
Can systematists help decide the relative worth of bits of biodiversity?

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Introduction

2010 is the United Nations' "International Year of Biodiversity" (www.cbd.int/2010/welcome/). Ostensibly, the year has been set aside for 'celebration', though this term is just the sugar-coating for the call to 'safeguard the variety of life on earth-' i.e. to do something. The United Nations knows that their member nations are in trouble, and a good deal of that trouble is due to the sad state of their biodiversity. The consensus view is that we are in the midst of a global biodiversity crisis.

Readers of this newsletter know well that the basic information on biodiversity (what bits are where) is generally produced by alpha taxonomists. As we venture ever deeper into the age of automated taxonomic identification (e.g. via various barcodes), this basic information will still be overseen by taxonomists, but no longer created by them. Will systematists and taxonomists become more peripheral? We argue here that, insofar as the Tree of Life is the true measure of first-order biodiversity (i.e. its moving parts), modern systematists must remain at the forefront of directed research on biodiversity and conservation. However, the argument we outline below is based on the premise that some bits of biodiversity are more worthy of our conservation efforts than others. This is contentious.

The argument

In an idiosyncratic but provocative essay, Brian Bowen and Joe Ramon suggested the "Orlog model" for characterizing biodiversity (Bowen & Ramon, 2005). In this Norse Mythological story, Urd, Verdandi, and Skuld are three sisters who tend the tree of life, and their names evoke the past, present and future. Bowen and Ramon suggested biodiversity could be viewed from a similar temporal set of perspectives. In this framework, phylogeny is the study of the past history, ecology is the study of present interactions, and evolution is the study of the future potential of some subset of biodiversity. According to the authors, all three perspectives should be considered when measuring the worth of any particular subset in the context of conservation.

Researchers working in systematics are ideally placed to inform the historically-minded handmaiden Urd's choices. Simply put, we can aid the process of making conservation decisions by providing additional information about species derived from the process of evolution. Vane-Wright et al. (1991) of the Natural History Museum (London) were perhaps the first to explicitly consider using phylogenies to establish the conservation priority of sets of taxa and this important concept has been quantified and continually refined by Faith (1992 and onwards). Importantly, Faith introduced the quantity "phylogenetic diversity" to mean the sum of branch lengths of the phylogenetic tree that connects

together all the taxa in a set.

We cannot predict the future course of evolution, and, therefore, betting on evolutionary winners and losers is likely to be nonsensical over relevant timescales (Bowen & Ramon, 2005; Barraclough & Davies, 2005). Instead, using Faith's phylogenetic diversity measure we can choose to conserve sets of species that maximise phylogenetic diversity, thereby maximising the past routes of evolution, and so carrying forward a varied portfolio of species into an uncertain future (Faith, 1992). But here lies the contention: By looking to maximise phylogenetic diversity, we are implicitly changing the mindset of conservation from one where a species' need for conservation attention is dictated by its probability of its extinction (e.g. the Red List; www.redlist.org), to one where we value species based on their ability to conserve past evolutionary history, and therefore, deciding instead, which species we cannot afford to lose.

Given this previous body of work, we appear to have a fledgling basis for using evolutionary history to make conservation decisions, and this might appear to be the end of the story for systematists in the realms of conservation decision making. Interestingly, however, there is some evidence of an agreement between the three sisters' points-of-view. The first hint of such an agreement comes from Faith's assertion that, in theory, 'phylogenetic diversity' is a robust index of the combined 'feature

diversity' of the set. By looking to maximise phylogenetic diversity we could, therefore, also maximize the 'features' contained by the species we are choosing to save.

Reconciling phylogeny and ecology

The precise nature of the 'feature diversity' assigned to the branches of a phylogeny by Faith (1992) can be interpreted in several different ways. One interpretation is any measurable heritable difference between species. Ignoring for a moment biases in phylogenetic construction, if branch lengths within a 'true' phylogeny are to accurately represent the number of physical differences between species, phenotypic changes would need to occur at the same rate(s) as DNA substitutions - or, if we assume a molecular clock, at a constant rate through time. Furthermore, for this relationship to be useful across taxonomies, this consistent relationship between genetic and phenotypic change would also need to be on the same scale across the tree of life. We know of no systematic test of these ideas, but it is a lot to ask of Nature.

Instead, we could look beyond the basic phenotypic differences between species. We could consider 'feature diversity' as measuring those evolutionary changes that affect a species' ecological role (i.e. 'features' are considered to be changes that are non-synonymous in terms of ecology). Here we may be on safer theoretical ground, since ongoing, continual evolution by natural selection may indeed allow for accumulation of ecologically-relevant change at some average rate, at least over long time periods. Again, in order to compare across taxa, this rate would have to be similar across very different biologies.

At the limit, we already know that rates of ecological change vary among groups. George Gaylord

Simpson, in his 1944 book *The Tempo and Mode of Evolution* coined the term 'bradytelic', which he used to describe those taxonomic groups who appear to have remained almost static in their measurable appearance, during their known fossil record. In this respect, Cyanobacteria are perhaps the organisms most unchanged by the process of evolution, as fossil Cyanobacteria dating from ~3.8 billion years ago appear to show similar biochemical patterns to those left by today's extant taxa. Other lineages are more readily modified; for example, the major phenotypic radiations of Angiosperms, birds and mammals have occurred within the last 100 million years. So, we know that the amount of evolutionary change is unlikely to be consistently correlated to time-based branch lengths, throughout the entire tree of life.

Setting aside these extreme examples, let us assume that within more restricted taxonomic groups (e.g. within the mammals) branch lengths might, on average, correlate with the build-up of ecologically-relevant traits. Then, by selecting the subset of species which contain the maximum possible 'phylogenetic diversity' value, we might suppose to reach some agreement between two of the Orlog handmaidens: by conserving the widest set of possible historical phylogenetic paths we also capture a wide array of ecological diversity. This way, we would not only look to maximise our historical portfolio but also our present day ecological one. This would be a property worthy of investigation, and, if proved correct, worthy of greater public attention.

What does previous work tell us? Forest and colleagues (Forest et al., 2007) considered phylogenetic diversity in a large scale conservation planning exercise in the South African fynbos. As part of their study, they found that a greater number of economically-relevant

species are conserved when phylogenetic diversity was used to choose sets of species than when species were chosen at random. This was because different types of economically-relevant traits were clustered in different parts of the tree. Devictor et al. (2010) show that, for birds, there is a general correlation between the amount of 'functional trait' diversity and phylogenetic diversity across grid cells in France ($R^2 = 0.26$), with areas of both surprising congruence and incongruence. Work by Suzanne Fritz & Andy Purvis (2010) may also be relevant: they present evidence that the variation in mammal body size for an ecoregion (a surrogate measure of total ecological diversity of mammals) is predicted to drop much more than both phylogenetic diversity and species richness if IUCN-listed mammals are lost. This is because at-risk mammals tend to be large. Whether overall phylogenetic diversity and body-size variation in mammals is correlated at various geographic scales is still an open (and simple-to-test) question, though we do know that related mammals do have similar body-sizes.

Marc Cadotte goes one step further in linking phylogeny to ecology, by testing whether greater phylogenetic diversity can lead to greater ecosystem productivity. Working with data from David Tillman's long-term community ecology plots in Minnesota, he and colleagues found that phylogenetic diversity measured in inferred substitutions was a better predictor of productivity (above-ground biomass) in these plots than species richness, and better than 12 other biodiversity measures (Cadotte et al., 2008, 2009). Phylogenetic diversity even outperformed total functional diversity. In other words, the total number of inferred DNA substitutions linking species sown into an experimental plot (or a rate-smoothed version of this that

produces a clock-like tree) was a better predictor of ecological function than compound measures of ecological differences measured from traits of the species themselves. As the authors state, their phylogenies may reflect integrated phenotypic differences among taxa and so be a more encapsulating measure than sets of singular, discretely measured traits. This is precisely Dan Faith's original argument in his seminal 1992 paper.

This tantalizing finding has the potential to bring past evolutionary history and the present, ecological, dimension of biodiversity closer together. The mechanism at work here could be that species from the least related (and most phenotypically different) evolutionary routes represent more complementary ecologies, providing a more efficient use of resources. This is a tempting idea but remains unproven. Furthermore, if we also consider that maximising past routes of evolution and wide sets of ecological characteristics puts us in good stead for riding out unknown future changes, this approach might also take into account the views of our final, forward-thinking handmaiden.

Urd as the standard bearer

But why do we suggest that Urd, the historically-minded handmaiden lead the other sisters into battle against biodiversity loss? We would not expect evolutionary information to ever perfectly predict evolutionary potential or the ecological or functional attributes of species. Any conservation importance index based on evolutionary information, therefore, will, to some degree, discount the importance of the other two biodiversity axes.

One good reason to use evolutionary information is that we appear to know more about our past than about either our present or

future. Large scale phylogenies for many mega-fauna groups have been around for several years; large scale databases containing information about the morphology and ecology of entire species groups are only slowly becoming available in a digital format; each museum or wild-caught specimen has to be painstakingly measured. Sequencing machines have, to some degree, mechanised molecular data collection; although molecular phylogenetics requires expert knowledge, it is not often taxon-specific.

We know even less about the future evolutionary or future functional roles of species. The young science of functional ecology, whose remit it is to establish the role of species on the productivity, resilience or biodiversity of its habitat (which one could call a species' 'keystone-ness') is yet to reach consensus on anything more than a handful of species. Furthermore, so little is known about many of the vast number of invertebrates groups that it seems reasonable to think that it would take decades to produce a meaningful measure of ecological importance for even a sizable fraction.

Depending on findings over the coming decade, information taken from molecular phylogenies may offer a cheap and dirty surrogate for precious information about the evolutionary and ecological importance of species. One potentially interesting but untested route here is the role of DNA barcoding. Work is ongoing to establish to what extent CO1 barcode data (in concert with taxonomic information) can provide a good approximation of phylogenetic diversity for birds and mammals, even if they produce fairly poor phylogenetic trees. Depending on the results, barcodes may offer a surrogate of a surrogate for informing conservation of taxa with limited phylogenetic

information.

Phylogenetic information and conservation policy

If we were eventually to conclude that by maximising 'phylogenetic diversity' we select a useful set of species in terms of ecological traits and even functional traits, there are still significant practical problems regarding current conservation policy. This is because most legally-binding conservation programmes assess the need for conservation attention on a species-by-species basis (Possingham et al. 2002). Problems arise because phylogenetic diversity is intrinsically a measure of group information content and not a characteristic that is easily attributable to a single species.

There have been several attempts to calculate a species-specific phylogenetic importance measure (stretching back at least to Vane-Wright et al., 1991). All work on the principle that species with fewer close relatives contain less redundant evolutionary information. The platypus, the ostrich, and the tuatara are examples of such species. And, indeed, those species with fewest close relatives are the ones most likely to complement any other random subset of species, and so sets of species chosen using importance values do capture more than random amounts of phylogenetic diversity (Redding et al., 2008). We note, however, there is no published importance score that has this as its goal.

There are some species-specific measures of phylogenetic importance that stand out from the rest as being, at least, partially interpretable in an evolutionary biology context: 'Species Age' – the amount of time since a species split from its most closely related, usually extant, sister species; and 'Evolutionary Distinctiveness' (see Isaac et al., 2007) – which, by pure chance, approximates the potential

contribution of species to future evolutionary trees (K. Hartmann, PhD thesis, 2008). Most other phylogenetic importance measures remain simply statistical approximations of tree topology and branch length. Though there is limited evidence that species chosen using importance scores span a wider than expected range of ecologies (Magnuson-Ford et al., 2009; Redding et al., 2010), most of the proposed phylogenetic conservation importance measures (there are approximately 10 published) have lost the clear objectives set out by Faith, that is, to maximize the 'feature diversity' of taxa being conserved. Therefore, if one of these measures were widely adopted, instead of choosing one representative from every branch on the tree of life (as we would under Faith's conservation approach), the over-arching aim of conservation becomes, instead, an attempt to conserve, in an evolutionary sense, the loneliest species on the planet.

The lack of a coherent conservation objective behind species-specific phylogenetic importance measures has not prevented the adoption of 'Evolutionary Distinctiveness' into one global conservation approach. The 'Evolutionary Distinct, Globally Endangered' (EDGE) project (www.edgeofexistence.org) has received significant media attention and successfully promoted the use of evolutionary information in conservation decision making.

Phylogeny on the landscape

Conservation does not operate solely at the species level either. Perhaps the principal agent of conservation mitigation is the nature reserve, and this was also the framework for the initial discussion of phylogenetic diversity (Vane-Wright et al., 1991; Faith, 1992). Under at least some models, choosing to maximise species

richness does a good job of conserving phylogenetic diversity (Rodrigues et al., 2005); given that so few new reserves are being created, maximizing total PD during reserve design might not often be practical.

A different approach was recently introduced by Dan Rosauer from the University of New South Wales. His "phylogenetic endemism" approach is a methodology that distributes the total phylogenetic diversity of a candidate clade over the landscape as a function of each member species' phylogenetic isolation and its range size (Rosauer et al., 2009). Overlapping small-range endemics that have few close relatives would represent the densest possible sample of phylogenetic history and the areas where they are found would have high phylogenetic endemism scores. It is even possible to include the probability of extinction of branches of the tree into these calculations, in order to identify areas where the long and threatened branches of the tree of life are concentrated. This is ongoing work in our labs.

There is also ongoing work mapping the location, or hotspots, of species with few close relatives, i.e. those species that score highly using the phylogenetic importance measures outlined above. Perhaps unsurprisingly, the species richness of an area is a good predictor of where the most distinctive ones are found: there are more species with few close relatives in the mega-diverse tropical rainforests than in the polar-regions, for instance. Given this, an approach to maximize species richness, such as Conservation International's Hotspots programme, should also adequately protect those species with the fewest close relatives. While this finding should be taken seriously in policy-making decisions, there are geographical discrepancies, where some areas have much higher numbers of evolutionary isolated species than

expected. For birds and mammals, for instance, these areas may include the sub-tropical mountains of sub-Saharan Africa, Eastern Madagascar, and coastal Papua New Guinea - all good candidates for a geographically-centric EDGE-style programme.

Conclusion

The science we have sketched out above is one at heart of triage. The handmaidens tend to the Tree of Life, but it is a tree that is being rapidly pruned back. It is important that the research in the area of phylogenetic conservation is robust enough to support the expanding and popular strategy of considering the path of evolution that every species has travelled along when making hard decisions about which species, and which geographical areas, we cannot afford to lose. It is heartening to note that one major UN-sponsored international biodiversity initiative, DIVERSITAS (www.diversitas-international.org) has recently set up a separate subprogramme called bioGENESIS, whose first core goal is to facilitate the creation and testing of new phyloinformatics tools and data to help produce the phylogenies needed to do this work.

More work is required to test the idea that some (sets of) species are more evolutionarily and ecologically important to conserve than others, and that phylogenies can help predict which. If they can, then readers of this newsletter, as the producers and interpreters of phylogenies, can indeed help decide which bits of biodiversity are most worthy of conservation. This might be a task with a moral dimension, and one that might carry some significant responsibility.

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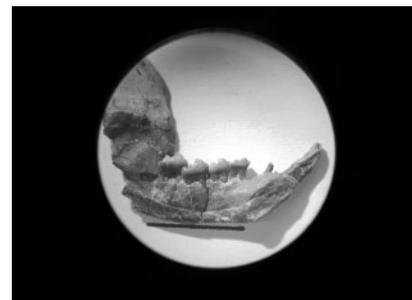
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research trip! I was in the USA to visit the University of California Museum of Paleontology (UCMP) in Berkeley, and the Museum of North Arizona (MNA), Flagstaff, in order to carry out research into a relatively obscure group of extinct animals, the Tritylodontidae. These are non-mammalian synapsids (previously mammal-like reptiles) that lived from the latest Triassic through to the Early Cretaceous, beneath the feet of the dinosaurs,



Tritylodontid jaw © Ian Corfe

alongside their close relatives the earliest mammals. This close relationship has seen them proposed as the sister group to Mammalia (Kemp 1982, 1983; Lucas & Luo 1993, Ji et al. 2002). This, in addition to the increasing number of genera and species described in recent years, and the extension to their 'traditional' Triassic-Jurassic presence provided by Lower Cretaceous taxa from Japan (Setoguchi et al. 1999, Manabe et al. 2000; Matsuoka & Setoguchi 2000) and Russia (Tatarinov & Matchenko 1999, Lopatin & Averianov 2006) has led to an increasing interest in the group. Given the large number of Mesozoic localities, it is surprising that the Americas were about 100 years behind the rest of the world in reporting the presence of tritylodontids. However, discoveries and publications in the last 25 years or so have allowed the naming of four new genera in addition to the identification of a possible new species of the genus *Oligokyphus*, previously known from Late Triassic and Early Jurassic deposits in Germany, England, Wales and

SRF Report

Flying into San Francisco at sunset with the Golden Gate Bridge visible out of the left window of the plane was a pretty spectacular start to a