Biodiversity conservation: **Does phylogeny matter?**

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To conserve biodiversity, it is necessary not only to maximize the number of taxa that are saved today, but also to guarantee the maintenance of high levels of biological diversity in the future. A recent analysis argues that, to achieve this, consideration of phylogeny is essential.

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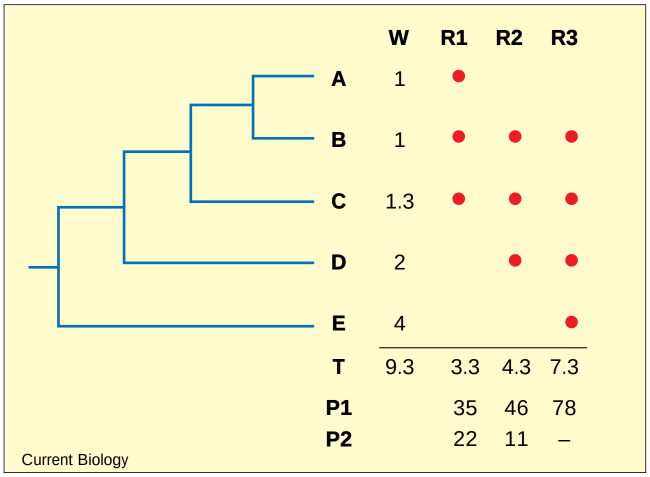
Nature is having a hard time — human activities are destroying ecosystems and their biota at an ever increasing rate. For example, about 200,000 km^2 of tropical forests are destroyed each year, representing about 1.2% of the total tropical forest cover, in which two thirds of the world's species reside [1]. So much habitat is being lost that we are facing what might be one of the major mass extinctions of the history of life [2]. Species extinction rates at present are between 10 and 100 times higher than the background, 'natural' extinction rates [3].

Many biologists argue that it is important to conserve geographically-rare species — 'endemics' — and much attention is therefore focussed on the conservation of endemic-rich areas, or 'hotspots' [3–5]. The hope is that, by conserving a relatively small area of the total land surface of the earth, it would be possible to save a large fraction of total global biodiversity. For example, Bibby *et al.* [5] identified 221 endemic bird areas around the world, which overall hold 70% of the endangered bird species and over 95% of those with restricted ranges. Areas such as the Atlantic forests of southeast Brazil, the Hawaiian Islands and Madagascar are at the top of the priority list.

This focus on hotspots, although useful for immediate conservation purposes, considers only a part of the problem. Is the set of species conserved in endemic-rich areas the right one for the maintenance, not only of present, but of future biodiversity? We do not know. It has been argued that phylogeny may be important for gauging the evolutionary potential of species [6]. According to this view, it is necessary not only to conserve as much species diversity as possible, but also to conserve sets of species that include as much 'evolutionary history' as possible [7,8]. If we consider that each species has diverged genetically from its relatives by an amount roughly proportional to the time since they diverged from their common ancestor, then the branch lengths in a phylogenetic tree scaled to the observed genetic divergence between species would provide a quantitative measure of diversity within a clade. From this perspective, old, monotypic taxa — that is, those with few or no sister taxa — often make relatively large contributions to diversity, and so should be accorded high priorities in conservation decisions [9].

Vane-Wright *et al.* [8] and Williams *et al.* [10] have proposed analytical methods by which the topology of a phylogenetic tree is used to establish the best representation of different clades within regions with high priority for conservation. Other methods for calculating phylogenetic diversity for conservation purposes have been proposed by several authors ([5,11–13], for example). Although a range of different algorithms have been suggested, they share the same objective: that of maximizing the number of clades that are represented, rather than the number of species conserved. In the method reported by Vane-Wright *et al.* [8], for example, the species in a cladogram — a type of

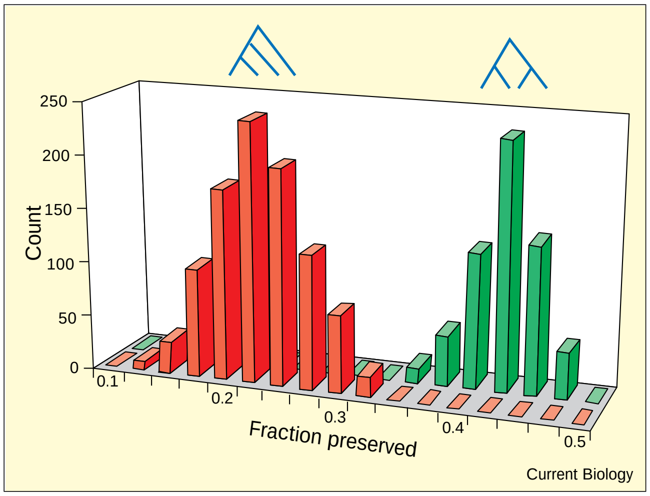
Figure 1



	W	R1	R2	R3
A	1	●		
B	1	●	●	●
C	1.3	●	●	●
D	2		●	●
E	4			●
T	9.3	3.3	4.3	7.3
P1		35	46	78
P2		22	11	–

Theoretical priority area analysis, based on the topology of phylogenetic trees and taxon weighting [8]. The distributions of the five terminal taxa among the three regions, R1–R3, are given in the three-column matrix on the right. Column W gives the weight for each taxon. Row T gives the aggregate weights for all five taxa, and for each of the three regions. Row P1 gives the percentage diversity scores for each of the three regions – the summed weights of the taxa for each region as a percentage of the aggregate weight for all the taxa. The values in row P1 indicate that R3 is the top-priority region. Row P2 gives the percentage diversity scores for the remaining two regions for the taxa they contain that are complementary to – not found in – R3. This indicates that R1 is the second priority region. Finally, the fact that the highest values of the first two steps sum to 100% indicates that the analysis is complete. (Adapted from [8].)

Figure 2



Frequency distributions of the fraction of evolutionary history saved by random sampling 12 species from sets of 64 related by phylogenic trees with either a comb-like topology (left) or a brush-like topology (right). In the simulation study, the times between nodes are the same for both topologies; the time between the i^{th} and (i + 1) node is 1/(i + 1), that is, the expected time interval under a pure birth process. (Adapted from data in [14].)

phylogenetic tree — are given different weights, according to their evolutionary history. 'Monotypic' taxa, which lie at the ends of long branches, are given higher weights than 'terminal' taxa, which have many sister taxa to which they are connected via short branches. The weights thus reflect the evolutionary history unique to each taxon.

The approach is best explained by a specific example, and one is illustrated in Figure 1. From species richness alone, it would be impossible to decide which of the three hypothetical areas shown in Figure 1 should have the highest priority for conservation — it would not be possible to distinguish between regions R1 and R3. The algorithm of Vane-Wright *et al.* [8] decides the relative priority of each region in two steps. The first step, P1, identifies the 'top-priority' region — the one in which the sum of the weights of the taxa contained in the region (the 'percentage diversity score') is highest. In the second step, P2, the remaining regions are assessed according to their 'complementarity' to the top-priority region — that is, by summing the weights of the taxa they contain that are not found in the highest priority region. Using this algorithm, in the example shown in Figure 1, region R3 is the top-priority region, R1 the second priority, and R2 the third.

Phylogenies are the end result of differential species extinction. Some taxa are obviously more susceptible to extinction than others; for example, the estimated average species' lifespan for mammals is around 1 million years, while for marine invertebrates it is 4–10 million years [2]. But how are differences in extinction rates related to the various patterns of evolutionary history that are observed? Nee and May [14] recently simulated phylogenetic trees and, guided by mathematical models, pruned different branches (clades) of the tree to simulate the effects of extinction. Two interesting results were found. First, when species are randomly eliminated from simulated trees, saving only a fifth of the species, the average loss of evolutionary history was found to be approximately 50%. But when species are optimally eliminated, using a more ruthless extinction algorithm that optimizes the loss in species-rich clades, then the loss of evolutionary history was found to be increased to approximately 60%. The second result concerns the effect of tree topology. Nee and May investigated the effect of removing species randomly from trees with either of two extreme topologies, 'comb-like' or 'bush-like' (Figure 2). By random selection of 12 species from 64-species clades, the frequency distribution of the fraction of evolutionary history lost by pruning either type of tree showed that almost twice as much evolutionary history is preserved with a bush-like tree.

These results have important implications. With the recent development of a body of analytical tools, more rigorous phylogenies are now available for identifying processes of evolution and patterns of extinction [15,16]. The detailed phylogenies that are now available have provided a window into speciation and extinction rates, the ecological and biogeographical causes of speciation and extinction, and the timing of these events, all of which were hitherto inaccessible. The phylogenetic approach also shows that losses of species number may not be devastating. All things being equal the loss of a lineage may not necessarily reflect the loss of biodiversity. All things generally are not equal, however; particular traits, for example large body size, slow reproduction and a bamboo diet, tend to make a species more vulnerable to extinction. The question is to what extent are the species that are vulnerable to extinction found in monotypic clades and have unusual biological characteristics [17]?

Let us return to the idea of hotspots. Taking the conclusion of Vane-Wright *et al.* [8] and Nee and May [14] together, it is clear that areas with a high concentration of different monophyletic groups related by comb-like phylogenetic trees will be more susceptible to loss of evolutionary history than areas with predominantly bush-like trees. It might be argued that, if we want to conserve as much evolutionary history as possible, we should protect areas that will allow us to maximize the amount of evolutionary history preserved. That is to say, we would like to have a similar idea to that of Myers' [4] 'hotspots' of endemism, but applied to phylogenies. This idea was first proposed by Ackery and Vane-Wright [18] under the name of ‘critical faunal analysis’. Following the simulation studies of Nee and May [14], it would seem important to prioritize areas in which there are aggregations of monophyletic taxa related by comb-like trees. For this, we need to know where lineages — not individual species — originate innovations in their evolution, and how these become distributed over some part of the planet.

It may be argued that centers of species endemism might also be centers for high levels of phylogenetic diversity. If this were the case, phylogenetic information would be redundant. But areas for species endemism and phylogenetic diversity do not necessarily overlap. Fjeldså and Lovett [19] recently analyzed the distribution of old and young species of birds and plants in African forests, and made three significant observations. First, that older, monotypic species tend to have much more widespread distributions than younger species. Second, that younger species tend to be clustered and more patchily distributed. And third, that young and old species that are biogeographically restricted tend to be clustered in the same areas.

The first of these three findings tells us that, if we want to conserve the maximum amount of evolutionary history, we cannot concentrate only on centers of endemism, because we would be disregarding the oldest taxa. On the other hand, their last finding gives us a hint: species with restricted ranges, which are those most likely to become extinct from habitat destruction, seem to be concentrated in the same place, regardless of their evolutionary history. The generality of these findings still needs to be assessed, however. We need to know how evolutionary history is distributed around the world, and for as many different taxa as possible. Only then will it be possible to prioritize areas for the conservation of biodiversity with a sound phylogenetic basis.

To know how evolutionary history is distributed around the world for many different taxa is clearly not an easy task; it will take considerable time and effort to gather and analyse the requisite data. Considering the high extinction rates of present times, it would not be wise to ‘sit and wait’ until we have the necessary information to decide which areas we should focus on to conserve the largest part of the Earth’s evolutionary history — by then, it might be too late. On the other hand, this information exists, or should be relatively easy to gather, for some well-known taxa, such as birds. We should begin to use the phylogenies for at least these taxa as guides in the selection of conservation areas. Conservation strategies should seek, not only to maximize the levels of biological diversity today, but also to include the patterns detected in cladistic studies, so as to maximize tomorrow’s levels of biodiversity. By preserving as much phylogenetic history as possible, it will be more likely that the evolutionary potential of our world’s biota is preserved too.

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