

Evolutionary heritage as a metric for conservation

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One of the many things that society considers worthy of conservation is biological diversity (Gaston & Spicer 1998). Many 'currencies of biodiversity' (Gaston 1994) have been proposed; the most common approach has simply been to count the number of species in an area (Gaston 1994) and thus identify 'hotspots', regions with high species richness (Reid 1998). Other species-based conservation efforts have focused on identifying endemic (Williams & Humphries 1994), threatened (see www.redlist.org) or ecologically important species (Risser 1995; Maddock & Du Plessis 1999). Species with attractive, peculiar, or otherwise special morphological attributes have often been used by conservation organizations for logos and mass appeal (Humphries *et al.* 1995). Beginning in the early 1990s, several research groups, based primarily in Australia (Faith 1992; Crozier 1992) and the UK (May 1990; Vane-Wright *et al.* 1991; see also Weitzman 1992), have made strong arguments for considering phylogenetic diversity (PD: some measure of the proportion of the tree of life that a species or group of taxa represents) when ranking conservation units. Because diversity is ultimately the product of descent with modification, branch lengths on a phylogenetic tree predict feature diversity (morphological, genetic) of the lineages they represent (Faith 1992). This suggests that metrics of evolution such as PD might point directly to attributes of diversity worthy of conservation and stewardship. Phylogenetic diversity has been examined at the global level: for instance, Sechrest *et al.* (2002) found that 839 million years of primate history is endemic to 25 biodiversity hotspots, and fully 70% of all primate and carnivore history is represented in hotspots.

Here, we suggest that because most conservation decisions are made at the level of the geopolitical unit (e.g. at the country level), rather than,

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say, at the level of ecosystem or hotspot, these geopolitical units might do well to consider the PD that they steward as their 'evolutionary heritage'. Frankel (1974) was the first to draw attention to the idea of a 'genetic estate which comprises the biological heritage [. . .] worthy of preservation' on non-utilitarian grounds; we push Frankel's analogy with the 'national estate' further in this chapter (see also Mooers & Atkins 2003). We first briefly discuss the background of conserving PD and its connection to species richness, and then present two examples of how the idea of evolutionary heritage might be applied, using the well-known taxa Carnivora and Primata. Rankings of countries based on total, endemic, or at-risk evolutionary heritage differ in potentially important ways with rankings based simply on counts of total, endemic, or at-risk species. We end with a consideration of some of the obvious problems and possible extensions of this formulation.

PHYLOGENETIC DIVERSITY AS A METRIC FOR CONSERVATION

Ross Crozier (1997) offers a clear formulation of the concept of PD, based on 'information content': when a phylogenetic tree depicts the information shared among taxa, then maximising the proportion of the tree preserved maximises the information preserved. For example, a sample from a larger assemblage containing a species of pine and a species of orchid would contain more information about the entire assemblage than would a sample of two orchid species, simply because the two orchids are more alike. Different samples of species from a larger assemblage contain different proportions of PD and therefore information, as highlighted in Figure 6.1. Crozier (1997) discusses how PD might be valued under different conservation perspectives. For instance, under a morally grounded conservation ethic, all species can be considered equally important (Crozier 1997), and PD would be of little use. Although an alternative moral argument might be constructed that favours PD, the perspective that most easily equates PD with worth involves utility: if we consider the products of evolution to have some immediate and future value to us (through ecosystem services, or as the basis for pharmaceutical or agricultural products), then our portfolio should be as diversified as possible. This argument may be the most compelling for evolutionary heritage in our present society. However, it risks diminishing in force as we learn more about ecosystem stability and move deeper into the age of genetic engineering. That said, the utility

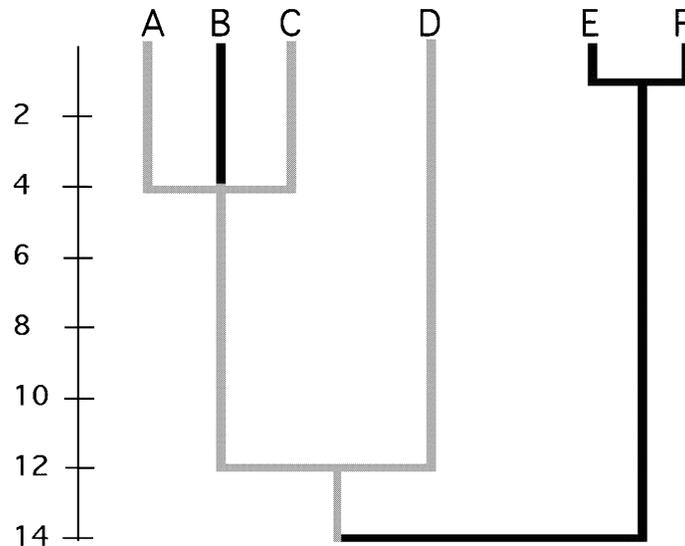


Figure 6.1. Definition of phylogenetic diversity (PD) and evolutionary heritage. For this ultrametric tree of six species, total PD = 49 my (million years), the total length of the tree. The assemblage of species A, C, D (in grey) encompasses 30 my of PD (more than 60% of the total PD). If Country 1 contained species A, C and D within its borders, its 'evolutionary heritage' would be 30 my. If species C were endemic to Country 1 (found nowhere else), Country 1 would steward 4 my of unique heritage; Country 2, with species A, D and E, would steward 40 my of heritage (more than 80% of the total); and 26 my of history, encompassed by the species assemblage (A, E), would be stewarded by both countries. If species A were listed as globally threatened, Country 1 would steward 4 my of 'at risk' heritage, and Country 2, 12 my (the difference being due to the presence of species C in Country 1).

argument strongly supports the use of PD as one measure of conservation worth.

Perhaps a more interesting application of PD to conservation involves the aesthetic argument: Wilson (1984; Kellert & Wilson 1993) has argued that humans may appreciate a variety of living forms for innate reasons, and derive psychological benefit from such variety. Nature-based tourism is worth billions of dollars worldwide (Gaston & Spicer 1998). Because diversity itself is valued (rather than some other attribute, such as ecosystem function, hypothesised to depend on diversity), this incentive for conservation may be robust. This aesthetic value of biodiversity (see also Williams & Gaston 1994; Rosenzweig 2003) informs our suggestion that evolutionary heritage may offer inspirational value.

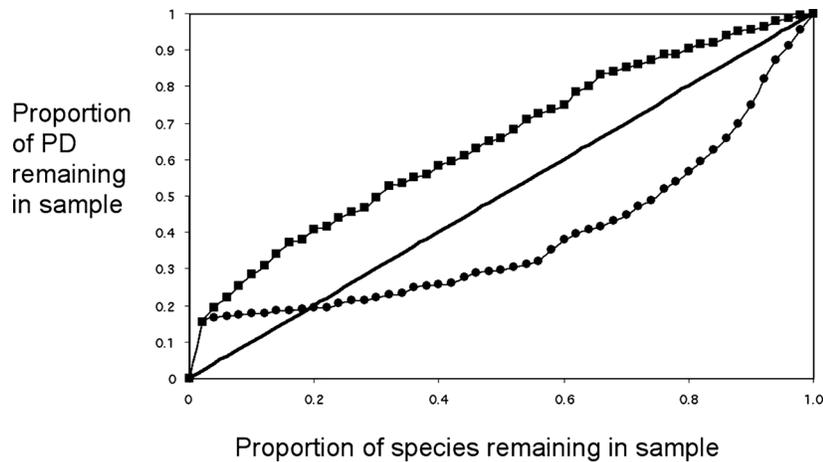


Figure 6.2. Phylogenetic redundancy. A plot of the phylogenetic diversity remaining in a sample as species are removed from a very unbalanced tree. Squares: average diversity remaining if species are sampled at random. This lies above the line of equality, indicating that proportionately more history is retained in these samples than species. Circles: diversity remaining if relictual lineages with slow diversification rates are systematically removed from the sample. Here we lose more than proportionate history. Modified from Heard & Mooers (2000, Figure 6.3d, ignoring the history common to the entire clade).

REDUNDANCY AND SPECIES RICHNESS

The idea that species vary in distinctiveness (represent different amounts of PD) leads directly to the notion that numbers of species may not be the best measure of diversity (or the loss of diversity). This is because, with respect to evolutionary history, phylogenetic trees exhibit considerable redundancy (Nee & May 1997). That is, much of the evolutionary history represented by a clade is shared by more than one species (for example, all the non-terminal branches in Fig. 6.1). The loss of a species by extinction erases only the evolutionary history uniquely represented by that species; any history shared with relatives remains as long as the relatives still exist. As a result, there need not be a 1 : 1 correspondence between the loss of species from a clade and the proportional loss of evolutionary history. Figure 6.2 depicts a plot of history retained as a function of species retained under random and non-random sampling for a particular model of diversification consistent with published phylogenetic trees (Heard & Mooers 2000). No matter what the shape of the tree, random samples of species (i.e. the diversity left after a bout of randomly acting extinction) retain more history than expected from sample size alone (top curve). Of course, the deviation of

the random-sampling line from a 1:1 species–history relation (i.e. the proportion of total history compared with the proportion of total species in a sample), and so how much ‘extra’ history is preserved during extinction, depends on the shape of the tree of life: some shapes contain more redundancy than others (Heard & Mooers 2000). The simplest models of diversification (e.g. Markov and steady-state) contain considerable redundancy (Nee & May 1997), whereas more star-like trees contain less.

Random extinction, however, may not be a good representation of real extinction events (Heard & Mooers 2002). Non-random extinctions could leave much greater surviving history (if the species lost are dispersed across the tree such that there remains considerable redundancy), or they could leave much less surviving history (if the species lost encompass a great deal of unique history, or, to a lesser extent, are phylogenetically clumped (Heard & Mooers 2000)). For instance, the bottom curve in Fig. 6.2 shows the case where the most relictual species are removed first. Because these lineages represent a lot of unique history, their removal means that the loss of evolutionary history is out of proportion to the loss of species (i.e. the loss curve is below the 1:1 species–history line). Past mass extinctions have often been phylogenetically clumped and/or non-random with respect to ecological and morphological traits (Erwin 1993; McKinney 1997; Heard & Mooers 2002). However, such non-randomness is only moderately costly in terms of evolutionary history lost (Heard & Mooers 2000) unless extinction risks are correlated with speciation rates across lineages. Evidence for such correlations, which lead to much more costly extinctions, is limited at best (Heard & Mooers 2002).

Extinction risks in the modern day, however, need not be patterned in the same way as in past mass extinctions (Heard & Mooers 2002). The consensus from several recent analyses of the loss of evolutionary history as a function of species loss (see, for example, Russell *et al.* 1998; Purvis *et al.* 2000; von Euler 2001; Sechrest *et al.* 2002; Mooers & Atkins 2003) is that we are currently losing (and risking) much more history than if anthropogenic extinctions were random. The poster child for this is the small clade of highly threatened species of tuatara, the last of a lineage of Rhynoccephalia that is sister to all the living squamates. If these species become extinct, we will lose so much PD that our remaining sample of reptiles will fall well below the 1:1 line. Another recent discovery concerns the Acanthisittidae, a small family (3 species) of threatened songbirds that also live on New Zealand. This family may be the sister to the rest of the Passeri (Ericson *et al.* 2002) and losing it would mean disproportionate loss of PD. However, and importantly, even if we are losing more history than expected based on such ‘field of bullets’ scenarios (Raup 1991; Nee & May 1997),

species richness might still be a good surrogate for history to the extent that any argument or approach that calls for increasing the number of species we want to preserve will have as a consequence at least as great an effect on preserving history. Unfortunately, direct comparisons of conservation strategies based on evolutionary history and species richness are few (but see Chapter 5 for a pertinent simulation study).

Three recent studies suggest that prioritising sites based on species richness yield rankings near-identical to those of schemes that explicitly consider PD (Polasky *et al.* 2001 for birds in North America; Rodrigues & Gaston 2002 for birds in South Africa; Whiting *et al.* 2000 for crayfish in Australia). A study of various taxa in South America by Posadas *et al.* (2001) can be interpreted in different ways: geographic samples of species were not random with respect to PD, but rankings of areas based on species richness and rankings based on total history were none the less strongly and positively correlated. Rodrigues *et al.* (Chapter 5) offer simulation work relevant to this question.

With regard to samples of endangered, extirpated or recently extinct species, the evidence is more equivocal: Johnson *et al.* (2002) recently presented intriguing data suggesting that we may be losing disproportionate amounts of Australian marsupial history (and so falling below the line of equality in Fig. 6.2). Purvis *et al.* (2000) present strong evidence that the probability of a species' being threatened is inversely related to the size of the genus to which it belongs for birds, primates and carnivores. However, for these groups worldwide, we do not risk losing proportionately more history than species. For primates, although between 16–60% of species are at risk, only 12–45% of total history is at risk. For carnivores, the statistics are 10–37% of species at risk vs. 7–24% of history at risk (data from Purvis *et al.* 2000). von Euler (2001) makes the point explicitly for birds: 12% of species are at risk, and 10% of evolutionary history will go with them if they are lost. Although these proportions are very rough, they clearly contradict the oft-cited statistic that we could lose 95% of species and yet retain 80% of the total PD of a tree (Nee & May 1997). They do, however, also suggest that saving species may be an efficient way to save PD. More case histories and comparative analyses will be critical to decide how efficient it is, and to identify why the evolutionary 'fail-safe' of redundancy works so poorly.

STEWARDSHIP OF EVOLUTIONARY HERITAGE BY NATIONS

Even if future work suggests that we will often do well by concentrating on species richness, PD may still be a useful metric for conservation. With

it, we can perform an accounting exercise that treats taxa within defined geopolitical units as independent samples of 'evolutionary heritage.' This concept is outlined in Fig. 6.1: every country is assigned the evolutionary heritage equal to the PD that its species encompass. This total heritage is not unique, since countries may share species, and deeper branches will be shared among many countries. This total heritage can be calculated in several overlapping ways: species or clades that are endemic to a single country will encompass its truly unique heritage; species or clades that are at risk in a country will contribute to that country's 'at risk' heritage, and a portion of a country's heritage may be both endemic and at risk.

This type of accounting is suggested by several observations, as follows.

1. Much of the policy concerning biodiversity is species-based (Europe, Australia, Canada, Mexico and the USA all have variations on a lineage-based endangered species act).
2. Almost all policy concerning biodiversity is geopolitically based. For instance, Canada's new Species at Risk Act is a direct response to similar national laws in Mexico and the USA and its obligations under the Convention on Biological Diversity. Indeed, much of the political lobbying was based on the fact that species given legal protection in one country were ignored or persecuted in another (see, for example, www.scientists-4-species.org). Only on occasion will a single geopolitical unit's jurisdiction encompass an entire clade of interest (island states such as Madagascar, the Philippines, Australia and New Zealand being important cases).
3. Some political policy already uses history as a conservation metric: under American Endangered Species Legislation from 1983 on, for example, the US Fish and Wildlife Service uses a priority system when listing and establishing recovery plans that explicitly considers 'genetic uniqueness', giving higher rank to species in monotypic higher taxa (see, for example, Anonymous, 1998).
4. Time (e.g. millions of years) allows for a common currency, in the sense that it is understandable to the public and comparable across regions and taxa. The metric may allow us to reduce our reliance on specific poster or flagship species (such as pandas or rhinos), and thereby may foster a more comprehensive appreciation of the tree of life;
5. 'Heritage' is a time-based, geographically defined concept: geopolitical units steward their individual monuments, and may define themselves in part by the sum of their tangible heritage. A graphic example of this

was the Taliban regime's decision to destroy part of Afghani Buddhist heritage in early 2001 (see, for example, Rosenberg, 2001). The international outcry that ensued also exemplifies how governments steward heritage both for both their own and the world's citizenry.

EXAMPLES OF EVOLUTIONARY HERITAGE

Mooers & Atkins (2003) were the first to catalogue the amount of PD of interest for a single country. Using compilations of species lists and conservation status, a time-based taxonomy and cytochrome b data, the authors estimated that Indonesia stewards between 670 and 750 million years of avian PD that is 'near threatened' or worse, and that over one third of this history (280 million years) is endemic to this country alone. This is a large amount of heritage, similar to the threatened PD for primates and carnivores over the entire globe. However, there is not yet a complete tree of the birds, and so these estimates are conservative and further comparisons are premature. Luckily, there are two groups of charismatic megafauna (Primata and Carnivora) for which all the requisite data exist: a well-studied taxonomy, a dated tree, conservation status reports, and range information allowing for reliable country lists. We present preliminary results for these two groups below.

Carnivore data

The dated 'supertree' of 271 carnivore species by Bininda-Emonds *et al.* (1999) formed our primary dataset. (The domesticated dog and cat were not considered.) This tree encompasses 2731 million years of evolutionary history. We were able to establish country lists for all these species for 151 countries. Our primary reference was Wilson & Reeder (1993), with supplementary information from various sources (Medway 1965; Dorst 1970; Diller & Haltenorth 1980; Jefferson *et al.* 1993; Nowak 1999). Cohen (2000) was used for geopolitical boundaries and name changes. Countries were excluded if they had no naturally occurring carnivores (Barbados, the Maldives) and species were excluded if range descriptions were too vague. This means that lists must be considered conservative; only descriptions that explicitly listed countries or obvious geographic locations were used to place a species on a country list. For example, the range for *Arctictis binturong* (Wilson & Reader 1993) is: 'Bangladesh, Bhutan, Burma, China (Yunnan), India (incl. Sikkim), Indonesia (Borneo, Java, Sumatra), Laos, Malaysia, Nepal, Philippine Isls (Palawan), Thailand,

Vietnam'. Because it was not explicitly listed, the species was not assigned to Brunei Darussalam, although its occurrence there seems likely; likewise, 'possibly into Venezuela' (Wilson & Reeder 1993) was not enough to include *Bassaricyon alleni* in Venezuela.

The species ranges were updated with the IUCN status in each country of a species range (for example, the IUCN provides information on extirpated species, such as the swift fox *Vulpes velox*, which was last classified in 1996 as regionally extinct in Canada). Because we restricted ourselves to the species in the 1999 tree, three red-listed carnivores were not included in the database.

Primate data

The dataset for primates was constructed similarly. Our tree for 233 species was that published by Purvis (1995, representing 1679 million years of history) and our country lists were based primarily on the Mammal add-on to the Bird Area software package (Santa Barbara Software Products, 2000) which in turn is based on Wilson & Reeder (1993) and various sources. Haphazard cross-referencing turned up no discrepancies. Forty-six species of primate listed by the IUCN either could not be synonymized with our species list or have been named since 1995. We chose to exclude *Homo sapiens* from our calculations, leaving us with eighty-seven countries to which we could assign at least one primate species besides ourselves.

Calculating evolutionary heritage

For both taxa, three lists were made for each country: total species, endemic species, and 'at risk' species. We used the IUCN categories (www.redlist.org, November 2002) to delineate risk, and considered any species with a 'data deficient', 'near-threatened' or worse designation to be 'at risk' in every country in which it was found. We used a simple program written in VisualBasic (Microsoft, Redmond, WA, USA) ('PhyloCommunity', available upon request from S.B.H.) to perform our heritage calculations. This program calculates the proportion of the total evolutionary history in a clade encompassed by a sub-tree (the tree defined by a subset of species). For our purposes, the sub-trees we used represented the total, endemic, and at-risk species lists for each country (giving us total heritage, endemic heritage, and at-risk heritage, respectively) (see Fig. 6.1). 'At risk' heritage included that portion of the sub-tree that was not represented by any other non-threatened species in a country (although it could

be represented in some other country). Endemic heritage included only that portion of the sub-tree that was not represented by any other species anywhere else in the world. Importantly, for total EH, if a country contained any carnivore species, its heritage included the total branch length back to the first split at the root (i.e. any single carnivore species represents 54 million years of history, equivalent to the depth of the tree). We did not, however, include the common single branch linking the carnivore (and primate) clade to its sister group (because these branch lengths are presently unknown). Although that branch should be included in a tally of evolutionary history represented by the clade, it could only be lost under the doomsday scenario in which *the entire clade* became extinct. We hope this is not likely; omission of this deepest branch means that some constant amount of EH is missing from each of our country measures.

Results

Figure 6.3 shows, for the 151 countries in our dataset, the proportion of the world's heritage stewarded by each country against the proportion of the world's carnivore species found in that country. The straight line represents a 1:1 correspondence between species and history; countries falling above and below the line would steward disproportionately more and less (respectively) history than expected. The correlation across all countries is strong (after square-root transformation of species number: carnivores, $R^2 = 0.95$; primates, $R^2 = 0.92$). For all countries, more history is stewarded than species, indicating substantial redundancy. This redundancy is not universal for 'at risk' heritage, however (Fig. 6.4): for some countries, 'at risk' species represent a large proportion of their total heritage, such that losing them would have a disproportionate effect on how much heritage remains. Tables 6.1–6.3 rank the top countries for both total and 'at risk' species, and for total, endangered and endemic history for both groups. Importantly from an immediate conservation perspective, the overlap between the top country rankings for most threatened species and for most threatened heritage is quite low, suggesting that some countries may be unaware of how much heritage they currently have at risk. Although the presence of some countries is not unexpected (for example, for both taxa, Indonesia is in the top ten for total heritage and China for threatened heritage), other states may be surprised to learn what they harbour (e.g. the total amount of carnivore heritage, and the 'at risk' primate heritage, partitioned among the countries of mainland southeast Asia; Bolivia's total primate and Guinea's 'at risk' carnivore heritage).

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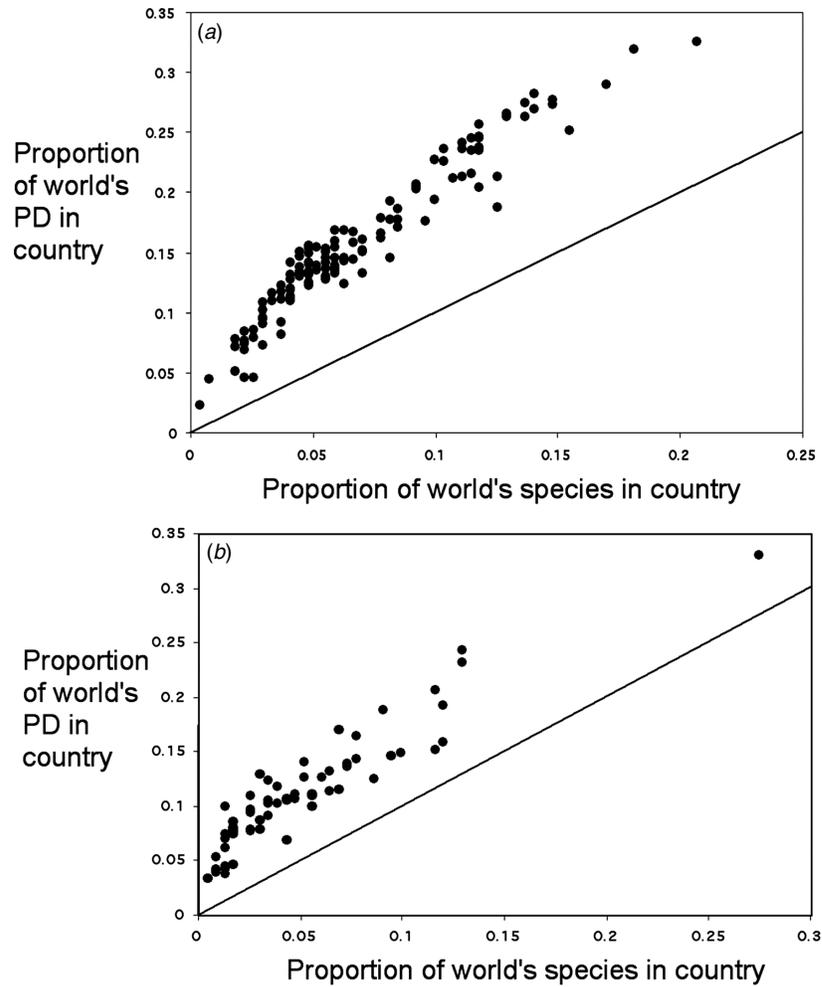


Figure 6.3. Plot of the proportion of the species in the world that a country stewards against the proportion of the world's total PD that a country stewards (which is that country's 'evolutionary heritage') for carnivores (a) and Primates (b). The line of equality is also depicted.

DISCUSSION

The relevance of time-based PD

Two issues concerning PD merit mention. The first is the tension between this somewhat static formulation of information content and the argument that society might consider preserving the process of evolution as

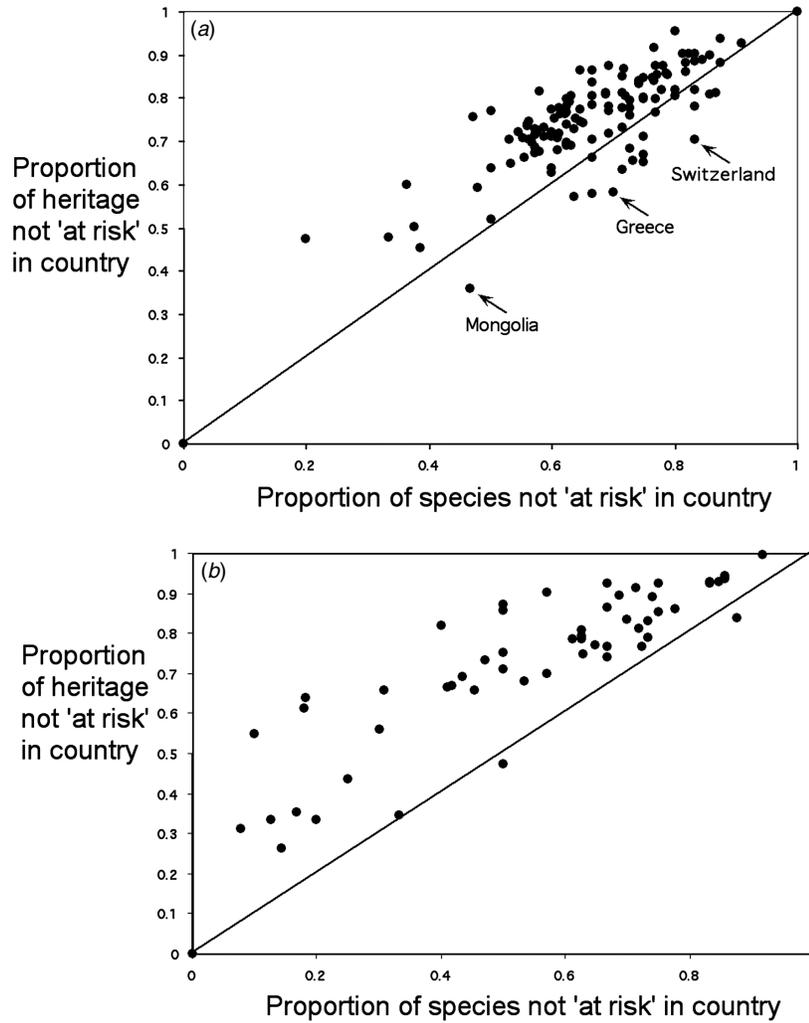


Figure 6.4. Plot of the proportion of the species in a country that are not 'at risk' ($1 - (\text{no. of threatened spp.} / \text{total no. of spp.})$) versus the proportion of the country's evolutionary heritage that is not at risk, for carnivores (a) and primates (b). The line of equality is also depicted: points above the line are countries where the amount of safe heritage is more than expected based on the number of safe species, and points below the line are countries that stand to lose more than proportionate history if their 'at risk' species are lost.

Table 6.1. Top ten countries for total species, ‘at risk’ species, total heritage and ‘at risk’ heritage for carnivores

Figures in parentheses indicate: no., number of species; my, millions of years of evolutionary heritage

Rank	Species (no.)	Heritage (my)	‘at risk’ species (no.)	‘at risk’ heritage (my)
1	India (56)	India (774)	India (25)	India (227)
2	China (49)	China (756)	China (19)	China (214)
3	USA (46)	USA (688)	Russia (18)	Guinea (203)
4	Russia (42)	South Africa (671)	Thailand (16)	Mongolia (198)
5	Thailand (40)	Malaysia (657)	Indonesia (16)	Bhutan (197)
6	Malaysia (40)	Myanmar (651)	Malaysia (15)	Russia (196)
			Viet Nam (15)	Nepal (196)
			Nepal (15)	
			Peru (15)	
7	Viet Nam (38)	Thailand (649)	—	—
8	South Africa (38)	Viet Nam (638)	—	Indonesia (189)
9	Indonesia (37)	Angola (630)	—	Laos (179)
10	Myanmar (37)	Indonesia (624)	Myanmar (14)	Ecuador (169)
			Laos (14)	
			Brazil (14)	
			Ecuador (14)	

well as its product. Prioritising samples that maximise PD means prioritising samples that include evolutionary ‘relicts’, lineages that have few close relatives. Erwin (1991) suggested that because these relicts are often ‘predictably on their way to extinction’, rapidly evolving clades or ‘evolutionary fronts’ might be worthy of consideration; Krajewski (1991), in his response to Erwin’s article, clearly formulated the question by asking whether we are better served by focusing on the ‘twigs’ or the ‘stems’ of the evolutionary tree. The idea of explicitly targeting process has recently been resurrected at an American National Academy of Sciences symposium (Cowling & Pressey 2001; Woodruffe 2001). One thread here is that of evolutionary triage: given that we are likely to lose many (perhaps very many) species to anthropogenic extinction, we should look to the future, and let evolutionary relicts such as the ginkgo shuffle off if necessary, carrying their history with them, while we concentrate on saving those species or those areas from which new diversity will spring. At the extreme, this sort of predictive book-keeping may be possible, but the timescales involved have very little to do with current conservation (indeed, human) thinking (see Chapter 18).

Table 6.2. Top ten countries for total species, 'at risk' species, total heritage and 'at risk' heritage for primates

Conventions as in Table 6.1.

Rank	Species (no.)	Heritage (my)	'at risk' species (no.)	'at risk' heritage (my)
1	Brazil (64)	Brazil (556)	Madagascar (24)	Madagascar (272)
2	Madagascar (30) Peru (30)	Madagascar (407)	Indonesia (23)	Cambodia (160)
3	—	Peru (390)	Brazil (18) China (18)	Sri Lanka (133)
4	Indonesia (28) Cameroon (28)	Colombia (348)	—	India (126)
5	—	Indonesia (323)	Cameroon (14)	Indonesia (125)
6	Colombia (27) Dem. Rep. Congo (27)	Bolivia (317) Eq. Guinea (13)	Nigeria (13)	Laos (114)
7	—	Ecuador (285)	—	Philippines (110)
8	Nigeria (23)	Congo (277)	India (12)	Bangladesh (106)
9	Eq. Guinea (22)	Cameroon (267)	Dem. Rep. Congo (10)	Brazil (105)
10	Bolivia (21)	Dem. Rep. Congo (255)	Gabon (9) Myanmar (9) Viet Nam (9)	China (94)

Table 6.3. Top five countries for endemic species and endemic heritage for carnivores and primates

Conventions as in Table 6.1.

Rank	Carnivores		Primates	
	Species (no.)	Heritage (my)	Species (no.)	Heritage (my)
1	Madagascar (8)	Madagascar (51)	Madagascar (24)	Madagascar (342)
2	Indonesia (3) India (3) USA (3) Mexico (3)	Indonesia (28) India (28)	Brazil (18) Indonesia (18)	Brazil (130)
3	—	—	—	Indonesia (89)
4	—	China (22)	India (4) China (4)	Philippines (16) Colombia (16)
5	—	Costa Rica (17) Panama (17)	—	—

The second, thornier issue is the equation of tree path length with information. Much has been written on the merits of tree-topology-, character-, genetic-, or time-based measures of distinctness among taxa (see, for example, Vane-Wright *et al.* 1991; Crozier 1992; Williams & Gaston 1994; Krajewski 1994; Owens & Bennett 2000; Faith 2002). In this chapter, we have used ultrametric trees where path lengths represent time. The reason is three-fold: (i) if the probability of character change within an evolving lineage is correlated with time (Crozier 1992) then this metric will be correlated with information measured on any other scale; (ii) time offers a metric that is directly comparable across taxa and so is fungible; and (iii) time is immediately understandable to the public and allows the concept of 'heritage' to be used with minimal loss of meaning.

Database instability

Another concern is the quality of the phylogenetic and conservation-status databases. Taxonomies are not static (and so often out of date; see, for example, our primates decisions above), even for well-studied groups, and ultrametric phylogenetic trees that purport to show the ages of clades are even more fluid (see, for example, Yoder *et al.* (2003) for a new perspective on the 'Viverridae' of Madagascar, and Vos & Mooers (2004) for an updated tree of Primates). The two supertrees used here (Purvis 1995; Bininda-Emonds *et al.* 1999) are statements of ignorance as much as of information: indeed, they were explicitly created to help highlight where more phylogenetic work is needed. It is extremely unlikely that the single endemic tarsier of the Philippines or the two endemic olingos from Costa Rica and Panama are as old as the tree depicts: in the face of no information, these species are placed as emanating from a genus-level polytomy. In any particular case, *ad hoc* decisions could be made, for instance by assigning the average species age to all species for which data are lacking. More generally, however, should we place specific conservation decisions on the shifting sands of phylogenetic inference (cf. Muir *et al.* 1998)? This issue must be faced squarely. In the end, allocation decisions for conservation are made on the basis of many types of information (see Chapter 4). More work is needed on the sensitivity of heritage rankings to changing phylogenetic information. Evolutionary heritage, and the rankings that can be made with it, should be seen as an alternative way to highlight and contrast countries who steward one aspect of conservation (information content). We suggest that international conservation monitoring bodies such as the IUCN and Conservation International set up updatable web-based 'league tables' of total, endemic and 'at risk' evolutionary heritage for various taxonomic groups, cross-referenced

to state-based conservation initiatives (e.g. legislation, budgeting, habitat protection). These might make the connection between an improving phylogenetic database, conservation activity, and the legal status of species clearer, and so spur further work at the interface of academic phylogenetics and practical conservation biology. We were surprised at the number of countries that do not even maintain accessible species lists, especially for local conservation status. Compiling such lists is an expensive endeavour, but is the absolute minimum required if state-sponsored conservation is going to be effective. In the absence of such detailed information, one is forced to make extrapolations of species status. It may be prudent to consider all species listed globally as 'at risk' as being at risk everywhere, but no such extrapolation is safe for other statuses: species listed at one level globally may be worse off in certain countries.

Geopolitical scale of conservation efforts

Finally, the basis of the exercise is that geopolitical units act independently: even though many of the countries in the top ten list share species (for example, Brazil, Peru, Bolivia and Ecuador for primates, or Myanmar, Thailand and Viet Nam for carnivores) the countries are listed separately. Ideally, of course, species would be managed and stewarded with no regard to arbitrary borders, but this is unlikely. More practicable would be a rational geopolitically based system for allocating resources: countries could 'trade' species stewardship as a function of relative burden and probability of success. Given limited resources, a country should not invest in a threatened population at the edge of its range that is doing well elsewhere. It is true too that co-operative programmes do exist (e.g. the North American Migratory Birds Convention Act of 1994). However, state-based conservation activities are more common. Critically, neighbouring states may have very different political systems (as in Myanmar and Thailand) or different political histories, economies, attitudes and priorities (as in the USA, Canada and Mexico). We suggest that it may be naïve and dangerous for a state to assume that some other country will properly steward shared species. That said, being on a 'top ten' list for 'at risk' species is a double-edged sword: one can lobby for international funds for one's endangered heritage, but also be hounded for doing too little. Some might worry that countries could leave marginal species off lists (or even allow them to disappear on the ground) in order to look better internationally. Future work should both consider how rankings might change under more refined measures of heritage (e.g. if countries are ascribed heritage over species as a function of the proportion of the total range they steward) and study the correlates of evolutionary

heritage across countries. Ideally, these extensions should be done in the context of present conservation activities and future threats. Only after such analyses will we know how evolutionary heritage, a concept appealing in principle, might actually help to advance practical conservation endeavours.

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