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Global protected areas seem insufficient to safeguard half of the world's mammals from human-induced extinction

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Protected areas (PAs) are a cornerstone of global conservation and central to international plans to minimize global extinctions. During the coming century, global ecosystem destruction and fragmentation associated with increased human population and economic activity could make the long-term survival of most terrestrial vertebrates even more dependent on PAs. However, the capacity of the current global PA network to sustain species for the long term is unknown. Here, we explore this question for all nonvolant terrestrial mammals for which we found sufficient data, ∼4,000 species. We first estimate the potential population size of each such mammal species in each PA and then use three different criteria to estimate if solely the current global network of PAs might be sufficient for their long-term survival. Our analyses suggest that current PAs may fail to provide robust protection for about half the species analyzed, including most species currently listed as threatened with extinction and a third of species not currently listed as threatened. Hundreds of mammal species appear to have no viable protected populations. Underprotected species were found across all body sizes, taxonomic groups, and geographic regions. Large-bodied mammals, endemic species, and those in high-biodiversity tropical regions were particularly poorly protected by existing PAs. As new international biodiversity targets are formulated, our results suggest that the global network of PAs must be greatly expanded and most importantly that PAs must be located in diverse regions that encompass species not currently protected and must be large enough to ensure that protected species can persist for the long term.

extinction risk | protected areas | mammals | land-use change | gap analysis

Significance

Protected areas are vital for conserving global biodiversity, but we lack information on the extent to which the current global protected area network is able to prevent local extinctions. Here we investigate this by assessing the potential size of individual populations of nearly 4,000 terrestrial mammals within protected areas. We find that many existing protected areas are too small or too poorly connected to provide robust and resilient protection for almost all mammal species that are threatened with extinction and for over 1,000 species that are not currently threatened. These results highlight that global biodiversity targets must reflect ecological realities by incorporating spatial structure and estimates of population viability, rather than relying simply on the total area of land protected.

Wild mammals are declining or being lost from ecosystems across the world (1, 2) as natural habitats are fragmented and replaced with human-dominated lands unsuitable for their survival (3) and as individual populations are reduced by hunting, collecting, human-wildlife conflict, climate change, and pollution (1, 4). If historical trends continue, global growing per capita consumption of food, timber, and other natural resources, combined with a global population of perhaps 10.5 billion to 11 billion people by 2100 (5), will likely require millions of square kilometers of land cleared for agriculture (6–9), timber, roadways, powerline and pipeline rights-of-way, and urban expansion. The resultant ecosystem destruction would also fragment remaining natural habitats (10), further isolating the few remaining habitat patches protected by either law or circumstances (11–15) and potentially resulting in much of the world having heavily modified, depauperate landscapes like those across much of Europe and the United States today.

These processes would fragment populations of wild mammals into smaller and more isolated populations within habitat patches. Each such population could be unlikely to survive in the long term, with a higher risk of it and its unique genetics going locally extinct (16, 17). These local extinction events—individual populations being lost from habitat fragments—may appear unimportant at a global level, but if most local populations are too small to survive in the long term, then the entire species may decline catastrophically and at worst become globally extinct (1). Ensuring that individual populations within PAs are large enough to survive in the long term is therefore of critical importance for conserving global biodiversity.

Ensuring the long-term persistence of sufficiently large patches of natural habitats will undoubtedly require proactive efforts to reduce demand for agricultural land (7, 9). However, even large surviving habitat fragments may not preserve biodiversity if they are not formally managed as PAs because of human use and management or natural resource exploitation. In contrast, when properly managed, PAs can, within their boundaries, slow or stop habitat destruction (18), reduce mortality from hunting and disturbance (19), and thus act as potentially the last remaining strongholds for many mammal species (14). Thus, while unprotected habitats will almost certainly remain

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important for some species, in many regions PAs may be the only sites capable of supporting the truly long-term survival of many species.

In response to this challenge, the international community committed to conserving 17% of Earth's terrestrial surface in representative and connected PAs by 2020 (20). However, determining if the 17% target, or alternative targets currently under consideration (21–23), are sufficient requires understanding the capacity of current PAs to conserve biodiversity and the nature of any shortfalls (21, 23, 24). In particular, the population of each species within a PA must be sufficiently large to survive long term in that PA or to be periodically rescued by movement from a nearby, well-connected PA. In addition, even those populations large enough to survive demographic and environmental stochasticity can be vulnerable to natural disasters (25), disease outbreaks (26, 27), and climate change (28) or to changes in governance (29) and social and political upheaval (30). An adequate PA network must therefore be resilient to the loss of individual populations and PAs and should include, for each species, multiple protected populations, preferably across multiple countries or regions, with a sufficient number of populations of each species large enough to have a realistic chance of long-term survival. Given the trends described above, it is plausible that the long-term survival of much of Earth's biodiversity will ultimately hinge on the network of PAs that are established and properly functioning in the near future (31). Timing is of the essence since ecosystem regeneration or restoration can take decades to a century and may not result in biological communities comparable to those present before disturbance, with habitat specialist species in particular likely to be lost (32, 33).

Previous analyses have identified considerable shortfalls in the global PA network, with many species having little suitable habitat, or only small proportions of their range, within PA boundaries (23, 24, 34, 35). Here we build on these insightful analyses by accounting for 1) the ecological spatial structure of the PA network, 2) the likely population sizes of each mammal species in each PA, and 3) for each species, the number and spatial distribution of its populations across all PAs (36, 37). In particular, we expand on previous work (23, 24, 34–40) to explore which, and how many, species of terrestrial mammals would be likely to avoid extinction if their long-term survival depended solely to the existing global network of PAs.

Our analyses include all nonvolant terrestrial mammal species for which we could find sufficient data, ranging from small to large bodied, from locally rare to locally abundant, from carnivore to herbivore to omnivore, and from range-restricted species to those found across multiple continents. For each of these 3,834 species (70% of all mammal species), we first adapted methods used in regional analyses (37–39) to estimate the potential size of each individual population within a PA (*Methods*). We then assessed whether each individual population in a PA was likely to be large enough to survive in the long term using a series of well-defined criteria. Finally, we evaluated the resilience of the global PA network for each species by determining how many viable protected populations exist for each species and by evaluating the distribution of these populations across countries and ecoregions (*Methods*).

Assessing whether a species' constituent populations are large enough to survive in the long term is critical for understanding a species' extinction risk (1, 41, 42). However, the minimum population size needed to survive will vary with a species' biology and ecology, with environmental and climatic factors, with the length of survival time (survival for 1,000 y will require a larger population than survival for 100 y), and with the desired certainty of survival (a 99% chance of survival will require a larger population than a 95% chance) (42). Performing a robust population viability analysis for each protected population of terrestrial mammals in the world is impractical, as such calculations require detailed knowledge of species' ecological and life-history traits, precise environmental conditions (e.g., environmental variability), and the presence and strength of anthropogenic pressures (e.g., hunting). Instead,to estimate population viability, that is, whether population size was large enough for its long-term survival, we compared each estimated population size against three previously defined criteria of population viability.

Trait-based viability criterion: First, we used relationships between life-history traits and body mass to estimate the minimum population size required for the population to have a 95% probability of surviving for 100 y (43), terming this the trait-based criterion. The estimated critical population sizes range from over 5,000 individuals for the smallest mammals, with body masses < 3 g (e.g., the Sulawesi tiny shrew *Crocidura levicula*, body mass of 1.8 g); to ∼60 individuals for a midsized mammal, with a body mass of around 1 kg; to fewer than 20 individuals for large-bodied mammals, with body masses over 50 kg. For most species, this was the least rigorous criterion (lowest population sizes) and can be viewed as sufficient only if PAs are to act as temporary refuges, rather than as a long-term solution to biodiversity loss.

500-individuals viability criterion: Second, we used a population size of 500 individuals (the 500-individuals criterion), based on a standard, if controversial, benchmark for population viability (44–47). This criterion required a higher population size than the trait-based criterion for 75.7% of species, representing a more robust target for longer-term conservation of most mammal species.

40-generations viability criterion: Finally, we used a population size of 6,020 individuals based on empirically derived estimates of the minimum population size required to provide a 99% probability of a population surviving for 40 generations (the 40-generations criterion). The value of 6,020 individuals was the median of 52 such estimates for terrestrial mammal species (42) and was the most conservative criterion for all but three species of tiny-bodied shrews. The 40-generation criterion is particularly relevant if PAs are likely to be the major locations that are of sufficient size and that provide sufficient protection to assure the long-term survival of most mammal species within them.

These three criteria therefore provide a range of estimates of how secure each population is, allowing us to understand the sensitivity of our conclusions to variation in estimates of the population size required for survival within a PA. When using each of these three criteria, we classified any mammal species with 10 or fewer viable protected populations worldwide as underprotected and those with no viable protected populations as unprotected.

Results

Our analysis shows that a large proportion of the world's mammals are unlikely to be adequately protected from extinction by the current global PA network. This result is robust to our choice of population viability criteria, assumptions about species dispersal, and the number of protected populations required to be classed as adequately protected. Underprotected species were found in all regions of the world and across all taxonomic groups, body mass classes, degrees of endemism, and levels of extinction risk.

Using the trait-based viability criterion (the least rigorous of the three viability criteria for most species analyzed), we estimate that 1,536 mammal species, which is 40.1% of species analyzed, are globally underprotected (≤10 protected populations) by the current network of PAs (Fig. 1). Reducing the number of populations required for a species to be classified as underprotected did not qualitatively change this result: 1,217 species (31.7%) had five or fewer viable protected populations (Fig. 2). There were 641 species (16.7%) with only a single such population and 248 species (6.5%) that did not have a single viable protected population based on our criteria (Fig. 2). Moreover, our analyses suggest that most species listed as threatened by the International Union for Conservation of Nature (IUCN) were underprotected: 69.1% of threatened species analyzed (621 of 899) had 10 or fewer viable protected populations, with 13.8% (124 species) unprotected (Figs. 1 and 2). These values were robust to the inclusion or not of dispersal between protected habitat patches, and henceforth, we report only results without dispersal (*SI Appendix*, Fig. S3).

The stricter 40-generations viability criterion identified a total of 56.2% of mammal species (2,156 species) as underprotected, including 91.0% of threatened species that we analyzed (818 species). Some 576 species (15.0% of the total) were classed as unprotected, including 319 of those already listed as threatened with extinction (35.5% of all threatened species). Results for the 500-individuals viability criterion were intermediate: 44.1% (1,691 species) having 10 or fewer viable protected populations and 7.5% (289 species) having none, with 702 and 155 of these, respectively, classified as threatened.

Both the number and the proportion of underprotected species were highest in the most biodiverse regions of the world (Fig. 3 and *SI Appendix*, Fig. S7). South, Southeast, and East Asia; Latin America and the Caribbean; and Africa all had both more underprotected mammal species and a higher proportion of their total mammal species underprotected than did other

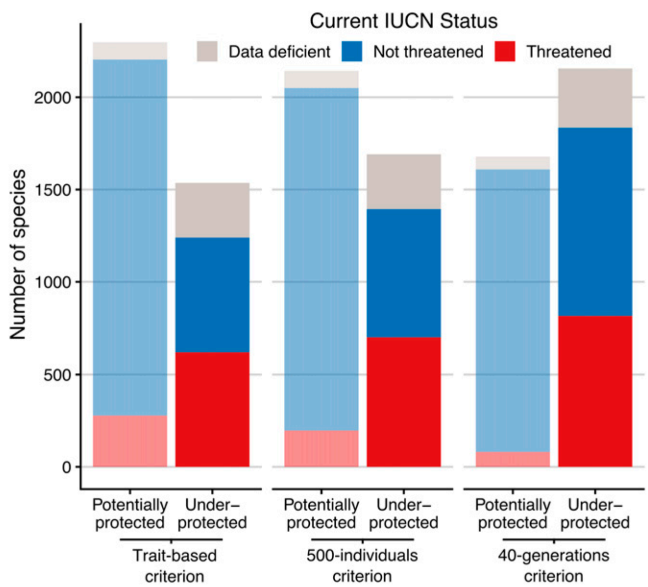

Fig. 1. Number of underprotected species, which have no more than 10 viable protected populations, evaluated for each of the three protection criteria. Dark bars are underprotected. Lighter bars are potentially protected species with more than 10 such populations. Species are divided by those listed as threatened (vulnerable, endangered, or critically endangered, in reds), lower risk (near threatened or least concern, in blues), or data deficient (in grays) by the IUCN (48).

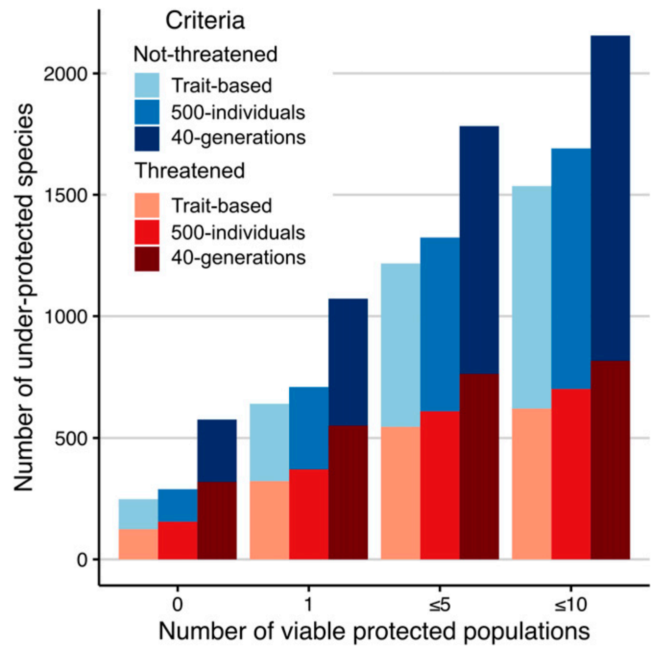

Fig. 2. The number of species with different numbers of viable protected populations based on the three different population criteria (light bars = trait-based criterion, medium bars = 500-individuals criterion, dark bars = 40-generations criterion) and on the number of viable populations used to classify a species as underprotected. Bar height shows the total number of species, separated into those classified as threatened by the IUCN (vulnerable, endangered, or critically endangered, in reds), and those classified as lower risk (near threatened or least concern, in blues).

regions, with the exception of Oceania, which also had high levels of underprotection. These three regions, respectively, had 494, 433, and 380 mammal species with 10 or fewer viable protected populations using the trait-based estimate for viability and 70, 62, and 65 species that were unprotected, with no viable protected populations. The numbers of underprotected mammal species in these three regions increased to 707, 623, and 557 species underprotected using the 40-generations criterion (62.9%, 52.9%, and 55.3% of all species in the respective regions), including over 200 species in each region currently listed as threated and 200, 131, and 164 classed as unprotected. In contrast, fewer than 100 species and less than 30% of all species present were deemed underprotected in North America or Europe, even under the 40-generations criterion, with 18 and 11 species, respectively, classed as unprotected.

Species endemic to a single country were particularly poorly protected: 67.7% of endemic species had 10 or fewer viable protected populations under the trait-based viability criterion, compared with 19.8% of nonendemic species (1,098 vs. 438 species). These numbers rose to 1,143 and 1,275 species (70.4% and 78.6%), respectively, under the 500-individuals and 40-generations viability criteria. Indeed, small-bodied endemic species constituted 65.3%, 60.9%, and 53.0% of all underprotected species under each viability criterion. While some of this effect occurs because endemic species have smaller ranges, and therefore are present in fewer PAs, we also found that 15.2% of endemic species were unprotected, with no viable protected populations, using the trait-based estimate for population viability, a percentage that rose to 16.5% and 25.7% under the 500-individuals and 40-generations viability criteria, respectively.

Underprotected species were found across all body masses (*SI Appendix*, Supplementary Results and Figs. S4 and S5) and taxa (*SI Appendix*, Supplementary Results and Figs. S6 and S7),

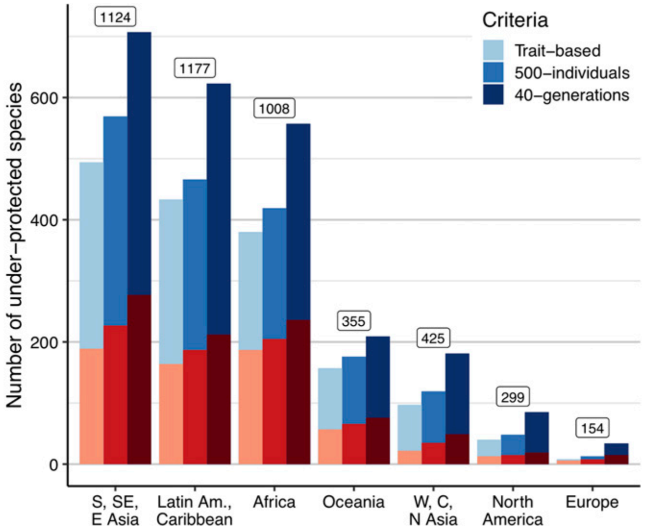

Fig. 3. Number of underprotected species (10 or fewer viable protected populations) in different regions based on the three different population criteria (light bars = trait-based criterion, medium bars = 500-individuals criterion, dark bars = 40-generations criterion; S = south, SE = southeast, E = east, W = west, C = central, N = north). Bar height shows the total number of species, separated into those classified as threatened by the IUCN (vulnerable + endangered + critically endangered, in reds), and those classified by the IUCN as lower risk (near threatened + least concern, in blues). Numbers above bars are the total number of species analyzed in each region. See *SI Appendix*, Fig. S4 for the proportion of species underprotected in each region.

although far more small-bodied species were underprotected due to their far higher species richness (*SI Appendix*, Supplementary Results and Fig. S5). Due to their relatively long generation times, large-bodied species such as even- and odd-toed ungulates, elephants, carnivores, and primates had relatively low proportions of underprotected species using the trait-based estimate of population viability, which was based on population survival for 100 y. In contrast, these groups had very high proportions of underprotected species using the more realistic 500-individuals and 40-generations viability criteria due to lower population densities requiring larger PAs for species to have sufficient population sizes. The number of small-bodied species, and taxa such as rodents and Eulipotyphla, classed as underprotected did increase with stricter viability criteria, but to a far lesser extent.

The majority of underprotected species only had viable protected populations in a single country, if any (*SI Appendix*, Fig. S9): 1,219 species using the trait-based viability criterion (79.4% of all underprotected species); 1,285 species (76.0%) using the 500-individuals viability criterion; and 1,551 species (71.9%) using the 40-generations viability criterion. Most underprotected species were also found in two or fewer ecoregions: 1,043 species (67.9% of all underprotected species), 1,086 species (64.2%), and 1,295 species (60.1%), respectively, under the trait-based, 500-individuals, and 40-generations viability criteria.

Discussion

Our results demonstrate that the current global PA network is extremely unlikely to safeguard the world's mammals on its own. In particular, we highlight three issues of critical importance for biodiversity conservation.

First, the vast majority of mammal species currently listed as threatened by the IUCN are estimated to be underprotected by the current PA network. These species included almost all of the largest land mammals—elephants and rhinoceroses—many large-bodied ungulates, such as antelope and wild horses; and medium-sized species, such as African wild dog *Lycaon pictus*. However, this group also includes some of the world's smallest species, particularly those with restricted ranges, such as the Sri Lankan shrew *Suncus fellowesgordoni*. This conclusion supports previous analyses highlighting the increase in the number and/or size of PAs and the overall conservation efforts and funding that will be required to conserve threatened species in the long term (23, 35, 49, 50). By including species-specific habitat suitability, species- and location-specific population densities, and the ecological spatial structure of populations, our results provide the clearest evidence yet that international targets for PA coverage need to explicitly include an understanding of which species are being protected within PAs and exactly what their habitat requirements are. Importantly, this finding supports previous calls for the strategic expansion of PAs into specific ecosystems that require additional protection, rather than relying on arbitrary area-based targets (21–23, 40, 51). Our results emphasize that the ultimate goal of PAs needs to be the avoidance of population extinctions: only by focusing on the maintenance of viable populations of species can regional or global extinctions be avoided. Conversely, focusing on area-based targets may distract from this aim or could even provide perverse incentives to expand PAs into remote areas with low opportunity costs that are unlikely to be at risk from agriculture or encroachment, rather than ensuring establishment of a PA network which is truly effective in maintaining global biodiversity (22, 51).

Second, our analyses estimate that over 1,000 additional mammal species that are not currently listed as threatened may also be underprotected. These species, which represent more than a third of nonvolant mammal species not classified as threatened, include several very large species, such as white rhinoceros *Ceratotherium simum*, American bison *Bison bison,* and giant eland *Tragelaphus derbianus;* medium-bodied species, including jungle cat *Felis chaus* and several howler monkey *Alouatta* spp.; and hundreds of small-bodied species of rodents and insectivorous species, such as the volcano shrew *Sylvisorex vulcanorum* native to central Africa and the short-faced mole *Scaptochirus moschatus* of China. Many of these smaller species in particular are poorly studied, lack detailed population data (48), and are unlikely to be the focus of current conservation efforts. They may therefore be at risk for unnoticed long-term declines or even regional or global extinctions as economic forces and human population growth drive widespread land-use change and restrict ever more species completely or largely to existing PAs. Our results suggest that these species merit increased consideration within conservation strategies. This is particularly important because proactive policies to prevent new extinction threats are likely to be more effective—and potentially easier to implement and much less expensive—than reversing habitat loss and population declines once they have occurred (52).

Third, our results highlight the need for policy makers and conservationists to take a holistic approach to safeguarding biodiversity by reducing the demand for additional land for agriculture, development, or timber harvest, as driven by a larger and wealthier populace, and by greatly expanding the PA network (9, 53). In the absence of international aid, expanding PAs to the extent required to adequately protect species may be politically, economically, and socially difficult (54) in low- and middle-income countries. Such countries often hold disproportionately large numbers of underprotected species but also are likely to see the greatest increases in economic and population growth and in future demand for agricultural, forestry, and urban lands (5, 7, 55, 56). PA expansion may also be unlikely or unfeasible for underresourced conservation budgets in such countries (49), particularly given the likely trade-offs between expansion and more effective management of existing PAs (57). In addition, established PAs may be at risk across the world. For example, recent controversies over PAs in the United States and Brazil highlight how even in countries with extensive conservation networks, political changes can rapidly lead to the downgrading, downsizing, or degazettement of PAs and the subsequent losses of habitats and species within them (58–61). However, proactive efforts to reduce demand for additional agricultural land through aid-supported policies to generate higher yields, to reduce food waste, to eat healthier diets, and to import those crops produced in excess in other countries could both increase food security and reduce the need for new agricultural lands, thus making conservation more feasible (7, 9, 62).

Our analyses suggest that the current PA network is too small and poorly connected to provide resilient protection for many mammalian species. We estimate that most underprotected species have a viable protected population in only one or two countries or ecoregions and will therefore be particularly vulnerable to perturbations such as climate change, disease outbreaks (63, 64), changes in public policy priorities and the downgrading of PAs (29), major societal transformations such as warfare (30), or economic downturns. The COVID-19 pandemic, for example, has resulted in widespread loss of tourism revenue to African PAs, potentially reducing management effectiveness and the ability to support local livelihoods (65).

As shown in Figs. 1–3, our findings are robust to uncertainties in minimum viable population estimates, dispersal capabilities, and the number of viable protected populations required to be classed as underprotected. Which of our three population criteria is viewed as most appropriate will depend on system- and species-specific factors and especially whether PAs are viewed, as done here, as essential long-term sanctuaries for biodiversity or, alternatively, as a short-term "ark" to conserve species while longer-term solutions are found. However, in the face of the ongoing increases in population, economic activity, food demand, land clearing, and habitat destruction globally (7), we suggest that PAs may well become the only secure habitats during the coming decades and centuries and that the most conservative of our three criteria should be adopted. Indeed, the short-term nature of the trait-based population criterion means they may be too low to provide resilient protection. For example, the trait-based criterion for 356 species was set at 25 or fewer individuals, but populations this small would be extremely vulnerable to environmental, political, and economic stochasticity and have a high probability of stochastic extinction for time periods greater than 100 y. We therefore suggest that a strict criterion, such as the 40-generations viability criterion, will be essential for minimizing species extinctions for the long term.

The high level of underprotection we identify occurs despite our inclusion of all biodiversity-centric PAs, including many that are ineffectively managed (40, 66), and despite our optimistic assumption that all PAs within a species' range and with suitable habitat would hold populations of a species even if, at present, they do not. Restricting PA coverage to effectively managed reserves would likely reduce coverage further, since only 22% of analyzed PAs were found to have adequate staffing and budgets (40) and since populations of wild species have been declining in many PAs (67). Additional data on the presence and abundance of species within each PA will be essential for improving the rigor of our estimates and for ensuring better planning of more efficient and effective PAs (68).

Perhaps because we analyzed the spatial structure and separation of populations, population density, and probability of population persistence, we identified additional species as underprotected compared with some prior estimates based on the sum total of species' range areas (34). Moreover, our analyses suggest that more large-bodied species will be at risk for extinction in the long term if future land clearing forces their survival to be reliant on PAs. This is particularly worrying for carnivores, ungulates, elephants, and primates for which there can be serious human-wildlife conflict because of crop raiding, livestock predation, or even human deaths (69) and because of hunting, whether for food or income. These types of species are unlikely to survive in, or even successfully move through, areas outside PAs if human-dominated lands expand as expected.

PAs form the basis of much biodiversity conservation across the world and are vital for maintaining populations and ensuring the persistence of habitats and species. However, our analyses suggest that the current PA network maybe insufficient to assure, on its own, the long-term survival of between 1,700 and 2,500 species of mammals, which represent 44% to 65% of terrestrial nonvolant mammals. These species seem to be at serious risk of local, regional, or even global extinction if current trends in the loss of their natural habitats continue and if PAs thus contain their only protected populations. The long-term survival of about half of Earth's terrestrial mammal diversity will likely require a coordinated plan to reduce humanity's demand for croplands, forestry lands, and other resources (31); concerted efforts to protect biodiversity outside of PAs; and an ambitious and strategic program to identify the best locations for additional PAs and to globally increase the size, number, and connectivity of PAs.

Methods

To assess the potential of the global PA network to safeguard wildlife, we need to know the following for each species and each PA: the number of individuals of that species that would likely occur within each PA, whether each such population is large enough to survive in the long term, and the number and distribution of these viable protected populations. It is vital to assess these questions for as many species as possible, but few empirical data exist on population sizes for the majority of species. We therefore modeled the potential of the global PA network to provide long-term protection using existing data on the ranges, habitat preferences, and potential population densities of 3,834 terrestrial mammal species. This analysis of the global PA network's ability to protect the majority of species within a taxon takes into account the spatial structure of the network.

To do this, we adapted methods (36, 37, 39) to first estimate the potential population size of each species within individual PAs and then assess the likelihood of their survival. Potential population size depends on the area of suitable habitat available and the population density of a species. As described below, we therefore 1) calculated the area of suitable habitat for each species within the world's PAs, splitting habitat patches in unconnected PAs, and 2) estimated the population density of each species within each PA based on phylogenetic, life-history, and environmental data, combining these data with those from step 1 to 3) provide estimates of potential population sizes in each PA. In step 4, we assessed each population as large enough to survive in the long term or not. Given the uncertainty over how large populations need to be to survive in the long term, we assessed each population against three different viability criteria. Finally, we evaluated the resilience of the global PA network for each species on the basis of the number of viable populations and their distribution across countries and ecoregions.

Step 1: Calculating the Area of Suitable Habitat within PAs Not every PA within a species' range will contain suitable habitat for that species and thus be relevant to its survival. We therefore quantified the overlap between suitable habitat and terrestrial PAs by clipping previously published maps of suitable habitat for each species (70) with the February 2019 edition of the World Database on Protected Areas (71), excluding all suitable habitat that was outside PA boundaries. We rasterized all spatial data to a 2.25-km^2 resolution and reprojected them to a Mollweide equal area projection. We followed recommendations for excluding nonbiodiversity-focused PAs and for estimating the boundaries of areas missing spatial data [(71); *SI Appendix* for details]. We excluded marine species, those for which habitat maps were not available, and bats (Chiroptera) due to a lack of data on species population densities (described later). This resulted in a total of 3,834 species across 25 orders (*SI Appendix* for details).

We examined the size of individual patches of protected habitat, rather than the total area protected across all PAs, as we were interested in the viability of individual populations. To do this, we categorized all habitat patches within a group of adjacent PAs (i.e., those that were not separated by unprotected land) as linked and supporting a single population. We categorized habitat patches within nonadjacent PAs as supporting separate populations, even if they were connected by unprotected suitable habitat (*SI Appendix*, Fig. S1). We then summed the area of all linked protected habitat patches to calculate the total area of habitat supporting each population. Categorizing habitat in this way assumes that species cannot effectively disperse from one population to another because of higher mortality rates outside of a PA and/or the hard barriers that surround many PAs (72). To test the sensitivity of our results to this assumption, we also performed analyses that allowed for size-dependent dispersal across unprotected land (*SI Appendix*, Fig. S2).

Step 2: Estimating Species- and Location-Specific Population Estimates Data on population densities, i.e., the observed number of individuals per square kilometer, are sparse for many species. We therefore followed Santini et al.'s (73) approach and estimated the population density of each species (D) in each PA based on body mass in grams (M), net primary productivity (NPP), seasonality of precipitation (P_{cv}), mammalian species richness (R), and phylogeny. To do this, we first used a database of 8,076 records of population densities for 616 mammal species (74) to model the relationships between these five variables and reported population densities. This database has broad geographic coverage (although with relatively few records in high latitudes in Asia and desert regions) and at least one record from 60% of families and 100% of orders included in our study (74). We used multimodel inference by first defining a maximal model, based on Santini et al. (73), with all explanatory variables–including order, family, and species as nested random effects; a cubic effect for body mass; and quadratic effects for *NPP* and seasonality–such that

$$\log_{10}D \sim \log_{10}M + \log_{10}M^2 + \log_{10}M^3 + \log_{10}NPP + \log_{10}NPP^2 + P_{cv} + P_{cv}^2 + R.$$

We standardized the variables by subtracting the mean and dividing by the SD, and we used the dredge() function from the {lme4} package (75) in R version 3.6.0 (76) to fit all feasible component models (i.e., only including quadratic and cubic terms if the linear term was also present in the model) using maximum likelihood. We weighted these models by Akaike's information criterion adjusted for small sample sizes ($wAIC_c$) and selected the subset of models in which $\sum wAIC_c > 0.99$. For coefficient estimation, we then refitted these models with the raw (nonstandardized) data, using restricted maximum likelihood and weighted the coefficients by $wAIC_c$ (77). This process resulted in two models being averaged, with $wAIC_c$ of 0.75 and 0.25, respectively, and Nakagawa's conditional pseudo-R^2 values (78) of 0.771 and 0.770, respectively. The averaged model used for prediction (i.e., with nonstandardized coefficients) was

$$\log_{10}D = -26.2 + 1.63\log_{10}M - 0.729\log_{10}M^2 - 0.0722\log_{10}M^3 + 4.81\log_{10}NPP - 0.208\log_{10}NPP^2 - 0.00495P_{cv} + 1.16P_{cv}^2 - 0.00197R.$$

After fitting the models, we used them to estimate the population density of each species in each protected population. We extracted NPP, P_{cv}, and species richness estimates for each protected habitat patch from step 1, taking the mean value for all the cells in a patch. We used these, together with species-specific estimates of body mass (79–81) and the weighted model coefficients, to estimate population density of each species in each protected habitat patch. We could only estimate species-specific random effect sizes for the 616 species in the database and so used the effect sizes for family and order for the remaining 3,218.

To estimate the potential population size of each species within each PA, we then multiplied the area of each protected habitat patch–from step 1–with the species' estimated population density.

Step 3: Estimating Viable Population Sizes A population, even if perfectly protected from anthropogenic threats, will only survive if it is large enough to avoid systematically declining due to demographic or environmental stochasticity or genetic effects (16). For a PA to meaningfully contribute to a species' long-term survival, it needs to have the potential to support a minimum viable population–the fewest number of individuals needed "for a population or species to have a predetermined probability of persistence for a given length of time" (82). The size of this minimum viable population will depend on species- and location-specific variables such as population growth rates and environmental variability, as well as–crucially for conservation planning–the probability of survival that is being aimed for and the time period that population viability is measured over.

The location-specific data requirements for estimating minimum viable populations mean that obtaining accurate estimates for individual species in individual PAs is unfeasible across large numbers of species and regions. Therefore, we instead used three different criteria to estimate if a population in a PA is likely to survive (42, 43, 83). One major difference among these criteria is the length of time during which a population seems likely to be viable. The criteria ranged from relatively short-term viability to those aimed at conserving evolutionary potential over far longer time periods (Table 1).

The first criterion (henceforth the trait-based estimate) uses relationships between life-history traits and body mass to estimate the minimum population size required for the population to have a 95% probability of surviving for 100 y (43). The trait-based estimate ranged from 15 individuals for the mammal species with the largest body mass, longest generation times, and lowest reproductive rates to 7,700 individuals for mammals with the smallest body sizes, shortest generation times, and highest reproductive rates (*SI Appendix*). In contrast, the other criteria did not vary among species. The second criterion (500 individuals) was set at 500 individuals for all species based on a standard target for maintaining populations in the face of demographic stochasticity, which–while controversial–is often used in conservation planning (44–47). The 500-individuals criterion was higher than the trait-based estimate for 75.7% of the mammal species we analyzed. The final criterion (40 generations) was based on empirically derived estimates of the minimum population sizes to provide a 99% probability of a population surviving for 40 generations (42). These estimates were most strongly influenced by population growth rates, but data on these are not available for most species and locations. We therefore set the target of 40 generations for all species as the median of the 52 species-specific estimates, a value of 6,020 individuals. These criteria differ in both the length of time they are targeted at and the probability of survival, providing a range of possible targets from relatively short-term protection to the long-term conservation of evolutionary potential. For all species with generation times > 2.5 y, the 40-generations criterion represents a longer-term target than the trait-based estimate, in addition to a higher probability of population survival (99% vs. 95%). These factors combined meant that the 40-generations criterion was higher than the trait-based estimate for all but three of the species we analyzed (all shrews) and is, by definition, higher than the 500-individuals target. In contrast, which of the 500-individual or trait-based criterion was higher depended on species, with 932 species (24.3%) having a trait-based estimate higher than 500 individuals. Almost all of these were small-bodied, rapidly reproducing species in the orders Eulipotyphla (shrews, hedgehogs, and moles; 340 species) or Rodentia (rodents; 483 species).

Step 4: Assessing the Resilience of the Global PA Network For each species, we used the results from steps 3 and 4 to calculate how many protected habitats were large enough to hold a species population greater than that set by each of the three criteria, and we defined each such habitat patch as a viable protected population for that species.

A resilient global PA system will require multiple, independent, viable populations, preferably spread across multiple countries and ecoregions. We therefore classified species with fewer than 10 viable protected populations as

Table 1. Different population viability criteria used in the analysis, their justification, and the population size used

Criterion	Description	Justification/reference	Population size
Trait-based estimate	Population size required for a 95% probability of surviving for 100 y	Based on body mass which scales with many life-history traits that determine probable minimum viable populations (43)	Species specific; min = 15, max = 7,700
500 individuals	Standardized target for conservation planning	Frequently used in conservation planning but not explicitly linked to the probability of persistence over a defined time period (44–47)	500
40 generations	Median estimates of population size required for a 99% probability of for 40 generations	Median of 53 species-specific estimates from published literature (42); the median value was used, rather than estimating sizes for individual species, due to a lack of data on population growth rates Note: Using generation times means the length of time populations were estimated to persist for varies considerably, from <80 to ∼1,000 y	6,020

underprotected, although as the number of such populations required for the long-term survival of a species will vary with environmental and human factors, we repeated analyses classifying species as underprotected with one and five viable protected populations. We classified species with no viable PAs as unprotected. For each species, we also calculated the number of countries that held viable protected populations.

Data Availability. R code data have been deposited at https://doi.org/10.5061/dryad.x3ffbg7md. All other study data are included in the article and/or supporting information.

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