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Phylogeny and conservation

ANDY PURVIS, JOHN L. GITTLEMAN
AND THOMAS M. BROOKS

WHY A BOOK ON PHYLOGENY AND CONSERVATION?

Of the many sub-fields of biology, phylogenetics and conservation biology are two of the fastest growing. On the one hand, the explosion of phylogenetics – the study of evolutionary history – has been stimulated over the past two decades by the emergence of new molecular methods and statistical techniques for modelling the tree of life. DNA sequence data are now typically freely available through public-access databases such as GENBANK, and much software for phylogeny estimation is cheap and easy to use. On the other hand, the tree of life is being heavily pruned by human activities; this pruning has helped to drive the emergence of the applied discipline of conservation biology.

Bibliometric data provide a rough-and-ready way to summarise the growth in the two disciplines. There was an exponential increase in the number of papers in both fields between 1992 and 2003, as shown by a search of the Science Citation Index with the keywords 'conservation biology' and 'phylogen*'. According to these searches (other terms would give slightly different results), numbers of papers in each discipline are growing at about 12%. The growth rate of the intersection set – papers linking conservation biology and phylogenetics – is slightly (although non-significantly) lower at 10.4%. Numbers of papers found by a search for 'phylogen*' in four conservation journals (*Conservation Biology, Biological Conservation, Biodiversity and Conservation* and *Animal Conservation*) over the same period have increased at about the same rate (13%) as phylogenetics papers overall. These results all suggest that, although phylogenetics has been permeating conservation biology over the past decade, there has so far been little synergy.

Why, then, are we interested in the overlap between these historically separate fields of biological endeavour? The main reason is the *direction* in which both fields are growing, rather than the speed. As the magnitude of the anthropogenic threat to biodiversity has become apparent, much conservation biology has focused on systematic conservation planning, priority-setting and monitoring trends, and on the biodiversity assessment required to provide the data for those activities. An effect of this transition is that conservation biologists are increasingly dealing with taxa whose natural history and even species membership is poorly known. The increase of available phylogenies is inversely related to the demise of basic descriptive taxonomy (Wheeler 2004; Wheeler *et al*. 2004). Proposals to base species descriptions upon DNA sequences instead of morphology, and even to build the complete tree of life – both unthinkable a few years ago – must now be taken seriously. Increasingly, an organism's position in phylogeny will be one of the few things we know about it with any precision (Mace *et al*. 2003). It is therefore timely to explore the ways in which the wealth of new phylogenetic information can benefit conservation biology. This book is the result of a Symposium of the Zoological Society of London, organised to investigate these issues. The meeting was held on 6–7 February 2003.

We have structured this book around four areas where phylogeny should give insights into conservation issues. First, phylogeny can help delimit the units and currencies of biodiversity assessment and management (Cracraft 1983; Vane-Wright *et al*. 1991). Second, phylogeny is a record (albeit only a partial one) of how biodiversity has come about: the evolutionary processes responsible for it (Harvey *et al*. 1996). Understanding origins can assist in the conservation of biodiversity by contrasting current versus historical patterns, and of the processes that have generated these patterns. Third, phylogeny provides a statistical framework for the rigorous investigation of how human processes – habitat loss, overexploitation, species introductions – are affecting biodiversity (Fisher & Owens 2004). Fourth, it is possible to extrapolate from the past and present into the phylogenetic future, in order to predict what might happen to biodiversity under possible scenarios (Rosenzweig 2001). We enlarge on each of these below.

UNITS AND CURRENCIES

Traditionally, the units of conservation biology have been species (Agapow *et al*. 2004). The severity of the current biodiversity crisis is often expressed in terms of numbers of species that have gone, are going, or are in imminent danger of going, extinct. Species provide an intuitive currency for comparing the biodiversity value of different locations. Management plans often focus on particular species. However, species can be hard to demarcate, with a great many decision rules available from which to choose (Hey 2001; Mayden 1997; Sites & Marshall 2003). Further, many species harbour considerable diversity among their populations, a fact with two important and related implications: the species should perhaps not be managed as a single entity (for example, translocating individuals among populations may be harmful to the species), and conservation of a single population of the species does not conserve all of the diversity. Phylogenetics made its first impressions on conservation biology by providing possible extra units (e.g. evolutionarily significant units (Avise 2000)) and currencies (e.g. phylogenetic distinctiveness (Faith 1992)) for conservation biology. The first two chapters of this book consider phylogeny's role in demarcating units; then the subsequent three chapters consider the use of currencies derived from phylogeny when trying to set conservation priorities.

Chapter 2 starts with an overview of how evolutionary relationships can be inferred both among and within species, focusing on practical issues of study design and on recent methodological developments (Felsenstein (2004) provides a general review of the whole field). The chapter concludes with two examples showing how the results of such analyses can help to demarcate species and, by revealing the patterns of gene flow, management units. Despite the rapid growth of phylogenetics, phylogenies of the detail and sophistication described in this chapter are still very much the exception. Many later chapters use less statistically justified phylogenies, or taxonomies as surrogates for phylogeny. This lack-of-fit is a transient phenomenon: phylogenies will improve, and it makes sense to use the best surrogate we have at any given time, whatever it is.

The use of phylogenetics in conservation is sometimes controversial, nowhere more so than in the application of the phylogenetic species concept (PSC). Formulations differ in the detail, but the essence of the proposal is that species are the least inclusive clades in phylogenies: they are the smallest sets of populations that can be told apart from other sets. The PSC has been gaining ground in recent years because of its ease of application: there is no difficult decision about whether two distinct lineages are sufficiently diverged to be recognised as separate species. In Chapter 3, Agapow reports that, on average, species lists based on PSC contain about twice as many species as lists for the same groups based on the biological species concept. He goes on to explore some of the problematic consequences of this change, and suggests ways in which conservation biologists might avoid such problems. Among these ways is the idea of using species' unique evolutionary history, or phylogenetic distinctiveness (PD), as a currency of biodiversity, rather than focus on counting species (Faith 1992). The last three chapters in Part 1 consider different aspects of PD.

Based on the emerging science of conservation genetics, with a foundation in phylogenetics, Avise (Chapter 4) considers two possibilities for how phylogenies may be effective in management decisions. First, using earlier work on comparing phylogenetic measures with trait or ecological diversity (see, for example, Faith 1992; Vane-Wright *et al.* 1991), Avise develops a ranking procedure for assessing how species in clades can be selected for conservation management based on differences in phylogenetic diversity relative to other measures such as rarity, endemism, ecology or charisma. Some examples show that this priority-based system can isolate a species such as the giant panda (*Ailuropoda melanoleuca*) because it has clearly high values relative to other bear species. However, analyses of other groups, such as horseshoe crabs or cats, are ambiguous. When ecological and phylogenetic diversity are relatively equal or, more often, when these measures are poorly known, then such a priority analysis is limited (for example, how can we decide between the polar bear (*Ursus maritimus*) and brown bear (*U. arctos*)?). In general, Avise is sceptical as to whether phylogenetic analysis has much to offer at the interspecific level. This conclusion can be confounded by other factors, however: conservation prioritisation generally considers areas rather than species (Margules & Pressey 2000), and combinatorial scoring of this kind will necessarily produce subjective results (Williams & Araújo 2002).

Second, Avise emphasises that because phylogenetic analyses have been successful at intraspecific levels for describing genetic diversity, adaptive variability to habitat change and the consequences of population fragmentation, it is at this level that phylogenies are beneficial. For example, he argues that the constructs of evolutionarily significant units (ESUs) and management units (MUs) are relevant to conservation prioritisation, with phylogeographic analyses setting the primary criteria for establishing these units for individual species (see Crandall *et al.* 2000). The future of phylogenies in conservation rests, Avise argues, with how to use the kind of information gleaned at intraspecific levels to inform conservation decisions at global levels.

In Chapter 5, Rodrigues *et al.* consider a separate question concerning PD: if it is used for priority-setting, does it lead area-selection algorithms to choose areas different from those selected solely on the basis of species data? The extra information about evolutionary history that phylogeny contains may suggest an efficiency gain, in terms of how much diversity is captured within a set of preferred areas. But is the gain large or small? Their simulation study finds that the gain will not in general be large unless four conditions are all met: the phylogeny must be unbalanced, the geography must show a phylogenetic pattern, old species must tend to have smaller geographic ranges, and these old species must tend to be endemic to species-poor areas. The first condition is usually met (Mooers & Heard 1997; Stam 2002) and the second is so common it is even a prerequisite for cladistic biogeography. Jones *et al.* (Chapter 7 below) report evidence for the third. Little is so far known about how often old species are endemic to species-poor areas, indicating that this is an important priority for future research. Later chapters contain several case studies that bear on the issue of whether phylogeny will affect choice of areas: some (e.g. Moritz, *et al.* Chapter 11) suggest that it will, others (e.g. Brooks *et al.*, Chapter 12) that it will not.

Mooers *et al.* (Chapter 6) round off Part 1 by attempting to bridge the gap between scientific precision and political reality with their discussion of 'evolutionary heritage'. Here, they propose measurements of PD at the national level, in order to inspire conservation both in its own country and through international aid. The idea of highlighting national heritage – especially of endemism, for countries have ultimate responsibility for their endemic species – is not a new one (Mittermeier *et al.* 1998). The novelty here is in incorporating phylogenetic history. Two caveats face this, however. On the one hand, it is unclear how well evolutionary heritage will resonate with policy-makers, especially given that many of the nations identified as having the greatest evolutionary heritage retain creationist beliefs at the state level. Second, the jury is still out as to how much the evolutionary precision added by this metric changes the results of conservation planning relative to consideration of species alone (Rodrigues *et al.*, Chapter 5).

INFERRING EVOLUTIONARY PROCESSES

Knowing how diversity arose is important for at least three related reasons in conservation. First, a process-based understanding of diversity patterns provides a null expectation against which today's state of play can be judged. Such use of null models can help to identify lineages whose distribution is narrower than might be expected, for example (see Webb *et al.* 2001). Second, an understanding of the mechanisms that generate diversity is essential if we are to safeguard their future through conservation of evolutionary process as well as of the pattern it has produced. Because phylogenies contain information about how they grew – about how biodiversity arose – some of the necessary understanding can be gleaned from careful analysis of phylogeny (Harvey *et al.* 1996). Lastly, knowledge of how particular lineages have responded to challenges in the past may help us to understand how they are now responding, or will soon respond, to anthropogenic changes.

The first chapter in Part 2 revisits one of the oldest conundrums in evolutionary biology – the relationship between the age and the extent of occurrence of a taxon (Willis 1922) – in an attempt to model the underlying process. Jones *et al.* (Chapter 7) offer new insight into age–area relations, using a remarkable dataset of the geographic distributions of all mammal species (compiled at the University of Virginia and now comprising the basis for the IUCN Global Mammal Assessment) plus two of the most complete supertrees compiled to date, for primates (Purvis 1995) and carnivores (Bininda-Emonds *et al.* 1999). For both taxa, Jones *et al.* tentatively support a model of declines in species' range sizes over time. Further, they find that, contrary to previous evidence (see, for example, Webb & Gaston 2003), there tends to be phylogenetic correlation across range sizes, for primates and carnivores at least. Based on these findings, they then ask whether currently threatened species have smaller range sizes than would be expected by their phylogeny, and, as expected, find that they do.

Although the importance of preserving pattern and process is readily acknowledged, the pattern is difficult to achieve in practice. The next four chapters in Part 2, however, illustrate ways of beginning to address evolutionary process. The field studies of Smith and colleagues (Chapter 8) on West African populations of the little greenbul (*Andropadus virens*) investigate the processes that cause differentiation resulting from isolation and ecological selection. Using a combination of molecular, behavioural and phylogenetic analyses at both intra and inter-specific levels, Smith *et al.* show that divergence in fitness-related characters (body mass, wing length) and parallel characters of male song types are mainly related to habitat rather than to geographic isolation. Analysis of sister species across the sunbird family are also consistent with gradients of speciation associated with different habitats. Different qualities of tree density and climate found within ecotones suggest that ecologically they are extremely important for areas of speciation, at least in the ecotones of West Africa. Unfortunately, these areas are also attractive to human settlements. Future work is needed to sort out how ecotones are structured worldwide, whether they are also cradles of speciation and, if so, how to protect them from habitat degradation.

What happens when a biodiverse area is shocked by climatic change or habitat degradation? A triad of chapters, from the Eastern Arc of eastern

Africa, the South African Fynbos and Succulent Karoo, and the wet tropics of Australia, show the processes by which species respond to these changes. Lovett *et al*. (Chapter 9) study geologically ancient rainforests in Africa, dating back perhaps to the Miocene, to assess the question of whether biodiversity can withstand change by community stability, or whether it is adaptable. The distributions of over 100 tree species along a gradient of 158 plots through the elevational range of the forests suggest the former. Further, these Eastern Arc rainforests appear more stable than other areas in sub-Saharan Africa. The phylogenetic implication is that such areas of high endemism hold numerous closely related species that respond in kind to temperature and rainfall gradients. Further analyses adopting a more explicitly phylogenetic perspective should find out whether other global centres of endemism hold closely related taxa.

It is commonly thought that Pleistocene climate change has dramatically influenced the unusually high plant endemism in the Fynbos and Succulent Karoo biomes of southern Africa. As with other species hotspots it is important to disentangle such historic from current ecological effects influencing regional differences in species richness. In Chapter 10, Midgley *et al*. pull together palaeoecological data, present biogeographic maps and phylogenetic information to assess these patterns. The clearest explanation is that climatic history produced shifts in geographic extents of the two biomes, resulting in speciation through vicariance and allopatry. Midgley *et al*. indicate that anthropogenic climatic change could result in a loss of 51–65% of the extent of the Fynbos biome, resulting in potentially significant species losses. Similar global effects have also been reported elsewhere (Thomas *et al*. 2004). The next generation of global change studies could usefully incorporate phylogenetic analyses in order to evaluate historical background climatic shifts from current levels.

Finally in Part 2, a detailed analysis reveals how the Eastern Australian rainforests are also under intense threat from predicted climate change (Williams *et al*. 2003). In Chapter 11, Moritz *et al*. show how past climate has influenced the diversification and present diversity of three reptile and amphibian clades within this region. They use phylogeographic insights from snails – whose low vagility and need for moisture make their current distribution a likely pointer to past refugia – to provide a backdrop against which to compare herpetofaunal patterns and processes. Interestingly, the groups studied show different evolutionary processes in response to the same environmental history. Such differences clearly complicate the use of one lineage as a surrogate for another. Furthermore, old lineages do tend to be restricted to small and species-poor locations: two of the requirements for PD to show patterns different from those of species-richness (Rodrigues *et al.*, Chapter 5). The study nicely shows how past refugia leave imprints on today's diversity patterns, and how even small areas can contain important phylogenetic diversity. The lineage-specificity of responses to a common climatic history provides another layer of challenges in predicting and mitigating what may happen in response to climate change.

EFFECTS OF HUMAN PROCESSES

Evolutionary processes such as those considered in the previous section mean that diversity is not spread evenly over the globe. Most clades show latitudinal gradients, with more species in tropical than in temperate regions (Gaston 2000), as well as more complex non-random patterns of richness (Davies *et al.* 2004). People also have more impact in some parts of the world than in others: densities, land use and technological advancement show complex patterns too. In the first chapter in Part 3, Brooks *et al.* (Chapter 12) examine the spatial concordance between the fruits of natural diversification processes and the threats caused by human actions. Their review and analyses of birds illustrate how threats to species, threats to habitats, evolutionary distinctness and endemism are all positively intercorrelated. The authors argue that an important consequence is that conservation strategy is quite tightly proscribed: arguments about whether to focus on areas of greatest biodiversity value or those facing the severest threat lose importance if these areas are one and the same.

As well as providing the backdrop against which human actions play out, phylogeny also gives a statistical and logical framework for analysing the pattern of casualties, survivors and beneficiaries of those actions (Fisher & Owens 2004). Because species biology tends to mirror phylogeny – i.e. close relatives tend to be similar – evolutionary relationships should be considered in any comparative study of present-day conservation patterns. The next two chapters use phylogeny in this way.

Using the primate and carnivore datasets discussed earlier, Purvis *et al.* (Chapter 13) find selectivity of threat status in phylogeny and geography so strong as to require consideration of phylogeny in all analyses of correlates of extinction risk. They then go on to tease apart the impacts of threat intensity *per se* from the interaction between biological characteristics and threat intensity in determining threat status (as Purvis *et al.* point out, intrinsic characteristics alone have a near-negligible impact on threat status). Two particularly important results emerge. First is the importance of an additional parameter – scale – in determining the relative strengths of these

Cambridge University Press
0521532000 - Phylogeny and Conservation
Edited by Andy Purvis, John L. Gittleman and Thomas Brooks
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factors. This notwithstanding, however, their second key result is the importance of incorporating biological characteristics in assessments of the determinants of extinction risk, rejecting recent suggestions that measurements of threat intensity such as human population density alone are relevant. This chapter does not differentiate among the different ways in which people endanger species; the remaining chapters in Part 3 probe more deeply into particular threatening processes.

A multitude of causal factors such as small population size, habitat depletion, and reduction in geographic range size all contribute to population decline in birds, with around 12% of species currently listed by IUCN as threatened. Can an explicit phylogenetic approach help in understanding the current processes of extinction, and will this aid in staving off levels of threat? In the face of many hypotheses, Bennett *et al.* (Chapter 14) begin by showing that the distribution of extinction risk is not random among birds: some families (e.g. parrots, Psittacidae, and cranes, Gruidae) face a significantly higher prevalence of extinction risk than would be expected under the 'hail of bullets' scenario. Similar patterns are known throughout most animal and plant taxa (Purvis *et al.* 2000; Russell *et al.* 1998; Schwartz & Simberloff 2001). A comparative phylogenetic approach reveals that threatened lineages have particular biological characteristics that may predispose them to a higher risk of extinction. Specifically, larger body mass and lower fecundity ratchet up threatened status as measured from the IUCN Red List. Such biological characteristics vary considerably, so the interesting problem is: how do species with divergent life histories respond to various human-related threats? Interestingly, the lineages for which larger body mass is associated with greater threat status are more vulnerable to human persecution or introduced predators, whereas breeding specialisations are more influenced by habitat loss. Further, there is evidence that ecological flexibility in diet and clutch size may allow some species with 'risky traits' such as large size to overcome sources of threat. The study by Bennett *et al.*, along with other recent work (e.g. that of Cardillo *et al.* 2004; Isaac & Cowlishaw 2004; Jones *et al.* 2003), clearly shows multiple routes to the biological underpinnings of extinction risk. Future comparative work is needed, based on multivariate analyses across large phylogenetic clades, to assess why some traits are more risky than others and whether these are traits that have been historically critical to adaptive radiations. In this way, speciation and extinction could be tied together and phylogenetic analyses would be increasingly valuable to conservation. The growing number of complete phylogenies and massive bioinformatic databases, together with the increasing sophistication of methods for dealing with missing data in comparative analyses (Fisher *et al.* 2003), give reason to be optimistic about the value of phylogenies for conservation.

In Chapter 15, Cardoso da Silva *et al.* focus on habitat loss, the most important single threatening process (Mace & Balmford 2000), at a finer scale of phylogenetic and geographic resolution. They consider a single taxon, primates, in a single region (albeit biologically the richest on the planet), Amazonia. Based on claims initially made by Wallace in the 1850s, they subdivide Amazonia into eight 'areas of endemism' and then examine primate diversity (including PD), likely deforestation around roads, and protected-area coverage among these eight regions. They find a strong trend in primate diversity from east to west (although this is at least partly driven by the fact that the western 'areas of endemism' are much larger than those in the east), but find that the eastern regions (especially Belém) are much the most threatened and least protected. The contrast between these results and those reported elsewhere in this volume (e.g. Brooks *et al.*, Chapter 12) of correlations between phylogeny and threat emphasise the result found by Purvis *et al.* (Chapter 13) that these correlations can swing in unexpected directions at fine scales.

Most biodiversity conservation attention focuses on diversity loss through the loss of species and habitats, but diversity is also lost through biotic homogenisation: the spread of invasive species reduces biological differences between places. Lockwood (Chapter 16) provides an important review of the literature on invasive success. She shows that, across a range of plants and animals, the fact that one species is a successful invader much increases the likelihood that a closely related species will also be. This does not mean that phylogeny alone can be used as a predictor of invasion success, but rather that phylogeny should be considered along with geography and extrinsic factors in the science of pre-empting likely biotic invasion, a result mirrored by that of Purvis *et al.* (Chapter 13) in considering extinction risk.

PROGNOSIS

Phylogeny helps us to understand both the distant and the recent past, putting present-day diversity and extinction patterns into context. What can we say of the future of phylogeny, given the intensity and breadth of anthropogenic disturbance?

The first problem that the chapters in Part 4 raise is how a phylogenetic perspective shows that we may be looking at the wrong biodiversity: