

Selective extinction and rapid loss of evolutionary history in the bird fauna

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The extinction of species results in a permanent loss of evolutionary history. Recent theoretical studies show that this loss may be proportionally much smaller than the loss of species, but under some conditions can exceed it. Such conditions occur when the phylogenetic tree that describes the evolutionary relationships among species is highly imbalanced due to differences between lineages in past speciation and/or extinction rates. I used the taxonomy by C. G. Sibley and B. L. Monroe Jr to estimate the global loss of bird evolutionary history from historical and predicted extinctions, and to quantify the ensuing changes in balance of the bird phylogenetic tree. In the global bird fauna, evolutionary history is being lost at a high rate, similar to the rate of species extinction. The bird phylogenetic tree is highly imbalanced, and the imbalance is increased significantly by anthropogenic extinction. Historically, the elevated loss of bird evolutionary history has been fuelled mostly by phylogenetic non-randomness in the extinction of species, but the direct effect of tree imbalance is substantial and could dominate in the future.

Keywords: birds; biodiversity; evolutionary history; extinction; phylogenetic tree shape; taxonomic distinctness

1. INTRODUCTION

Human expansion is causing a mass extinction of geological magnitude. Extinction not only reduces the number of species, it also erodes the evolutionary heritage, the history that species represent. History is comprised in the underlying phylogenetic tree that describes the temporal sequence of lineage branching and diversification. Faith (1992) quantified evolutionary history (what he called 'phylogenetic diversity', PD) as the cumulative length of the branches connecting the root of the phylogenetic tree (the common ancestral lineage) to the discrete, evolving tips (species) (figure 1). A species without close relatives represents more unique evolutionary history than a species with close relatives. Thus the loss of evolutionary history caused by extinction depends on which species are lost.

Recent theoretical work has addressed the rate at which history is lost. Nee & May (1997) showed that in many cases, evolutionary history may be lost much more slowly than species go extinct. However, Heard & Mooers (2000) demonstrated realistic scenarios under which extinction can result in a more rapid loss of history than of species. Two conditions characterize such scenarios: (i) the phylogenetic tree is imbalanced as a result of substantial differences between lineages in past speciation rates, extinction rates, or both; and (ii) species extinction is phylogenetically non-random (selective) (McKinney 1997). In birds and mammals, species extinctions cause (and are predicted to cause) a greater-than-expected loss of higher taxa (genera, families, etc.) (Bennett & Owens 1997; Gaston & Blackburn 1997; Russell *et al.* 1998; Hughes 1999), and so are phylogenetically non-random. An increased loss of evolutionary history (Purvis *et al.* 2000) is therefore expected.

Here, I estimate the historical (since 1600) and future predicted, relative loss of evolutionary history (PD) in the

global bird fauna. I compare this loss to expectations under random extinction. Finally, I quantify the shape and imbalance of the bird phylogenetic tree, estimate the relative impact of imbalance on the loss of evolutionary history and demonstrate how extinctions are changing the shape of the phylogenetic tree.

2. MATERIAL AND METHODS

(a) *Phylogenetic and extinction data*

I estimated the structure of the evolutionary tree of the global avifauna from a standard taxonomic classification (Sibley & Monroe 1990, 1993). Using a taxonomy instead of a phylogeny has both advantages and disadvantages. Phylogenies are in continuous flux, and some taxa are better known than others. Because taxonomies have less detail, they change less frequently and are computationally easier to handle. On the other hand, the lack of detail means that phylogenetic patterns due to 'recent' evolution (species level) could be underestimated. The taxonomy is based on the Sibley & Ahlquist (1990) molecular phylogeny, includes 9702 species and summarizes the phylogenetic branching pattern at 13 taxonomic levels above the root node (subclass Neornithes). Each level corresponds to a particular range of genetic distinctness (in units of $\Delta T_{50}H$, a measure of nuclear DNA incompatibility) between divergent lineages. I used the following distinctness weights ($\Delta T_{50}H$, are given in brackets) (Sibley & Ahlquist 1990, p. 254): species (1.1), genus (3.35), tribe (5.75), subfamily (8), family (10), superfamily (12), parvorder (14.25), infraorder (16.75), suborder (19), order (21), superorder (23.25), parvclass (25.75), infraclass (28). As a basis for estimating branch lengths, I assumed that genetic distinctness was proportional to absolute time. This assumption is not without problems, as the rates of different 'molecular clocks' may depend on factors such as metabolic rate and generation time (Martin & Palumbi 1993; Ayala 1997), and Sibley & Ahlquist's (1990) hypotheses have been questioned by Mindell (1992) and others. However, several independent

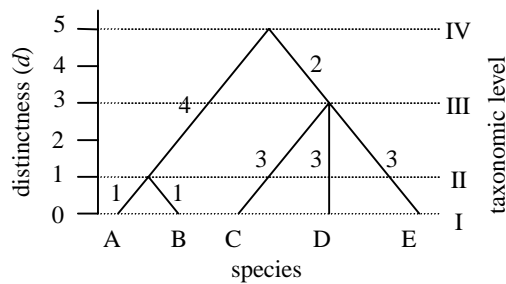


Figure 1. A hypothetical tree (clade), showing the branching pattern as it is summarized in a taxonomy with four levels (I–IV). The estimated evolutionary history (PD) contained in species A–E, equals the sum (= 17) of the lengths (labels) of individual branch segments, in units of distinctness.

analyses support the overall topology and temporal scaling of the Sibley & Ahlquist phylogeny (Mooers & Cotgreave 1994; Cooper & Penny 1997).

In compiling the list of extinct species, I adhered closely to Russell *et al.* (1998). Most species recorded as extinct since 1600 are included in the Sibley & Monroe (1990, 1993) taxonomy. One species, *Dromaius ater*, is mentioned in the text but not listed. I added this and a further 25 extinct species listed by the World Conservation Monitoring Centre (1992). These additional extinct species usually have close living relatives and could easily be accommodated in the taxonomic framework of Sibley & Monroe (1990, 1993). My total data set contained 105 extinct species (category EX) and 9623 extant species. Extant species were classified into four threat categories based on Collar *et al.* (1994): critically endangered (CR), endangered (EN), vulnerable (VU) and the remainder (not presently threatened or data-deficient species).

(b) Phylogenetic diversity loss

Under random extinction, all species are at equal risk. The expected loss of evolutionary history when one species is lost is therefore equal to the average length of terminal lineages in the clade. In a perfectly balanced tree, which has grown exponentially (figure 2a), terminal lineages represent a moderate fraction of the total PD. They represent much more PD in a tree that is imbalanced (figure 2b) or non-exponential with no recent nodes (figure 2c). If most nodes are recent, the terminal branches may contain only a small fraction of the total PD even while the number of species is high (figure 2d). These examples show how evolutionary history may be lost at a high relative rate in the absence of selectivity. Some degree of tree imbalance is obviously required for selectivity to have an additional effect on PD loss. For example, with the perfectly balanced tree in figure 2c, the extinction of up to three species from a single parent taxon is indistinguishable from the extinction of three random species, in terms of PD loss.

PD loss was determined by deleting entire species categories (EX, CR, EN and VU) from the taxonomy as of 1600, and calculating PD for the pruned trees. To estimate the PD loss that would be expected had extinction been random, the same numbers of species as before were deleted, but were chosen randomly rather than according to category. This was repeated 1000 times and the results averaged. To quantify the effect of imbalance, I replaced the estimated tree by a completely balanced but otherwise identical taxonomic tree (see §2(c)). Species were then deleted randomly as before, and PD

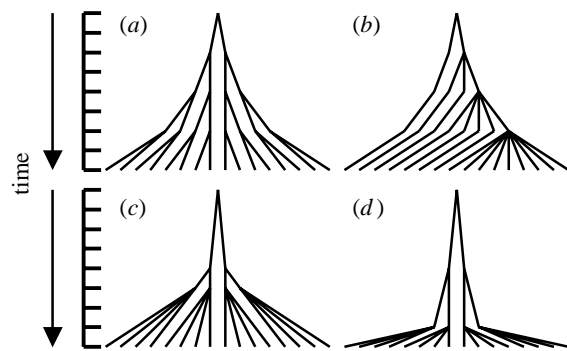


Figure 2. Examples illustrating the effects of tree shape on the loss of evolutionary history (PD). All clades span the same time-period, and comprise 16 species. (a) Balanced, exponential growth; (b) imbalanced ('comb-shaped'), exponential growth; (c, d) balanced, non-exponential growth (differing temporal distribution of nodes). Clades a–c contain identical amounts of PD (*d* contains less). For each clade, respectively, the loss of PD when four species (25%) go extinct, expressed as a fraction of species loss, is as follows (minimum loss, random extinction, maximum loss): (a) (0.53, 0.59, 0.93), (b) (0.53, 0.90, 1.60), (c) (0.80, 0.80, 0.87), (d) (0.44, 0.44, 0.78).

calculated for the pruned trees. This was repeated 100 times to obtain average values.

(c) Tree shape

I use 'tree shape' to include two properties: (i) balance, i.e. the more or less equitable distribution of daughter lineages among parallel parent lineages; and (ii) temporal distribution of nodes. To quantify the shape of the bird phylogenetic tree I used a recently developed measure (Clarke & Warwick 1998; Von Euler 1999) (here called TD). TD is the average taxonomic distinctness, counted over all possible pairs of species: $TD = 2 \sum_i \sum_{j < i} d_{ij} / (s(s-1))$, where s is the total number of species, and d_{ij} is the taxonomic distinctness between species i and species j . For example, in figure 1, species A and B have a distinctness of 1, the height of the first node connecting them, and species A and C have a distinctness of 5. For the full set of species in figure 1, TD equals 4. The expected value of TD is independent of the number of species under random sampling (Clarke & Warwick 1998), so random extinction of species would not change TD significantly.

Indices of imbalance, such as Colless' I_C , typically do not apply to trees with polytomies (three or more daughter lineages linked to the same node) (Mooers & Heard 1997). I introduce a new measure of imbalance (I_E), defined as $I_E = (TD_{\max} - TD_{\text{obs}}) / (TD_{\max} - TD_{\min})$, where TD_{\max} and TD_{\min} are the maximum and minimum values that TD could theoretically take, given the observed number of lineages at different taxonomic levels. $I_E = 0$ with a completely balanced tree (such as figure 2a), and $I_E = 1$ for a completely imbalanced tree (such as figure 2b). For any given observed tree I created a completely imbalanced reference tree by assigning each consecutive species to a new genus until the number of 'occupied' genera equalled the observed number minus one. Remaining species were lumped in the last genus. Genera were then assigned to tribes in a similar fashion, and so on at higher taxonomic levels. I created a completely balanced reference tree by assigning species to groups of as far as possible equal size, beginning with

the taxonomic level next to the root and proceeding with each successive level. Changes in I_E may be compared to a null model, obtained by replacing TD_{obs} in the expression above, with the TD-value expected under random extinction (which is a constant; Clarke & Warwick 1998).

Within the range of the present data, imbalance (I_E) was found to be tightly (negatively) correlated with shape (TD), so only TD was used for temporal analyses. I calculated TD for each year when at least one species was lost after 1600. Following Russell *et al.* (1998), I also calculated the expected number of extinct species at five future dates (2016, 2036, 2056, 2076 and 2096). This was done by randomly deleting, from within each threat category, the expected number of extinct species after z years (E_z , from equation 4 in Russell *et al.* (1998)):

$$E_z = S \left(1 - \left(1 - \frac{x}{100} \right)^{z/y} \right),$$

where S is the number of species in the threat category, and x is the percentage expected to go extinct in y years (Russell *et al.* 1998). I then calculated TD for the 'pruned' trees. This procedure was repeated 100 times to obtain means and standard deviations. For two points in time, I estimated the distribution of TD from 1000 simulated extinction episodes (from 1600–1996; and from 1996–2096), assuming random extinction. Limits of the 95% confidence interval for the expected TD were determined as the 2.5% and 97.5% quantiles of these distributions.

3. RESULTS

Between 1600 and the present, bird species and bird evolutionary history (PD) has been lost at similar rates (table 1). The relative rate of history loss will probably decrease in the future, but not below 80%. If extinctions had been random, history would be lost at 74–75% of the extinction rate, in good agreement with the estimated contribution of terminal taxa to total branch length in the phylogenetic tree. If extinctions had been random, and operating on a perfectly balanced tree (with the original numbers of species, genera, tribes, etc.), the history loss rate would be constant at 62%. This is practically identical to the theoretical minimum loss rate obtained by removing species from the actual tree according to the 'maximizing algorithm' (Nee & May 1997) (results not shown).

The present global bird taxonomic tree is highly imbalanced ($I_E = 0.253$), and tree shape has been and will be changed by extinction (figure 3). TD (essentially expressing balance) in the global avifauna has decreased significantly, but not monotonically, due to extinctions after 1600. Extinctions before 1880 account for the entire historical decrease in TD. There is no downward trend in TD from 1880 to 1996—the massive extinction of Fringillid species (tribe Drepanidini) in Hawaii has even produced short-term increases. Predictions of extinctions do not allow the trend in future TD to be described in similar detail, but it is clear that there is a significant, long-term trend of declining TD.

4. DISCUSSION

The relative loss of evolutionary history in the bird fauna has historically been very high, and will remain

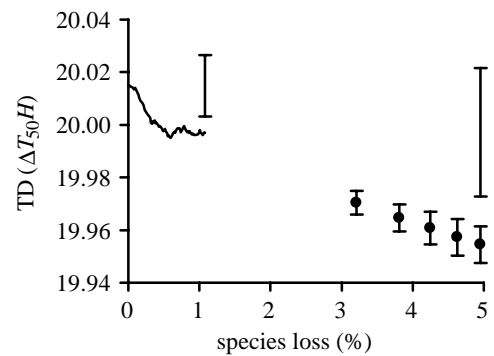


Figure 3. Change in global bird taxonomic distinctness (TD) versus species loss. Solid line, change in TD between 1600 and 1996. Dots, predicted TD in 2016, 2036, 2056, 2076 and 2096 (with standard deviations). Left vertical bar, 95% confidence interval for TD in 1996, given random extinction from 1600 to 1996. Right vertical bar, 95% confidence interval for TD in 2096, given random extinction from 1996 to 2096.

high in the foreseeable future. The predicted loss of history is a minimum estimate because the taxonomy used does not account for evolutionary branching patterns within the broadly delimited and taxon-rich species level; all congeneric species are considered to represent the same amount of evolutionary history. Extinction non-randomness at this level probably increases history loss beyond the results presented. Grouping data-deficient species with non-threatened species could also have resulted in conservative estimates of history loss.

Island species account for about 90% of historical extinctions (between 1600 and the present), while the corresponding percentage for predicted extinctions is less than 60% (Collar *et al.* 1994; Manne *et al.* 1999). Although the historical record is imperfect and probably biased towards island species, this difference indicates that threats to continental species are now accumulating faster. Figure 3 shows that for extinct (predominantly island) species, taxonomically highly distinct species were lost first, mostly before 1900, followed by species with less taxonomic distinctness. The long-term trend of declining TD suggests that continental species will follow the same pattern.

Global 'extinction management' (choosing which taxa to sacrifice) (Heard & Mooers 2000) appears to have limited potential benefit in the case of birds and could theoretically only reduce the future history loss rate to 62% of the extinction rate. This result, however, should be compared to the worst-case scenario. In the light of work by Heard & Mooers (2000), and assuming that taxonomic (I_E) and phylogenetic (I_C) imbalance measures are interchangeable, the highly imbalanced bird phylogeny implies that the future loss of evolutionary history in the bird fauna could potentially be much more rapid than the loss of species (> 100%).

Proactive extinction management focused on minimizing loss of evolutionary history at the global scale is probably unrealistic, because of the many non-scientific conservation factors that override strictly evolutionary considerations (Nee & May 1997). 'Evolutionary' management at local scales may be less controversial, since the extinction of individual species is usually not a premeditated consequence of such actions. Spatial TD trends among bird communities (species assemblages within

Table 1. *Estimated and expected loss (%) of evolutionary history (PD) from the avifauna as of 1600*

(Estimated PD loss is based on loss of identified, extinct and threatened species (categories). Expected PD loss is based on loss of corresponding numbers of random species. Numbers in parentheses, PD loss expressed as a fraction of species loss. EX, extinct species; CR, critically endangered species; EN, endangered species; VU, vulnerable species.)

categories	number of species	species loss (%)	PD loss (%)		
			estimated	expected (random extinction)	expected with balanced tree (random extinction)
EX	105	1.08	1.04 (0.97)	0.80 (0.74)	0.67 (0.62)
EX+CR	261	2.68	2.34 (0.87)	1.99 (0.74)	1.66 (0.62)
EX+CR+EN	486	5.00	4.16 (0.83)	3.72 (0.74)	3.09 (0.62)
EX+CR+EN+VU	1171	12.04	9.93 (0.82)	9.01 (0.75)	7.46 (0.62)

landscape units of size 25–100 km²) in Europe and North America, are surprisingly consistent with the demonstrated temporal TD trend for the global bird fauna. Although few globally threatened species occur in these regions, community TD is lower where land use is intensive (Von Euler 1999; F. von Euler, unpublished data). However, a decrease in local TD is often not associated with lower local species richness, indicating that taxonomically highly distinct species (in the context of the local community) are being replaced by less-distinct species. This tangible taxonomic homogenization corresponds to a widely observed biotic homogenization (McKinney & Lockwood 1999). Parallel local- and global-scale trends in TD invite the hypothesis that taxonomically distinct species are particularly vulnerable to human activities, rather than intrinsically susceptible to background extinction. At any rate, the consistency with which species contributing the most to TD are threatened by global extinction and local extirpation make such species, and their habitats, prime candidates for conservation.

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