Mammal diversity will take millions of years to recover from the current biodiversity crisis

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The incipient sixth mass extinction that started in the Late Pleistocene has already erased over 300 mammal species and, with them, more than 2.5 billion y of unique evolutionary history. At the global scale, this lost phylogenetic diversity (PD) can only be restored with time as lineages evolve and create new evolutionary history. Given the increasing rate of extinctions however, can mammals evolve fast enough to recover their lost PD on a human time scale? We use a birth–death tree framework to show that even if extinction rates slow to preanthropogenic background levels, recovery of lost PD will likely take millions of years. These findings emphasize the severity of the potential sixth mass extinction and the need to avoid the loss of unique evolutionary history now.

phylogenetic diversity | mammals | mass extinction | diversification rate | evolutionary distinctiveness

As we enter a potential sixth mass extinction (1), triaging species and prioritizing limited conservation funds grow increasingly urgent if we wish to preserve biodiversity (2). However, taxonomic species richness (SR), the most used metric for measuring biodiversity among researchers, governments, and managers, is insufficient for these purposes because it implicitly treats all species equally (3). Functional diversity (FD), a richer metric that captures species' ecological adaptations and contributions to ecosystem function is growing in popularity, but it is difficult to measure and hard to compare between different taxonomic groups (2–4). Phylogenetic diversity (PD), the amount of independent evolution within a phylogeny (5), is a complementary metric that measures lineage history and may be correlated to functional trait diversity and evolutionary potential (4, 6, 7, but cf. ref. 8). PD is generally considered a better metric of biodiversity than SR because it incorporates both SR and phylogeny, is less influenced by arbitrary taxonomic decisions, and provides a powerful metaphor of "national heritage" for conservationists (5, 9). Furthermore, unlike FD index values, which are relative to each idiosyncratic analysis, PD is typically measured in millions of years of independent evolution (the sum of all branch lengths connecting a set of species to the root of their phylogenetic tree), a meaningful common currency that allows comparisons across a wide range of taxa and studies (2, 5). It is difficult to understand and measure the FD contribution of every species in a community, but with the rapid advancement of environmental DNA methods and computational capabilities, we could potentially place all those species on the tree of life to measure their contribution to PD (6, 10).

The incipient sixth mass extinction that started during the Late Pleistocene has been diagnosed by extremely elevated modern extinction rates compared with background levels (1). However, one can also put our current biodiversity crisis in perspective by estimating the time necessary for global diversity to recover to a preanthropogenic state (11). Although regional losses in biodiversity might be lessened by restoration activities such as species reintroductions and rewilding (12), at the global scale, lost

PD can only be restored by time as species evolve and create new evolutionary history. For example, although as few as 500 individuals of the critically endangered (CR) pygmy sloth (*Bradypus pygmaeus*) remain (13), global PD would recover from the extinction of this species in less than 2 y (11). This is not to say that a new species of pygmy sloth would evolve within this time or that the sloth's ecological functions would be restored, but that the 8,900-y loss in unique evolutionary history brought about by the sloth's extinction could be countered simply by all 5,418 remaining mammal species existing, and hence evolving, for an additional 1.64 y. The pygmy sloth, however, is one of the youngest mammal species, splitting from its congener during a vicariance event in the Holocene. The extinction of the aardvark (*Orycteropus afer*) would cause a much larger drop in PD, over 75 My, because the aardvark is the sole representative of an entire order. Such deep cuts into the mammal tree are increasingly likely, given that over one-fifth of current mammal species are threatened with extinction (14). How much PD will mammals lose during the ongoing sixth mass extinction, and can they recover this lost biodiversity?

Massive Losses of Evolutionary History

We randomly sampled 30 phylogenies from the posterior distribution reported by Faurby (15), which includes all extant and extinct Late Quaternary mammal species. Combining these trees

Significance

Biodiversity is more than the number of species on Earth. It is also the amount of unique evolutionary history in the tree of life. We find that losses of this phylogenetic diversity (PD) are disproportionally large in mammals compared with the number of species that have recently gone extinct. This lost PD can only be restored with time as lineages evolve and create new evolutionary history. Without coordinated conservation, it will likely take millions of years for mammals to naturally recover from the biodiversity losses they are predicted to endure over the next 50 y. However, by prioritizing PD in conservation, we could potentially save billions of years of unique evolutionary history and the important ecological functions they may represent.

and ranked threat statuses from the International Union for the Conservation of Nature (IUCN), we calculated the loss of PD since the Last Interglacial (~130,000 y ago) and the expected loss of PD, given probabilities that currently threatened species will go extinct in the near future (16). Unlike most previous studies, here, we use the Last Interglacial as a baseline instead of the present day because it better represents the typical, megafauna-rich state that existed through much of the Cenozoic (17). Leaving prehistoric extinctions out of analyses undercounts biodiversity loss and ignores the many large impacts these extinctions have had on modern ecology (17). To put global PD losses in perspective compared with species losses, we randomly shuffled species' IUCN statuses 250 times so that taxonomic losses during simulated extinctions were of the same severity but random with respect to phylogeny (*SI Appendix*).

Several unique mammal lineages (notably the endemic South American orders Litopterna and Notoungulata) were completely lost during the likely human-linked extinctions of the terminal Pleistocene and early Holocene (18). These extinctions also decimated the sloth and anteater, armadillo, odd-toed ungulate, and elephant lineages, all disproportionately rich in PD (Fig. 1 and *SI Appendix*, Fig. S1). Human-linked prehistoric extinctions saddled global mammal diversity with a PD loss of 2 billion y of unique evolutionary history. Historic extinctions since 1500 CE caused an additional 500 My of loss, leaving PD levels far worse

than expected, given null expectations of random extinctions (Fig. 2 and *SI Appendix*, Table S1). This is partly because prehistoric and historic extinctions were highly size-biased (19), devastating large mammals (*SI Appendix*, Fig. S2), a group shouldering a disproportionate share of PD. Evolutionary history has its own intrinsic value (20), but these lost years also represent a loss of instrumental value in the extinction of unique functional traits (2, 10). Human-linked extinctions have already left the world in an atypical state: depauperate of large animals and the important ecosystem functions and services they provide (17).

If current lineages simply persisted without any new speciation or extinction, it would take nearly 500,000 y for the ~5,400 current mammal species to evolve enough new history to restore net PD to preanthropogenic levels. But there will be new extinctions. The IUCN's own definitions for ranks predict the loss of 99.9% of CR species and 67% of endangered species within the next 100 y (16), eliminating even more ecosystem functions and services and further increasing mammals' already large PD debt. At the same time, mammals will also continue to diversify; if every lineage speciated into two distinct lineages, PD could be restored in half the time. The larger the speciation rate (λ) is compared with the extinction rate (μ), the shorter the amount of time (t) that it will take for mammals to naturally evolve back their lost PD. Given realistic background speciation and extinction rates, how long would it take mammals to regain this
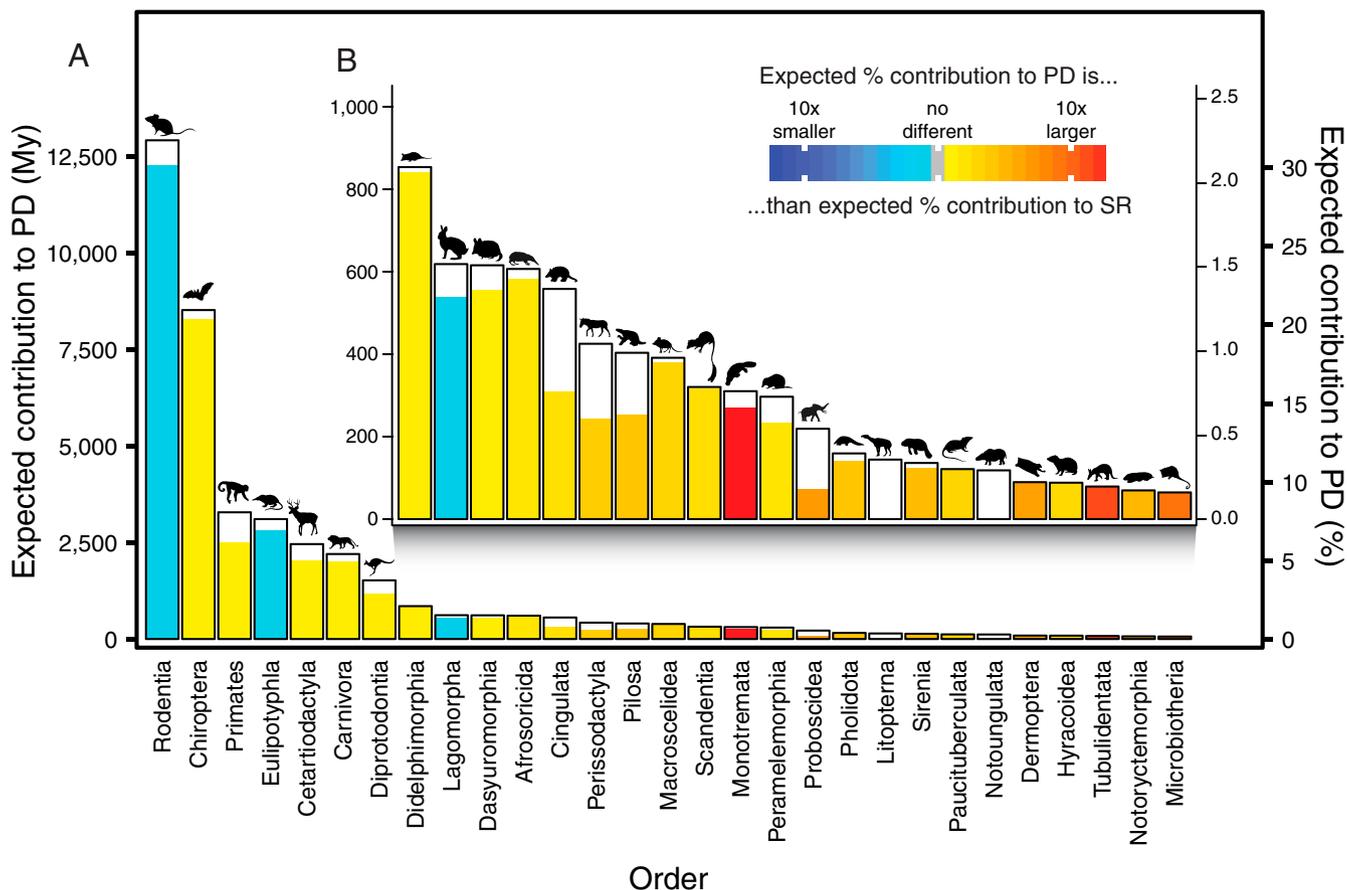
Fig. 1. Loss of evolutionary history is variable across mammalian orders. The heights of the bars show the amount of unique evolutionary history attributable to each mammal order at a preanthropogenic baseline (130,000 y ago). The right-hand *y* axis shows this same value as a percentage of global mammal PD at this baseline. The heights of the colored bars show the contribution to global PD projected to remain after 50 y of status quo conservation. Warm colors represent proportional contributions that are high for an order's SR; cool colors show the reverse. The orders Didelphimorpha to Microbiotheria are shown at standard (*A*) and enlarged (*B*) scales.
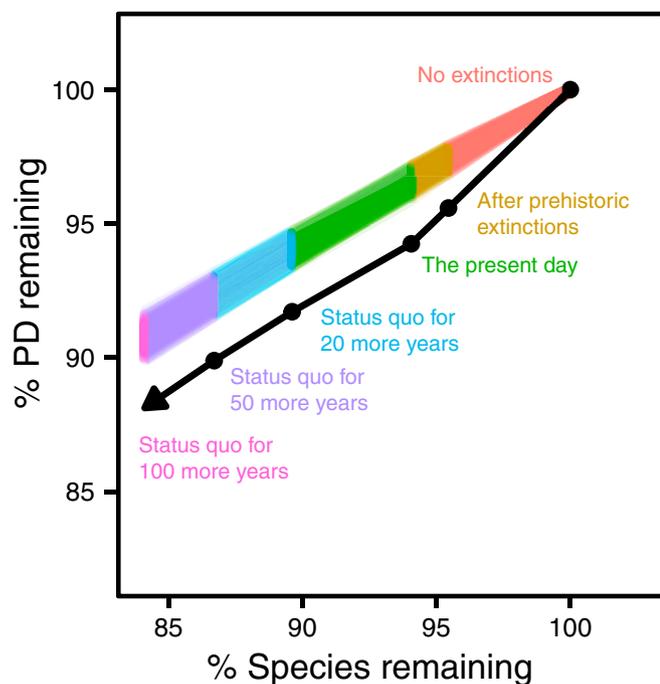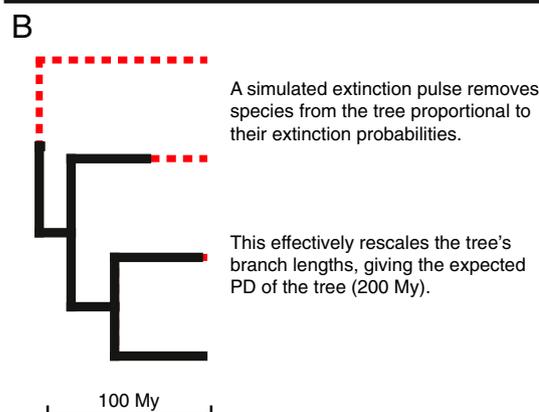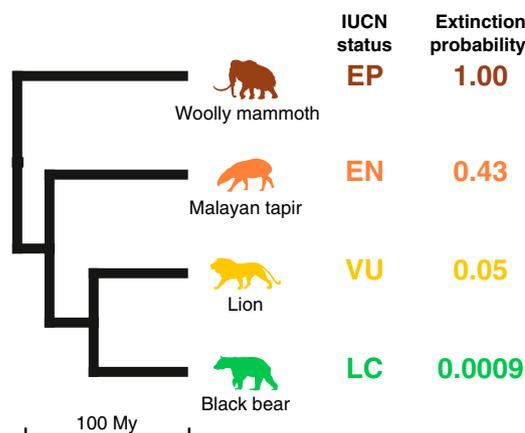
Fig. 2. Projected extinctions show a greater loss of PD in mammals than expected, given species loss. The black line shows the percentage of PD and SR remaining compared with a preanthropogenic baseline (130,000 y ago). Colored lines show 250 null simulations where extinctions are of equal magnitude, but random with respect to phylogeny. Lines correspond to the extinction scenarios labeled with the same color. Results from one randomly selected phylogenetic tree are shown. Summary results for all trees are shown in *SI Appendix*, Table S1, and results using the present day as a baseline are shown in *SI Appendix*, Table S5.
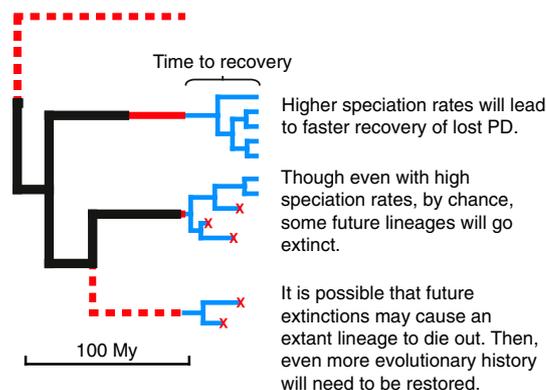
evolutionary history? Put another way, given a human time scale, can mammals evolve fast enough to recover from the sixth mass extinction?

We considered a "best-case" counterfactual model where the average global extinction rate drops down to background levels (21) before mammals are allowed to recover and start evolving new evolutionary history (Fig. 3). This could happen either because of a massive, global paradigm shift toward increased conservation efforts or because human populations have somehow collapsed to a point at which we are no longer a dominant and threatening ecological force. Using extinction probabilities extrapolated from IUCN definitions (16), we examined five scenarios for when PD was allowed to recover. Mammals could start recovering immediately or after 20, 50, or 100 y of status quo conservation efforts. If they started recovering immediately, only the PD lost during historic and prehistoric extinctions would need to be recovered. However, if mammals were not allowed to recover until sometime in the future, there would be a large chance that many extant species would also go extinct (*SI Appendix*, Table S2), creating even more lost PD compared with the baseline of all species alive at the Last Interglacial. To determine how large of an effect prehistoric extinctions had (18, 22), we also measured what would happen if mammals were allowed to recover from a 1499 CE baseline (i.e., before any "historic" or potential future extinctions). Using a birth–death tree framework (23) and a range of preanthropogenic background extinction rates (21), we then determined the speciation rate necessary to generate enough new PD through the evolution of new branch lengths to equal the PD lost during prehistoric and historic extinctions and potential future extinctions (Fig. 3 and *SI Appendix*).

A The prehistoric baseline tree has 340 My of evolutionary history (PD). After 50 years of status quo conservation, species will have the following probabilities of extinction:

	IUCN status	Extinction probability
Woolly mammoth	EP	1.00
Malayan tapir	EN	0.43
Lion	VU	0.05
Black bear	LC	0.0009

100 My

B

A simulated extinction pulse removes species from the tree proportional to their extinction probabilities.

This effectively rescales the tree's branch lengths, giving the expected PD of the tree (200 My).

100 My

C To restore the lost 140 My of PD, surviving lineages are allowed to diversify with background extinction rates until the tree has regained its original length.

Time to recovery

Higher speciation rates will lead to faster recovery of lost PD.

Though even with high speciation rates, by chance, some future lineages will go extinct.

It is possible that future extinctions may cause an extant lineage to die out. Then, even more evolutionary history will need to be restored.

100 My

Fig. 3. Diagrammatic explanation of how we modeled the loss and recovery of PD. The total PD of a prehistoric tree containing all mammals is used as a preanthropogenic baseline before (*A*) a simulated extinction pulse removes species from the tree proportional to their probability of extinction (*B*). IUCN status abbreviations: EN, endangered; EP, extinct in prehistory (a status added here); LC, least concern; VU, vulnerable. (*C*) After the extinction pulse, lineages are allowed to diversify at background extinction rates until they have generated enough new branch lengths to restore lost PD (red branches).

Recovery Times for PD

Although PD losses may be highly variable across clades and regions, previous studies predict that, globally, expected mammal PD losses should not be disproportionally severe (24–26, but cf. ref. 27 in which disproportionate losses of higher taxonomic units, although not necessarily PD, are predicted). Phylogenetic traits like lineage age, lineage richness, and evolutionary distinctiveness (ED) show no significant relationships with extinction risk (28), and simulations suggest that even though extinctions may be highly phylogenetically clustered (29), this is not enough to cause large losses in PD (30). However, when considering a baseline of the Last Interglacial, we found that global PD losses were much worse than expected (Fig. 2 and *SI Appendix*, Table S1), although losses did vary greatly across different taxonomic groups (*SI Appendix*, Fig. S3). Although extinction risk did not show a strong phylogenetic signal in our data, species that went extinct prehistorically (before 1500 CE) were significantly larger, older, and more evolutionarily distinct than other species (*SI Appendix*, Figs. S2, S4, and S5). Considering only terrestrial species, extinct megafauna (≥45 kg) were, on average, 48% older than surviving species and 61% more evolutionarily distinct. This is partly just a function of size, but even among large terrestrial mammals, extinct megafauna stood out. On average, they were 49% older and 57% more evolutionarily distinct than surviving megafauna. This means that prehistoric and historic extinctions were close to worst-case scenarios for PD loss, as many of the most phylogenetically distinct species were lost first, a pattern that has little analog in the fossil record (31). Even when excluding the strong effect of these extinct species by using the present day as a baseline like previous studies (24–26), we still found disproportionate (albeit much smaller) losses in PD compared with SR in 14 of the 30 phylogenetic trees examined (*SI Appendix*, Fig. S6 and Table S5).

If the status quo of mammal conservation continues for 50 y before mammals are allowed to recover, speciating and going extinct at their average preanthropogenic background rates of $\lambda = 0.276$ and $\mu = 0.272$ (roughly, one to two extinctions per 1,000 y) (21), it would take 5–7 My to restore the PD debt from prehistoric and historic extinctions (Fig. 4 and *SI Appendix*, Fig. S7). Even if background extinction rates effectively slowed to a stop ($\mu = 0$), speciation rates in mammals would still have to be about twice as high as their highest levels during the Cenozoic to restore PD debt within 500,000 y. Rates this high would mean that all mammals on Earth would have to speciate as fast as the Lake Victoria and Lake Malawi cichlids (32), the textbook vertebrate clade for extremely rapid evolution, without a single lineage going extinct. These high rates are not merely due to using the Late Pleistocene as a baseline. Of the 4,280 My of total PD debt we expect to have accrued after 50 y of status quo conservation, less than 60% comes from historic (509 My) and prehistoric (1,995 My) extinctions. Speciation rates and recovery times would still be excessive using the modern day as a baseline by completely ignoring historic and prehistoric extinctions (*SI Appendix*, Fig. S8). If the extinction rate fell to its average preanthropogenic level ($\mu = 0.272$), mammals would have to speciate faster than their highest Cenozoic rate (21) ($\lambda = 0.969$) for 1 My just to restore the amount of evolutionary history we are expected to lose in the next five decades (*SI Appendix*, Fig. S8). More realistically, average preanthropogenic speciation rates suggest a recovery time of 3–5 My (*SI Appendix*, Fig. S8).

Lagged Functional Recovery Times

Functional recovery from the sixth mass extinction would likely take even longer than PD recovery. We estimated mass distributions of future mammals using simulated birth–death trees and a neutral Brownian motion model of evolution on log-transformed weight with rates conditioned on the full trees
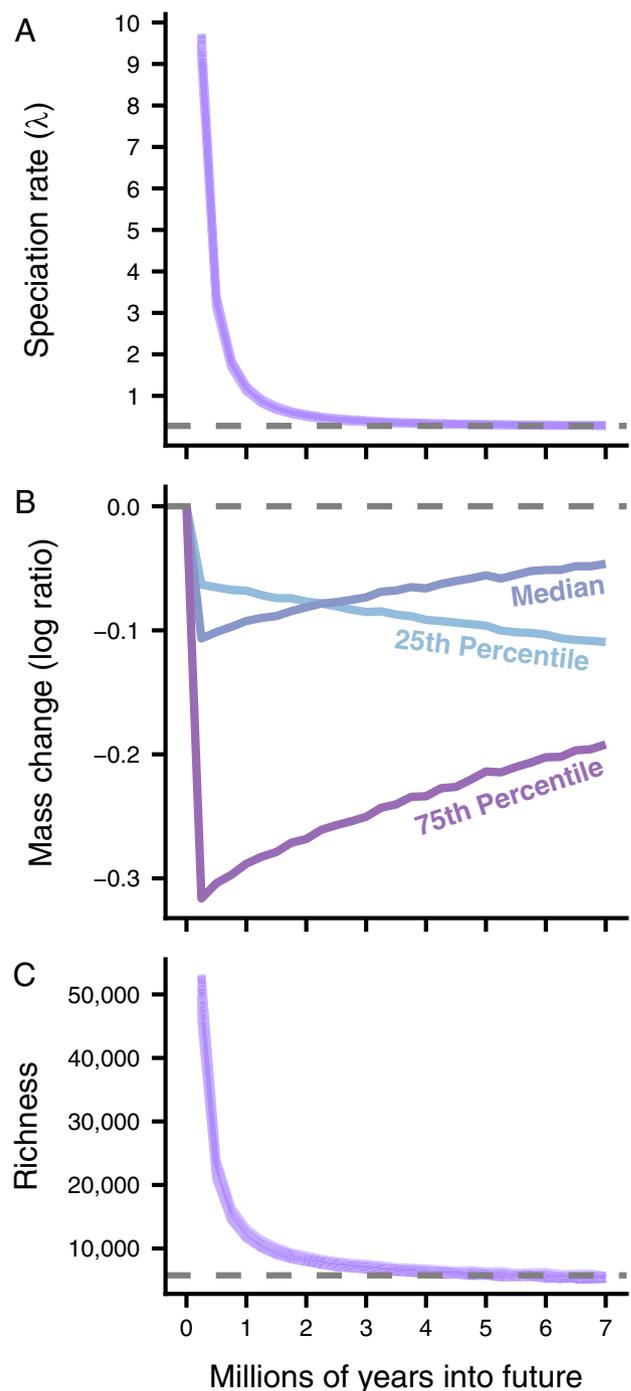
Fig. 4. (*A*) Speciation rate (λ) needed to recover PD lost over the past 130,000 y (a preanthropogenic baseline) assuming status quo conservation is allowed to continue for 50 more years before extinction rates drop to their average background levels ($\mu = 0.272$). The x axis shows how many millions of years (*t*) it would take for PD to recover with a given λ value (y axis, lineages per million species years). The gray dotted line is the average background λ of 0.276 for comparison. (*B*) The log ratios of mammal body masses at PD recovery, given a *t* and λ in *A*, to their preextinction masses. The colored lines represent how much the lower quartile, median, and upper quartile of mammal body mass will decrease from their preanthropogenic baselines represented by the dotted line. (*C*) Global mammal SR at recovery generated with a given *t* and λ in *A*. The dotted line shows a preanthropogenic SR of 5,761 mammals.

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(Fig. 4*B*). Currently, median mammal body mass (72.7 g) is 14% lower than its preanthropogenic level of 84.3 g. Stopping extinctions right now ($\mu = 0$) could restore PD within 500,000 y, given a very high speciation rate (*SI Appendix*, Fig. S7), but it would still take 4–5 My before median body mass returned to its pre-Pleistocene extinction level (*SI Appendix*, Fig. S9). If all extinctions stopped 50 y from now, it could take over 7 My for body sizes to recover (*SI Appendix*, Fig. S9). Although Faith (5) originally developed PD as a measure of the total number of features in an assemblage, PD is now often implicitly treated as equivalent to the range of trait values in an assemblage (33, 34) (i.e., functional richness, a component of FD). Prioritizing PD is generally a reasonable method for conserving FD (4), but restoring one does not always restore the other (24, 33, 35). This is partly because, even if traits are perfectly phylogenetically conserved, not all evolutionary time is equal. For example, one could say that losing 500 My of PD is roughly equivalent to losing a monotypic phylum (27). However, because the expected variance of traits evolving through Brownian motion increases linearly with time, a 1-My-old clade with 500 species would have only 1/250th of the expected trait variance of a pair of sister species that split apart 250 Mya despite both clades having the same rate of trait evolution and representing 500 My of PD (36). Even if PD is equal, for trait diversity, recovery at short time scales and high speciation rates is not equivalent to recovery at long time scales and lower speciation rates. This means that given neutral evolution, the unique traits of threatened, phylogenetically isolated taxa (10) cannot be easily replaced by short, rapid bursts of speciation, greatly prolonging the time needed for full functional recovery.

Even recovering such a large amount of PD through a rapid burst of speciation is highly unlikely. This is made clear by examining the expected number of species generated if PD lost during prehistoric and historic extinctions and the next 50 y was restored (Fig. 4*C*). To generate this much PD within 500,000 y and with an average background extinction rate ($\mu = 0.272$), new lineages would have to rapidly split, creating many functionally similar species on short branches. The world would have over 22,000 mammal species, 6,000 of them rats (Muroidea) (Fig. 4*C*). The existence of a strict carrying capacity for SR is debatable even at local scales (37); however, it seems unlikely that the globe could support almost fourfold the number of species that it harbored during the Late Pleistocene without some major geographical alterations. More reasonable speciation rates are likely those where the Earth maintains a taxonomic diversity close to its current level ($\lambda \approx 0.276$), leading to a recovery time of 5–7 My. Even then, each order's proportional contribution to global PD could change greatly in the future. After 50 y of status quo conservation, rodents are predicted to show a large increase in proportional PD. Bats, eulipotyphlans, carnivorans, opossums, rabbits and pikas, and hyraxes are expected to make smaller gains (*SI Appendix*, Fig. S10). All other orders are predicted to decrease in their proportional contribution to global PD. Primates and many Australasian marsupials could show large losses.

Avoiding a Mass Extinction

Is there any way to avoid the grim predictions of our model and speed recovery of PD and FD? The preferential extinction of older lineages seen in the Late Pleistocene and early Holocene is rare in the deeper fossil record (31), making mechanistic comparisons with past extinction events uncertain. Although the size bias of recent extinctions could lead to a "Lilliput effect" where small, surviving species rapidly evolve into vacant niches (38), the correlation between genetic substitution rates and high diversification rates necessary for this pattern have not been found in mammals (39). In general, mammals may not have the elevated speciation rates (21) shown by other taxa after mass

extinctions (40). However, even with strong selection for mammals to fill vacant niche space, recovery times on the order of millions of years are probably realistic. The maximum body mass of terrestrial mammals took over 10 My to first evolve from horse-sized to elephant-sized (41).

The results reported here show that it is unlikely that mammals can evolve fast enough to restore their lost PD on any kind of time scale relevant to humans. Just the PD that mammals are expected to lose in the next few decades would realistically take millions of years to recover (*SI Appendix*, Fig. S8). Even after this PD recovery, FD (*SI Appendix*, Fig. S9) would likely remain highly altered for millions of years more. The lost evolutionary history from previous and ongoing extinctions is already affecting ecosystems (42), a trend that will likely only get worse. If anything, our grim predictions of long recovery times are conservative. Unlike our best-case scenario model, there is little reason to expect that humans will be able to bring extinction rates down to background levels within the next century with a rising human population and increasing anthropogenic climate change. The only real option to speed PD recovery is to save unique evolutionary history before it is already lost. In addition to increasing overall conservation efforts, we should use available PD methods to prioritize action for evolutionarily distinct species and dedicate more research to exploring PD's relationship with FD and ecosystem services (4, 7). If we could momentarily stop extinctions for mammals, we would save as much evolutionary history in the next 100 y as what our ancestors lost in the last 100,000 y (*SI Appendix*, Table S1). Extinction is part of evolution, but the unnatural rapidity of current species losses forces us to address whether we are cutting off twigs or whole branches from the tree of life.

Materials and Methods

We developed a counterfactual model to investigate how fast current mammal species would have to evolve to replace the amount of evolutionary history they have already lost and are expected to lose during the ongoing sixth mass extinction. This model assumes a best-case scenario, where the average global extinction rate for mammals drops down to background levels (21) before they are allowed to recover and start evolving new evolutionary history (Fig. 3). Using a birth–death tree framework (23) and a combination of simulations and algebraic solutions, we iteratively determined the speciation rate (λ) necessary to recover lost PD with a given time span (t) and extinction rate (μ). Both λ and μ were measured in lineages per species per million years, and t was measured in millions of years.

Mammal phylogenies and body mass data came from a prerelease (version 1.1) of the PHYLACINE database (15). Average background diversification rates for mammals were from Alroy (21). Extinction probabilities for extant species were based on studies by Mooers et al. (16) and Isaac et al. (43). To partition expected PD (44) fairly among taxa, we developed a missing PD metric, expected ED, a probabilistic version of ED (45). To facilitate the use of the expected ED metric, we created an R package ("mallorn") that can quickly calculate expected ED and expected PD (10.5281/zenodo.1286923, available at https://megapast2future.github.io). All analyses were carried out in R version 3.4 (46). Detailed information on data and methods is provided in *SI Appendix*. The complete data and code necessary to replicate this analysis are archived at Zenodo (doi.org/10.5281/zenodo.1286876).

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