

Fossils, phylogenies, and the challenge of preserving evolutionary history in the face of anthropogenic extinctions

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Anthropogenic impacts are endangering many long-lived species and lineages, possibly leading to a disproportionate loss of existing evolutionary history (EH) in the future. However, surprisingly little is known about the loss of EH during major extinctions in the geological past, and thus we do not know whether human impacts are pruning the tree of life in a manner that is unique in the history of life. A major impediment to comparing the loss of EH during past and current extinctions is the conceptual difference in how ages are estimated from paleontological data versus molecular phylogenies. In the former case the age of a taxon is its entire stratigraphic range, regardless of how many daughter taxa it may have produced; for the latter it is the time to the most recent common ancestor shared with another extant taxon. To explore this issue, we use simulations to understand how the loss of EH is manifested in the two data types. We also present empirical analyses of the marine bivalve clade Pectinidae (scallops) during a major Plio–Pleistocene extinction in California that involved a preferential loss of younger species. Overall, our results show that the conceptual difference in how ages are estimated from the stratigraphic record versus molecular phylogenies does not preclude comparisons of age selectivities of past and present extinctions. Such comparisons not only provide fundamental insights into the nature of the extinction process but should also help improve evolutionarily informed models of conservation prioritization.

extinction | phylogenetic diversity | phylogeny | fossil record | bivalves

Extinguishment of any species or higher taxon invariably results in some loss of existing evolutionary history (EH), but a major concern about extinctions driven by anthropogenic impacts is that they may remove a disproportionately large amount of such history (1–3). In groups as varied as birds, mammals, and plants, studies have shown that extinctions of species currently on the International Union for the Conservation of Nature Red List of Threatened Species would lead to a much larger loss of EH than expected under randomly distributed extinction of the same number of species (4–6). This disproportionate loss of EH stems from phylogenetic clustering of anthropogenic extinctions (1) with a bias toward the loss of species-poor and geologically old taxa (7–9). Such predictions, along with the realization that not all species currently threatened by human activities can be saved, have motivated the development of various strategies for minimizing the loss of EH (8, 10, 11). These approaches primarily target lineages that are old but species poor in an attempt to protect large amounts of EH and, presumably, also unique traits and functions that may affect future evolutionary potential (10, 12).

Although the disproportionate loss of EH caused by anthropogenic extinctions is increasingly evident, surprisingly little is known about the loss of EH during extinctions in the geological past. The rich archive of extinctions preserved in the fossil record has been the main source of insights about the nature of the extinction process (13–15), and it provides the baseline against which the magnitude of the current crisis has been measured

(16). Comparisons of ecological and biogeographic components of past and present extinctions also hold great potential for predicting the nature of future losses (17, 18). Although paleontological studies have tested for age-related bias in extinction vulnerability (19–22), such analyses have focused primarily on background extinctions rather than on selectivity across major extinction events (23). However, without a better understanding of patterns of loss of EH during major pulsed extinctions in the geological past, we cannot answer the fundamental question of whether we, as a species, are pruning the tree of life in a unique manner. Such an understanding requires developing a comparative framework that includes both paleontological and neontological data.

A major impediment to comparing anthropogenic impacts on EH with those during past extinctions is that the methods used in each case differ. Analyses of future losses caused by anthropogenic extinctions primarily have used tree-based measures of EH (24, but see ref. 25) that are not easily applicable to extinct taxa for which large phylogenies are still lacking. More importantly, even when phylogenies of extinct taxa are available, the differences in the nature of paleontological and molecular phylogenies complicate direct comparisons. In paleontological phylogenies, a species maintains its identity over time as long as its traits remain relatively constant. This property allows “budding cladogenesis” in which a parent species remains unaffected while giving rise to a daughter (Fig. 1) (26, 27). In contrast, molecular (or cladistic) phylogenies allow only “bifurcating cladogenesis” in which the parent lineage is replaced by two daughters (or more daughters

Significance

Anthropogenic impacts are endangering many species, potentially leading to a disproportionate loss of evolutionary history (EH) in the future. However, surprisingly little is known about the loss of EH during extinctions in the geological past, and thus we do not know whether anthropogenic extinctions are pruning the tree of life in a manner that is unique in Earth's history. Comparisons of EH loss during past and ongoing extinctions is difficult because of conceptual differences in how ages are estimated from paleontological data versus molecular phylogenies. We used simulations and empirical analyses to show that the differences between the two data types do not preclude such comparisons, which are essential for improving evolutionarily informed models of conservation prioritization.

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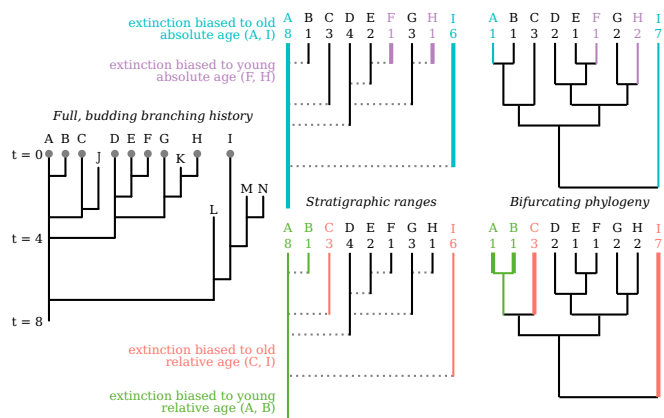


Fig. 1. A simple tree showing how the full branching history of a clade can be reduced to either stratigraphic ranges or a bifurcating phylogeny. A clade undergoes speciation (assumed here to be budding, with survival of the parent) and extinction, with nine lineages (A–I) surviving to the focal time ($t = 0$). The stratigraphic range and absolute age of each surviving species are determined by the time of its first appearance in the fossil record, without reference to species relationships. The bifurcating phylogeny is determined by the divergence times of surviving species relative to one another, without regard for their original times of speciation. Colors illustrate the four scenarios of age-dependent extinction at the focal time. Note that the oldest species differ—in both identity and age—between the absolute and relative age definitions, as do the youngest species. Thus, stratigraphic and phylogenetic diversity are differently affected by the loss of species.

in the case of multifurcation), even for speciation events that were, in fact, budding (Fig. 1) (26). Thus, the discrepancy between the stratigraphic and cladistic representations depends on the frequency of budding versus bifurcating speciation, which remains unknown at present despite well-documented cases of budding cladogenesis in the fossil record (26–28).

Whether cladogenesis is viewed as budding or bifurcating has important consequences for assessing what the “age” of a species is and consequently for analyses of age selectivities as well as other aspects of evolutionary dynamics (29). For budding cladogenesis, the age of a taxon is its entire stratigraphic range (hereafter absolute age) regardless of daughter taxa it may have produced, whereas for bifurcating cladogenesis the age of the taxon is the time to the most recent common ancestor shared with another extant taxon (hereafter relative age) (Fig. 1) (26, 29). Comparing paleontological insights about evolutionary dynamics with those inferred from molecular phylogenies requires us to understand better the consequences of this difference for empirical analyses. For the question addressed here, the age definition used will affect empirical tests of age selectivity during extinctions. It also will affect simulation tests, such as when choosing taxa for removal during an age-biased extinction event (Fig. 1). We emphasize, however, that these two age definitions are simply different conceptualizations of a given biological history. Extinction selectivity is expected to be based on traits (e.g., geographic range, body size) rather than on age per se, so any signal of age-dependent extinction more likely reflects its relationship to other traits.

Our goal here is to understand how the loss of EH is manifested in budding versus bifurcating phylogenies. We start with simulations to illustrate how a given extinction event erodes EH on each of these types of phylogenies. We then explore this issue empirically using a phylogeny of living and extinct marine scallops (Pectinidae) that experienced elevated extinction during the Plio–Pleistocene transition (30).

Measuring the Loss of Evolutionary History

Although many metrics are available to quantify loss of EH (12, 31), the one most commonly used to estimate potential losses of EH caused by anthropogenic extinctions is phylogenetic diversity (PD), defined as the sum of branch lengths on a phylogenetic

tree (24). Because of its widespread application (1, 4, 32–34), we focus on PD here.

As discussed above, although reconstructed bifurcating phylogenies estimate the relative divergence time of two lineages, stratigraphic range data approximate the absolute duration of each taxon (35) independent of other taxa derived from it. When branches are pruned off a clade, the loss of EH may look quite different from a paleontological perspective (Fig. 1). We define stratigraphic diversity (SD), analogously to PD, as the sum of the stratigraphic ranges of taxa within a clade. Loss of PD and SD may scale differently with extinction intensity and selectivity in the two types of trees (Fig. 1).

One window into how extinction erodes EH comes from its age selectivity. Paleontological studies have long tested for age bias in extinctions, starting with the work of Simpson (36) and the much-cited conclusion of Van Valen (19) that the extinction risk of a taxon is independent of its age. Subsequent studies at different taxonomic levels and across various extinction intensities instead have found evidence for preferential extinctions of either older (21) or younger taxa (20). However, virtually all these analyses focused on background rather than on pulsed extinctions. For anthropogenic extinctions, disproportionately large losses of PD predicted for many groups (4–6, 9) suggest the preferential endangerment of older and species-poor lineages, although a recent study of mammals failed to find such age bias (37).

Simulations

Loss of EH. We designed a set of simulations to compare the loss of EH under the same extinction event using paleontological and molecular phylogenies, considering different effects of species ages on extinction risk. Our central question is whether excessive loss of older (or younger) taxa as measured on one phylogeny type is detectable using the other.

We simulated phylogenies under a constant-rates birth–death process with budding speciation, retaining only species that survived to the time of observation. By assuming that all speciation events are budding, we maximize the difference between absolute and relative ages and hence the discrepancy between SD and PD. Our analyses are based on these histories and do not incorporate uncertainty in estimating phylogeny or stratigraphic range. Two alternative simulation programs were used, SimTreeSDD (Figs. 2 and 3) (38) and paleotree (39) (Figs. S1–S3 and *SI Materials and Methods*). We then reduced the outcome of the branching process to either stratigraphic ranges, which define the “absolute age” of each species, or to a bifurcating phylogeny on which the terminal branch length is the “relative age” of each species (Fig. 1 and *SI Materials and Methods*).

Trees were simulated for two pairs of speciation and extinction rates, capturing relatively low and high extinction [$\epsilon = \mu/\lambda = 0.2$ or 0.8 , where λ is the origination rate and μ the extinction rate (40)] while holding the net diversification rate ($r = \lambda - \mu$) constant. We subjected each simulated tree to five different forms of age bias in extinction risk (Fig. 1 and *SI Materials and Methods*): extinction risk independent of both absolute age and relative age, extinction risk increasing linearly with absolute or relative age, or extinction risk decreasing linearly with absolute or relative age. We considered four different extinction intensities (m) for each age structure of extinction, removing between 10% and 80% of species. Note the distinction between the background extinction rate of the clade (μ , used to simulate the trees) and the intensity of the specific extinction event (m). We are interested in age bias associated with the latter.

For each simulation outcome, we computed the loss of EH measured by PD (24) as the sum of all of the branch lengths (terminal and internal) removed from the phylogeny. We also computed the corresponding loss of EH measured by the paleontological metric SD, the loss of which is defined here as the sum of all absolute ages removed. Letting the subscript “observed” denote EH remaining after the extinction event in any particular outcome and “random” denote EH remaining when age does not influence extinction risk, we quantify the excess loss

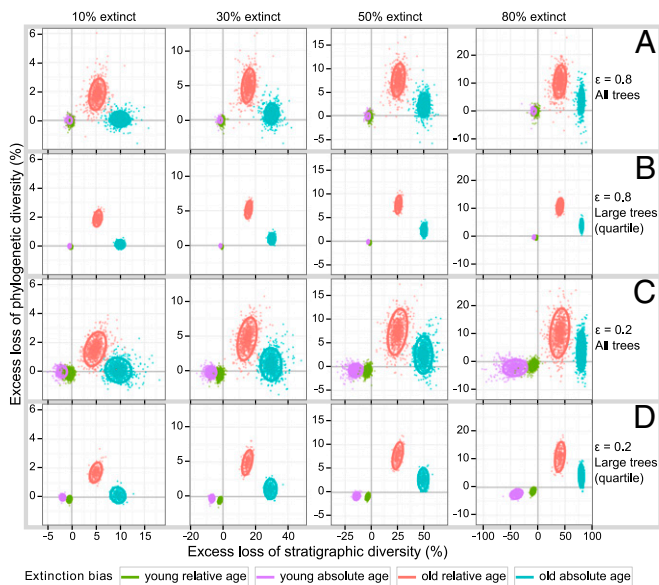


Fig. 2. PD_{excess} based on bifurcating phylogenies versus the corresponding SD_{excess} for the same extinction event under four age-biased extinction regimes. Individual colors depict extinction probability increasing linearly with absolute age (stratigraphic range) or with relative age (phylogenetic tip length) or decreasing linearly with absolute age or with relative age. Excess-over-random losses (see main text) are shown for four extinction intensities ($m = 10, 30, 50,$ or 80%) and trees simulated with two pairs of speciation (λ) and extinction (μ) rates ($\epsilon = \mu/\lambda = 0.2$ or 0.8). (A) One thousand trees with $\epsilon = 0.8$. (B) Largest quartile of trees (250) with $\epsilon = 0.8$. (C) One thousand trees with $\epsilon = 0.2$. (D) Largest quartile of trees (250) with $\epsilon = 0.2$.

of EH with $EH_{\text{excess}} = (EH_{\text{random}} - EH_{\text{observed}})/EH_{\text{random}}$ (41), where EH may be either PD or SD. This excess quantity is positive when more EH is lost than expected by chance and negative when less EH is lost.

When loss of species during an extinction event is independent of both absolute and relative age, we find that SD loss is greater than PD loss (Fig. S1). This effect is driven by the extinction of older species. When species of large absolute age go extinct, they take their entire EH with them, whereas when species of large relative age go extinct, part of their shared history (internal branches) may remain on the phylogeny (e.g., species A in Fig. 1).

When an extinction event preferentially removes taxa with older absolute ages, SD_{excess} values are strongly positive because less SD remains than under random extinction, but PD_{excess} values are smaller or even negative (Fig. 2, blue). The discordance between SD_{excess} and PD_{excess} decreases with increasing tree size and extinction intensity. When extinction most affects taxa with older relative ages, both SD_{excess} and PD_{excess} are generally positive (Fig. 2, red). These results together show that when an extinction event preferentially affects older species—by either definition—paleontological studies are more likely to detect the effect than are neontological studies.

When extinction preferentially removes species of younger absolute or relative age, both SD_{excess} and PD_{excess} values are often negative although many are near zero (Fig. 2, green and purple). We see the largest effect of young-biased extinction and the greatest consequent loss of EH when μ is low but m is high.

These age-biased extinction results are determined by three factors. First, SD loss is generally greater than PD loss under any extinction regime, as discussed above (Fig. S1). Second, the age distribution of an exponentially growing clade is dominated by the continual production of younger species (42). Thus, even when risk during an extinction event is independent of age, more extinctions are of younger species simply because younger species are more numerous. This inherent feature of random extinction overshadows much of the signal of young-biased extinction while

highlighting the signal of old-biased extinction. Third, the frequencies of absolute and relative ages within a clade differ. Because the birth of a new species reduces the relative but not absolute age of the parent lineage, the relative age distribution is even more strongly biased toward the young. Consequently, there is less scope for extinctions biased by relative age, reducing the size of PD_{excess} relative to SD_{excess} .

Taxon Age Selectivity. We used the same simulations to test whether age bias during extinction events is manifested statistically in phylogenetic and stratigraphic data. Following Finnegan et al. (20), we used a binomial logistic regression model to test for the effect of age on the survival of a species. The odds ratio of a logistic regression conveniently summarizes the results: the log-odds are expected to be negative when extinction preferentially removes older taxa and positive when younger taxa suffer greater extinction. Our central question is again whether an extinction event biased by absolute age can be recognized by studies using relative age, and similarly whether absolute age studies can detect relative age-biased extinction.

When extinction risk is independent of age, no statistically significant age bias is detected for either definition of age (Fig. 3 I and J). We do see a slight influence of extinction intensity (m) on effect size, however, with positive log-odds (in the direction of young-biased extinction) for low m and negative log-odds for high m . We attribute this difference to the age distributions, discussed above. With an overrepresentation of young species, especially as measured by relative age, old species are less likely to be captured in any one extinction episode.

When extinction risk is biased to older absolute or relative age, log-odds almost always are negative. If absolute age drives the risk (Fig. 3 A and B), the signal is strongest when measured by absolute age, as expected, but also generally is significant when

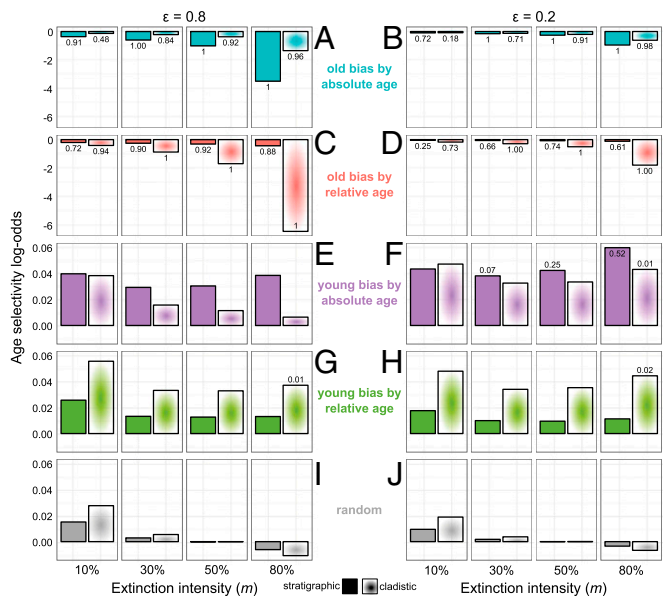


Fig. 3. Taxon age selectivity under four age-biased extinction regimes plus a null model of random, age-independent extinction. (A–J) Bars represent the natural logarithm of the odds ratio (log-odds) based on a binomial logistic regression model. Log-odds are expected to be negative when extinction preferentially removes older taxa and positive when younger taxa are more likely to go extinct. Solid colors represent log-odds calculated based on absolute ages from stratigraphic ranges; shaded colors represent log-odds calculated using relative ages from bifurcating phylogenies. Shown are log-odds under four extinction intensities ($m = 10, 30, 50,$ or 80%) for trees simulated with two pairs of speciation (λ) and extinction (μ) rates ($\epsilon = \mu/\lambda = 0.2$ or 0.8). Numbers above or below bars represent the proportions of trees that show a statistically significant effect of age on species survivorship.

measured by relative age except for low extinction intensity. If relative age drives the risk (Fig. 3 C and D), the age bias of extinction is detected less reliably when measured by absolute age. We ascribe this difference to the smaller pool of species of old relative age, compared with the absolute age distribution. As in the previous case, the results for the two types of age match best when both m and ε are high, and the mismatch is worst for very low extinction intensities, especially when ε is low (Fig. 3).

In cases where we preferentially remove younger taxa, using either relative or absolute ages, the log-odds are always positive, as expected (Fig. 3 E–H). The effect size is larger for absolute age when extinction risk is based on absolute age, and likewise for relative age. The results rarely are statistically significant, however. We again attribute this difference in effect size to the overrepresentation of young species in a clade: young-biased extinction then has less effect on the age distributions of victims and survivors.

Plio–Pleistocene Extinctions

Paleontological analyses of age-related bias in extinction vulnerability (19–22) have focused on background extinctions rather than on selectivity across major extinction events (23), whereas analyses of anthropogenic extinctions are focused on a single, unfolding event. As a first step toward reducing this information gap, we tested for age-related bias in the Plio–Pleistocene extinction of marine scallops (family Pectinidae) in California.

The Late Cenozoic fossil record of California preserves a rich assemblage of shallow marine molluscan species, which suffered a major extinction during the Plio–Pleistocene transition (30), a time of elevated extinctions of mollusks in other regions of the world as well (43–45). The bivalve family Pectinidae suffered particularly heavy losses in California during this extinction event with little subsequent evolutionary rebound (46). The systematics of the Neogene pectinids of California also is well studied, making this an ideal group for phylogenetic analyses of extinction selectivity (47–49). To perform these extinction analyses, we used Bayesian methods to infer a time-calibrated phylogeny of living and Neogene pectinid species based on molecular and fossil data, generating a posterior set of 1,000 fully resolved trees (SI Materials and Methods). Of the 50 species of Plio–Pleistocene scallops known from California, 25 were lost during this extinction event (Fig. 4). Despite this 50% reduction in species richness, the loss of PD in this case was significantly less than expected across the 1,000 posterior trees (Fig. S4), suggesting a preferential loss of younger species during this extinction. Comparisons of relative ages produce a qualitatively similar result, with the age selectivity log-odds being larger than under age-independent extinctions, although this finding is not significant across all trees (Fig. S5). The loss of SD using absolute ages shows that SD_{excess} is negative, but the confidence interval (CI) is broad and overlaps with zero (mean $SD_{\text{excess}} = -0.11$, 95% CI = -0.38 to 0.08 based on 1,000 iterations). The log-odds using absolute ages are also positive (0.02), but, again, are not significant ($P = 0.75$). Taken together, although all metrics indicate a preferential loss of younger scallop species during this extinction event, only PD loss using relative ages shows a significant signal.

We also tested for selectivity in absolute ages of other bivalve species during the Plio–Pleistocene extinction using stratigraphic ranges from Hall (30) because a phylogeny for nonpectinid species involved in this event is not currently available. In contrast to the scallops, species across all families of bivalves show an overall negative log-odds (-0.03 , $n = 286$), as do Veneridae, the most species-rich family in this fauna (-0.05 , $n = 33$), but neither effect is significant ($P = 0.16$ overall and $P = 0.52$ for Veneridae). Thus, the bias toward a loss of younger species seen in the pectinids is not reflected in other families, suggesting that clades can differ in their patterns of species age selectivity during the same extinction event.

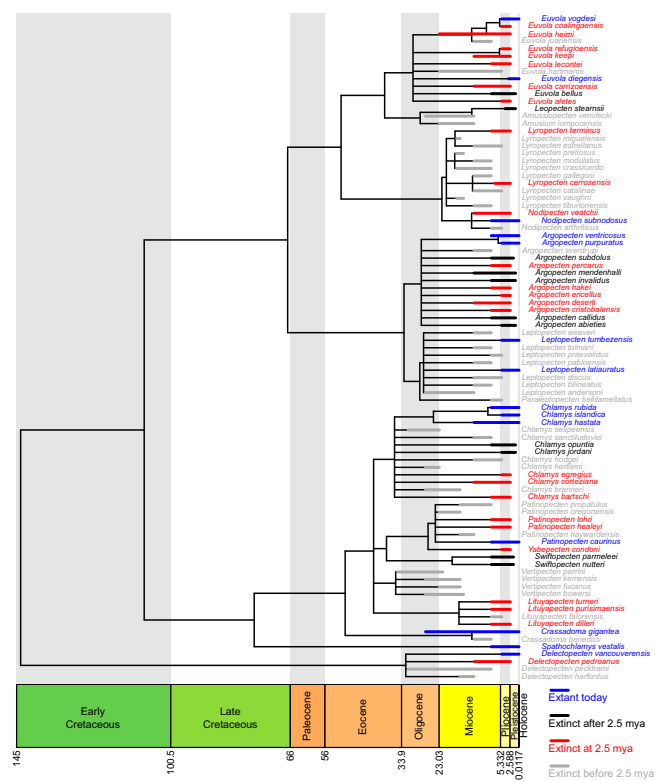


Fig. 4. Stratigraphic ranges (thick lines) and phylogenetic relationships (thin lines) of 89 Late Oligocene to Recent species of scallops (Pectinidae) known from California. The tree shown forms the backbone for generating 1,000 fully resolved Bayesian posterior trees used to analyze extinctions occurring at the Plio–Pleistocene transition, ~2.5 Mya, which removed 25 of the 50 species present at that time. Species names and stratigraphic ranges are colored according to times of extinction relative to the Plio–Pleistocene transition.

Discussion

Comparing the loss of EH during major extinction events using paleontological versus molecular phylogenies can be difficult because of the conceptual difference in how ages are estimated. However, our simulations and empirical analyses show that estimated EH losses during major extinction events tend to be qualitatively similar despite this difference. The simulations also show that extinction generally removes EH more rapidly in paleontological data than in molecular phylogenies, where the loss is buffered by shared history. Preferential extinction of older taxa leads to large losses of EH in both cases, but the magnitudes differ among the two data types with molecular phylogenies again providing the more conservative estimates. This asymmetry when comparing phylogeny-based EH losses with those from the fossil record indicates that analyses of major extinction events in the geologic past can provide a meaningful baseline for comparing patterns of endangerment in ongoing extinctions. The absence of excess loss of EH observed during past extinction events would indicate that there is little natural analog for the preferential endangerment of older lineages currently seen from anthropogenic impacts. Furthermore, our results suggest that such comparisons can be based on either the sum of the ages or the age distributions themselves, although conceptually the latter may be preferable.

When extinctions preferentially remove younger species, the signal is muted in paleontological data and more so in phylogenies. We ascribe this lower power to the age distributions of species at any point in time being skewed toward the younger ages. Therefore, these results caution that type II errors are most likely to arise when a bias toward younger ages in species-level extinctions is suspected. Such a bias should be easier to detect at

higher taxonomic levels where the age distributions contain a larger proportion of older taxa. Available empirical evidence is generally consistent with this view, with at least one previous study finding a significant bias toward younger genera during background extinctions (20). Our empirical results show that species loss of pectinids during a major extinction event in California involved preferential loss of younger taxa; however, the effect is significant only using PD, indicating that the age bias in this case is more closely tied to relative than to absolute age. Because these extinct species had geographic ranges significantly smaller than those of the survivors (50), we hypothesize that the ranges of parent species were reduced by giving rise to daughters; speciation made the parent taxa younger and range-restricted (e.g., refs. 51 and 52), and thus more extinction prone.

In addressing our central question of whether we are currently trimming the tree of life in a manner different from in the past, our results are encouraging in that they identify ways of making comparisons across extinction events using paleontological data and molecular phylogenies. As discussed above, virtually all paleontological analyses of the age selectivity of extinctions have focused on background extinctions, integrating over a substantial history of individual clades (20, 21, 23), but the best analogs of the current extinction crisis are the more severe extinction pulses of the past, either regional or global (16). Furthermore, the incomplete nature of the fossil record and the difficulties involved in identifying fossil species have led previous analyses to focus on higher taxa rather than species (but see ref. 21). Because the age distributions of higher taxa are different from those of species, it is difficult to compare patterns of age selectivity across taxonomic levels. Thus, existing studies do not readily allow direct comparisons of past losses of EH with those predicted for anthropogenic extinctions. Although temporal durations of species in the fossil record are more difficult to estimate reliably than those of higher taxa (23), a number of paleontological studies have used fossil species successfully to test important evolutionary and biogeographic hypotheses (21, 51–56) as well as various aspects of the extinction process (57–59). With the increasing availability of large, taxonomically standardized paleontological databases, analyses of age selectivity of extinctions at the species level, such as the one undertaken here, are now feasible, especially on regional scales. In addition, molecular sequence data for living species continue to accumulate in GenBank and other repositories, and novel approaches for integrating fossil species into molecular phylogenies are now available (60, 61), making it feasible to undertake age-selectivity analyses of past and present extinctions using a common currency of relative ages estimated from phylogenies.

Although much remains to be learned about how extinctions, past and present, remove EH, the long-term evolutionary consequences of age-biased extinctions are even less understood. The use of PD in conservation is based primarily on a proposed correlation between PD and trait diversity (24, 62, 63). Under this model, excessive loss of PD would result in a disproportionate loss of traits and consequently in a greater effect on future evolutionary trajectories. Species in geologically old and species-poor lineages are considered to be particularly important from this perspective because they alone represent millions of years of trait evolution, and considerable effort is being put into identifying such taxa, generally known as “Evolutionarily Distinct and Globally Endangered” (EDGE) species (8, 11, 64). However, empirical analyses using molecular phylogenies of living species often fail to find a strong correlation between PD and trait diversity (33, 65). In

addition, paleontological data show that many geologically old lineages tend to be morphologically unremarkable (66). Finally, some species-poor, long-lived lineages are likely to fit the “dead clade walking” model of Jablonski (67, 68), in which formerly diverse groups are bottlenecked by an extinction event without subsequent recovery. These patterns suggest that we need to better understand how age-biased extinctions, especially those that preferentially remove older taxa, affect future evolutionary trajectories. Given the problems of estimating extinction rates from molecular phylogenies of extant species (69, 70) and the uncertainties associated with ancestral state reconstructions (71), data from the fossil record are critical for addressing this issue. However, although much of our insight into the extinction process comes from paleontological studies, the issues of age bias and trait loss during major extinction events and their effects on subsequent recoveries still remain poorly explored.

Our finding that the signal of preferential extinctions of young species can be hard to detect through the approaches commonly used to study age-biased extinctions also has important implications. As discussed above, evolutionary conservation studies have focused on the endangerment of older lineages, but many young species can have unique traits and important functional and ecological roles. Adaptive radiations, in particular, often contain many unique young species, and examples abound of such species being negatively affected by anthropogenic impacts (e.g., refs 72–75). A focus on the loss of EH alone is likely to underestimate the erosion of trait and functional diversity resulting from such extinctions in young radiations, especially for smaller clades. Such losses of young species also would suggest that anthropogenic impacts have the potential to suppress origination rates in some clades, although the effect remains to be quantified. The same lack of power also can plague analyses of past extinctions of species, as seen for the pectinids here. Thus, although a bias toward younger genera of marine invertebrates during background extinction has been documented, establishing whether a similar bias exists for species, especially during major extinctions, may require alternative analytical approaches.

Conclusions

Although there is little doubt that anthropogenic impacts are endangering many long-lived species and lineages, potentially leading to their extinction and thus a disproportionate loss of existing EH, whether this bias is likely to be a unique evolutionary legacy of our species remains unknown. The rich archive of past extinctions preserved in the fossil record holds the key to answering this question, and our results show that the conceptual difference in how ages are estimated from the stratigraphic record versus phylogenies does not preclude comparisons of age selectivities of past and present extinctions. Such comparisons can provide fundamental understanding about the nature of the extinction process and also can help us develop more evolutionarily informed models of conservation prioritization.

Materials and Methods

Further details about simulations, data, and analytical methods are provided in *SI Materials and Methods*.

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Supporting Information

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SI Materials and Methods

Simulations. Phylogenies were simulated under a constant-rates birth–death process (1) using the program SimTreeSDD (2). The program was updated to return not only the resulting phylogeny of extant species but also the time of speciation for each species. This new version of SimTreeSDD is now available (3).

For each of the simulated trees, we quantified the change in EH for four extinction intensities (m) corresponding to the loss of 10, 30, 50, or 80% of the tips on the tree. Trees were subjected to five extinction regimes—old bias based on absolute or relative age, young bias based on absolute or relative age, or random with respect to age. For each extinction regime and rate, 100 replicates were performed. Before and after each extinction event, we computed the PD of each tree, given as the sum of all branch lengths of the phylogeny (4), and the corresponding SD, given as the sum of absolute ages of species on the tree. We then compared each of the old- or young-biased extinction regimes against a null model represented by the random regime (5–8) using PD_{excess} and SD_{excess} (9).

To explore the effect of age on species survivorship, we fit a binomial logistic regression model with either absolute or relative age as the explanatory variable and survivorship during the simulated extinction event as the binary response variable. The regression coefficient is the natural logarithm (log-odds) of the odds ratio $p/(1-p)$, where p is the probability of surviving through the event (10). We fit the model separately for each of the five extinction regimes and four extinction intensities described above.

We also repeated our analyses on trees generated by the R (11) package, paleotree (12). We simulated morphotaxa and their relationships in the fossil record under the budding cladogenesis model (13), based on the same speciation and extinction parameters and minimum number of extant taxa outlined above. Similarly, we generated 1,000 sets of absolute ages each for the high and low amounts of background extinction (ϵ). These sets then were converted into time-scaled phylogenies for analyses. SimTreeSDD trees are used in the main text (Figs. 2 and 3), and results using paleotree trees are presented here as Figs. S2 and S3.

Plio–Pleistocene Extinctions in California. To reconstruct the phylogeny of extant and extinct species of California Pectinidae, we first assembled from GenBank a molecular dataset comprising six markers—the mitochondrial 12S rRNA, 16S rRNA, and cytochrome c oxidase subunit I, as well as nuclear 18S rRNA, 28S rRNA, and histone H3—covering 76 living pectinid species worldwide and three outgroup species from the Propeamussiidae (14). Extinct species were added to the dataset as topological

constraints based on their genus identities. More specific constraints were implemented based on refs. 15–19.

Fossil node calibrations were carried out based on the first appearance of pectinid genera obtained from an existing global marine bivalve database (20, 21). For nodes for which fossil data were available, we used as prior a truncated normal distribution with the mean set to the earliest date (stage midpoint) among sister clades and an SD of 2.5 Ma. Calibration was carried out at the genus level and above for taxa with molecular data, so a species' time of bifurcation with its sister on the phylogeny can occur after its first appearance in the fossil record. The root of the tree, representing the origin of Pectinidae was designated a truncated normal prior with a mean of 251 Mya and SD of 5 Ma. Based on stratigraphic ranges of pectinid species compiled from primary literature (18, 22–26), the origin of each extinct species was assigned a truncated normal prior with a mean based on first appearance and an SD of 1 Ma, with its termination represented by noncontemporaneous tip dates based on the species' last appearance and a uniform distribution of ± 0.25 Ma (27).

Based on the molecular data, topological constraints, and fossil calibrations, we used an uncorrelated lognormal relaxed clock implemented in BEAST 1.8 (28–30) to infer the pectinid phylogeny comprising 79 living (global) and 75 extinct (California) species. Four separate Markov chain Monte Carlo runs of 60 million generations were carried out with a sampling interval of 1,000. The first 10 million of all posterior trees were discarded upon convergence that was checked in Tracer 1.5 (31), and the remaining trees were subsampled to every 200,000 iterations to generate 1,000 fully resolved trees.

Species not present in California as well as those that were extinct before the Plio–Pleistocene extinction event 2.5 Mya were trimmed from the trees, resulting in a 50-species phylogeny with 25 of the tips going extinct at this time. Because we were analyzing an extinction that happened around 2.5 Mya (Plio–Pleistocene), we trimmed back to this date the branch lengths of living species that survived the extinction event. We also carried out a separate reconstruction based on the 14 living and 75 extinct Californian species, excluding at the onset species not present in California, to determine if our results were sensitive to the amount of data used to reconstruct the phylogeny. All subsequent calculations were performed for each of the 1,000 posterior trees, separately for the global species and Californian species calibrations.

Following the procedure for the simulated trees, we computed PD_{excess} and performed the binomial logistic regression to obtain the log-odds of survivorship with respect to relative age for this particular extinction event. We also computed log-odds for the null model with the same extinction rate.

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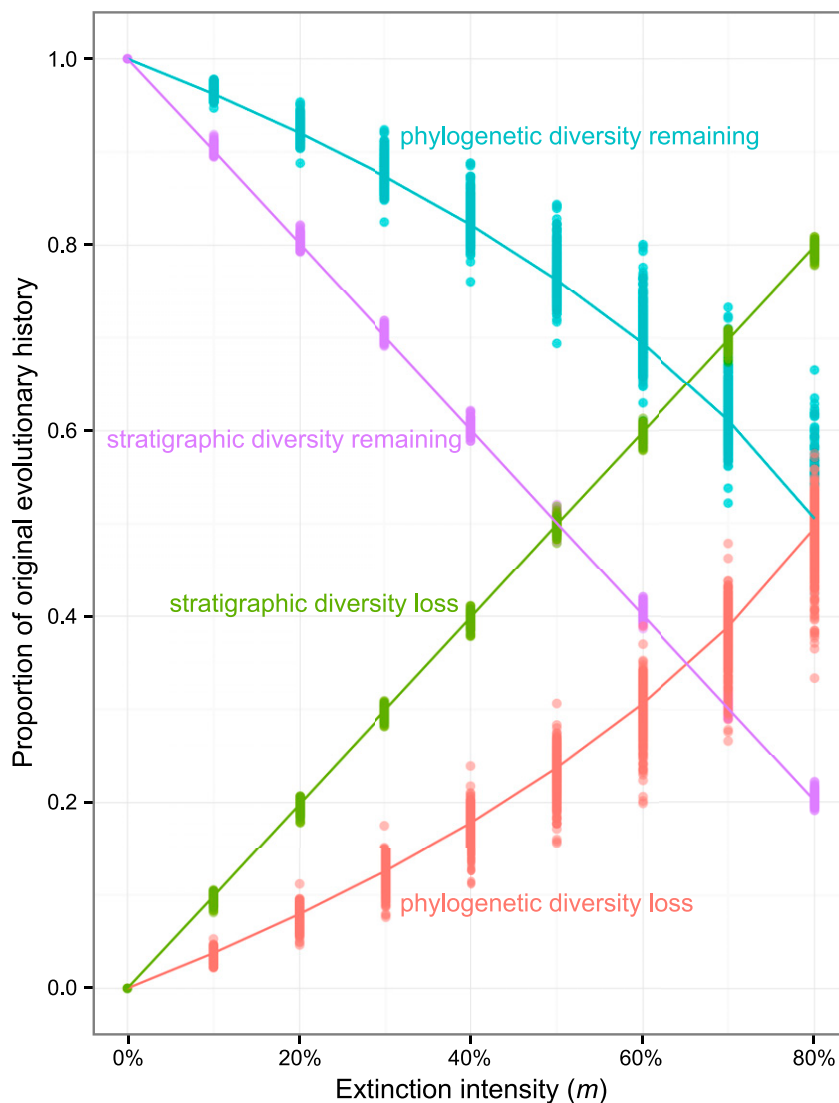


Fig. S1. Proportion of original EH lost or remaining after simulated species extinction independent of absolute or relative age. Shown are outcomes of PD based on bifurcating phylogenies as well as SD for extinction intensities (m) between 10% and 80%. Trees were simulated using SimTreeSDD under $\varepsilon = \mu/\lambda = 0.8$. Patterns are similar for trees simulated under $\varepsilon = 0.2$ and with paleotree (12).

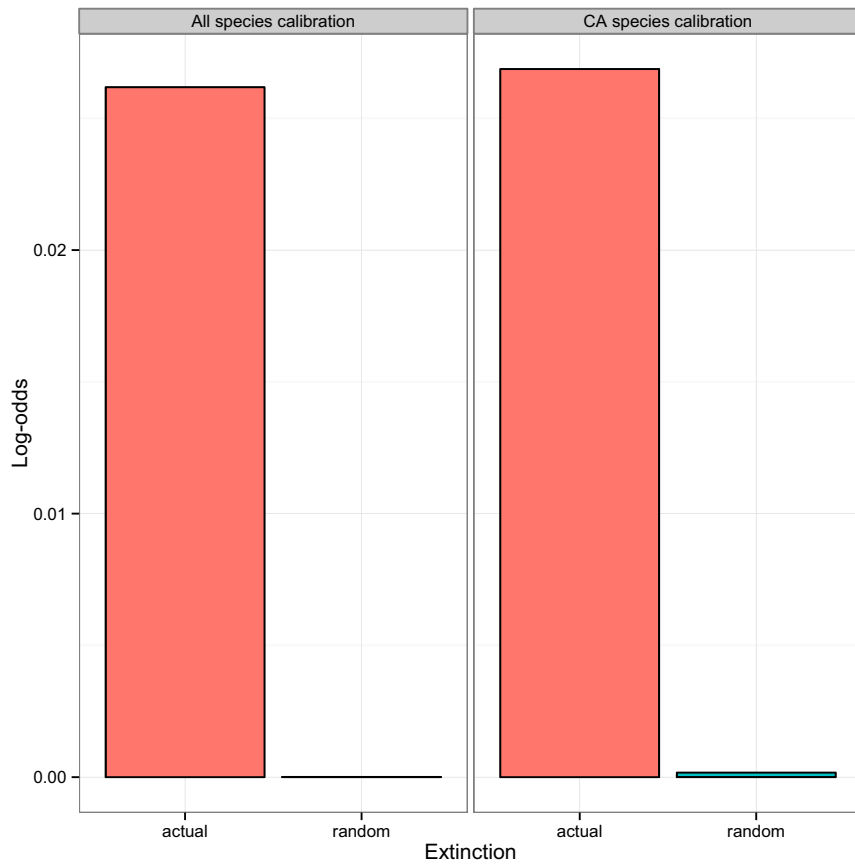


Fig. S5. Age selectivity log-odds of survival during the Plio-Pleistocene extinction event (~2.5 Mya) in which 25 of the 50 species present at that time went extinct. Results are similar for each posterior set of 1,000 trees calibrated with a global molecular dataset of 79 living and 75 extinct species (*Left*) and a California dataset (*Right*) of 14 living and 75 extinct species (*Right*). None of the log-odds computed for trees of both calibrations show statistical significance based on a binomial logistic regression model for the actual event (red) and random, age-independent species loss (cyan).