

# Indonesia's threatened birds: over 500 million years of evolutionary heritage at risk

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## Abstract

Using published IUCN red-lists for the threatened bird species of Indonesia (Stattersfield & Capper, 2000), we document that the species at risk in Indonesia are not a taxonomically random sample, consistent with patterns seen at the global scale (Purvis *et al.*, 2000). This implies that a greater than random proportion of Indonesia's and the world's (through the loss of endemics) phylogenetic diversity (PD) is at risk (Von Euler, 2001). Using cytochrome b (Johns & Avise, 1998) and a distance-based taxonomy, we attempt to quantify this projected loss of PD in millions of years and conclude with a brief discussion of the conservation implications for Indonesia, and of the use of 'evolutionary heritage' as a measure for conservation at the geopolitical level.

## INTRODUCTION

When a species becomes extinct, the evolutionary history it embodied is lost with it (Nee & May, 1997). The more distantly related a species is to its nearest relatives, the more history is lost. If one important metric of conservation value is evolutionary distinctness (Wilson, 1992), then measuring the loss of evolutionary history (also called phylogenetic diversity or PD) through anthropogenic-mediated extinction is an important component of conservation biology (Faith, 1992; Crozier, 1997; see also Morowitz, 1991).

Theoretical work (Vane-Wright, Humphries & Williams, 1991; Nee & May, 1997; see also Vazquez & Gittleman, 1998; Heard & Mooers, 2000) has quantified the expected pattern of evolutionary loss, and several groups have projected the worldwide amount of loss we might expect under reasonable scenarios of extinction for several taxonomic groups (McKinney, 1998; Russell *et al.*, 1998; Purvis *et al.*, 2000; Von Euler, 2001, Sechrest *et al.*, 2002). However, conservation decisions are normally made at much smaller scales, and here we present the first analysis of projected loss of evolutionary history at the scale of a geopolitical unit, using the birds of Indonesia as a test case. Two-thirds of the world's bird species are threatened by habitat loss and degradation (Beissinger, 2000) and deforestation is the major threat in Indonesia; at current rates, most of Indonesia's species-rich lowland forests will have disappeared completely by the year 2010 (Jepson *et al.*, 2001).

Using published IUCN red-lists for the threatened bird species of Indonesia (Stattersfield & Capper, 2000), we investigate whether a significantly higher proportion of Indonesia's, and the world's (through the loss of endemics) evolutionary history is at risk than if extinction risk were random with respect to taxonomic position (Von Euler, 2001). The amount of PD a particular country (or other geopolitical unit) stewards might be considered that country's 'evolutionary heritage'.

## METHODS

### Data collection

The Indonesian species list is from Andrew (1992), augmented with data from Stattersfield & Capper (2000), Coates, Bishop & Gardner (1997), MacKinnon & Phillipps (1993) and Beehler, Pratt & Zimmerman (1986). Taxonomy is based on Sibley & Monroe (1990). Conservation status data are from Stattersfield & Capper (2000). Where taxonomy data differed between authors, Stattersfield & Capper (2000) was preferred (e.g. species versus subspecies rank: see 'speciesnotes' at [www.sfu.ca/~amooers/evolheritage](http://www.sfu.ca/~amooers/evolheritage) for taxonomic decisions). Breeding and non-breeding species are included in the analysis. We considered Indonesia to include East Timor and Irian Jaya (Papua) and its satellites, but not Sarawak, Sabah or Brunei. Exclusion of these areas did not affect the species list since there are no species endemic to Sarawak, Sabah or Brunei.

We classified each species two ways, as follows. (1) endemic status: found only in Indonesia (endemic) versus found in at least one other country (non endemic);

(2) threat status: not threatened (S), near threatened (nt), vulnerable (VU), endangered (EN), critically endangered (CR). Species lacking information on threat status (data-deficient: DD) were excluded from further analyses. According to Purvis *et al.* (2000), most data-deficient species are likely to have a high extinction risk, making our approach conservative. We then constructed three data sets by classifying our species following Purvis *et al.* (2000), producing sets of increasing conservation concern. The most inclusive data set (NTplus) considered as 'threatened' those species listed as nt, VU, EN and CR (Table 1). The other two data sets were designated VUplus (and so lumping nt species with the not threatened category) and ENplus (considering those species listed as nt and VU as not threatened).

## Analysis

### Patterns of risk

Each of our three data sets corresponds to an extinction regime. We compared the observed taxonomic patterns of threat with patterns created by randomly sampling species repeatedly 2000 times across the taxonomy, using a simple macro written in Microsoft Excel (available from the authors). Each extinction regime specified a different proportion of threatened species to be sampled (Table 1). We evaluated patterns of loss at the level of country (Indonesia) by comparing observed numbers of all higher taxa at risk with simulated values created by allocating the same proportion of species at risk randomly to the species list. We evaluated patterns of loss to the world by repeating this but recording only the number of endemic taxa affected. Actual patterns from Indonesia were considered remarkable if they were larger than the most extreme 5% of the simulations.

**Table 1.** Projected loss of avian evolutionary history to Indonesia and worldwide

Region <sup>c</sup>	Risk <sup>d</sup>	Taxa at risk <sup>a</sup>				Projected loss (MY) <sup>b</sup>	
		Species	Genera	Families	Orders	ERM	Comb
Indonesia	EN+	44	5***	0	0	78	85
	VU+	114	23***	1*	0	228	263
	NT+	306	56***	5***	1**	674	751
World	EN+	36	3**	0	0	62	66
	VU+	75	8***	0	0	134	146
	NT+	158	11***	0	0	270	288

<sup>a</sup>Asterisks denote significant deviations from taxonomically random patterns of risk: \* $P < 0.1$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.0005$ .

<sup>b</sup>Millions of years (MY) of evolutionary history at risk. ERM assumes a log-linear relationship between genus size and age and random (Equal Rates Markov) diversification; Comb assumes every genus is 4.54 MY old and has the shape in Fig. 1(b). See text for further details.

<sup>c</sup>Species and higher taxa at risk of being lost to Indonesia, or, being wholly endemic to Indonesia, at risk of being lost worldwide.

<sup>d</sup>Nested sets of risk: 'NT+' includes all near threatened, vulnerable, endangered, or critically endangered; 'VU+' excludes nt species; 'EN+' includes only endangered and critically endangered species. Data Deficient species are excluded. See text for more detail.

### Evolution history at risk

Given that no full tree of the birds yet exists, we drew on Sibley & Monroe's (1990) genetic distance-based taxonomy, a compilation of cyt. b data from Johns & Avise (1998; G. Johns, pers. comm.), and the standard 2% per million years 01 divergence for avian cyt. b (Moore & DeFilippis, 1997; Johns & Avise, 1998 and references therein) to make rough but very conservative calculations of the amount of Indonesia's evolutionary history at risk. Preliminary analyses confirmed that estimates using the entire data set were statistically indistinguishable from those made using only genera with representatives in Indonesia (results not shown). We therefore used the entire data set and calculated the evolutionary history as follows:

*Species.* We took the *minimum* genetic distance between sister species for 51 genera from 33 families and 11 orders and calculated a taxonomically corrected (Harvey & Mace, 1982) average as a conservative estimate of a species' age ( $T_s$ ).

*Whole genera.* Using data from 88 genera, 42 families and 12 orders, we calculated genus ages using a Model 1 regression of *maximum* intrageneric distance on (Log) number of species sampled for cyt. b. The maximum distance is most likely to incorporate the first split in the genus (see Fig. 1). We then assumed that genus trees could be approximated by a pure birth process. The appendix by Sean Nee explicates how this assumption leads to the expression for their PD:

$$PD = \frac{T_g(N-1)}{\sum_{i=2}^N \frac{1}{i}}$$

with  $T_g$  being the age of a genus with  $N$  species (see Fig. 1a). Random extinction in an expanding genus will lead to fewer deep branches than this model, meaning this expression will overestimate total PD. However, if there has been an adaptive radiation in the genus (much speciation early in its history), branches will be longer, making this expression conservative. It is also conservative if the genus has been at a stable size for a long time (see Nee & May, 1997 for a discussion of this last model).

As an alternative, more ignorant approach, we also (1) took a taxonomically weighted average genus age  $T'_g$  and (2) assumed the genus form presented in Fig. 1(b), leading to  $PD = 2*T'_g + (N-2)*T_s$ . We report values from both methods.

*Entire Families.* Using data from 36 families in 12 orders, we calculated a taxonomically corrected average *maximum intergeneric* cyt. b distance and used this to calculate the amount of added history lost if an entire family goes extinct. Because the families involved were very small (<3 spp.) this could be done without recourse to a pure birth model; this model is likely to be invalid at

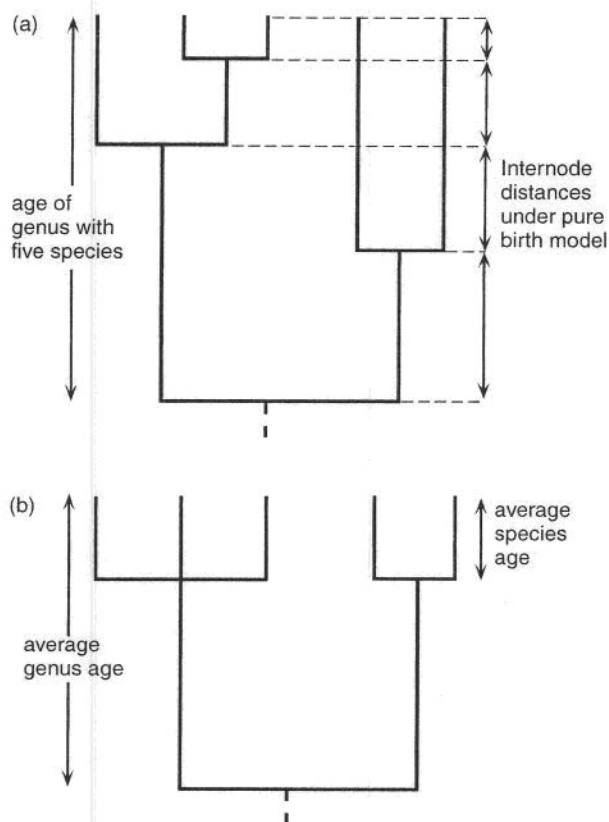
deeper levels in the avian tree (Von Euler, 2001). We simply added a single branch of the requisite length to the PD estimated in the genera within that family.

*Higher taxa.* We treated PD for higher taxa on a case-by-case basis (see results).

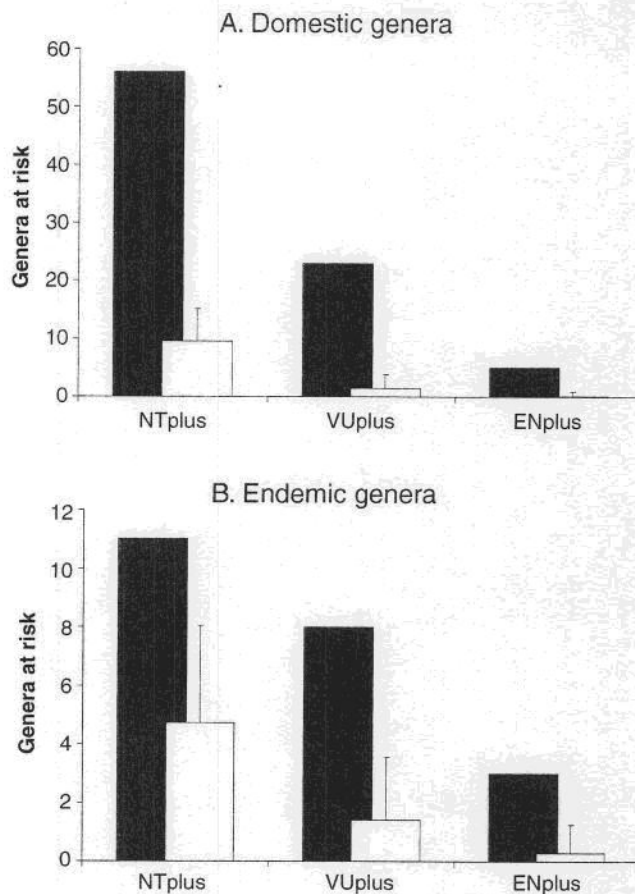
## RESULTS

### Patterns of risk

Indonesia is home to fully 15% of the world's bird species, and harbours a similar proportion of species at risk as the rest of the world (~19% NTplus species; see [www.redlist.org](http://www.redlist.org), table 4a). The phylogenetic patterns within Indonesia mirror birds on the global scale (Fig. 2). Corresponding *P*-values from the raw simulation data and the observed numbers of birds in the different risk



**Fig. 1.** Evolutionary history (EH) is the sum of the lengths of all branches (in time) a tree. If the actual tree is unknown, EH can be estimated in several ways. (a) Given the number of species in a genus, one can use an empirical relationship to estimate its age, and then use the mean internode distances under random diversification to calculate the total EH. Note that the actual relationship among species (topology) will not change this sum. (b) Given only the average species age and average genus age, one can assume a simplified tree with two nodes and use this to estimate EH. Again, the sizes of the two subclades (here 3,2; 4,1 is also possible) will not change the total EH the genus embodies.



**Fig. 2.** Observed number of complete genera lost under the three extinction regimes (black bars, see text for extinction regimes) and the average number of complete genera lost after 2000 simulations under a random extinction regime of equal magnitude (white bars), for all Indonesian species (A) and for endemic species (B). Error bars show two standard deviations of the simulation distribution (figures after Purvis *et al.*, 2000).

categories and higher taxa are summarized in Table 1: risk is phylogenetically clumped in Indonesia, as it is at the level of the planet (Purvis *et al.*, 2000; Von Euler, 2001). Combined with the fact that endemic taxa are more likely to be red-listed (*G*-test on 1 d.f.,  $P < 0.0001$ ), the proportion of the world's evolutionary history at risk in Indonesia is much greater than any random expectation.

### Threatened evolutionary heritage

The weighted average minimum sister-species divergence was 3.2% (=1.6 MY). Model 1 regression suggested a strong relationship between  $\ln(\text{number of species sampled})$  and genus age ( $F_{1,86} = 27.4^{***}$ ,  $R^2_{\text{adj}} = 23.4\%$ ), but also revealed differences between the two major groups (Passeriformes vs. non-Passeriformes, Partial  $F_{1,85} = 8.3^{**}$ ). We therefore decided to calculate genus ages for the two groups separately. The estimate of the overall taxonomically weighted genus age was 9.1% (4.55 MY, or roughly a genus of size 3 based on the regressions). The



taxonomically weighted average family age was 18% (9 MY), after removing a single extreme outlier in the Piciformes; 18% is the level of divergence where cyt. b divergence ceases to be linear with DNA-DNA hybridization distances and so perhaps with time (Moore & DeFilippis, 1997).

Using our two tree shapes and these estimates leads to projections of Indonesia's (and the world's) threatened evolutionary heritage given in Table 1. We note that the sole higher taxon entirely at risk in Indonesia is the infraclass Ratitae, represented by the three 'at risk' Cassowary species (2 VU, 1 nt). We conservatively set the age of this taxon at the KT boundary (64 million years; Fedducia, 1995), though some molecular estimates are nearly twice this (see references in Cooper & Fortey, 1998).

## DISCUSSION

Much has been written about 'the agony of choice' (Vane-Wright *et al.*, 1991). With only limited time and resources for conserving the world's biodiversity, choices have to be made regarding which species should be the focus of conservation action. Conserving future biodiversity, i.e. species or areas with future evolutionary potential, only adds to the agony of limited choice.

As our results show, a greater number of higher taxa are at risk in Indonesia than would be expected by chance alone. This observation supports work done at the global scale (Purvis *et al.*, 2000), and has several implications for conservation in Indonesia.

Although our analysis shows many more taxa are at risk than if risk were randomly allocated to species, this potential loss is confined to lower taxonomic levels for endemics, meaning that global loss of PD through Indonesian species will be limited. This is good news. Furthermore, 48 of the 56 domestically threatened genera (nt and higher, 86%) only have one species in Indonesia. Other things being equal, this means that the probability of losing the genus from Indonesia may be quite high, but the relative loss to the world may not be as great. However, the reason that Indonesia only harbours one species is that these 56 genera are generally small worldwide (mode and median size = 1, max size = 12; see also Purvis *et al.*, 2000). If the species is at risk in Indonesia, it may also be at risk elsewhere; given that many of these genera are monotypic, the amount of world PD at risk goes up. In addition, previous studies on primates and carnivores have already shown that Sundaland and Wallacea are hotspots not only for biodiversity, but also for PD (Sechrest *et al.*, 2002). If this is also the case for birds, Indonesia's (threatened) evolutionary heritage may encompass a relatively large proportion of the world's avian PD.

Several factors in this analysis might lead to conservative estimates of the amount of PD lost in MY. DD species are excluded from the analysis, although according to Purvis *et al.* (2000), most data-deficient species are likely to have a high extinction risk. Furthermore, the cyt. b estimates of taxonomic age seem,

on the face of it, to be conservative themselves (e.g. species age = 1.6 MY and family age = 9 MY). Research on the origins of passerine birds shows that several genera, some also present in Indonesia, might be far older than previously believed (Ericson *et al.*, 2002). Revising the age of these genera would increase Indonesia's evolutionary heritage. Finally, our analyses assume that the higher taxa at risk are of average age: previous work at the world scale implies that they may indeed be older than the average taxon (Gaston & Blackburn, 1997). It may be also that endangered species are older than average (e.g. represent relictual lineages); this seems to be the case for Australian marsupials (Johnson, Delean & Balmford, 2002). Further work is needed to address these questions.

Even using our conservative estimates, if current rates of habitat destruction continue and the red list is a good predictor of extinction, Indonesia stands to lose up to 751 million years of evolutionary history, of which up to 288 millions years will be lost to the world forever. These values should also be evaluated with reference to global avian PD and to total evolutionary heritage across different countries, and the next step will be to produce these estimates, probably with the help of 'supertree' techniques (see Bininda-Emonds, Gittleman & Steel, 2002). Regardless, the numbers for this single country are large, on the order of magnitude of projected losses to the primates and carnivores worldwide (Purvis *et al.*, 2000). We call for inventories of threatened evolutionary heritage for many countries and for other well-known taxonomic groups (and particularly for plants), in the hopes that this metric may bolster conservation activities.

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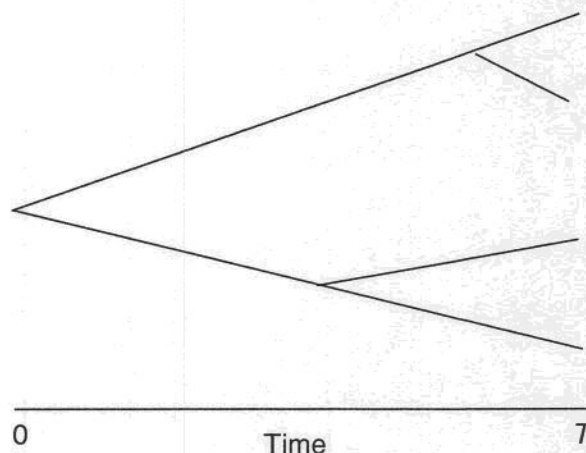
## APPENDIX 1. TOTAL EVOLUTIONARY HISTORY UNDER THE PURE BIRTH PROCESS

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This Appendix derives a simple formula for the expected amount of evolutionary history in a phylogenetic tree that has grown according to a pure birth process. It may be useful for theoretical work or as a benchmark against which real trees can be compared.

I present an explicit derivation for the case of a tree with four species: the generalization then follows immediately.



The tree begins with two lineages at time zero. For the sake of simplicity, I assume that a new species originates at exactly time  $T$ , so the tree actually consists of five species. The time from the root of the tree to the first (second, third) split is exponentially distributed with parameter  $2b$  ( $3b$ ,  $4b$ ), where  $b$  is the birth rate. If these times are taken as the means of the exponential distributions, then we have

$$\text{total evolutionary history} = 2^* \frac{1}{2b} + 3^* \frac{1}{3b} + 4^* \frac{1}{4b} = \frac{3}{b}. \quad (\text{A.1})$$

So, in general,

$$\text{total evolutionary history} = \frac{n-1}{b}, \quad (\text{A.2})$$

where  $n$  is the number of species in the phylogeny (not counting the invisible 'fifth' species which was introduced solely for convenience).

$$\text{Now, } \frac{1}{2b} + \frac{1}{3b} + \frac{1}{4b} = T. \quad (\text{A.3})$$

So, rearranging, we have

$$\text{total evolutionary history} = \frac{T(n-1)}{\left(\frac{1}{2} + \frac{1}{3} + \dots + \frac{1}{n}\right)}. \quad (\text{A.4})$$

An approximation to this expression, which may be useful in some contexts, is:

$$\frac{T(n-1)}{\log_e(n) + C - 1} \quad (\text{A.5})$$

where  $C$  is Euler's constant, 0.57722.

Further expressions can be derived using the expected value for  $n$ ,  $E(n)$ , under a pure birth process:

$$E(n) = 2e^{bT}. \quad (\text{A.6})$$