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Prioritizing global land protection for population persistence can double the efficiency of habitat protection for reducing mammal extinction risk

Graphical abstract

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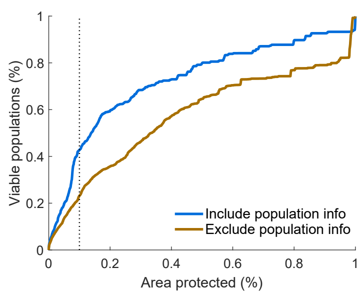
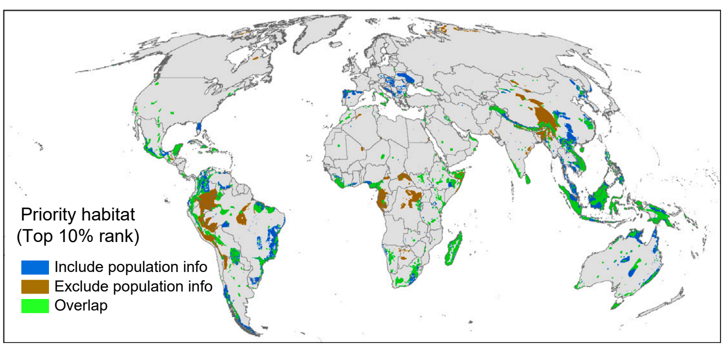


A. When information on the persistence needs of individual populations (blue) was included in habitat prioritization, the identified top 10% sites (dotted line) could support the viability of nearly twice (84% more) as many populations compared to a solution based on species distribution information only (red).

B. The differences in protection efficiency between prioritization approaches translates to some divergence in global locations of priority habitat. A comparison of the two approaches demonstrates that the locations of over 56% of the top 10% sites are distinct from each other. Ignoring population persistence needs could drive conservation actions towards places that inefficiently reduce extinction risks.

B



Highlights

- Prioritizing population-level habitat needs nearly halved species' extinction risk
- Only 8% of priority habitat for persistence falls within strict protection categories
- Over 50% of the global extent of priority habitat falls within just 7 countries
- Including conversion threat alters locations of over 50% of priority habitat extent

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In brief

To address the species extinction crisis driven by habitat loss, the Global Biodiversity Framework established preservation targets. Achieving these goals is hindered by limited resources and urgency. Our global prioritization merges data from 70,492 unique population maps and life history traits for 861 endangered terrestrial mammals. With the same amount of protection, this population-level integration doubles species' persistence compared to a conventional species distribution-based approach. Our evaluation of existing protection of identified priority areas will help nations reach conservation targets.

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Prioritizing global land protection for population persistence can double the efficiency of habitat protection for reducing mammal extinction risk

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SCIENCE FOR SOCIETY Amid an alarming surge in species extinction, the international community responded by endorsing the Kunming-Montreal Global Biodiversity Framework (GBF) in December 2022. This framework includes the ambitious "30 × 30" goal to safeguard 30% of Earth's surface by 2030. The challenge now lies in efficiently achieving these targets and minimizing extinction risks. Traditional global prioritizations ignore that global extinctions result from the local extinction of all individual populations. They are limited in focusing on efficiently protecting a fixed percentage of species' global distributions while neglecting the habitat needs for individual species populations to endure. To address this, we introduce an innovative prioritization that predicts the likelihood of population persistence based on habitat loss projections for threatened mammals. Our study will help nations and other actors reach conservation targets and curb extinction—the goal of the GBF.

SUMMARY

Halting the alarming rate of species extinction, driven primarily by habitat destruction, motivated the international community to adopt the Global Biodiversity Framework (2022) and its targets aimed at reversing habitat and species loss. Because of urgency and resource constraints, a key challenge is meeting targets effectively and efficiently. Here we conduct a global prioritization linking 70,492 unique population maps and life history characteristics for 861 threatened terrestrial mammal species. Incorporating individual population data to identify priority areas for conservation nearly doubled the likely long-term persistence of species for the same amount of land compared with a typical approach based on species distributions alone. We map and rank global mammal persistence priority areas and assess how well the current protected area (PA) system captures these important regions. Our results offer a clearer, quantifiable link between conservation actions and global extinction risk than previously possible at a global scale.

INTRODUCTION

Preventing the extinction of species is a core goal of biodiversity conservation and a task of increasing urgency. Species extinction rates are thousands of times the background rate,[1] and habitat loss and fragmentation are the primary driver of species decline globally.[2–5] Partly in response to this threat, various forms of habitat protection are pursued by governments, nongovernmental organizations, and private individuals and will form a core component of the Kunming-Montreal Global Biodiversity Framework (GBF).[6,7]

Terrestrial mammals are one of the most threatened species groups globally[8] and are often used to inform conservation prioritizations as direct conservation targets themselves (e.g., Brum et al.,[9] Carwardine et al.,[10] and Wilson et al.[11]) and as proxies for biodiversity in general (e.g., Visconti et al.[12] and Waldron et al.[13]). The objective of these prioritizations is to guide habitat protection actions toward areas that will be most cost efficient for conserving biodiversity. Most commonly, prioritizations have focused on efficiently protecting a percentage of species' global distributions,[10,14,15] sometimes adjusted for different dimensions of diversity.[9]

Conservation prioritizations typically ignore the fact that most species have multiple geographically distinct populations. Global extinctions are the result of all individual populations going extinct; thus, the percentage of the global species distribution that is protected may not be a good proxy of extinction risk.[16,17] The weak relationship between the portion of a species range protected and extinction risk is a well-recognized challenge for global-scale conservation planning.[18] Data and modeling advances in the last two decades have contributed to prioritization methods that account for habitat configuration on population-level persistence[19,20] or specifically account for population dynamics and species interactions.[21] However, these studies are confined to local or regional scales because of lack of global data and the computational challenge involved in dealing with complex non-linear interactions within these more realistic conservation problem formulations.

An additional challenge in global conservation prioritization is to effectively combine known factors that contribute to local and global extinction risk (e.g., habitat loss) and apply them to strategically prioritize habitat conservation efforts that effectively mitigate those risks. Despite the repeated calls for conservation actions that address habitat risks,[22–24] most conservation prioritizations ignore what would happen in the absence of potential protection or assume a simplistic scenario where all unprotected habitat becomes unsuitable for native species;[25,26] these simplistic assumptions result in overestimation of the expected benefits of conservation and misplacement of efforts toward areas that are *de facto* already protected by virtue of being "high and far" or "rock and ice" that ultimately deliver limited conservation additionality.[27] This problem is especially acute for global prioritization studies, given the scarcity of counterfactual analyses that estimate the potential impact of protected areas on conservation outcomes.[15,28,29]

Future habitat loss will be exacerbated by an increasing global human population that is expected to exceed 9 billion by 2050.[30] Combined with dietary shifts and increasing consumption of biofuels, this population is projected to require a doubling of current crop production.[31] To meet these rising demands, scenarios for 2050 envisage an expansion of urban areas[32] and cropland, with a concomitant conversion of forest and other natural habitats.[30] From a conservation planning perspective, the growing number of global land use projections offers an opportunity to assess biodiversity risk.[33,34] However, the coarse resolution and substantial heterogeneity across land use models[35] diminishes their utility for quantifying population-level persistence. An approach that does show promise for identifying population-level threats from habitat loss, and that we explore here, forgoes the extensive uncertainties associated with highly parameterized land use models to instead quantify spatially explicit development potential.[36,37]

Here, we conduct a prioritization, using the conservation planning software Zonation, to inform habitat protection investments of governments and other conservation actors as they seek to meet GBF targets. We do this by linking population maps and life history characteristics for 861 threatened terrestrial mammal species (excluding bats) to identify the best places to target for minimizing overall extinction risks. We then assess how well the current protected area (PA) systems capture these priority areas or how they can be expanded to avert mammal extinction risk. We also quantify how this prioritization changes when focused on areas likely to be under high development pressure in the future. We demonstrate that integration of population-level extinction risk nearly doubled the security of long-term species persistence compared with traditional prioritization approaches that only consider species distributions. We found that just 7 countries contain over 50% of the most important habitat for extinction risk reduction. Approximately 20% of this priority habitat is currently protected by the global PA network, with only 7.9% in strict protection categories. Finally, the urgency of the biodiversity crisis and the spirit of the GBF require the global community to not only provide efficient conservation solutions but also solutions that will be effective at halting how extinction occurs, one population at a time.

RESULTS

Global priorities for minimizing mammal extinction

The sites where habitat loss would result in the greatest global increase in extinction risk for threatened non-volant mammal species are distributed widely around the globe (Figure 1A) and not exclusively concentrated in areas of high richness of threatened mammal species (Figure 1B). Approximately one-third (33.7%) of top-ranked Zonation solutions (top 10% of habitat for avoiding mammal extinction, here called top-ranked or high-priority habitat) overlap sites with the top 10% highest species richness (5 species or more). Countries with the largest areas of high-priority habitats are also those with high biodiversity and high endemism more generally (Figure 2; Table S1). Just 7 of the 143 countries with high-priority habitat contain over 50% (51.6%) of these important areas. Indonesia has more than 1 million km^2 of high-priority habitat, and Brazil, Australia, and China each have over 500,000 km^2. Among countries with a high proportion of their land area in the top-ranked solutions, Brunei and Liberia stand out, with more than 90% of their area in high-priority habitat for threatened mammal persistence (Figure 2). Other countries with very high proportions

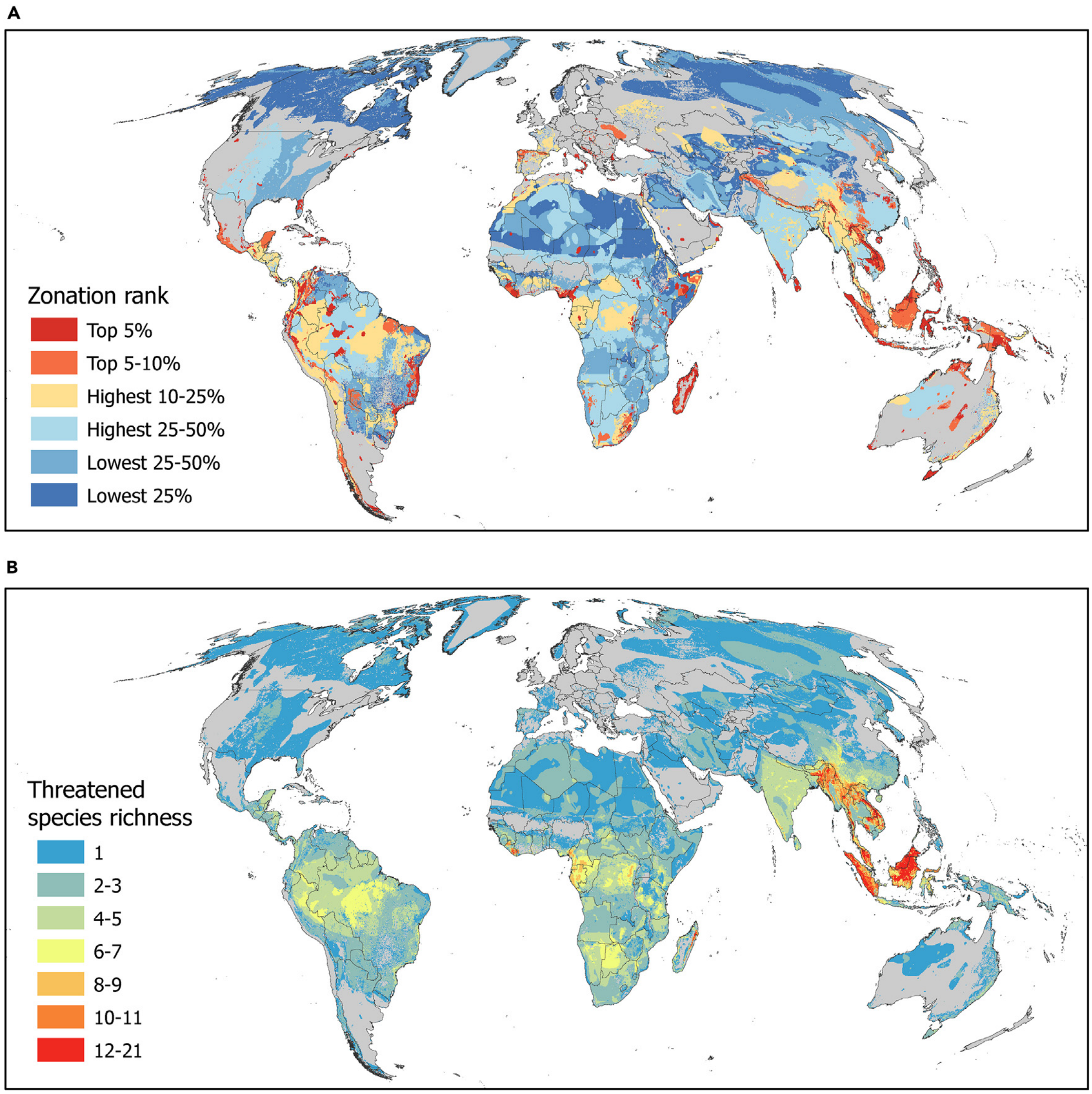

Figure 1. Zonation results from habitat prioritization for minimizing threatened mammal extinction
(A) Zonation percentage rank. Habitat with a higher rank is more important for mammal persistence.
(B) Species richness from mammal distribution data used in Zonation analysis. Gray regions are outside of threatened mammal species range (zero occurrence).

(>70%) of their land area in important habitat and with a very large (>250,000 km^2) total area of importance include Papua New Guinea, Malaysia, Indonesia, and Madagascar (Table S1).

Comparing prioritization approaches

Accounting explicitly for population persistence in the prioritization significantly improved the likely long-term persistence of species in comparison with a more traditional species-level prioritization (Figure 3). When information on the persistence needs of individual populations was included in the prioritization, the identified top 10% sites could support the viability of nearly twice (84% more) as many populations (30,132, 42.7% of total populations) in comparison with a solution based on species distribution information only (16,347, 23.2% of total). This means that, with the same amount of area, on average, twice as many populations could be preserved per species, increasing the security of their long-term persistence. Compared with the species-level prioritization, the population-level prioritization offers greater protection efficiency (for population persistence) at nearly every percent of habitat protected; the results do not merge until nearly 100% of habitat is protected. For example, only 13.8% of habitat protection is needed to maintain the persistence of 50% of the populations under the population-level approach compared with over 33% of habitat protection needed to offer the same persistence under the species-level approach.

The differences in protection efficiency between prioritization approaches translates to some divergence in global locations of priority habitat (Figure S1). A comparison of the two approaches demonstrates that the locations of over 56% of the top 10% sites are distinct from each other (Figure S1B). Perhaps

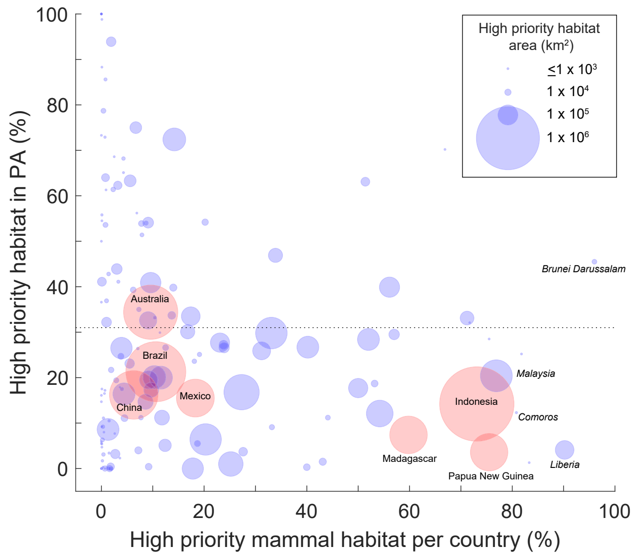

Figure 2. Scatterplot showing the percentage of high-priority (top 10%) habitat and the percentage protected by country

The size of each bubble represents the km^2 of high priority habitat for each country (N = 143 countries). Shown in red, and labeled, are the seven countries that cumulatively capture more than 50% (51.6%) of global high-priority habitat. Labeled in italics are additional countries that have greater than 75% of their land and at least 1,000 km^2 covered by high-priority habitat. The dotted line represents mean country protection (31.0%) of high-priority habitat. Information for each country is shown in Table S4. Note that resampling population distributions from 300 m to 5 km introduced a positive bias of approximately 8% to species footprints (km^2).

unsurprisingly, many of the top-ranked sites selected only by the species-level prioritization correspond to species-rich locations (e.g., in the Amazon and central Africa) at a sacrifice to areas important for population persistence found scattered throughout the globe (Figure S1B). In fact, the amount of overlap between the top-ranked sites from the species-level prioritization with the highest species richness sites (Figures 1B and S1B) was 42.8%. Compared with the overlap observed between the population-level prioritization and the high-diversity sites described above, this translates to a 26.4% increase in area of overlap (807,938 km^2).

Current protection of priority habitat

Approximately 20% (1,828,733 km^2) of top-ranked solutions are currently protected by the global PA network (Table 1). The portion of each International Union for Conservation of Nature (IUCN) PA category that contains high priority-habitat ranges from a high of 61.7% (category Ia) to a low of 20.2% (category VI). The strict protection categories (I–IV) contain 35.9% high-priority habitat and contribute 39.3% to the protected portion of this habitat but only contain 7.9% of the total habitat (Table 1).

On average, each country only has 31% of its high-priority habitat protected (Figure 2; Table S1). Indonesia has legally protected 14.2% of its priority habitat, less than half of the global country average. Australia protects over 34% of the high-priority habitat within its borders and contributes more than any other country to the current square kilometers of this habitat that is protected (Figure 2; Table S1).

Our analysis also identifies which PAs protect the highest-priority habitat. Indonesia and Australia also stand out in this regard (Table 2; Table S2). The Tropical Rainforest Heritage of Sumatra, in Indonesia, is the PA with the largest amount of high-priority habitat, and Australia contains 2 of the top 10 PAs in terms of amount of this habitat that is under protection.

Countries notable for having large areas of top-ranked sites but very low protection of these habitats include Somalia (113,000 km^2 with 0% protected), Ukraine (151,000 km^2 with <1% protected), and Papua New Guinea (351,228 km^2 with only 3.6% protected; Table S1). In Somalia, the 8 species driving the selection of these top-ranked sites include the leopard (*Panthera pardus*, vulnerable), Thomson's gazelle (*Gazella spekei*, endangered), and the African wild ass (*Equus africanus*, critically endangered). The four species in Ukraine include the endemic sandy mole-rat (*Spalax arenarius*, endangered) and the Russian desman (*Desmana moschata*, endangered), and the 32 species in Papua New Guinea include the black-spotted cuscus (*Spilocuscus rufoniger*, critically endangered) and Poncelet's giant rat (*Solomys ponceleti*, critically endangered) (see Table S3 for a complete list of species by country).

"Last chance" habitats to prevent extinctions

The 80% of top-ranked sites currently outside of legal PAs encompass 7.3 Mkm,^{2} roughly the size of Australia. Within the top-ranked sites, we further identified the most critical, or "last chance," locations, where protection would likely prevent the extinction of the last population for as many species as possible (Table S4). Specifically, we evaluated the protection required for 90% of species to have at least one population persisting long term (1,000 years) with a 75% probability. We found that avoiding habitat loss from just 462,479 km^2 (just slightly larger than the land area of Papua New Guinea) would allow 90% of threatened mammal species to have a greater than 75% probability of long-term persistence (Figure S2; Table S4). The unprotected portion of this high-persistence-probability area is only 306,012 km^2 (64%), 24 times smaller than the unprotected portion of top 10% ranked areas. However, we stress that, within these areas, the persistence of species may be down to a single population, leaving them vulnerable to uncontrollable stochastic events, such as disease and natural catastrophes, which cannot be accounted for in our analysis. While protecting the very minimum to avoid the loss of the last population of a species is appealing because of the relative spatial ease and efficiency, there are high risks involved in placing the burden of protection in a narrower set of geographies.

Additional priorities because of habitat conversion threat

Targeting critical areas where habitat conversion will likely increase species extinctions altered the global distribution of top-ranked sites (Figure 4). When conversion threat was considered, over 3 million km^2 of different habitat areas were ranked in the top 10% compared with the solution without consideration of habitat conversion threat. Australia and Russia had particularly large increases (>400,000 km^2) in high-priority habitat, with large

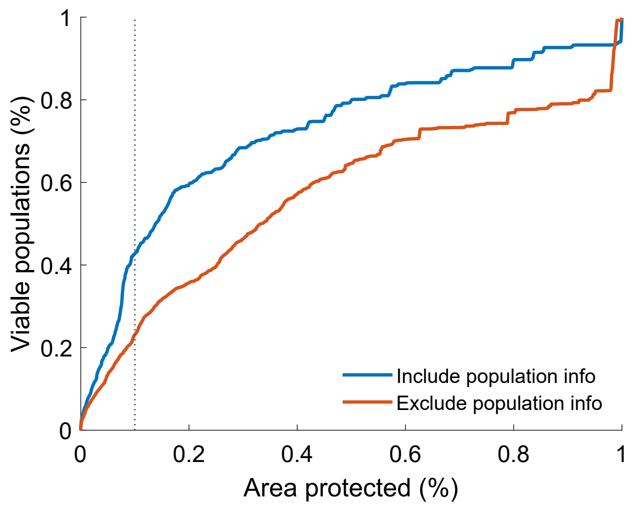

Figure 3. Persistence of threatened mammal populations using population-based vs. species-based Zonation prioritization

Zonation results showing the percent of all populations that are viable as area protected increases. Results are shown for the population-level analysis used in this study (blue) and a more typical species-level analysis (red) where no data on populations are used to inform the prioritization. The dotted vertical line marks the top 10% ranked solutions used to summarize results. n = 70,492 individual populations. A population was considered viable when it had at least a 75% probability of persisting. Results were similar when 50% and 90% probability of persisting thresholds were used. See Figure S1 for mapped results.

increases (>100,000 km^2) also observed in South Africa, Bolivia, Peru, Argentina, Somalia, and Brazil (Figure 3; Table S5).

Importantly, many sites were identified as top ranked with and without habitat conversion threat included in the prioritizations (Figure 4). Globally, 46% of the top-ranked solutions spatially overlapped. Indonesia, Brazil, and Australia contain large extents (>640,000 km^2) of overlapping top-ranked sites. The countries with the highest proportion (>90%) of overlapping high-priority habitat (and at least 10,000 km^2 of overlapped area) include Costa Rica, Liberia, Cuba, Belize, and the United States (Table S5).

DISCUSSION

We incorporate life-history characteristics and population-level abundance and habitat information to identify areas where habitat loss disproportionately increases extinction risk to threatened terrestrial non-volant mammal species. These are places where avoiding habitat loss can have the greatest global impact on reducing the risk of extinction for threatened mammal species—an important objective for global conservation.[22,24,25]

Global conservation prioritizations have typically focused on the representation of different dimensions of biodiversity.[9,38] While representing a part of the range of each species is an essential first step in protection prioritization, it does not easily translate into long-term persistence of species, for which habitat needs vary greatly.[17,39,40] Optimizing for species persistence is challenging because it requires a detailed understanding and joint consideration of species traits, the spatial configuration of their habitat, and their non-linear relationships that drive population survival. To our knowledge, this is the first global prioritization where selection of priority sites is based on estimates of population persistence. Unlike species-area-based approaches to global conservation prioritization, the explicit consideration of reducing extinction risk used here indicates that important places for habitat protection are spread widely around the globe and not influenced disproportionately by underlying mammalian diversity. For instance, habitat loss in parts of southern Patagonia could be more significant for additive global extinction risk than the equivalent habitat loss in Borneo, where the total number of threatened mammal species is higher than anywhere on the globe. This illustrates the importance of considering the impact of habitat loss at the population level for different species. Importantly, our results demonstrate that including the ongoing persistence of populations when prioritizing conservation efforts considerably enhanced the probability of long-term species persistence, surpassing the outcomes of a conventional approach that solely focused on individual species distributions. In summary, prioritizations that only use species-level information run the risk of selecting sites that offer individual populations poor persistence outcomes.

PAs are a conservation mechanism that exists in most countries and in many places forms the backbone of conservation action.[41,42] Of the important areas for ameliorating mammal extinction risk identified in this analysis, 20.1% are already inside PAs. This is higher than the background rate of protection (14.7%) because PAs are frequently designated as important mammal habitat (e.g., the Gobi Desert PA in Mongolia) and because in many places the ranges of threatened mammal populations have contracted to within PA boundaries (e.g., *Rhinoceros unicornis*, *Addax nasomaculatus*, and *Saiga tatarica*).[43] Our analysis is likely to underestimate the lands under protection because in some places, such as South Africa and the United States, there are large numbers of private PAs that do not appear in the World Database on Protected Areas (WDPA). However, we explicitly do not assume that habitat inside existing PAs is safe from loss.[44,45] This analysis highlights PAs where future loss of habitat would be particularly detrimental to global extinction risk for mammals. Determining which of these PAs are at high risk of habitat loss, and how management could be strengthened to avoid this loss, requires greater local contextual knowledge than is possible in a global analysis.

Explicitly considering the threat of future habitat loss in our prioritization identified additional areas likely to be important for reducing mammal extinction risk. Regions where large areas were elevated in rank based on projected land conversion pressure include South America, west Africa, and Russia. Accounting for potential future habitat loss can enable conservation practitioners to focus on strategies that protect habitat from subsequent development pressure, thereby ensuring the additionality of conservation action.[46,47] The exact location of habitat clearing from development expansion is hard to predict,[48] and any loss of habitat from the highly ranked areas is likely to have a meaningful consequence for extinction risk. Further, selecting sites for protection based on development pressure may increase the risk of PA downgrading, downsizing, and degazettement (PADD) events because of demands for resource extraction and development.[49] Therefore, we see the results with and without

Table 1. Top-ranked area (top 10%) within each IUCN PA category

IUCN PA category	Top-ranked area (km^2)	Top-ranked area within each PA category (%)	Contribution to global top-ranked PA area (%)	Contribution to global top-ranked total area (%)
Ia	63,154	61.7	3.5	0.7
Ib	23,467	42.3	1.3	0.3
II	461,543	35.9	25.2	5.1
III	30,288	31.5	1.7	0.3
IV	140,994	30.6	7.7	1.6
V	216,742	29.1	11.9	2.4
VI	305,144	20.2	16.7	3.4
Other	587,403	27.5	32.1	6.5
Category groups				
I–IV	719,444	35.9	39.3	7.9
I–VI	1,241,330	29.1	67.9	13.7
All	1,828,733	28.6	100	20.1

"Other" includes PAs with IUCN categories designated by the WDPA as "not reported," "not assigned," and "not applicable."

projected risk as complementary in their information rather than substitutable.

We recognize that countries develop and execute conservation plans based on national priorities, preferences, and constraints. However, the successful implementation of the Kunming-Montreal GBF requires collective efforts and collaboration among national governments, stakeholders, indigenous peoples and local communities, civil society organizations, and the private sector. One strength of the Zonation analysis producing a global rank order of sites rather than a portfolio of places is that it is amenable to supporting decisions at different scales and particularly within different geopolitical units. For example, if the prioritization were restricted to a single region or country, then the results would still give a rank order of priority within that region. But the full optimality is only achieved when all parts of the identified network of priority areas are protected. In other words, because species population distributions cross political borders, global coordination of conservation efforts is necessary to achieve the most efficient biodiversity benefits.[50] We recognize that this global coordination will be politically challenging. Many developing countries, such as Indonesia, Papua New Guinea, and Liberia, have proportions of priority habitat that exceed 50% of their land. Expecting these countries to exceed GBF protection targets (e.g., "30 × 30") is unreasonable. Instead, our results can inform where PA target gaps might be filled and prioritize sustainable land use practices that could meet development and biodiversity goals. Finally, the increasing availability of fine-scale global habitat data combined with advancements in cloud computing resources means that we are close to the moment where global prioritizations can be performed at a resolution sufficient to meet national needs. Reaching this technical threshold will help strengthen global coordination.

This analysis focuses on identifying priority locations to avert mammal extinction in relation to habitat loss, which, although important, is only one threat to mammal populations. We do not consider important and significant risks to species that are not related to habitat loss; for instance, invasive species,[51] poaching,[52] or disease.[53] The analysis also does not consider the potential impact of climate change on mammal population distribution or abundance. We also emphasize that our results are not a conservation plan. We do not consider what specific protection actions are required to achieve conservation outcomes in any place, only what the impact of doing so could be. We assume that, in any country, the loss of habitat can be prevented through multiple mechanisms. We also recognize that mammals represent only a component of threatened biodiversity in need of conservation. Sufficient density[54] and dispersal[55] information currently exists to extend this analysis to include bird populations, and equivalent data for amphibians and reptiles are progressing.[56] It is important to recognize that the inclusion of other taxa will likely alter prioritization results.

We explicitly do not consider conservation costs because funding is rarely globally fungible, and availability and ease of funding are largely unrelated to cost.[10] In addition, opportunity, management, and transaction costs would depend on which type of management is adequate for each site,[57] which we do not identify here. We do, however, implicitly include opportunity costs by looking at future conversion threat, and in this sense, we actually prioritize areas with higher opportunity costs arising from forgoing extractive or productive activities. This is not to suggest that cost is not a critical factor in determining efficient use of funds, but it is a difficult factor to incorporate meaningfully at a global scale. The cost of habitat protection is highly variable at a fine scale, often varying several orders of magnitudes more than the benefits with which they are being compared.[58] In current spatial prioritization tools (including Zonation and Marxan), the inclusion of costs can dominate the results so that priority areas are frequently the inverse of the cost map. At the same time, costs are also highly variable temporally (even in the absence of large system shocks such as coronavirus disease 2019 [COVID-19]), meaning that prioritizations inclusive of them would quickly become outdated.[58,59]

There is an abundance of global-scale prioritizations in the conservation literature, but most remain academic exercises with little impact on conservation resource allocation. In contrast, this analysis was explicitly designed to inform priorities for The Nature Conservancy's global terrestrial protection work.

Table 2. The PAs with the greatest overlap with top-ranked (top 10%) Zonation solutions

Country	PA	Designation	IUCN category	Reported PA area (km^2)	Top-ranked area in PA (km^2)
Indonesia	Tropical Rainforest Heritage of Sumatra	World Heritage Site	NA	25,951	25,950
Paraguay	Gran Chaco	Biosphere Reserve	NR	47,073	25,025
Niger	Termit et Tin-Toumma	Nature Reserve	IV	90,507	21,625
Chile	Bernardo O'Higgins	National Park	II	35,259	20,850
Australia	Coongie Lakes	Ramsar Site, Wetland of International Importance	NR	21,762	20,700
Venezuela	Alto Orinoco-Casiquiare	Biosphere Reserve	VI	84,000	20,300
South Sudan	Sudd	Ramsar Site, Wetland of International Importance	NR	57,000	19,125
Bolivia	Kaa-iya del Gran Chaco	Natural Integrated Management Area and National Park	NR	34,677	19,125
Australia	Kakadu	National Park	II	19,112	18,400
Brazil	Parque Nacional Do Pico Da Neblina	National Park	II	22,524	16,075

NA, not applicable; NR, not reported.

This work is not just about establishing PAs but often about engaging with the sectors responsible for habitat loss in a location.[60] There is a wide range of government and non-government conservation actors around the world who either explicitly or implicitly seek to link habitat protection with reducing species extinction risk. Although only reflective of threatened mammals, the approach described here allows a more direct and quantifiable linkage between conservation action and extinction risk than what has been possible previously at a global scale. The ability to look at conservation priority this way, globally but also regionally, gives this work broad utility to support efficient conservation spending and, therefore, greater impact in addressing the extinction crisis facing this planet.

EXPERIMENTAL PROCEDURES

Resource availability

Lead contact

Further information about data and code should be directed to and will be fulfilled by the lead contact, Nicholas H. Wolff (Nicholas.wolff@tnc.org).

Materials availability

This study did not generate new unique materials.

Data and code availability

All input data and information required to conduct the Zonation analyses presented in this study have been deposited at Zenodo (https://doi.org/10.5281/zenodo.8290612) and are publicly available as of the date of publication. Zonation output files are also deposited under the above DOI.

Methods overview

We mapped 861 threatened non-volant mammal species, representing 367,915 individual populations, at 300-m^3 resolution, which were resampled to 5-km resolution for the prioritization exercise. We then modeled extinction probability based on the relationship between population size and extinction risk using 40 different population starting points and 31 separate models based on body size. Each simulation was run 500 times for 1,000 years to estimate extinction probability. The threat of conversion was modeled using Zhou et al.[32] for urban growth and the development potential index (DPI)[36] for other development pressures. We used Zonation to identify global priority areas for protecting habitat whose loss would cause mammal populations to drop below the 50% probability of survival threshold. We also looked at triaging protection to populations most likely to benefit from it versus those that would more likely persist even in the absence of protection.

Mammal distribution data

We obtained the geographic range polygons from the IUCN Red List[61] and refined them by filtering out unsuitable habitat and elevations following Rondinini et al.[62] We used the habitat preferences reported by the IUCN Red List[61] following the habitats classification scheme level 1 (IUCN Habitat Classification Scheme 2019) to identify the suitable habitat categories per species. We then converted these categories into ESA CCI Land Cover categories (https://www.esa-landcover-cci.org/) by using the cross-walk presented in Table S6. Next, we used the suitable elevation range reported by the IUCN Red List (IUCN 2019) to filter out unsuitable elevations using the digital elevation model EarthEnv-DEM90.[63]

We further refined these models by identifying patches of suitable habitat potentially able to support viable populations for each species.[17,18,39] We followed the procedure described in Santini et al.,[17] which consists of clumping patches of suitable habitat within a species-specific dispersal distance, excluding patches smaller than the area needed to support at least 10 individuals of the species (potential stepping stones). We estimated dispersal distance using the allometric models in Santini et al.[64] and species body mass and/or home range area and the models in Whitmee and Orme[65] for species for which additional information about population density and weaning age information were available. We estimated species average population density using species body mass, diet, and taxonomic information using the models in Santini et al.[56] Population density estimates were used to estimate the average number of individuals expected per suitable habitat patch. The species body mass, diet, home range area, population density, and weaning age were obtained from the PanTHERIA database,[66] EltonTrait 1.0,[67] and TetraDENSITY database.[68]

We conducted all spatial analyses using Geographic Resources Analysis Support System (GRASS) GIS v.7.4[69] and ArcGIS 10.4.1 (ESRI, 2016), with all further data processing performed in R v.3.5.1.[70] All spatial data used a Mollweide equal-area projection. For each threatened terrestrial mammal species (n = 861 species) analyzed, a map was produced at 300-m resolution, showing the distribution of each unique population (assigned by a unique population ID).

Because our goal was to identify where protection would reduce extinction risk, we focused on threatened mammals (861 species representing 367,915 individual populations), defined by the IUCN Red List[61] as vulnerable, endangered, or critically endangered (hereafter called "threatened"). We excluded

CellPress
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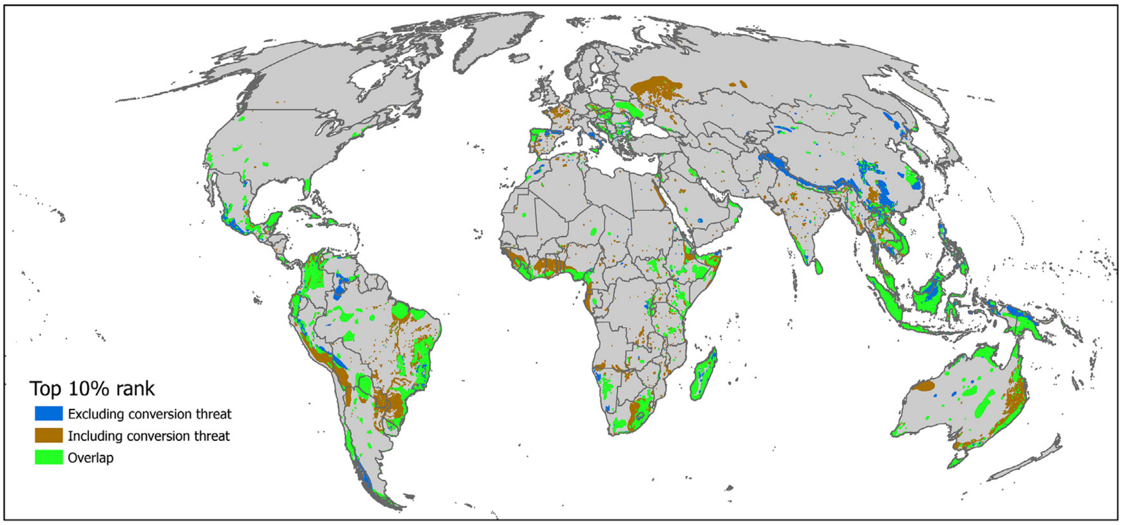

Figure 4. Global distribution of high-priority habitat for minimizing threatened mammal extinction

Shown are the high-priority areas (top 10% Zonation ranks) when habitat conversion threat is excluded (blue) versus included (red) in the prioritization. Approximately half of the total priority areas overlap (green) across both prioritizations. See also Figure S3 for full Zonation rank results.

bats (Chiroptera) because of a lack of sufficient dispersal and density information. In preparation for the prioritization analysis (see below for details), individual global maps were created for each independent population at 5-km resolution via resampling ("nearest neighbor") of the original 300-m data, resulting in 70,492 population maps for the 861 threatened species (Table S7). Simple linear regression demonstrated that the footprint (km^2) of species distributions from the original 300 m explained 99.5% of the variation in the footprint from the resampled 5-km distributions (F (1, 860) = 170,505, $p < 0.001$). With the intercept set to zero, the slope of the fit was 1.0773, demonstrating that the resampling inflated species footprints by an average of nearly 8% (Table S7).

Relationship between extinction risk and population size

We used methods and data from Hilbers et al.[71] to model the probability of persistence over different population sizes of archetypical mammal species in 31 body-size classes (spaced logarithmically). The parameters of the Ricker logistic growth were derived from allometric relationships and are described in Hilbers et al.[71] Model simulations were run for 1,000 years and repeated 500 times for each carrying capacity and body-size class. For each simulation, we recorded how many times the population persisted until the end of the simulation.

We first tested incrementally larger starting population sizes (set at population carrying capacity) until the population persisted for 1,000 years in all 500 replicates of the stochastic population dynamics simulation and then tested even larger population sizes to make sure we were capturing the right-hand tail of the probability of persistence as a function of starting population size. We then identified an optimal set of 40 starting population sizes for each of the 31 body masses, which adequately captured the distribution of probability of persistence. We therefore had, in total, 20,000 simulations of population dynamics for each of the 31 body-size classes.

With these data we fitted a Gomperz sigmoid model to extrapolate how probability of persistence scales with population size for each body mass class. The Gompertz function fitted was

$$p = e^{-10e^{-cx}}, \qquad \text{(Equation 1)}$$

where p is the probability of persistence of the population over 1000 years, c is a body-mass-specific parameter, and x is the population size. The values of p were obtained from simulating the Ricker logistic model from Hilbers et al.[71] with maximum growth rate equal to 80% of what is physiologically possible for the species. The values of c were obtained using a simulated annealing solver, using the optim function in R (Stats package). The c values identified yielded $R^2 > 0.9$ for all body mass classes smaller than 70 kg and between 0.76 and 0.9 for the remaining 8 body mass classes. A locally estimated scatterplot smoothing (LOESS) interpolation was then used to estimate values of c in Equation 1 to all mammal species in our database.

Equation 1 was then solved to identify, for each species, the population size needed to achieve a probability of persistence of any given population of at least 50% for 1,000 years. This value was used in Zonation as the parameter T_j in Equation 3 as described below. We recognize a trade-off associated with the selected probability of persistence value: a higher probability confers greater likelihood that population size thresholds are sufficient for persistence but also implies that any current population abundances already below this threshold are no longer viable and not worth protecting. We settled on 50% probability or greater for this study because it allowed most current populations to be considered in the analysis while remaining sensitive to changes in habitat extent but acknowledge that this value is idiosyncratic to organizations and individuals.

Habitat conversion threat

We captured future threat of habitat conversion based on a cumulative development pressure map that identifies lands highly suitable for expansion by 14 industrial sectors based on the presence of large quantities of unexploited resources and infrastructure that supports their extraction and transportation. We used previously published, spatially explicit land suitability maps at 1-km resolution for renewable energy (concentrated and photovoltaic solar power, wind power, and hydropower), oil and gas (conventional and unconventional), mining (coal, metallic, and non-metallic mining), and agriculture (crop and biofuels expansion) sectors[36] and created an urban pressure map using global urban growth projections from 2020–2050.[32] Each DPI map has standardized 0–1 values that indicate low to high suitability for development expansion based on (1) sector-specific land constraints that restrict development (e.g., suitable land cover, slope), (2) land suitability for sector expansion based on resource availability (sector-specific yields), and (3) siting feasibility of new development (e.g., ability to transport resources or materials, access to demand centers, existing development, and other economic costs associated with resource siting).[36] The urban DPI was based on global urban growth probabilities for 31 years at 30 arc-seconds (~1-km) resolution and based on the SLEUTH urban growth model that accounts for slope, land cover, excluded regions (i.e., PAs, water bodies), urban land cover, transportation, and hill shade and calibrated based on the historical distribution of global population from LandScan (Oak Ridge National Laboratory; https://landscan.ornl.gov/landscan-datasets).[32] We summed urban growth probability values across the 31-year time interval, resulting in values ranging from 1 (1% probability of expansion in 2050) to 3,100 (100% probability of expansion for all 31 years). Given the right-skewed distribution of these data (skewness = 4.3619), we log-transformed all urban cell values and scaled urban DPI to 0–1 values using min-max normalization.

For each DPI, we binned the range of values into six classes based on standardized Z score ranges as follows:[36] very low (≤ -1.282), low (> -1.282 to -0.675), medium-low ($\gg -0.675$–0.000), medium-high (>0.000–0.675), high (>0.675–1.282), and very high (>1.282). With normally distributed data, these Z scores approximately correspond to percentile breaks of 10, 10–25, 25–50, 50–75, 75–90, and >90, respectively.[36] We calculated Z scores by mean-standardizing values per country under the assumption that national-level domestic demand and global demand will drive resource extraction in areas of highest suitability within each country. Because urban DPI was derived from urban expansion probabilities based on population growth projections that were more restrictive than the DPI values of other sectors (e.g., excluded suitable areas like flat land, near roads, and existing urban areas when demand was met), we binned the non-zero urban DPI values that were below and above the mean (i.e., standardized Z score <0.00 and >0.000) into high or very high classes, respectively. All classified DPIs were assigned numeric values ranging from 1 (very low) to 6 (very high). Finally, we created a cumulative development pressure map across all sectors by assigning pressure scores that also ranged from 1 (very low) to 6 (very high) by retaining the highest cell value of each classified DPI. All lands without a pressure category were assigned a value of 0. Final preparation of the cumulative development pressure map for use within Zonation prioritization is described in the next section.

Identifying global priorities for minimizing mammal extinction

Prioritizing population persistence

We used the conservation prioritization software Zonation v.4.0[72] to identify areas that should be targeted for protection to minimize mammal extinction. In this optimization, we used maps of each independent population (n = 70,492) from 861 threatened mammal species as our input, mapped on a uniform lattice at 5-km resolution with a total global distribution covering 91,436,625 km^2.

Zonation is a backward-heuristic maximum-utility optimization tool[15,73] that starts by assuming that all grid cells are protected and then iteratively removes those grid cells that cause the smallest marginal loss δ in the conservation of populations. The cell removal is repeated until no cells are left, and the removal order of cells indicates their protection priority, with the most important cells being removed last. A central component of the algorithm is how the value of marginal loss of cell i is calculated across populations. Here we used the General Benefit Function mode of Zonation,[73] which defines marginal loss as a sum of values across populations:

$$\delta_i = w_j \sum_j V_j(R_j) \qquad \text{(Equation 2)}$$

where $V_j(R_j)$ is the conservation benefit of not removing cell i for population j, defined as a function of population j's remaining representation R_j in the landscape, and w_j is the weight of population j. We defined the conservation benefit functions for each population as

$$V_j(R_j) = \begin{cases} 0.5 \times \left(\frac{R_j}{T_j}\right)^x & \text{when } R_j \leq T_j \\ \left(\frac{R_j - T_j}{1 - T_j}\right)^y & \text{when } T_j < R_j < 1 \end{cases} \qquad \text{(Equation 3)}$$

where R_j is the remaining relative size of the population j, updated at each point of the cell removal. Equation 3 is a sigmoid function, where parameters x and y define the steepness of the slope below and above T_j, respectively. Values for these parameters can be empirically derived where such data exist; here we set x and y to 4 and 1/x = 0.25, respectively, following the widely used power value of 0.25 in species-area relationships. The inclination point is defined by the relative population size, T_j, at which the population drops below its 50% persistence threshold (see Relationship between extinction risk and population size). This point was calculated individually for each population, given their population size calculated from current range (from 300m resolution layers) and estimated population density (Tables S7 and S8). During cell removal, the optimization algorithm tries to avoid removing cells that push the population below their viability threshold because this introduces the largest single drop in conservation benefit, inflating the marginal loss δ_i. Effectively, the optimization aims to retain as many populations above their persistence thresholds as long as possible. Eventually, as more grid cells are removed and some populations drop below their threshold, the remaining parts of their area are removed rather quickly in favor of maintaining the viability of other populations. This way, the number of viable populations is maximized for any fraction of the top-ranked grid cells. To account for the fact that some species have different numbers of populations left, and that these populations may disproportionally represent the global population, each population was weighted (w_j in Equation 1) as abundance of population j/total abundance of species (abundance = number of individuals). During the cell removal, 10,000 cells (0.27% of cells) were removed at each iteration from a total of 3,657,465 effective cells (non-empty cells, occupied by at least 1 population), and we allowed cells to be removed only from the edges of remaining areas.

PA gap analysis of top-ranked sites

Zonation produces a priority map, where each grid cell is ranked from the least important to the most important. We use the top-ranked results, which we defined as the top 10% most important cells (9,143,663 km^2), when reporting our country level results. In addition to rankings, Zonation also reports how much of each population j is captured at any percentage of the top-ranked cells (e.g., top 10%), allowing us to estimate a population's probability of persisting at each percentage of interest (see Supplemental methods for details).

We also identify the proportion of overall top-ranked areas that are currently protected by each country with threatened mammals. Additionally, we identify PAs of particular importance; i.e., those containing a relatively large area of high-priority habitat. To do this, Zonation must be agnostic to the protection status of a grid cell and treat each cell purely based on their conservation value rather than any legal designation. Finally, we recognize that substantial habitat can still be lost from PAs as well as their legal status threatened or downgraded.[44,45] Therefore, we do not consider PAs within the Zonation analysis itself and instead conduct a PA gap analysis using Zonation results. To conduct the country-level gap analysis, we overlaid the top-ranked mammal areas with the WDPA (downloaded July 2020 from https://www.protectedplanet.net). The WDPA PA polygons were processed according to the Digital Observatory of PA s (DOPA) methodology,[74] which retains PAs that lack an IUCN management category designation but eliminates PAs lacking legal designations and certain international PAs.

Influence of habitat conversion threat on persistence

Next, we explored how the location of priority areas for mammal persistence is altered when accounting for future threat of habitat conversion (see Habitat conversion threat). To do this, we modified the Zonation prioritization to maximize future habitat retention for all populations.[23,75] This is achieved by focusing conservation efforts on regions where populations are at highest risk of being pushed below their viability threshold in the future. In Zonation, this is done using the built-in retention feature,[15,76] which alters the weighting of individual populations in the prioritization depending on how much of their current habitat is likely to be lost without intervention. Specifically, a retention map describes for each grid cell i the amount of original habitat that is likely to be retained in the future in the absence of conservation intervention, with values ranging between 0 (all habitat lost) and 1 (all habitat retained). Here we apply the cumulative development pressure map as a relative measure of the potential threat of future habitat loss instead of estimating an actual amount of loss. Operationally, this is done as follows.

First, the cumulative development pressure map, with values ranging from 0 (no development pressure) to 6 (very high development pressure), was inverted and rescaled between 0 and 1 to similarly match Zonation retention values. Next, the layer was resampled from the original 1-km resolution to 5-km resolution via bilinear resampling to match the grid size of the mammal population features. The final retention layer had continuous values ranging from 0 (very high threat of habitat loss) to 1 (very low threat of habitat loss).

Second, the distribution map of each population j (*current habitat$_j$*) is multiplied with the retention map, which then gives the total amount of habitat left in the future if development proceeds as predicted without any conservation intervention (= the counterfactual scenario). The difference between the original habitat map and the counterfactual map is the amount of habitat loss that can theoretically be prevented with conservation (*difference*$_j$).

Third, for each population j, the population-specific weight w_j (Equation 4) is adjusted according to the proportional value gain of protecting population j's habitat:

$$w_j^* = \frac{difference_j}{current\ habitat_j} w_j \quad \text{(Equation 4)}$$

The adjusted weights w_j* are then used instead of w_j when calculating the conservation value of grid cells in the prioritization (Equation 4).

Effectively, the approach prioritizes areas where populations are more threatened by future development, which could lead to a loss of large proportions of their current habitat in the absence of intervention, increasing their extinction risk. Conversely, the approach also de-prioritizes (1) sites that may be important for persistence but have a lower threat of being converted in the future and (2) sites that are highly threatened by conversion but whose loss does not cause proportionally large losses to populations. The logic is that scarce conservation resources should be targeted at populations whose status is most improved by the action of land protection.

Comparing population with species level prioritization

To quantify the benefit of explicitly considering the long-term persistence of individual populations, we also ran a traditional species-level prioritization. We then compared the number of individual populations that may persist under different levels of protection across the population level and species distribution prioritizations. For the species-level prioritization, we used the Additive Benefit Function mode of Zonation,[73] which defines conservation benefit for each species as

$$V_j(R_j) = R_j^z \quad \text{(Equation 5)}$$

where R_j now represents the remaining relative size of species j instead of populations. Equation 5 is a power function, and, as in Equation 3, we set the power parameter z to 0.25, which produces a concave downward-shaped benefit curve with no inclination points. Each species was weighted as w_j = 1/number of populations (Equation 2) to mimic the weighting scheme of the population-level prioritization and, hence, make the two prioritizations more comparable.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.oneear.2023.10.001.

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AUTHOR CONTRIBUTIONS

Conceptualization, N.H.W., P.V., H.K., L.S., J.F., H.P.P., and E.T.G.; methodology, N.H.W., P.V., H.K., L.S., J.P.H., J.R.O., and C.M.K.; investigation, N.H.W., P.V., H.K., and L.S.; writing – original draft, N.H.W., P.V., H.K., L.S., J.R.O., C.M.K., and E.T.G.; writing – review & editing, J.P.H., H.P.P., J.K., and J.F.; supervision, E.T.G. and J.F.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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