

FORUM Evolutionary biology

Birds of a feather

A phylogenetic reconstruction of the diversification of birds across space and time provides a novel resource for evolutionary studies. But the methods used to construct this tree, and what insights can be inferred from it, are a source of debate. Two evolutionary biologists provide opinions on how to draw the lines. SEE LETTER P.444

THE PAPER IN BRIEF

- Geographical and ecological features, such as climate and niche opportunities, influence the evolutionary processes that generate new species.
- Jetz *et al.*¹ (page 444 of this issue) combined genetic and taxonomic information to construct a phylogenetic tree of the almost 10,000 species of extant birds that also considers

their historical locations*.

- The authors report that the diversification rates of bird species vary across the globe, with greater differences in rates between the Eastern and Western hemispheres than across latitudinal lines.
- The phylogeny also reveals ‘hot spots’ of recent diversification in regions characterized by strong climatic fluctuation over the past 5 million years.

Disconnects in diversity

ROBERT E. RICKLEFS

Ever since biologists began cataloguing the diversity of life on Earth, they have sought to understand the origin and maintenance of global patterns of species richness — for example, that life is most diverse where the climate is warm and wet or where mountains vary the landscape. Biological diversity reflects a balance between the tendency of evolutionary lineages to form new species and the variety of living things that an environment can support. Furthermore, diversification depends on the availability of space, the dispersal of life forms among shifting continents, and variations in climate and resources at different locations and over time. Therefore, to understand the distribution of diversity is to interpret evolutionary diversification in historical and geographical contexts — and this is the key to Jetz and colleagues’ remarkable accomplishment.

By integrating their reconstruction of the ancestral relationships of all of the approximately 10,000 known extant species of bird with maps of their distributions, Jetz *et al.* derived a detailed picture of average diversification rates over the surface of the globe. The patterns revealed are intriguing. One might expect more species where the diversification rate is higher, but the authors find that

diversity and diversification rate correspond poorly around the planet — evolutionary lineages split more frequently, on average, in the Western than the Eastern Hemisphere, but not in the tropics compared with higher latitudes. They also find that the overall diversification rate is higher in passerines (songbirds) than in non-passerines (ducks, raptors, shorebirds and others), as expected given the species richness of the former group. But, surprisingly, the data show that the relative contribution of each group to the diversification rate differs between regions. Particularly intriguing is the relative evolutionary quiescence of modern passerines in Australia and New Guinea, where the passerines, now the largest group of birds, originated around 60 million years ago² (Fig. 1).

Biologists will debate whether Jetz and colleagues’ phylogenetic reconstruction is up to the task. Although some DNA-sequence information is available for around two-thirds of bird species, the genomes of only a few have been well sampled. Jetz *et al.* built their phylogeny on a backbone of 158 major bird clades whose relationships had previously been defined³ (a clade represents a ‘branch’ of a phylogenetic tree, including an ancestor and all its descendants). To this, they attached new phylogenetic detail, using a complex algorithm based on taxonomic distinctions to determine the placement of species for

which sequence data are not available.

The result is perhaps not perfect, but it is probably the best possible for now, and is certainly the most ambitious. Moreover, the sequence data that would be required for a substantial improvement might not be worth the effort, because any inference on rates of species production depends on how we circumscribe species. For example, the authors’ method for calculating diversification rate — on the basis of the lengths of branches close to the tips of the phylogeny — may provide inflated estimates in regions in which bird populations are finely distinguished at the species level, such as Europe and North America. So additional sequencing without taxonomic revision

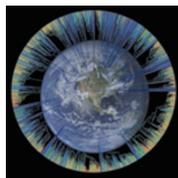
might be an empty exercise.

“The result is perhaps not perfect, but it is probably the best possible for now.”

The apparent absence of a latitudinal gradient in the diversification rates of birds is consistent with a recent analysis for mammals⁴. This

result implies that the great species richness of tropical environments is a matter of age: Earth was mostly tropical before temperate and boreal environments began to expand around 30 million years ago. However, an assessment based on a different phylogenetic approach⁵ concluded not only that the recent speciation and extinction rates of birds both increase towards higher latitudes, but also that the difference between the two (the diversification rate) has nevertheless been higher in the tropics. These conflicting interpretations and other enigmatic patterns arising from Jetz and colleagues’ new phylogeny — for example, that extinction compared with speciation has been relatively infrequent, or that the overall rate of diversification has increased towards the present, particularly with the expansion of cold and arid environments — will motivate further work for some time to come.

Robert E. Ricklefs is in the Department of Biology, University of Missouri-St. Louis, St. Louis, Missouri 63121, USA. e-mail: ricklefs@umsl.edu



NATURE.COM
For more on bird diversification, see: go.nature.com/jvlqnv

*This article and the paper under discussion¹ were published online on 31 October 2012.



Figure 1 | Birds in space and time. These Cape sparrows (*Passer melanurus*) are one of around 5,000 species of songbird (passerine), which make up around half of the known species of bird. Jetz and colleagues¹ have constructed a phylogenetic

tree of all known avian species and mapped this to spatial data of species distribution to assess how bird diversity and diversification rates compare at different times in history and in different regions.

First steps for birds

MARK PAGEL

Jetz and colleagues' bird phylogeny joins several other attempts to reconstruct the history of entire classes of organism, including the 5,000 or so mammals⁶ and the roughly 6,000 amphibian species⁷. These large phylogenetic trees have a value that extends beyond describing the evolutionary relationships among a group of organisms: they grant unprecedented statistical power to attempts to reconstruct the probable historical events and processes of evolution⁸, such as our understanding of ancestral states, or rates of morphological change and speciation. This statistical power allows researchers greater confidence in ruling some proposals in and others out. But it also means that, if the phylogeny is wrong, it might confidently return wrong, biased or misleading answers to tests of evolutionary questions.

And this is why we must receive Jetz and colleagues' tree with a measure of caution. Rather than seeking to infer the avian tree from gene-sequence or other information, such as data on morphology and behaviours, Jetz *et al.* relied on the findings of previous studies to fix the tree's major outlines and the broad placement of most of its species. In fact, the authors assigned positions in the tree to roughly one-third of the bird species on the basis of previous taxonomic classifications alone. As a consequence, the authors' method never explores the possible universe of avian relatedness, and so we are left wondering whether there might be other trees that provide equally good or even better descriptions

of avian evolution, given what we know about birds' genetic, morphological and behavioural similarities and differences.

The authors could have avoided this nagging worry by gathering data on as many species as possible and then inferring the tree by a more conventional route that did not place such strong prior constraints on the outcome. Curiously, for instance, Jetz *et al.* seem to have ignored recently published gene-sequence data⁹ on around 4,000 passerine bird species that were used to infer a tree of this group — the largest within the class Aves.

Jetz and colleagues press their tree into service to study avian speciation rates, concluding that these rates have increased through time

“If the phylogeny is wrong, it might confidently return biased or misleading answers to tests of evolutionary questions.”

and that they are, for example, higher in the Western than the Eastern hemisphere, with latitude generally having a smaller influence. These are the sorts of broad questions that such large trees should be used to test, but here we must not lose sight of the statistical power this tree grants. For example, the authors' methods for estimating speciation rates depend on how well one can estimate the lengths of the branches of the phylogeny in units of time. As has been previously discussed¹⁰, there are reasons to be cautious about the branch lengths that are returned by methods used to infer time-dated trees, and even small biases in branch-length estimation, when integrated over so many species, can produce apparent trends that may or may not be real.

So it is difficult to know what to make, in evolutionary terms, of the 'hemisphere' effect

the authors report. It is not just that there are questions about the tree and the estimation of speciation rates — hemisphere boundaries are arbitrary constructions, and the regions they separate, whether north–south or east–west, are vast and each harbour a wealth of ecological and climatic conditions. Furthermore, when seeking associations between characteristics of species, or between characteristics of species and their environments, it is vital to identify multiple evolutionarily independent instances of the two traits changing in tandem¹¹. But Jetz *et al.* have not done this for the features of climate and ecology that they suggest influence speciation rates.

So these are still 'first steps' towards a phylogeny of birds and our understanding of their rates of speciation. The important questions Jetz and colleagues raise invite careful second steps towards confirming or refuting their proposals in this tricky area. ■

Mark Pagel is in the School of Biological Sciences, University of Reading, Reading RG6 6AS, UK.
e-mail: m.pagel@reading.ac.uk

1. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. *Nature* **491**, 444–448 (2012).
2. Ericson, P. G. P., Irestedt, M. & Johansson, U. S. *J. Avian Biol.* **34**, 3–15 (2003).
3. Hackett, S. J. *et al. Science* **320**, 1763–1768 (2008).
4. Soria-Carrasco, V. & Castresana, J. *Proc. R. Soc. B* **279**, 4148–4155 (2012).
5. Weir, J. T. & Schluter, D. *Science* **315**, 1574–1576 (2007).
6. Bininda-Emonds, O. R. P. *et al. Nature* **446**, 507–512 (2007).
7. Fritz, S. A. & Rahbek, C. *J. Biogeogr.* **39**, 1373–1382 (2012).
8. Pagel, M. *Nature* **401**, 877–884 (1999).
9. Huggall, A. F. & Stuart-Fox, D. *Nature* **485**, 631–634 (2012).
10. Venditti, C., Meade, A. & Pagel, M. *Nature* **463**, 349–352 (2010).
11. Harvey, P. M. & Pagel, M. D. *The Comparative Method in Evolutionary Biology* (Oxford Univ. Press, 1991).