

methods like phylogenetic footprinting (8).

In studies of the vast diversity of microbes that have never been cultured in the laboratory, DNA can be isolated directly from the environment. To know what organisms that DNA came from, one needs a phylogenetic anchor sequence [e.g., ribosomal RNA (rRNA)] to link the DNA to the tree of life. This approach led to the identification of a novel form of phototrophy in the open ocean (9) and has revolutionized environmental microbiology.

In addition, the tree of life can be used to select species that “bracket” major evolutionary transitions. For example, comparing genomes on either side of the prokaryote–eukaryote transition has identified features conserved among eukaryotes but apparently absent from prokaryotes (10). The importance of this approach is one reason to sequence the genomes of monotremes (the earliest branching group in mammalian evolution that still has living species, including the echidna and the duck-billed platypus). A detailed knowledge not only of the structure of the tree but also of the origin of particular features is important for such studies, so as to avoid artificially grouping together features that evolved independently multiple times such as multicellularity (11).

The concept of a single tree implies that evolution of species follows a branching pattern in which genes and genomes are transmitted vertically from parents to offspring. However, this is not the only mode of evolution—genes can also be passed from one evolutionary branch to another in a process known as lateral gene transfer (LGT). Although the occurrence of LGT was known for many years, analysis of whole genomes has reinvigorated its investigation (12). The value of complete genome sequences is great in these studies since it allows one to screen for genes that may have unusual origins, without any preconceived notions of what those genes might be. This has allowed, for example, the identifica-

tion of “pathogenicity islands” in bacteria (13–15). Analysis of complete genomes has contributed to better understanding of one of the most common forms of LGT—that of genes from organellar genomes (mitochondria and chloroplasts, which used to be free-living bacteria and still have their own genomes) to the nuclear genomes of eukaryotes. Analysis of complete genomes has been used to identify genes that are likely derived from chloroplasts in plant (16) and *Plasmodium* genomes (17).

Unfortunately, many of the claims of LGT turn out to be incorrect [e.g., the claim that the human genome was “infected” with hundreds of bacterial genes (18) has since been refuted (19–21)]. In practice, identifying cases of LGT is quite difficult, and distinguishing it from other phenomena that cause genes to look anomalous, such as unusual rates of evolution, strong selection, or gene loss, has been difficult (22). When done carefully, whole-genome studies suggest that LGT has been rare over the course of evolution and that it has not completely distorted the structure of the tree. Therefore, we should view claims of LGT with appropriate skepticism and ask whether alternative possibilities have been tested.

The value of evolutionary analysis in genomics goes beyond simply using the relationships among species. For example, the prediction of gene function is greatly improved by phylogenetic analysis of gene families (23, 24). Evolutionary reconstructions have revealed that in bacteria the most common major rearrangements are inversions that are symmetric about the origin of replication (25, 26), that the entire genome of the plant *Arabidopsis thaliana* has apparently been duplicated (27), and that many segmented duplications may have occurred in human history (28). Evolutionary analysis also allows the determination of the age of duplication events, which in turn can greatly aid in functional studies (i.e., recent duplications suggest the expansion of an activity in a species, old duplications likely reflect divergent functions) (29, 30). In all such cases, evolu-

tionary analysis helped by allowing homologous genes in different species to be divided into groups of orthologs and paralogs, which in turn allows the identification of duplication events.

In conclusion, there is an ever-growing list of examples in which cross-talk between these two disciplines has enabled scientists to design better experiments and generate new insights. Just as development biology has embraced evolution and become known as EvoDevo, genomics and evolution should become one.

References

1. J. A. Eisen, P. C. Hanawalt, *Mutat. Res.* **435**, 171 (1999).
2. J. A. Eisen, D. Kaiser, R. M. Myers, *Nature Med.* **3**, 1076 (1997).
3. V. Daubin, M. Gouy, G. Perrière, *Genome Res.* **12**, 1080 (2002).
4. M. D. Katinka *et al.*, *Nature* **414**, 450 (2001).
5. T. D. Read *et al.*, *Science* **296**, 2028 (2002).
6. R. D. Fleischmann *et al.*, *J. Bacteriol.* **184**, 5479 (2002).
7. P. Hugenholtz, *Genome Biol.* **3**, reviews0003.1 (2002).
8. D. L. Gumucio *et al.*, *Mol. Cell. Biol.* **12**, 4919 (1992).
9. O. Beja *et al.*, *Science* **289**, 1902 (2000).
10. V. Wood *et al.*, *Nature* **415**, 871 (2002).
11. J. A. Eisen, *Nature* **415**, 845 (2002).
12. W. F. Doolittle, *Trends Cell Biol.* **9**, M5 (1999).
13. J. Parkhill *et al.*, *Nature* **413**, 523 (2001).
14. H. Tettelin *et al.*, *Science* **293**, 498 (2001).
15. H. Tettelin *et al.*, *Science* **287**, 1809 (2000).
16. T. Rujan, W. Martin, *Trends Genet.* **17**, 113 (2001).
17. M. J. Gardner *et al.*, *Nature* **419**, 498 (2002).
18. E. S. Lander *et al.*, *Nature* **409**, 860 (2001).
19. S. L. Salzberg, J. A. Eisen, *Science* **293**, 1048 (2001).
20. M. J. Stanhope *et al.*, *Nature* **411**, 940 (2001).
21. J. Roelofs, P. J. Van Haastert, *Nature* **411**, 1013 (2001).
22. J. A. Eisen, *Curr. Opin. Genet. Dev.* **10**, 606 (2000).
23. J. A. Eisen, *Nucleic Acids Res.* **26**, 4291 (1998).
24. J. A. Eisen, *Genome Res.* **8**, 163 (1998).
25. J. A. Eisen, J. F. Heidelberg, O. White, S. L. Salzberg, *Genome Biol.* **1**, research0011.1 (2000).
26. M. Suyama, P. Bork, *Trends Genet.* **17**, 10 (2001).
27. The *Arabidopsis* Genome Initiative, *Nature* **408**, 796 (2000).
28. J. A. Bailey *et al.*, *Science* **297**, 1003 (2002).
29. I. K. Jordan, K. S. Makarova, J. L. Spouge, Y. I. Wolf, E. V. Koonin, *Genome Res.* **11**, 555 (2001).
30. J. F. Heidelberg *et al.*, *Nature* **406**, 477 (2000).

VIEWPOINT

Preserving the Tree of Life

Georgina M. Mace,¹ John L. Gittleman,² Andy Purvis³

Phylogenies provide new ways to measure biodiversity, to assess conservation priorities, and to quantify the evolutionary history in any set of species. Methodological problems and a lack of knowledge about most species have so far hampered their use. In the future, as techniques improve and more data become accessible, we will have an expanded set of conservation options, including ways to prioritize outcomes from evolutionary and ecological processes.

If a species is at risk of extinction, its close relatives have a higher than average chance of being at risk too (1). As well as predicting extinction risk, phylogeny provides a powerful metaphor for biodiversity—the Tree of Life. If

the lengths of all the branches are summed, phylogeny can go beyond metaphor to yield a natural measure of biodiversity (“evolutionary history” or “phylogenetic diversity” (2, 3) (Fig. 1).

Counting Extinctions

Documentation of the extinction crisis has tended to be about lists of species—those regarded as extinct, as committed to extinction, or as threatened with extinction. The

¹Institute of Zoology, Zoological Society of London, Regent’s Park, London NW1 4RY, UK. ²Department of Biology, Gilmer Hall, University of Virginia, Charlottesville, VA 22904, USA. ³Department of Biological Sciences, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK.

length of these lists should be an indicator of the severity of the problem. Moreover, changes in the length of lists—over time, from place to place, or across higher taxa—should inform us about the nature of the current extinction spasm, the rate at which it is proceeding, and its foci. Recent experience suggests that the length of the lists, especially with respect to changes over time and space, is more affected by the rules used to delimit species than by extinction processes.

The phylogenetic species concept (PSC), in which any diagnosably distinct taxa are recognized as species (4), appeared to open the path to an objective, evidence-led way of delimiting species. In well-worked taxa, most new species have been recognized under PSC. However, it seems that PSC often deflects the issue onto the choice of methodological tools, and phylogenetic methods tend to inflate the number of species at a rate driven by the sophistication of markers and techniques (5). This has serious consequences for conservation biologists' lists. Of the primates added to the latest compilation of threatened species, 17 were newly recognized taxa based on PSC, compared to 7 from actual changes in status (6). Taxonomic changes have always plagued threatened-species lists [they caused 27% of the 295 additions to the World List of Threatened Birds (7)], but widespread adoption of PSC adds to the problem.

The objectivity claimed for PSC comes at a high price: The nature of the species taxon has been changed, and because PSC has had more impact in some taxa and regions than on others, comparisons of the lengths of lists are seriously undermined. For example, at least 140 new amphibian species from Sri Lanka were reported after intense survey and phylogenetic analyses of mitochondrial DNA—a new hotspot of diversity, given that previously only 18 species were known (8). Phylogenies may provide a way to avoid the problem: We can measure directly the evolutionary history that we seek to preserve. Hence, in theory we need no longer bother about the units at the ends of the branches; we can simply build trees based on the total variability in the genetic material of all individuals from a region or clade. The shapes and structures of these trees could be compared across time, space, and taxa to detect the fingerprint of a mass extinction or the impending loss of an entire clade. Such approaches have shown that mammal and bird species on long branches (i.e., without close relatives) are particularly likely to be at risk (9), whereas the opposite pattern may hold for plants (10); they also indicate that the Tree of Life is currently being pruned by extinction very much more rapidly than it is regrowing.

However, serious practical difficulties must be overcome before such analyses can be precise. Accurate estimation of phylogenetic topology faces many pitfalls (11), and accurate dating may be even more difficult (12). Even if all these practical difficulties could be solved, we still must deal with the fact that “saving species” has a resonance that “saving accumulated phylogenetic branch lengths” clearly lacks.

We also face difficulties in providing reliable information on which species are actually going extinct, for several reasons: (i) Most species are poorly known; (ii) very rare species tend to persist for long periods before finally succumbing to extinction; and (iii) conservationists are understandably reluctant to name species as extinct before being abso-

record can tell us (18, 19). Phylogenetic analyses clearly indicate that the current loss of species is focused on the large, long-lived, slowly reproducing forms with specialized habitats and high endemism (20, 21). They can also reveal how patterns of susceptibility can depend on the detail of the threatening process; for example, overharvesting is especially bad for slow reproducers, whereas habitat loss takes its heaviest toll of habitat specialists (21). Extrapolating such results into the future suggests that we are heading for a biota consisting of widespread and weedy species, and that specialized adaptations are being lost much more rapidly than could be inferred simply from lists of the casualties. Some of the most charismatic and distinctive lineages could be lost soon if currently threatened taxa do go extinct, such as the rhinos and kiwis, the giant panda and the elephants; meanwhile, whole radiations of generalists such as small rodents and carnivores stand ready to invade globally.

Devising the Plans

Phylogenetic comparative approaches have modeled extinction risk as a function of species' biological characteristics; some of these models have good explanatory power and could be used as a basis for evaluating the status of species whose risk of extinction is unknown. These methods also highlight species (e.g., the black-footed cat or black spider monkey) (20) that are not yet declining steeply but whose biology renders them susceptible to human impact. Preemptive conservation strategies, likely to be much cheaper than remedial actions, could usefully be developed for such species.

Habitat conservation often provides better value for money than do species-centered approaches. The conservation value of areas has typically been computed from lists of species (or endemic or threatened species) in some well-known taxon, such as birds or vascular plants (22). We have seen that evolutionary history provides an alternative basis for comparing the value of different places. Leaving species concepts aside, does phylogeny make a difference? Apparently the answer is yes, but only under certain conditions: (i) if phylogenies are unbalanced, (ii) if phylogeny reflects geography, (iii) if old species tend to have smaller ranges, and (iv) if old species are in species-poor areas (23). The first two conditions are usually met, and the most thorough studies indicate that the third condition is also met; hence, the last condition is a particularly important one for future research. As suggested in carnivores and primates (24), we should soon know whether “hotspots” of species diversity are also hotspots of evolutionary history.

But what of the evolutionary future? Conservation thinking is increasingly switching

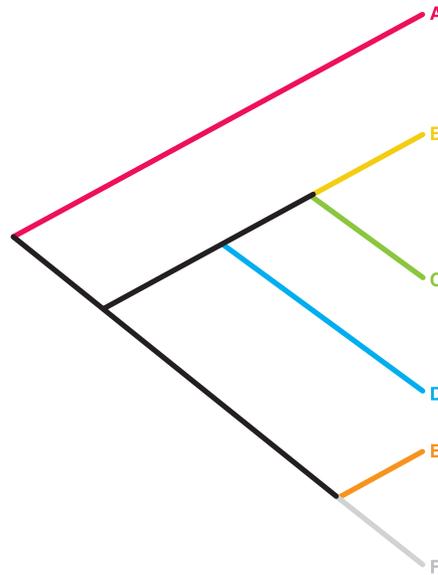


Fig. 1. Loss of species leads to loss of evolutionary history. In this example phylogeny, species A to F each have some unique (colored) and some shared (black) evolutionary history. Extinction of any one species leads to the loss of the unique history it represents. In this case, loss of species A is the most serious.

lutely certain that the last individual has died. Hence, lists of extinct species are far shorter than numerical estimates of the number of extinctions based on indirect methods such as loss of habitat area (13), observed population declines (14), and numbers of threatened species believed to be committed to extinction (15, 16).

Evolutionary Patterns

Dated interspecies phylogenies contain information about rates and distributions of species extinctions and about the nature of radiations after previous mass extinctions (12, 17). These insights are largely independent of those gained from paleontology, which is especially important given current concerns about what large-scale patterns in the fossil

from preservation of the pattern of biodiversity to preservation of the processes that have generated the pattern. Phylogenies retain the imprint of many of these processes. Geographical structure in within-species phylogenies can pinpoint habitats or topographical features that may have been important drivers of diversification (25). At larger scales, phylogenies permit easy identification of clades such as Old World monkeys that are diversifying rapidly, clades such as parrots that have always had high rates of speciation and extinction, and lineages such as the giant panda that are (to be politically correct) speciationally challenged (26). Combined with character data, they highlight key innovations repeatedly associated with high species richness (27), as well as clades where evolution along lineages—another important facet of biodiversity—has been unusually rapid or slow (28). When combined with geographic information, phylogenies may allow us to distinguish “cradles” of diversity (where diversity is generated) from “museums” (where it persists). Such analyses can indicate which taxa and which places are currently most active in the growth of the Tree of Life, and which may therefore be particularly important to conserve. But the priority taxa based on process are bound to differ from those based on pattern: Species in rapidly diversifying lineages must have close relatives, and thus represent little unique evolutionary history. They are unlikely to be priority taxa, given current choices for rarity, endemism, and distinctiveness. In any case, the large-scale history of life has many examples of major radiations with unprepossessing origins (29), showing how difficult it is to pick long-term winners.

The main problem facing all approaches to biodiversity conservation is lack of knowledge. Although we have plentiful Linnaean taxonomic lists, these are not necessarily a surrogate for phylogenetic diversity. In addition, area selection algorithms require distributional data on all taxa; to this already stringent criterion, we now add the need for a complete and well-resolved phylogeny. At present, we cannot even evaluate the extent to which different major groups show common patterns of evolutionary history; biogeography tells us, however, that the patterns will often differ. If so, the information bias toward charismatic vertebrate groups—present in phylogenetics as elsewhere in biology—is serious: A big attraction of numerical algorithms for selecting conservation areas is that they can go beyond subjective preferences for the cute and the cuddly—but if phylogenies are available for only cute and cuddly groups, then we are no further forward. Given the rate at which sequence data in the public domain are accumulating, with initiatives to sequence the entire biota (30) on the horizon, it seems likely that within a decade or two, phylogenetic data will cease to be the limiting factor: It could even be that an organism’s place in the Tree of Life often will be one of the few things we know about it.

References and Notes

1. G. J. Russell, T. M. Brooks, M. L. McKinney, C. G. Anderson, *Conserv. Biol.* **12**, 1365 (1998).
2. S. Nee, R. M. May, *Science* **278**, 692 (1997).
3. D. P. Faith, *Biol. Conserv.* **61**, 1 (1992).
4. J. Cracraft, *Curr. Ornithol.* **1**, 159 (1983).
5. K. A. Crandall *et al.*, *Trends Ecol. Evol.* **15**, 290 (2000).
6. C. Hilton-Taylor, *2000 IUCN Red List of Threatened Species* (IUCN, Gland, Switzerland, 2000).
7. N. J. Collar, M. J. Crosby, A. J. Stattersfield, *Birds to Watch 2—The World List of Threatened Birds* (BirdLife International, Cambridge, 1994).
8. M. Meegaskumbura *et al.*, *Science* **298**, 379 (2002).
9. A. Purvis, P.-M. Agapow, J. L. Gittleman, G. M. Mace, *Science* **288**, 328 (2000).
10. M. W. Schwartz, D. Simberloff, *Ecol. Lett.* **4**, 464 (2001).
11. S. Gribaldo, H. Philippe, *Theor. Popul. Biol.* **61**, 391 (2002).
12. L. Bromham, M. J. Phillips, D. Penny, *Trends Ecol. Evol.* **14**, 113 (1999).
13. R. M. May, J. H. Lawton, N. E. Stork, in *Extinction Rates*, J. H. Lawton, R. M. May, Eds. (Oxford Univ. Press, Oxford, 1995), pp. 1–24.
14. G. Ceballos, P. R. Ehrlich, *Science* **296**, 904 (2002).
15. V. H. Heywood, G. M. Mace, R. M. May, S. N. Stuart, *Nature* **368**, 105 (1994).
16. T. M. Brooks *et al.*, *Conserv. Biol.* **16**, 909 (2002).
17. S. B. Heard, A. Ø. Mooers, *Syst. Biol.* **51**, 889 (2002).
18. J. Alroy *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 6261 (2001).
19. S. E. Peters, M. Foote, *Nature* **416**, 420 (2002).
20. A. Purvis, J. L. Gittleman, G. Cowlishaw, G. M. Mace, *Proc. R. Soc. London Ser. B* **267**, 1947 (2000).
21. I. P. F. Owens, P. M. Bennett, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 12144 (2000).
22. N. Myers, R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, J. Kent, *Nature* **403**, 853 (2000).
23. A. S. L. Rodrigues, T. M. Brooks, K. J. Gaston, in *Phylogeny and Conservation*, A. Purvis, T. M. Brooks, J. L. Gittleman, Eds. (Cambridge Univ. Press, Cambridge, in press).
24. W. Sechrest *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 2067 (2002).
25. J. C. Avise, *Phylogeography* (Harvard Univ. Press, Cambridge, MA, 2000).
26. S. Nee, T. G. Barraclough, P. H. Harvey, in *Biodiversity: A Biology of Numbers and Difference*, K. J. Gaston, Ed. (Blackwell Science, Oxford, 1996), pp. 230–252.
27. T. G. Barraclough, A. P. Vogler, P. H. Harvey, *Philos. Trans. R. Soc. London Ser. B* **353**, 241 (1998).
28. P. S. Soltis, D. E. Soltis, V. Savolainen, P. R. Crane, T. G. Barraclough, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 4430 (2002).
29. A. Cooper, R. Fortey, *Trends Ecol. Evol.* **13**, 151 (1998).
30. E. O. Wilson, *Trends Ecol. Evol.* **18**, 77 (2003).
31. We thank the UK Natural Environment Research Council for support, N. Isaac and A. Rodrigues for information, and the National Center for Ecological Analysis and Synthesis (University of California, Santa Barbara) for a working group on Phylogeny and Conservation (run by J.L.G.).

Turn a new page to...

www.sciencemag.org/books

— Science —
Books et al.
 == HOME PAGE ==

- ▶ the latest book reviews
- ▶ extensive review archive
- ▶ topical books received lists
- ▶ buy books online