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Financing conservation by valuing carbon services produced by wild animals

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Filling the global biodiversity financing gap will require significant investments from financial markets, which demand credible valuations of ecosystem services and natural capital. However, current valuation approaches discourage investment in conservation because their results cannot be verified using market-determined prices. Here, we bridge the gap between finance and conservation by valuing only wild animals' carbon services for which market prices exist. By projecting the future path of carbon service production using a spatially explicit demographic model, we place a credible value on the carbon capture services produced by African forest elephants. If elephants were protected, their services would be worth $20.8 billion ($10.3 to $29.7 billion) and $25.9 billion ($12.8 to $37.6 billion) for the next 10 and 30 y, respectively, and could finance antipoaching and conservation programs. Elephant population growth would generate a carbon sink of 109 MtC (64 to 153) across tropical Africa in the next 30 y. Avoided elephant extinction would also prevent the loss of 93 MtC (46 to 130), which is the contribution of the remaining populations. Uncertainties in our projections are controlled mainly by forest regeneration rates and poaching intensity, which indicate that conservation can actively reduce uncertainty for increased financial and biodiversity benefits. Our methodology can also place lower bounds on the social cost of nature degradation. Poaching would result in $2 to $7 billion of lost carbon services within the next 10 to 30 y, suggesting that the benefits of protecting elephants far outweigh the costs. Our methodology enables the integration of animal services into global financial markets with major implications for conservation, local socioeconomies, and conservation.

ecosystem services | megafauna | financial economics | nature-based solutions | climate change

Significance

The involvement of financial markets is critical to deliver effective and long-lasting solutions to mitigate climate change and reverse biodiversity loss. However, financial markets have not invested in ecosystem services because these are often valued based on non-market prices, which deter investments. Based on existing carbon market prices, we value the carbon services produced by forest elephants and show that wild animals' carbon services are valuable enough to attract investors. This framework would facilitate financing of conservation programs and local communities and broaden the portfolio of nature-based solutions to mitigate climate change.

The collapse of biodiversity and ecosystems threatens the long-term sustainability of the biosphere and human society(1). Large investments are needed to protect and restore natural ecosystems. Yet relatively few resources have been committed to protecting nature (2). Global financial markets cannot promote significant investment into natural capital until credible valuations of natural resources become widely available. Current valuations use shadow prices, willingness to pay, or other implicit or indirect measurements (3, 4) and are thus disconnected from market prices. This disconnect discourages investors who rely on market price information and has created a shortfall in social spending on nature protection known as the "global biodiversity financing gap" (5). Estimates of the global need for financing range from $265 to $440 billion annually (6, 7), while global biodiversity investments are only $120 billion (8).

Bridging the biodiversity financing gap may require a more modest approach to valuation, focusing only on services produced by nature that both have market prices and can be utilized without harming biodiversity. This approach rules out most markets for nature products, which rely on extractive or lethal activities or impose monocultures on ecosystems. Currently, carbon storage and sequestration produced by species and ecosystems (9–11) are the only market-valued services that could support investments and trading in the near term. Several national and transnational carbon markets already exist, and a global market will likely emerge (12). In some markets, carbon prices have been steadily rising toward the carbon price range of $40 to $80 needed to meet the 2° Paris Agreement goals (13). Given the limited supply and increasing demand for carbon offsets (14), carbon prices are forecasted to rise globally toward the $40 to $80 range, at least during the next few decades (13, 15). Carbon prices are forecasted to increase even if carbon dioxide removal technologies were to be implemented at large scales (16). However, these technologies have not yet proven to be scalable (17), which leaves natural solutions as one the main options to offset emissions (14). This scenario, however, presumes that carbon services produced by natural entities are sufficiently valuable and that investor interest is sufficiently high to support the development of a market for this instrument.

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Mounting evidence shows that wild animals influence carbon fluxes, promote carbon storage (9, 10, 18), and should be part of nature-based solutions to mitigate climate change (19). Yet wild animals have not been widely associated with the nature-based solution narrative (14). Research on the role of wild animals in the carbon cycle has developed recently, and an increasing number of species are being identified as important contributors to the carbon cycle in marine and terrestrial ecosystems (9). The effects of animals on carbon cycling are through direct or indirect interactions with primary consumers (via the trophic web), through nutrient redistribution, or by storing carbon in their bodies, part of which is stored in long-term carbon pools after death (9, 20). For example, some wild mammal species seem to exert a particularly strong additionality in carbon stored in plant and kelp biomass (9). On land, large herbivores, such as wildebeest, can increase plant and soil carbon stocks by reducing the frequency and intensity of wildfires through removing combustible biomass. In the ocean, sea otters can facilitate carbon storage by reducing herbivory pressure on kelp and seagrass biomass. The magnitude of these effects likely depends on the species population size and their ecological functions (21). Other species with potentially important contributions to carbon cycling are beavers and burrowing rodents because of their ecosystem engineering role (22), and large marine fish sinking to the ocean after death (20).

Carbon services are produced by other natural entities (4, 11), but valuing and protecting animals have some advantages compared with other habitat-centered emission reduction initiatives. First, animal conservation, particularly for umbrella species, inherently involves conserving and restoring natural habitats, with cascading benefits for biodiversity. This reduces the "empty forest" effect observed in other CO_2 emission reduction schemes centered on habitat carbon services, such as United Nations Reducing emissions from deforestation and forest degradation program (REDD+) (23). Habitat-centered schemes do not offer sufficient protection for animals and lead to defaunation, which also undermines carbon storage (23). Second, once animal species become extinct, their reintroduction is either impossible or complicated and costly if captive populations exist, whereas the replanting of trees or seagrass is achievable through the use of seed banks and nurseries. Third, animals might appeal to a broader audience because they include charismatic species that attract public interest. Consequently, investing in animal carbon services would provide a win-win model to preserve ecosystems, reduce biodiversity loss, mitigate climate change, and avoid irreversible animal species extinctions. These added benefits cannot be valued but are nonetheless increasingly important because of the rise of environmental, social, and governance (ESG) investing during the past decade (24). The financial crisis, and increased public pressure for ESG reporting, incentivize investments with positive outcomes for the environment and society (25). The high-ESG rating of our proposed financial framework makes it more likely to attract investors.

Results

Financing Conservation through Market-Valued Services. Modern finance provides a framework for establishing markets in natural services through a new class of financial assets that consists of claims on these services. These claims establish the ownership of the services, which may be sold to other individuals, corporations, nongovernment organizations, and governments. Under this model, governments retain ownership of natural resources and hold the initial claims on the services they produce. Investors could purchase the rights to the flows of services to receive income from them or in anticipation of capital gains from reselling the rights later. Income should be considered not necessarily in monetary terms. In the case of carbon services, "income" would be carbon credits, and the primary purpose of such investments will likely be to offset carbon emissions given the limited supply of carbon offsets in the near future (14). The claims on the services decrease in value or become worthless if the resources producing them are harmed or destroyed. Consequently, investors would require that part of the proceeds of the sales be earmarked for protecting and restoring the resources, including payments to local and indigenous populations for stewardship services. Permanent endowments charged with looking after the natural resources are well suited to collect and disburse these funds through the use of distributed ledger technology ensuring transparency and traceability (e.g., blockchain). Such technology facilitates verification that conservation and restoration programs, as well as the local community members they claim to employ, actually receive the proceeds from carbon or other environmental services sales (26). Payments for ecosystem services with blockchain have been implemented in rural livelihoods with limited access to technology and low literacy levels (27, 28). Where this might not be possible, long-standing payments for ecosystem services programs can offer guidance (29). In addition, governments will be motivated to extend or enhance legal status, protections, or rights to their natural assets (30) as well as enforce them more rigorously. This increases the likelihood that degradation or destruction would result in significant fines or penalties, which motivates further actions to protect natural entities. In these ways, the creation of natural asset-backed securities would provide both incentives for preservation of nature as well as the funding mechanism for it. This scheme incentivizes both the public and private sectors to make long-term financial commitments to nature conservation.

Case Study: Forest Elephant Carbon Services. Given the demand for carbon services and high-ESG investments, we examine the extent of a market based on wild animals' carbon services through the case study of the African forest elephant (*Loxodonta cyclotis*). The forest elephant was chosen for several ecological, conservational, and methodological reasons. 1) Elephants contribute to increasing rainforest aboveground carbon (AGC) by reducing the density of small trees primarily through trampling and partly due to consumption and by dispersing seeds of particularly large trees (18, 31). Lower tree density leads to less competition for resources, allows trees to grow larger, and promotes late-succession trees, which store more carbon per volume than other types of trees. Overall, mature closed-canopy forests with elephants store 3 to 15% more carbon compared with forests without them (18). 2) Forest elephants are in rapid decline due to poaching, but they were once widespread across tropical Africa (32) and have been recently identified as critically endangered by the International Union for Conservation of Nature. 3) Forest elephants are a keystone species performing other critical and unique ecological functions, such as seed and nutrient dispersal (32). 4) Elephants are considered an umbrella species because they require large areas and their protection would benefit the whole ecosystem and promote biodiversity. 5) Human–elephant conflict is on the rise in central Africa because of shrinking forest habitat, and funding is needed to mitigate this conflict. 6) Elephants are one of the few animal species for which a correlation was established between population density and an increase in carbon storage (18). This is particularly critical as it allows us to relate changes in population growth to carbon fluxes. All these conditions make the valuation of elephant

services an important proposition for funding their conservation across countries and obtaining carbon and additional ecosystem-wide benefits.

We valued the carbon services of elephants in 79 tropical rainforest protected areas (PAs) across nine African countries, under three conservation scenarios reflecting different population growth rates: natural as well as 50 and 75% reduced growth due to poaching. Estimates of elephant contribution to AGC (18) were integrated in a spatially explicit demographic model based on empirical observations (33). This demographic model permits the quantification of the effect of rebounding elephant populations on the AGC of PAs in the next 100 y. We accounted for the variability in the major factors that could influence carbon gains: forest regeneration rates, elephant growth rates, and the relative contribution of elephants to AGC annual accumulation (*Materials and Methods*). Upper and lower bounds for these factors were used to calculate the uncertainty in our results. These results were then used in a financial framework to value elephant services and the losses due to poaching within the next 10 to 30 y, a timescale in line with management and carbon policy targets. The financial framework evaluated the annual cash flow of carbon capture services produced by current elephants and their contribution to future elephant generations (*Materials and Methods*). We used the carbon price of \$51.56/tCO_2 based on the European Union-Emissions Trading System (EU-ETS) market discounted at 2% to calculate the future value of elephant services (*Materials and Methods*). We also performed the same calculation using a carbon price of \$5/tCO_2 (10% of the EU-ETS price and below the \$40 to \$80 World Bank recommended price range) to provide a comparison with a low–carbon price scenario. All results are based on the \$51.56/tCO_2 unless specified. The magnitude of African forest elephants' contributions to carbon capture are large enough and the price of carbon has recently become high enough to imply that a sizable market for investment in elephant-related carbon credits could be created.

Elephant Populations and PAs. The selected 79 tropical rainforest PAs cover 537,722 km^2 and host an estimated population of ∼99,000 elephants (Fig. 1*A* and Dataset S1). Most of the PAs ($n = 69$) are in central African countries: Cameroon (20), Central African Republic (CAR; 3), Democratic Republic of Congo (DRC; 13), Equatorial Guinea (1), Gabon (17), and Republic of the Congo (15). The others are in Nigeria (5), Rwanda (2), and Uganda (3). Current population density varies greatly among PAs (0 to 0.92 elephants/km^2) (Dataset S1). PAs are mostly national parks (40) and natural or forest reserves (13). The demographic model predicted that after 30 y without poaching, the elephant population would double from ∼99,000 to ∼201,000 individuals (183,000 to 219,000) and quadruple in 100 y to 389,000 (356,000 to 416,000) (*SI Appendix*, Fig. S1).

Carbon Sequestration and Valuation. The elephant population growth would result in ∼109 MtC (64 to 153) stored in forests due to elephants in 30 y (∼1.8% increase from current AGC). At a carbon price of \$51.56/tCO_2, this growth would result in a potential market value of \$20.8 billion (\$10.3 to \$29.7 billion) and \$25.9 billion (\$12.8 to \$37.6 billion), for the next 10 and 30 y respectively, across all nine countries (Fig. 2, *Insets*). At a carbon price of \$5/tCO_2, the market value would be \$2.02 billion (\$1.00 to \$2.89 billion) and \$2.51 billion (\$1.24 to \$3.64 billion) for the next 10 and 30 y, respectively. These present values are the cumulative contribution of current elephant populations to AGC and the yearly increase in AGC due to future population growth. The totality of these sums would be reserved for implementing the conservation program and ensuring its success: protecting forests and elephants, helping local communities with human–wildlife conflicts, and improving socioeconomics conditions. Any return on investment will be independent of these sums. These results assume that anthropogenic disturbances, such as deforestation or degradation, would be minimal within PAs but include the variability in elephant population growth, relative contribution of elephants to AGC sink, and forest regeneration rates (*SI Appendix*, Figs. S2–S4). The latter factor is initially the most important contributor to the variance in the value of services (relative contribution: 60 to 80%) (*SI Appendix*, Fig. S5). However, in the longer term, the level of conservation effort becomes the second most important factor as it explains 20 to 38% of the variance in the valuation (*SI Appendix*, Figs. S2–S5). This implies that forest-specific regeneration rates should be used for more localized studies. Most importantly, it shows that conservation efforts to reduce poaching can have an important effect on reducing uncertainties in future values of carbon services (*SI Appendix*, Figs. S2 and S4). The value of services in individual countries varies widely between \$10 to \$17,160 million (range: \$3 to \$23,000 million) because of differences in present-day population and the extent of PAs (Figs. 1*B* and 2 and Dataset S1). Nigeria, Rwanda, and Uganda are at the edges of the forest elephant range and have a few small PAs (Figs. 1*A* and 3). Uganda has, however, higher chances of approaching its maximum carbon sink potential given its high elephant density (Figs. 1*B* and 3*A*). Gabon and the Republic of Congo are also well positioned to optimize elephant services due to their large PAs and more abundant populations (Figs. 1*B* and 3*A*). The other countries have extended PAs but small populations, particularly the DRC (the second largest extent of PAs) (Fig. 3). This reduces their potential for carbon capture and value (Fig. 3), which is nonetheless still the third largest and offers sizable sums to jump-start conservation efforts based on the contribution of remaining populations. The negative effect of small populations is also observed in the carbon capture value per kilometer squared, which is low in the DRC and CAR compared with the potential offered by their large PAs (Fig. 1*C*). Small current populations result in unrealized carbon value as it takes longer to restore populations and fully benefit from their services (Fig. 3*A*). Small PAs limit the country-level value of carbon services because elephant range is restricted. Extending PAs could be a solution if matched with increased protection to avoid poaching and reduction in elephant–human conflict. Similarly to other herbivores, elephants emit methane when digesting plant material, which might offset some of their carbon sink potential. A population of 200,000 elephants would emit 0.024 TgCH_4/y, equivalent to 0.16 MtC/y (*SI Appendix*). Elephant methane emissions are thus trivial, particularly when compared with ∼100 TgCH_4/y emitted by livestock (34).

The Cost of Poaching. In 30 y, medium and medium–high poaching intensities [50 and 75% reductions in population growth rates (33)] (*Materials and Methods*) would limit population growth to ∼151,000 (122,000 to 180,000) and ∼125,000 (112,000 to 138,000), respectively (*SI Appendix*, Fig. S1). Consequently, at a carbon price of \$51.56/tCO_2, the cumulative value of carbon services is severely reduced by \$5 billion (20%) and \$7 billion (27%), respectively, compared with the no-poaching scenario (Fig. 2). Within the first 10 y, the losses are between \$2 to \$3 billion (Fig. 2). High losses due to poaching are observed in Gabon, the DRC, and Congo, and losses

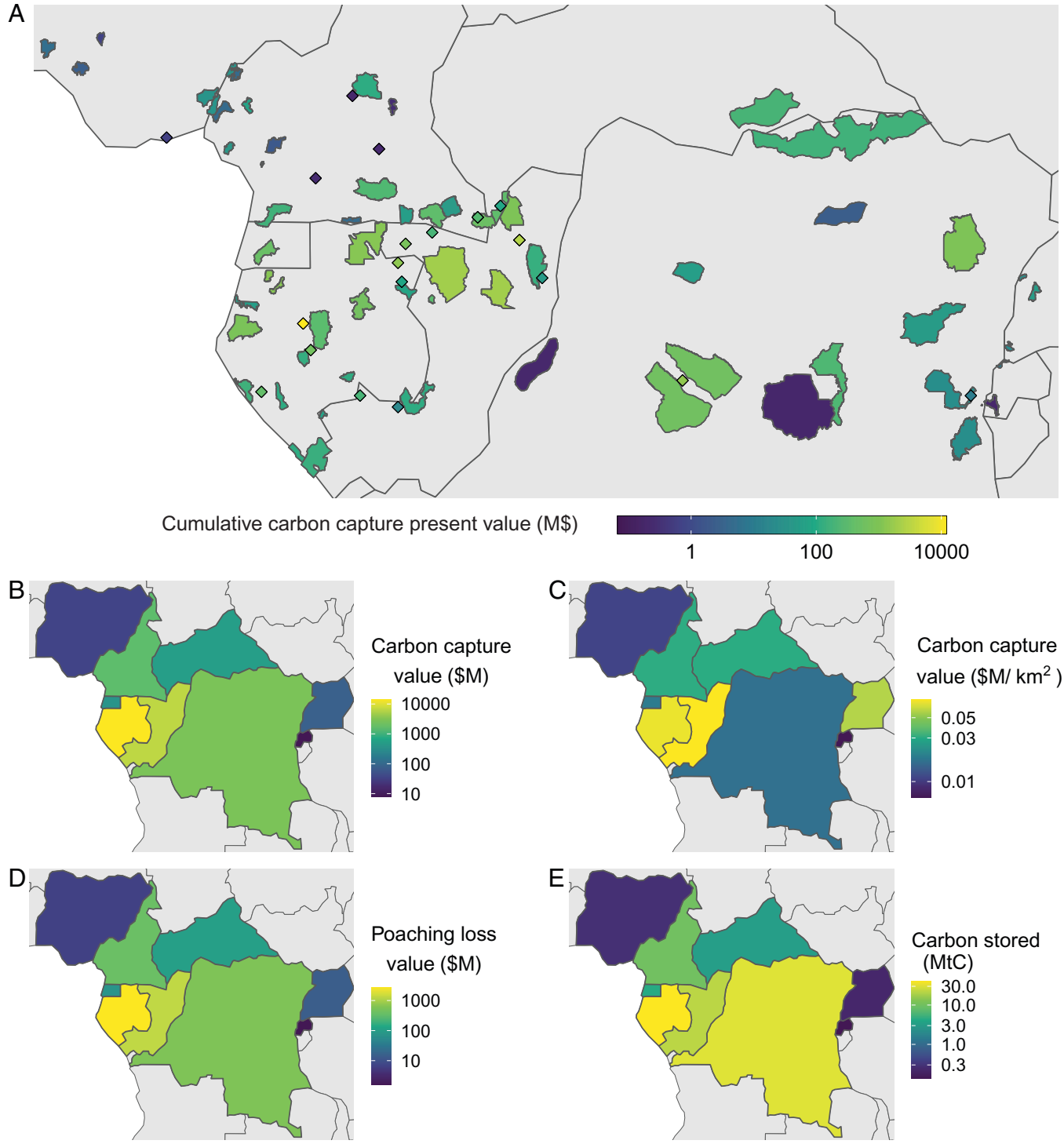

Fig. 1. Carbon capture value (carbon price \$51.6/tCO_2) and stored carbon due to forest elephant activity in 30 y. (*A*) Diamonds represent PAs not present in the World Database on Protected Areas. The extent of some PAs does not fully match with elephant habitat (*Materials and Methods*). The PA "Rest of Gabon" is not displayed as it covers ~54% of the country (value \$11.8 billion). (*B*) Total value of elephant carbon service and (*C*) per kilometer squared value (ratio of total value to total extent of PAs). (*D*) Loss of value caused by depressed population growth (50% of natural growth rate) under the medium-protection scenario. (*E*) Sum of carbon stored across all PAs within each country.

are intermediate in the CAR, Cameroon, and Equatorial Guinea (Figs. 1*D* and 2). The losses incurred in the different conservation scenarios are initially small, but after 30 to 50 y, they already amount to \$6 to \$11 billion (*SI Appendix*, Fig. S2). Long-term losses would be ~\$10 billion or more depending on the variability associated with forest regeneration rates, the relative contribution of elephants to AGC and their population growth rate (*Materials and Methods* and *SI Appendix*, Fig. S2), and differences in local poaching rates. The case of declining population was not considered as it would not generate any value. Only population growth can be associated with additional carbon storage. This makes very intensive poaching very harmful not only for the species, but also for local economies. A decline of current elephant populations would essentially cost between \$20 and \$25 billion within the next 10 to 30 y. After 30 y, roughly a third of the carbon sink potential due to

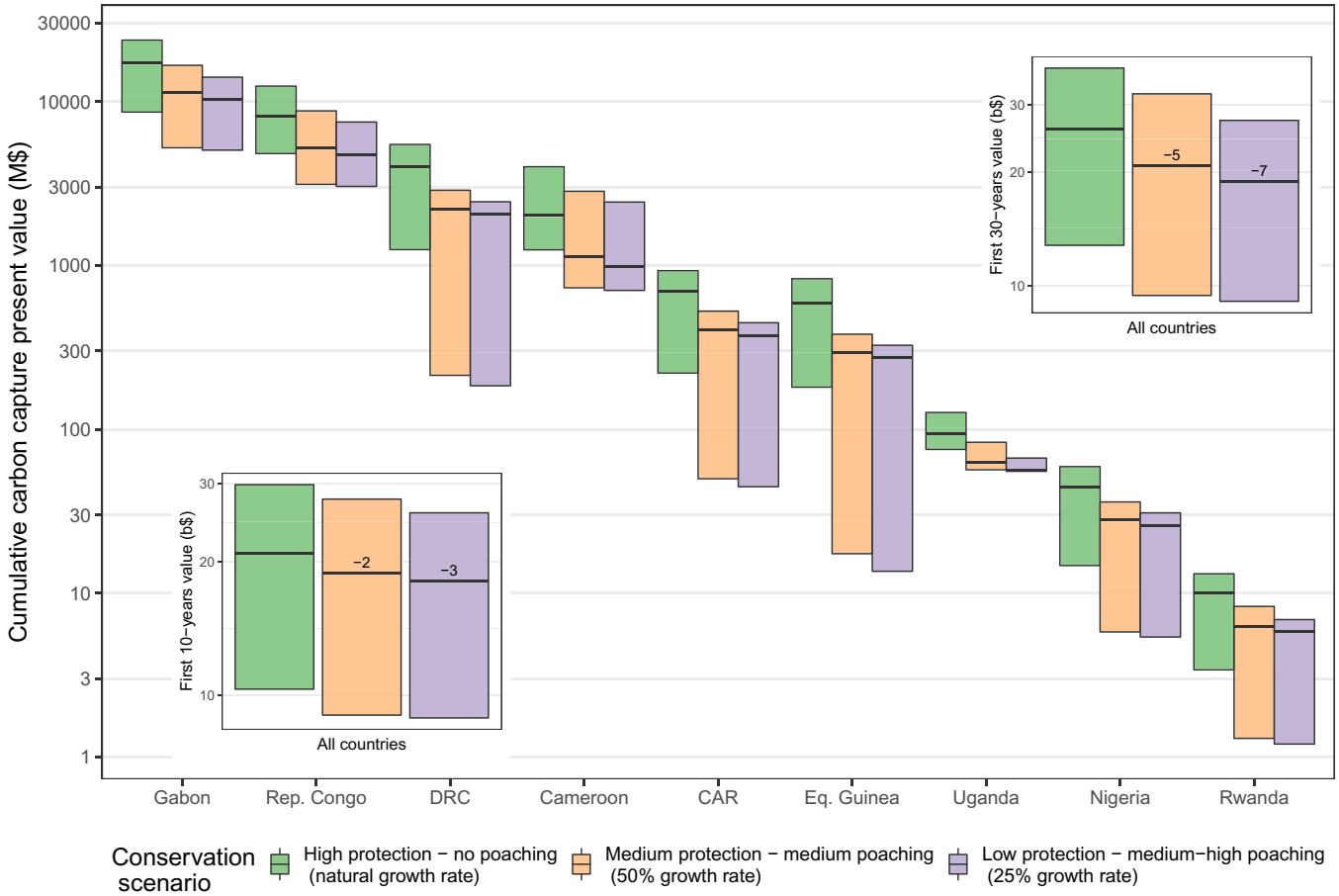

Fig. 2. Value of forest elephant services in African countries under different conservation scenarios at a carbon price of \$51.6/tCO_2. Present values are the cumulative sum of yearly carbon service in PAs over an investment horizon of 30 y and include the contribution of present and future generations of elephants. *Insets* show the total cumulative present value of carbon services within the first 30 y (*Upper Right Inset*) and first 10 y (*Lower Left Inset*) for all countries. Box plot upper and lower bounds show the uncertainty associated with the forest regeneration rate, the contribution of elephants to AGC accumulation, conservation scenarios, and elephant population growth (*Materials and Methods*). The numbers inside the bars show the difference in billions of dollars compared with the high-protection conservation scenario.

elephants is realized in Gabon, Congo, and Uganda (Figs. 1*E* and 3*B*). Instead, the other countries would attain only between 15 and 20% of their potential carbon sequestration (Fig. 3*B*). All nine countries have small carbon footprints, implying that elephants could further expand their role as enhancers of carbon sinks for several years. A larger potential carbon sink of 341 MtC (206 to 463) would only be accrued after 100 y as current populations are small compared with their historical levels and geographically constrained (Dataset S1).

Discussion

Creating Markets around Conservation. To contextualize these calculations in terms of single PAs, consider Nouabale-Ndoki National Park (Republic of Congo) hosting ∼1,800 elephants at a density of 0.45/km^2. The carbon capture services provided by these elephants would be worth ∼\$286 million (\$261 to \$912 million). This amount is comparable with the average market capitalization of a publicly traded company in the Russell 2000 index, a measure of 2,000 US small stocks having a median value of slightly less than \$1 billion. This comparison implies that the size of the Nouabale-Ndoki market alone would be large enough to attract institutional investors whose participation is essential to the success of nascent markets. In a wider financial context, even at the low carbon price of \$5/tCO_2, the revenue generated by elephants (∼\$200 million/y) would finance the entire cost of anti-poaching measures across central Africa (\$16.9 million/y) (35) and likely cover the majority of the budget of PAs in our study case (36), with benefits for the whole ecosystem. At a price of \$51/tCO_2, the revenue would be ∼\$2 billion/y, a sum greater than most conservation funding sources combined for all of Africa (36), which would allow for significant investments to improve local socioeconomic conditions. This revenue would be considerable for the countries discussed in this paper where tourism is not well developed (35) or to reduce the dependency of PAs on tourism revenue (36).

The above calculations show that restoring the carbon capture services of African forest elephants could form the basis of an investment market worth over \$25 billion. Our carbon price is market based and in line with Intergovernmental Panel on Climate Change reports, the literature, and the recommended price range needed to reach the 2° goals (13, 16, 37), but it is much lower than the social cost of carbon used in other valuations (4). Fluctuations in the price and its variation across regions (13, 37) might also affect these kind of valuations, but in the foreseeable future, the demand for carbon offsets will far exceed the supply (14). Forest elephant services are only one part of a potentially much larger global market in animal carbon services, which could generate billions of dollars annually to reduce the biodiversity financing gap. Creating these markets would involve the associated costs for the protection (e.g., antipoaching activities,

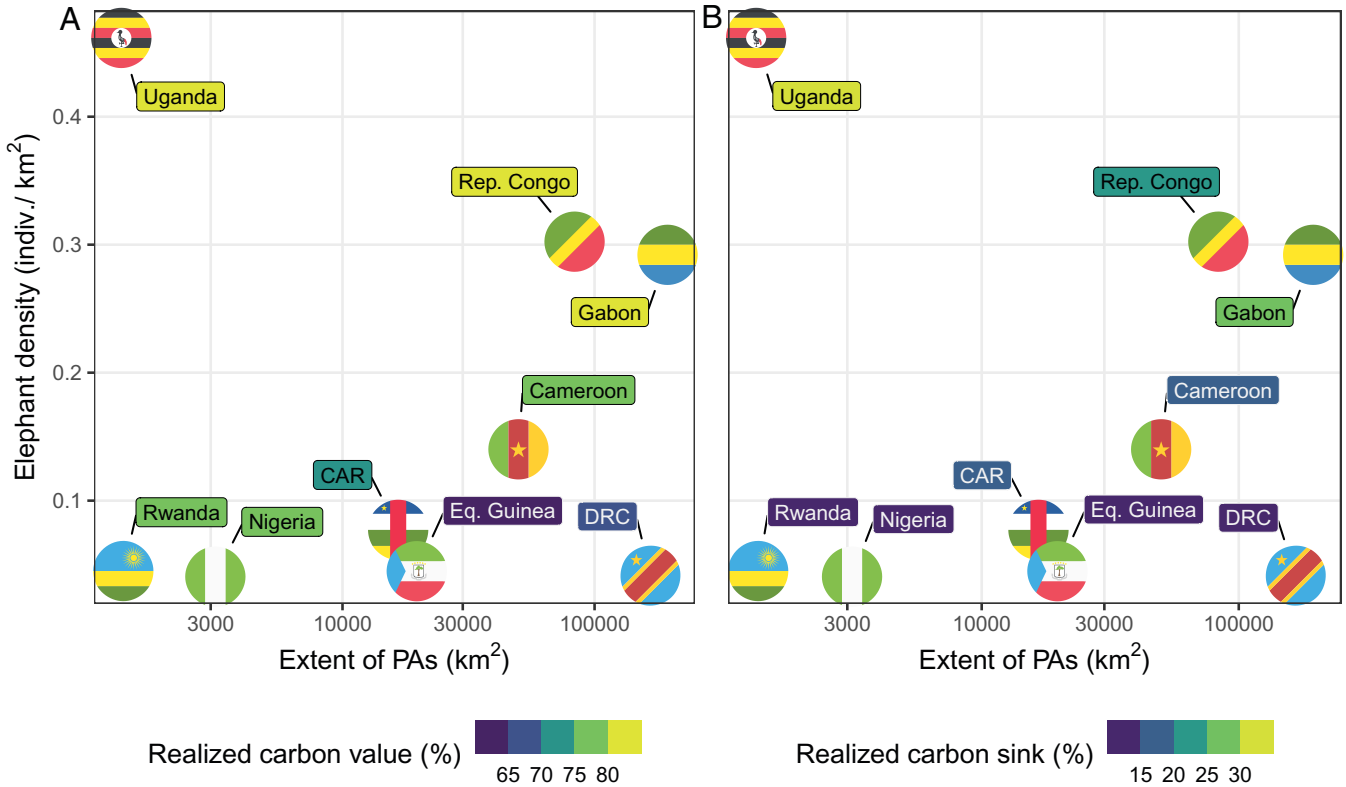

Fig. 3. Carbon value and carbon sink potential attained by countries within the first 30 y under the "high-protection" scenario, in which elephant populations grow at their natural rate. The percentage represents the fraction of (*A*) value or (*B*) AGC stored under no poaching compared with the value attainable in 100 y if elephant populations quadrupled compared with today.

creation of PAs), species reintroduction, and restoration of ecosystems (e.g., rewilding) and compensations for lost income for local communities and their direct involvement throughout the project (e.g., policy, implementation, and management) (38). Added benefits of restoring and preserving ecosystems include their increased resilience to future climate disturbances (39), which threaten ecosystems' health and services. The protection of one species might not guarantee the protection of all others, but the valuation of services provided by umbrella species could provide ecosystem-wide benefits through habitat conservation and law enforcement. Researchers are establishing that many other animals, including marine and terrestrial vertebrates (9, 10) and invertebrates (9), play important roles in carbon cycling. More research is needed to establish the correlation between carbon cycling and wild animals. However, the decline of many wild populations has likely compromised the functioning of ecosystems, including their carbon storage potential; this suggests that rewilding could enhance carbon storage across a wide range of ecosystems (18, 19). The total market value of carbon services may be measured in the trillions of dollars—smaller than global equity markets but as large as the markets for important types of bonds, such as commercial paper. More broadly, the techniques used in this paper can be applied to any animal service that can be measured and to which market prices may be assigned. Animal services, therefore, represent an entire asset class whose market potential may rival that of existing financial instruments.

Challenges and Opportunities. Given the mixed experiences that many countries have had with related schemes, such as debt for nature swaps (DNSs) and payment for environmental services (PESs), convincing governments to participate in natural asset markets may be difficult. DNSs generally result in only small amounts of debt reduction (40, 41) and in some cases, have impaired the ability of local and indigenous populations to earn a living (42). Likewise, PESs are intended to fund the protection of land or other natural assets, but they are often significantly lower than the returns from alternative uses of these resources (43, 44). The organizers of natural asset markets must convince governments (and in turn, the local and indigenous communities) that this innovative approach will deliver larger and more dependable benefits than existing arrangements.

The organizers' case can be built in part on the fact that market prices for carbon capture services, rather than bilateral creditor–debtor negotiations, will determine what countries earn from their participation. In this paper, we have documented that such cash flows could be quite substantial. A valid concern, however, is that the price of carbon, like other commodity prices, may be volatile and fall to levels that make participation in this scheme unattractive. However, as the carbon market develops, tools, such as futures and options contracts for managing this risk, will almost surely be introduced, enabling both the producers and the end users of carbon credits to maintain participation in the natural asset–backed carbon market despite carbon price volatility.

The final question is how to develop these markets as quickly as possible in order to enable actual investments to fund preservation and restoration of vanishing species and habitats. Many steps are involved in financial market development (45). Certification of the carbon sequestration produced by forest elephants (and other species) is necessary for investor acceptance of financial instruments based on this service. The best approach is to start small with a demonstration case in a few PAs with a good record of elephant protection and intact habitat. PAs should be kept intact as much as possible before and while elephant populations

are recovering, and synergies with other climate change mitigation strategies could further preserve biodiversity and carbon stocks (46). Collaboration between governments, including local communities, and institutional investor representatives over the design of the financial instrument will greatly increase the likelihood of successful issuance.

If certification and instrument design obstacles can be overcome, the outlook is positive. The increasing global demand for carbon offsets, driven by corporate and government pledges to reach carbon neutrality, and household investment into high-ESG portfolios present an unprecedented opportunity to develop financial markets that support conservation backed by the services produced by the nature being protected.

Materials and Methods

Carbon Capture Services of African Forest Elephants. African forest elephants (*L. cyclotis*) facilitate the capture of large quantities of carbon through different mechanisms. First, the average body mass of a mature forest elephant contains 720 kg of carbon (47). After death, the carbon contained in bodies is mostly released back into the atmosphere in the form of CO_2. However, a stable population of elephants will continually store carbon in proportion to the number of individuals. Any increase to the stable population implies that additional carbon is captured and stored in elephant bodies. The plant biomass consumed by elephants through their lifetime is much higher compared with their body mass. Here, we do not consider consumed biomass because forest elephants consume mostly grass and fruit (32). Thus, elephant consumption does not directly reduce closed-canopy forests AGC, which is stored mainly in tree trunks and branches. Consumption should be considered in cases where it might have more direct effects on carbon storage: for example, through defecation that might affect soil carbon and nutrients.

Most importantly, African forest elephants facilitate carbon sequestration through their effect on the forest ecosystem. While moving through the forest and foraging for food, elephants reduce the density of trees smaller than 30 cm in diameter. This reduction in tree density changes light and water availability in the forest, leading to an increase in the proportion and the average size of late-succession trees. Late-successional trees are slow-growing, canopy-dominant trees with a higher carbon density (kilograms of carbon per meter cubed) compared with other tree types. As late-successional trees become larger and more abundant, there is a net increase in the forest AGC due to elephant activity (18). This effect was only quantified for closed-canopy forests and mostly in relation to elephant-induced mortality on small trees due to trampling or to reaching for foliage and fruit. It does not consider the effect of browsing on leaf litter quality or photosynthetic rates nor the effect of elephants in secondary forests, where more leaf biomass might be within reach of elephants. Forest elephants might also influence carbon capture through other mechanisms: for example, by dispersing large seeds produced by high–wood density trees or by depositing dung that could increase plant productivity or soil carbon. However, these mechanisms have not been adequately studied and quantified to be included in our calculations.

Projecting the future population of elephants is essential to estimating the full value of the carbon capture services they produce. The quantities of services produced are proportional to population, and current populations are much smaller than their natural preindustrial levels due to poaching and habitat loss. The population is currently estimated at less than 100,000 compared with more than 1 million individuals before widespread poaching (48). Thus, we initially define a demographic model to project future changes in elephant populations under different poaching scenarios. The demographic model is then used to calculate the value of carbon in elephant bodies and of their carbon-capturing services.

Elephant Population Model. We forecast population growth using a logistic model under three scenarios: 1) "high protection," natural population rate growth under no poaching; 2) "medium protection," 50% of the natural growth rate under medium poaching rates; and 3) "low protection," 25% of the natural growth rate under medium to high poaching rates (see below for further details on mortality rates). We do not consider the case of declining elephant populations because it would generate no value as only population growth is associated with additionality in carbon storage. The logistic model was chosen because it allows us to estimate the evolution of the forest elephant populations in PAs across Africa as populations approach their carrying capacity.

The annual growth rate of elephants is given by

$$\frac{1}{P(t)}\frac{dP(t)}{dt} = \begin{cases} v(0)\left[1-\frac{P(t)}{P^*}\right] & \text{for } P(t) \leq P^* \\ 0 & \text{for } P(t) > P^*, \end{cases} \quad [1]$$

where $P(t)$ is the population at time t and P^* is the population carrying capacity estimated at 1 elephant/km^2 based on conservative estimates found in the literature (48, 49). The left-hand side of Eq. **1** is the per capita change in the elephant population. The right-hand side of Eq. **1** indicates that when $P(t)$ is less than or equal to P^*, the growth rate starts at $v(0)\left[1-\frac{P(0)}{P^*}\right] = 0.0351$ (SD 0.006) in the natural mortality scenario and $v(0)\left[1-\frac{P(0)}{P^*}\right] = 0.018$ (SD 0.01) in the medium protection scenario. These population growth rates were determined following the only long-term studies of forest elephant demography at Dzanga Bai in the CAR (33, 50). We added a low-protection scenario where the initial growth rate is $v(0)\left[1-\frac{P(0)}{P^*}\right] = 0.009$ (SD 0.0045), which is half the growth rate under poaching reported in refs. 33 and 50. In our low-protection scenario, the growth rate is roughly four times less than the natural growth rate and half of the growth rate with poaching at Dzanga Bai. The proportion of illegally killed elephants (PIKE) was estimated at Dzanga to be around 0.5, which is lower than the central Africa average of 0.8 (51). The low protection is representative of other national parks having higher PIKE compared with Dzanga Bai, which is a relatively well-protected area. These scenarios account for the high variability in poaching rates across central Africa in the case where poaching still allows elephant populations to grow. The SDs associated with different conservation scenarios capture the interannual variability in relation growth and are used in combination with the other variable factors (see below) to produce operator lower-bound ranges for our results. The $-\frac{P(t)}{P^*}$ term represents a decrease in the growth rate of elephants as the population approaches carrying capacity. The initial growth rate at $P(0)$ decreases toward zero until $P(t) = P^*$.

The solution to Eq. **1** as t goes from zero to infinity follows (52, 53):

$$P(t) = \frac{P(0)}{\frac{P(0)}{P^*}\left[1-e^{-v(0)t}\right] + e^{-v(0)t}} \text{ for } P(t) \leq P^*. \quad [2]$$

The initial population $P(0)$ and the population at carrying capacity P^* are required to solve Eq. **1** for P at each iteration. These parameters were determined for each PA following the African Elephant Database (54) (AED) and the literature (35). We use the term PA in a broader sense as the AED identifies "input zones," which are sometime outside PAs. Further, because the AED does not distinguish between forest and savanna populations, we retained only the PAs covered by tropical rainforests within potential forest elephant range. We excluded forest concessions, mountainous areas, and the savanna part of mixed vegetation PAs. These data were used to determine current population density, potential range (i.e., PA extent), and average AGC (Dataset S1). Population density at equilibrium was set at 1 elephant/km^2. Note that estimates of historical populations are uncertain, and our estimate might be conservative compared with observed densities in some PAs.

Value of Carbon Capture in Elephant Bodies. The value of carbon stored in elephant bodies is marginal compared with the carbon captured by elephants through their interactions with the forest. We performed the calculations for completeness and because it might be of interest for species attaining larger total population biomass, such as ocean vertebrates (10). We estimate that an average elephant weighs 3,000 kg, of which 24% is carbon (47). The carbon sequestered in the body is multiplied by 3.667 to obtain its CO_2 equivalent (C_b):

$$C_b = 0.24 \times 3{,}000 \text{ kg} \times \frac{11}{3} = 2{,}640 \text{ kg } CO_2. \quad [3]$$

The value of carbon sequestered per elephant body is calculated by multiplying C_b by the price of CO_2 per kilogram $\times 10^3$ (C_p). The average CO_2 price reported in the European Union Emissions Trading System market in 2021 was \$51.56 (55). This price is the average over the period 1 January 2021 to 20 June 2021 using historical futures prices: European Climate Exchange European Union Allowance Futures, Continuous Contract #1. One European Union allowance

gives the holder the right to emit 1 tCO_2. This price is converted from euros to US dollars using the average US/euro exchange rate over the same time period from the St. Louis Federal Reserve Bank. We acknowledge that the price of carbon might vary through time following demand and supply. However, according to recent reports, the price of carbon is projected to rise sharply until 2050 because demand far outweighs supply, and a price range of \$40 to \$80 is needed to reach the Paris Agreement 2° goal (13–16). The price of carbon used in our simulations is thus conservative compared with forecasted prices and the \$40 to \$80 price range. We also perform the calculations using a carbon price of \$5 for a comparative scenario with a much lower price. The yearly value of CO_2 captured in the population is equal to the increase in population multiplied by the CO_2 captured per elephant multiplied by C_p so that the market value for this service during period $t+i$ is given by

$$V_b(i) = C_p C_b [P(i) - P(i-1)]. \quad \textbf{[4]}$$

To find the present value of current and future carbon capture, we must assume a discount rate (d), which is the return on \$1 after 1 y. The present value of a future cash flow of \$1 is discounted by an interest rate, d, by $\frac{1}{(1+d)^k}$. Here, k is the numbers of years into the future. This procedure identifies the amount of money needed today equivalent to \$1 in k years into the future. Once the dollar value is placed into the same time period, all the future values can be added together. We chose a 2% discount rate, reflecting both market evidence and the practices in the existing literature (56, 57). Using $d = 0.02$, the present value of carbon content in the body of all elephants in a PA is

$$V_1 = PV(Body\ Carbon) = C_p C_b P(0) + \sum_{i=1}^{\infty} \frac{V_b(i)}{(1+d)^i}. \quad \textbf{[5]}$$

Value of Carbon Capture Enhancement through Interaction with Tropical Forest. The enhancement of AGC triggered by elephants is determined by their population density and the state of AGC in relation to the equilibrium AGC with elephants (18). Here, we assume that PAs are not subject to intense anthropogenic disturbances, as are areas outside PAs; thus, perturbations to carbon cycling should be within the natural variability in the forest regeneration rate for which we account (see below). For example, we excluded areas that are selectively logged. We also assume no large-scale effects of fires as these are currently not a major source of forest loss within the Congo basin (58). In our case, at a density of 1 elephant/km^2, Berzaghi et al. (18) estimated that equilibrium AGC is 15.7% (±0.1) higher compared with AGC in a closed-canopy forest without elephants. The effect of elephants on AGC was simulated by using a state-of-the-art process-based vegetation model that simulates forest dynamics as a function of environmental variables (climate, microclimate, and soil conditions), competition for resources (light and water) among plants, and variable elephant densities (18). Berzaghi et al. (18) simulated the effects of elephants on a generic mature lowland Congo basin rainforest and acknowledged that the contribution of elephants might vary in space and time. Our statistical approach is based on the results of the vegetation model used by Berzaghi et al. (18) and integrated with current remote sensing estimates of AGC to produce spatially explicit results as a function of time. In our simulations, we consider only the effect of elephants in mature closed-canopy forests. The effects of elephants on AGC in secondary forests might be different, but currently, not enough information is available to model this effect. We used a conservative 13% as our baseline for the contribution of elephants to AGC. An SD of 2% was used to simulate upper and lower bounds covering a broad range of conditions, and it is still conservative compared with Berzaghi et al. (18). As elephants are removed from the system, AGC starts to decrease until it reaches a new equilibrium relative to a lower elephant density. The time to transition from one equilibrium AGC to another depends on the rate of elephant population decline and the mortality rate of trees. These two rates are needed to estimate how much of the 13% (±2%) gain has been lost since their decline and to calculate the future contribution of elephants to AGC. Once the potential gain (13% − percentage lost since decline) is determined, the equilibrium AGC at a density of 1 elephant/km^2 can be estimated from the current AGC in each PA. Historical rates of population decline were not available for most of the PAs in our study. Instead, we used the current population density in each PA as an indication of years since decline. The majority of populations across central Africa declined between 20 and 100 y ago, with some exceptions in areas afflicted more recently with intensive poaching. A density close to zero might suggest that local populations declined 100 y ago or more. At higher population densities, the years since decline would be less. Following these assumptions, we use a linear function to determine the years since decline (t_d) as a function of current population density for each PA. We acknowledge that local declines might not follow linear patterns:

$$t_d = 100 \times (1 - P_d), \quad \textbf{[6]}$$

where P_d (elephants per kilometer squared) is the population density in a particular PA.

Tree mortality rate provides an indication of how fast a forest regenerates itself. Observed mortality rates in tropical forests are highly variable (2 to 6%/y) and are affected by drought and extreme climatic events (59, 60). Observed mortality rates of African tropical forests suggest rates between 1 and 2% (61, 62). However, estimating mortality rates requires long-term studies, which are limited in Africa compared with other tropical areas (61). We account for this uncertainty by setting the mortality rate (m_r) at 1.5% and by performing a sensitivity analysis by setting this parameter at 1 and 2% to account for the effect of regional differences and extreme climatic events. A yearly mortality of 1.5% implies that 67 y are needed to replace most adult trees with new recruits. Under these conditions, where elephant density is close to zero, t_d would be approaching 100 y. Most adult trees would have been replaced, and AGC likely reached its equilibrium without elephants, so the potential future gain in AGC would be around 13%. We used t_d and m_r to calculate the equilibrium AGC if elephants would return to their original density of 1 elephant/km^2. The three study cases used for the sensitivity analyses are further explained in *SI Appendix, Supplementary Text*:

$$AGC_e = \begin{cases} AGC_p \times (1 + 0.0013 \times t_d) & \text{for } t_d \geq t_r \\ AGC_p \times \left(1 + 0.0013 \times t_d \times \frac{t_d}{t_r}\right) & \text{for } t_d < t_r, \end{cases} \quad \textbf{[7]}$$

where AGC_e (tonnes of carbon) is the equilibrium AGC with elephants, AGC_p (tonnes of carbon) is the present-day AGC, and t_r (years) represents the forest regeneration time calculated as $100/m_r$. AGC_p was calculated as the average AGC within each PA according to the boundaries indicated by the United Nations World Database on Protected Areas (63) and the most recent AGC map (64).

When elephant density starts to increase, the time to reach AGC_e will depend on various factors: the number of years needed to reach 1 elephant/km^2 (t_e), the spatial heterogeneity of elephant density, and m_t. Because in the majority of PAs, t_e is 1.5 to 5 times larger than m_t, we conservatively use t_e as an indication of the time taken to reach AGC_e. In all cases, the elephants' contribution to AGC is maximized only when the population reaches carrying capacity; consequently, at least t_e years are needed for this process to complete. We assume that AGC increases at a constant rate irrespective of the initial AGC_p. Therefore, we calculate the yearly rate of change in AGC attributable to elephants with the following:

$$r = \frac{AGC_e - AGC_p}{t_e}. \quad \textbf{[8]}$$

We assume that r is constant through the simulation of each PA, but as PAs have different AGC at present and equilibrium, our model captures the spatial variability in r. This implies that, even though population density might vary spatially within a PA, an average increase in AGC per kilometer squared per year is applied in areas that are reclaimed by elephants. As populations grow, their density will homogenize across the landscape, and their effect on AGC will converge to r. This assumption is needed because there is no current knowledge on the heterogeneity of elephant densities inside each PA or how elephants might reclaim the previously occupied range after a population rebound. The average value of r across PAs is 0.0754 × tonnes of carbon per hectare per year (SD 0.03), which is a small fraction compared with the net growth rates of AGC observed in the African rainforest of 0.66 to 4 × tC/hectare per year (65, 66). Our estimated r is thus conservative compared with previously published estimates of elephant contribution to AGC (18). We use r and yearly changes in population to calculate the value of carbon capture provided by elephants. The calculation is as follows. At time 1, there is an increase in population of $P(1) - P(0)$ following the population growth model (Eq. **2**). This new generation enters a plot of forest with AGC_p and increases it to AGC_e over t_e. The size of the plot is adjusted so that the density of elephants in the forest is maintained constant throughout the PA. At time 2, a new generation of elephants is born with size

$P(2) - P(1)$, which occupies a new plot and contributes to the growth of AGC as described above. We repeat this process for 1,000 generations to ensure convergence of the elephant population to its steady state, at which point the total increase in carbon capture converges to zero. The present value of the carbon capture by current and future generations of elephants has three components given by

$$V_2 = \begin{cases} C_p \times AGC_p \times 0.13 \times \ P(0) + C_p \ \times \ r \ \times \ P(0)\frac{1}{d}\left[1 - \left(\frac{1}{1+d}\right)^T\right] + \sum_{g=1}^{T} V_g & \text{for } t_d \geq \ t_r \\ C_p \times AGC_p \times 0.13 \times \left(1 - \ \frac{t_d}{t_r}\right) \times \ P(0) + C_p \ \times \ r \ \times \ P(0)\frac{1}{d}\left[1 - \left(\frac{1}{1+d}\right)^T\right] + \sum_{g=1}^{T} V_g & \text{for } t_d < \ t_r. \end{cases} \quad [9]$$

Here, T is the investment horizon of the investor, which is the number of years the investor expects to receive payments from the investment. Let g be the number of generations and V_g be the value of each generation contribution to carbon capture given by

$$V_g = \frac{C_p \ \times \ r \ \times \ [P(g) - P(0)]}{d}\left[1 - \left(\frac{1}{1+d}\right)^{t_e}\right]\left(\frac{1}{1+d}\right)^g. \quad [10]$$

All other variables were defined previously. The first term in Eq. **9** is the 13% contribution to AGC by the current population of elephants, $P(0)$, multiplied by the price of carbon credits, C_p. If $t_d \geq \ t_r$, the current population is equal to the population density times the area of the PA. Otherwise, we assume that the current population has realized its contribution to AGC_p. The choice between the first and second lines in Eq. **9** is determined by the mortality of the forest and the initial elephant density in the PA. For example, when the mortality is 1.5% per year, the first line is relevant if the initial density is less than or equal to $\frac{1}{3}$. In addition, $\left(1 - \frac{t_d}{t_r}\right) = \frac{1}{2}[3P_d - 1]$ for an initial density greater than $\frac{1}{3}$, so that the current population does not contribute to the present value of the elephants in the PA when the initial density is $\frac{1}{3}$.

The next two terms in Eq. **9** include the contribution of future generations, $P(g)$. The population in each generation can be decomposed into a contribution from the initial population, $P(0)$, to the current generation and the change in the population from the initial population, $[P(g) - P(0)]$ [i.e., $P(g) = P(0) + P(g) - P(0)$]. The first part $P(0)$ adds for each time step the change in AGC times the market price of carbon capture, so that the second term in Eq. **9** is $C_p \ \times \ r \ \times \ P(0)$. This leads to the second contribution in Eq. **9**. This contribution is multiplied by the present value of an annuity at the discount rate, d, which pays this contribution for the investment horizon, $\frac{1}{d}\left[1 - \left(\frac{1}{1+d}\right)^T\right]$. An annuity is a financial contract that pays the same amount each year for a fixed number of years given a discount rate d. In the calculations, we use an investment horizon of 100 y. Adding additional years does not have a significant impact on the valuation in Eq. **9** because the discount rate lowers the valuation over longer investment horizons. The second part of the contribution from the future generation is the change in population from the initial size, $[P(g) - P(0)]$, for t_e years resulting in the increase in AGC and r multiplied by the price of carbon credits. This third contribution in Eq. **10** is multiplied by the present value of an annuity, which pays this contribution for t_e years, $\frac{1}{d}\left[1 - \left(\frac{1}{1+d}\right)^{t_e}\right]$. Generation g contributes from time g for t_e years into the future, so we must discount this benefit by $\left(\frac{1}{1+d}\right)^g$ to determine the present value of generation g in Eq. **10**. Consequently, the present value of each generation g's contribution to carbon capture in Eq. **10** is added in the last term of Eq. **9** for each generation 1 to T, which is denoted $\sum_{g=1}^{T} V_g$. This leads to Eq. **9**, which adds together the present value of the three components of the contributions of current and future generations of elephants. The total value of the elephants is equal to $V = \ V_1 + \ V_2$ following Eqs. **5** and **9**, respectively.

Sensitivity Analysis and CIs. The different parameters used to model changes in AGC as a function of elephant population growth contain some uncertainties and sources of variation. We generate upper and lower bounds for our results through a sensitivity analysis covering a total of 81 different simulations through the combination of the four factors that are associated with an SD or a scenario. These four factors, described in detail in the previous sections, are contribution of elephants to AGC growth, elephant population growth associated with interannual variability, elephant population growth associated with conservation scenarios, and forest regeneration rate (i.e., tree mortality rate). The results of this sensitivity analysis are included in the upper and lower ranges provided in the main results and are visualized in *SI Appendix*. Additionally, we estimated the relative contribution of each factor to the variance of the value of carbon services.

Data Availability. All study data are included in the article and/or supporting information.

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