Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines

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The population extinction pulse we describe here shows, from a quantitative viewpoint, that Earth's sixth mass extinction is more severe than perceived when looking exclusively at species extinctions. Therefore, humanity needs to address anthropogenic population extirpation and decimation immediately. That conclusion is based on analyses of the numbers and degrees of range contraction (indicative of population shrinkage and/or population extinctions according to the International Union for Conservation of Nature) using a sample of 27,600 vertebrate species, and on a more detailed analysis documenting the population extinctions between 1900 and 2015 in 177 mammal species. We find that the rate of population loss in terrestrial vertebrates is extremely high—even in "species of low concern." In our sample, comprising nearly half of known vertebrate species, 32% (8,851/27,600) are decreasing; that is, they have decreased in population size and range. In the 177 mammals for which we have detailed data, all have lost 30% or more of their geographic ranges and more than 40% of the species have experienced severe population declines (>80% range shrinkage). Our data indicate that beyond global species extinctions Earth is experiencing a huge episode of population declines and extirpations, which will have negative cascading consequences on ecosystem functioning and services vital to sustaining civilization. We describe this as a "biological annihilation" to highlight the current magnitude of Earth's ongoing sixth major extinction event.

sixth mass extinction | population declines | population extinctions | conservation | ecosystem service

The loss of biological diversity is one of the most severe human-caused global environmental problems. Hundreds of species and myriad populations are being driven to extinction every year (1–8). From the perspective of geological time, Earth's richest biota ever is already well into a sixth mass extinction episode (9–14). Mass extinction episodes detected in the fossil record have been measured in terms of rates of global extinctions of species or higher taxa (e.g., ref. 9). For example, conservatively almost 200 species of vertebrates have gone extinct in the last 100 y. These represent the loss of about 2 species per year. Few realize, however, that if subjected to the estimated "background" or "normal" extinction rate prevailing in the last 2 million years, the 200 vertebrate species losses would have taken not a century, but up to 10,000 y to disappear, depending on the animal group analyzed (11). Considering the marine realm, specifically, only 15 animal species have been recorded as globally extinct (15), likely an underestimate, given the difficulty of accurately recording marine extinctions. Regarding global extinction of invertebrates, available information is limited and largely focused on threat level. For example, it is estimated that 42% of 3,623 terrestrial invertebrate species, and 25% of 1,306 species of marine invertebrates assessed on the International Union for Conservation of Nature (IUCN) Red List are classified as threatened with extinction (16). However, from the perspective of a human lifetime it is difficult to appreciate the current magnitude of species extinctions. A rate of two vertebrate species extinctions per year does not generate enough public concern, especially because many of those species were obscure and had limited ranges, such as the Catarina pupfish (*Megupsilon aporus*, extinct in 2014), a tiny fish from Mexico, or the Christmas Island pipistrelle (*Pipistrellus murrayi*, extinct in 2009), a bat that vanished from its namesake volcanic remnant.

Species extinctions are obviously very important in the long run, because such losses are irreversible and may have profound effects ranging from the depletion of Earth's inspirational and esthetic resources to deterioration of ecosystem function and services (e.g., refs. 17–20). The strong focus among scientists on species extinctions, however, conveys a common impression that Earth's biota is not dramatically threatened, or is just slowly entering an episode of major biodiversity loss that need not generate deep concern now (e.g., ref. 21, but see also refs. 9, 11, 22). Thus, there might be sufficient time to address the decay of biodiversity later, or to develop technologies for "deextinction"—the possibility of the latter being an especially dangerous misimpression (see ref. 23). Specifically, this approach has led to the neglect of two critical aspects of the present extinction episode: (*i*) the disappearance of populations, which essentially always precedes species extinctions, and (*ii*) the rapid decrease in numbers of individuals within some of the remaining populations. A detailed analysis of the loss of individuals and populations makes the problem much clearer and more worrisome, and highlights a whole set of parameters that are increasingly critical in considering the Anthropocene's biological extinction crisis.

Significance

The strong focus on species extinctions, a critical aspect of the contemporary pulse of biological extinction, leads to a common misimpression that Earth's biota is not immediately threatened, just slowly entering an episode of major biodiversity loss. This view overlooks the current trends of population declines and extinctions. Using a sample of 27,600 terrestrial vertebrate species, and a more detailed analysis of 177 mammal species, we show the extremely high degree of population decay in vertebrates, even in common "species of low concern." Dwindling population sizes and range shrinkages amount to a massive anthropogenic erosion of biodiversity and of the ecosystem services essential to civilization. This "biological annihilation" underlines the seriousness for humanity of Earth's ongoing sixth mass extinction event.

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In the last few decades, habitat loss, overexploitation, invasive organisms, pollution, toxification, and more recently climate disruption, as well as the interactions among these factors, have led to the catastrophic declines in both the numbers and sizes of populations of both common and rare vertebrate species (24–28). For example, several species of mammals that were relatively safe one or two decades ago are now endangered. In 2016, there were only 7,000 cheetahs in existence (29) and less than 5,000 Borneo and Sumatran orangutans (*Pongo pygmaeus* and *P. abelli*, respectively) (28). Populations of African lion (*Panthera leo*) dropped 43% since 1993 (30), pangolin (*Manis* spp.) populations have been decimated (31), and populations of giraffes dropped from around 115,000 individuals thought to be conspecific in 1985, to around 97,000 representing what is now recognized to be four species (*Giraffa giraffa*, *G. tippelskirchi*, *G. reticulata*, and *G. camelopardalis*) in 2015 (32).

An important antecedent to our work (25) used the number of genetic populations per unit area and then estimated potential loss on the basis of deforestation estimates and the species–area relationship (SAR). Given the recognized limitations of the use of SAR to estimate extinctions, our work provides an approach based on reduction of species range as a proxy of population extirpation. The most recent Living Planet Index (LPI) has estimated that wildlife abundance on the planet decreased by as much as 58% between 1970 and 2012 (4). The present study is different from LPI and other related publications in several ways, including that here we use all decreasing species of vertebrates according to IUCN, mapping and comparing absolute and relative numbers of species, and focusing on population losses. Previous estimates seem validated by the data we present here on the loss of local populations and the severe decrease in the population size of many others (see also refs. 3, 4, 6–8, 26). Here we examine the magnitude of losses of populations of land vertebrate species on a global system of 10,000-km^2 quadrats (*Methods*). Species vary from common to rare, so that our analysis, which includes all land vertebrate species (amphibians, birds, reptiles, and mammals) deemed as "decreasing" by IUCN, provides a better estimate of population losses than using exclusively IUCN data on species at risk. Obviously, common species decreasing are not ordinarily classified as species at risk. IUCN criteria provide quantitative thresholds for population size, trend, and range size, to determine decreasing species (28, 33). We also evaluate shrinking ranges and population declines for 177 species of mammals for which data are available on geographic range shrinkage from ∼1900 to 2015. We specifically focus on local extinctions by addressing the following questions: (*i*) What are the numbers and geographic distributions of decreasing terrestrial vertebrate species (i.e., experiencing population losses)? (*ii*) What are the vertebrate groups and geographic regions that have the highest numbers and proportions of decreasing species? (*iii*) What is the scale of local population declines in mammals—a proxy for other vertebrates? By addressing these questions, we conclude that anthropogenic population extinctions amount to a massive erosion of the greatest biological diversity in the history of Earth and that population losses and declines are especially important, because it is populations of organisms that primarily supply the ecosystem services so critical to humanity at local and regional levels.

Results

Patterns of Variation in Population Loss Among Vertebrates. Considering all land vertebrates, our spatially explicit analyses indicate a massive pulse of population losses, with a global epidemic of species declines. Those analyses support the view that the decay of vertebrate animal life is widespread geographically, crosses phylogenetic lineages, and involves species ranging in abundance from common to rare (Figs. 1–4). The losses, however, are not uniform: some regions exhibit higher concentrations of species with local population extinctions than others, including a strong latitudinal signal corresponding to an intertropical peak (i.e., roughly between the Tropics of Cancer and Capricorn) of number of decreasing species, particularly strong in mammals and birds, which largely drive the overall land vertebrate pattern (Fig. 3, *Center*). Notably, some parts of the planet harbor low absolute numbers of vertebrate species undergoing decline (Figs. 2 and 3), such as those areas of low species richness located in hypercold (northernmost locations, particularly of the Western Hemisphere) and hyperarid (Saharan Africa and Central Asia) regions. However, it is instructive to examine their corresponding proportional numbers, an aspect we discuss in detail in another section below.

The number of decreasing species of all land vertebrates in each of the 10,000-km^2 quadrats over Earth's land surface ranges from a few to more than 365 (Fig. 2). As expected, large concentrations of decreasing vertebrate species occur in species-rich areas of moist tropical forests adjacent to mountainous regions, such as the Andes–Amazon region, the Congo basin-adjacent eastern African highlands, and the Himalayas–south Asian jungle belt. The distribution of the number of decreasing species considering vertebrate classes separately reveals notable differences. First, the maximum number of decreasing species in a 10,000-km^2 quadrat varies from a high value of 296 decreasing birds per quadrat, to a low maximum of 60 decreasing reptiles in a quadrat. Second, mammals and birds have relatively similar distribution patterns of

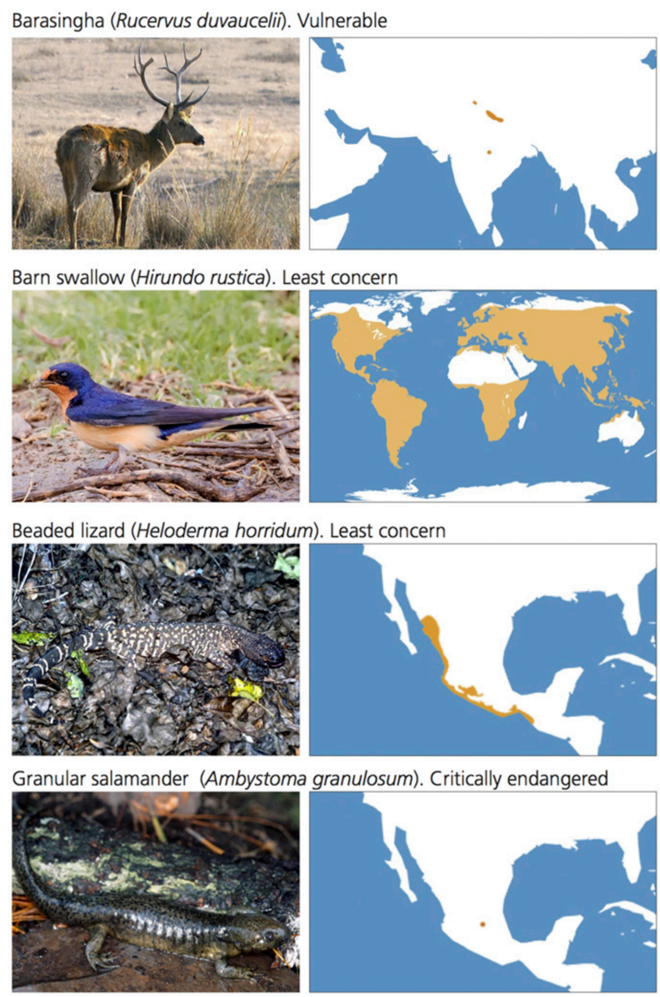

Fig. 1. Decreasing land vertebrates, as exemplified with these four species, include taxa with different conservation status (e.g., low concern, critically endangered), current geographic range (e.g., large, very restricted), and abundance (e.g., common, rare). The data on conservation status, current geographic range, and abundance are from IUCN (28). Barn swallow image courtesy of Daniel Garza Galindo (photographer).

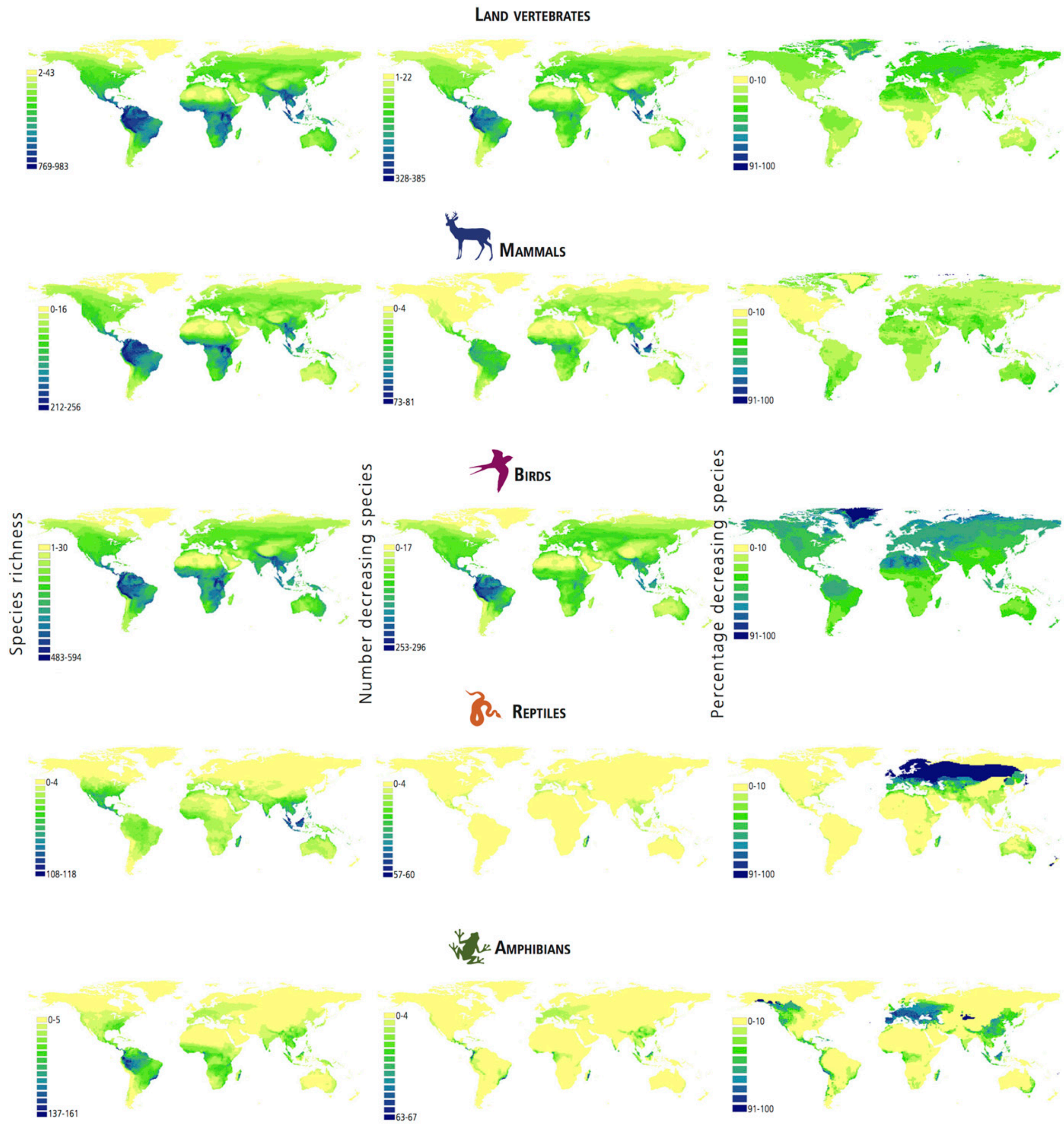

Fig. 2. Global distribution of terrestrial vertebrate species according to IUCN (28). (*Left*) Global distribution of species richness as indicated by number of species in each 10,000-km^2 quadrat. (*Center*) Absolute number of decreasing species per quadrat. (*Right*) Percentage of species that are suffering population losses in relation to total species richness per quadrat. The maps highlight that regions of known high species richness harbor large absolute numbers of species experiencing high levels of decline and population loss (particularly evident in the Amazon, the central African region, and south/southeast Asia), whereas the proportion of decreasing species per quadrat shows a strong high-latitude and Saharan Africa signal. In addition, there are several centers of population decline in both absolute and relative terms (Borneo, for example).

decreasing species, except that birds have more decreasing species in the temperate zones. Third, mammals and birds have patterns of decreasing species quite distinct from those of reptiles and amphibians (Figs. 2 and 3), given that the latter are rarer in the northern and southern temperate and subpolar regions (both are essentially absent from the Arctic and are missing from the Antarctic). Fourth, reptiles and amphibians clearly differ from each other in regions where decreasing species are concentrated. For example, there are more decreasing reptiles in the Eurasian and African continents, and more decreasing amphibians in the Americas.

There is also great variation in the total population size and geographic ranges among individual species. Although there is no

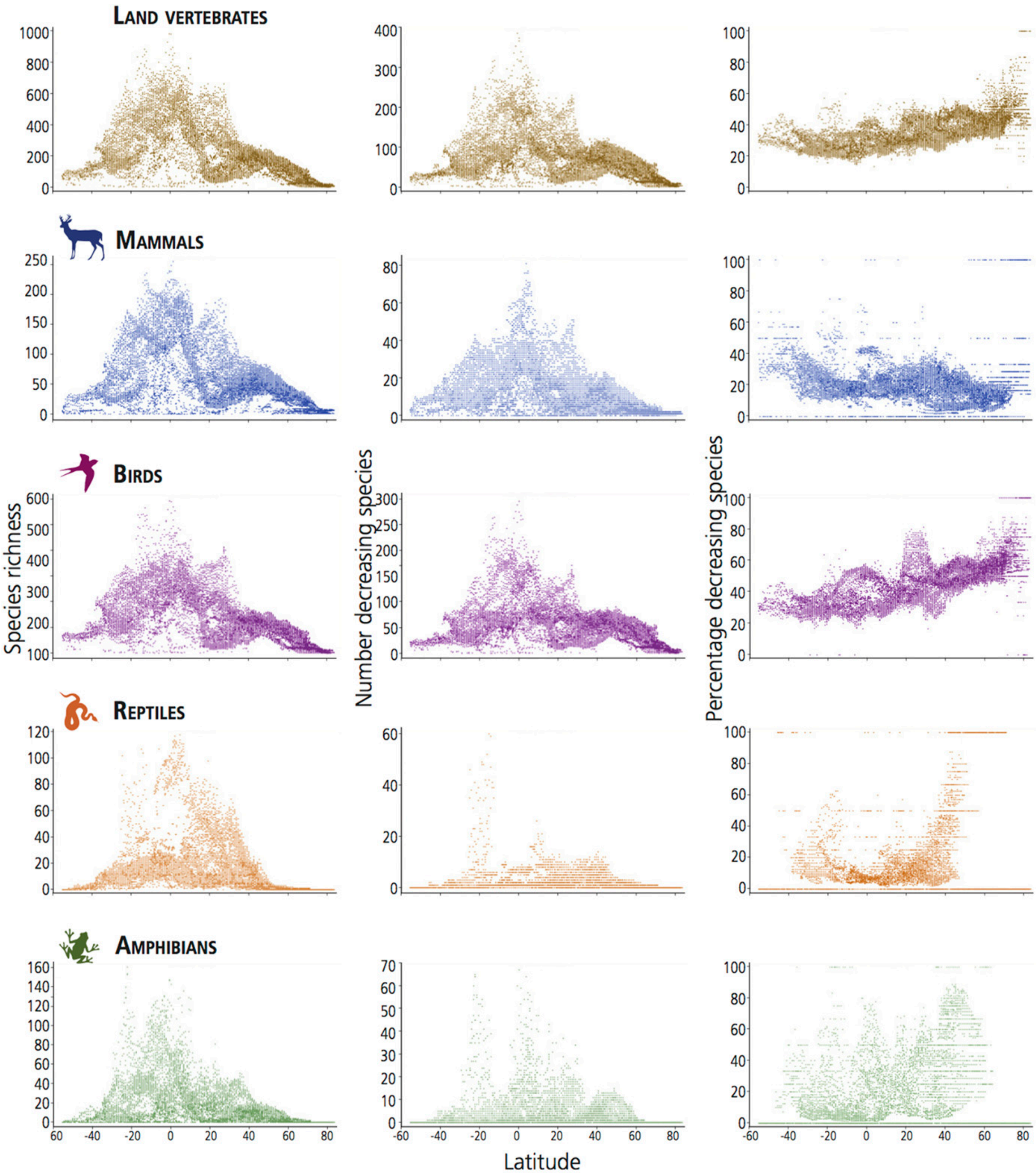

Fig. 3. Latitudinal distribution of species richness (*Left*), decreasing species (*Center*), and the percentage of species (*Right*) that are suffering population losses in relation to total species richness, in each 10,000-km^2 quadrat. Patterns of species richness in relation to latitude are similar in all vertebrates, although there are more species per quadrat in birds and mammals and, as expected, a scarcity of reptiles and amphibians at high latitudes. The patterns of number of species with decreasing populations indicate that regions with high species richness also have high numbers of decreasing species, but the percentage of decreasing species in relation to species richness shows contrasting patterns between mammals and birds compared with reptiles and amphibians. In mammals and birds, the percentage of decreasing species is relatively similar in regions with low and high species richness. In contrast, there are proportionally more decreasing species of reptiles and amphibians in regions with low species richness.

accurate information on population size for most taxa, whatever is available indicates that the total population size in species with decreasing populations varies from fewer than 100 individuals in critically endangered species such as the Hainan black-crested

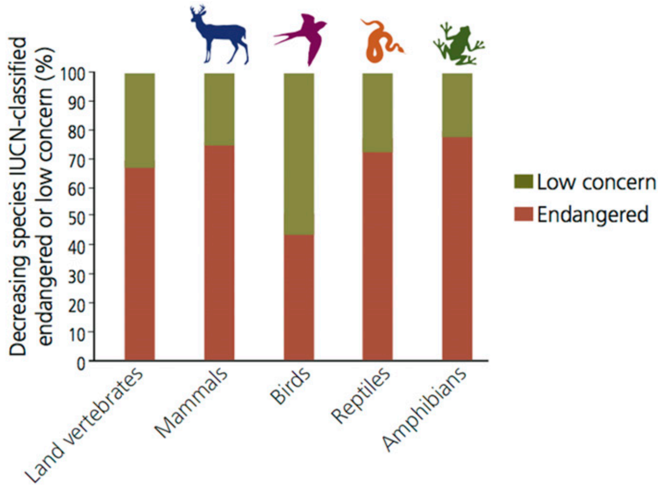

Fig. 4. The percentage of decreasing species classified by IUCN as "endangered" (including "critically endangered," "endangered," "vulnerable," and "near-threatened") or "low concern" (including "low concern" and "data-deficient") in terrestrial vertebrates. This figure emphasizes that even species that have not yet been classified as endangered (roughly 30% in the case of all vertebrates) are declining. This situation is exacerbated in the case of birds, for which close to 55% of the decreasing species are still classified as "low concern."

gibbon (*Nomascus hainanus*), to many millions of individuals in decreasing common species such as the barn swallow (*Hirundo rustica*). Similarly, the smallest ranges (i.e., <1 km^2) are seen in species such as the Carrizal seedeater (*Amaurospiza carrizalensis*) from Venezuela and Herrera's false coral snake (*Lampropeltis herrerae*) from Mexico, both denizens of tiny islands. The largest ranges are hundreds of thousands of square kilometers, as in the bush dog (*Speothos venaticus*) from South America and the common lizard (*Zootoca vivipara*) from Eurasia. The sum of the 10,000-km^2 quadrats representing the current ranges of the 8,851 decreasing vertebrate species is 1,350,876 quadrats. A highly conservative estimate would indicate a similar number of local populations facing extinction. This is, of course, a very rough estimate of the total number of populations, as the number of populations of a decreasing species in each quadrat largely depends, aside from suitable habitat distribution within the quadrat, on animal body mass and trophic position (e.g., ref. 34). The assumption of one population per 10,000 km^2 might seem very conservative, as this area could accommodate many populations of small animals (e.g., 0.1-kg rodents), most of which could have been extirpated. However, 10,000 km^2 may not be sufficient for, or can barely accommodate a viable population of large carnivores (say a 330-kg Siberian tiger; ref. 34). Nonetheless, our results provide evidence of the extremely large numbers of vertebrate populations facing extinction, compared with the number of species.

Proportion of Vertebrate Species Decreasing. The proportion of decreasing vertebrates shows that there are areas across the planet with high concentrations of decreasing species in all vertebrates and regions with high proportions of decreasing species of a particular group (Figs. 2, 3, and 5). For example, in mammals, the highest percentage of decreasing species is concentrated in tropical regions, mostly in the Neotropics and Southeast Asia, whereas in reptiles, the proportional decline concentrates almost exclusively in Madagascar. Decreasing amphibians are prominent in Mexico, Central America, the northern Andes, and Brazil's Atlantic forest in the Americas; West Africa and Madagascar in Africa; and India and Southeast Asia, including Indonesia and Philippines in Asia–Southeast Asia. Finally, decreasing species of birds are found over large regions of all continents (Fig. 2).

Roughly a third (8,851/27,600) of all land vertebrate species examined are experiencing declines and local population losses of a considerable magnitude (Figs. 2–4). Such proportion of decreasing species varies, depending on the taxonomic group, from 30% or more in the case of mammals, birds, and reptiles, to 15% in the case of amphibians. Furthermore, of the decreasing species, many are now considered endangered (Fig. 4). Beyond that, roughly 30% of all decreasing species are still sufficiently common that they are considered of "low concern" by IUCN, rather than "endangered." That so many common species are decreasing is a strong sign of the seriousness of the overall contemporary biological extinction episode.

In our 10,000-km^2 quadrats, the proportion of decreasing species ranges from less than 10% to more than 50% (Fig. 2). The geographic distributions of absolute (i.e., number) and relative (i.e., percentage) of decreasing species is contrasting. Whereas tropical regions have larger numbers of decreasing species, as expected, given their higher species richness, their corresponding proportions are relatively low. In contrast, temperate regions tend to have similar or higher proportions of decreasing species, a trend dramatically prominent in the case of reptiles.

Local Population Extinctions in Mammals. Our most detailed data allow comparison of historic and present geographic range of a sample of 177 mammal species (Figs. 5 and 6). Most of the 177 mammal species we sampled have lost more than 40% of their geographic ranges in historic times, and almost half have lost more than 80% of their ranges in the period ∼1900–2015. At the continental and subcontinental level, some patterns become evident (Fig. 5). The predominant category of range contraction is ≥80% in Africa (56% of the sampled mammal species), Asia (75% of the species), Australia (60% of the species), and Europe (40% of the species). In the Americas, range contractions are less marked but still considerable: 22% of the species in North America and 17% of the species in South America have experienced range contractions of at least 80%. Nevertheless, 50% of the species in North America and 28% of the species in South America have experienced a range contraction of 41% or more.

The comparison of the 1900–2015 geographic ranges showed that the 177 species of mammals have disappeared from 58,000 grid cells. On the assumption that on average each of the 10,000-km^2 occupied quadrats held a single population of the species found within it, this implies that roughly 58,000 populations of the 177 mammals we examined have gone extinct. Consider the following emblematic cases: The lion (*Panthera leo*) was historically distributed over most of Africa, southern Europe, and the Middle

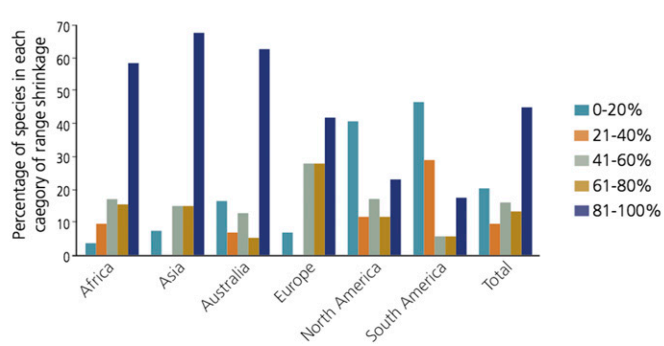

Fig. 5. The percentage of species of land mammals from five major continents/subcontinents and the entire globe undergoing different degrees (in percentage) of decline in the period ∼1900–2015. Considering the sampled species globally, 56% of them have lost more than 60% of their range, a pattern that is generally consistent in Africa, Asia, Australia, and Europe, whereas in South America and North America, 35–40% of the species have experienced range contractions of only 20% or less. (See text for details.)

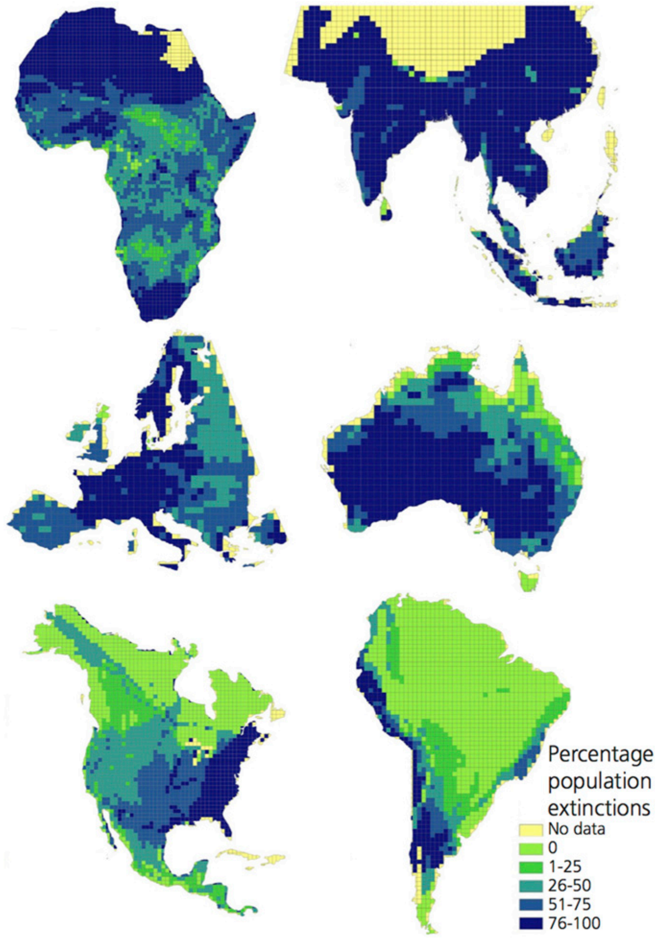

Fig. 6. Percentage of local population extinction in 177 species of mammals in 1° × 1° quadrats, as an indication of the severity of the mass extinction crises. The maps were generated by comparing historic and current geographic ranges (49) (*SI Appendix, SI Methods*). Note that large regions in all continents have lost 50% or more of the populations of the evaluated mammals. Because of the small sample size, biased to large mammal species, this figure can only be used to visualize likely trends in population losses.

East, all the way to northwestern India (*SI Appendix*, Fig. S1). It is now confined to scattered populations in sub-Saharan Africa and a remnant population in the Gir forest of India. The vast majority of lion populations are gone. In its African stronghold, it historically occupied roughly two thousand 10,000-km^2 cells, and now it is reduced to some 600 cells. Other species, such as the mountain lion (*Puma concolor*), are known to be doing better. The mountain lion has lost some of its local populations in North America, but has not suffered such disastrous losses as its Old World relative, adapting relatively well to human-dominated landscapes, and it is still found across 85% of its historic range.

Clearly, the extinction of mammal populations, although varying from species to species, has been a global phenomenon (Fig. 6). Strikingly, the predominant color code in the mammalian map is that of 70% or more of population losses, with the exception of some areas of South America and high latitudes of North America. Particularly hard hit have been the mammals of south and southeast Asia, where all of the large-bodied species of mammals analyzed have lost more than 80% of their geographic ranges. The Cape and Sahara regions in Africa, central Australia, the eastern United States, and the Atlantic forest in South America have also suffered severely from population extinctions.

Discussion

It has recently been shown, using conservative estimates of current and background species extinction rates, that Earth is now in a period of mass global species extinction for vertebrate animals (11). But the true extent of this mass extinction has been underestimated, because of the emphasis on species extinction. This underestimate largely traces to overlooking the accelerating extinction of populations. Whereas scientists have known for a long time that several relatively well-studied species have undergone major contraction of their ranges, experienced considerable population decreases, and suffered many population extinctions, the global extent of population shrinkage and extirpation has previously not been recognized and quantified.

In addition, some studies document that invertebrates and plants are suffering massive losses of populations and species (35–38). Here we extend investigation of mass extinction to terrestrial vertebrate population decreases and losses, and give estimates of the number of their species with decreasing populations. The accuracy of the estimates is strongly dependent on an unknown parameter, namely, the actual average area occupied by a vertebrate population (e.g., refs. 35, 39–41). However, even if a population would, on average, occupy an area five times larger than what we have used here (i.e., 50,000 km^2) there would still be hundreds of thousands of populations that have suffered extinction in the past few centuries. On the other hand, most vertebrates (~70%) are small species of mammals, birds, reptiles, and amphibians. If, on average, they have one population every 10 km^2 then vertebrates would have suffered more than a billion population extinctions.

Our results show that population extinction in land vertebrates is geographically omnipresent, but with notable prominence in tropical, species-rich regions. It is interesting, however, that when population extinctions are evaluated as the percentage of total species richness, temperate regions, with their typical low species diversity, show higher proportions of population loss.

There are some illustrative qualitative examples of population decreases and their consequences within terrestrial and marine vertebrates, but ours is an attempt at a quantitative evaluation of global trends in population extinctions. Recent reviews indicate that species extinctions, population decreases, and range contraction (implying population extinctions) among terrestrial invertebrates and plants are as severe as among vertebrates (e.g., refs. 35–38). For example, long-term monitoring of insect populations in the United Kingdom shows that 30–60% of species per taxonomic order have contracting ranges (36). The situation in plants has been less evaluated; thus it is difficult to compare them with animals, but there is little reason to believe that the extinction situation in plants is dramatically different (37). Furthermore, research shows that the loss of animal populations indirectly leads to changes in plant communities (20, 37, 39), frequently causing the reduction of local species richness and dominance of a few plant taxa that either experience "ecological release" in response to decreasing herbivore pressures (42, 43), and/or experience population reductions due to the decline of animals responsible for pollination or dispersal (e.g., refs. 2–3, 20). The status of biodiversity among microorganisms is too poorly known to permit us to make any comparison and generalizations about the current pulse of extinctions, although some recent research has unraveled feedbacks between local large herbivore defaunation and mycorrhizal richness (44, 45). Given what we know about genetic population differentiation, it is expected that the range contractions and declines we document here imply a considerable loss of intraspecific genetic diversity (23) but this is, clearly, an aspect that warrants further investigation.

In sum, by losing populations (and species) of vertebrates, we are losing intricate ecological networks involving animals, plants, and microorganisms (e.g., refs. 2, 8, 18, 45, 46). We are also losing pools of genetic information that may prove vital to species' evolutionary adjustment and survival in a rapidly changing global environment.

This suggests that, even if there was not ample sign that the crisis extends far beyond that group of animals, today's planetary defaunation of vertebrates will itself promote cascading catastrophic effects on ecosystems, worsening the annihilation of nature (2, 3, 46). Thus, while the biosphere is undergoing mass species extinction (11), it is also being ravaged by a much more serious and rapid wave of population declines and extinctions. In combination, these assaults are causing a vast reduction of the fauna and flora of our planet. The resulting biological annihilation obviously will also have serious ecological, economic, and social consequences (46). Humanity will eventually pay a very high price for the decimation of the only assemblage of life that we know of in the universe.

Conclusion

Population extinctions today are orders of magnitude more frequent than species extinctions. Population extinctions, however, are a prelude to species extinctions, so Earth's sixth mass extinction episode has proceeded further than most assume. The massive loss of populations is already damaging the services ecosystems provide to civilization. When considering this frightening assault on the foundations of human civilization, one must never forget that Earth's capacity to support life, including human life, has been shaped by life itself (47). When public mention is made of the extinction crisis, it usually focuses on a few animal species (hundreds out of millions) known to have gone extinct, and projecting many more extinctions in the future. But a glance at our maps presents a much more realistic picture: they suggest that as much as 50% of the number of animal individuals that once shared Earth with us are already gone, as are billions of populations. Furthermore, our analysis is conservative, given the increasing trajectories of the drivers of extinction and their synergistic effects. Future losses easily may amount to a further rapid defaunation of the globe and comparable losses in the diversity of plants (36), including the local (and eventually global) defaunation-driven coextinction of plants (3, 20). The likelihood of this rapid defaunation lies in the proximate causes of population extinctions: habitat conversion, climate disruption, overexploitation, toxification, species invasions, disease, and (potentially) large-scale nuclear war—all tied to one another in complex patterns and usually reinforcing each other's impacts. Much less frequently mentioned are, however, the ultimate drivers of those immediate causes of biotic destruction, namely, human overpopulation and continued population growth, and overconsumption, especially by the rich. These drivers, all of which trace to the fiction that perpetual growth can occur on a finite planet, are themselves increasing rapidly. Thus, we emphasize that the sixth mass extinction is already here and the window for effective action is very short, probably two or three decades at most (11, 48). All signs point to ever more powerful assaults on biodiversity in the next two decades, painting a dismal picture of the future of life, including human life.

Methods

For full methods, please see *SI Appendix*. We determined the number of decreasing vertebrate species using the IUCN (28) Red List of Threatened Species. In the IUCN, species are classified as decreasing, stable, or increasing (see also ref. 33). Either range contraction (population extinction) or reduction in numbers in extant populations determines whether a species is decreasing. We used the IUCN maps of terrestrial vertebrates (i.e., mammals, birds, reptiles, and amphibians) to create the global maps of number of species (richness) and of decreasing species, and percentage of decreasing species in relation to total species richness. The distribution of all of the species was superimposed in a 22,000 grid of 10,000-km^2 quadrats covering the continental lands. For the grid, a Lambert azimuthal equal-area projection was used (see ref. 49 for details of the projection methods). In our analyses a critical issue is how grid squares and populations correspond. This is a very difficult problem that varies with definitions of species. (In this paper, we stick with the classic biological definition of species.) The number of populations also varies from species to species; for example, a highly phylopatric species would have more populations per square than a very vagile species, and species with different mating systems would have different estimates of numbers of Mendelian populations, and these would not be the same as estimates of number of demographic units (50). For the purposes of understanding the annihilation, these differences are not critical. For example, if we have lost 90% of the lion's geographic range, whether this amounts to 10,000 demographic units or 4,000 Mendelian populations is trivial in the present context. It would be extremely useful if we had much more information on population structure for all vertebrates, but this is a major, pending agenda.

The population extinction analysis was conducted on 177 mammalian species occurring on five continents. Specifically, we analyzed 54 species in Africa, 14 in Asia, 57 in Australia, 15 in Europe, and 35 in America. The historical distribution was gathered from specialized literature (see details in ref. 26) and the current distribution from IUCN (28). Historic and current ranges were digitized as geographic information system polygons and elaborated in ArcGis 10.1 (51). For each species, we calculated the area of the historical and present distribution (in square kilometers) to estimate the percentage of lost area and the percentage of area where the species are extant. A caveat of these estimates regards how representative the sample of 177 species is. We recognize a bias in that the data include a large number of medium- and large-sized species, for which the best information is available. However, given that such medium and large species are the most seriously threatened by the predominant proximate drivers of defaunation (2, 3), the likely bias against small-sized species should not affect our overall interpretation of results.

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