In praise of the big picture

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When ambitious large-scale projects are proposed, like the Paleobiology Database (Alroy et al. 2001) and Panama Paleontology Projects (Jackson and Johnson 2001), there is inevitably a negative reaction from various quarters, which is quickly forgotten when the projects start to yield results. Given that, it may be useful to sing the praises of ''big picture'' science more generally and I will do so after briefly addressing this discussion starter in the context of my own research.

Albeit a truism, it is also a profound truth that the kinds of patterns we observe and the kinds of explanations for these patterns are different at different scales (e.g., Willis and Whittaker 2002). A decade ago I studied the early evolution of the birds using a molecular phylogeny (Nee et al. 1992). In particular, we analyzed the rate of cladogenesis at the root of the phylogeny, the rate of diversification of those lineages that gave rise to all extant species—clearly a global measure of biodiversity dynamics. We wanted to see if the data fit an exponential model of radiation (they do not). This could be construed as ''meaningless'' by objecting that it is meaningless to talk of a ''rate'' when there is, inevitably, rate heterogeneity—not all lineages are the same and the devil is in the detail.

I reject this view, of course. By way of analogy, it is perfectly reasonable to compute and analyze *the* rate of increase of the human population, ignoring heterogeneity. One then discusses this meaningful global observation in terms of the Haber-Bosch system of nitrogen fixation and so on. At a different scale, we may invoke female emancipation to explain the declining populations of Europe. Finally, we could discuss my own childlessness by reference to my personality. ''Meaningless''–ness would arise if and only if we mixed scales and,

for example, tried to think about global population trends in terms of personality. One may not be *interested* in global patterns, but that is a separate matter. It is also a commonplace in ecology and evolution to observe that it is only at a large scale that many important patterns can be seen—the latitudinal gradient in species richness, for example.

In any case, sometimes heterogeneity is actually what is of interest. We identified the Passeri (songbirds) and Ciconiiformes (roughly shorebirds, herons, plovers, flamingos etc.) as text-book exponential radiations, with the Ciconiiformes radiating at a substantially higher rate. This is probably not unconnected with the breakup of Gondwanaland that was occurring at the time (Cotgreave and Harvey 1994).

The molecular phylogeny of Sibley and Ahlquist (1990) that we used to study the tempo of bird diversity dynamics is a useful example of the value of big-picture science that illustrates many points that are important in this discussion. While they were constructing their gigantic single phylogeny of birds, starting from the root of the tree, using what is now considered to be a rather crude molecular method—DNA-DNA hybridization—their work was subjected to the kind of vituperative abuse at which taxonomists excel. Fortunately, they persevered.

One of their major discoveries concerned Australian passerines: birds like fairy-wrens, Austra-Papuan robins and woodswallows had all been placed in different groups of Old World birds, as suggested by their names. Sibley and Ahlquist discovered that they all belonged to a single, ancient family (Corvidae). This discovery was partly owing to Sibley and Ahlquist's use of molecules rather than morphology. But it was also due to the fact that

they were looking at the big picture: many morphological taxonomists had felt that these species were problematic but, only looking at one or two groups at a time, failed to see the simple, overall solution.

Sibley and Ahlquist's phylogeny arrived at a time when comparative biologists had solved their serious statistical problems (Harvey and Pagel 1991). The solution requires large phylogenies, and Sibley and Ahlquist's was seized upon by comparative biologists as an invaluable tool. Owens and Bennet (2000) used it to study extinction risk across contemporary bird lineages: they found two ecologically distinct mechanisms of extinction risk. Human persecution is significantly more likely to endanger large-bodied species with slow life histories, whereas habitat loss is significantly more likely to threaten small-bodied species that are habitat specialists—a global truth.

Two other large phylogenies have since been constructed: a large carnivore phylogeny (Bininda-Emonds et al. 1999) and a complete phylogeny of primates (Purvis 1995). These are different to Sibley and Ahlquist's in that they are assembled from studies carried out by many people on small clades—making these phylogenies, in effect, databases. Both have been studied from the point of view of the following, global, question: if species that are currently endangered do ultimately go extinct, which is likely, what are the consequences for the loss of evolutionary history? The precise definition of this last term is simply the sum total of branch lengths lost from the phylogeny and, thus, corresponds to independent evolution. The answer is unsettling and contrary to theoretical expectations (Nee and May 1997): it is as if a malign intelligence has chosen to extinguish precisely those species that will maximize the loss of evolutionary history (Purvis et al. 2000; von Euler 2001).

Although Sibley and Ahlquist's phylogeny has largely stood the test of time, it was argued while they were constructing it that, perhaps, it would be better to really nail down the phylogeny of a small group than go for the big picture with the inevitably greater error rate that that must entail. Interestingly, it was discovered about five years after the publication

of their phylogeny that you are *less* likely to make errors constructing large phylogenies than small ones (Hillis 1996). Hence, it is not safe to assume that small scales will give you greater accuracy.

Other ''big picture'' studies readily come to mind. It is difficult to recall now the high levels of opposition to the Human Genome Project when it was proposed: I was contemptuous. But now, ignoring the unfolding revolution in medical genetics, just the knowledge that I have as many genes as mustard cress and that my genome consists mainly of selfish genetic elements has changed the way I see myself in the world (IHGSC 2001; but see Shouse 2002). Sepkoski's renowned data set almost had a more widespread and profound cultural impact—imagine if it were true that we are visited every 26 million years by a death star (Raup 1984, Raup 1985; Sepkoski 1992)? So we are not: it could have been otherwise. Here are two more examples from further afield that illustrate that the big picture usually contains big surprises. The goal of producing a magnetic map of the world's oceans had the entirely unexpected consequence of confirming the theory of plate tectonics. Producing a large-scale map of the galaxies revealed unsuspected large-scale structure—gigantic holes—with implications for the origin of the universe.

A common source of criticism of the large-scale approach is that the data will be flawed or incomplete. Well, obviously, data can be corrected and added to over time. But, most interestingly, theory can be used to study and even correct the imperfections. In the 1940s, Corbet was cataloging the butterflies of Malaya. He posed the great R. A. Fisher a rather odd question: How many species did he *not* have specimens of—how incomplete was his data set? Being a genius, Fisher invented the statistical theory to actually answer this question using Corbet's butterfly sampling data (Fisher et al. 1943). The same theory could also be used to address the question: If Corbet went out and caught another hundred butterflies, how many would be of new species, how many would have been seen once before, etc.? This version of the theory was used to authenticate a new poem by Shakespeare discovered

in the 1980s (how many words in the poem had Shakespeare never used before, used once before etc.) (Kolata 1986). Returning to paleobiology, sampling biases, for example, are a clear problem for global biodiversity studies: ingenious ideas are being used to solve this problem (Alroy et al. 2001).

Never mind biodiversity dynamics; what about biodiversity per se? Efforts are currently underway to catalog all the named species on Earth using modern information technology (Bisby 2000). This effort provides further examples of the theme that problems and weaknesses may, in fact, be opportunities. The obvious problem is that species are not unambiguously defined and one person's ''species'' may be another person's subspecies and so on. The solution is to list all names that have been given for a species and information about how inclusive the name is. This allows entirely new sorts of questions to be asked: for example, are there any interesting biological generalizations about what organisms are more or less likely to be divided into subspecies?

Finally, the blindingly obvious. The globe is not an abstraction and important processes affecting biodiversity occur on a global scale: the oxygenation of the atmosphere, ocean circulation, the fluctuating CO_2 concentration of the air, the breakup of Gondwanaland, habitat destruction, global trade and the spread of alien invasive species, and so on. Global processes produce global patterns.

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