Revisiting the impacts of non-random extinction on the tree-of-life

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The tree-of-life represents the diversity of living organisms. Species extinction and the concomitant loss of branches from the tree-of-life is therefore a major conservation concern. There is increasing evidence indicating that extinction is phylogenetically non-random, such that if one species is vulnerable to extinction so too are its close relatives. However, the impact of non-random extinctions on the tree-of-life has been a matter of recent debate. Here, we combine simulations with empirical data on extinction risk in mammals. We demonstrate that phylogenetically clustered extinction leads to a disproportionate loss of branches from the tree-of-life, but that the loss of their summed lengths is indistinguishable from random extinction. We argue that under a speciational model of evolution, the number of branches lost might be of equal or greater consequences than the loss of summed branch lengths. We therefore suggest that the impact of non-random extinction on the tree-of-life may have been underestimated.

1. Introduction

Each time a species goes extinct, a branch of the tree-of-life is pruned. Because the branches of the tree-of-life are expected to capture ‘feature diversity’ [1,2] important for ecosystem function and stability [1,3], this pruning is a major conservation concern. Early simulation models, assuming random extinctions, indicated that 80 per cent of the tree-of-life would remain intact, even under a scenario of very high (95%) species loss [4], but were based on an unrealistic model of diversification [5]. In addition, there is increasing evidence that extinction events are non-random [6–13], and thus that the loss of phylogenetic diversity (PD) might be greater than previously thought [6]. To date, empirical evidence has been mixed, with greater than random losses reported in some analyses [6,8], but not in others [14].

In a recent study, Parhar & Mooers [15] demonstrated that non-random extinction alone was insufficient to explain greater than random losses of PD. However, non-random extinction might target specific locations on the tree-of-life (e.g. internal versus terminal branches; [14]), affecting tree structure more than suggested by the loss of summed branch lengths. Here, we suggest that the number of branches lost might be greater under a model of non-random extinction, even when the loss of summed branch lengths is no different from random extinction (figure 1). We test our hypothesis using simulations and the observed distribution of extinction risks in three well-studied mammal clades: Primates, Carnivora and Artiodactyla. The sum of branch lengths may best capture feature diversity when assuming a gradual model of trait diversification, in which trait variance increases in proportion with time. However, we argue that under a speciational model of evolutionary change, in which trait evolution occurs in bursts at speciation, the number of branches (or nodes, which represent speciation events on a phylogenetic tree) might be of equal, or greater, importance than their summed lengths.
of phylogenetic signal as defined by genetic signal where 0 equates to no signal, and 1 matches to a death tree (under our different branch length models. We generated an index the relationships between non-random extinction and PD loss.

2. Material and methods
We focus our analysis on mammals because they are a well-studied taxonomic group for which we have a comprehensive phylogeny, and they have been the subjects of several extinction risk studies in the past [16–19]. Specifically, we analyse three well-resolved clades: Primates, Carnivora and Artiodactyla. We quantified extinction risk using the global IUCN Red List of Threatened Species (http://www.iucnredlist.org). First, we transformed Red List categories into extinction probabilities, $p(\text{ext})$, following the study of Mooers et al. [20] and assuming IUCN designations projected to 50 years. Second, we estimated the phylogenetic signal in $p(\text{ext})$, using Pagel’s $\lambda$ [21]. Third, for each clade, we calculated the expected loss of PD for the observed branch lengths and the equivalent loss of diversity assuming that all branches had equal weight (approx. a speciational model of evolution), following the approach of Witting & Loeschcke [22]. We then used simulations (1000 replicates) to compare observed losses to expectations from the same distribution of $p(\text{ext})$, but randomly assigned to species at the tips of the phylogeny.

Finally, we used an additional set of 100 simulations to explore the relationships between non-random extinction and PD loss under our different branch length models. We generated an index of extinction risk by evolving traits along the branches of a birth–death tree ($b = 0.2$, $d = 0$, size $n = 240$), assuming various levels of phylogenetic conservatism as defined by $\lambda$, a measure of phylogenetic signal where 0 equates to no signal, and 1 matches to a Brownian motion model of evolution. We increased $\lambda$ from 0.1 to 1.0 in 0.1 intervals. Based on the simulated trait values, a constant fraction of species (here the top 25% as this broadly matches the proportion of threatened mammal species in the IUCN Red List) were then assigned high risk of extinction ($p(\text{ext}) = 0.75$ and 0.95). We then compare expected losses to a null model of random extinction, as mentioned earlier. All simulations were conducted in the R statistical package [23] using the GEIGER [24] and APE [25] R-libraries.

3. Results
Phylogenetic signal in extinction risk varied across clades (Carnivora, $\lambda = 0.32$; Artiodactyla, $\lambda = 0.57$; Primates, $\lambda = 0.84$). Predicted loss of diversity assuming a gradual trait evolution was never greater than the random expectation, and in Artiodactyla the loss was marginally lower than expected (Carnivora, $p = 0.819$; Primates, $p = 0.943$; Artiodactyla, $p = 0.035$; figure 2a). However, we generally lose a greater diversity under speciational evolution than predicted from the null, although only marginally so for Artiodactyla (Primates, $p < 0.001$; Carnivora, $p = 0.047$; Artiodactyla, $p = 0.08$).

In our tree and trait simulations, we found that loss of diversity under gradual evolution was not significantly greater than predicted from random extinctions, although absolute losses tended to increase with $\lambda$ (figure 2b,c). The diversity loss under a scenario of speciational evolution also increased with $\lambda$, but was significantly greater than random expectations when $\lambda$ was high (figure 2b,c).

4. Discussion
We demonstrate that more branches from the tree-of-life are pruned when extinction is phylogenetically non-random, but that the loss of their summed lengths is no greater than expected by chance. Furthermore, in some cases (e.g. Artiodactyla), non-random extinction can reduce the loss of branch lengths, presumably because threatened species tend to cluster within young, species-rich clades, while the number of branches being pruned may still be greater than random expectations. We suggest that number of branches, rather than branch lengths, might be important if trait variation accumulates in bursts at speciation events (represented by the nodes in the phylogenetic tree), as would be expected under a model of punctuated equilibrium [26]. If evolution follows a speciational model (and this may be the case for body size in mammals [27]), short branches separating rapidly diverging lineages might capture as much feature diversity as longer branches in more slowly diversifying clades, although extinctions in the early diversification of a clade may uncouple the link between branching events and feature diversity deeper in the phylogeny.

Our simulations reveal that, under a model of non-random extinction, the loss of PD generally increases with the strength of phylogenetic signal, but not significantly so when only considering branch lengths (see also [15]). The significant deviation of diversity loss under speciational evolution from the null can be explained by the lower variance in number of pruned branches with random extinction, indicating that random extinctions of equivalent intensity prune more or less the same number of branches. By contrast, there is large variance in the loss of summed branch lengths under random extinction, such that observed losses typically overlap to a greater extent with the null distribution.

Over the last decade, there has been increasing emphasis on the conservation of PD [28–30]. Traditionally, PD has been quantified by summing the branch lengths connecting a set of taxa [1], although a variety of metrics are available to quantify species evolutionary distinctiveness [31]. Implicit within this approach is an assumption that evolutionary distance translates more or less directly into ecological distance [12], for example, as might be modelled under a Brownian motion process. However, at the same time, there has been a growing awareness that the evolutionary trajectory of many traits depart from assumptions of Brownian motion and that models of evolution may differ between traits and clades [32–35]. To date, there has been little consideration...
of alternative evolutionary models in the conservation phylogenetics literature (but see [36]). We suggest, therefore, that the impact of non-random extinction on the tree-of-life may have been underestimated.

References