

Conclusions

The strength of this workshop was in the exchange it promoted between new theory and new data. Both are allowing us not only to ask new questions, but also to return to old ones using tools that were not available to the contemporaries of Fisher, Haldane and Wright. It seems probable that progress in population genetics will continue apace with the rapid accumulation of sequence data, which contain a wealth of genealogical information amenable to analysis by coalescent theory¹. Much of these data will no doubt continue to come from research on the human genome. Indeed, as one contributor to the workshop commented, this avalanche of molecular data from *Homo sapiens* is turning our species into an unexpectedly good model organism for the study of other systems such as *Drosophila*.

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References

- 1 Fu, Y.X. and Li, W.H. (1999) Coalescing into the 21st century: an overview and prospects of coalescent theory. *Theor. Popul. Biol.* 56, 1–10
- 2 Hudson, R.R. (1990) Gene genealogies and the coalescent process. In *Oxford Surveys in Evolutionary Biology*, Vol. 7 (Futuyma, D.J. and Antonovics, J., eds), pp. 1–44, Oxford University Press
- 3 Lewontin, R. (1980) Theoretical population genetics in the evolutionary synthesis. In *The Evolutionary Synthesis: Perspectives on the Unification of Biology* (Mayr, E. and Provine, W.B., eds), pp. 58–68, Harvard University Press
- 4 Stroheck, C. (1987) Average number of nucleotide differences in a sample from a single subpopulation: a test for population subdivision. *Genetics* 117, 149–153
- 5 Wright, S. (1939) The distribution of self-sterility alleles in populations. *Genetics* 24, 538–552
- 6 Vekemans, X. and Slatkin, M. (1994) Gene and allelic genealogies at a gametophytic self-incompatibility locus. *Genetics* 137, 1157–1165
- 7 Wright, S. (1951) The genetical structure of populations. *Ann. Eugen.* 15, 323–354
- 8 Whitlock, M.C. and Barton, N.H. (1997) The effective size of a subdivided population. *Genetics* 146, 427–441
- 9 Maynard Smith, J. and Haigh, J. (1974) The hitchhiking effect of a favourable gene. *Genet. Res.* 219, 1114–1116
- 10 Hill, W.G. and Robertson, A. (1966) The effect of linkage on the limits to artificial selection. *Genet. Res.* 8, 269–294

The calculus of biodiversity: integrating phylogeny and conservation

Recently, several algorithms – a ‘calculus of biodiversity’¹ – have been proposed to provide a more objective, phylogenetic basis for conservation decisions^{2–4}. But, do such quantitative approaches yield the purported objectivity or can the conservation value of species and areas be measured using phylogenetic information? To answer these, and similar, questions, John Gittleman (University of Virginia, Charlottesville, USA) and Michael McKinney (University of Tennessee, Knoxville, USA) established a ‘Phylogeny and Conservation’ working group sponsored by the National Center for Ecological Analysis and Synthesis (NCEAS) in Santa Barbara, CA, USA. The first of three annual meetings last August represented a collaborative effort among ecologists, evolutionary biologists, paleontologists, systematists and conservation biologists from the USA, Canada, Australia and England.

The first two days laid the groundwork for the rest of the week. Paul Williams (Natural History Museum, London, UK) impressed the participants with a demonstration of his WORLDMAP software program (<http://www.nhm.ac.uk/science/projects/worldmap>) for exploring geographical patterns in biodiversity, rarity and conservation priorities. Quick introductions to the online ‘Tree of Life’ project

(<http://phylogeny.arizona.edu/tree/phylogeny.html>) and the TreeBASE archive (<http://www.herbaria.harvard.edu/TreeBASE>) as potential sources of phylogenetic trees also were provided.

Initial discussion centered on two recent publications by Nee and May⁵, and Warwick and Clarke⁶. Both papers represent important attempts to integrate phylogenetics and conservation biology. The former demonstrated that surprising amounts of phylogenetic diversity might remain even under high rates of (random) extinction. The latter suggested that recent extinction events (e.g. owing to pollution), at least in the marine environment, could be detected through missing phylogenetic diversity. Discussions about both articles prompted the creation of two subgroups. One subgroup extended previous work examining the issues of quantifying the distribution of traits, such as extinction risk, across taxonomic groups (‘taxonomic selectivity’)^{7–9}. A second subgroup explored the phylogenetic and conservation implications of geographic concentrations of biodiversity (‘hotspots’). The remaining members of the working group formed a third subgroup, which examined the value of the evolutionarily significant unit (ESU) concept¹⁰ for designating units for conservation action below the species level.

Taxonomic selectivity or random extinctions?

A fundamental assumption made in Nee and May’s simulation study was that extinction was random with respect to phylogeny. Recent studies, many by members of the working group, indicate that this is not realistic; within taxonomic groups as diverse as mammals⁸, birds^{8,9} and plants¹¹, extinctions and invasions were highly clumped and were not distributed randomly. However, these studies used different measures of the ‘clumpiness’ of the desired traits (‘taxonomic selectivity’), which complicates comparisons across studies and taxonomic groups. Furthermore, the measures used in the studies probably are influenced by various characteristics of the underlying phylogenies or taxonomies. Recognizing these limitations, the ‘selectivity subgroup’ sought to discover a statistic that could detect taxonomic selectivity independent of tree size (i.e. number of species), tree shape (i.e. degree of balance of the tree) or prevalence of the desired trait (e.g. proportion of all species that are endangered or invasive). Moran’s *I*, adapted as a measure of phylogenetic autocorrelation¹², received the most attention as a likely candidate statistic.

The rest of the meeting was devoted to testing the performance of Moran’s *I* at detecting selectivity. The subgroup simulated trees in which tree balance, tree size and the degree of clumpiness of a trait were manipulated to study the degree of dependence of the *I* statistic on these characteristics. Preliminary results were promising; Moran’s *I* seems to accurately detect selectivity, regardless of tree size or shape.

Once the performance of Moran's *I* and alternative statistics have been tested sufficiently, the subgroup plans to propose one statistic that will allow standardized comparisons of the selectivity of extinctions, rarity and invasions among different real data sets. This will allow the subgroup to address several questions, including: how selectivity varies across a wide variety of taxonomic groups; how selectivity varies across geographical regions; how selectivity varies between 'higher' and 'lower' taxonomic units; and how selectivity for extinction is related to selectivity for invasion within taxonomic groups. By developing a suitable statistic, the subgroup hopes to provide an important fundamental tool for evaluating hypotheses about the causes and the consequences of taxonomic selectivity in extinctions and in invasions.

Hotspots

Scientists use many criteria to determine the relative conservation value of different areas (e.g. whether the areas hold many species, many threatened species, many endemic species or large numbers of species across different groups). Following these criteria, many quantitative methods have been proposed to choose important areas to protect with accountability; however, few methods incorporate phylogenetic information. When constrained to choose only a limited number of areas for conservation, the combination of areas containing more 'phylogenetic diversity' (PD)² is an appropriate choice because it should represent the most biodiversity value in the form of different genes, characters or 'features'^{2,3}.

The 'hotspots' subgroup is extending earlier explorations of the link between PD and the spatial distribution of biodiversity. What is the utility of phylogenetic information for selecting appropriate areas for conservation action? Within a given taxonomic group, what are the phylogenetic consequences of losing all the species in a particular geographic location or all the currently threatened species? If hotspots of species richness and PD do not coincide, this might drastically change how candidate conservation areas are chosen.

The subgroup looked at comparing the additional PD gained for two different taxonomic groups when adding a protected area to an existing network. This problem is linked to the general problem of surrogate evaluation¹³. Realistic planning methods that trade-off costs and biodiversity require surrogate information that predicts marginal gains ('complementarity values') for areas. If the gains are not comparable in size, two taxa cannot indicate one another's, or the complete, PD in that particular region. A protocol

was developed for assessing complementarity predictions for surrogates and this was implemented in WORLDMAP. Preliminary results showed good prediction of complementarity patterns between taxonomic groups.

A second project extends the first subgroup's findings of taxonomically non-random extinction risk by comparing the spatial distribution of PD both before and after projected extinction given present threat scenarios. A third project examines whether phylogenetic patterns of threat could predict the amount of ecological disturbance in an area, following on from Warwick and Clarke⁶.

In the future, the hotspots subgroup will expand their work to other regions and other taxonomic groups. Another goal is to examine those species that provide additional PD. Perhaps these species also provide many unique features (*sensu* Faith²). Part of this problem involves how best to calculate branch lengths for PD (Ref. 3). The subgroup will explore this issue by simulation and by selected real taxonomic data sets with both morphological and molecular character data.

Below the species level

The final subgroup originated from a desire of Robert Wayne (University of California, Los Angeles, USA) and Georgina Mace (Zoological Society of London, London, UK) to examine the long-standing problem of how to designate conservation units below the species level. Although the ESU is the accepted standard in this regard [together with management units (MUs)], members of the subgroup felt that the concept is hampered by an over-emphasis on genetic information that can lead to the designation of too many small, and isolated, subunits. A survey of the recent literature revealed that most studies follow the guidelines of Moritz¹⁴, which advocate a purely genetic definition of ESUs. However, a large fraction of papers based conservation decisions on both genetic and ecological evidence, in keeping with the original description of the ESU (Refs 10,15).

Discussions within the subgroup revolved around how to improve the ESU concept or whether to scrap it entirely. This was done using a diverse set of difficult case studies [e.g. red wolf (*Canis rufus*), dusky seaside sparrow (*Ammodramus maritimus nigrescens*), Florida panther (*Puma concolor coryi*) and Gila topminnow (*Poeciliopsis occidentalis occidentalis*)] to pinpoint limitations. It was agreed that decisions should be based on both genetic and ecological evidence, in the context of ecological and genetic exchangeability. Together with an examination of recent and historical processes, this provides a

more fine-grained and, therefore, more flexible categorization than the current system. Future topics the subgroup hopes to address include how hybrids should be managed and how well ESU-like concepts might apply above the species level.

Prospects

The 'Phylogeny and Conservation' working group provided an invaluable opportunity for a diverse group of biologists to agree on what was important and to merge various solutions, all with a view to integrating phylogeny and conservation through quantitative analysis. However, the integration was done with a critical eye. Although it was agreed that phylogenetic information should play a larger role in most areas of conservation biology (e.g. selectivity and hotspots), it was also felt that it had played too large a role in others (e.g. designating ESUs). The key point is that phylogenetic information is another important tool for decision making in conservation biology, along with ecology and numerous human or political considerations. To date, phylogeny generally has been vastly underutilized in conservation biology; but, like any tool, there are times when its use is more or less appropriate.

Pending renewal of the NCEAS award from the National Science Foundation (NSF) early this year, the working group is slated to meet annually for another two years. Future meetings will build on the work already begun and will probably move in new directions with the invitation of new participants. Information about the working group – including a full participant list, links to related websites and information about future meetings – can be found at the NCEAS website (<http://www.nceas.ucsb.edu>) under 'Research Projects' (look for Gittleman and McKinney).

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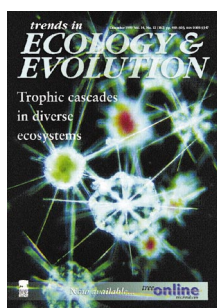
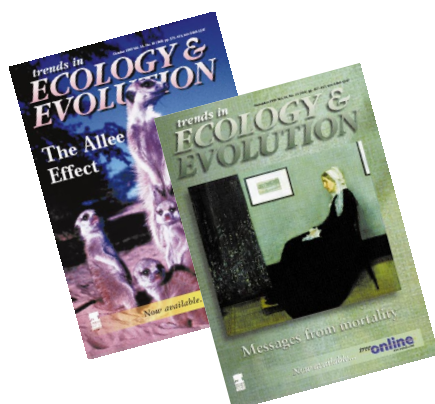
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References

- 1 May, R.M. (1990) Taxonomy as destiny. *Nature* 347, 129–130
- 2 Faith, D.P. (1994) Phylogenetic diversity: a general framework for the prediction of feature diversity. In *Systematics and Conservation Evaluation* (Forey, P.L. *et al.*, eds), pp. 251–268, Oxford University Press
- 3 Williams, P.H. *et al.* (1994) Do conservationists and molecular biologists value differences between organisms in the same way? *Biodiv. Lett.* 2, 67–78
- 4 Crozier, R.H. (1997) Preserving the information content of species: genetic diversity, phylogeny, and conservation worth. *Annu. Rev. Ecol. Syst.* 28, 243–268
- 5 Nee, S. and May, R.M. (1997) Extinction and the loss of evolutionary history. *Science* 278, 692–695
- 6 Warwick, R.M. and Clarke, K.R. (1998) Taxonomic distinctiveness and environmental assessment. *J. Appl. Ecol.* 35, 532–543
- 7 McKinney, M.L. (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Syst.* 28, 495–516
- 8 Russell, G.J. *et al.* (1998) Present and future taxonomic selectivity in bird and mammal extinctions. *Conserv. Biol.* 12, 1365–1376
- 9 Lockwood, J.L. (1999) Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. *Conserv. Biol.* 13, 560–567
- 10 Ryder, O.A. (1986) Species conservation and systematics: the dilemma of subspecies. *Trends Ecol. Evol.* 1, 9–10
- 11 Daehler, C.C. (1998) The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. *Biol. Conserv.* 84, 167–180
- 12 Gittleman, J.L. and Kot, M. (1990) Adaptation: statistics and a null model for estimating phylogenetic effects. *Syst. Zool.* 39, 227–241
- 13 Faith, D.P. and Walker, P.A. (1996) How do indicator groups provide information about the relative biodiversity of different sets of areas? On hotspots, complementarity and pattern-based approaches. *Biodiv. Lett.* 3, 18–25
- 14 Moritz, C. (1994) Defining 'evolutionarily significant units' for conservation. *Trends Ecol. Evol.* 9, 373–375
- 15 Waples, R.S. (1991) Pacific salmon, *Oncorhynchus* spp., and the definition of 'species' under the Endangered Species Act. *Mar. Fish. Rev.* 53, 11–22

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