups mean that the research needs in relation to these are different from those in other taxa. The genetic variability present in marine organisms is relatively little known and this is likely to be another area requiring substantial research effort. Recent advances in our understanding of soil biota have necessitated considerable advances in analytical techniques, and it seems likely that novel genetic tools will allow greater insight in the study of soil biodiversity.

Sustainable development

We need to establish how to put conservation at the centre of sustainable development, and this is likely to require an improved understanding of how to undertake realistic economic valuation of charismatic and/or rare species. From a genetic perspective, cultural needs can be satisfied by manipulation, since most people are most concerned with which species are present, rather than which genes are present!

Rarity and the emphasis on uniqueness within conservation

How important is the idea of 'pure British ancestry'? Perhaps rarity and endemism have been given too much emphasis? Has nature conservation been resistant to the introduction and movement of 'foreign' units of diversity, including genes? The translocation of foreign ecotypes is excluded by policy (as a precautionary measure, due to uncertainty with regard to outcome), but is this a realistic or sensible strategy given the dynamic nature of biological systems? It may be considered a parochial attitude, or even racist! Should translocation be a last resort? Population augmentation is perhaps still preferable to allowing a local population to become extinct before introducing new genetic material, as at least some genes may be conserved. However, if the introduced genes are not well adapted, they will in any case die out and be lost from the population.

For the conservation of which taxa is genetic information important?

Should we be concerned with all taxa? Should these be treated equally? To date, rare taxa have received a disproportionate amount of attention. There are insufficient funds for the research of all taxa. As a consequence, we need a strategic approach. One way forward might be to consider those species that would be representative of other taxa, from which we could extrapolate. There is a need to establish some general principles, particularly with respect to how we use genetic information. Compromises will also be needed, as the timescales involved for the delivery of conservation actions are often very tight (e.g. in relation to climate change).

Key knowledge gaps

- how does genetic variability within species affect their interactions with other species in a community?
- to what extent are functionally adaptive genes represented in some populations?
- what are the relative merits of being well adapted vs future adaptability?
- how can we enhance our ability to predict future problematic species, in terms of genetic swamping or invasiveness resulting from hybridisation?
- does increasing population connectivity increase the risk of swamping of populations at the edge of a species' range with non-adaptive genes?

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- do we need to adopt different approaches depending on the longevity of the species involved?
- improvements are needed in the communication of the conservation-relevance of genetic techniques and information to practitioners.

Can the recommended actions be prioritised?

- 1. Assessments of local adaptation in terms of interactions within biological communities.
- 2. Involvement of population geneticists in the prioritisation of conservation-oriented research (link to policy)
- 3. Historical studies of populations (any bottlenecks in the past). How well can this be deduced? What work can be done to provide this information?
- 4. Action is needed in areas with very low biodiversity.
- 5. Monitoring of adaptive variation is needed, but is likely to be VERY expensive!
- 6. Documenting genetic diversity in invertebrate animals.
- 7. We are currently 'monitoring to death'? We need practical action on the ground!
- 8. Environmental justice involve local stakeholders in decision making.

5. Session 2: Where are we going?

5.1. Conservation of adaptive genetic variability – insights from comparative studies of marker gene and quantitative trait differentiation

Juha Merilä, Department of Biological and Environmental Sciences, University of Helsinki, Finland

In genetics, quantitative traits are those functional characteristics, such as height or weight, with a genetic basis and which vary over a continuum. These traits are typically encoded by several different genes, and therefore, are also known as polygenic traits. The amount of genetic variability in quantitative polygenic traits, within and among different populations, can be estimated with quantitative genetic methods (Falconer & MacKay 1996). The information gained using quantitative genetic methods is fundamentally different from that gained by analyses of neutral marker genes such as microsatellites. Most importantly, while the neutral marker genes allow inferences about population history and demography, quantitative genetic analyses allow us to estimate the degree of local adaptation among populations with respect to genes coding quantitative traits of interest. Therefore, information obtained from quantitative genetic studies of wild populations is highly relevant to conservation biology: this is information about genetic variation in traits influencing individual and population fitness.

 F_{ST} is a measure of the subdivision of populations. This coefficient is defined as the probability that two neutral marker genes taken at random, from different subpopulations, are identical by descent.

 Q_{ST} is equivalent to F_{ST} , calculated using gene frequencies for quantitative traits. The relationship between levels of F_{ST} and Q_{ST} can be used to infer patterns of evolution.

Box 1. Definitions of F_{ST} and Q_{ST}

Here, I aim to provide a short overview of what is currently known regarding the variation in genes coding quantitative traits among different populations of the same species. I will do this by focusing on comparative studies of quantitative traits and marker gene variation, and will reflect upon the use of such markers in conservation and the information that can be obtained from such studies.

In traditional population genetic analyses the degree of genetic differentiation among populations at neutral loci (e.g. allozymes, microsatellites) is often described using the F_{ST} index to estimate the fraction of total genetic variability that differs among populations. This index ranges between zero and one, with an F_{ST} value of zero indicating no differentiation and equal allele frequencies in different populations, while a value of one signifies the maximum degree of differentiation with populations fixed for different alleles at all loci. An equivalent index, Q_{ST} , can be estimated for quantitative traits, and comparison of the two indices provides a basis for inferring causes of population differentiation in quantitative traits.

Since the degree of differentiation in neutral marker genes is determined by the joint action of genetic drift and migration, F_{ST} gives us a reference point for the degree of population differentiation expected in the absence of selection. Hence, if the differentiation in a given trait
is a consequence of genetic drift (i.e. non-adaptive differentiation), F_{ST} should equal Q_{ST} . If $Q_{ST} > F_{ST}$, then the population differentiation in the trait in question must have been caused by natural selection that has favoured different traits in different populations, which would be considered as evidence for local adaptation. If, on the other hand, $Q_{ST} < F_{ST}$, this means that the mean trait values among populations differ less than would be expected due to genetic drift alone and that selection is acting to maintain the current form.

The basic theory and tools for comparative studies of quantitative trait and marker gene differentiation have been available for around 50 years, but they were first used in empirical studies during the mid–1980's. Between 1993 and 2000, there were around twenty empirical studies that compared F_{ST} and Q_{ST} estimates in the same sets of populations. A meta-analysis of these studies revealed that Q_{ST} typically exceeds F_{ST} , suggesting that genetic differentiation in mean values of different quantitative traits is typically higher than that in neutral marker genes (Merilä and Crnokrak 2001). Since this finding, the number of empirical and theoretical studies using Q_{ST}/F_{ST} -comparisons has more than tripled but the big picture appears to remain the same: Q_{ST} estimates are typically, but not always (see below), larger than F_{ST} estimates for the given study. In other words, the available data suggest that there is more genetic variation among wild populations than is suggested by traditional marker gene analyses. It is also worth emphasising the fact that many species showing no or very little differentiation in marker genes ($F_{ST} < 0.2$) often appear to be almost fixed ($Q_{ST} > 0.8$) for different alleles in loci coding quantitative traits, i.e. species with very little differentiation at neutral markers can show very large differentiation in functional quantitative traits.

Another observation highly relevant to practical conservation and population management is that the correlation between the F_{ST} and Q_{ST} estimates across different studies and populations is weak at best. As a consequence, it is not possible to predict the degree of genetic differentiation in quantitative traits from data regarding genetic variation at neutral marker genes. Furthermore, the correlation between the amount of genetic variability within populations in quantitative traits (as measured by heritability of the traits) and the amount of genetic variability in neutral marker genes (as measured by heterozygosity) is effectively zero (e.g. Pfender *et al.* 2000). Hence, the amount of genetic variability in neutral marker genes tells us little about the evolutionary potential of any given population.

The conclusions above are generalisations, and are contradicted by the findings of some studies. For instance, there are some studies where $Q_{ST} < F_{ST}$, suggesting that natural selection has favoured the same phenotypes in different populations (Edmands & Harrison 2003). It is possible that many rare and specialised species could be found with little differentiation in the quantitative traits relevant for their specialisation. For example, species adapted to a particular type of habitat may be rare because this habitat is rare. If the selection pressures on quantitative traits in these rare habitats are conservative, this could mean that $Q_{ST} < F_{ST}$ in rare species.

Another situation that is currently understudied in the wild is the possibility that local adaptation in small populations is hampered because of low levels of genetic variability and the inefficiency of selection relative to drift. From studies of laboratory models, we know that selection in small populations is less efficient than selection in large populations (e.g. Wright 1931; Jones *et al.* 1968; Weber & Diggins 1990). If so, we would also expect the degree of quantitative trait differentiation among small populations, (e.g. those subject to habitat fragmentation) to be less than that observed among larger populations, such as those residing in more continuous landscapes. The opposite pattern is expected for neutral marker genes, which evolve mainly under the influence of genetic drift. Some unpublished studies suggest that this might actually be the case, but more research on this subject is needed. Several problems and issues are related to the use of quantitative traits and neutral marker genes as a means of inferring patterns of selection in natural populations. First, obtaining Q_{ST} estimates is typically difficult as this requires breeding experiments conducted with individuals from several different populations. Secondly, the statistical properties of Q_{ST} estimates and their standard errors are problematic: they are difficult to estimate accurately, and therefore, comparisons based on small number of populations may often be quite uninformative. Furthermore, as pointed out by Hedrick (1999, 2005), the F_{ST} estimates based on highly variable markers are often bounded by values less than one, meaning that the F_{ST} estimates may in general be underestimated. Whether the same problem applies to Q_{ST} estimates, and to what extent, remains to be investigated.

In conclusion, the current evidence suggests that there is typically more genetic variation among natural populations than previously thought. Studies of neutral marker genes seem to generally underestimate the degree of genetic population subdivision in quantitative traits. In other words, there may be much more genetic heterogeneity, even over short distances, than is currently estimated; as most measures of genetic diversity from wild populations are based on studies of neutral marker genes. Furthermore, since the degree of differentiation in marker genes and quantitative traits is uncorrelated, we cannot predict the degree of genetic differentiation among populations from the studies of markers genes alone. Since one of the main goals of conservation genetics is to maintain genetic diversity within and among different populations of the same species, translocation, restocking and restoration projects should be concerned about disrupting local adaptations by mixing populations of different origin. They should also perhaps worry about basing management decisions on underestimates of genetic diversity among different populations.

5.2. Conserving the generation of biodiversity

Richard Ennos¹, Pete Hollingsworth², Ashley Robertson¹ and Graham French^{1,2}

Biological diversity at the species level is determined by a balance between the generation of novel taxa through speciation processes and the loss of species by extinction. The vast majority of research on genetic aspects of biodiversity conservation has been concerned with understanding population genetic processes that accelerate the rate of extinction, and with devising management strategies that will alleviate these problems. However, it should also be remembered that if, over the long term, there is a reduction in the generation of novel taxa, this too will ultimately reduce the equilibrium level of species diversity. Thus another important role for genetics in biodiversity conservation is to elucidate the processes leading to the generation of novel species and to recommend management that will ensure continuation of these processes.

Conserving processes that generate novel taxa is of special practical relevance in the context of the British flora. As a consequence of glaciation, we have a flora that is very largely derived from continental Europe by migration. Many of our rare endemic species are the products of 'speciation' events occurring within the last 10,000 years. These are rightly afforded high conservation status, with over 25% of the taxa on the UK BAP list being the products of recent evolution. However, the fact that these taxa are recently evolved also means that their taxonomy may be very complex and fluid, with a plethora of described entities. There may be serious problems with identification and this, coupled with the large number of described taxa, means that a conventional Species Action Plan (SAP) approach to conservation may be unworkable.

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An alternative conservation strategy for these groups of plants is to invest effort in understanding the evolutionary processes that have in the past generated the novel taxonomic diversity that we see today (Ennos *et al.* 2005). This knowledge can then be used to define management practices that will facilitate continued evolution in these groups and so circumvent the problems that would arise if each described taxon were allotted a separate SAP. The objective is thus to conserve the evolutionary processes that generate novel taxa, rather than to preserve the named products of these processes. This approach to conservation can be illustrated by reference to two genera with endemic taxa in the British Flora, *Sorbus* (whitebeams) (Figure 9) and *Euphrasia* (eyebrights).



© Richard Ennos **Figure 9.** Novel *Sorbus* (whitebeams) taxon at Catachol Burn.

The Isle of Arran is one of a number of hotspots of *Sorbus* biodiversity in Britain. Two endemic taxa have been described, Arran whitebeam *S. arranensis* and Arran service-tree *S. pseudofennica* (Robertson *et al.* 2004a). The application of genetic analysis using molecular markers has shown that *S. arranensis* is the triploid, apomictic product of hybridisation between diploid, sexual *S. aucuparia* (rowan), and tetraploid, apomictic *S. rupicola* (rock whitebeam). This hybridisation event has taken place on at least three occasions. The second endemic taxon, *S. pseudofennica*, is a tetraploid hybrid between the triploid *S. arranensis* and the diploid *S. aucuparia*, and has been formed on at least five different occasions on Arran. Approximately 20% of the offspring of *S. pseudofennica* are produced sexually. Further studies of the Arran populations have detected a further hybrid with novel leaf morphology (Robertson *et al.* 2004b). This is apparently the product of a *S. pseudofennica* and *S. aucuparia* backcross (Figure 2).



Figure 10. Novel leaf morphology, a product of a backcross between *S. pseudofennica* and *S. aucuparia*. © Ashley Robertson.

The situation on Arran is thus one of continuing hybridisation between a common sexual diploid (*S. aucuparia*) and both an apomictic tetraploid and its hybrid products, generating at least three novel taxa (Figures 10 and 11). There is the potential for more taxonomic diversity to evolve in the future. A traditional SAP, preserving the named entities *S. arranensis* and *S. pseudofennica ex situ*, would be inadequate either for conserving existing diversity or for safeguarding future evolutionary processes on Arran. We advocate *in situ* conservation of the evolving complex, comprising the named endemic taxa, the unnamed novel hybrid and the common diploid *S. aucuparia* that has been instrumental in the generation of biodiversity. *In situ* conservation on Arran is essential because the special geology of the region brings together the acidic and base rich habitats necessary for the coexistence of the parents and their hybrid products.



Figure 11. Evolution of *Sorbus* on Arran. © Richard Ennos.

The arguments for basing conservation on an understanding of the genetic origins and continuing evolution of taxa are even more compelling in the case of the annual hemiparasitic genus *Euphrasia*, where species delimitation is often, but not invariably, problematic. Both diploid and tetraploid taxa are present in Britain and molecular marker studies show that little gene exchange occurs between the ploidy levels. The two diploid endemics on the UK BAP list, *E. vigursii* and *E. rivularis* are taxonomically and geographically well delimited, and are apparently the result of rare hybridisation between diploid and tetraploid taxa (Figure 12). Conventional SAPs are therefore appropriate for conserving these taxa.



Figure 12. Conservation of endemic *Euphrasia*; a genus containing 9 named species, with 6 endemics on the UK BAP list. © Graham French.

However, among the endemic tetraploids, species limits are ill defined and adopting a conventional SAP approach is impracticable. Analysis of the mating system indicates that many of these tetraploid taxa are highly inbreeding (French *et al.* 2005). It appears that the endemic taxa have originated on multiple occasions as segregating selfing lines derived from crosses between the widespread outcrossers (*E. arctica/E. nemorosa*) and the widespread inbreeding taxa (*E. micrantha/E. scottica/E. frigida*). In these circumstances, conservation is best achieved by programmes that facilitate hybridisation of widespread tetraploid outcrossers and inbreeders in ecologically heterogeneous habitats where selection of differentially adapted selfing lines can take place. The whole focus of conservation for these taxa is thus switched from futile attempts to classify and preserve the diverse products of multiple hybridisation events, to the management of habitats for coexistence and hybridisation of well defined and widespread *Euphrasia* species that can be identified by competent botanists.

5.3. Adaptation to climate change

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Introduction

Global temperatures have increased recently, and the world has seen alarming patterns of changes in precipitation and extreme weather (Houghton *et al.* 2001). In the British Isles, increasing spring temperatures and changes in precipitation patterns have also been observed, as well as biological responses to these changes. For example, earlier arrival dates for swallows *Hirundo rustica* along the coast of England and earlier laying dates for many British birds may have occurred in response to warmer springs and greater insect abundance. All wildlife species confronted with systematic changes in environmental conditions and increased environmental variability face three possible outcomes: they can move elsewhere, adapt, or go extinct. Here I focus on the second outcome of adaptation in the context of climate change.

Adaptation

The term 'adaptation' is used in more than one context in the literature. It is used in a 'plastic' context where it refers to physiological, behavioural, or other flexible and non-genetic responses to climate change. In an evolutionary context, adaptation describes genetic responses to environmental change. The question I wish to address here is whether phenotypic plasticity, which is the 'change in the average phenotype expressed by a genotype in different environments' has the capacity to evolve. This is because the degree of plasticity itself may be adaptive, as it could allow a population to persist in variable environments.

Microevolution

Quantitative genetics provides the appropriate statistical framework to study small-scale evolutionary changes, known as microevolution, for continuously distributed, quantitative characters. The evolutionary response of a trait is a function of the trait heritability, reflecting genetic variation, and the strength of directional selection.

Evidence for microevolution comes from changes in gene frequency or predicted breeding values, and generally requires long-term studies of marked individuals in the wild. Simply recording changes in population means over time in cross-sectional studies is insufficient to understand the evolutionary implications because it is impossible to separate plastic responses from evolutionary change.

Separating plasticity from microevolution

The first study to use longitudinal data to separate plasticity from microevolution in the wild was published by Pryzbylø et al. (2000). They used longitudinal data on breeding over 16 years to show that collared flycatchers Ficedula albicollis from Gotland lay their clutches earlier following warm wet winters. However, they found no change in laying date over time, which indicated that the changes were purely plastic.

Genetic changes were first documented in North American red squirrels Tamiasciurus hudsonicus from the Yukon, Canada, (Réale et al. 2003). Spring temperatures in the Yukon have increased by 2°C since about 1970, and mean food (spruce cone) abundance has also increased. Birth dates have advanced by 6 days per generation in response to these changes. Using a matrilineal pedigree, Réale et al. (2003) showed that birth date is heritable and could estimate that a genetic trend accounted for 0.8 days of the advance per generation. Plasticity, therefore, accounted for most (87%) of the adaptive response.

Is plasticity a trait that may evolve in response to changing environments?

Modelling can be used to separate traits statistically into fixed and plastic components. Brommer et al. (2005) used this approach to study reproductive characters in collared flycatchers. They found that individuals varied and that selection favours earlier and more plastic laying dates. However, they found little genetic variation for mean laying date or for plasticity. This may explain why Pryzbylø et al (2000) did not find changes in laying date over time despite advancing spring temperatures (Figure 13). Collared flycatchers therefore lack genetic variation to adapt to these changing conditions.



© Juha Merilä.

Figure 13. Collared flycatcher *Ficedula albicollis* and graph showing the relationship between mean laying date (±SE) of 2-year old female collared flycatchers and NAO-index (North Atlantic Oscillation) over the study period (observations weighted by sample size in each year; Pearson r=-0.535, n=15, p=0.040). Pryzbylø et al. (2000).

A lack of genetic variation may not be the only mechanism that can prevent evolutionary change. In the Netherlands, caterpillar peak biomass date has advanced by 9 days over 23 years in response to warmer springs (Visser et al. 1998). In Dutch great tits Parus major the date of laying has failed to respond, partly because the cue to lay eggs (caterpillar emergence) did not advance as much as the availability of the resource (caterpillar peak biomass due to rapid growth). This mismatch generates increasing selection on the date of laying by Dutch great tits. Nussey et al. (2005) subsequently showed that plasticity varies between females, and that earlier breeders are more plastic. Plasticity is also genetically determined. They also showed increasing selection for plasticity as well as an early mean laying-date. However, lack of a phenotypic response, and the fact that fitness in this population is decreasing, suggests that the rate of the evolutionary response is just too slow to track environmental change.

Conclusions

These studies provide a powerful framework in which to study adaptation to climate change. They also illustrate a number of mechanistic constraints on adaptation. There may be limited genetic variation for selection to act on, as life history traits often have low heritability and many populations are small or declining, and may have low genetic variation. The genetic basis of plasticity is likely to be a consequence of multiple genes, or multiple effects of individual genes; which means that adaptation may be constrained by selection on genetically correlated traits.

Selection also fluctuates in time and space, and increased climatic variability may lead to more variable selection regimes. There may be insufficient time for adaptation to occur, especially for long-lived organisms. Adaptive responses may be masked by other phenomena such as inbreeding depression, which accumulates in small, isolated populations. Population size may also be important, as genetic drift may overwhelm adaptation in small populations. Finally, gene flow into peripheral populations under pressure to adapt may cause them to act as sinks for immigrants from maladapted source populations, especially if the peripheral populations are small. However, these are all theoretical possibilities and we have a very narrow base of empirical data upon which to draw a few generalisations.

It is clear that we need more quantitative genetic data and long-term studies to assess the potential for genetic adaptation. Intuitively, it seems unlikely that microevolution can keep pace with climate change, especially for long-lived organisms. Small populations have limited adaptive potential for many reasons and must be at increased risk of extinction due to genetic factors, especially when generation times are long.

Summary

- adaptation can originate from phenotypic plasticity and/or genetic change;
- evolutionary responses are determined by the amount of genetic variation a population possesses and the strength of the selection pressure at work;
- experimental studies can separate phenotypic plasticity and genetic change;
- phenotypic plasticity itself can be genetically determined and subject to evolutionary pressures;
- factors including limited genetic variability, levels of heritability, population size and gene flow will influence adaptability;
- there may be insufficient time for adaptation to occur;
- fluctuation in selection pressures may increase with increasing climate variability;
- more quantitative data and long term studies are required to assess the potential for genetic adaptation.

6. Discussion

Three key questions relating to the papers presented in Session 2 were addressed in parallel breakout groups, as follows:

- 1. What strategies do we need to adopt to conserve the processes that sustain diversity?
- 2. How should we strike a balance between conserving local adaptation, avoiding inbreeding depression and promoting future adaptability?
- 3. Protected areas or landscapes: a simple choice?

The outputs from these groups are given in the following section. A synthesis of the main points is provided in the final section of this report, which identifies knowledge gaps and the research needed to fill these.

6.1. Breakout group 4: What strategies do we need to adopt to conserve the processes that sustain diversity?

- Do we know when hybridisation between species, population size or movement of individuals between populations is important in promoting or sustaining genetic diversity?
- How should we approach the conservation of these processes?

Discussion Notes

It is important to clarify whether our focus is on processes that generate biodiversity or those that sustain biodiversity. Furthermore, how broad is our definition of processes? Do these include management?

Hybridisation

Hybridisation can be considered a good thing when introgression is occurring but there are instances when hybridisation reduces genetic diversity. It is a wasted process when it produces sterile hybrid offspring, and may be perceived as bad when hybridisation with alien species occurs. An example in the UK is that of red deer/sika deer hybridisation. Changes in habitat management can bring together species that would not normally meet. In the USA the red wolf/coyote interaction is considered by some to be a natural process; however, it has been facilitated by anthropogenic habitat modification.

Management implications

These issues raise the generic question: do we want to restore things to some previous condition? A major problem is that we often have no data about what conditions were like during the chosen time period.

In practical terms, it is hard to oppose some degree of introgression. Human activities bring together many compatible but normally allopatric species, so that they can hybridise in genetic hotspots – these are disturbed, rapidly changing 'unnatural' habitats. Are these what we want to conserve?

There is a problem in that too much international and national legislation focuses on named species, and we have to accept that instances of hybridisation are widespread. This presents a problem with Special Areas of Conservation (SACs), i.e. where citations are for pure species, not hybrids. There is an argument that says that site designations should be maintained in order to allow genetic process to occur. However, under the present system, rarity of parents is a stronger

justification for preserving a population as a whole than is the origination of hybrids. This is not necessarily the right approach, particularly in a changing world! So, can we reach a point where the two goals coincide? That is to say, can we maintain rare species and, in the process, help to ensure that hybridisation occurs, whilst ensuring that the source population is protected from hybridisation? How feasible is this?

Population size

An understanding of genetics becomes ever more important as population size decreases. Population size could well be the main restriction in promoting or sustaining genetic variability, but may not be working alone. Geneticists are reluctant to give precise numbers to define minimum population size. What is clear is that there is a low number below which genetic drift overrides the hybridisation process. Rather than consider *minimum population size*, we should be focusing on *effective population size*, based on the number of breeding adult individuals (it might also be considered to be the *functional population size*). Geneticists need to be clear about what this means when communicating, particularly with policymakers and practitioners.

Key knowledge gaps

In order to address these, we should break the question down into separate parts, to consider:

- hybridisation between species;
- population size;
- movement of individuals.

Hybridisation

Are we taking a snapshot in time? Do we need to be conserving the process? Or should we be conserving the habitats? And are we looking at the 'right' habitat (i.e. not the one in which the species evolved)?

Population size

Neither practitioners nor researchers have a clear understanding of what constitutes a *minimum viable population size*. The minimum viable population size needs to be understood in relation to the accumulation of detrimental variance, or mutational meltdown. Unfortunately, this is not known, so geneticists cannot give advice to practitioners and policymakers. As a result, targets set in the UKBAP may not have a firm evidence base and there may have been insufficient genetic input.

The *effective population size* is considered to be 10–50% of the census size. However, for management purposes a greater population size is needed, and clonal species are currently excluded from consideration.

Genetic pressures are expressed at population levels of 'a few tens', e.g. a suggested threshold of 50 individuals. However, is it worth taking action if we have already reached this point? The conservation effort needed may be too great, e.g. lady's slipper orchid *Cypripedium calceolus*. Perhaps efforts should focus only on endemic species that have reached these levels, accepting that we cannot sustain the others. Establishing an effective population size for invertebrates can be particularly difficult. Year on year variation in population size means that it is difficult to find an effective mean. There are many examples of invertebrates with very small population sizes in the UK, which are abundant in continental Europe.

As a general point, should we not focus on declining species, rather than those that have already declined?

How do we approach the conservation of these processes?

In the UK, we have the best monitored and best mapped biota in the world, so numerical and distributional targets are based on solid information. However, we need more information on ecological processes. Habitat conservation will take care of species, but does this also preserve the processes? Should not our management go further, in order to conserve combinations of habitats, and the creating and recreating processes? Networks and connectivity are particularly important. We need to recognise that the species composition of communities is in constant flux and that management needs to permit evolutionary adaptation through consideration of ecological processes.

6.2. Breakout group 5: How should we strike a balance between conserving local adaptation, avoiding inbreeding depression and promoting future adaptability?

- Is local provenance important when restoring populations?
- Should we pro-actively import genes into genetically depleted or inbred populations?

Discussion Notes

Is there a conflict?

Conservation of local adaptation does not necessarily conflict with the need to avoid inbreeding depression and to promote future adaptability where populations are large. However, where populations are small, gene flow needs to be encouraged. In the UK, populations are increasingly fragmented.

How do we define gene flow?

Geneticists define gene flow in terms of the successful establishment of individuals, but from a conservation perspective there is a need to take account of unsuccessful establishment (e.g. in relation to pollen flow), as natural selection acting today may act differently tomorrow. The definition of gene flow means that, within continuous populations, local adaptation is considered as selection within a generation, which potentially undermines its conservation importance. Even so, translocations short-cut some of the selection processes and very small populations still have the potential to be swamped.

Should existing declines in populations be addressed before increasing gene flow or is there a need to act now given the potential rate of future environmental change?

Disrupting local genetic variation may be abhorrent to some conservationists but there is no way of establishing whether there is a problem in genetic diversity using markers. UK habitats have been fragmented by intensive land use in recent decades and time lags to extirpation mean that they may currently often support populations that are not genetically viable. There is a need to take account of changes in ecological processes and not simply await declines. Some species naturally increase gene flow when populations are reduced; therefore, it may be inappropriate to apply universal policies across all taxa.

History is all-important. Key questions are:

- Was the population originally large or was it always small?
- Has the effective population declined recently?
- Does fragmentation prevent adequate gene flow?
- Could fragmentation increase gene flow (e.g. tree seeds in woods compared to across open ground)?

For some species fragmentation is serious but for others it may be beneficial. Physical fragmentation may not equal functional fragmentation. This may be a question of scale; for example, a population that goes from 10,000 to 1,000 individuals may not be an issue but one that declines from 1,000 to 10 individuals is definitely a concern.

Other questions in this context are:

- What is the causal relationship between fitness and heterozygosity?
- Can numerical thresholds be used as the basis to management decisions?
- Is gene flow there anyway?
- How important are rare and chance long-distance dispersal events?
- How much migration is necessary to avoid inbreeding depression and promote future adaptability?
- How much gene flow would lead to loss of local adaptation? This would depend on effective population size, degree of divergence, extent of selection pressure, and whether the species is a generalist species or specialist species.

Increasing gene flow should be achieved through enhancing landscape permeability, in preference to restocking and translocating species.

Can F_{ST}/Q_{ST} give us clues as to what sorts of species we need to worry about?

The risk of inbreeding depression depends on the effective population size. Decisions to promote future adaptability should bear in mind effective population size, the rate of environmental change, and the potential for rapid evolution, of which there are lots of examples (e.g. Jowlett 1964).

Habitat creation

Habitat creation to buffer and extend habitats is not undertaken primarily for genetic reasons, although it may have genetic implications. There is a need to consider what it may mean for gene flow of non-target species and to what extent it will promote community change or increase invasion. However, unless the resilience of habitats is increased through buffering and extending them, they will be vulnerable to invasion anyway. Some people are concerned that genetic diversity has intrinsic value and action should only be taken when the consequences of doing so are known. A practical example would be in relation to restoration of plantations on ancient woodland sites: should we regenerate from one or two remnant trees or bring in stock? It is argued that the precautionary approach should be to use 'local provenance' as far as possible. However, in reality there are practical constraints on conservation actions. It should also be borne in mind that 'local provenance' does not mean 'local' but is defined by population boundaries, which themselves are a matter of debate. Populations of many species in the UK might be regarded as continuous.

Key knowledge gaps

- do we understand local adaptation?
- what is the genetic basis of local adaptation (in order to better understand how gene flow may disrupt it)?
- what is the spatial or temporal scale of local adaptation?
- how should population boundaries be defined?
- at what scale does outbreeding depression occur?
- how much migration is needed to promote adaptability?
- with reference to existing effective population size, can we rank how much migration would lead to: loss of local adaptation (high migration); inbreeding depression (low migration); promotion of future adaptability (intermediate migration)?
- can F_{ST}/Q_{ST} give us clues as to what sorts of species we need to worry about?

- can we generalise about the degree to which plants are likely to be locally adapted based on whether they are selfers or outbreeders?
- does the rate of evolution of local adaptation undermine its importance?

6.3. Breakout group 6: Protected areas or landscapes: a simple choice?

- What is the role of protected areas in the conservation of genetic diversity?
- To what extent should we consider the need for gene flow at broader spatial scales to conserve adaptability?

Discussion Notes

What is a protected area?

The sizes of protected areas vary hugely, from SLINCs to National Parks or AONBs. All these areas have varying levels of protection. However, protection does not necessarily equate to/or imply management, or vice versa. Designation of a protected area may be for specific reasons with other values of the area being ignored or overlooked, e.g., its genetic diversity.

Are they an adequate ark (should they be an ark)?

Protected areas should not be viewed as a stand-alone ark. We do not really know if protected areas are 'adequate'. There is protection provided for some species and habitats through the EU Habitats Directive but there is a need for a landscape-scale, nation-wide strategy that incorporates the role of protected areas. From a genetic perspective, common as well as rare species and especially declining species need to be considered. It is important to remember that rare species localities do not necessarily correlate with biodiversity hotspots.

Genetic risks

- common species the genetic risk posed by fragmentation varies dependent on their capacity to disperse;
- widespread species that occur at low abundance may have special needs based on the history of the species. It may be difficult to cater for these species within protected areas;
- rare species landscape context may be less of an issue;
- marginal populations special issues (see below).

How do we monitor and demonstrate the role of protected areas in conserving genetic diversity?

- are protected areas a source of genes?
- are they diverse for historical reasons or due to management? Before and after studies are needed but generally these are not available, e.g., in no-fishing zones;
- how much of the total genetic diversity do protected areas contain?
- the signature of gene flow may be detectable by assignment tests and reductions in inbreeding are also rapid and detectable but the signature of increasing genetic diversity due to increased effective population may be very slow to reveal itself;
- there is a difference between 'colonisation distance' and migration distance. It is difficult to estimate colonisation distance. Similarly, there are differences in movement in different habitat types that are not well understood;
- it is important for policy-makers to see a return. This may present a serious time-scale problem with some manipulations.

Habitat networks

Networks of habitats are required at a landscape-scale in order to allow communities to persist. But how should landscapes be managed and what specific strategies are needed from a genetic perspective?

- make patch sizes bigger, if possible;
- manage the intervening landscape to be more 'wildlife-friendly' with existing seminatural habitats remaining as the critical core;
- increase disturbance to promote species diversity e.g. felling/coppicing?
- encourage species to move 'naturally' rather than move them because only a very low level of gene flow is needed, especially for advantageous alleles, and facilitating natural movement works for multiple species whereas artificial movement only aids targeted species;
- consider increasing connectivity at range margins with care. Is it best to maintain the uniqueness of marginal isolates and avoid swamping by gene flow from their core range, or is it better to enhance genetic variation in isolates to facilitate adaptation to change?

Recommendations

- from a genetic point of view, it is more important to manage landscapes than protected sites. Connecting islands, or increasing island size, is better than creating new islands but the creation of 'stepping stones' may be a good way to enhance matrix permeability;
- artificial movement (genetic rescue) should be a last resort for attempting to save a population or species under immediate threat from inbreeding depression, e.g. 'Florida panthers'. Even here some people might consider that re-introduction after extinction would be a better option than deliberate hybridisation.

Key knowledge gaps

- what do current levels of protection in designated areas currently achieve from a genetic perspective?
- is it possible to quantify dispersal distances, colonisation distances and permeability of unsuitable habitat? This is a major undertaking, and is species specific. The extent to which the answers can be generalised is itself a knowledge gap;
- what level of connectedness is needed for 'optimum' gene flow?

These questions could be addressed by:

- studying colonisation of new habitats, e.g. ponds, farm woodlands, headlands, etc;
- testing, e.g., movement of a suite of species between populations, such as ponds, using assignment approaches;
- targeting taxa most likely to have genetic problems, e.g., amphibians, ideally with varying intervening landscapes.

7. Session 3: the next steps

7.1. Conservation and genetics: a broad, shallow and personal perspective

John Hopkins, English Nature, UK.

Available evidence clearly indicates that genetics has played only a small part in the practice of biodiversity conservation in the UK. For example there is no mention of genetics in UK wildlife legislation, there are no genetic guidelines for the selection of Sites of Special Scientific Interest (SSSIs) and genetics is not mentioned in the England Biodiversity Strategy.

However, the null hypothesis that genetics is irrelevant to conservation policy and practice is not entirely supportable. Genetics, along with species and habitat/ecosystems, is one of the three cornerstones of biodiversity in the UN Convention on Biological Diversity. More practically, genetic analysis increasingly plays a part in species recovery programmes and other species and population-focussed conservation actions, not least in testing the taxonomic validity of rare species, in relation to closely related, congeneric species. Somewhat haphazardly, but not infrequently, conservationists mention genetic phenomena such as in breeding depression, founder effects, and genetic isolation. It would appear that, if asked, most practising conservationists would see genetics as an important consideration in decision making, despite its absence in much current practice.

Currently the barriers between genetic science and conservation practice appear to be lowering due to the availability of new genetic tools which can be applied to conservation problems, and a widespread but not always well-informed awareness of them in the conservation community.

I would like to suggest that there are other issues that explain this apparent dysfunctional relationship between conservation and genetics and if addressed could result in a far more satisfactory interaction, at a time of rapid global genetic impoverishment.

Values

A large part of conservation genetics concerns the use of genetic information to protect populations and species from extinction. To a lesser extent, or at least through more complex ecological mechanisms, genetics plays a role in the maintenance of species diversity at the community level, but this has been little explored by conservation practitioners.

I would like to ask if it is not also time for us to think carefully and more clearly about alleles and genetic loci themselves as entities to be conserved, lest we allow the current rapid loss of global genetic diversity to proceed simply out of complacency. It has rapidly become a media cliché that species share a high proportion of their 'genes', even across wide phylogenetic ranges, suggesting the global genome is much less diverse and rich than might have been thought in the past. It may be that a large part of this global genome is found outside the current priorities for conservation, as for example amongst *Archaea* and other extremophiles.

Of course one issue that should influence our thinking about genetic conservation *sensu stricto* is the degree to which alleles and genetic loci are replaceable. Given that genetic material is simply chemical it would appear possible that alleles and genetic loci have a high potential recreatability. Here, caution would seem appropriate, given that currently genetically manipulated organisms of all types involve transfers of genes between organisms, not brand new genes, and the use of mutagens in commercial breeding programmes has not proved to be a

highly successful approach. We should also be cautious, for clearly some genetic loci are extremely ancient. If also rare their loss might be associated with a significant source of regret.

I would posit that, independent of issues of recreatability, genetic variation is an inherently interesting property of species and habitats that deserves to be conserved. Genetics is a rich and increasingly available source of meaning about evolution, past environments (including some of the earliest phases of life on earth), biogeography and ecology, some of which has very direct relevance to current environmental crises.

More pragmatically, one might also ask to what degree the diversity of the global and more local genomes underpins the delivery of ecosystem services such as nitrogen fixation and decomposition. Might the provisioning by living things of products such as food, fibre and pharmaceuticals also be seen as genetic services?

Science

Although by no means a problem unique to genetics, it is in my experience unclear to most conservation practitioners where there is scientific consensus amongst geneticists (policymakers and practitioners shy away from areas of scientific uncertainty where possible), and which areas of this consensus are relevant to conservation practice.

A further impediment to the wider uptake of genetic information is caused by the scientific methods adopted in genetics. These often emphasise probabilistic solutions to problems and are historically rooted in this approach. Notoriously, the human mind is poorly designed to deal with probabilistic information and formal logic. In contrast the discipline of ecology has sought to develop more deterministic solutions to problems, although it can be argued this causes the misrepresentation of the behaviour of ecosystems. It is notable that demographic research by ecologists, which also emphasises probabilistic solutions, despite its high academic profile, has had a surprisingly modest impact upon conservation practice, where objectives and targets are seldom set in probabilistic ways.

More prosaically, the availability of new methods in genetics, and their widespread reporting in the media, has lead to an over-simplistic expectation amongst conservationists of how cheap and easy they are to use. For example, the extremely slow progress made over several decades in the application of remote sensing to conservation practice has lead to widespread cynicism about the approach, and should make us cautious about over-selling the value of newly-developed methods.

Education

A significant problem may not be the training of the next generation of conservation practitioners in conservation genetics, but the knowledge and understanding of those already working in the field of conservation, *inter alia* because some will have been educated at a time when genetic conservation was in a primitive stage of its development. The absence of inservice training and continuing professional development opportunities may mean that the uptake of genetic advances is likely to continue to be slow amongst conservationists.

Sociology

A striking distinction between ecology and genetics (if I am allowed to artificially treat these as disciplines hermetically sealed against each other) is that, whilst conservation policymakers and practitioners usually have a rich and varied set of collaborations with ecologists, the conservation community has had relatively sparse links to the genetics community. Conservation practitioners are more likely to attend ecological conferences than genetics conferences. In the statutory sector this may be due to a subtle 'founder effect', given the founding fathers of the UK conservation agencies, notably Sir Arthur Tansley, were mainly ecologists. I suggest the more

limited social interaction between conservationists and geneticists is related to a slower and more hesitant take-up of genetic advances than is true for ecology, given the appliance of science advances as much through informal communication as formal publication.

Conclusion

I believe that in future decades conservationists will realise that some, perhaps many, of the policies and practices we undertake today have been unsuccessful because genetic aspects of the problems were not well enough understood. There is therefore in my view an important need to improve the links between genetics and conservation. None of the problems outlined above are insurmountable, although unless the issues are addressed in the round, the end result is likely to be continued poor communication.

7.2. The Country Agencies' view on the conservation of genetic diversity

Barbara Jones, The Countryside Council for Wales, Wales

Staff in the conservation agencies have a number of priorities which take up most of their time, such as habitat protection and restoration, management agreements, site designation, management plans and liaison with landowners, statutory and voluntary bodies, meeting (inter)national conservation targets, research into monitoring effects of conservation management and the effects of pollution and climate change on habitats and species; with all these priorities and the number of pressures on British wildlife and habitats such as pollution, overgrazing, undergrazing, drainage, development pressures and climate change, so far, consideration of genetics has almost been considered a 'luxury'.

In addition there is the problem of a general lack of knowledge of genetics in conservation organisations. Ecologists often do not know which questions should be asked to conserve genetic diversity (or even if there is a question). This is important, as the sophisticated techniques now available are often only as effective as the questions asked. However, recent research together with increased knowledge and improved collaboration between geneticists and ecologists has highlighted the importance of considering genetic factors in conservation management for both species and habitats. Conservationists are becoming increasingly aware of this and a series of issues where genetic research is likely to prove most useful are emerging. These include:

- the effects of habitat fragmentation on species distribution and viability. How many populations need to be retained to ensure that a species, and its gene pool, are conserved? Should populations be kept separate or do they form part of a large metapopulation, the components of which need to be linked via gene flow?
- In an example involving work on lesser horseshoe bats Rhinolophus hipposideros, research focussed on the importance of mating roosts in the promotion of genetic diversity, connectivity and isolation among roosts and the genetic consequences of small colony size (G Jones, unpublished);
- currently evolving genera how to conserve a 'species' or should we be looking at processes and concentrating on the habitat needed for the genus to evolve? This is currently an important issue for conservation agencies who are discussing this with genetics researchers in regard to the genus Euphrasia;
- when does genetics become a factor in the conservation of a species and, conversely, when does it cease to be a factor? This relates often to small/edge-of-range population viability and future persistence under environmental change. An example includes the arctic-alpine species Saxifraga cespitosa (tufted saxifrage) in its tiny population in North

Wales. Is this population now so small that stochastic factors are more likely to impact on the species here, rendering genetic factors almost irrelevant?

- amount of genetic variability is this important for adaptability and long-term survival, and is evolutionary history a factor, or is current management more likely to be the deciding aspect?
- the taxonomic status of a species is it a distinct species, sub-species, native or endemic? For example, the recent research into the Limonium group (sea lavender) and the Loxia scotica (Scottish crossbill). Species status makes a huge difference in terms of funding;
- the significance of hybridisation;
- inbreeding and outbreeding scenarios how to avoid these. Is selfing a problem in specific small populations? If so, what do we need to do?
- if collections of material for ex situ conservation are needed, what is required?
- recovery and restoration situations. When is it advisable to (re)introduce species and what is the best way of going about it? When to mix gene pools and when not to? How important is it to consider the origins and relatedness of source stock?
- would it be possible to produce generic points from research data such as that from species and populations at the southern limit of their range? We usually concentrate on single-species results, but generic points, if there are any, to help guide conservation decision-making generally would be extremely useful.

Habitat management

Habitat management questions in genetics are increasingly important. Questions such as: how can we best develop habitat management to improve the demographic and genetic performance of a species? Much conservation relies on the existence of protected areas to conserve both habitat and species diversity, but what about the representation of genetic variation (of priority species) in protected areas. Is this adequate or do we need more? Can genetics tell us about how much habitat we really need for the long-term viability of British wildlife? This is what the Biodiversity Action Plan (BAP) refers to as 'secure status'. If so, what is it and how will we know when we've got it? Politics in recent years has determined that we concentrate on rarities. However, should we be looking at globally uncommon species that may be relatively abundant in the UK, such as bluebell and heaths? If so, can we justify the landscape and habitat scale actions these may require, which can be costly and difficult?

Challenge of a 'new' approach

The Scottish crossbill is a case in point where molecular work has indicated that it is indistinguishable from common and parrot crossbills (Piertney *et al* 2001). How does this alter the status of what was recognised as Britain's only endemic bird? This research may appear to have devalued the importance of the Scottish crossbill in our rarity centred culture. However, if an entity is of interest and an important component of biodiversity, then we should conserve it. Our aims should be to conserve variability and biodiversity and not necessarily just 'static' organisms. The species concept sits with increasing unease alongside more powerful molecular techniques showing increasing amounts of variation. This is leading some ecologists and conservationists to consider it fundamental to take a Darwinian approach to conservation, i.e. conserve the processes producing genetic variation within species to enable future evolution, rather than a Linnaean approach of treating species as unchanging entities.

The future

The results of genetic research, particularly the political consequences of taxonomic decisions, can have significant impacts on conservation status, prioritisation and resource allocation. Genetic research is potentially, therefore, a powerful tool for conservation management and should be integrated into the way we think about conservation. To achieve this it needs to be integrated into policy. There is some way to go but it is slowly happening, an example being in

the new higher tier agri-environment scheme in England, which has genetic conservation as an objective (Defra 2005). So the future is looking brighter for the integration of genetics into conservation management decisions in the UK. However, there is still the potential for 'interesting' genetics research to be undertaken for its own sake. There is absolutely nothing wrong with this but to ensure that genetics is taken on board fully by conservation organisations, it needs to be appreciated that the role of genetics in the conservation world is to help conservation as opposed to what might be considered 'conservation genetics'.

7.3. UK policy on conserving genetic variation in natural populations – is there one?

Richard Ferris, JNCC, UK

The resources represented by genetic diversity have been recognised at an international level within the Convention on Biological Diversity (CBD)³ and at a national level in the UK Biodiversity Action Plan (UK BAP)⁴. When formulating and implementing policy aimed at conserving genetic diversity, consideration should be given to the full range of scales, from genes to landscapes.

International Principles

The importance of genetic resources is highlighted in the CBD with one of the three objectives set out in Article 1 stating:

"...fair and equitable sharing of the benefits arising out of the utilisation of genetic resources, including by appropriate access to genetic resources and by appropriate transfer of relevant technologies, taking into account all rights over those resources and to technologies..."

The focus is on genes as exploitable commodities but what about the role of genetic variation in natural populations? In addition, Article 2 defines biological diversity as:

"...the variability among living organisms from all sources...; this includes diversity within species."

However, many of the obligations of the CBD are not specific and are conditioned by phrases such as "as far as possible" and "as appropriate". Nevertheless, there is a strong legal basis for actions to conserve and manage genetic variation in a sustainable manner although most references to genetic *resources* within the CBD focus largely, but not exclusively, on agricultural biodiversity. They aim to promote:

- i. the conservation and sustainable use of genetic resources of actual or potential value for food and agriculture;
- ii. the fair and equitable sharing of benefits arising out of the utilisation of genetic resources.

Subsequent developments include the COP Decision VII/30, which focused on "Progress towards the 2010 target." The Action, *Protecting the components of biodiversity*, incorporates Goal 3: to "promote the conservation of genetic diversity."

³ The Convention on Biological Diversity (CBD) was an important component of the Earth Summit, and was signed at Rio in 1992 by over 150 countries, including the United Kingdom (and the European Community). The United Kingdom ratified the Convention on 3 June 1994.

⁴ In January 1994, the United Kingdom Government published *Biodiversity: The UK Action Plan.* This was in response to the commitment given by the United Kingdom at the Earth Summit in 1992.

"Genetic diversity of crops, livestock, and of harvested species of trees, fish and wildlife and **other valuable species** conserved..."

But, does this take us any further forward? The problem is that the CBD defines genetic resources as "material of actual or potential value", rather than acknowledging explicitly that they have value in terms of maintaining functions and hence integrity of ecosystems.

The UK BAP view

The UK BAP recognises that genetic variation is an important component of the UK's biodiversity, and it needs to be considered from two points of view:

- i. conserving the variation of the UK's species and
- ii. deliberate or accidental introduction of non-local genetic material.

Again, the value of genetic diversity is recognised in relation to maintaining agricultural productivity:

"... in maintaining the productivity of our crops, we depend on a reservoir of wild relatives, and a pool of genetic material that we can go back to, in order to reinforce our selection."

The UK BAP view states little about enhancing species' ability to adapt to change but rather is focused on maintaining the status quo. Furthermore, it stresses the linkage between species and habitats, and includes a section on variation within species in the UK, but a clear policy position is not outlined.

However, within UK policy, the costing of Species Action Plans uses a checklist of action points including:

- surveys to determine distribution and population size;
- genetic and population dynamics studies and
- *ex situ* conservation.

At the habitat scale, the UK BAP considers genetic variation, e.g., referring to native *Pinus sylvatica* (Scots pine) forests, states:

"A group of protected habitats, spanning the natural range of the habitat in the UK, is probably the only way to conserve the genetic variation of species that occur in that habitat type."

It also recognises that:

"...there is a risk that groups of sites may not be the best way of conserving the genetic variation of any particular species."

Country strategies

Country strategies vary in their approach to genetic diversity:

- Defra's *Working with the grain of nature: A biodiversity strategy for England* says nothing about genes or genetic conservation!
- The Welsh Assembly Government's consultation on the *Environment Strategy for Wales* makes no reference at all to genes or genetic conservation in its chapter on biodiversity!

The conservation of genetic diversity: science and policy needs in a changing world

- The Scottish Executive's *Scotland's Biodiversity: It's in your hands* states that "...genetic diversity within species is better understood and actions to conserve this diversity for priority species are in place" and proposes the development of "...cost-effective indicators relating to... genetic diversity..."
- The Northern Ireland Biodiversity Group's *Northern Ireland Biodiversity Strategy* makes reference to genetic resources within a section concerned with "Business and Tourism", recognising that "...biodiversity is much wider than saving species and habitats..."

Two sides to every story

Despite recognising that there are gaps in biodiversity conservation policies, we should consider whether the blame for this lies solely with policymakers. After all, population genetics has been described as an "opaque and esoteric discipline, of dubious relevance to practical issues," and as having a lack of ecological context, which "commonly precludes a useful interpretation of the data" (Ennos, 2003).

In 2001 a Conservation Genetics Workshop held at the Royal Botanic Gardens, Kew reported that conservation practitioners wanted to gain a basic understanding of the issues raised by genetics research. It recommended that researchers needed to relate information to the needs of those involved in conservation management. Put simply, knowledge transfer needs to be improved, with the flow of information between the different communities increased and delivered in a format that is understood easily.

Is there still a gap between the research and policymaking communities in the UK? If so, what can we do to ensure that conservation genetics becomes a truly applied discipline, integral to biodiversity conservation in the UK? I propose that:

- 1. Researchers must focus on the questions that practitioners and policymakers ask and need:
 - to understand what conservation practitioners want to know;
 - to know how their work is relevant in a policy context;
 - to tease out the important applied issues.
- 2. Policymakers and researchers need to get out more.
- 3. Researchers need to speak the language of end-users.
- 4. Practitioners need:
 - to gain a basic understanding of conservation genetics;
 - to ask the right questions;
 - to know about techniques and their limitations.

These steps are necessary, in order to:

- develop policies with a firm evidence-base and that are developed according to sound genetic principles;
- improve dialogue between the research–policymaker–practitioner communities to communicate, understand, implement and continually review policies.

Workshops such as this are one way in which the different communities can be brought together to share ideas. However, there is a continual need to encourage integration of genetics in a wide range of conservation actions, and make this explicit in policy. Formalising of the links between policymakers, researchers and practitioners is likely to be necessary in order to ensure effective and lasting knowledge transfer, and may be achieved through the involvement of organisations such as the UK Biodiversity Research Advisory Group (UK BRAG), the British Ecological Society, and the Environmental Research Funders' Forum (ERFF).

8. Discussion

Breakout groups 7, 8 & 9: Critical issues for the effective conservation management of genetic diversity

The following key questions were each addressed in the three final breakout groups, as follows:

- 1. Which issues are most critical to effective conservation management of genetic resources?
- 2. What are the benefits of using genetic information in conservation management?

1. Which issues are most critical to the effective conservation management of genetic resources?

There was a broad consensus on some of the principles of conservation genetics that can be communicated to policymakers and practitioners with a high degree of confidence. These include the following generalisations:

- high levels of genetic diversity within populations are almost always desirable to ensure that they are genetically sustainable;
- adaptability is correlated with diversity and should be an important driver for conservation in response to environmental change;
- genetic diversity is broadly correlated with population size, hence conservation should seek to maintain or create large populations;
- low levels of genetic diversity are detrimental to populations when they lead to inbreeding depression but can be of special scientific interest and may indicate ongoing evolution and speciation;
- gene flow between populations is desirable but care may be required where small populations have been isolated for a long period and local adaptation may be swamped;
- action to increase landscape permeability for one species may be bad for another but what is good for most species should take precedence.

2. What are the benefits of using genetic information in conservation management?

The benefits to using genetic approaches in a conservation framework were examined in terms of: 'what have we got?' (existing biodiversity) and 'what are the threats to this?' There was general agreement that to allow effective conservation management it is important to improve the levels of interaction and understanding among the research, practitioner and policy-making communities ('what are the geneticists talking about?'). In addition to considering the knowledge and information gaps and the research needed to address these, the delegates also considered knowledge transfer and other means to facilitate the implementation of the recommendations. The conclusions, knowledge gaps and recommendations outlined below are in no particular order of priority.

• How can genetic approaches provide clear definitions for our natural heritage? (What have we got?)

Knowledge and information gaps

There is a need to better to understand the biogeographical heritage of the British Isles. Many species lie at the edge of their range in the British Isles and have unusual histories and distributions. This applies to the geographical origins of our native and exotic flora and fauna

and knowledge of the historical processes that resulted in their acquisition. In terms of the processes that have given rise to our biodiversity, a wide range of temporal perspectives can be taken and the relative rates and routes of gene flow can illustrate historical change in species and communities, which may then be used to inform conservation decisions.

Research needs

- undertake phylogeographic analyses of genetic variation, to improve understanding of its historical distribution within British species;
- determine what species or sub-species are present, and carry out an assessment of their distinctiveness at a British Isles, national, regional and local level. Use this information to identify conservation priorities at each appropriate level.
- How can genetic research identify problems and provide solutions? (What are the threats to what we have?)

Knowledge and information gaps

Three main genetic threats were identified: fragmentation of species ranges and patterns of gene flow, loss of genetic diversity, and inbreeding versus outbreeding with their implications for the management of gene flow. These three threats are examined in more detail below.

Fragmentation: The most pressing threat in terms of the conservation of genetic diversity appears to be species range fragmentation resulting from habitat fragmentation. However, there is relatively little information about how the spatial scale and pattern of fragmentation may affect gene flow or how much of a genetic problem fragmentation poses for conservation. The effect of fragmentation will be species dependent and is contingent on a species' ability to disperse (vagility). In this respect, genetic tools can be used to delineate functional boundaries between populations and to assess the importance and abundance of the demographic units contributing to populations.

Loss of diversity: What are the means of assessing the relative genetic risks for species and communities from fragmentation? In addition, what is the importance of genetic diversity in terms of its relationship with the capacity of populations and species to respond to environmental change?

Inbreeding versus outbreeding; managing gene flow: A major concern for conservation practitioners and a knowledge gap for researchers is the question of whether gene flow between distant populations threatens the breakdown of local adaptation, causing outbreeding depression.

Research needs

- use genetic approaches to identify functional population boundaries, adopting a case study approach for selected key species in a range of landscape types (showing different degrees of habitat fragmentation);
- undertake studies to provide quantitative measures of perturbations to population structure or gene flow caused by fragmentation in order to assess the risks posed;
- investigate contemporary and historical levels of gene flow, as baselines for determining targets and assessing the success of management interventions.

How do we interpret technical information? (What are geneticists talking about?) – The need for effective knowledge transfer and implementation

Knowledge and information gaps

Researchers, policymakers and conservation practitioners have an equal responsibility to communicate and improve understanding, so that the knowledge gaps addressed are of the highest relevance to conservation.

Mechanisms for knowledge transfer exist but are in the early stages of development; *UKPopNet* and *Quercus* may serve as suitable models. There is a need for a mechanism to steer research and target statutory funding, but also enhance the process of application and communication of science. For the scientific literature to reach conservation practitioners, this requires specialist writers, equipped with the necessary skills to interpret and communicate technical detail. This is particularly true in the field of conservation genetics.

Conservation biology (and conservation genetics as a sub-discipline) needs to mature as a respected academic endeavour. Genuinely co-operative research between policymakers and practitioners and academic units is relatively scarce. Much of the support for molecular ecology research comes through the Research Councils, is academically driven and is not always relevant to policy and practice.

Considerable barriers remain in terms of communication between population and conservation geneticists and conservation managers. These include the understanding of fundamental technical terms, without which the central messages of published studies may be obscured. In addition, there is uncertainty surrounding the terms *population* and *species*. What defines a population? More specifically, what relevance does the term *effective population size* have for practitioners and how can it be used in the assessment of conservation priorities? Furthermore, as we gain a better understanding of the continuum of speciation, can we justify the taxonomic absolutism of policy designations?

Research needs

- establish a UK conservation genetics forum to facilitate knowledge transfer between diverse stakeholders;
- produce a non-technical and accessible handbook for conservation practitioners, defining important concepts and supporting informed communication with geneticists;
- encourage the review of management plans from a genetic perspective, to foster a culture of consultation between managers and conservation geneticists.

Genetic Conservation Forum

This workshop has recognised the importance of improving communication between all stakeholders, and proposes that a Genetic Conservation Forum be established to aid knowledge transfer, to:

- enable practitioners to incorporate genetic concepts and information into their management strategies;
- to raise awareness of the latest analytical tools, their potential applications within conservation, and their limitations;
- enable the research community to be updated on the most pressing conservation-related questions to be addressed;
- synthesise and disseminate the existing evidence relating to the conservation of genetic diversity, making it accessible to policymakers and practitioners;
- enable consultation on and peer review of specific management problems, with the involvement of academic scientists.

Actions

Establishment of a conservation genetics forum or specialist group, to steer research, target statutory funding, improve science communication and aid implementation of research recommendations.

Genetic Conservation Handbook

Recognising that genetic conservation has many difficult conceptual aspects, the need for a common terminology was identified in order to ensure clarity of communication. Examples of potentially confusing terms include *local*, (*effective*) population size, and poorly defined concepts such as *MU* (*Management Unit*).

Actions

This workshop recommended that a Genetic Conservation Handbook be produced, providing definitions of terms used in genetic conservation in a form accessible to researchers, policymakers and practitioners. This should be written and reviewed by representatives of each stakeholder group. Its primary audience is envisaged as being managers without the technical knowledge of genetics, and it should include a glossary of key terms.

Integrated conservation planning

The need for genetic issues to be considered fully in conservation management plans was given strong support, particularly species and Habitat Action Plans as part of the UK Biodiversity Action Plan. A decision support tool identifying key genetic factors at critical points of the management plan and involving a timeline for action was suggested. This tool would need to take into account:

- current and historical demography;
- population size;
- past management history of populations;
- historical distribution and connectivity of populations;
- level of on-going gene flow and species vagility;
- mating system;
- current levels of genetic diversity;
- presence of adaptation;
- population genetic differentiation.

The decision tool would facilitate prioritisation when making decisions about the conservation of populations that have had a continuously large size, and for which there is evidence of adaptation. It would also encourage population connectivity where historical evidence or current genetic differentiation indicates past gene flow among populations.

Actions

Production and dissemination of a flow chart or appropriate table with guidelines that allow managers, in the first instance, to formulate conservation management plans accounting for conservation genetic needs.

Peer review of management plans by experts in conservation genetics. This would be facilitated by the establishment of a database of people with expert knowledge, who would be available for consultation and review of species management plans.

9. Synthesis

The first six breakout groups covered a range of topics relevant to the conservation of genetic diversity and using genetic principles to enhance conservation. Discussion in these groups was wide ranging and often overlapping in scope. In the following section and tables, the key conclusions, recommendations, and knowledge gaps, along with arising research questions identified by the breakout groups, are summarised by combining the key themes covered in their discussions. The order of items in the tables does not imply priority or precedence of some conclusions or recommendations over others.

9.1. A case for using genetic concepts and information within conservation

It was generally agreed that there are three main areas where conservation has underlying genetic concerns:

- The maintenance of species' adaptive potential in the face of environmental change;
- Avoiding the loss of genetic diversity;
- Avoiding inbreeding and outbreeding depression.

In practice conservationists are currently concerned with:

- Identifying situations where genetic constraints limit population viability;
- Learning whether species can be grouped meaningfully according to the level of genetic risk, in order to identify generic conservation policies;
- Conserving habitats and processes to facilitate evolutionary responses to changing environmental conditions;
- Potential conflicts between species and genetic conservation.

9.2 General conclusions and knowledge gaps

The following points constituted common themes in the first six breakout groups, and are summarised below. The recommendations in the table are by no means exhaustive and provide a basis for future discussions. They reflect opinions expressed at the workshop and are not prioritised in any way.

and benefits to such definitions are.

Knowledge gaps	Research Questions	Recommendations
Definition of a population.	How can populations and their boundaries best be defined?	Apply genetic approaches that define
	What is the relative importance of geographic and genetic	populations or identify migrant
	criteria in defining populations?	individuals, in order to address these
	Which attributes of the population concept do we need to	questions, e.g. assignment tests or
	consider most, to facilitate effective conservation and the	measurements of contemporary gene flow
	assessment of conservation priorities?	based on genetic markers.
	How does the scale of populations vary for different taxa	
	(UK/regional/European e.g. consideration of 2010 targets)?	Improve our understanding of the scale of
	How does our definition of a population allow us to define	populations, to determine at what scale
	more accurately units such as ESUs or MUs, and are these	species should be managed.
	useful concepts?	
There is limited understanding of what	Is the concept of effective population size useful to the	Synthesise existing evidence on what
constitutes an 'effective population size'	management of all UK taxa?	constitutes an effective population size
and its relevance to conservation?	What is the best way to measure effective size if it is to be a	and its relevance to conservation, and
	meaningful concept?	initiate further research to support the
	Are current effective population sizes in the British Isles	development of new recommendations.
	adequate to sustain genetic diversity?	
• Defining units of conservation		
Knowledge gaps	Research Questions	Recommendations
There is a limited understanding of how we	Are protected areas more effective in ensuring genetic	Undertake comparative studies of the
can define units of conservation to ensure	conservation than non-site based approaches?	genetic composition of populations in
effective site protection, and what the costs	How can critical units of conservation such as ESUs and	protected areas versus the wider

landscape.

MUs be defined?

	What are the ESUs, MUs, dispersal distances, colonisation	Investigate the potential application of
	distances, boundaries and permeability of unsuitable	selectivity measures and conservation of
	habitats?	'management units'.
An understanding is required as to whether	Does knowledge of a species' breeding system, functional	Undertake meta-analysis of existing
life-history and demographic information	group, or life history allow inferences about expected levels	research to establish relationships.
could be used as a surrogate for measuring	of population neutral and adaptive diversity, or	Develop and test models based on life
genetic diversity to inform conservation (as	susceptibility to genetic risks such as inbreeding depression?	history/demographic information and
'conservation short-cuts').	Can we use such short cuts to make generic conservation	genetic diversity, and in partnership with
	protocols?	practitioners and policymakers, apply this
		knowledge to issues of practical
	What are the costs and benefits of this approach?	conservation.

Conserving evolutionary processes that generate and sustain genetic and taxonomic diversity

Here we consider the evolutionary processes of population size and inter-specific hybridisation. The process of gene flow among populations, which can also sustain genetic diversity, is dealt with in a separate section. There is a need to consider the conservation of evolutionary processes rather than just of *status-quo* taxonomic units; this has genetic implications.

Networks and connectivity of populations, related species and habitats are likely to be particularly important in the context of conserving the ecological processes that support biodiversity.

Knowledge gaps	Research Questions	Recommendations
Limited understanding of the key evolutionary processes <i>in situ</i> .	Which evolutionary processes sustain and generate biodiversity, and what is their relative importance? Should the focus of conserving processes generating biodiversity be upon identifying and conserving the	Conservation actions should take into account the evolutionary processes generating and sustaining diversity as well as named taxa and units of biodiversity
	processes themselves, or upon conserving the habitats and landscapes that allow those processes to occur? What conservation value should we place on processes and the novel taxa that they generate or sustain? To what extent does the current conservation approach (including guidelines for designating protected areas, such as SACs, and rare species) foster or restrict the processes that are currently generating novel taxa and/or genetic diversity?	Research projects should aim to analyse evolutionary processes as well as simply describing the extent and distribution of neutral genetic diversity.

Hybridisation		
Knowledge gaps	Research Questions	Recommendations
Understanding hybridisation.	How many species have been generated by hybridisation? How often does hybridisation result in genetic introgression, reduction in genetic diversity within parental types, sterile offspring, the generation of new taxa or the exclusion of one of the two parental types?	Undertake the meta-analysis of existing data to establish past hybridisation rates. Assess the frequencies of negative outcomes of hybridisation including laboratory and field based approaches.
Managing the products and outcomes of hybridisation.	How should we value the results of hybridisation that occur through human-mediated environmental change - should these be the object of conservation actions (e.g. what is the value of SAPs for <i>in situ</i> conservations)? How much of a risk are the negative outcomes of hybridisation?	Recommendations must await cost- benefit analyses of the possible outcomes of hybridisation and their value to biodiversity and conservation. Hybridisation can have little discernable effect on fitness or viability, yet still be judged as 'negative' (e.g. the Scottish wildcat).

Understanding and managing gene flow in the context of adaptation and species' adaptability

Understanding and managing gene flow is central to the application of genetics in conservation. There is an inherent tension between

- an emphasis on conserving potentially well-adapted local ecotypes, and
- general maximisation of genetic diversity in every location to promote future adaptability.

Knowledge gaps	Research Questions	Recommendations
Methods to adequately and accurately	What are the best ways to assess gene flow?	The effects of different levels of gene
measure gene flow.	When and where is it beneficial to manage gene flow?	flow should be investigated in species
	How do measures of gene flow compare?	with a range of effective population sizes
	When and at what scales should we seek to increase	and varying longevity and with different
	landscape permeability to gene flow?	dispersal rates/mechanisms.
There is an incomplete knowledge of	What are the best methods for assessing habitat	Undertake a review of existing landscape
species dispersal ability, colonisation ability	permeability?	metrics to assess reliability and possible
and the permeability of habitats.	What is the relative permeability of different habitats to	need for new measures.
	different taxa?	

	Over what distances can different species disperse and	Undertake studies of dispersal in key
	colonise?	species/taxa in a range of landscape types.
	How frequent are long-distance dispersal events and what is	
	their genetic significance?	Synthesise existing research on species
	Does knowledge of species' life history or breeding system	dispersal and colonisation abilities and the
	help us to predict dispersal and colonisation ability?	relative permeability of different habitats.
There is a poor understanding whether there	How have the genetic constituents of populations changed	Undertake the meta-analysis of historical
is any relationship between historical events	or persisted over historical time scales?	data.
and genetic composition of current	To what extent are functionally adaptive genes represented	
populations?	in some populations?	
Gene flow and outbreeding depression.	How, and at what scales does outbreeding depression affect	Study inbreeding and outbreeding in a
	the genetic composition and fitness of populations?	range of taxa and populations, including
		those undergoing environmental
		fluctuation and/or change.
Adaptation and invasive species.	Do invasive species have genetic characteristics that may	Initiate comparative studies on invasive
	allow problems to be predicted?	species to establish whether genetic
	Does the extent of adaptation in non-native species predict	factors play a role in their invasiveness.
	their invasiveness within UK habitats?	

• Understanding adaptation

Clear and meaningful definitions of local adaptation are needed that are accessible to practitioners and policymakers alike.

Knowledge gaps	Research Questions	Recommendations
Mechanisms of adaptation.	To what extent can genetic variation facilitate adaptation,	Review current data to establish current
	and through which mechanisms?	knowledge and initiate research where
	How rapidly does local adaptation occur?	necessary to assess local adaptation in
	Are local adaptations constant over time, or does fluctuating	terms of community interactions;
	environments cause them to shift and change in nature?	Compare habitat type and distance in
		driving the differentiation of ecotypes.
Measuring adaptation.	Are there useful surrogates for adaptation, such as common	Investigate the use of reciprocal transplant
	garden and reciprocal transplant experiments?	experiments to identify adaptive diversity;
		Undertake further studies on quantitative
		traits and local adaptation in wild
		populations, and compare results with

	Do comparisons of F_{ST} and Q_{ST} provide useful indications	those from common garden and reciprocal
	of the presence of adaptation?	transplant experiments;
	Is it possible or useful to measure adaptive diversity in small	Undertake studies on quantitative traits
	populations?	and adaptation in small populations.
The extent and distribution of adaptive	How much adaptive diversity can we expect to encounter	Review existing research on the extent
diversity.	within natural populations in the UK and species' wider	and distribution of adaptive diversity and
	ranges?	initiate further studies for key taxa.
	How do species breeding systems affect the extent and	
	distribution of adaptive genetic diversity?	Study inbreeding and outbreeding in a
	How does outbreeding affect the genetic composition and	range of taxa and populations and
	fitness of populations?	examine how they effect genetic
		composition and fitness of populations.
Adaptation and the response to	How do populations with different levels of neutral and	Review existing research on how
environmental change.	adaptive genetic diversity respond to change?	populations with different levels of neutral
	Can locally adapted populations cope with changing and	and adaptive genetic diversity respond to
	variable environments?	change and initiate studies of populations
	How do adaptable (genetically diverse or plastic)	subject to environmental fluctuations
	populations cope with changing and variable environments?	and/or change.
Plasticity and adaptation to change.	What are the relative contributions of phenotypic plasticity	Review existing research that has
	and microevolution on adaptation to changing	partitioned out components of variability
	environments?	and, if necessary, instigate new research.
	Does plasticity itself evolve with changing environments?	

Management of species, populations, habitats and landscapes

• Conservation of species and populations

Knowledge gaps	Research Questions	Recommendations
A lack of generic strategies for conservation	How do methods of setting conservation priorities compare	Undertake a review and meta-analysis of
of species with certain breeding systems and	across species with different breeding systems and	methods of setting conservation priorities
historical demography.	populations characteristics?	across species with different breeding
	What are their costs and benefits?	systems and population characteristics,
	Should our approach to managing genetic diversity be	including cost-benefit analysis by relating
	different for endemic species?	to genetic data.
Taxa that are poorly studied from a genetic	What levels of neutral and adaptive genetic diversity are	Undertake studies to document genetic

view	point.	present in poorly studied taxa such as invertebrates and	diversity in invertebrates including key
		marine taxa?	functional or indicator groups.
Genetic diversity, historical events and		How have patterns of genetic diversity changed or persisted	Synthesise the existing literature.
dem	ography.	over historical time?	
		How well can we reconstruct species genetic and	
		demographic history?	
Inco	mplete knowledge of how genetic	What are the key evolutionary and ecological processes	Undertake meta-analysis of research
mar	kers inform species conservation	driving change in the levels of genetic diversity contained	relating genetic data to conservation
•	The meaning of changes in genetic	within populations?	actions.
	diversity.	Do meaningful baselines exist for genetic measures that	
•	Baseline measures of genetic diversity	may be useful conservation indicators, such as effective	Construct a conservation management
	and their relationship to population	population size, heterozygosity, F_{ST}/Q_{ST} ? Which baselines	decision assistance tool, to facilitate the
	fitness.	are 'desirable': those at present, or in the past; when in the	use of genetic information on a species-
•	The integration of information from	past?	specific basis.
	genetic studies into conservation	Is there a relationship between genetic measures and	
	actions.	population fitness?	Pilot this tool using case studies whose
		What are the costs and benefits of different genetic marker	management outcomes were known to see
		systems to conservation?	whether it can be used to recommend
		How can different genetic indicators inform conservation	appropriate actions.
		actions?	
		How should we incorporate and weight genetic information	Synthesise and disseminate costs and
		with other data such as ecological, habitat, life history,	benefits of the existing molecular marker
		historical and past management information on a species of	systems.
		interest?	
The	significance of genetic diversity for	How does genetic diversity within species influence species	Review existing genetic and ecosystem
community species diversity and ecosystem		interactions within a community and ecosystem	function research and facilitate closer
func	tion	functioning?	working between these research
•	Little is known about the relationships	Are species replaceable?	communities.
	between genetic diversity and species	Does local adaptation facilitate species coexistence or alter	
	interactions within a community.	community dynamics?	
•	Local adaptation and community	To what extent are genes that affect the function of	
	interactions.	ecosystems represented in some populations?	

Conservation of habitats and landscapes		
Knowledge gaps	Research Questions	Recommendations
The scale of gene flow.	At what scales should we seek to increase landscape permeability to gene flow?	Undertake a review of the existing landscape matrix to assess permeability and the possible need for new agri- environment measures; Undertake studies of dispersal in key taxa in a range of landscape types.
Habitat fragmentation.	How does habitat fragmentation affect gene flow? At what scales does fragmentation become problematic to the maintenance of gene flow?	Assess the impacts of fragmentation at different scales.
Population connectivity and range-edge populations.	Does increasing population connectivity increase the risk of swamping adaptation at the edge of a species' range with non-adaptive genes? Will enhanced population connectivity help to alleviate inbreeding depression at the range edge?	Initiate landscape-scale field studies in near-natural systems and compare genetic impacts across a range of taxa.
Management of connectivity at large spatial scales.	What are the costs and benefits of encouraging landscape connectivity at a UK scale relative to a pan–European scale? Do we need to worry about the genetic distinctiveness of UK populations?	Compare genetic parameters in British and other populations and review the existing DNA literature of the genetic distinctiveness of British populations.
The benefits of encouraging landscape connectivity at a UK scale relative to a pan– European scale have not been fully explored. Limited understanding of the benefits of maintaining and conserving genetic diversity of species within the UK compared to wider geographic ranges.	Do UK populations represent sub-species or are they genetically indistinguishable from those in other geographical regions? What are the costs and benefits of adopting genetic conservation strategies at a range of geographical scales?	Comparison of genetic measures in UK and other populations.
There is little knowledge of how increasing connectivity may impact upon populations at the edge of their ranges.	Does increasing population connectivity increase the risk of swamping of populations at edge of a species' range with non-adaptive genes?	Initiate landscape-scale field studies in near-natural systems and compare impacts across a range of taxa.

The role of protected areas.	What role should protected areas play in a wider landscape	The use of selectivity measures and
	strategy to conserve genetic diversity and evolutionary	management units should be considered
	processes?	when conserving genetic diversity and
	How can we manage the landscape between protected areas	evolutionary processes in the wider
	to make it more 'wildlife friendly' in order to encourage	landscape.
	natural gene flow among populations?	Review existing research and promote
	Are protected areas more effective in ensuring genetic	discussion between policymakers and
	conservation than non-site based approaches?	practitioners on the management of the
		landscape between and within protected
		areas to encourage gene flow.
How effective are protected areas at	To what extent do protected areas conserve genetic	Undertake comparative studies of the
conserving diversity?	diversity?	genetic composition of populations in
		protected areas vs. those in the wider
	To what extent does the protected area network facilitate the	landscape are needed.
	operation of natural evolutionary processes such as gene	Studies on the dynamics of gene flow
	flow, adaptation, etc?	between protected and unprotected areas
		are needed, as well as a better
		understanding of the process of
		colonisation.

Policy limitations and responses

The current legal framework and obligations emphasise the importance of conserving existing taxa and patterns of biodiversity. Policy needs reconsidering in context, taking into account the need for dynamic change in biodiversity and to include processes that generate and sustain diversity.

Limitations of Current Policy	Recommendations
The present need of policymakers to see a return on investments in conservation efforts presents a serious problem with the time-scale required to carry out and achieve some conservation objectives.	Given the current state of our knowledge regarding the role of genetic diversity in biodiversity, conservation policies need to be set within a longer timescale than at present.
Continued application of the precautionary principle (preserving distinctive units of biodiversity) in the conservation of species' genetic diversity may be practically difficult and biologically unsound if species' genetic diversity and adaptive potential is to be maintained.	A flexible interpretation of the precautionary principle is needed, in which adaptability is accepted as an important conservation objective. The precautionary principle may be too conservative, and actually be detrimental to the long-term-sustainability of declining populations that have experienced some genetic depletion.
Future conservation strategies require a combined approach that can maintain existing species and populations but also allow for demographic dynamism and future environmental changes, e.g. those expected due to the climate.	There is a need to develop strategies that permit adaptation to environmental change.

9.3 Follow-up

The workshop agreed that the following actions should be progressed as a matter of priority:

• Genetic Conservation Forum

Establish a genetic conservation forum or specialist group, to steer research, target statutory funding, improve science communication and aid implementation of research recommendations.

• Genetic Conservation Handbook

Produce a Genetic Conservation Handbook. The handbook should, provide definitions of terms used in conservation genetics, in a form accessible to researchers, policymakers and practitioners. This should be written and reviewed by representatives of each stakeholder group. Its primary audience is envisaged as being managers without the technical knowledge of genetics, and it should include a glossary of key terms.

• Integrated Conservation Planning

Produce and disseminate a flow chart or appropriate table with guidelines that allow managers, in the first instance, to formulate conservation management plans accounting for conservation genetic needs.

• Peer Review Database

Establish a database of people with expert knowledge, who would be available for consultation and review of species management plans.

Glossary of Terms

Adaptation A process of genetic change of a population, owing to natural selection, whereby the average state of a character becomes improved with reference to a specific function, or whereby a population is thought to have become better suited to some feature of its environment.

Adaptive evolution Changes in the genetic composition of populations due to natural selection that improve their reproductive fitness in a particular environment.

Allele One of the several forms of the same gene or DNA sequence, e.g. A_1 , A_2 , A_3 , A_4 ; presumably differing by mutation of the DNA sequence, and capable of segregating as a unit Mendelian factor. Alleles can be recognized by their phenotypic effects.

Allopatric Of a population or species, occupying a geographic region different from that of another population or species; populations or species whose geographic distributions do not overlap.

Apomictic Vegetative, asexual reproduction. Seeds produced are identical to the parent plant.

Archaea Like bacteria, single-celled organisms lacking nuclei and are therefore classified as Prokaryota.

Bottleneck A restriction in population size.

Ecotype A form, variety, or genotype of any species possessing distinctive inherited characteristics that are assumed to enable it to succeed in a particular habitat.

Edge effect Collective term to describe the many possible consequences that occur specifically when an organism occupies the edge of a habitat, population or geographic range.

Evolutionary significant units (ESU) Populations that are at least partially genetically differentiated and so are considered to require management as separate units.

Ex situ Away from its normal habitat, such as an endangered species being conserved in captivity, or an endangered plant being preserved in a seed bank or via cryopreservation.

Extremophile An organism, usually unicellular, which thrives in or requires "extreme" conditions.

Fragmentation The breaking up of formerly contiguous landscape features into disjunct, isolated, or semi-isolated patches as a result of land-use changes.

 F_{ST} is a measure of the subdivision of populations. This coefficient is defined as the probability that two neutral marker genes taken at random, from different subpopulations, are identical by descent.

Gene flow The incorporation of genes into the gene pool of one population from one or more other populations.
Genetic Drift Changes in genetic composition of a population due to stochastic sampling in small populations. It results in loss of genetic diversity, random changes in allele frequencies and diversification among replicate populations. Also referred to as random genetic drift.

Genetic load The load of deleterious alleles in a population, some due to the balance between deleterious mutations and selection (mutation load) and some due to heterozygote advantage and other forms of balancing selection (balanced load).

Genotype The set of genes possessed by an individual organism; often, its genetic composition at a specific locus or set of loci singled out for discussion.

Habitat permeability The extent to which organisms or their offspring, seeds, or gametes may migrate or travel through any particular habitat type.

Hardy-Weinberg equilibrium The equilibrium genotype frequencies achieved in a random mating population with no perturbing forces from mutation, migration, selection or chance. If two alleles A_1 and A_2 have frequencies of p and q, the Hardy-Weinberg equilibrium frequencies for the A_1A_1 , A_1A_2 and A_2A_2 genotypes are p^2 , 2pq and q^2 , respectively.

Heterozygote An individual with two different forms alleles at a genetic locus, e.g. A_1A_2 .

Heterozygosity A measure of genetic variability among individuals within populations and variability among populations. The extent to which any organism is expected to be a heterozygote at one or more genetic loci.

Homozygote An individual with two copies of the same allele at a gene locus, e.g. A_1A_1 .

Hybrid An individual formed by mating between unlike parental forms, which usually originate from genetically differentiated populations or species; occasionally in genetics, the offspring of a mating between phenotypically distinguishable genotypes of any kind.

Hybrid zone Region in which hybrid offspring are formed, usually corresponding to a point of spatial contact between parental types.

Inbreeding Production of offspring from the mating of individuals related by decent, e.g. self-fertilization, brother-sister, or cousins mating.

Inbreeding depression Reduction in reproduction, survival or other quantitative characters due to inbreeding.

Indicator species A species whose status provides information on the overall condition of the ecosystem and of other species in that ecosystem. Species that respond to and indicate changes in biotic or abiotic conditions. They reflect the quality and changes in environmental conditions sometimes including aspects of community composition.

In situ conservation The conservation of biodiversity within the evolutionary dynamic ecosystems, habitat or natural environment from which it originates.

Introgression Introduction of genetic material from another species or sub-species into a population.

Invasive Species An introduced or "non-native" species whose range is expanding within the area of introduction, sometimes with detrimental impact to native biodiversity.

Management unit (MU) A population within a species that is sufficiently genetically differentiated from other populations to warrant separate management.

Meta-analysis A statistical analysis that combines information from several different studies, or several different species to assess the overall evidence for or against any hypothesis or statement.

MHC: Major histocompatibility complex A large family of loci that play an important role in the vertebrate immune system. They produce molecules that bind foreign antigens. These loci show extraordinarily high levels of genetic diversity.

Outbreeding depression A reduction in reproductive fitness due to crossing of two genetically differentiated or differentially adapted populations, or sub-species, or species.

Phylogeny The evolutionary development and history of a sub-species, species or higher taxa. Often visualised as a *phylogenetic tree*.

Phenotype The morphological, physiological, biochemical, behavioural, and other characteristics of an organism, manifested throughout it life, that develop through the action of genes and environment; or any subset of such properties, especially those affected by a particular allele or other proportion of the genotype.

Phylogenetics The study of evolutionary relatedness among various groups of organisms (e.g., species, populations).

Phylogenetic tree A tree reflecting the relationships between different species or populations.

Plasticity The extent to which an organism can make modifications to its phenotype which are induced by changes in the environment and which do not require underlying changes in genotype.

Population A group of conspecific organisms that occupy a more or less well defined geographic region and exhibit reproductive continuity from generation to generation; it is generally presumed that ecological and reproductive interactions are more frequent among these individuals than between them and members of other populations of the same species.

 Q_{ST} is equivalent to F_{ST} , calculated using gene frequencies for quantitative traits. The relationship between levels of F_{ST} and Q_{ST} can be used to infer patterns of evolution.

Speciation The process by which populations diverge and become reproductively isolated so that they develop into different species.

Stochastic Having a chance element.

Vagility The capacity or tendency of an organism or a species to move about or disperse in a given environment.

List of Acronyms

AFLP	Amplified fragment length polymorphism
AONB	Area of Outstanding Natural Beauty
BRWG	Biodiversity Research Working Group
CBD	Convention on Biological Diversity
cpDNA	Chloroplast DNA sequence
ERFF	Environmental Research Funders' Forum
ESU	Evolutionarily Significant Unit
HAP	Habitat Action Plan
IUCN	World Conservation Union
MHC	Major histocompatibility complex
mtDNA	Mitochondrial DNA sequences
MU	Management Unit
NERC	Natural Environment Research Council
PCR	Polymerase chain reaction
SAC	Special Area of Conservation
SAP	Species Action Plans
SLINC	Site of (Local) Importance for Nature Conservation
SSSI	Site of Special Scientific Interest
UKBAP	UK Biodiversity Action Plan
UKBRAG	UK Biodiversity Research Advisory Group
UKPopNet	UK Population Biology Network

Species List

Binomial Name	Common Name
Agrostis spp	Bent or bentgrass
Bufo calamita	Natterjack toad
Canis latrans	Coyote
Canis lupus	Grey wolf
Canis rufus	Red wolf
Cypripedium calceolus	Lady's slipper orchid
Euphrasia spp	Eyebrights
Felis silvestris grampia	Scottish wild cat
Ficedula albicollis	Collared flycatchers
Hirundo rustica	Swallows
Hyacinthoides hispanica	Spanish bluebell
Hyacinthoides non-scripta	Bluebell
Limonium binervosum	Rock sea-lavender
Limonium group	Sea lavender
Littorina spp	Winkles
Loxia scotica	Scottish crossbill
Loxodonta Africana	Elephant
Meles meles	Badger
Mercurialis annua	Annual mercury
Mercurialis Perennis	Dog's mercury
Oncorhynchus tshawytscha	Chinook salmon
Oxyura jamaicensis	Ruddy duck
Oxyura leucocephala	White-headed duck
Parus major	Great tit
Pinus sylvatica	Scots pine
Populus tremula	Aspen
Puma concolor coryi	Florida panther
Rhinolophus hipposideros	Lesser horseshoe bats
Saxifraga cespitosa	Tufted saxifrage
Senecio squalidus	Oxford ragwort
Sorbus	Whitebeams
Sorbus arranensis	Arran whitebeam
Sorbus aucuparia	Rowan
Sorbus pseudofennica	Arran service-tree
Sorbus rupicola	Rock whitebeam
Tamiasciurus hudsonicus	North American red squirrel
Triturus marmoratus	Marbled newt
Triturus cristatus	Great crested newt

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Annex A: Delegates List

Full Name	Organisation
Zanete Andersone-Lilley	Biodiversity and Landscape Branch, Natural Resources & Rural Affairs Science Division, Defra
Richard Bateman	The Natural History Museum, London
Trevor Beebee	University of Sussex, School of Life Sciences
David Boshier	University of Oxford. Department of Plant Sciences
Mike Bruford	Cardiff University, Biodiversity and Ecological Processes Group
Terry Burke	University of Sheffield, Department of Animal and Plant Sciences
Roger Butlin	University of Sheffield, Department of Animal and Plant Sciences
David Coltman	University of Alberta, Canada; Department of Biological Sciences
Joan Cottrell	Forest Research, Northern Research Station
Joanna Drewitt	Scottish Executive
Richard Ennos	University of Edinburgh, Institute of Evolutionary Biology
Mike Fay	Royal Botanic Gardens Kew
Richard Ferris	Joint Nature Conservation Committee
Sara Goodacre	University of East Anglia Norwich, School of Biological Sciences
John Harvey	National Trust
Phil Hedrick	Arizona State University, USA; Department of Zoology
Helen Hipperson	University of Sheffield, Department of Animal and Plant Sciences
Dr Rus Hoelzel	University of Durham, Department of Biological Sciences
John Hopkins	English Nature
Ruth Jenkins	Forestry Commission
Barbara Jones	Countryside Council for Wales
Grant Luscombe	Landlife, National Wildflower Centre
Donald MacIntyre	Flora Locale
Robbie McDonald	Quercus, Queen's University Belfast
Juha Merilä	University of Helsinki, Finland; Ecological Genetics Research Unit
Robert Ogden	Wildlife DNA Services
John Pannell	University of Oxford, Department of Plant Sciences
Paulo Prodöhl	Queen's University Belfast
Simon Pryor	Forestry Commission Cambridge
Ilik Saccheri	University of Liverpool, School of Biological Sciences
Richard Smithers	The Woodland Trust

Full Name	Organisation
Jane Squirrel	Royal Botanic Garden Edinburgh
Athayde Tonhasca	Scottish Natural Heritage
Eric Verspoor	FRS Marine Laboratory
	University of Sheffield, Department of Animal and Plant
Raj Whitlock	Sciences

Annex B: Background documents

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Annex C: The roles of UKBRAG & UKPopNet

The role of the UK BRAG

The UK Biodiversity Research Advisory Group (UK BRAG) has been charged with identifying both knowledge gaps and the research needed to fill these in order to facilitate successful delivery of the UK Biodiversity Action Plan. UK BRAG's work plan 2003–2006 has had at its core, six broad cross-cutting research themes, determined by the Biodiversity Research Working Group (BRWG) in its report Science in Action for Biodiversity (Defra 2001). One of these themes concerned science for the conservation of genetic and native species diversity, and was a driver for the workshop that has led to this report.

The key issues identified by BRWG were:

To develop, for native species, a better understanding of genetic variation, functional ecology and the taxonomy of lesser-known groups, to guide policy and practical action for biodiversity conservation and restoration.

The drivers for this work are:

- The need for clear objectives with regard to the conservation of genetic and native species diversity at the landscape level, to compliment the UKBAP actions via Species Action Plans (SAPs) and Habitat Action Plans (HAPs);
- The need for better information on threats to the genetic integrity of native species, on the numbers and systematics of species, and on how species interact to maintain ecosystem dynamics, functions and processes. This would allow an assessment of the adequacy of current and potential new measures for species conservation at the landscape level.

BRAG's vision was for research within six main areas:

- 1. Understanding genetic variability. Improve current knowledge of how much genetic variation is present within some of our species and how it is distributed within populations, between populations, between geographical areas and between different habitat units. This could be focused on priority species, with these species being identified through consideration of aspects such as which species are priorities for conservation, generic categories or functional groups of species, or the selection of model species.
- 2. Understanding areas of risk. Research to assess the potential impacts of pressures such as introduced genes, habitat loss and landscape change, and to inform species (re)introductions and translocations policy and practice.
- **3. Formulating action.** Research needed to support the development of strategies and policies for the conservation of native species genetics. This should include consideration of the impacts of management, including introductions, and of policy.
- **4. Functional species in the marine environment.** Research on the ecology of keystone species (including, e.g. succession, turnover, spatial dynamics etc.) and on the roles and relationships between individual species and guilds of species. The identification of indicator species is required for the assessment of habitat and ecosystem health.

- 5. Maintenance of species populations and essential interactions between species at the landscape level. Research on the ecology of keystone species in terrestrial environments, and on the roles and relationships between individual species and guilds of species. This should guide research to assess the ability of different landscape types to sustain different key species or functional groups over time. The identification of indicator species is required for the assessment of habitat and ecosystem health.
- 6. Improved knowledge of taxonomy and systematics in lesser-known groups. Research guided by a review of the current status of taxonomic knowledge in relation to native species groups, and taxonomic and systematics research, for the lesser-known groups. This need was identified especially for marine organisms, but is likely to be relevant for other species groups as well.

UK BRAG's purpose in supporting this workshop approach has been to bring together a diverse community of experts working in conservation genetics research, practical biodiversity conservation and policymaking; in order for them to improve understanding of the role of genetic conservation, learn about the 'current state of the art' in conservation genetics, identify information requirements, and consider the research priorities in order to fill the knowledge gaps. A specific output from the workshop has been to produce a list of priority research actions – a research strategy for promotion to major funding agencies.

The role of the UK Population Biology Network (UKPopNet)

The UK Population Biology Network (UKPopNet) is a network of institutions funded by the Natural Environment Research Council (NERC) with additional funding from English Nature. It was founded by researchers from some of Britain's leading research Universities including Aberdeen, East Anglia, Leeds, Sheffield, York and the Centre for Ecology and Hydrology. UKPopNet funds or participates in eight inter-institutional projects and a series of working groups and workshops. UKPopNet's work focuses on two questions of pressing importance to science and society:

- How will biodiversity change affect the sustainability of ecosystems, landscapes, and livelihoods?
- How can we mitigate those effects?