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Future threats to biodiversity and pathways to their prevention

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Tens of thousands of species are threatened with extinction as a result of human activities. Here we explore how the extinction risks of terrestrial mammals and birds might change in the next 50 years. Future population growth and economic development are forecasted to impose unprecedented levels of extinction risk on many more species worldwide, especially the large mammals of tropical Africa, Asia and South America. Yet these threats are not inevitable. Proactive international efforts to increase crop yields, minimize land clearing and habitat fragmentation, and protect natural lands could increase food security in developing nations and preserve much of Earth's remaining biodiversity.

Hence the environment are imperilling the species and ecosystems of Earth at ever-increasing rates¹⁻³. Land-use change and habitat fragmentation⁴, overhunting, invasive species and pollution⁵ already threaten 25% of all mammal species and 13% of all bird species, as well as more than 21,000 other species of plants and other animals, with extinction⁶. In one of the few remaining centres of terrestrial large mammal diversity worldwide, an area that comprises southeast Asia, India and China (referred to as SAIC in this Review), rapid increases in wealth, land clearing and population density in the last 50 years have resulted in almost two-thirds of mammals that weigh 10 kg or more being threatened with extinction⁶.

Another such centre — sub-Saharan Africa — is likely to be swept by a similar wave of human impacts in the coming decades. Indeed, various analyses suggest that Earth's most biodiverse regions will experience elevated extinction risks in the near future if human impacts continue along current trajectories^{7–10}. To prevent and reduce threats to global biodiversity, more substantial conservation efforts will be needed and proactive policies, such as shifts in agricultural practices, increased agricultural trade and improved land-use planning, will also be essential¹⁰.

Human-influenced extinctions began when modern humans moved out of Africa. Successive waves of extinctions in Australia (50,000 years (50 kyr) ago), North America and South America (10–11 kyr ago) and Europe (3–12 kyr ago) were driven largely by a combination of hunting by humans and natural climate change. By 3 kyr ago, Earth had lost half of all terrestrial mammalian megafauna species (with a mass of more than 44 kg) and 15% of all bird species^{11–14}. Since 1500 AD, the impacts of humans have accelerated⁶. Extinction rates for birds, mammals and amphibians^{15–17} are similar at present to those of the five global mass-extinction events of the past 500 million years (500 Myr) that probably resulted from meteorite impacts, massive volcanism and other cataclysmic forces¹³.

With the human population worldwide now 25 times greater than 3 kyr ago and projected to increase by about 4 billion people by the end of the twenty-first century¹⁸, extinction rates will accelerate in the absence of large-scale conservation actions. Here, we explore current patterns of extinction risks and their drivers, and discuss where and

how these risks may change in the coming 50 years, which species groups are most likely to be jeopardized and how future risks might be minimized or prevented.

Human-driven extinction risks

In this Review, we focus on terrestrial mammals and birds because of the comprehensive assessments of the threats to and stresses on these two groups conducted by the International Union for Conservation of Nature (IUCN). We expect that human-driven changes in the environment will increasingly threaten these and other groups of terrestrial, marine and freshwater species¹⁹.

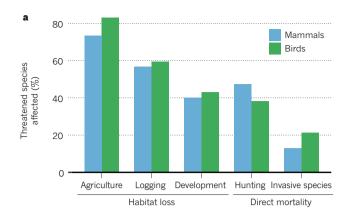
The IUCN has assessed the risk of extinction for 61,000 animal species, including essentially all known species of mammals and birds, against its Red List categories and criteria^{6,20} and classified the status of each as one of the following: 'least concern' (extinction risk (ν) of 0); 'near threatened' (ν =1); 'vulnerable' (ν =2); 'endangered' (ν =3); 'critically endangered' (ν =4); and 'extinct' or 'extinct in the wild' (ν =5). We have adopted the IUCN terminology, in which a species is considered to be threatened if it is listed as vulnerable, endangered or critically endangered. We also used two metrics of the extinction risks faced by a particular country's mammal and bird species: the percentage of all species that are threatened with extinction; and the mean extinction risk value for all of the species in a country. In these calculations, we excluded the few 'data deficient' and 'not evaluated' species (see Supplementary Methods).

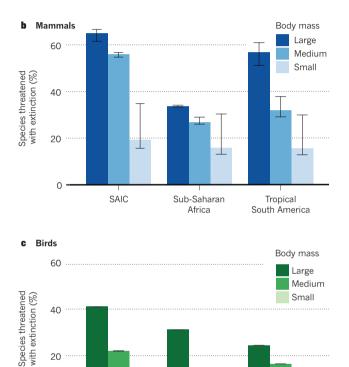
Land-use change is associated with declining biodiversity worldwide⁴. Habitat loss and degradation pose the most frequent direct threats to terrestrial mammals and birds¹⁹ (Fig. 1a) by decreasing the size of the area that a species can occupy, and therefore its abundance²¹, and by fragmenting populations and species ranges into small, isolated patches. About 80% of all threatened terrestrial bird and mammal species are imperilled by agriculturally driven habitat loss (Fig. 1a). Other considerable drivers of habitat destruction include logging, urbanization, mining and the establishment of transport corridors.

Hunting by humans and other forms of direct mortality imperil 40–50% of all threatened bird and mammal species (Fig. 1a) and an even greater proportion of large herbivores²². Hunting for valued body parts (such as rhinoceros horn and elephant ivory) is also a serious threat

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Figure 1 | Anthropogenic threats to mammals and birds and the role of body mass. a, Major threats for terrestrial mammals and birds, separated by the mechanism of the threat (habitat loss or direct mortality). Categories are aggregations of various stresses and threats, as defined by the IUCN (see Supplementary Methods). b, Percentage of large (mass ≥ 10 kg), medium (<10 kg and ≥ 2 kg) and small (<2 kg) terrestrial mammals that are classified as threatened (critically endangered, endangered or vulnerable) by the IUCN⁶ in the three geographic regions in our analysis (see Supplementary Methods for the countries that are included in each region). Error bars represent the uncertainty introduced by data deficient species. c, Percentage of large (mass ≥ 2 kg), medium (<2 kg and ≥ 0.5 kg) and small (<0.5 kg) terrestrial birds that are classified as threatened by the IUCN⁶. Error bars represent the uncertainty introduced by data-deficient species.

that is yet to be addressed adequately, despite widespread attention^{23,24}. Moreover, the consumption of bushmeat threatens many more species²⁵ and has led to catastrophic declines of Asian and sub-Saharan mammals^{26–29}. Between 1970 and 1998, bushmeat consumption in Ghana resulted in a 76% decline in the biomass of 41 mammalian species, with some species being extirpated locally³⁰. Bushmeat hunting and illegal livestock grazing are often vital for the nutrition of local communities.

But even in large protected areas, unlawful hunting and grazing can reduce species populations to well below their carrying capacities³¹. Because of the threats that they pose to humans³² and livestock, large carnivores may also experience high mortality as a result of problem animal control strategies^{33,34}.

Relatively few terrestrial mammals are threatened by invasive species (Fig. 1a) but introduced predators threaten, and have even extirpated, many species of island bird³⁵. Invasive and other problematic species threaten 21% of terrestrial birds (Fig. 1a), a figure that rises to 26% if seabirds are included. Water pollution, often from agriculture, is a modest threat to mammals and birds yet a considerable threat to amphibians⁶. Exotic diseases can be a major threat to amphibians and to some bird, mammal and plant species. Anthropogenic climate change does not yet represent a considerable threat to biodiversity⁶ but, as we will discuss, will probably pose challenges in the future^{36–38}.

Large-bodied species are especially vulnerable to human-driven impacts^{22,39}. For both mammals (Fig. 1b) and birds (Fig. 1c), such species are about three times more likely to be threatened than smallbodied species. In the SAIC region, tropical South America and sub-Saharan Africa, all of which have high numbers of mammal or bird species, 30–60% of large mammals (weighing more than 10 kg) and 25–40% of large birds (weighing more than 2 kg) are classified as threatened with extinction.

The geography of current endangerment

The degree of spatial overlap between human activity and biodiversity is a crucial determinant of the impacts of humans on biodiversity. Here, we discuss patterns of diversity and threats at the sub-continental scale, but show and use data for individual countries (Figs 2–4) because most environmental policy is set at the national level. Most taxonomic groups have highest diversity in the tropics: mammal diversity is greatest in the SAIC region (1,500 species), followed by sub-Saharan Africa (1,200 species) and tropical South America (900 species) (Fig. 2a). For birds, both tropical South America and the SAIC region have about 3,100 species and sub-Saharan Africa has 2,100 species (Fig. 2c).

Anthropogenic threats are determined largely by income, density of the human population and development activities. As incomes and the population grow, the demand for agricultural land and animal protein increases, which threatens biodiversity through habitat loss and hunting^{40,41}. Between 1960 and 2010, the human population worldwide increased by 130% and the global constant-dollar gross domestic product (GDP) (at purchasing power parity) increased by 490%^{42,43}. During this time, SAIC was the fastest growing region: per capita, its GDP grew sevenfold and its population grew by 2 billion people, giving it the greatest population density of the three tropical centres of terrestrial diversity. By contrast, although sub-Saharan Africa underwent economic and population growth during this period, its population density and GDP per capita in 2010 were about one-fifth and one-third, respectively, of those of the SAIC region. Tropical South America's growth resulted in a GDP per capita in 2010 that was only 20% lower than that of SAIC, but with a far lower population density. These regional differences are reflected in the greater percentages of mammals and birds being threatened in the SAIC region and tropical South America than in sub-Saharan Africa, at present (Fig. 2b, d).

These biodiversity threats are the greatest for large terrestrial mammals, which attain their greatest regional diversity in SAIC (155 species), followed by sub-Saharan Africa (125 species). The next most diverse region, tropical South America, has only 38 species of large mammal because of prehistoric megafaunal extinctions that also left North America, Australia, Europe and northern Asia depauperate (Fig. 3a). The SAIC region also has the highest percentage of large mammals that are threatened with extinction (Fig. 3b). On a country-by-country basis, 40–90% of the large mammal species of SAIC are threatened and, for the region as a whole, 62% of these species (96 of 155 species) are threatened. The mean of the national extinction risk for large mammals in the SAIC region is 2.1, which is equivalent to the average species being classified as vulnerable. By comparison, 34% of sub-Saharan Africa's large mammal species (42 of 125 species) are threatened (Fig. 3b) and the mean extinction risk is 0.7, which is equivalent to the average species being classified as somewhere between least concern and near threatened. Across tropical South America, 50% of large mammal species (19 of 38 species) are threatened (Fig. 3b) and the mean extinction risk is 1.2 (near threatened). Although about one-third of the large mammals of sub-Saharan Africa are threatened, at present, they are still more secure than those in the other two centres of large mammal diversity.

We focused our analyses of extinction risks (see Supplementary Methods) on these three biodiverse tropical regions because much of their growth and development occurred after 1961, a period for which we have relevant data. Countries in these regions with greater increases in per capita income and cropland between 1961 and 2010 also had higher mean extinction-risk values. In particular, national extinction risks for mammals and for birds were positively correlated with the proportion of a country under cropland in 1961, as well as to subsequent growth in the extent of cropland and GDP per capita by 2010. They were also dependent on the body mass of the species of interest and on the two- and three-way interactions between growth in cropland, growth in GDP per capita and body mass. (The overall extinction-risk regression is: $R^2 = 0.69$, $F_{12,110} = 20.6$, N = 123 and P < 0.0001 for mammals; and $R^2 = 0.84$, $F_{12,110} = 48.5$, N = 123 and P < 0.0001 for birds; statistical models can be found in Supplementary Table 1.) The percentage of mammal or bird species that are threatened in the countries of the three biodiverse tropical regions showed similar patterns (Supplementary Table 2), which reflects a strong positive correlation between national mean extinction-risk values and the percentage of a country's species that are threatened ($R^2 = 0.97$, $F_{1,250} = 8,599$, P < 0.0001 and N = 252).

Current conservation efforts

Conservation programmes saved at least 31 species of bird from extinction in the last century⁴⁴ — 16 of which were saved between 1994 and 2004 (ref. 45) — and prevented an estimated 20% of threatened vertebrates from moving closer to extinction⁴⁶. Designated protected areas now cover about 14% of Earth's terrestrial surface⁴⁷ and are often instrumental in reducing habitat conversion⁴⁸, hunting⁴⁹ and extinction risks⁵⁰ within their confines. Other forms of legal protection have improved species population trends⁵¹. The control of invasive species, particularly on islands, has enabled the recovery of some vulnerable populations⁵². Conservation efforts that involve intensive species management, captive breeding and reintroductions have also saved some severely threatened species, including the Arabian oryx (*Oryx leucoryx*), which was extinct in the wild in 1972 but is now listed as vulnerable^{6,46}, and the California condor (*Gymnogyps californianus*)⁴⁴.

Despite such efforts, biodiversity continues to decline worldwide^{22,46,53,54}. For example, lion populations in many parts of Africa have fallen to 10% of their potential, largely as a result of increasing human pressures, as well as poor infrastructure and inadequate management budgets in protected areas³¹. The prevention of further extinctions will require both accelerated conservation efforts and proactive approaches that are designed to address potential future threats.

The geography of future extinction risks

In the next 50 years, threats to biodiversity are likely to grow as both human populations and per capita incomes increase. Regions that have already undergone, or are now experiencing, habitat loss on a large scale will probably face increased extinction risks — for example, southeast Asia in response to oil palm cultivation⁵⁵, as well as other conservation hotspots with high levels of endemism^{56,57}. New hotspots of threats and extinction risk that are related to human population density⁷, consumption^{8,9} and the characteristics of species⁵⁸ will no doubt emerge.

Between 2010 and 2060, the population worldwide is projected to increase by 3.2 billion people^{59,18}, and the majority of this growth (an increase of 1.7 billion people) is expected to occur in sub-Saharan Africa

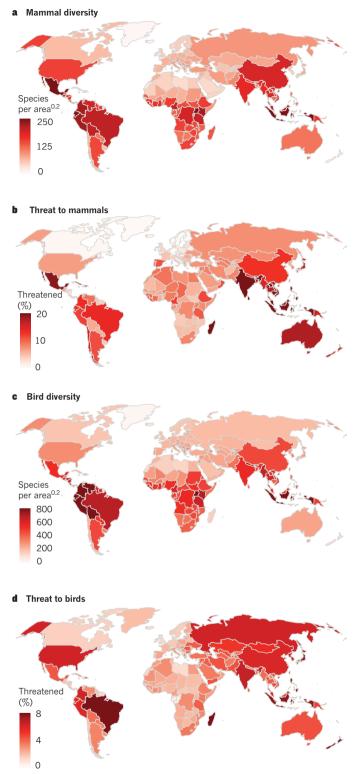


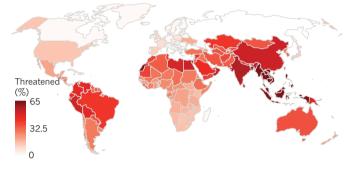
Figure 2 | **Diversity of mammals and birds worldwide and the extent of the extinction threat. a**, Based on the species–area scaling relationship, the number of mammal species in each country is scaled by the area of each country (as 100,000 km²) as (number of species per country)/area^{0.2}. This provides an index of diversity that is independent of the size of each country. **b**, Percentage of mammal species threatened with extinction in each country. **c**, The number of bird species in each country (scaled by area, as in **a**). **d**, The percentage of bird species that are threatened with extinction in each country. Data are from ref. 6. Country-level patterns are shown to highlight issues in individual nations because most environmental policy is set at the national level. For fine-scale maps of mammal and bird diversity and threats, see refs 9, 14 and 45.

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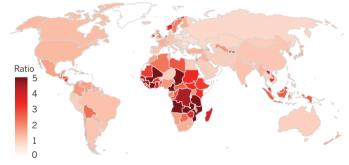
a Large mammal diversity



b Threat to large mammals



c LDR (BAU scenario)



d LDR (closed yield gap)



Figure 3 | The current extent of large mammals and projected land clearing worldwide. a, Based on the species–area scaling relationship, the number of large (mass $\geq 10 \text{ kg}$) mammal species in each country is scaled by the area of each country (as $100,000 \text{ km}^2$) as (number of species per country)/area^{0.2}. This provides an index of diversity that is independent of the size of each country. **b**, The percentage of large mammal species in each country that are threatened with extinction. Data for **a** and **b** are from ref. 6. **c**, The LDR, calculated by dividing the forecasted cropland area for 2060 by the cropland area of 2010, under BAU yield trajectories. **d**, The LDR if yield gaps were reduced by 80% by 2060. See also Supplementary Methods and Supplementary Table 3.

(Fig. 4a). Of the three regions of diversity on which we have focused, sub-Saharan countries had the lowest GDP per capita in 2010; however, this measure may triple by 2060 (ref. 38 and Supplementary Methods), becoming similar to the 2010 incomes of the SAIC region. It is fore-casted that, by 2060, SAIC will have grown by 0.7 billion people and tropical South America by fewer than 0.1 billion people and that both regions may have an average GDP per capita that is about three times larger than their 2010 level^{59,18} (see Supplementary Methods).

The growing demand for cropland, and the habitat destruction and fragmentation that are associated with it, will be considerable drivers of future extinction risks. We used projected populations and incomes, as well as observed income-dependent changes in per capita crop demand^{42,43,18,60} (Supplementary Fig. 1), to predict the national total crop demand of each country^{60,61} in 2060 (see Supplementary Methods). We then calculated a country's land demand ratio (LDR), which is the cropland area forecasted for 2060 divided by the cropland area in 2010, under the 'business-as-usual' (BAU) assumptions that the increased demand for crops is met mainly through domestic production and that yields continue to increase along the trajectories that were observed during the last 50 years. The largest 2060 LDRs in this BAU scenario are found in sub-Saharan Africa (Fig. 3c). Thirteen sub-Saharan countries have projected LDRs for 2060 of greater than 4. Mozambique, Zambia, Angola, Chad, Cote d'Ivoire, Cameroon, Tanzania, Mali and Guinea would need to clear between 380 and 760% more land for use as cropland by 2060. Assuming that yields increase along past trajectories, a further 710 million hectares of cropland worldwide would be cleared to meet the projected global demand for food in 2060, of which 430 million hectares (equivalent to half the area of the continental United States) is predicted to be cleared in sub-Saharan Africa⁶¹. The relationship that is observed between GDP per capita, cropland and extinction risk (Supplementary Table 1) highlights the potential consequences for biodiversity of future land clearing and increases in GDP per capita. To this end, we used the extinction risk regressions (described previously), in combination with projected land clearing and GDP per capita for 2060, to forecast BAU extinction risks for mammals and birds in 2060 for the SAIC region, sub-Saharan Africa and tropical South America (Fig. 5). The actual risks of extinction will depend on how and where threats develop but, for more than half of the countries we analysed, the projected 2060 mean BAU extinction risks for at least one species group were unprecedented, being higher than any current observations of mean national risk.

Mammals and birds of all body masses are predicted to face elevated extinction risks in all three of the regions analysed (Fig. 5). According to our calculations, the greatest increases will be experienced by mammals in sub-Saharan Africa: if present trends and relationships continue, medium and large mammals in this region could face extinction risks that are much greater than those faced now by large mammals in SAIC. Mean extinction risk values for large and medium mammals in both the SAIC region and sub-Saharan Africa may increase by 1.5–2 Red List categories by 2060 (Fig. 5). For the medium and large mammals of tropical South America, and for the medium and large birds of all three diverse regions, extinction risks are forecasted to increase by about 1–1.5 Red List categories (Fig. 5).

The effects of an increase in risk of 1.5 categories can be visualized by comparing the current status of large mammals in the SAIC region with those in sub-Saharan Africa. Large predators have been lost from much of SAIC, with lions restricted to about 400 animals in a single population and cheetahs extirpated fully. By contrast, despite contractions in range size and decreases in population, about 20,000–30,000 lions and 7,500 cheetahs remain in sub-Saharan Africa. For all members of the subfamily Bovinae, which include relatives of cattle and spiral-horned antelope, 10 of 11 species in the SAIC region are threatened with extinction, whereas only 1 of 10 sub-Saharan African species is currently threatened. Although threatened worldwide, numerous species of primate, as well as elephants and rhinoceroses, are rarer or more severely threatened in SAIC than in sub-Saharan Africa, at present.

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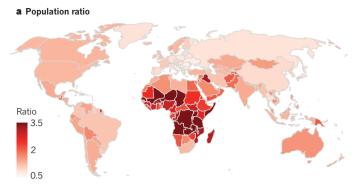


Figure 4 | **Projected growth rates for the human population and current crop yields worldwide. a**, The ratio of the United Nations 'medium fertility' population projection for each country in 2060 to the population in 2010 of each country (ref. 60). A ratio of 2, for example, indicates that the

Reducing future risks of extinction

Safeguarding biodiversity from impending threats will require substantial increases in established conservation practices and policies, as well as proactive approaches such as national land-use planning and yield increases that reduce both habitat fragmentation and the demand for land clearing. Although our analyses have focused on broad geographic regions and groups of species, on-the-ground conservation requires national and local analyses and actions, often targeted at individual species. However, actions that decrease the level of land clearing and habitat fragmentation, and that create further protected areas, can benefit large numbers of species simultaneously, as well as reduce the need for species-specific conservation activities.

Expanding conservation practices

Conservation efforts have had mixed amounts of success in the last century, and large-scale efforts and comprehensive strategies will become increasingly urgent in the future^{31,62,63}. The existence of a greater number of economically developed countries will heighten pressures on global biodiversity through their disproportionate consumption of natural resources, and such countries should become major contributors to conservation efforts that take place beyond their borders^{64–66}, directing funds strategically to regions with the greatest current, or future, threats or the largest potential return on investment⁶⁷.

The safeguarding of biodiversity will require the expansion and more

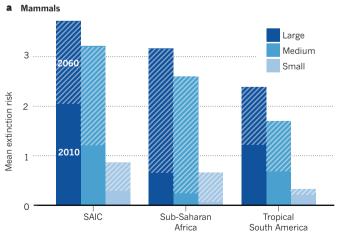




population is expected to double by 2060. **b**, Yields in 2010 for all nutritious crops, calculated for each country by summing the caloric production of each crop and dividing this amount by the total area harvested. See also Supplementary Methods.

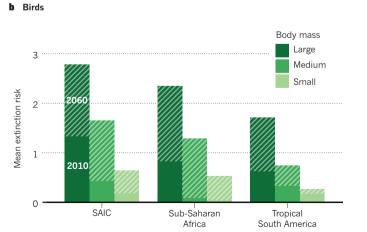
effective management of areas set aside to protect species^{47,68,69}, as many species lack adequate protection⁴⁷. New protected areas should be both sufficiently large and appropriately situated to optimize the protection of biodiversity while ensuring that countries can meet the food security and sovereignty needs of local people^{70,71}. Land clearance by humans often leaves only small fragments of habitat intact, which may initially harbour high diversity^{72–74}. However, the associated increase in edge habitats⁷³ and isolation⁷⁵, and the reduction in patch size⁷⁶, lead to an increase in long-term extinction risks, especially for large-bodied species^{72,73}. Habitat fragmentation has also driven declines of migratory species worldwide⁷⁷ and blocked the migration routes of large mammals such as wildebeest⁷⁸. Protected areas could be linked together by corridors that enable the movement of animals between them or they could be managed as parts of larger metacommunities, such as in the case of large carnivores in the smaller reserves of South Africa³¹.

Protected areas are unable to protect species that live beyond their boundaries, and species may continue to decline even within their boundaries^{48,79}. The hunting of endangered species can be reduced outside of protected areas by the enforcement of protective legislation^{49,80}, although enforcement is more difficult for highly valued species⁸¹. The ultimate drivers of hunting and poaching must be addressed, for example, by providing people with alternative livelihoods or sources of protein^{29,82,83}. In Africa and South America, local communities consume less bushmeat when other protein sources are available^{30,84}, but social norms



SAIC Sub-Saharan Tropical Africa South America Figure 5 | Current and projected regional extinction risks for mammals and birds. a, b, Current (2010) and projected (to 2060) mean extinction risk values for large, medium and small species of mammal (a) or bird (b)

risk values for large, medium and small species of mammal (**a**) or bird (**b**) in the three geographic regions we investigated. Extinction risk values (ν) are assigned to each species in a country based on IUCN risk status: least concern; ν = 0; near threatened, ν = 1; vulnerable, ν = 2; endangered, ν = 3;



critically endangered, $\nu = 4$; and extinct or extinct in the wild, $\nu = 5$ (see also Supplementary Methods). The mean of these values across all mammal or bird species in a country and body-mass class represents the extinction risk value for an individual nation. The mean of these national values is shown for the SAIC region, sub-Saharan Africa and tropical South America for mammals (**a**) and birds (**b**).

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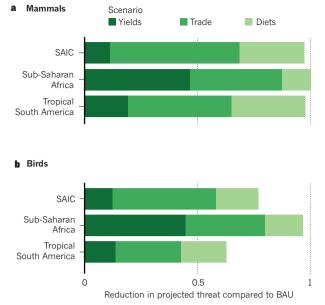


Figure 6 | **Potential benefits to biodiversity of proactive conservation**. The estimated reductions in the mean 2060 extinction risk values that would result from closing yield gaps (dark green), increasing agricultural trade (medium green) and healthier diets (light green) for larger (large and medium) bodied mammals and birds. Each shaded portion of a horizontal bar shows the independent effects of each of the three proactive policies for a given region and species group. Estimates are made on the basis of the regression model of Supplementary Table 1, using data in Supplementary Table 4. See Supplementary Fig. 4 for the total reductions from the three approaches combined and for separate projections for body-mass classes.

and customs make the elimination of bushmeat consumption challenging. Government-led efforts and publicity campaigns, such as those that successfully decreased the consumption of shark-fin soup⁸⁵, could reduce the use of endangered species as food or pets, or in medicines and fashion.

Climate change has resulted in range shifts and the local extirpation of species^{86,87}, but uncertainty remains over how many, and which, species will be threatened in the future^{37,38}. Species have survived past fluctuations in climate through migration. However, the velocity of the projected changes in climate is unprecedented⁸⁸, and habitat fragmentation will limit migration pathways. Reducing the rate and degree of climate change is important because of the direct threat that climate change poses and the even greater extinction risks posed by the combination of climate change and habitat fragmentation^{13,86,89}. Although much of the attention on mitigating greenhouse gases is focused on the use of fossil fuels⁹⁰, agriculture contributes about 30% of greenhouse gas emissions worldwide, mainly through land clearing, the application of nitrogen fertilizers and methane production by ruminants and in rice paddies⁴¹. Greater agricultural efficiencies and a reduced demand for the meat of ruminants would therefore help to slow climate change^{60,61} and confer considerable biodiversity benefits.

Conservation actions must be sensitive to the needs of local communities, especially in developing nations. Protected areas can provide localized benefits, but they may also harm local people⁹¹, as can protective legislation⁹², by denying access to wild game and other resources. Participatory approaches, whereby local people contribute their expertise, can reduce conflict between local populations and protected areas⁹³. Tools such as those developed for systematic conservation planning⁹⁴ can minimize the costs of local-scale conservation opportunities by designating regions of higher biodiversity as protected areas and by concentrating food production in areas of relatively higher crop-yield value⁹⁵. Quantifying and monetizing the value of clean water, carbon sequestration and other ecosystem services that are provided by protected areas can also improve outcomes for biodiversity⁹⁶⁻⁹⁹ and increase local support for conservation, as can the construction of physical barriers to protect people from dangerous animals³¹ and other community-based approaches to resolving conflict between humans and wildlife^{34,100,101}.

Proactive policies for reducing extinction risks in the future

Proactive conservation efforts could potentially decrease the underlying societal drivers that threaten species. Land is a limiting resource for both humans and nature, so reducing human demand for land and changing the pattern of land clearing to minimize habitat fragmentation is crucial for proactive conservation. Here, we evaluate the implications for extinction risks of increasing crop yields, modifying diets and establishing conservation-based agricultural trade, and then discuss the benefits of land planning and zoning at the national scale.

Closing yield gaps The amount of land that is needed to meet the future crop demands of a country will depend on the land's yields, which are quantified as the amount of food production per hectare. Reducing the difference between the forecasted BAU yield and the attainable yield — known as the yield gap — could greatly decrease the demand for future land clearing. Ninety-six countries, especially in Africa, but also in South America and the SAIC region, have actual yields that are less than half of those that could be attained if yield-enhancing methods and technologies were adopted^{102,103} (Fig. 4b and Supplementary Methods). If yield gaps were closed progressively (Supplementary Fig. 2), the demand worldwide for new cropland between 2010 and 2060 and the LDRs for most countries in sub-Saharan Africa could be reduced substantially (Fig. 3d). Under the BAU scenario, 13 sub-Saharan African countries would have LDRs of greater than 4 (Fig. 3c); however, closing yield gaps by 80% would decrease the demand for further cropland in sub-Saharan Africa by 55% and leave just one country with an LDR of more than 4 (Fig. 3d). For this region as a whole, the demand for new land clearing between 2010 and 2060 could be reduced from 430 million hectares to 195 million hectares, if yield gaps were closed by 80%. This land-sparing estimate is likely to be conservative, as further yield improvements by 2060 are probable. But because higher yields can lead to increased profitability, and can also encourage the local expansion of agriculture¹⁰⁴, agricultural zoning and other 'active' land-sparing strategies are also needed¹⁰⁰.

The relationship between extinction risks and anthropogenic drivers (Supplementary Table 1) suggests that closing yield gaps by 80% would reduce extinction risks in comparison to the BAU scenario, especially for medium and large species in sub-Saharan Africa (Fig. 6 and Supplementary Fig. 4).

Yield gaps should be narrowed through practices that minimize the negative environmental impacts of the intensification of agriculture. Methods include: planting legumes to increase soil fertility; using manure, cover crops and other strategies to increase the amount of organic matter in soil; using improved seed varieties; and appropriately timing the application of fertilizers, pesticides and irrigation^{59,105-108}. Often, such inputs can also be reduced. For example, many farmers in developed nations can maintain high yields with the application of about 25% less fertilizer than is currently used^{108,109}. Furthermore, region-appropriate crops could decrease the need for irrigation; crop rotation can decrease the incidence of disease and increase fertility; and drip irrigation can increase the efficiency of water use¹⁰⁸. At the country scale, agricultural subsidies in Malawi¹¹⁰, Rwanda, Zambia, Ghana, Mali and Senegal¹¹¹ have increased crop yields by 20-80% through increasing access to fertilizer and improved seeds. At smaller scales, integrated pest-management systems¹¹² and the growth of nitrogen-fixing plants alongside crops or during fallow periods, among other methods, have increased yields in countries with lower yields^{113,114}. The widespread implementation of similar, locally tailored, programmes that incorporate both new and conventional expertise and techniques could result in large and environmentally sustainable increases in yield.

Dietary change In many wealthier nations, modifying diets can reduce the environmental impacts of food production while improving human health⁶¹. As incomes have risen, so too has the per capita consumption of animal products, sugars and starches and total calories¹¹⁵.

Such diets are land-intensive, lead to the emission of considerable amounts of greenhouse gases¹⁸ and are contributing to a worldwide epidemic of diabetes and heart disease^{116–119}. Healthier diets include the greater consumption of vegetables, fruits, nuts and plant-based oils rather than animal products, and require less cropland, potentially decreasing the demand for land clearing¹⁸ and reducing the risks of developing chronic disease^{116–120}.

To explore how plant-rich diets might affect future extinction risks, we assumed that, by 2060, the per capita meat consumption in each country would be reduced by half, in comparison to the BAU incomedependent diet of 2060 (Supplementary Methods). The extinction risks for mammals and birds of all body sizes benefitted from this dietary change, with medium- and large-bodied mammals of tropical South America and the SAIC region having the greatest reduction in risk (Fig. 6).

Conservation-based agricultural trade At present, most countries import about 5-15% of their food and animal feed. As developing nations close yield gaps and reach their sustainable yield potentials, trade agreements could further decrease the global demand for land by concentrating crop production in higher-yield regions¹²¹⁻¹²³. A simple scenario in which a further 20% of each country's total crop demand is met by imports from nations with the highest yields for each crop group (Supplementary Methods) predicts a reduction in land clearance and extinction risks, in comparison to the BAU scenario (Fig. 6). Medium- and large-bodied species from all three of the diverse regions that we analysed are projected to have reduced extinction risks that are comparable to those that would result from closing yield gaps in sub-Saharan Africa (Fig. 6). However, the potential benefits of agricultural trade would be constrained by preferences for locally produced foods, crop prices, transport costs and national policies that promote domestic food security and sovereignty.

Benefits of proactive policies Combining the policy tools of yieldgap closure, dietary change and the development of conservation-based agricultural trade could potentially offset about half to two-thirds of the projected increases in extinction risk by 2060 for medium- and largebodied species (Figs 5 and 6). Small mammals and birds also benefit (Supplementary Fig. 4); however, because the extinction risks of such species are projected to increase the least (Fig. 5), the benefits they receive from proactive conservation are smaller.

Although proactive land-sparing is essential for conserving biodiversity, the benefits that it confers will depend on which lands are spared, their spatial distribution and how natural and undisturbed they are. Our empirical model, which forms the basis of the extinction-risk forecasts in Fig. 5, assumes that past trends and spatial patterns of fragmentation would continue. However, appropriate land-use planning and spatial zoning could greatly enhance the benefits of a decrease in land demand. Appropriate zoning could focus agricultural land clearance on selected fertile areas, providing food security and sovereignty, while minimizing habitat fragmentation and its associated extinction risks in regions that are spared from clearing by increased yields, the development of conservation-based agricultural trade and dietary shifts. Conservation also requires the support of local people. Policies must therefore be fair and provide local benefits, such as increases in yields and income, that more than compensate for the costs that the policies impose. With forethought, planning and investment, fair and effective conservation policies and programmes have the potential to increase both the protection of biodiversity¹²⁴ and the social acceptability of conservation by reducing the food-versus-nature conflict that has arisen over Earth's remaining natural lands.

The future for biodiversity

Earth has entered an era of rapidly escalating environmental changes that are being driven by increases in the human population and in wealth. Tens of thousands of species are already threatened with extinction worldwide. In the next 50 years, the number of threatened species and the severity of their extinction risks will rise greatly, especially in many of the world's most biodiverse countries. The policies and actions that we adopt now will therefore be instrumental in determining which, and how many, species will survive the present era of environmental change.

The actions of humans eliminated half of Earth's large animal species during prehistoric times. The remaining large-mammal species of sub-Saharan Africa, the SAIC region and tropical South America have extinction risks that are on trajectories to reach unprecedented levels in the coming decades, including many species in sub-Saharan Africa that are not yet under considerable threat. Moreover, the large mammal species that are already threatened in the SAIC region would face even graver risks. The extinction risks of birds are also projected to increase markedly, and the actions that threaten mammals and birds also jeopardize many other species of animal and plant worldwide. Urgent conventional and proactive approaches to conservation are needed to ensure that sufficient habitats will remain to preserve the viability of these species in the long term and to guarantee that such habitats are well managed. Proactive policies, including land zoning and programmes to rapidly close yield gaps, can reduce societal demand for land clearing and ensure that any land clearing that is necessary minimizes the resultant fragmentation of habitats.

All species could benefit from the intensification of current conservation policies, as well as from policies that reduce underlying anthropogenic threats. Developing and enacting such policies, however, will require an unprecedented degree of engagement between stakeholders, policymakers, natural scientists and social scientists. Earth is capable of providing healthy diets for 10 billion people in 2060 and preserving viable habitats for the vast majority of its remaining species. The benefits for biodiversity and humanity of pursuing these goals are great, and with forethought and timely action, these goals can be achieved.

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- 1. Steffen, W., Crutzen, P. J. & McNeill, J. R. The Anthropocene: are humans now overwhelming the great forces of nature? *Ambio* **36**, 614–621 (2007).
- Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O. & Ludwig, C. The trajectory of the Anthropocene: the Great Acceleration. *Anthropocene Rev.* 2, 81–98 (2015).
- Vitousek, P. M., Mooney, H. A, Lubchenco, J. & Melillo, J. M. Human domination of Earth's ecosystems. *Science* 277, 494–499 (1997).
- Newbold, T. et al. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50 (2015).
- Maxwell, S. L., Fuller, R. A., Brooks, T. M. & Watson, J. E. M. The ravages of guns, nets and bulldozers. *Nature* 536, 143–145 (2016).
- 6. IUCN. *The IUCN Red List of Threatened Species. Version 2016-2.* http://www.iucnredlist.org. (2016).
- McKee, J. K., Sciulli, P. W., Fooce, C. D. & Waite, T. A. Forecasting global biodiversity threats associated with human population growth. *Biol. Conserv.* 115, 161–164 (2004).
- Visconti, P. et al. Future hotspots of terrestrial mammal loss. Philos. Trans. R. Soc. B 366, 2693–2702 (2011).
- Visconti, P. et al. Projecting global biodiversity indicators under future development scenarios. Conserv. Lett. 9, 5–13 (2016).
- Balmford, A., Green, R. E. & Scharlemann, J. P. W. Sparing land for nature: exploring the potential impact of changes in agricultural yield on the area needed for crop production. *Glob. Change Biol.* **11**, 1594–1605 (2005).
- Barnosky, A. D., Koch, P. L., Feranec, R. S., Wing, S. L. & Shabel, A. B. Assessing the causes of late Pleistocene extinctions on the continents. *Science* **306**, 70–75 (2004).
 This work shows that the interaction of human activity with climate change led to considerable increases in extinction rates during the Pleistocene
- epoch, especially for large mammals. 12. Barnosky, A. D. Megafauna biomass tradeoff as a driver of Quaternary and
- future extinctions. Proc. Natl Acad. Sci. USA 105, 11543–11548 (2008).
 Barnosky, A. D. et al. Has the Earth's sixth mass extinction already arrived? Nature 471, 51–57 (2011).
- Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. The future of biodiversity. *Science* 269, 347–350 (1995).
- Ceballos, G. et al. Accelerated modern human-induced species losses: entering the sixth mass extinction. Sci. Adv. 1, e1400253 (2015).
- Pimm, S. L. *et al.* The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 1246752 (2014).
 A review of the state of the knowledge of biodiversity, species distributions
- and extinction rates, as well as how these are likely to change in the future. 17. May, R. M., Lawton, J. H. & Stork, E. in *Extinction Rates* (eds Lawton, J. H. & May,

INSIGHT REVIEW

- R. M.) 1–24 (Oxford Univ. Press, 1995).
- United Nations, Department of Economic and Social Affairs, Population Division. World Population Prospects: The 2015 Revision, Key Findings and Advance Tables. Working Paper No. ESA/P/WP.241 (United Nations, 2015)
- Joppa, L. N. *et al.* Filling in biodiversity threat gaps. *Science* **352**, 416–418 (2016).
- Mace, G. M. et al. Quantification of extinction risk: IUCN's system for classifying threatened species. Conserv. Biol. 22, 1424–1442 (2008).
- Ceballos, G. & Ehrlich, P. R. Mammal population losses and the extinction crisis. Science 296, 904–907 (2002).
- Ripple, W. J. et al. Collapse of the world's largest herbivores. Sci. Adv. 1, e1400103 (2015).
- Di Minin, E. et al. Identification of policies for a sustainable legal trade in rhinoceros horn based on population projection and socioeconomic models. *Conserv. Biol.* 29, 545–555 (2015).
- 24. Wittemyer, G. *et al.* Illegal killing for ivory drives global decline in African elephants. *Proc. Natl Acad. Sci. USA* **111**, 13117–13121 (2014).
- 25. Ripple, W. J. *et al.* Bushmeat hunting and extinction risk to the world's mammals. *R. Soc. Open Sci.* **3**, 160498 (2016).
- Corlett, R. T. The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica* 39, 292–303 (2007).
- Lindsey, P. A. et al. The bushmeat trade in African savannas: impacts, drivers, and possible solutions. *Biol. Conserv.* 160, 80–96 (2013).
- Maisels, F. et al. Devastating decline of forest elephants in central Africa. PLoS ONE 8, e59469 (2013).
- Strauss, M. K. L., Kilewo, M., Rentsch, D. & Packer, C. Food supply and poaching limit giraffe abundance in the Serengeti. *Popul. Ecol.* 57, 505–516 (2015).
- Brashares, J. S. et al. Bushmeat hunting, wildlife declines, and fish supply in West Africa. Science 306, 1180–1183 (2004).
- Packer, C. et al. Conserving large carnivores: dollars and fence. Ecol. Lett. 16, 635–641 (2013).
- 32. Packer, C., Ikanda, D., Kissui, B. & Kushnir, H. Lion attacks on humans in Tanzania. *Nature* **436**, 927–928 (2005).
- Kissui, B. M. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. *Anim. Conserv.* 11, 422–432 (2008).
- Hazzah, L. et al. Efficacy of two lion conservation programs in Maasailand, Kenya. Conserv. Biol. 28, 851–860 (2014).
- Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L. & Kevin, J. Avian extinction and mammalian introductions on Oceanic islands. *Science* **305**, 1955–1958 (2004).
- Thomas, C. D. et al. Extinction risk from climate change. Nature 427, 145–148 (2004).
- Macleán, I. M. D. & Wilson, R. J. Recent ecological responses to climate change support predictions of high extinction risk. *Proc. Natl Acad. Sci. USA* 108, 12337–12342 (2011).
- Urban, M. C. Accelerating extinction risk from climate change. Science 348, 571–573 (2015).
- Cardillo, M. et al. Multiple causes of high extinction risk in large mammal species. Science 309, 1239–1241 (2005).
 This paper demonstrates that both biological and environmental factors and an antisemental factors.
- This paper demonstrates that both biological and environmental factors make large-bodied animals more predisposed to extinction.
- Grossman, G. & Krueger, A. Economic growth and the environment. Q. J. Econ. 110, 353–377 (1995).
- Balmford, A. et al. Capturing the many dimensions of threat: comment on Salafsky et al. Conserv. Biol. 23, 482–487 (2009).
- 42. The World Bank. World Development Indicators 2016 https://openknowledge. worldbank.org/handle/10986/23969 (2016).
- The Conference Board. Total Economy Database https://www.conference-board. org/data/economydatabase/ (2016).
- Rodrigues, A. S. L. Are global conservation efforts successful? Science 313, 1051–1052 (2006).
- Butchart, S. H. M., Stattersfield, A. J. & Brooks, T. M. Going or gone: defining 'possibly extinct' species to give a truer picture of recent extinctions. *Bull. Br. Ornithol. Club* 126, 7–24 (2006).
- Hoffmann, M. et al. The impact of conservation on the status of the world's vertebrates. Science 330, 1503–1509 (2010).
- Butchart, S. H. M. et al. Shortfalls and solutions for meeting national and global conservation area targets. *Conserv. Lett.* 8, 329–337 (2015). This paper highlights that meeting goals for protected-area coverage will be insufficient to protect biodiversity unless such areas are also well managed and properly located.
- 48. Geldmann, J. *et al.* Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biol. Conserv.* **161**, 230–238 (2013).
- Barnes, M. D., Craigie, I. D., Dudley, N. & Hockings, M. Understanding local-scale drivers of biodiversity outcomes in terrestrial protected areas. *Ann. NY Acad. Sci.* http://dx.doi.org/10.1111/nyas.13154 (2016).
- Butchart, S. H. M. et al. Protecting important sites for biodiversity contributes to meeting global conservation targets. *PLoS ONE* 7, e32529 (2012).
- Donald, P. F. et al. International conservation policy delivers benefits for birds in Europe. Science 317, 810–813 (2007).
- Jones, H. P. et al. Invasive mammal eradication on islands results in substantial conservation gains. Proc. Natl Acad. Sci. USA 113, 4033–4038 (2016).
- Butchart, S. H. M. et al. Global biodiversity: indicators of recent declines. Science 328, 1164–1168 (2010).
- Ripple, W. J. et al. Status and ecological effects of the world's largest carnivores. Science 343, 1241484 (2014).

- Sodhi, N. S., Koh, L. P., Brook, B. W. & Ng, P. K. L. Southeast Asian biodiversity: an impending disaster. *Trends Ecol. Evol.* **19**, 654–660 (2004).
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858 (2000).
- Mittermeier, R. A. et al. Wilderness and biodiversity conservation. Proc. Natl Acad. Sci. USA 100, 10309–10313 (2011).
 Cardillo M. Maco G. M. Gittlemen LL & Bundie A. Latent estimation site and
- Cardillo, M., Mace, G. M., Gittleman, J. L. & Purvis, A. Latent extinction risk and the future battlegrounds of mammal conservation. *Proc. Natl Acad. Sci. USA* 103, 4157–4161 (2006).
- 59. Johansson, Å. et al. Looking to 2060: Long-term Global Growth Prospects. OECD Economic Policy Paper 3 (OECD, 2012).
- Tilman, D., Balzer, C., Hill, J. & Befort, B. L. Global food demand and the sustainable intensification of agriculture. *Proc. Natl Acad. Sci. USA* 108, 20260–20264 (2011).
- Tilman, D. & Clark, M. Global diets link environmental sustainability and human health. *Nature* 515, 518–522 (2014).
- McCarthy, D. P. et al. Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. Science 338, 946–949 (2012).
- Balmford, A. & Whitten, T. Who should pay for tropical conservation, and how could the costs be met? Oryx 37, 238–250 (2003).
- Lenzen, M. et al. International trade drives biodiversity threats in developing nations. Nature 486, 109–112 (2012).
- Weinzettel, J., Steen-Olsen, K., Hertwich, E. G., Borucke, M. & Galli, A. Ecological footprint of nations: comparison of process analysis, and standard and hybrid multiregional input–output analysis. *Ecol. Econ.* **101**, 115–126 (2014).
- Wiedmann, T. O. *et al.* The material footprint of nations. *Proc. Natl Acad. Sci. USA* 112, 6271–6276 (2015).
- Brooks, T., Mittermeier, R. & Da Fonseca, G. A. B. Global biodiversity conservation priorities. *Science* **313**, 58–61 (2006).
- Ricketts, T. H. et al. Pinpointing and preventing imminent extinctions. Proc. Natl Acad. Sci. USA 102, 18497–18501 (2005).
- 69. Balmford, A. Conservation conflicts across Africa. Science **291**, 2616–2619 (2001).
- Joppa, L. N. & Pfaff, A. High and far: biases in the location of protected areas. PLoS ONE 4, 1–6 (2009).
- Wilson, K. A., McBride, M. F., Bode, M. & Possingham, H. P. Prioritizing global conservation efforts. *Nature* 440, 337–340 (2006).
- Laurance, W. F. et al. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv. Biol. 16, 605–618 (2002).
 This study shows that large fragments of habitat are crucial for preserving biodiversity and the function of ecosystems in the face of habitat loss.
- Haddad, N. M. et al. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1, e1500052 (2015).
 This paper demonstrates that forest fragments, especially small and isolated patches, experience declines in ecosystem function and lose diversity over time, providing empirical evidence for the extinction debt.
 Coursins, S. A. O. Extinction debt in fragmented grasslands: paid or not? *J. Veg.*
- 74. Cousins, S. A. Ö. Extinction debt in fragmented grasslands: paid or not? J. Veg. Sci. 20, 3–7 (2009).
- 75. Laurance, W. F. et al. Averting biodiversity collapse in tropical forest protected areas. *Nature* **489**, 290–294 (2012).
- Ferraz, G. et al. Rates of species loss from Amazonian forest fragments. Proc. Natl Acad. Sci. USA 100, 14069–14073 (2003).
 Harris, G., Thirgood, S., Hopcraft, J. G. C., Cromsigt, J. P. G. M. & Berger, J. Global
- Harris, G., Thirgood, S., Hopcraft, J. G. C., Cromsigt, J. P. G. M. & Berger, J. Global decline in aggregated migrations of large terrestrial mammals. *Endanger. Species Res.* 7, 55–76 (2009).
- Msoffe, F. U. et al. Spatial correlates of land-use changes in the Maasai-Steppe of Tanzania: implications for conservation and environmental planning. Int. J. Biodivers. Conserv. 3, 280–290 (2011).
- 79. Craigie, I. D. *et al.* Large mammal population declines in Africa's protected areas. *Biol. Conserv.* **143**, 2221–2228 (2010).
- Butchart, S. H. M., Stattersfield, A. J. & Collar, N. J. How many bird extinctions have we prevented? *Oryx* 40, 266–278 (2006).
- 81. Gross, M. The plight of the pachyderms. *Curr. Biol.* **26**, R865–R868 (2016). 82. Damania, R., Milner-Gulland, E. J. & Crookes, D. J. A bioeconomic analysis of
- bushmeat hunting. *Proc. R. Soc. B* **272**, 259–266 (2005). 83. Price, S. A. & Gittleman, J. L. Hunting to extinction: biology and regional
- economy influence extinction risk and the impact of hunting in artiodactyls. Proc. R. Soc. B 274, 1845–1851 (2007).
- Bodmer, R. E., Eisenberg, J. F. & Redford, K. H. Hunting and the likelihood of extinction of Amazonian mammals. *Conserv. Biol.* **11**, 460–466 (1997).
- 85. Fabinyi, M. & Liu, N. The Chinese policy and governance context for global fisheries. *Ocean Coast. Manage.* **96**, 198–202 (2014).
- 86. Pounds, J. A. *et al.* Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161–167 (2006).
- Sinervo, B. et al. Erosion of lizard diversity by climate change and altered thermal niches. Science 328, 894–899 (2010).
- Burrows, M. T., Schoeman, D. S. & Richardson, A. J. Geographical limits to species-range shifts are suggested by climate velocity. *Nature* 507, 492–495 (2014).
- Benning, T. & LaPointe, D. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. *Proc. Natl Acad. Sci. USA* **99**, 14246–14249 (2002).
- Rogelj, J. et al. Paris Agreement climate proposals need a boost to keep warming well below 2 °C. Nature 534, 631–639 (2016).
- Brockington, D. & Wilkie, D. Protected areas and poverty. *Phil. Trans. R. Soc. B* 370, 20140271 (2015).



- Williams, R., Burgess, M. G., Ashe, E., Gaines, S. D. & Reeves, R. R. U.S. seafood import restriction presents opportunity and risk. *Science* **354**, 1372–1374 (2016).
- de Vente, J., Reed, M. S., Stringer, L. C., Valente, S. & Newig, J. How does the context and design of participatory decision making processes affect their outcomes? Evidence from sustainable land management in global drylands. *Ecol. Soc.* **21**, 24 (2016).
- Margules, C. & Pressey, R. Systematic conservation planning. *Nature* 405, 243–253 (2000).
- Polasky, S. et al. Where to put things? Spatial land management to sustain biodiversity and economic returns. *Biol. Conserv.* 141, 1505–1524 (2008).
 Bateman, I. J. et al. Bringing ecosystem services into economic decision-
- making: land use in the United Kingdom. Science 341, 45–50 (2013).
 27. Lawler, J. J. et al. Projected land-use change impacts on ecosystem services in
- the United States. *Proc. Natl Acad. Sci. USA* **111**, 7492–7497 (2014). 98. Ouyang, Z. *et al.* Improvements in ecosystem services from investments in
- natural capital. *Science* **352**, 1455–1459 (2016). 99. Polasky, S. *et al.* Are investments to promote biodiversity conservation and
- ecosystem services aligned? Oxf. Rev. Econ. Policy 28, 139–163 (2012). 100. Phalan, B. et al. How can higher-yield farming help to spare nature? Science 351, 450–451 (2016).
- 101.Jackson, R. M., Mishra, C., McCarthy, T. M. & Ale, S. B. in *The Biology and Conservation of Wild Felids* Ch. 19, 417–430 (Oxford Univ. Press, 2010).
- 102.Mueller, N. D. et al. Closing yield gaps through nutrient and water management. Nature **490**, 254–257 (2012).
 - This study predicts that crop yields in many developing nations can be doubled or tripled by appropriate fertilization and irrigation, potentially reducing the need for land clearing.
- 103.Global Yield Gap and Water Productivity Atlas. Global Yield Gap Atlas http:// www.yieldgap.org/ (accessed in September 2016).
- Stevenson, J. & Villoria, N. Does intensification slow crop land expansion or encourage deforestation? *Glob. Food Sec.* 3, 92–98 (2014).
 Wezel, A. *et al.* Agroecological practices for sustainable agriculture. A review.
- Agron. Sustain. Dev. **34**, 1–20 (2014).
 106.Matson, P. A., Parton, W. J., Power, A. G. & Swift, M. Agricultural intensification
- and ecosystem properties. Science 277, 504–509 (1997).
- 107.Godfray, H. C. & Garnett, T. Food security and sustainable intensification. *Phil. Trans. R. Soc. B* **369**, 20120273 (2014).
- 108. Robertson, G. P. et al. Farming for ecosystem services: an ecological approach to production agriculture. *Bioscience* 64, 404–415 (2014).
- 109. Vitousek, P. M. et al. Nutrient imbalances in agricultural development. Science 324, 1519–1520 (2009).
- This work shows that high crop yields can be retained, even when the rate of nitrogen fertilization is reduced, by matching application rates to the current needs of crops.
- 110.Dorward, A. & Chirwa, E. The Malawi agricultural input subsidy programme: 2005/06 to 2008/09. Int. J. Agric. Sustain. 9, 232–247 (2011).
- 111.Druilhe, Z. & Barreiro-Hurlé, J. Fertilizer subsidies in sub-Saharan Africa. ESA Working Paper No. 12–04 (FAO, 2012).
- 112.Khan, Z. R. et al. Achieving food security for one million sub-Saharan African poor through push–pull innovation by 2020. *Philos. Trans. R. Soc. B.* **369**, 20120284 (2014).

- Hall, N. M. et al. Effect of improved fallow on crop productivity, soil fertility and climate-forcing gas emissions in semi-arid conditions. *Biol. Fertil. Soils* 42, 224–230 (2006).
- 114.Garrity, D. P. et al. Evergreen agriculture: a robust approach to sustainable food security in Africa. *Food Secur.* **2**, 197–214 (2010).
- 115. Popkin, B. M. The nutrition transition in low-income countries: an emerging crisis. *Nutr. Rev.* **52**, 285–298 (1994).
- 116. Key, T. J., Thorogood, M., Appleby, P. N. & Burr, M. L. Dietary habits and mortality in 11,000 vegetarians and health conscious people: results of a 17 year follow up. *Br. Med. J.* **313**, 775–779 (1996).
- 117. Mann, J. I., Appleby, P. N., Key, T. J. & Thorogood, M. Dietary determinants of ischaemic heart disease in health conscious individuals. *Heart* 78, 450–455 (1997).
- 118.Lagiou, P. *et al.* Mediterranean dietary pattern and mortality among young women: a cohort study in Sweden. *Br. J. Nutr.* **96**, 384–392 (2006).
- 119. Brunner, E. J. et al. Dietary patterns and 15-y risks of major coronary events, diabetes, and mortality. Am. J. Clin. Nutr. 87, 1414–1421 (2008).
- 120. Martínez-González, M. A. et al. Adherence to Mediterranean diet and risk of developing diabetes: prospective cohort study. Br. Med. J. 336, 1348–1351 (2008).
- 121. Johnson, J. A., Runge, C. F., Senauer, B., Foley, J. & Polasky, S. Global agriculture and carbon trade-offs. *Proc. Natl Acad. Sci. USA* **111**, 12342–12347 (2014).
- 122.West, P. C. et al. Trading carbon for food: global comparison of carbon stocks vs. crop yields on agricultural land. Proc. Natl Acad. Sci. USA 107, 19645–19648 (2010).
- 123. Johnson, J. A., Runge, C. F., Senauer, B. & Polasky, S. Global food demand and carbon-preserving cropland expansion under varying levels of intensification. *Land Econ.* **92**, 579–592 (2016).
- 124.Erb, K.-H. et al. Exploring the biophysical option space for feeding the world without deforestation. Nature Commun. 7, 11382 (2016).

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Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this paper at go.nature.com/2qvpqz8. Correspondence should be addressed to D.T. (tilman@umn.edu).

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