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Source: *Philosophical Transactions: Biological Sciences*, Vol. 349, No. 1327, New Uses for New Phylogenies (Jul. 29, 1995), pp. 113-118

Published by: The Royal Society

Stable URL: <http://www.jstor.org/stable/56130>

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Uses of molecular phylogenies for conservation

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SUMMARY

Conservation requires the accurate targeting of resources together with information on population processes. Molecular phylogenies can potentially contribute in both areas. Interspecific molecular phylogenies can identify clades undergoing rapid diversification or extinction and can assess the contribution of individual lineages to overall genetic diversity. Whether and how this should translate to conservation priorities is open to debate. Within species, molecular phylogenies along with information on allele frequencies can be used to identify evolutionarily significant population units or areas. In relation to population processes, molecular phylogenies may provide a perspective on population growth and connectivity over evolutionary time. As threatened species typically have undergone rapid changes in population size and/or migration rate, phylogeny-based estimates may be misleading about contemporary population processes. However, the comparison between historical and current estimates may identify significant changes to long-term trends, thus identifying population in need of urgent management. This information can potentially suggest strategies for managing declining or fragmented species, but this requires further theoretical and experimental study.

INTRODUCTION

Phylogenies of species are producing important insights into taxonomy, the evolution of characters and the long-term patterns and dynamics of adaptation and divergence (Brooks & McLellan 1991; Harvey & Pagel 1991). Molecular characters provide a rich source of information for analysis of species phylogeny and, within limits, can indicate the approximate timing as well as sequence of events (Hillis & Moritz 1990). Molecular systematics can also reveal the phylogeny of alleles within species, revealing previously inaccessible details of historical biogeography and population processes (Avice 1989, 1994; Hudson 1990). Whether these new tools and concepts will prove of practical and general use of conservation remains to be demonstrated. In this paper, I consider the use of molecular phylogenies in two areas relevant to wildlife conservation: description of biodiversity and inference of population processes.

DESCRIBING BIODIVERSITY

Identification of 'evolutionarily significant units'

The definition of conservation units within species is fundamental to prioritize and conduct management (see, for example, Daugherty *et al.* 1990). Moritz (1994*a, b*) suggested a distinction between two types of conservation unit (figure 1): *management units* (MUS), representing sets of population that are currently demographically independent; and *evolutionarily, significant units* (ESUS), which represent historically isolated sets of populations that together encompass the evolutionary diversity of a taxon. Both types of unit are

significant for conservation, the former primarily to short-term management and the latter more to strategic, long-term issues. For example, MUS are the logical unit for monitoring responses of populations to impacts and management. Their value is as important functional components of the (usually) larger evolutionary entity. ESUS constitute the larger entities that conservation actions seek to preserve and can be seen as a complement to species as defined under broader criteria (Moritz 1994*b*) or as essentially equivalent to species under a phylogenetic species concept (Vogler & DeSalle 1994).

Whereas MUS often are best defined by differences in allele frequency (Hudson *et al.* 1992), the suggested definition of ESUS incorporates information on allele phylogeny, specifically the phylogeny of mitochondrial DNA (mtDNA) alleles in relation to their distribution (see also: Dizon *et al.* 1992; Vogler & DeSalle 1994). The definition proposed (Moritz 1994*b*) is that ESUS should be reciprocally monophyletic for mtDNA alleles and also differ significantly for the frequency of alleles at nuclear loci (figure 1). Reciprocal monophyly of mtDNA was selected not because this is evolutionarily significant in itself, but because theory and simulations suggest that isolated sets of populations reach this condition after a specific amount of time, of the order of $4N$ generations (Neigel & Avice 1986), although allele coalescence may be more rapid in a declining population (Avice *et al.* 1984). This criterion is stringent, has the advantage of being qualitative rather than quantitative and has a sound basis in population genetics theory. Whether nuclear genes should show concordant phylogenetic structuring (Avice & Ball 1990) is open to debate. This may be overly restrictive given that nuclear genes are

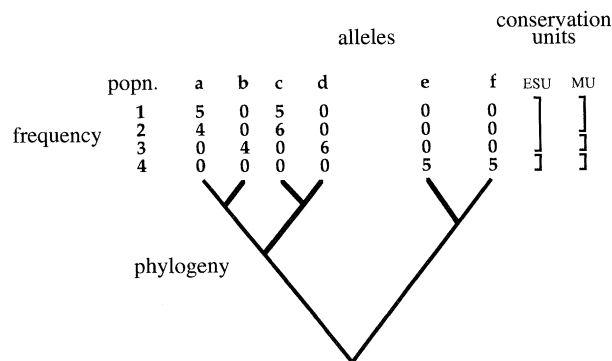


Figure 1. Different types of conservation unit defined by allele phylogeny and frequency. Management units can be recognized as populations with distinct allele frequencies. e.g. populations 1 + 2 vs 3 vs 4, whereas evolutionarily significant units are defined by having reciprocally monophyletic mtDNA alleles, e.g. populations 1 + 2 + 3 vs 4 as well as divergence in allele frequencies at nuclear loci. Modified from Moritz (1994a).

expected to retain ancestral polymorphisms for longer than mtDNA and clearly demarked species that are reciprocally monophyletic for mtDNA often retain ancestral polymorphisms at nuclear loci (see, for example, Slade *et al.* 1994).

A clear example of a species with multiple ESUs, as defined above, is provided by the ghost bat, *Macroderma gigas*. This species has undergone a marked contraction of its range and is now restricted to a series of disjunct breeding populations around the humid north coast of Australia. Each regional population has monophyletic alleles for mtDNA (Worthington Wilmer *et al.* 1994) and significant divergence of allele frequencies at microsatellite loci (J. Worthington Wilmer, unpublished data). Thus, each regional population is a separate ESU and warrants conservation effort.

This approach has proved useful for documenting the evolutionary diversity within species, but, in general, resources or political will are inadequate to conserve all ESUs. A significant and more practical extension of this approach is to identify geographic areas between which many species show phylogeographic structure (Avice 1992, 1995; Brooks *et al.* 1992), i.e. to identify *evolutionarily significant areas*. These could be targeted separately for establishing protected areas or development of off-park conservation measures. A dramatic example is provided by the wet tropical rainforests of northeast Australia. Comparison of mtDNA sequences from several species of rainforest restricted vertebrates revealed geographically congruent phylogeographic structuring about a historical barrier predicted by previous palaeoclimatological modelling (Joseph *et al.* 1995). The rainforests to the north and south of this site are already included in a World Heritage Area and protected accordingly, but the molecular data have enhanced appreciation of the evolutionary significance of the smaller northern block of rainforest.

Representation and conservation value

The above use of molecular information in defining ESUs was confined to consideration of phylogenetic pattern; it was not the intention to ascribe conservation value on the basis of the magnitude of sequence divergence between populations. By contrast, several authors (for example: Crozier 1992; Faith 1992) have derived algorithms for assessing the conservation priority of taxa, and thus areas, based on branch lengths of molecular phylogenies (see, for example, Crozier & Kusmierski 1994). This builds on the suggestion that the priority accorded to taxa should take account of their phylogenetic distinctiveness (Vane-Wright *et al.* 1991).

The usual goal is to measure biodiversity to ensure that reserve systems are representative. The 'taxic diversity' approach of Vane-Wright *et al.* (1991), Faith (1992) and others emphasizes phylogenetically divergent lineages or a set of such lineages that best represents the breadth of the evolutionary diversity. Molecular phylogenies can contribute significantly to the estimation of species phylogenies for this purpose, regardless of branch lengths, but the inclusion of molecular distance does, at least crudely, add a time dimension. However, it should be borne in mind that single-gene trees are subject to variation in rates of evolution (Gillespie 1986) and also may depart from the true phylogeny of the species (Pamilo & Nei 1988; Slade *et al.* 1994).

A very different, and potentially conflicting, approach accords higher priority to *currently diversifying* taxa as these may provide the basis for 'faunal reconstruction' following the current mass extinction (Erwin 1991; Brooks *et al.* 1992). Molecular phylogenies can be used for this purpose to distinguish between geographic areas that contain rapidly speciating lineages ('evolutionary fronts'; Erwin 1991) and those with predominantly old lineages. For example, using DNA-DNA hybridization data of Sibley & Ahlquist (1990) and Fjeldsa (1994) identified areas of Amazonian rainforest with concentrations of young species and suggested that these could provide a better basis for protection and reservation than the more dispersed areas with old species that would receive high priority under the taxic diversity approach.

To a large extent, the conflict between conservation of old and conservation of young lineages stems from differences in conservation goals and philosophy. Taxic diversity explicitly focuses on pattern, attempting to identify areas that will include the greatest phylogenetic breadth of species without making assumptions about future processes. By contrast, Fjeldsa (1994; see also Brooks *et al.* 1992) argues that an understanding of process, and the use of this information, is necessary to take differences in vulnerability and sustainability into account. Towards this end, Nee *et al.* (1994) have developed methods for measuring lineage speciation and extinction rates from molecular phylogenies and suggest that these could be used to identify clades of species that are under threat.

The contradictions between 'taxic diversity' and 'evolutionary front' approaches suggests that to use

phylogenetic criteria as a primary means to attach conservation value to species is fraught with unresolved ethical and conceptual problems and thus may be premature. The issue of conserving pattern versus process is considered further below.

INFERRING POPULATION PROCESSES

Species management typically requires information on population size and connectivity, particularly for harvested or declining species. These parameters are central to the dynamics and viability of meta-populations, but connectivity in particular is difficult to measure by traditional ecological methods. Traditional population genetics provides measures of migration (gene flow) among populations (Slatkin 1987) and, at least potentially, changes in population size (Nei *et al.* 1975; cf. Leberg 1992). More recently, there has been intense interest in methods for estimating gene flow and trends in population size from molecular phylogenies (see, for example: Slatkin & Maddison 1989; Ball *et al.* 1990; Slatkin & Hudson 1991; Nee *et al.* 1995), neutrality being assumed (cf. Rand *et al.* 1994).

In applying these measures for conservation, it needs to be kept in mind that (i) it is difficult to discriminate between current and historical processes and (ii) most species in need of conservation have undergone dramatic changes in population size, structure and connectivity within the recent past. For example, ten species of Australian marsupial have gone extinct in the past 200 years and a further 23 species have undergone dramatic (> 50%) reductions in range, many in the past 100 years (Kennedy 1992).

Estimation of gene flow

Slatkin & Maddison (1989) introduced an approach for measuring gene flow among populations from the geographic distribution of alleles in relation to their phylogeny. The basic concept is to estimate the minimum number of migration events consistent with the phylogeography and, from this, to estimate the value of N_m , the average number of migrants per generation at equilibrium under an island model. Subsequently, this approach was developed to test for different types of population structure, e.g. isolation by distance (Slatkin & Maddison 1990) and panmixia (Maddison & Slatkin 1990). In general, these methods are unable to distinguish between historical and current gene flow (but see Slatkin 1993) and are best regarded as providing a long-term perspective on connectivity, that may or may not correspond with contemporary processes.

In a different approach, Neigel *et al.* (1991) developed a method for estimating single-generation dispersal distance from the variance in geographic ranges of specific mtDNA lineages and this was subsequently extended to distinguish between non-equilibrium and equilibrium situations (Neigel & Avise 1993). These methods do not assume an equilibrium between gene flow and drift, but do require a constant

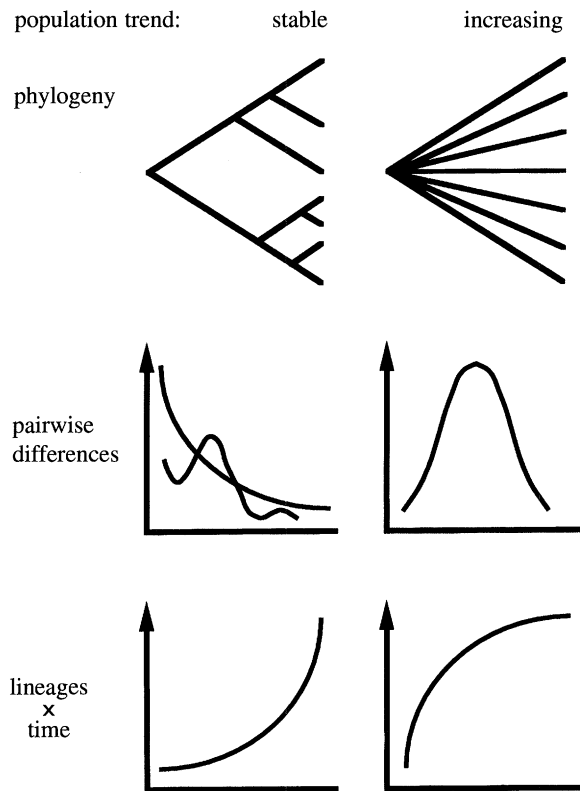


Figure 2. Diagrammatic summary of inferences from DNA sequences about trends in population size (see text).

rate of base substitution. The behaviour of these models for species undergoing a rapid contraction in size or range is not clear, although it is notable that the variance in geographic distribution of lineages did not appear to be affected by cyclic range contractions simulating Pleistocene events (Neigel & Avise 1993).

The distinction between long- and short-term processes of migration is well illustrated by an analysis of mtDNA variation in red kangaroos (*Macropus rufus*; Clegg *et al.*, in preparation). There is no phylogeographic structure of mtDNA from the west coast of Australia to central Queensland, covering most of the species range and a distance of > 3000 km. Yet, in larger sample sizes screened for restriction fragment length polymorphisms (RFLPs), there was evidence for significant heterogeneity of allele frequencies over distances as small as 60 km. This apparent contradiction can be resolved by proposing that kangaroos exhibit considerable long-distance gene flow in the long term, creating a phylogenetically random geographic distribution of alleles, but may have transiently isolated populations, resulting in locally heterogeneous allele frequencies. For the purpose of management, this distinction is critical, with the short-term population structure being more significant for identifying and managing stocks subject to control and harvesting.

Estimation of population trajectories

Another development stems from the realization that population expansion affects a number of parameters for DNA sequences (figure 2). Because of increased retention of gene lineages, expanding popu-

lations are expected to contain DNA sequences with a star-like phylogeny and a Poisson distribution of pairwise differences between alleles, unlike stable populations which are more likely to have strongly structured allele phylogenies with non-Poisson (e.g. geometric or multimodal) distributions of pairwise differences (Slatkin & Hudson 1991; Rogers & Harpending 1992; Felsenstein 1992). However, for pairwise differences, the signature arising from exponential growth at a constant rate is indistinguishable from that due to rapid expansion followed by a period of stasis (or by a selective sweep; Rand *et al.* 1994). This approach was extended by Nee *et al.* 1995 who, by analysing the number of lineages through time, were able to distinguish qualitatively different forms of population growth.

It is not yet clear how these measures respond to large fluctuations in population size in the short term, i.e. tens to hundreds of generations, but, being based on the dynamics of mutations, they are most likely to be relevant to long-term processes. Rogers & Harpending (1992) found that the distribution of pairwise differences responds relatively rapidly to sharp population declines, but 'rapid' was still measured in thousands of generation (i.e. of the order of the inverse of mutation rate), possibly because this method is oversensitive to deep branches in the genealogy (Felsenstein 1992). [Nee *et al.* (1995) used a large set of mtDNA sequences from humpback whales (Baker *et al.* 1993) to make inferences about population history and concluded that population size has been roughly constant, except for a slow increase in the recent past. It is of concern that the rapid reduction from ca. 125 000 to < 5000 individuals at the cessation of harvesting is not evident from the genetic signature. This is part of a larger problem of recognizing changes in the distribution of lineages due to changes in population size on an ecological timescale when these are superimposed on processes operating on evolutionary timescales.]

Another striking example of the disparity between population trends inferred from molecular phylogeny and current status concerns the coconut crab, *Birgus latro*. A study of mtDNA variation (Lavery *et al.* 1995) revealed extremely high allelic diversity, but mostly low sequence divergences. Populations from the Pacific Ocean revealed the genetic signature of an exponentially expanding population: the phylogeny was star-like, the pairwise differences fitted a Poisson distribution, and the lineage \times time plots suggested exponential growth at a constant or, more recently, an accelerating rate. In fact, the species has recently declined in numbers to the point where it is now extinct from most of its former range. Lavery *et al.* 1995 suggested that the current phylogenetic signature reflects rapid population expansion during periods of lower sea level in the Pleistocene, rather than the recent population declines.

CONSERVATION OF PROCESSES INSTEAD OF ENTITIES

From the theory and examples reviewed above, it appears that the most robust contributions of molecular phylogenies to conservation are in defining conservation units, specifically ESUs, and, perhaps, in making inferences about population processes over evolutionary time. Conversely, analyses of molecular phylogenies could be misleading about current or very recent population processes if the species concerned have undergone dramatic declines, as is often the case for species requiring active conservation management.

One option is to use phylogenies just to define entities for conservation and avoid making inferences about process. This would be reasonable if the goal was simply to identify areas containing substantial evolutionary diversity and place them into reserves. However, adaptive management of such reserves and of their surrounds requires information on population size and connectivity, both to assess current status and to predict outcomes of specific management actions. Conceivably, molecular phylogenies could contribute here by providing insights into long-term population trends and patterns of gene flow, against which current behaviour can be compared (Milligan *et al.* 1994). Dramatic differences between long-term and contemporary processes that can be attributed to human modification of the landscape may signal the need for intervention. Of course, common sense should dictate the extent to which historical processes can be maintained in the current human-modified landscape.

For example, around the world a large number of amphibian species appear to be declining precipitously (Blaustein & Wake 1990; Richards *et al.* 1993). While most ecologists view this with alarm, another view is that this could be part of a natural cycle of population contractions and expansions (Pechmann *et al.* 1991), rather than a set of anthropogenic extinctions. This hypothesis is difficult to assess without information on long-term population sizes, data that are virtually non-existent; molecular phylogenies may be informative.

A second issue for which information on long-term versus current processes may be useful relates to translocations and the related questions of managing gene flow or hybridization. On one hand, it is often suggested that a low level of managed migration within a metapopulation may prevent inbreeding and loss of genetic variation through drift (see, for example, Lacy 1987). On the other hand, there are concerns that introduction of foreign genes could result in the loss of local adaptation and cause 'outbreeding depression' (Templeton 1986). Unfortunately, with the exception of dramatic differences in karyotype, our ability to predict the outcomes from the extent of genetic differences among populations is limited (Avisé & Aquadro 1982; Lynch 1991; Vogler & DeSalle 1994).

The approach often adopted by wildlife managers – do not cross genetically distinct stocks – appears conservative, at least from the perspective of maintaining entities. However, this approach, which at the extreme can border on 'genetic typology', may be inappropriate when compared with the long-term processes

that operate in the species concerned (Wayne *et al.* 1994). From the perspective of long-term process, translocation of individuals within ESUs is unlikely to be detrimental and may well be an advantage, whereas deliberate translocation of individuals between ESUs should be avoided (see also: Vrijenhoek 1989; Woodruff 1989). The focus should be on maintaining the overall process, i.e. historical levels of gene flow, rather than the specific entities, e.g. MUS within ESUs.

An interesting situation arises where there is evidence from molecular studies for occasional hybridization between otherwise distinct species. For example, Degnan (1993) found paraphyly of mtDNA between two species of silveryeye (*Zosterops lateralis*) with monophyletic nuclear alleles, a combination strongly suggestive of one or more episodes of historical hybridization. Such hybridization is commonly considered aberrant and to be avoided in managing species. However, several recent studies have suggested that, far from being detrimental, occasional hybridization may be an important part of the evolutionary process (see, for example, Demarias *et al.* 1992), injecting genetic variance back into populations that would otherwise lose their diversity through genetic drift (Grant & Grant 1992, 1994).

CONCLUSION

Information on gene phylogeny can make a significant contribution to conservation through the more rigorous definition of entities and by contributing to better understanding of historical population processes. It is important that the potential limitations of phylogenetic information in making inferences about contemporary processes be explored and recognized. There is need for further development of theory, particularly in relation to the response of measures of gene flow or population trends to rapid fluctuations in size and connectivity of populations. This area is also ripe for experiments to determine whether management recommendations based on inferences from molecular data about long-term processes are valid or general. Such experiments are needed for a variety of species, vertebrate and invertebrate, and can be in the laboratory or in the field, perhaps taking advantage of reintroductions underway as part of existing conservation programs.

I thank M. Bruford, M. Cunningham, S. Degnan, S. Lavery, R. Slade, C. Schneider and J. Worthington Wilmer for critiques, discussion and/or permission to discuss unpublished data. The research described was funded by the Australian Research Council, the Queensland Department of Environment and Heritage and the Collaborative Research Centre for Tropical Rainforest Ecology and Management.

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