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Distribution and correlates of carnivore phylogenetic diversity across the Americas

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Abstract

Digital maps and a dated supertree of global carnivore species were used to assess the distribution of American carnivores' phylogenetic diversity (PD, measured in millions of years) both from a geopolitical perspective ('evolutionary heritage' or EH) and on the basis of species' range size and conservation status. A new measure, range-weighted EH, is introduced. This measure partitions the total PD of the tree between countries based on the proportion of species' ranges within each country. Sociopolitical correlates of these measures were explored. Only 3% of the total PD in the Americas is endemic to any one country. As expected, the measures of PD are positively correlated with each other and with species richness. The USA contains the most species, the most EH and the second most range-weighted EH after Brazil. Indeed, larger and richer countries, and those with the lowest state-corruption-rate hold most EH. No significant differences were observed in the amount of PD remaining if species are removed at random, or following more plausible sequences based on IUCN conservation status and range size. Eighty percent of the American carnivores' PD would remain safe if only the set of not threatened species were to remain. Roughly the same is true if only the 50% most widespread species were to persist. Samples of wide-ranging species represent more of the entire tree than do samples of narrow-ranging species, highlighting the importance of the former for conservation strategies. We suggest that similar approaches be applied to more groups across the globe to assess which countries and areas steward the most PD, as well as which species and taxa do, in order to plan conservation actions consequently.

INTRODUCTION

Human activities are pruning the tree of life at a drastically elevated rate (for reviews, see Pimm *et al.*, 1995; Wilson, 2002; Mace, Gittleman & Purvis, 2003). Limited resources and limited ability to protect 'nature's variety' at all levels of relevance (from genes to populations to species to higher taxa: Humphries, Williams & Vane-Wright, 1995) emphasise the need for appropriate ways to measure the diversity of life, in order to best prioritise conservation efforts (Gaston, 1994, 1998; Williams, Gaston & Humphries, 1994).

Species richness is often used as a crude measure of biodiversity (Gaston, 1994, 1996). However, this measure operates under the implicit assumption that all species are equal and that maximising the number of species will maximise biodiversity measured in other ways. This method might overlook old lineages that encompass relatively few species whose loss incurs a substantial loss of evolutionary history (May, 1990; Vane-Wright, Humphries & Williams, 1991; for a recent example of a surprising relictual lineage, see Roca *et al.*, 2004).

A biodiversity currency that takes into account not only the number of species, but also an estimation of their distinctiveness might provide a more comprehensive description of the biodiversity of areas for the identification of conservation priorities. Measuring biodiversity using phylogenetic diversity (PD: Faith, 1992), as defined by Crozier (1997), focuses on measuring the amount of genetic information shared among species and is a more sophisticated currency that does not treat all species as equivalent (Faith, 1992; Wilson, 1992; Crozier, 1997; Mace *et al.*, 2003). As such, phylogenies can be used to set conservation priorities for maximising the amount of evolutionary history preserved. Branch lengths in ultrametric phylogenies represent the length of time in which evolutionary processes have created unique characters in lineages and, thus, can serve as measures of evolutionary distinctiveness (Faith, 1992; Nee & May, 1997; Mace *et al.*, 2003). Hence, PD allows for the identification of assemblages of organisms that are likely to represent the broadest array of diversity. Because time is a measure of

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independent evolution, it is not focused on any particular suite of phenotypic characters but should be correlated with them all. Measures of PD that consider particular phenotypic traits are also possible (for an example using body size, see Diniz-Filho, 2004).

Here, we consider the carnivores of the Americas (North, Central and South) and assess patterns of PD from two perspectives: one that recognises that conservation decisions are made primarily at the level of the geopolitical unit and one that considers the loss of PD under various extinction scenarios. For the first, we refer to the amount of phylogenetic diversity that a country stewards as its evolutionary heritage (Mooers & Atkins, 2003; Mooers, Heard & Chrostowski, 2005). Recent conservation studies that use the country as the level of analysis (e.g., Smith *et al.*, 2003; Sutherland, 2003) have shown how, at a broad scale, important social and political factors can be incorporated into conservation. For instance, countries assess their own at-risk species (taxa, communities, ecosystems) and implement strategies to preserve the biodiversity they steward. Plans are optimised according to the country's available resources and priorities. However, given a measure of the evolutionary heritage contained in individual countries, the international conservation community could prioritise geopolitical units for conservation effort. Importantly in this context, Smith *et al.* (2003) found a negative correlation between both the amount of biodiversity and the level of endemism found in a country and a composite measure of state corruption they called governance. When combined with socioeconomic variables such as governance scores, wealth, and population density, a ranking of countries based on the evolutionary heritage they harbour could highlight countries that might benefit from international involvement to offset the negative effects of these variables on national conservation efforts.

One consideration in creating such a ranking is that of shared responsibility – most species occur in more than one country, and, due to the redundancy in the hierarchical phylogeny, much of the tree (i.e. the deeper branches) is represented in many, if not most, countries. Below, we outline a novel strategy that apportions the total PD represented in a group of species to a country in relation to the proportion of the total ranges of the species that that country stewards. This approach emphasises the difference between a simple patriotic view of evolutionary heritage (more and more different species are good) and a more complex view that apportions responsibility between countries as a function of the relevant habitat they steward.

An alternative approach is to assess patterns of PD and identify priorities not on the basis of geopolitical units, but of species traits such as range size and conservation status. For instance, Nee & May (1997) showed that a tree that loses 50% of its species randomly may retain as much as 70–80% of its total PD. In such cases, extinction management offers only marginal improvement. Simulation work has shown that with realistic trees (i.e. imbalanced; see Mooers & Heard, 1997), the amount of PD lost is very sensitive to non-random patterns of species loss (Heard & Mooers, 2000) and several recent analyses (e.g. Russell *et al.*, 1998; Purvis *et al.*, 2000*a*; Von Euler, 2001; Sechrest *et al.*, 2002) indicate that we risk losing more PD than suggested by the random scenarios described by Nee & May (1997). Whether information about that relationship offers more than marginal improvement over interventions based on species richness is still not clear (Mooers *et al.*, 2005). Thus, for conservation purposes it is important to understand the actual relationship between species loss and the loss of phylogenetic diversity. Consequently, we compared the amount of PD of the American carnivores remaining under several different extinction scenarios.

MATERIALS AND METHODS

Range data

Data on the distribution of American carnivores were obtained from the recently released *Digital distribution maps of the mammals of the western hemisphere* (Patterson *et al.*, 2003). This database provides distribution maps for all terrestrial mammals of the Americas, stored as ArcView shapefiles and associated tables of attributes. They were used to calculate species' range size (measured as extent of occurrence: see e.g. Gaston & Blackburn, 2000) and the fraction of their distribution within each American country. For the few species for which both polygons and points were provided, only polygons were considered in the analyses. A total of 84 carnivore species is included in the database. *Herpestes javanicus* was excluded from our analysis, as it is not native to the Americas. The extinct *Procyon gloveralleni* was also excluded. In contrast, we added another species, the polar bear (*Ursus maritimus*), not included in the original database. Information on this species' distribution was obtained from the IUCN/SSC Polar Bear Specialist Group (1998). Throughout the analysis the taxonomy follows B. Patterson's systematic database on Neotropical mammals and NatureServe's database on North American mammals (see www.natureserve.org/explorer).

Although *Digital distribution maps of the mammals of the western hemisphere* is the best dataset of its kind available, the maps are probably incomplete in that they do not include areas where a species is actually present but has not been recorded yet. Moreover, while for some species the portions of their range where they have recently gone extinct are indicated in the database, many species have probably undergone range contractions that are not recorded on the maps. Conversely, for the majority of species, mapped ranges are gross overestimates of locations where species truly occur. Thus, they are likely to include relatively extensive areas from which the species are actually absent. Hence, for consistency we used the 'original' ranges that the maps represent, with the exception of the black-footed ferret, *Mustela nigripes*, which is extinct in the wild and was given a range size of zero. We trust that the areas we use are correlated in some non-trivial way with relevant attributes of actual species ranges (e.g. latitudinal and longitudinal extent, population size, representation in country, etc).

Maps were plotted using ArcView 3.2 and then projected onto an equal-area cylindrical projection using

ArcView's 'Projector!' extension. Each species' range size (i.e. the area of the polygon representing a species' geographical range) was then calculated using the 'Xtools' extension and the results are included in Appendix 1. Countries' maps were extracted from the world map shapefile included with ArcView and then projected in the same manner. Species distribution maps and countries' maps were subsequently intersected using the 'Geoprocessing' extension and the area of these new polygons (representing the area of each species' distribution lying within each country) calculated using the 'Xtools' extension.

Nine out of the 83 species analysed are not restricted to the Americas and the database does not provide world maps of those species. Therefore, maps of their world range were obtained from the literature (see Appendix 1) and approximate distribution maps were plotted using ArcView. Those maps were then subjected to the same procedures to estimate the size of their world distribution. We followed the same procedure to calculate the (approximate) fraction of the polar bear distribution within each country.

Phylogenetic information

We used Bininda-Emonds, Gittleman & Purvis' (1999) dated supertree of global carnivore species to obtain phylogenetic information on the American carnivores. The domesticated dog and cat were not considered in our analysis. Five species were added to the original supertree to account for recent taxonomic changes. *Pseudalopex fulvipes* was added as a sister species to *P. griseus* (Patterson *et al.*, 2003), *Vulpes macrotis* as sister to *V. velox* (Dragoo *et al.*, 1990) and *Spilogale gracilis* as sister to *S. putorius* (Jones *et al.*, 1992). *Oncifelis colocolo* was replaced by *Lynchailurus colocolo, L. braccatus* and *L. pajeros* (García-Perea, 1994).

Although the tree is fairly well resolved below the genus level, our final dataset included species' ages for only 42 out of the 83 American carnivores we analysed. These ages are from the original supertree and are a combination of literature best estimates and interpolations from a pure birth model (Bininda-Emonds *et al.*, 1999). For the remaining 41 species, Bininda-Emonds *et al.* had reasonably assigned the species to the age of their most recent common ancestor (e.g. the age of the first split in the genus), producing deep polytomies (see Fig. 1(a)). However, this means that these species all have biased (old) ages and their genus a biased (high) amount of PD (a star phylogeny has the maximum possible pathlength because no internal branches are shared). In order to best ameliorate this, we re-calculated species' ages using a conservative, model-based approach, as outlined in Appendix 2. We applied a pure birth model to each genus to estimate the total PD for a genus of the same age and diversity. We then assigned all species the age that would lead to this pure-birth PD. This retains the shape of the genus tree (a polytomy), but produces unbiased estimates of the genus and less-biased species PD. Polytomies above the genus level were left unresolved, as a pure birth model is entirely unreasonable due to extensive exinction.

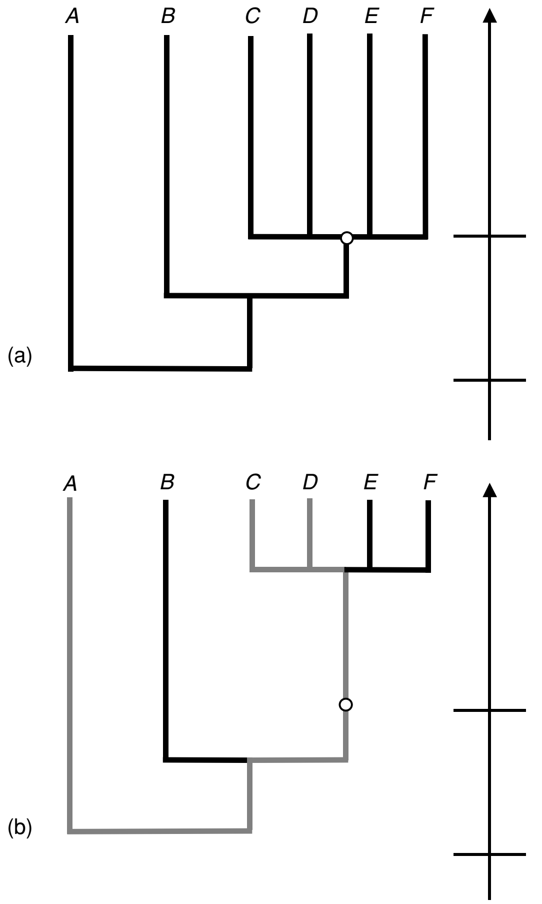

Fig. 1. Evolutionary Heritage (EH). (a) A partially resolved tree. The species C–F are given species ages equal to the known age of the genus, which is an overestimate of both their ages and of the total phylogenetic diversity (PD) in the clade. Using a pure birth model, a clade of this age and size would have the total PD equal to the tree in (b) and so the modified tree places the species on branches of shorter length. (b) This also highlights (in grey) the PD encompassed by the group of species A, C and D. A country with only these species would have an EH equal to this PD.

Evolutionary heritage per country

The 26 countries with native carnivores were assigned evolutionary heritage (EH) values using the software 'PhyloCommunity' (written by and available from SBH) in three ways. The first (endemic evolutionary heritage (endemic EH)) scores the proportion of the total tree that is represented by species restricted to one country only. The second (EH) considers only the presence and absence of species in each country (Mooers *et al.*, 2005) and is equal to the PD (or pathlength) of the subtree defined by each country's species (see Fig. 1(b)). This measure ignores the fact that species and higher taxa are shared by countries, since most country subtrees will overlap for the deeper branches. Due to this multiple counting, the summed PD across all countries will be much greater than the total PD in the tree. The third measure (range-weighted EH) incorporates the actual ranges of the species within each country and proportionally partitions the total PD of the tree between countries. This is done by apportioning the

PD of a branch (its length in million years (MY)) to a country as the:

> (sum of the country range of all the species that share
> the branch)/(sum of the world range of all the
> species that share the branch).

For a tip branch, this is just the proportion of a species' range in a particular country. Deeper branches are shared by many species and are apportioned between the subtending species relative to their range sizes. The branch is then apportioned to countries based on which species are present and what proportion of their range is found in that country. For example, take three species endemic to North America with the relationship ((A:1,B:1):3,C:4), such that species A and B are sister species that diverged 1 MY ago and their ancestor diverged from lineage C 3 MY before that. With these branch lengths, the total PD of the group is 9 MY. Then give Canada, the USA and Mexico the following ranges for these species: species A: 0, 2000, 1000; species B: 0, 500, 500; species C:100 000, 0, 0; Canada only governs species C, but shares it with no other country, while the USA and Mexico share both A and B. The range-weighted EH of the USA for this group would be (branch length A * proportion of A's range in the USA) + (branch length B * proportion of B's range in the USA) + (common branch length AB * proportion of the range of the clade AB in the USA), which is 1 * (2000/3000) + 1 * (500/1000) + 3 * (2500/4000) = 3.04 MY. Mexico would be apportioned 1.96 MY of EH and Canada would get 4 MY, which is all of the EH associated with its lone species C. This apportions the 9 MY between the three countries. If raw EH were employed, Mexico and the USA would each have 5 MY and Canada 4 MY (for a total of 14 MY of EH).

It is important to note that this third measure does not correct for geographical overlap of species' ranges, because ranges are simply summed up across species. It therefore cannot differentiate a country whose range-weighted EH is composed of spatially separated species and one whose species' ranges overlap. Although other formulations are possible we prefer this for several reasons: (1) multi-species management is still in its infancy, (2) most states still consider species separately in their legislation and (3) ranking areas by the number of relevant species they harbour seems desirable in any case.

Correlates of evolutionary heritage

We first considered the relationships of these measures of EH with each other and with the number of species in each country. We then looked at the rankings of the 26 countries on these measures of heritage and highlighted how the rankings differ for the different measures. Finally, we explored how these measures varied with a suite of country-based socioeconomic variables using both univariate and multiple regressions. For the multiple regression analysis, we started with the completely saturated model and used backwards elimination to find the simplest predictive model. We applied both non-parametric and parametric tests where appropriate: for parametric tests we removed three extreme outliers (the island nations). The final transformations without these nations produced very well-behaved data (Shapiro–Wilk W tests for normality): ln (spp), $P = 0.11$; arcsin (sqrt (EH)), $P = 0.62$; ln (EHrange), $P = 0.39$; ln (popsize), $P = 0.82$; ln (area), $P = 0.36$; ln (ln (governance)), $P = 0.37$; ln (purchasing power parity or PPP, a measure of wealth), $P = 0.75$; ln (ln (PPP/head), $P = 0.43$. The country analyses are exploratory in nature, so nominal P-values are presented throughout.

Random versus deterministic loss of PD

In order to explore the effects of species loss on the PD of our assemblage, we calculated the amount of PD remaining after removing species at random and following two more realistic and one less-realistic sequence: (1) in order of increasing range size (such that small-range species are lost first), (2) in order of decreasing threat following IUCN designations and, for comparison, (3) in order of decreasing range size (such that large-range species are lost first). Species' conservation status followed IUCN (2003). We assigned the IUCN status NT (near threatened) to all species in the *Lynchailurus* group as they were classified as NT when considered a single species. We did the same with *V. macrotis*, which is a sister species of the LR/cd *V. velox*. *Pseudalopex fulvipes* was considered as NT given its restricted range. The patterns of PD loss were then compared using two-sample Kolmogorov–Smirnov tests (Zar, 1999). Finally, we evaluated whether species at either higher threat levels or with smaller ranges represented more distinct species, measured as their unique PD (or tip length; see Sechrest *et al.*, 2002).

RESULTS

Patterns of evolutionary heritage

The total phylogenetic diversity of American carnivores is 657 MY. Using range-weighted EH, 85% of this phylogenetic diversity is apportioned between the 26 countries and the 73 native carnivores endemic to the Americas and still found in the wild, 14% is encompassed by portions of the ranges of the nine species also found outside the Americas and approximately 1% is harboured by *Mustela nigripes*, the species that no longer exists in the wild. Table 1 lists the number of carnivore species each American country stewards, together with the total EH, range-weighted EH (EHrange) and endemic EH (endemicEH) that these species represent. Because of the generally large ranges of carnivores, little of the total EH is endemic to any one country: only seven countries have any endemic EH at all (and all but two have only a single species) and the total across all these countries is just 18.5 million years, less than 3% of the total. As expected, the former two measures of PD are positively correlated, to varying degrees, with each other and with species richness at $P < 0.05$ (Spearman rank correlation with ($n = 26$) and without ($n = 23$) the island nations, respectively: spp

Table 1. Species numbers and Evolutionary Heritage for native terrestrial carnivores in the Americas.

Country	Number of species	EH	EHrange	EndemicEH	Governance[1]	Area (km^2)[2]	Population (millions)[3]	GDP (PPP US$ billions)[3]
Argentina	31	0.5491	0.0594	0	3.8	2776889	37.5	424.4
Bahamas	1	0.0818	0.0008	0.0008	–	11404	0.3	5.0
Belize	15	0.477	0.0007	0	–	22965	0.2	1.4
Bolivia	**32**	0.6242	0.0342	0	2.23	1098581	8.5	19.6
Brazil	29	0.5841	**0.2058**	0.0028	4.37	8511965	174.0	1268.6
Canada	25	0.5713	**0.1114**	0	9.85	9976128	31.0	843.2
Chile	20	0.3996	0.0114	0.0006	3.57	756945	15.4	141.6
Colombia	29	**0.6397**	0.0408	0	3.35	1138914	42.8	302.8
Costa Rica	21	0.5488	0.0161	**0.0087**	4.95	50700	4.0	36.7
Ecuador	27	0.616	0.0092	0	3.5	283561	12.6	42.3
El Salvador	16	0.5095	0.0007	0	–	21393	6.3	33.7
French Guiana	15	0.4391	0.0018	0	–	91000	–	–
Guadeloupe	1	0.0818	0.0008	0.0008	–	1779	–	–
Guatemala	18	0.5257	0.0034	0	2.08	108889	11.7	51.4
Guyana	17	0.4854	0.0044	0	2.18	214969	0.8	3.6
Honduras	18	0.5257	0.0034	0	2.37	112088	6.6	18.6
Mexico	30	**0.6743**	0.0719	**0.0048**[4]	3.28	1952500	100.5	838.2
Nicaragua	19	0.5546	0.0035	0	3.96	128410	5.2	12.4
Panama	23	0.6172	0.0057	0	2.12	77081	3.0	16.7
Paraguay	20	0.4642	0.0099	0	2.59	406752	5.6	29.4
Peru	**32**	0.6318	0.044	0	2.69	1285210	26.4	120.4
Surinam	15	0.4391	0.0031	0	2.63	163266	0.4	1.92
Trinidad and Tobago	4	0.238	0	0	–	5129	1.3	11.9
Uruguay	17	0.4382	0.0033	0	2.87	177508	3.4	28.2
USA	**36**	**0.6931**	**0.1723**	**0.0089**[5]	8.31	9166598	288.0	9792.5
Venezuela	24	0.6158	0.0348	0	3.5	912050	24.8	139.5

Total number of species = 83; total PD = 657 million years. The top three countries on each measure of diversity are indicated in bold type.

[1]Smith *et al.* (2003); [2]The Columbia Encyclopedia (2001–04); [3]UNDP (2003): PPP-corrected GDP for Nicaragua and Suriname was measured as GDP per capita (UNDP, 2003) x population size; [4]three endemic species; [5]two endemic species.

versus EH, Rho = 0.89, 0.84; spp versus EHrange, Rho = 0.92, 0.90; EH versus EHrange, Rho = 0.76, 0.69). Parametric correlations excluding the island nations are very similar (in the same order, $R = 0.84, 0.89, 0.67$, respectively, all $P < 0.05$).

Perhaps more interesting are those countries whose rankings on these three measures differ substantially (see Table 1). Panama and Belize both have more EH than their species' numbers might suggest (moving from 11th to 6th spot and 23rd to 18th spot, respectively), while Chile has much less (dropping from 13th to 23nd in the rankings). Bolivia drops furthest from the species richness to the EHrange ranking (from 2nd to 9th), while Canada rises highest (9th to 3rd). Comparison of EH with EHrange highlights Chile's increased importance when range is considered (from 22nd to 11th) and El Salvador and Panama's decline, as their small size forces them to drop eight spots (starting at 16th and 6th, respectively; minute Belize also drops seven places to 25th). The USA contains the most species, the most EH and the second most range-weighted EH (after Brazil, with 21%): fully 70% of the American Carnivore tree is represented in the USA (versus 43% of the species) and 17% when the tree is uniquely apportioned to countries based on the species' ranges. When ranges are taken into account, the three largest countries, Brazil, Canada and the USA, together encompass 49% of the entire American carnivore tree.

Exploratory univariate analyses using Model 1 regression (which is more flexible than correlation analysis because all variables have been normalised – R can be interpreted as sqrt (R^2)) revealed several important and differential correlates (strictly speaking, predictors) of our measures of biodiversity. Larger, richer and more populous countries contain more diversity regardless of what measure is used (area versus EH, species, EHrange: $R^2 = 0.26^*$, 0.64, 0.87; PPP versus EH, species, EHrange; $R^2 = 0.35^{**}$, 0.60, 0.71; population versus EH, species, EHrange, $R^2 = 0.43$, 0.67, 0.69, all $n = 23$ and all P values are < 0.001, except $^*P < 0.05$ and $^{**}P < 0.01$). If we use as a benchmark the 95% confidence interval (CI) on values used in the Model I regressions, then Chile stewards less EH than predicted from its size, population or wealth, Costa Rica more EHrange than predicted from its area, El Salvador less EHrange than predicted from its population and wealth and Bolivia more species than predicted from its population and wealth. Governance shows a similar pattern overall: weakest for EH ($R^2 = 0.07$, $P = 0.25$), stronger for species richness ($R^2 = 0.17$, $P = 0.072$) and strongest and significant for EHrange ($R^2 = 0.42$, $P = 0.002$, all three with $n = 20$), such that countries that have higher governance scores steward more range-weighted EH. For governance, no country seems anomalous.

In the Americas, larger countries are richer, more populous and have better governance. In the multiple regressions, area, total wealth and population are always better predictors of biodiversity than is governance (partial $F_{1,17}$ for area and population always 10× that for governance, with associated P for governance never < 0.05). When population (or total wealth, with which it is tightly correlated) and area are considered together, contrasting patterns emerge: to predict EH, population is the more important term (partial $F_{1,19}$ for population $= 6.6$, $P = 0.02$, partial $F_{1,19}$ for area $= 0.11$, $P > 0.5$); for species richness, both are important predictors (partial $F_{1,19}$ for population $= 6.5$, $P = 0.02$, partial $F_{1,19}$ for area $= 3.8$, $P = 0.07$), while for EHrange, area is the strongest predictor, as expected (partial $F_{1,19}$ for area $= 36.4$, $P < 0.001$, partial $F_{1,19}$ for population $= 3.8$, $P = 0.06$). Neither human density nor per capita wealth (both from UNDP, 2003) present illuminating patterns with diversity ($P > 0.1$ for all comparisons save per capita wealth, which is correlated with EHrange at $P = 0.04$).

Expected loss of phylogenetic diversity

Eighty percent of the American carnivores' PD would remain safe if only the species considered as being of 'least concern' remained (54% of the total species). If the six 'data deficient' species also survived, then total PD remaining would increase to 82% (Fig. 2). These proportions are not significantly different from those expected if extinctions were to occur at random ($D_4 = 0.033$, $P > 0.5$). If species are removed from the tree from smallest to largest range, the pattern of PD loss is not significantly different from that expected if species were removed at random ($D_{83} = 0.082$, $P > 0.5$: Fig. 2). Interestingly, if the reverse is done and more widespread species are removed first, much more history is lost: the small-to-large and large-to-small curves are significantly different ($D_{83} = 0.170$; $P < 0.02$), with a drop of up to four standard deviations (Fig. 2). The large-to-small curve is also marginally significantly different form the random curve ($D_{83} = 0.141$; $0.1 > P > 0.05$).

Finally, there is no significant correlation between species' unique PD or age and either conservation status (Spearman rank correlation with $n = 77$, Rho $= -0.019$, $P = 0.87$) or range size (Spearman rank correlation with $n = 83$, Rho $= 0.143$, $P = 0.20$). The results are similar when *Mustela nigripes* is removed from the analysis (Spearman rank correlation with $n = 76$, Rho $= -0.04$, $P = 0.74$; $n = 82$, Rho $= 0.147$, $P = 0.18$, respectively).

DISCUSSION

Patterns of evolutionary heritage

This is the first analysis of the correlates of evolutionary heritage across a group of countries, linked here by geography, history and politics. The motivation for such a comparison is multifaceted: On the one hand, the comparison highlights how biodiversity is measured and managed primarily as a national concern. Endangered species law is rarely supranational in scope and reserve design and management is still primarily done at the national level, to its detriment (Rodrigues & Gaston, 2002*b*). On the other hand, because species do not respect national boundaries, this type of analysis documents the redundancy that exists across political entities – for instance, by documenting how much of the entire evolutionary history of American carnivores is found in countries such as the USA (EH) or Brazil (EHrange).

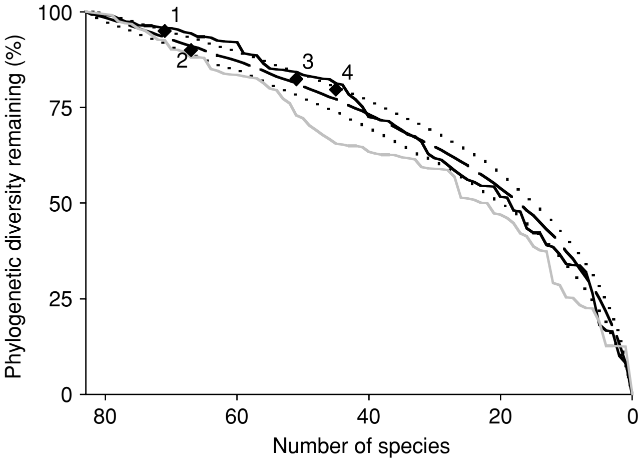

Fig. 2. The consequences of three extinction scenarios on the loss of American carnivores' phylogenetic diversity (PD). Dashed line shows expected PD loss when species are removed randomly (dotted lines indicate ± 1 SD); solid line shows PD loss when species are removed sequentially starting with the most geographically restricted and finishing with the most widespread; the grey line represents the opposite cull, where widespread species are removed first. Diamonds indicate PD remaining if more threatened species are removed first: 1. EX, EW and EN species removed; 2. EX, EW, EN and VU species removed; 3. EX, EW, EN, VU and NT species removed; 4. EX, EW, EN, VU, NT and DD species removed. Abbreviations are IUCN category codes.

A previous paper (Mooers *et al.*, 2005) ranked countries of the world by the total carnivore PD that they stewarded (EH), a measure that counts common PD multiple times. This approach was justified by the point made above: given that conservation in different countries is often uncoupled, the safest bet may be to assume the worst and ignore what other countries harbour, since they may cease to harbour it in the future. A more nuanced approach may be the range-weighted EH measure introduced here, where countries that steward more of a taxon's range are ranked higher. This reflects the differences between countries in their shares of the continent's evolutionary history (its heritage) and offers more EH to large countries and less to countries on the edge of species' ranges.

The four measures considered here (species richness, endemic, range-weighted and total EH) are complementary and none is necessarily more informative than the others (just as species richness and evenness are complementary in ecological contexts). Total EH recognises that two sites with the same number of species may harbour very different phylogenetic diversities. A comparison of total EH values with range-weighted EH values allows the distinction of countries that harbour species that together encompass a large amount of PD, but contain only a tiny portion of their range, from countries that include large portions of the range of those species. From the country perspective, total EH is probably more relevant; from an international conservation perspective, range-weighted EH may be more useful. The range-weighted EH comparisons illustrate how larger countries might bear extra responsibility for entire clades.

This last sort of calculus offers American carnivores good news, since the largest countries are also richer and politically more stable, suggesting that these countries should be more able to conserve their species. The range edge issue is less straightforward, as there is both evidence for, and anticipation that, peripheral populations may be critically important for species persistence (see, e.g. Channell & Lomolino, 2000*a*,*b*).

Our results should also be considered alongside recent work that suggests that prioritising sites based on species richness yields similar rankings as schemes that explicitly consider PD (Whiting *et al.*, 2000 for crayfish in Australia; Polasky *et al.*, 2001 for birds in North America; Rodrigues & Gaston, 2002*a* for birds in South Africa; see Mooers *et al.*, 2004 for a discussion). In the present study as well, species richness and measures of heritage are strongly positively correlated. However, our measures draw attention to countries such as Panama that steward more EH than expected simply from species richness; to Costa Rica, with surprisingly more range-weighted EH than expected from its size; and to Brazil and Canada, which steward large amounts of range-weighted EH. (Costa Rica also contains one seemingly old endemic species – *Bassaricyon lasius* – that is a member of a poorly investigated genus whose age is probably still overestimated.) Organisations interested in conserving carnivores should look to institutions in such countries for multi-species management. In fact, while our analysis was applied at the continental level and used countries as the units for comparison, this kind of analysis could be applied to prioritising sites based on species composition at any spatial scale.

Phylogenetic diversity, range size and risk

In American carnivores neither conservation status nor range size is correlated to the amount of species-unique PD. The relationship between the loss of evolutionary history and species loss matches that predicted by Nee & May (1997). Around 75% of American carnivores' PD would remain intact even if 50% of the species were gone, regardless of whether these species are marked by conservation status, small ranges or randomly. These results are consistent with data on carnivores worldwide (Purvis *et al.*, 2000*a*; Sechrest *et al.*, 2002) and in contrast with patterns for primates and other groups, where projected losses are significantly greater than random (e.g. Russell *et al.*, 1998; Purvis *et al.*, 2000*a*; Von Euler, 2001; Johnson, Delean & Balmford, 2002; Sechrest *et al.*, 2002). The contrasting results for carnivores and other groups draw attention to the need for more in-depth assessment of theory with actual phylogenies. Although balanced trees may show more redundancy than unbalanced ones (Nee & May, 1997) and recent work suggests that phylogenetic trees are often more unbalanced than those produced under reasonable models of diversification (see e.g. Mooers & Heard, 1997), more work is needed: extinction management has the highest pay off where extinction risks are negatively correlated with speciation rates (Heard & Mooers, 2000) but it is an open question how often this is the case (see e.g. Johnson *et al.*, 2002)

An unexpected finding is the greater initial rate of loss of PD when species are ranked from larger to smaller ranges than when they are ranked from smaller to larger ranges (Fig. 2). One possibility is that many younger species have not yet expanded their range (Webb & Gaston, 2000); although we found no general relationship between species-unique PD age and range size. Little is known about the inheritance of range size and the rate of its change. A related possibility is that widespread species are found in more unbalanced subtrees and, hence, with every new loss the probability of losing an entire branch of the subtree increases more rapidly. Although we can envision scenarios that might lead to such a pattern, it is important to note that the tree we are working with was shorn of all its non-American species: a full phylogenetic study of range size in the Carnivora is beyond the scope of this paper, but should be considered in the future. If it is true that wide ranging species embody more PD, this will inform the debate on the relative merits of investing in small-range species whose ecological importance is sometimes questionable (Ehrenfeld, 1988) and whose conservation may be most difficult (Mace & Lande, 1991; Purvis *et al.*, 2000*b*) and of investing in large-range, less threatened species, which may additionally offer more evolutionary potential (Rosenzweig, 1995). We may need to focus conservation efforts in protecting not only those species that are most likely to be pruned out of the tree of life, but also those whose loss would entail the largest loss, both from an ecological and an evolutionary perspective.

CONCLUSIONS

Here we propose and demonstrate a simple way to integrate phylogenetic information into prioritisation exercises. Furthermore, we introduce a simple measure of biodiversity (range-weighted Evolutionary Heritage) that explicitly encompasses three different levels of its hierarchical complexity (Humphries *et al.*, 1995; Gaston, 1998) in a single figure: the distribution across countries of populations within species and the distribution across phylogenies of species and higher taxa. The major constraint to this kind of approach is the number of well-resolved phylogenies available. Fortunately, this is likely to become less of a problem in the near future (Mace *et al.*, 2003). However, the net advantage of using this kind of approach for setting conservation priorities and designing networks of protected areas, instead of simply using species richness, still remains uncertain. What is clear is that PD solves the problem of how to select between areas with the same number of species but different taxonomic compositions (e.g. Mares, 1992; Gaston, 1996), since preserving more PD will often be preferred.

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APPENDIX 1 Species range size (extent of occurrence) of terrestrial American carnivores

Species	Range[1] (km^2)	Species	Range[1] (km^2)
Alopex lagopus[2]	13 000 000	*Mustela felipei*	125 050
Atelocynus microtis	6 627 692	*Mustela frenata*	12 303 849
Bassaricyon alleni	906 998	*Mustela nigripes*	0
Bassaricyon beddardi	440 309	*Mustela nivalis*[5]	41 500 000
Bassaricyon gabbii	676 882	*Mustela vison*[6]	30 000 000
Bassaricyon lasius	3834	*Nasua narica*	2 355 146
Bassaricyon pauli	1400	*Nasua nasua*	11 526 852
Bassariscus astutus	3 897 501	*Nasuella olivacea*	194 812
Bassariscus sumichrasti	621 421	*Oncifelis geoffroyi*	4 289 472
Canis latrans	17 016 568	*Oncifelis guigna*	189 098
Canis lupus[2]	49 000 000	*Orealilurus jacobita*	929 605
Cerdocyon thous	9 456 504	*Panthera onca*	16 355 791
Chrysocyon brachyurus	5 027 442	*Potos flavus*	12 732 552
Conepatus chinga	3 376 492	*Procyon cancrivorus*	13 328 746
Conepatus humboldtii	706 906	*Procyon insularis*	398
Conepatus leuconotus	217 012	*Procyon lotor*	11 644 502
Conepatus mesoleucus	2 281 454	*Procyon maynardi*	226
Conepatus semistriatus	1 733 062	*Procyon minor*	1416
Eira barbara	13 470 410	*Procyon pygmaeus*	490
Galictis cuja	4 578 366	*Pseudalopex culpaeus*	2 908 410
Galictis vittata	11 430 115	*Pseudalopex fulvipes*	8520
Gulo gulo[3]	21 500 000	*Pseudalopex griseus*	1 538 071
Herpailurus yaguaroundi	15 476 295	*Pseudalopex gymnocercus*	2 882 830
Leopardus pardalis	15 525 196	*Pseudalopex sechurae*	74 484
Leopardus tigrinus	11 503 204	*Pseudalopex vetulus*	1 483 344
Leopardus wiedii	13 899 314	*Pteronura brasiliensis*	10 391 610
Lontra canadensis	11 668 506	*Puma concolor*	23 791 151
Lontra felina	709 690	*Speothos venaticus*	10 718 496
Lontra longicaudis	14 484 373	*Spilogale gracilis*	3 814 267
Lontra provocax	801 196	*Spilogale putorius*	2 947 033
Lynchailurus braccatus	932 413	*Spilogale pygmaea*	94 060
Lynchailurus colocolo	179 676	*Taxidea taxus*	8 834 350
Lynchailurus pajeros	2 327 850	*Tremarctos ornatus*	1 036 583
Lyncodon patagonicus	1 078 053	*Urocyon cinereoargenteus*	8 623 227
Lynx canadensis	8 222 616	*Urocyon littoralis*	511
Lynx rufus	9 661 667	*Ursus americanus*	9 597 130
Martes americana	7 587 123	*Ursus arctos*[7]	21 000 000
Martes pennanti	3 465 935	*Ursus maritimus*[8]	22 500 000
Mephitis macroura	1 784 242	*Vulpes macrotis*	1 783 830
Mephitis mephitis	12 231 748	*Vulpes velox*	670 178
Mustela africana	4 390 374	*Vulpes vulpes*[2]	68 000 000
Mustela erminea[4]	38 000 000		

[1] Range based on polygons drawn in ArcView using published maps as the information source; area calculated using the 'Xtools' extension on an equal-area cylindrical projection.

[2] Ginsberg & Macdonald (1990).

[3] Pasitschniak-Arts & Larivière (1995).

[4] King (1983).

[5] King (2000).

[6] Larivière (1999).

[7] Pasitschniak-Arts (1993).

[8] IUCN/SSC PBSG (1998).

All others are from Patterson *et al*. (2003).

APPENDIX 2

Changes made to the Bininda-Emonds *et al.* (1999) supertree of the carnivores.

We assumed that the genus-level phylogenies could be approximated by a pure birth process (See Appendix by S. Nee in Mooers & Atkins, 2003) and first calculated total tree length (S_n) using the equation:

$$S_n = T(n-1)/(1/2 + 1/3 + \cdots 1/n) \qquad (1)$$

where T represents known genus age. We then created a new polytomous tree equal to this in total length. Branch lengths (x) for included species were estimated using the following equations:

$$x + y = T \text{ and } nx + y = S_n \qquad (2)$$

$$\text{to give, } x = (S_n - T)/(n-1) \qquad (3)$$

This method provided estimates of 'average species ages' that were less than the genus ages (see Fig. 1(a)).

For clades where some, but not all, species ages were previously known from the literature, estimated branch lengths for species in the taxon were corrected by the difference of the sum of the known branch lengths (k) and tree length (S_n), before being assigned to species of unknown age. The following equation was used to calculate corrected branch length (x_c):

$$X_c = (S - k)/(n - n_k) \qquad (4)$$

where n_k represents the number of species of known age in a taxon.

We were left with one further complication. Where the topology, but not species ages, was known in the original supertree, Bininda-Emonds *et al.* (1999) applied a pure birth model to estimate nodes. If taxa were fully resolved, we used this estimate for species ages. However, if T for a particular unresolved taxon was itself an estimated node in the original supertree, we did not use it. Instead, we moved down the tree to the first 'known' age, e.g. where the genus first split from its sister group. An expanded form of Eqn1 allowed us to calculate S' as the total tree length for a group under the pure birth model starting from when it originated (rather than when it first split: S. Nee, pers. comm.):

$$S' = (n \cdot T')/(1 + 1/2 + 1/3 + \cdots 1/n) \qquad (5)$$

where T' represents the age of origination of the genus. Given an estimate of S', T for a taxon of n species was estimated as:

$$nT + Y_1 = S' \text{ and } T + Y_1 = T' \qquad (6)$$

After obtaining an estimate for T, the estimated branch lengths were then calculated as before.

We note that our method of estimating unknown evolutionary history using the pure birth model iteratively as we work down a partially resolved genus may potentially give different values of b (instantaneous birth rate, where $b = (n - 1)/S$) for different subtaxa – e.g. the realized b in a resolved subtaxon may not be the same as the estimated b used to modify branch lengths elsewhere. However, we find this method to be acceptable because the b for the more inclusive taxon is just the average of locally variable birth rates across the phylogeny and this method retains as much of the original dating as possible.