ECOLOGY

Gaps and weaknesses in the global protected area network for safeguarding at-risk species

Yiwen Zeng[1]†*, **Rebecca A. Senior**[2]†*, **Christopher L. Crawford**[1], **David S. Wilcove**[1,3]*

Protected areas are essential to biodiversity conservation. Creating new parks can protect larger populations and more species, yet strengthening existing parks, particularly those vulnerable to harmful human activities, is a critical but underappreciated step for safeguarding at-risk species. Here, we model the area of habitat that terrestrial mammals, amphibians, and birds have within park networks and their vulnerability to current downgrading, downsizing, or degazettement events and future land-use change. We find that roughly 70% of species analyzed have scant representation in parks, or occur within parks that are affected by shifts in formal legal protections or are vulnerable to increased human pressures. Our results also show that expanding and strengthening park networks across just 1% of the world's land area could preserve irreplaceable habitats of 1191 species that are particularly vulnerable to extinction.

INTRODUCTION

Human activities such as logging and agriculture continue to alter the world's natural environments and show few signs of abating (*1*). As a result, an increasing number of species are likely to face extinction, with current assessments placing between 13 and 41% of terrestrial vertebrates at risk (amounting to more than 7400 species) (*2*, *3*). Despite setbacks in global commitments to biodiversity conservation, there has been a growing recognition across private and public sectors of the need to expand current conservation efforts to stem the tide of species loss (*4*).

One of the most effective and widely implemented strategies to conserve biodiversity is through the creation of protected areas (often referred to as parks). By establishing boundaries and restricting most anthropogenic disturbances within key areas, whether through legislative or other effective means, ecosystem processes and connectivity can be maintained, redounding to the benefit of species within them (*5*–*8*). Currently, ~17% of the world's terrestrial area is recognized by the United Nations Environment Programme (UNEP) and the International Union for Conservation of Nature (IUCN) as having some form of protected status (*5*, *7*, *9*). This includes areas that are classified as protected areas as well as other effective area-based conservation measures, which can include lands managed by indigenous groups or local communities (*7*, *10*). This achievement, while in line with the Aichi Biodiversity Target 11 for 2020, still leaves more than a thousand terrestrial vertebrate species lacking protected area coverage (*5*, *7*, *9*). Promisingly, as awareness of the need to expand conservation efforts continues to grow, more countries such as the United States, China, and Germany, are committing to expand protected areas to 30% of terrestrial environments by 2030 (*7*, *11*).

Yet, increasing the amount of nominally protected land is not enough if those parks do not successfully exclude harmful human activities (*12*, *13*). Weaknesses in current protected area networks can stem from insufficient enforcement, lack of political backing, and suboptimal park placements, which limit their ability to support species populations in the long term (*13*–*16*). Parks can also become less effective at safeguarding species when they experience official downgrading, downsizing, or degazettement (often termed PADDD), which occurs when a government decides to roll back the legal protections governing a park, thereby diminishing the degree or extent of protection afforded to it (*17*, *18*). Such decisions can stem from funding shortfalls and competing interests, but importantly, they reflect a level of recognition among policymakers of increasing human activities in parks (or a desire and motivation to facilitate these activities) and a willingness to adjust legal definitions to reflect existing or planned land uses (*17*, *18*). These legal changes can translate to the loss or degradation of habitats. More than 278 million hectares of parks are known to have been cumulatively subject to PADDD events as of 2021 (*17*–*19*).

With the inclusion of protected area targets within the Kunming-Montreal Global Biodiversity Framework, many studies have investigated and discussed the benefits of achieving expanded targets for park coverage (*7*, *20*, *21*). Similarly, studies have also identified gaps in park placement and their impact on population viability (*13*, *15*, *22*). However, studies identifying species with habitats that currently lack sufficient protection in parks or that are disproportionately found in parks affected by PADDD are scarce, even though such knowledge is essential to averting future extinction events (*23*). Here, we identify species that (i) currently lack formal protection in parks; (ii) are protected by parks that are vulnerable to PADDD events; and (iii) are protected by parks that are projected to experience to future land-use change. We also identify (iv) the habitat locations of all the above types of species and the areas that would benefit those species if parks were expanded or restored or if management of existing parks were improved. Our objective is to broaden the current (deserved) focus on global park expansion to also include the strategic buttressing of existing protected areas (*12*).

Specifically, we focus on 4946 terrestrial vertebrate species that are likely to benefit from efforts to expand and strengthen protected areas. We define these as terrestrial mammals, amphibians, and birds that both require natural ecosystems and have already

---

[1] Princeton School of Public and International Affairs, Princeton University, Princeton, NJ, USA. [2] Conservation Ecology Group, Department of Biosciences, Durham University, Durham DH1 3LE, UK. [3] Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA.
*Corresponding author. Email: yz0467@princeton.edu (Y.Z.); rebecca.senior@durham.ac.uk (R.A.S.); dwilcove@princeton.edu (D.S.W.)
†These authors contributed equally to this work.

experienced a degree of anthropogenic stress in these habitats (such as habitat degradation or conversion; see Materials and Methods for details). We determined the location and amount of suitable habitat (also known as area of habitat) remaining for each species by matching the habitat classifications, standards, and spatially explicit range data in the IUCN database to an optimized 2015 map of habitat types (*3*, *24*, *25*). We then further refined area of habitat maps based on species' recorded elevational ranges and elevation maps (*26*). We also updated these area of habitat maps to 2019 by excluding anthropogenic land cover changes that occurred between 2015 and 2019 (*27*). We calculated the proportion of suitable habitat for each species that is contained within parks, strictly focusing on parks that are formally protected as documented in the World Database on Protected Areas (*9*). We cross-referenced these parks with a database of detected PADDD events (from PADDDtracker.org Version 2.1) to identify those that are likely affected by human pressures, differentiating between species affected by downgrading, downsizing, or degazettement events, as well as the reversal of PADDD events (*17*, *18*). We then identified species that have yet to be affected by detected PADDD events but may be vulnerable to land-use change in the future because of their dependence on parks that are predicted to experience future cropland and urban expansion (*28*). Last, we mapped the suitable habitats of these identified species across 238 countries worldwide and assessed the conservation benefits of expanding, restoring, and reinforcing parks within each country.

RESULTS AND DISCUSSION

Species that lack protection in parks

Overall, we find that 1463 species (30%) of the terrestrial mammals, amphibians, and birds we assessed have less than 10% of their suitable habitat safeguarded by existing parks (Fig. 1 and table S1). These species, which we hereby describe as lacking protection in parks, consist of 329 mammals, 651 amphibians, and 483 birds (Fig. 1 and table S1). Among them are 184 Critically Endangered species, 391 Endangered species, 363 Vulnerable species, 296 Near-Threatened species, and 199 Least Concern species, according to assessments by the IUCN Red List (Fig. 1 and table S1). Overall, a substantially greater proportion of threatened species (i.e., classified by the IUCN Red List as Critically Endangered, Endangered, or Vulnerable) were found to be unrepresented in parks (Critically Endangered, 32%; Endangered, 31%; Vulnerable, 31%) compared to species that are classified as Least Concern (23%) (table S1). This link between threat status and lack of protected area coverage is especially pronounced when considering the area of habitat that each species has remaining.

Specifically, we find that species excluded from parks and with limited remaining habitat tend to be at greater risk of extinction than species with larger amounts of remaining habitat (Fig. 1). This likely stems from the fact that species lacking habitat protection are particularly vulnerable to land-use changes (e.g., deforestation and agricultural expansion) as well as stochastic events (e.g., wildfires and hurricanes) when insufficient habitat is present (*29*, *30*). We find that more than 80% of species with limited area of habitat (i.e., <2000 km^2 of suitable habitat remaining) that lack protected area coverage (i.e., <10% of their habitat contained in parks) are classified as threatened (table S1).

Broadly speaking, we find that the habitats of highly range-restricted species tend to fall entirely within or outside parks as compared to species with greater amounts of habitat (as shown in Fig. 1), suggesting that increasing park coverage could benefit a larger number of species with limited range sizes (*23*). Our analyses highlight a transition from unimodal to bimodal patterns of percent habitat protection as area of habitat decreases, wherein a larger number of species is more likely to have an intermediate degree of protected area coverage, with the number of species exhibiting either very high or very low protected area coverage peaking at smaller areas of habitat (Fig. 1) (*31*). This trend is especially pronounced for species with less than 10 km^2 of suitable habitat remaining, with 195 species in this category having less than 10% of their habitats in parks and 121 species having more 90% of their habitats in parks; in comparison, only 61 species had 10 to 90% of their habitat in parks (table S1).

Expanding the global network of protected areas to ensure adequate representation of small-ranged species that currently lack habitat protection could greatly mitigate further threats from land-use change for species that are already at high risk of extinction (*29*, *30*). Moreover, because these species are limited in terms of the area of habitat, the total amount of land that would need to be protected to safeguard them is small in absolute terms. For instance, protecting an additional 330 km^2 of natural landscapes within Indonesia would safeguard the suitable habitats of 53 species that currently lack protected area coverage and have limited area of habitat (49 of which are threatened) (table S2). This is less than 0.02% of Indonesia's total land area and is well within the various commitments Indonesia has made to expand conservation areas within its borders (*32*).

Species occurring in parks with recorded PADDD events

Our findings indicate that 70% of the at-risk terrestrial mammals, birds, and amphibians assessed have more than 10% of their habitats protected, but inclusion within protected areas confers limited benefits to species if those parks are poorly protected and managed. Studies have identified continued habitat loss and degradation within protected areas, albeit at a lower rate than in unprotected areas (*8*, *33*). Parks can lose formal protections through downgrading, downsizing, or degazettement (PADDD events) for many reasons ranging from local land claims to infrastructure expansion to mining. These PADDD events may not necessarily result in negative biodiversity impacts, as in the case of legal changes made to enhance conservation efficiency of park networks (*17*, *18*). However, most PADDD events are associated with extractive activities (*17*, *18*). This can lead to reductions in species' habitat quality or quantity, which is likely to affect a growing number of species, especially considering the increasing number of PADDD events since the 1960s (*17*–*19*, *34*).

We find that 2308 species (47%) have at least 100 hectares of their habitat falling within parks with documented PADDD events (Fig. 2 and table S1). Among these species, those with smaller areas of habitat tend to be more dependent on parks with at least one PADDD event recorded (Fig. 2). Concerningly, 182 species have >50% of their available habitat falling within parks that have experienced PADDD events, and 87% of these species have limited areas of habitat remaining (<2000 km^2) inside or outside parks (table S1).

The negative trend between species' areas of habitat and the proportions of their habitats with recorded PADDD events is more

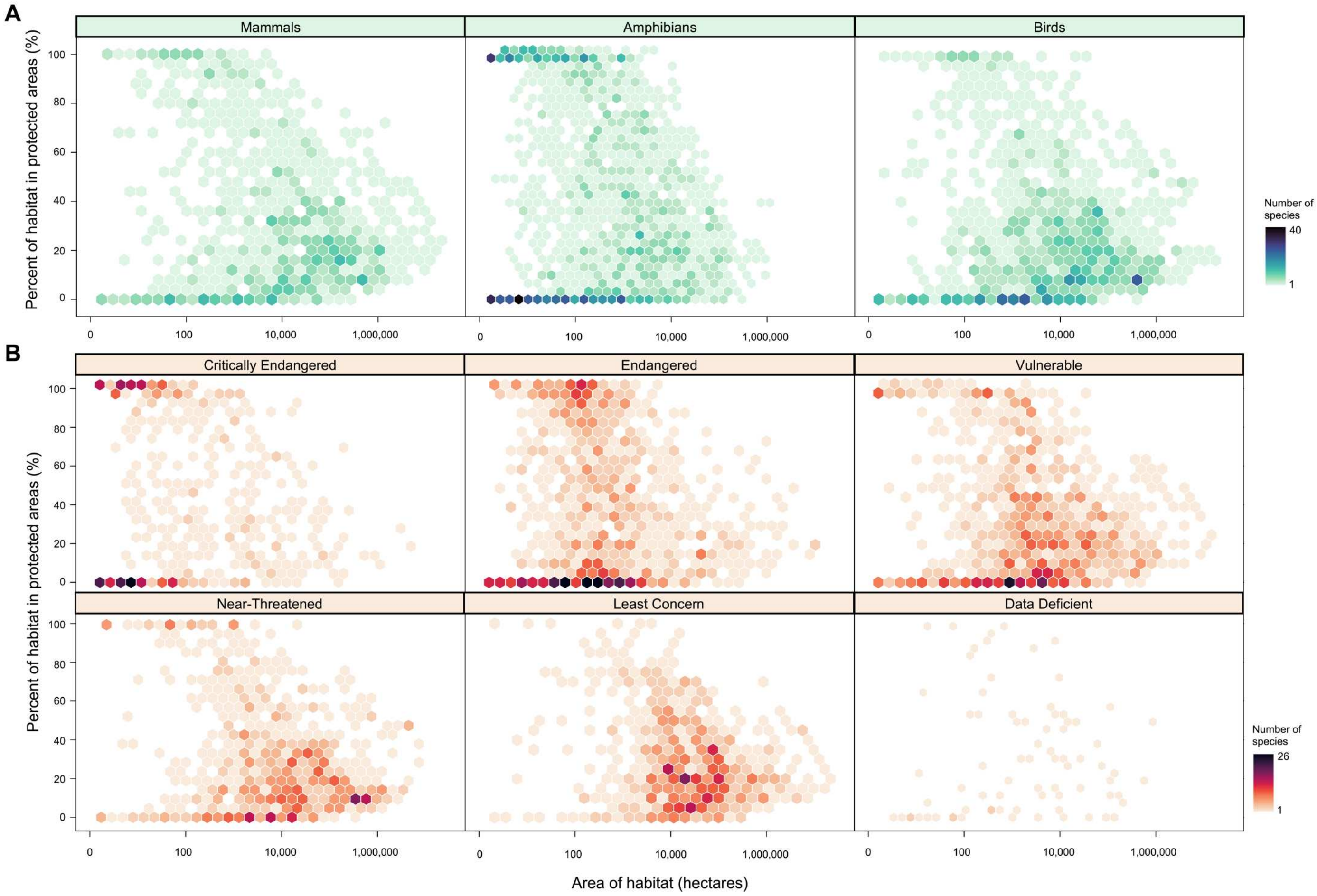

Fig. 1. Relationship between the area of suitable habitat available to 4946 species of mammals, birds, and amphibians and the proportion of their habitat that is safeguarded by parks. The relationship is depicted as mulitple hexbin plots (a representatoin of a three-dimensional histogram) that are (**A**) separated by taxa and (**B**) separated by threat status according to the IUCN Red List. The greater intensity of color indicates a greater number of species that have a specific area of habitat and protected area coverage.

pronounced for species that are at greater risk of extinction—as indicated by an increasing magnitude of slope as threat level increases (from Least Concern to Critically Endangered; Fig. 2). This could stem from the fact that PADDD indicates a continued expansion of human pressures that inform the classification of species as threatened, especially those species with small area of habitat.

Downgrading, downsizing, and degazettement events could also affect species to different degrees given the spatial distribution (and clustering) of those events, as well as the extent to which these rollbacks weaken, constrict, or remove formal legal protections (*17*, *18*). We find that 107 species are likely affected by a reduction in the number (or magnitude) of legal restrictions afforded to parks in downgrading events (Fig. 2). These 107 species have more than half of their available habitats contained within parks with at least one recorded downgrading event. In this same way, we find that 35 species are vulnerable to the reduction in spatial extent of parks through downsizing events, and 5 species are at risk because of the complete loss of protections arising from degazettement events (Fig. 2). We also find that 40 species are likely affected by more than one type of event and have more than half of their available habitats within parks that have experienced a combination of downgrading, downsizing, and degazettement events (Fig. 2).

Our data do not allow us to calculate the amount of species habitat in parks that has been affected by PADDD events. This is especially important for downsizing events because our data do not distinguish which sections of protected areas were excised; in contrast, degazettement and downgrading events are likely to affect the entire park (*17*). While there is a link between PADDD events and impacts to species habitats, shifts in legal protection do not necessarily lead to population declines of species (*17*, *19*, *34*). Nonetheless, the fact remains that these species are highly dependent on vulnerable parks. In other words, the parks they inhabit are analogous to leaky arks. Patching these leaky arks would require reversing the impacts of PADDD events through legal measures and through habitat restoration (*17*).

Already, many enacted PADDD events have been reversed in areas such as Colombia and Peru because of changes in national-level laws (*17*). These reversals could mean a substantial reduction in pressure for 102 species that are reliant on these leaky arks for survival (i.e., species for which >50% of their available habitat occurs within parks that experience reversals) (Fig. 2). That said,

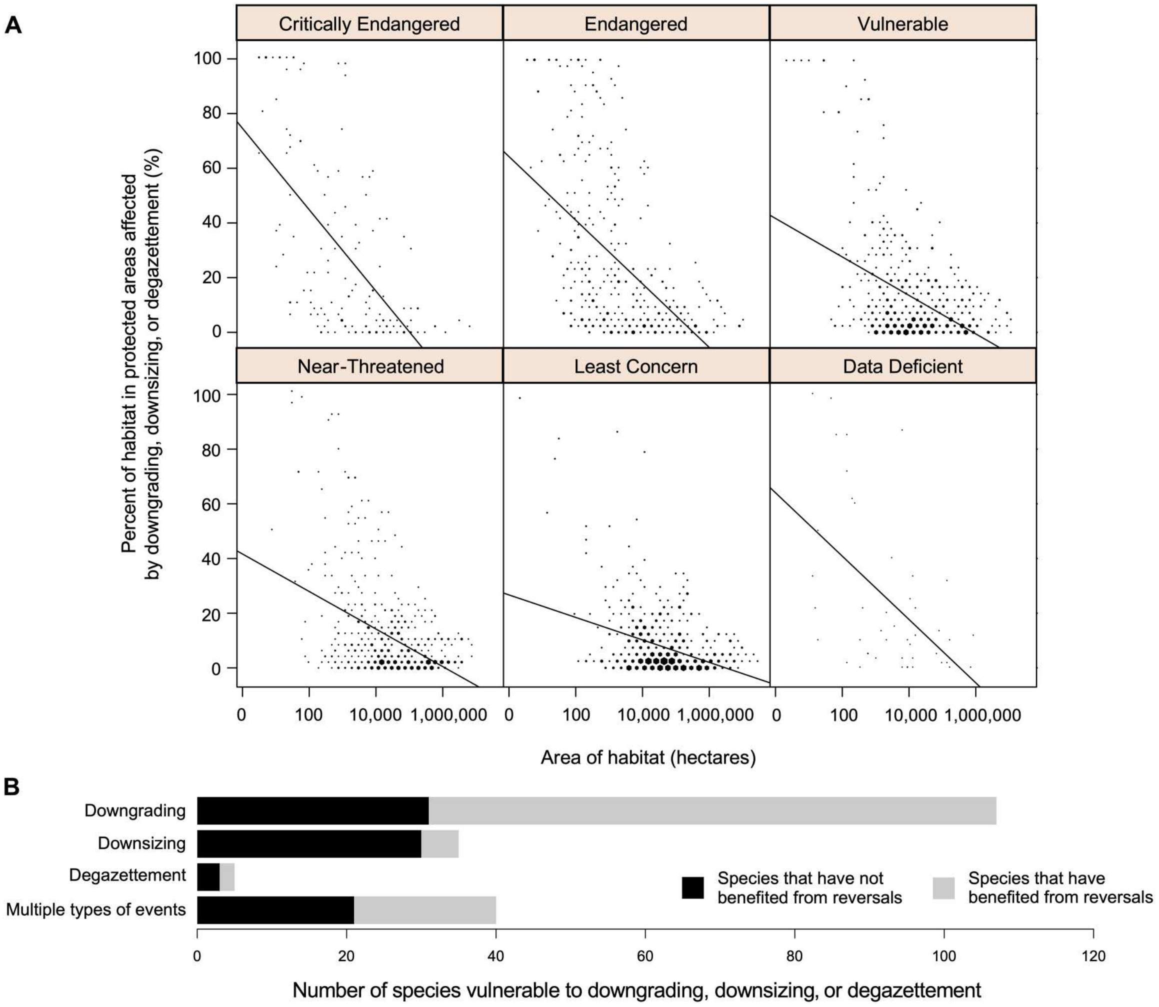

Fig. 2. A majority of the species assessed have habitats that occur in parks affected by PADDD events. (**A**) Relationship between the area of habitat available to species (affected by PADDD) and the percent of area of habitat contained in parks affected by PADDD events and (**B**) the number of species that are vulnerable to PADDD events (defined as having > 50% of available habitats in affected parks). Size of hexagon reflects the number of species associated with the area of habitat and parks affected by PADDD events.

reversals do not guarantee a reduction in species impacts if they are not coupled with restoration of the original habitats or ecological processes (*17*).

Species protected by parks but especially vulnerable to extinction

Looking ahead, limiting the number of species affected by leaky arks by ensuring that parks are adequately protected will be critical to preventing future extinctions (*17*). We find that 407 species (8%) have not yet been affected by PADDD events (as documented by our data sources) but are indeed reliant on parks, with more than 90% of their remaining habitat occurring within park boundaries (table S1). Among these species, 104 would be extremely vulnerable to future land-use change because they have <10 km^2 of habitat remaining globally (table S1).

While many parks are likely to remain effective at excluding harmful human activities, myriad factors could lead to increased vulnerability in the future (*17*, *35*). For instance, if we use well-known modeled projections of future cropland and urban expansion to identify which parks have a high risk of experiencing future land-use change within their borders (see Materials and Methods for more details), we find that 42 species are particularly at risk over the next 30 years (table S1). These 42 species represent terrestrial vertebrates that have <10 km^2 of habitat remaining, of which >90% occurs within parks predicted to be eroded by more than 50% because of cropland and urban expansion under four scenarios of projected socioeconomic global changes (i.e., Shared Socioeconomic Pathways 1, 2, 3, and 5) (*28*). Most of these 42 species are already threatened, with species such as *Balebreviceps hillmani* (Bale Mountains tree frog) continuing to face extinction due to ongoing habitat deterioration despite its supposed complete protection in national parks (*3*, *36*). These results highlight the importance of strengthening parks (e.g., restoring and reinforcing existing parks) as global efforts toward protected area expansion gain traction (*12*, *17*).

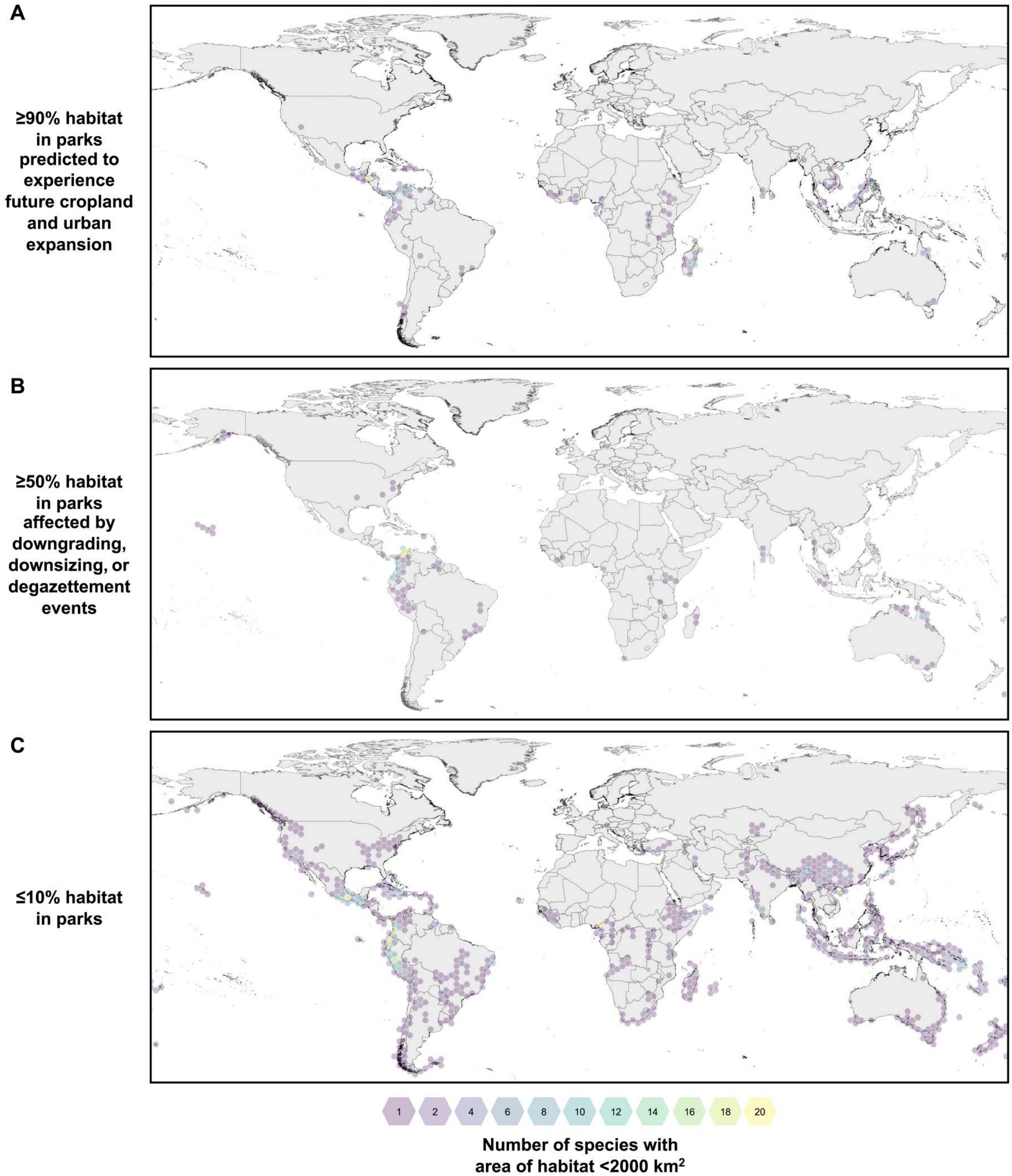

Fig. 3. Geographic distribution of habitat-limited species (area of habitat < 2000 km^2) that could benefit from reinforcing existing parks, restoring existing parks, or creating new parks. (**A**) Species protected by parks but are vulnerable to future land-use change. (**B**) Species contained within parks with recorded PADDD events. (**C**) Species that currently lack protection in parks. Colors within hexagons denotes the number of habitat-limited species within each location.

Geography of arks: Where to create new parks, and restore and reinforce existing parks

In summary, roughly 70% of the species we analyzed either have no apparent representation in parks, occur in parks that have experienced PADDD events, or would be especially vulnerable to extinction from future land-use change. Our identification of where these species occur can aid conservation planning, particularly when these species are at risk because they lack suitable habitat. We map the distributions of a subset of species we consider to be especially in need of attention. These include: (i) 816 species that would benefit greatly from the creation of new parks because they have ≤10% of their habitat currently within parks, and they are habitat-limited, which we define as having <2000 km^2 of habitat remaining; (ii) 163 species that would benefit from habitat restoration and improved management within parks because they are habitat-limited and have ≥50% of their habitat in parks affected by PADDD events; and (iii) 212 species that are highly dependent on continued park protection because they are habitat-limited and have ≥90% of their habitat in parks, yet are predicted to lose ≥50% of their habitat under all four scenarios of future cropland and urban expansion. In all three cases, we apply a threshold of 2000 km^2 to the area of habitat. This matches the area of occupancy threshold used by IUCN to classify a species as Vulnerable (provided that associated subcriteria are also met) (*3*). Given that area of occupancy represents a subset of locations within a species' area of habitat, species with <2000 km^2 of habitat remaining are likely to meet a key criterion to be classified as threatened (*3*, *25*).

We find that the greatest concentration of species that would benefit from the creation of new parks occur in biodiversity hot spots such as the Mesoamerican, Chocó-Darién, and West African forests (Fig. 3). These areas represent a subset of the biodiversity hot spots identified by Myers *et al.* (*37*) (Fig. 3).

Our analysis suggests that restoration of habitats in protected areas around the Tropical Andes, Eastern Afromontane, and Indo-Burma region would benefit large numbers of species that we have identified as being especially vulnerable to PADDD events (Fig. 3) (*17*). Last, reinforcing management of parks and preventing future cropland and urban expansion within their boundaries, for instance by ensuring continued funding and staffing, would limit the risk to rare, park-dependent species in these same regions as well as in Madagascar (Fig. 3) (*4*). However, these conservation interventions must be informed by the needs of local communities as well (*7*, *38*).

We find that the 816 species that are habitat-limited and currently unrepresented in parks, occupy a total of 7.1 million hectares of natural landscapes (measured as the total area of habitat across all species) (Fig. 3 and table S2); the 163 species that are habitat-limited and heavily dependent on parks vulnerable to PADDD events occupy a total of 5.9 million hectares; and the 212 species that are

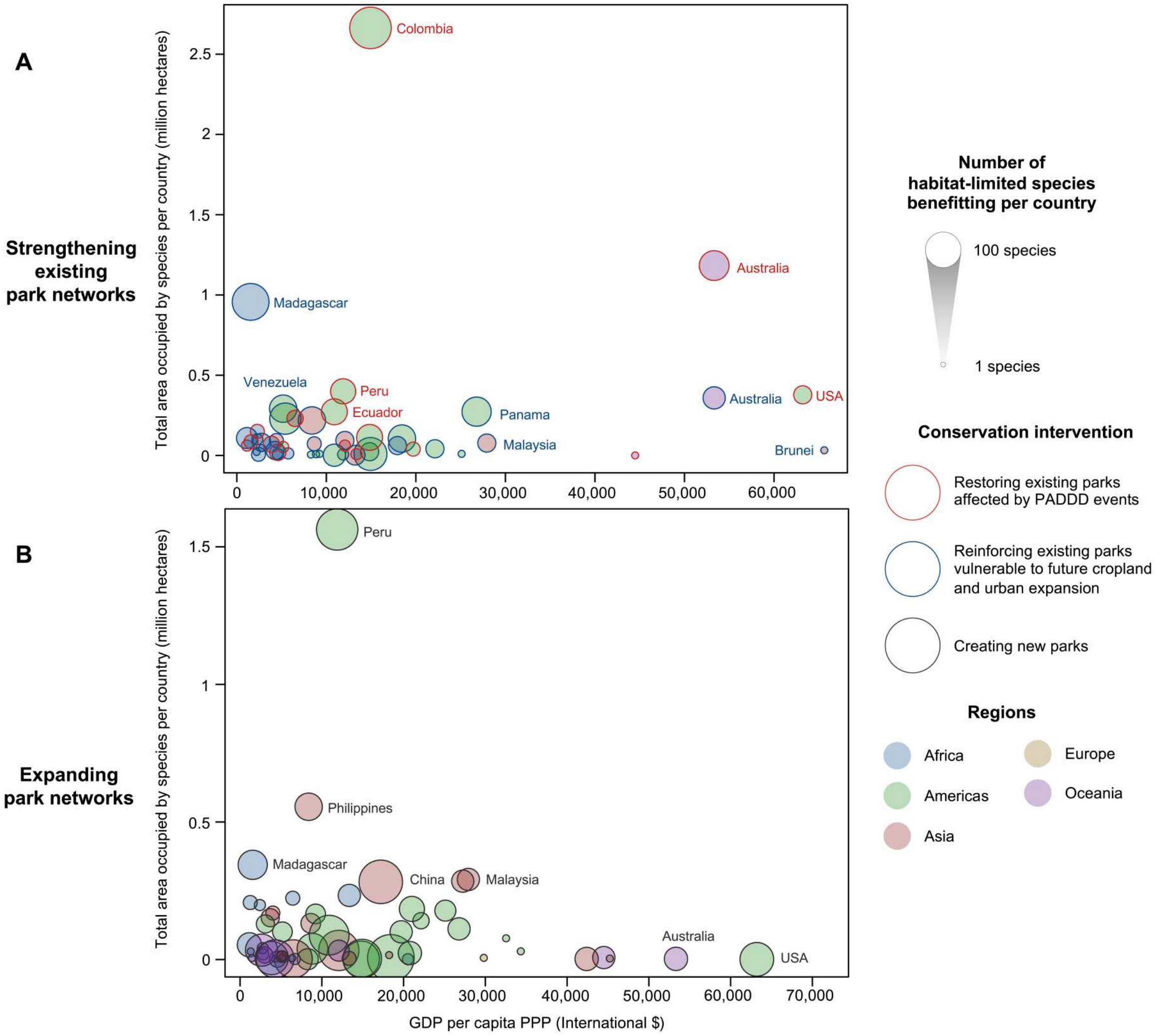

Fig. 4. Relationship between total area of habitat of species within a country that could benefit from strategic strengthening and expanding of park networks in reference to the gross domestic product (GDP) per capita based on purchasing power parity (PPP). (**A**) Strengthening of existing parks includes both the restoration of parks affected by PADDD events and reinforcing of existing parks vulnerable to future cropland and urban expansion and (**B**) expanding park networks refers to the creation of new protected areas. Size of each circle indicates the number of species within each country that could benefit from the conservation intervention, and the outline of circles and country text color indicate the type of intervention. Circle interiors are colored by region.

habitat-limited and highly dependent on habitats in parks that are vulnerable to future land-use change occur across 3.6 million hectares (Fig. 3 and table S2). In total, this represents 1191 species occupying <1% of global land area whose future extinction risk could be greatly reduced by strategically creating new parks and strengthening existing ones (table S2). Such optimized placement of conservation interventions would be spatially efficient and could reduce costs and some of the other barriers to meeting global targets (*15*). Our estimate, however, does not account for important on-the-ground considerations such as impacts to local land rights and economic conditions, as well as the potential for the creation or restoration of parks in one location to raise pressures on parks elsewhere (*7*, *39*).

Our study uses data from World Database on Protected Areas, which mainly features formally recognized protected areas (*9*). It has a tendency to leave out community-managed lands, such as the many that exist in Indonesia, Mexico, and Canada, that can provide substantial safeguards to biodiversity apart from park designation (*40*–*42*). This dataset also has gaps that stem from discrepancies between global databases and national-level inventories, which might include areas that permit a degree of human use while also providing suitable habitat to some species (*7*, *43*). A more inclusive consideration of what qualifies as protected areas would likely lead to fewer species requiring conservation interventions (*7*, *40*, *41*, *43*). Conducting downscaled analyses that focus on a single country or region would allow researchers to use more diverse and inclusive datasets that account for such alternative conservation governance systems (*41*, *43*). Nevertheless, our results show that a relatively large number of at-risk species could benefit from prioritizing conservation interventions over a small amount of land. This focus remains key to minimizing trade-offs and maximizing the limited funding available for the establishment and maintenance of protected areas (*4*, *11*, *38*, *44*).

We do not prescribe a minimum or maximum threshold of protected area coverage that is adequate for species survival, instead using arbitrary thresholds of 10 and 90% of species′ habitats to delimit species that would benefit greatly from expansion of parks and from better protection of existing parks, respectively. However, more conservative or relaxed thresholds can also be applied. For example, applying a 5 and 95% threshold, respectively, would have resulted in 704 species that would benefit from creating new parks and 195 species that would benefit from reinforcing existing parks; a 15 and 85% threshold would have resulted in 923 species that would benefit from creating new parks and 286 species that would benefit from reinforcing existing parks (tables S1 and S2 and fig. S1). Similarly, if we reduced the area of habitat threshold for habitat-limited species to 500 km^2, matching the area of occupancy threshold used by IUCN to classify a species as Endangered, we find that 617 habitat-limited species would benefit from creating new parks, 125 habitat-limited species would benefit from restoring existing parks, and 208 habitat-limited species would benefit from reinforcing existing parks (tables S1 and S2) (*3*). Regardless of the threshold used, we feel that a focus on these three groups of species provides tangible, valuable guidance for targeting areas for protection, restoration, or reinforcement. Countries with the largest number of species in these categories are largely located throughout the tropics (Figs. 3 and 4). By aggregating priority species and sites to their associated political borders (i.e., countries/territories), we find that potential biodiversity conservation benefits are concentrated in less affluent countries (Fig. 4). This is especially pronounced if we consider the area required to achieve this benefit and the global share that falls within individual countries. For example, the expansion of parks in Peru, Philippines, and Madagascar could safeguard an additional 60, 15, and 18 species from our list, respectively, but doing so requires establishment of parks covering up to 1.6, 0.6, and 0.3 million hectares (Fig. 4 and table S2). This amounts to ~35% of the global total identified in our study, falling within just three countries each of whose gross domestic product per capita (purchasing power parity) does not exceed $12,000. Similarly, 60% of the parks identified as urgently requiring restoration fall within Colombia, Australia, and Peru, and 45% of the parks requiring vigilance to prevent future species loss due to land-use change fall within Madagascar, Venezuela, and Australia (Fig. 4 and table S2). These results point to the tremendous conservation burdens potentially being placed upon a small number of countries with high levels of biodiversity, most of which likely have limited financial resources to expand and strengthen their network of protected areas (*45*, *46*). This issue was a source of contention at the 15th Conference of Parties to the UN Convention on Biological Diversity, which led to a number of delegates from developing countries walking out of negotiations. To meet some of these funding shortfalls, it has been suggested that richer nations should redirect US$ 10 billion in aid per year to support biodiversity conservation in developing countries across the world (*4*, *11*). Our results highlight the need to divert a larger proportion of conservation funds and foreign assistance to the countries with the greatest conservation burdens, particularly those less able to meet such requirements domestically.

Besides these twin considerations of expanding and strengthening protected area networks, there are many other goals associated with area-based conservation. For example, enhancing connectivity between patches of protected areas is important to maintain resilience to multiple threats, including climate change (*47*, *48*). In addition, it has been argued that species with very small ranges should have virtually all of their remaining habitat protected and that only species that exceed >250,000 km^2 should require as little as 10% of their habitat to be safeguarded (*23*).

Ultimately, we find that while the global burden of establishing, restoring, and reinforcing protected areas for the most at-risk species tends to fall within a small number of less affluent countries, the total area required to rapidly increase biodiversity conservation benefits is, in absolute terms, relatively small. This highlights the potential utility of a more nuanced understanding of where individual species′ habitats occur and the current conservation interventions that exist for them. Given the urgent need to implement conservation measures to conserve species and the need to balance socioeconomic constraints, such an approach is vital to finding a balanced solution to the global biodiversity crisis.

MATERIALS AND METHODS

Calculating available habitat of focal species

We created maps of the available suitable habitats for 4946 species of terrestrial mammals, amphibians, and birds following Brooks *et al.* (*25*). These species were selected from among the terrestrial mammals, amphibians, and bird species assessed by the IUCN Red List of Threatened Species (*3*) to reflect species that require the maintenance of natural landscapes and conditions within their range to use it as habitat. Hence, we limited the species analyzed to those that (i) are unable to use anthropogenic habitats (i.e., artificial habitats or habitats dominated by introduced vegetation) and (ii) have been recorded as having experienced anthropogenic stresses to their habitat or ecosystem. These data were directly obtained from the habitat classification scheme (Version 3.1) in the IUCN Red List of Threatened Species and followed the Level 2 habitat classification (e.g. 1.5 Subtropical/tropical dry forest; 3.6 Subtropical/tropical moist shrubland) (*3*).

Using the Level 2 habitat classification allows us to match a species quantified range to the areas of suitable habitats within its range boundaries (*3*, *24*, *49*). The range boundaries (polygons) of the 4946 species were obtained from IUCN (mammals and amphibians) and BirdLife International (*3*, *49*). These polygons, which we limited to extant and native ranges, were then used to mask the 2015 map of Level 2 terrestrial habitat types characterized by Jung *et al.* (*24*). In addition, we also limited a species' area of habitat to its suitable elevational range, based on species' elevational preferences listed IUCN and a recent elevation map (*3*, *26*). Last, we updated the area of habitat of each species to 2019 by excluding any areas that experienced an expansion of anthropogenic land cover (i.e., cropland and built-up areas) between 2015 and 2019 (*27*).

Protected area coverage and downgrading, downsizing, or degazettement events

We assessed current protected area coverage based on spatially explicit data from the World Database of Protected Areas (*9*). This includes all areas recognized as protected areas (in all categories) as well as other effective area-based conservation measures, according to the standards of UNEP and IUCN, and represents the most comprehensive database of terrestrial protected areas available on a global level (*9*). We cross-referenced these protected areas identities to parks that have affected by downgrading, downsizing, or degazettement events (often referred to as PADDD events) recorded in PADDDtracker.org (Version 2.1) (*50*). Location and extents of degazettement events were obtained from PADDDtracker.org when degazettement led to removal from the protected area database. Specifically, parks can be affected by a single downgrading, downsizing, or degazettement events or multiple events (same or combination of event types). Parks can also experience enacted and proposed PADDD events, and some parks also experience PADDD reversals (*17*). Using these two sources of data, we calculated the proportion of each species' area of suitable habitat that occurs (i) within protected areas and (ii) within protected areas previously affected by PADDD events. We further classify this into the proportion of each species' area of suitable habitat that occurs in parks affected by (ii-a) downgrading, (ii-b) downsizing, or (ii-c) degazettement events alone, or (ii-d) the combination of multiple types of events, as well as (ii-e) parks that have experienced reversals. This includes parks that experience multiple events within its boundaries. To account for potential time lags, we also assume that proposed PADDD events would carry the same degree of risk to species vulnerability as enacted PADDD events and assess the combined risk of both in this study.

Future expansion of human activities into protected areas

We estimated the potential for future human activities, namely, cropland and urban expansion, to encroach into existing protected areas by using data from the Land-Use Harmonization (LUH2) project (*28*). Here, we focused on four specific shared socio-economic pathways (SSPs) that reflect different scenarios of future global socioeconomic development and the degree of associated land-use change. Briefly, we considered the following: SSP1, which represents a sustainability narrative, where there is a strong degree of land-use change regulation; SSP2, which represents a middle-of-the-road narrative, with a medium degree of land-use change regulation; SSP3, regional-rivalry and rocky-road narrative, with limited degree of land-use change regulation; and SSP5, fossil-fueled development narrative, where there remains a medium level of land-use change regulation (*28*). We used the summed total of cropland and urban expansion predicted to occur by 2050 in each 1-km grid cell as an indicator the degree of increased human pressures likely to be faced by protected area in those grid cells. This allows us to estimate the relative increase in human pressures on protected areas that would in turn threaten species that depend on these protected areas for the maintenance of natural habitats.

Categorizing species based on risk

With these modeled results, we were able to calculate the following: (i) the area of suitable habitat available to each species, (ii) the proportion of species habitat currently contained within protected areas, (iii) the proportion of species habitat currently in protected areas affected by PADDD events collectively, and (iv) the proportion of species habitat in protected areas that could be affected by expanding human pressures in the future.

With the above information, we categorized species into three groups. These were (i) species that currently lack protection in parks, (ii) species protected by parks but affected by PADDD events, and (iii) species protected by parks that are at risk of experiencing future land use change. Species that have less habitat are assessed to be at greater risk of extinction, and this provides us with a means of identifying a subset of habitat-limited species that will likely benefit from area-based conservation interventions. We define habitat-limited species as those with <2000 km^2 of total area of habitat remaining (iv).

1) Species that currently lack protection in parks: We categorized habitat-limited species with ≤10% of this habitat currently in protected areas that would benefit from the creation of new protected areas.

2) Species protected by parks, but affected by PADDD events: We categorized habitat-limited species with ≥50% of habitat in parks affected by PADDD events that would benefit from the restoration of parks.

3) Species protected by parks that are at risk of experiencing future land-use change: We categorized habitat-limited species with ≥90% of their habitat in parks that are not currently affected by PADDD yet are predicted to lose ≥50% of habitat in parks under all four scenarios of future cropland and urban expansion that will most benefit from the prevention of future human encroachments into protected areas.

In addition, we conducted uncertainty analyses on the protected area coverage and the habitat-limited species area thresholds. For example, we find that more stringent protected area coverage thresholds of 5 and 95% will result in a 14 and 17% decrease in number of species that would benefit from the creation of new protected areas and the prevention of future human encroachments into protected areas, respectively (fig. S1). In addition, defining habitat-limited species with an area of habitat threshold of 500 km^2 would reduce the number of species benefiting from new parks by 24%, the number of species benefiting from restored parks by 25% and the number of species benefiting from avoided future human encroachments by 17% (fig. S1).

Mapping the benefits of conservation interventions

We modeled the number of species and area of habitats that would benefit from each of the three conservation interventions across the world. First, we aggregated the species richness maps to a 1° hexagonal grid for illustrative purposes. Next, we calculated the number of species within the boundaries of 238 countries/territories and the total (overlapping) area of habitat of all these species within each country. We then assessed the relationship between a country's affluence or economic output, measured by gross domestic product per capita (in purchasing power parity) (*51*), and the total area of habitat of occupied by the species within each country that (i) currently lack protection in parks; (ii) are protected by parks but affected by PADDD events; (iii) are protected by parks but prone to extinction.

All raster resolutions were formed at 1-km resolution following the native resolution of Jung *et al.* (*24*). Coarser resolutions (i.e., LUH2 maps) were resampled to a 1-km resolution. All analyses was performed in R version 3.6.0 (*52*), using the package "terra" for processing and calculations of raster layers (*53*), "sf" for shapefiles (*54*), and "fasterize" for the rasterization algorithm (*55*). Map visualizations were formed in QGIS (*56*).

Supplementary Materials

This PDF file includes:
Fig. S1
Legends for tables S1 and S2

Other Supplementary Material for this manuscript includes the following:
Tables S1 and S2

REFERENCES AND NOTES

1. P. G. Curtis, C. M. Slay, N. L. Harris, A. Tyukavina, M. C. Hansen, Classifying drivers of global forest loss. *Science* **361**, 1108–1111 (2018).
2. S. Ducatez, R. Shine, Drivers of Extinction Risk in Terrestrial Vertebrates. *Conserv. Lett.* **10**, 186–194 (2017).
3. IUCN, "The IUCN Red List of Threatened Species. Version 2021–1" (2021).
4. L. Coad, J. E. M. Watson, J. Geldmann, N. D. Burgess, F. Leverington, M. Hockings, K. Knights, M. di Marco, Widespread shortfalls in protected area resourcing undermine efforts to conserve biodiversity. *Front. Ecol. Environ.* **17**, 259–264 (2019).
5. S. L. Maxwell, V. Cazalis, N. Dudley, M. Hoffmann, A. S. L. Rodrigues, S. Stolton, P. Visconti, S. Woodley, N. Kingston, E. Lewis, M. Maron, B. B. N. Strassburg, A. Wenger, H. D. Jonas, O. Venter, J. E. M. Watson, Area-based conservation in the twenty-first century. *Nature* **586**, 217–227 (2020).
6. L. Santini, S. Saura, C. Rondinini, Connectivity of the global network of protected areas. *Divers. Distrib.* **22**, 199–211 (2016).
7. Y. Zeng, L. P. Koh, D. S. Wilcove, Gains in biodiversity conservation and ecosystem services from the expansion of the planet's protected areas. *Sci. Adv.* **8**, eabl9885 (2022).
8. P. Shah, K. Baylis, J. Busch, J. Engelmann, What determines the effectiveness of national protected area networks? *Environ. Res. Lett.* **16**, 074017 (2021).
9. WDPA, The World Database on Protected Areas (WDPA) (2021).
10. G. G. Gurney, E. S. Darling, G. N. Ahmadia, V. N. Agostini, N. C. Ban, J. Blythe, J. Claudet, G. Epstein, Estradivari, A. Himes-Cornell, H. D. Jonas, D. Armitage, S. J. Campbell, C. Cox, W. R. Friedman, D. Gill, P. Lestari, S. Mangubhai, E. McLeod, N. A. Muthiga, J. Naggea, R. Ranaivoson, A. Wenger, I. Yulianto, S. D. Jupiter, Biodiversity needs every tool in the box: use OECMs. *Nature* **595**, 646–649 (2021).
11. Convention on Biological Diversity, "Zero draft of the post-2020 global biodiversity framework" (Convention on Biological Diversity, 2020).
12. V. M. Adams, G. D. Iacona, H. P. Possingham, Weighing the benefits of expanding protected areas versus managing existing ones. *Nat. Sustain.* **2**, 404–411 (2019).
13. D. R. Williams, C. Rondinini, D. Tilman, Global protected areas seem insufficient to safeguard half of the world's mammals from human-induced extinction. *Proc. Natl. Acad. Sci.* **119**, e2200118119 (2022).
14. S. H. M. Butchart, M. Clarke, R. J. Smith, R. E. Sykes, J. P. W. Scharlemann, M. Harfoot, G. M. Buchanan, A. Angulo, A. Balmford, B. Bertzky, T. M. Brooks, K. E. Carpenter, M. T. Comeros-Raynal, J. Cornell, G. F. Ficetola, L. D. C. Fishpool, R. A. Fuller, J. Geldmann, H. Harwell, C. Hilton-Taylor, M. Hoffmann, A. Joolia, L. Joppa, N. Kingston, I. May, A. Milam, B. Polidoro, G. Ralph, N. Richman, C. Rondinini, D. B. Segan, B. Skolnik, M. D. Spalding, S. N. Stuart, A. Symes, J. Taylor, P. Visconti, J. E. M. Watson, L. Wood, N. D. Burgess, Shortfalls and solutions for meeting national and global conservation area targets. *Conserv. Lett.* **8**, 329–337 (2015).
15. O. Venter, R. A. Fuller, D. B. Segan, J. Carwardine, T. Brooks, S. H. M. Butchart, M. di Marco, T. Iwamura, L. Joseph, D. O'Grady, H. P. Possingham, C. Rondinini, R. J. Smith, M. Venter, J. E. M. Watson, Targeting global protected area expansion for imperiled biodiversity. *PLOS Biol.* **12**, e1001891 (2014).
16. C. A. Bonham, E. Sacayon, E. Tzi, Protecting imperiled "paper parks": potential lessons from the Sierra Chinajá, Guatemala. *Biodivers. Conserv.* **17**, 1581–1593 (2008).
17. R. E. G. Kroner, S. Qin, C. N. Cook, R. Krithivasan, S. M. Pack, O. D. Bonilla, K. A. Cort-Kansinally, B. Coutinho, M. Feng, M. I. M. Garcia, Y. He, C. J. Kennedy, C. Lebreton, J. C. Ledezma, T. E. Lovejoy, D. A. Luther, Y. Parmanand, C. A. Ruíz-Agudelo, E. Yerena, V. M. Zambrano, M. B. Mascia, The uncertain future of protected lands and waters. *Science* **364**, 881–886 (2019).
18. M. B. Mascia, S. Pailler, R. Krithivasan, V. Roshchanka, D. Burns, M. C. J. Mlotha, D. R. Murray, N. Peng, Protected area downgrading, downsizing, and degazettement (PADDD) in Africa, Asia, and Latin America and the Caribbean, 1900–2010. *Biol. Conserv.* **169**, 355–361 (2014).
19. J. L. Forrest, M. B. Mascia, S. Pailler, S. Z. Abidin, M. D. Araujo, R. Krithivasan, J. C. Riveros, Tropical deforestation and carbon emissions from protected area downgrading, downsizing, and degazettement (PADDD). *Conserv. Lett.* **8**, 153–161 (2015).
20. J. R. Allan, H. P. Possingham, S. C. Atkinson, A. Waldron, M. di Marco, S. H. M. Butchart, V. M. Adams, W. D. Kissling, T. Worsdell, C. Sandbrook, G. Gibbon, K. Kumar, P. Mehta, M. Maron, B. A. Williams, K. R. Jones, B. A. Wintle, A. E. Reside, J. E. M. Watson, The minimum land area requiring conservation attention to safeguard biodiversity. *Science* **376**, 1094–1101 (2022).
21. M. Jung, A. Arnell, X. de Lamo, S. García-Rangel, M. Lewis, J. Mark, C. Merow, L. Miles, I. Ondo, S. Pironon, C. Ravilious, M. Rivers, D. Schepaschenko, O. Tallowin, A. van Soesbergen, R. Govaerts, B. L. Boyle, B. J. Enquist, X. Feng, R. Gallagher, B. Maitner, S. Meiri, M. Mulligan, G. Ofer, U. Roll, J. O. Hanson, W. Jetz, M. D. Marco, J. M. Gowan, D. S. Rinnan, J. D. Sachs, M. Lesiv, V. M. Adams, S. C. Andrew, J. R. Burger, L. Hannah, P. A. Marquet, J. K. M. Carthy, N. Morueta-Holme, E. A. Newman, D. S. Park, P. R. Roehrdanz, J.-C. Svenning, C. Violle, J. J. Wieringa, G. Wynne, S. Fritz, B. B. N. Strassburg, M. Obersteiner, V. Kapos, N. Burgess, G. Schmidt-Traub, P. Visconti, Areas of global importance for conserving terrestrial biodiversity, carbon and water. *Nat. Ecol. Evol.* **5**, 1499–1509 (2021).
22. O. Venter, A. Magrach, N. Outram, C. J. Klein, H. P. Possingham, M. di Marco, J. E. M. Watson, Bias in protected-area location and its effects on long-term aspirations of biodiversity conventions. *Conserv. Biol.* **32**, 127–134 (2018).
23. W. Jetz, J. McGowan, D. S. Rinnan, H. P. Possingham, P. Visconti, B. O'Donnell, M. C. Londoño-Murcia, Include biodiversity representation indicators in area-based conservation targets. *Nat. Ecol. Evol.* **6**, 123–126 (2022).
24. M. Jung, P. R. Dahal, S. H. M. Butchart, P. F. Donald, X. de Lamo, M. Lesiv, V. Kapos, C. Rondinini, P. Visconti, A global map of terrestrial habitat types. *Sci. Data* **7**, 256 (2020).
25. T. M. Brooks, S. L. Pimm, H. R. Akçakaya, G. M. Buchanan, S. H. M. Butchart, W. Foden, C. Hilton-Taylor, M. Hoffmann, C. N. Jenkins, L. Joppa, B. V. Li, V. Menon, N. Ocampo-Peñuela, C. Rondinini, Measuring terrestrial area of habitat (AOH) and its utility for the IUCN red list. *Trends Ecol. Evol.* **34**, 977–986 (2019).
26. S. E. Fick, R. J. Hijmans, WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
27. M. Buchhorn, M. Lesiv, N. E. Tsendbazar, M. Herold, L. Bertels, B. Smets, Copernicus global land cover layers—collection 2. *Remote Sens. (Basel)* **12**, 1044 (2020).
28. A. Popp, K. Calvin, S. Fujimori, P. Havlik, F. Humpenöder, E. Stehfest, B. L. Bodirsky, J. P. Dietrich, J. C. Doelmann, M. Gusti, T. Hasegawa, P. Kyle, M. Obersteiner, A. Tabeau, K. Takahashi, H. Valin, S. Waldhoff, I. Weindl, M. Wise, E. Kriegler, H. Lotze-Campen, O. Fricko, K. Riahi, D. P. v. Vuuren, Land-use futures in the shared socio-economic pathways. *Glob. Environ. Chang.* **42**, 331–345 (2017).
29. I. R. Staude, L. M. Navarro, H. M. Pereira, Range size predicts the risk of local extinction from habitat loss. *Glob. Ecol. Biogeogr.* **29**, 16–25 (2020).

30. E. W. Seabloom, A. P. Dobson, D. M. Stoms, Extinction rates under nonrandom patterns of habitat loss. *Proc. Natl. Acad. Sci. U.S.A.* **99**, 11229–11234 (2002).
31. L. Cantú-Salazar, C. D. L. Orme, P. C. Rasmussen, T. M. Blackburn, K. J. Gaston, The performance of the global protected area system in capturing vertebrate geographic ranges. *Biodivers. Conserv.* **22**, 1033–1047 (2013).
32. F. Meehan, L. Tacconi, K. Budiningsih, Are national commitments to reducing emissions from forests effective? Lessons from Indonesia. *Forest Policy Econ.* **108**, 101968 (2019).
33. Z. Meng, J. Dong, E. C. Ellis, G. Metternicht, Y. Qin, X. P. Song, S. Löfqvist, R. D. Garrett, X. Jia, X. Xiao, Post-2020 biodiversity framework challenged by cropland expansion in protected areas. *Nat. Sustain.* 10.1038/s41893-023-01093-w, (2023).
34. R. E. G. Kroner, R. Krithivasan, M. B. Mascia, Effects of protected area downsizing on habitat fragmentation in Yosemite National Park (USA), 1864–2014. *Ecol. Soc.* **21**, 10.5751/ES-08679-210322, (2016).
35. W. S. Symes, M. Rao, M. B. Mascia, L. R. Carrasco, Why do we lose protected areas? Factors influencing protected area downgrading, downsizing and degazettement in the tropics and subtropics. *Glob. Chang. Biol.* **22**, 656–665 (2016).
36. D. J. Gower, R. K. Aberra, S. Schwaller, M. J. Largen, B. Collen, S. Spawls, M. Menegon, B. M. Zimkus, R. de Sá, A. A. Mengistu, F. Gebresenbet, R. D. Moore, S. A. Saber, S. P. Loader, Long-term data for endemic frog genera reveal potential conservation crisis in the Bale Mountains, Ethiopia. *Oryx* **47**, 59–69 (2013).
37. N. Myers, R. A. Mittermeier, C. G. Mittermeier, G. A. da Fonseca, J. Kent, Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
38. R. Chaplin-Kramer, K. A. Brauman, J. Cavender-Bares, S. Díaz, G. T. Duarte, B. J. Enquist, L. A. Garibaldi, J. Geldmann, B. S. Halpern, T. W. Hertel, C. K. Khoury, J. M. Krieger, S. Lavorel, T. Mueller, R. A. Neugarten, J. Pinto-Ledezma, S. Polasky, A. Purvis, V. Reyes-García, P. R. Roehrdanz, L. J. Shannon, M. R. Shaw, B. B. N. Strassburg, J. M. Tylianakis, P. H. Verburg, P. Visconti, N. Zafra-Calvo, Conservation needs to integrate knowledge across scales. *Nat. Ecol. Evol.* **6**, 118–119 (2022).
39. C. Wyborn, M. C. Evans, Conservation needs to break free from global priority mapping. *Nat. Ecol. Evol.* **5**, 1322–1324 (2021).
40. D. B. Bray, L. Merino-Perez, P. Negreros-Castillo, G. Segura-Warnholtz, J. M. Torres-Rojo, H. F. M. Vester, Mexico's community-managed forests as a global model for sustainable landscapes. *Conserv. Biol.* **17**, 672–677 (2003).
41. R. Schuster, R. R. Germain, J. R. Bennett, N. J. Reo, P. Arcese, Vertebrate biodiversity on indigenous-managed lands in Australia, Brazil, and Canada equals that in protected areas. *Environ. Sci. Policy* **101**, 1–6 (2019).
42. J. S. Sze, D. Z. Childs, L. R. Carrasco, D. P. Edwards, Indigenous lands in protected areas have high forest integrity across the tropics. *Curr. Biol.* **32**, 4949–4956.e3 (2022).
43. L. M. Dreiss, J. W. Malcom, Identifying key federal, state, and private lands strategies for achieving 30 × 30 in the United States. *Conserv. Lett.* **15**, e12849 (2022).
44. A. Waldron, V. Adams, J. Allan, A. Arnell, G. Asner, S. Atkinson, A. Baccini, J. Baillie, A. Balmford, J. A. Beau, L. Brander, E. Brondizio, A. Bruner, N. Burgess, K. Burkart, S. Butchart, R. Button, R. Carrasco, W. Cheung, V. Christensen, A. Clements, M. Coll, M. D. Marco, M. Deguignet, E. Dinerstein, E. Ellis, F. Eppink, J. Ervin, A. Escobedo, J. Fa, A. Fernandes-Llamazares, S. Fernando, S. Fujimori, B. Fulton, S. Garnett, J. Gerber, D. Gill, T. Gopalakrishna, N. Hahn, B. Halpern, T. Hasegawa, P. Havlik, V. Heikinheimo, R. Heneghan, E. Henry, F. Humpenoder, H. Jonas, K. Jones, L. Joppa, A. Joshi, M. Jung, N. Kingston, C. Klein, T. Krisztin, V. Lam, D. Leclere, P. Lindsey, H. Locke, T. Lovejoy, P. Madgwick, Y. Malhi, P. Malmer, M. Maron, J. Mayorga, H. V. Meijl, D. Miller, Z. Molnar, N. Mueller, N. Mukherjee, R. Naidoo, K. Nakamura, P. Nepal, R. Noss, B. O'Leary, D. Olson, J. P. Abrantes, M. Paxton, A. Popp, H. Possingham, J. Prestemon, A. Reside, C. Robinson, J. Robinson, E. Sala, K. Scherrer, M. Spalding, A. Spenceley, J. Steenbeck, E. Stehfest, B. Strassborg, R. Sumaila, K. Swinnerton, J. Sze, D. Tittensor, T. Toivonen, A. Toledo, P. N. Torres, W. V. Zeist, J. Vause, O. Venter, T. Vilela, P. Visconti, C. Vynne, R. Watson, J. Watson, E. Wikramanayake, B. Williams, B. Wintle, S. Woodley, W. Wu, K. Zander, Y. Zhang, Y. Zhang, Protecting 30% of the planet for nature: Costs, benefits and economic implications. Campaign for Nature (2020); http://pure.iiasa.ac.at/id/eprint/16560/.
45. V. Hickey, S. L. Pimm, How the World Bank funds protected areas. *Conserv. Lett.* **4**, 269–277 (2011).
46. A. Waldron, A. O. Mooers, D. C. Miller, N. Nibbelink, D. Redding, T. S. Kuhn, J. T. Roberts, J. L. Gittleman, Targeting global conservation funding to limit immediate biodiversity declines. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 12144–12148 (2013).
47. S. A. Parks, C. Carroll, S. Z. Dobrowski, B. W. Allred, Human land uses reduce climate connectivity across North America. *Glob. Chang. Biol.* **26**, 2944–2955 (2020).
48. R. Sreekar, Y. Zeng, Q. Zheng, A. Lamba, H. C. Teo, T. V. Sarira, L. P. Koh, Nature-based climate solutions for expanding the global protected area network. *Biol. Conserv.* **269**, 109529 (2022).
49. BirdLife International and Handbook of the Birds of the World, Bird species distribution maps of the world. Version 2020.1 (2020); available at http://datazone.birdlife.org/species/requestdis.
50. Conservation International and World Wildlife Fund, "PADDDtracker: Tracking protected area downgrading, downsizing, and degazettement" World Wildlife Fund, Conservation International, Ed. (Conservation International, World Wildlife Fund, 2021), vol. 2022.
51. The World Bank, GDP per capita, PPP (current international) (2021); available at https://data.worldbank.org/indicator/NY.GDP.PCAP.PP.CD.
52. R Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2020).
53. R. J. Hijmans, terra: Spatial Data Analysis, R package version 1.5-21 (2022); https://CRAN.R-project.org/package=terra.
54. E. Pebesma, Simple Features for R: Standardized Support for Spatial Vector Data. *R. J.* **10**, 439–446 (2018).
55. N. Ross, fasterize: Fast polygon to raster conversion, R package version 1.0.3 (2020); https://CRAN.R-project.org/package=fasterize.
56. QGIS Development Team, QGIS Geographic Information System. *Open Source Geospatial Foundation Project* (2016); http://qgis.osgeo.org.

Acknowledgments: We thank S. Z. Zainul Rahim, L. Ma, A. Wiebe, and F. Guo for contributions to improving the manuscript. **Funding:** Funding for this research was provided by the High Meadows Environmental Institute and the High Meadows Foundation. **Author contributions:** Y.Z., R.A.S., and D.S.W. conceived the study. Y.Z. collated the data and carried out the analyses. All authors contributed discussions and modeling insights. All authors wrote the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Codes used in this manuscript are available on Zenodo (10.5281/zenodo.7758709).

Submitted 28 November 2022
Accepted 1 May 2023
Published 2 June 2023
10.1126/sciadv.adg0288