Small room for compromise between oil palm cultivation and primate conservation in Africa

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Despite growing awareness about its detrimental effects on tropical biodiversity, land conversion to oil palm continues to increase rapidly as a consequence of global demand, profitability, and the income opportunity it offers to producing countries. Although most industrial oil palm plantations are located in Southeast Asia, it is argued that much of their future expansion will occur in Africa. We assessed how this could affect the continent's primates by combining information on oil palm suitability and current land use with primate distribution, diversity, and vulnerability. We also quantified the potential impact of large-scale oil palm cultivation on primates in terms of range loss under different expansion scenarios taking into account future demand, oil palm suitability, human accessibility, carbon stock, and primate vulnerability. We found a high overlap between areas of high oil palm suitability and areas of high conservation priority for primates. Overall, we found only a few small areas where oil palm could be cultivated in Africa with a low impact on primates (3.3 Mha, including all areas suitable for oil palm). These results warn that, consistent with the dramatic effects of palm oil cultivation on biodiversity in Southeast Asia, reconciling a large-scale development of oil palm in Africa with primate conservation will be a great challenge.

oil palm | primate | vulnerability | biodiversity | biofuel

Land conversion for agriculture is a primary threat to biodiversity (1), resulting in contracted species distributions with fragmented, often isolated populations (2, 3). Currently, 38.5% of global terrestrial area is dedicated to agriculture (4, 5), and this percentage is expected to increase, driven by wealthier economies and a growing global population (3). Forecasting where land use changes could potentially affect biodiversity can inform the development of guidelines to mitigate negative impacts of future agricultural expansions (6, 7).

Amongst emerging crops, large-scale cultivation of oil palm (*Elaeis spp.*) constitutes a major cause of concern for biodiversity conservation (8–13), with various studies reporting the dramatic effects this is having on tropical forest ecosystems (14, 15). Oil palm, which is most suited to low-lying tropical ecosystems, is largely cultivated in Indonesia and Malaysia, and supplies about 30% of the world's vegetable oil (15, 16). Now gaining importance as a biofuel source (17), palm oil represents a major economic resource in tropical developing countries (18). It has been argued that future population growth will be paired with a dramatic increase in palm oil demand [more than twice that observed in 2005 by 2050 (16)], and that a considerable amount of future land conversion to cope with this will occur in Africa (8, 14, 19). This calls for studies aimed at predicting how such a scenario could affect African ecosystems, so as to orient policies toward more-sustainable paths. Here we tackle the issue by providing a broad assessment of the expected future impact of oil palm expansion on African primate biodiversity.

The choice of focusing on African primates stems from several aspects. First, primates are a conservation priority. Populations of many primate species are declining due to human activities such as agriculture (including oil palm cultivation), logging, and mining (20–24). African primates are already under threat, with 37% of species in mainland and 87% of species in Madagascar threatened with extinction (22). Second, primates are a good proxy for overall biodiversity. They play an important role as seed dispersers in maintaining the composition of forest ecosystems (22, 25), and their diversity can be correlated to the species richness of other taxonomic groups (26). Third, most of African primate species ranges are relatively well known in comparison with other taxonomic groups, which makes it possible to confidently use them in large-scale analyses (22).

Results and Discussion

We combined information on distribution of all African primate species ($n = 193$) and their threat status at a scale of 10×10 km (see *Materials and Methods*) to obtain a map of cumulative primate vulnerability (Fig. 1*A*), which we compared with a

Significance

Although oil palm cultivation represents an important source of income for many tropical countries, its future expansion is a primary threat to tropical forests and biodiversity. In this context, and especially in regions where industrial palm oil production is still emerging, identifying "areas of compromise," that is, areas with high productivity and low biodiversity importance, could be a unique opportunity to reconcile conservation and economic growth. We applied this approach to Africa, by combining data on oil palm suitability with primate distribution, diversity, and vulnerability. We found that such areas of compromise are very rare throughout the continent (0.13 Mha), and that large-scale expansion of oil palm cultivation in Africa will have unavoidable, negative effects on primates.

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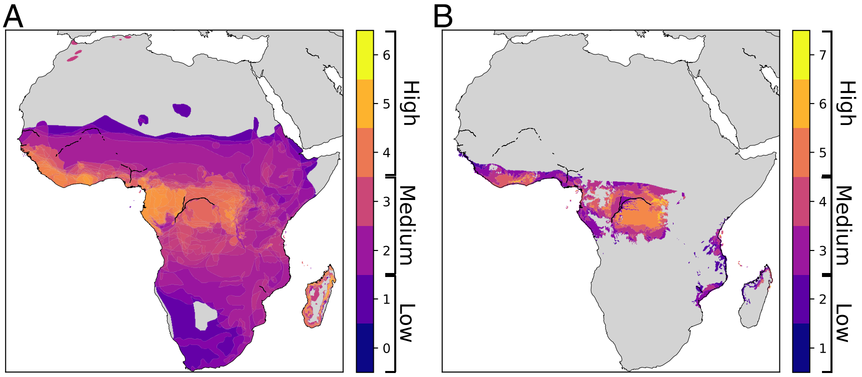

Fig. 1. (*A*) Cumulative primate vulnerability and (*B*) oil palm suitability mapped at 10 × 10-km resolution. Cumulative primate vulnerability was obtained by converting IUCN threatened status of each primate species to a numeric value (see *Materials and Methods* for details), and by summing up the vulnerability values of all species present in each 100-km^2 cell (see also *SI Appendix*, Fig. S2). Oil palm suitability was obtained from The International Institute for Applied Systems and The Food and Agriculture Organization of the United Nations Global Agro-Ecological Zones database (27). We used the map corresponding to a rainfed-only model, based on baseline climate, and under an intermediate-level inputs/improved management assumption (see ref. 27 for details). Suitability categories from 1 to 7 indicate attainable yields larger than 0%, 5%, 25%, 40%, 55%, 70%, and 85%.

map of oil palm suitability in Africa (Fig. 1*B*). The two maps revealed striking similarities in distribution patterns across sub-Saharan Africa, with areas of high vulnerability for primates and oil palm suitability largely overlapping in equatorial and forested regions in West and Central Africa. Oil palm suitability and primate vulnerability were significantly correlated (*SI Appendix*, Fig. S1; Spearman's rank correlation coefficient = 0.29; P value $< 2.2\text{e-}16$; correlation was evaluated only for the 100-km^2 cells with at least minimum suitability to oil palm cultivation, to avoid inflation due to the large extent of desert areas where both oil palm suitability and primate diversity are null; including such areas led to a correlation coefficient of 0.997). We quantified the overlap between areas of oil palm suitability and primate vulnerability focusing on nine different categories obtained by combining three levels of oil palm suitability (low, medium, and high) and three levels of primate vulnerability (low, medium, and high) (Fig. 1). We excluded protected areas and lands falling into one of the following categories: permanent and temporary water bodies, cropland, urban, and bare or sparse vegetation; and the land that has already been assigned a concession for growing oil palm (see *Materials and Methods*).

Over the African continent (about 3,037 Mha), under rainfed practices and intermediate input model for cultivating oil palm, 2.8% of the land (84 Mha) has a low suitability to grow oil palm (ranging from very low to less than moderate suitability), 4.6% (139 Mha) has a medium suitability, and only 1.6% (50 Mha) has a high suitability. The remaining 91.0% of land is unsuitable for oil palm cultivation (Fig. 1*B*). Over the entire Africa, we identified only a few, very small areas (for a total of 0.13 Mha) with high oil palm suitability and low primate vulnerability (Fig. 2). When considering all of the area suitable for oil palm with low primate vulnerability, this number only reaches 3.3 Mha (Fig. 2), which highlights how reconciling oil palm development with primate conservation in Africa will be challenging. These results are robust to the choice of the input model for cultivating oil palm (intermediate input model we focused on, low input subsistence-based model, or high input market-oriented model (Fig. 3). Notably, most of these areas of compromise are located in Madagascar where, however, due to the exceptional endemism (>80%) across most of the taxonomic groups (28), focusing on primates provides only a partial picture of biodiversity and conservation value.

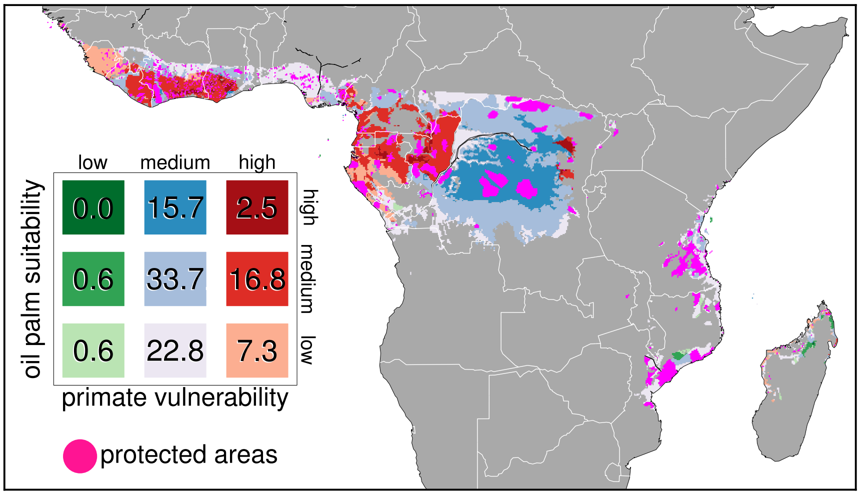

Fig. 2. Spatial overlap between oil palm suitability and primate vulnerability, mapped at 100-km^2 resolution. Numbers in the legend indicate the proportion of each class relative to the total suitable land. For areas (in megahectares) corresponding to each category, see Fig. 3.

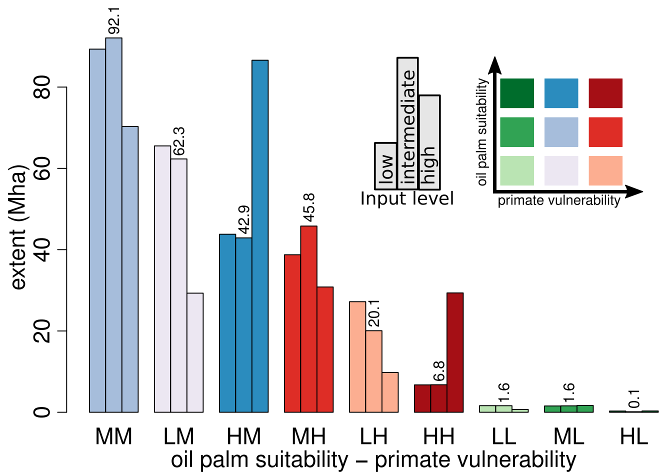

Fig. 3. Differences in the extent (in megahectares) of the nine oil palm suitability/primate vulnerability categories (L, low; M, medium; H, high) between the intermediate input scenario we focused on (central bars) and either a low input (subsistence based and not necessarily market-oriented, left bars) or a high input (mainly market-oriented, right bars) one (see ref. 27 for details). Numbers above bars indicate the extent (in megahectares) of the different categories in the intermediate input scenario.

From the results of previous studies (5, 16, 17), we have estimated (see *Materials and Methods*) that 53 Mha of additional land (44 Mha for edible palm oil and 9 Mha for biofuel) would have to be converted to oil palm plantations to meet the future demand in palm oil in 2050, in comparison with the 20 Mha of palm oil plantations already existing in 2015. If we consider all areas suitable to oil palm with low primate vulnerability, our results indicate that only 6.2% of this area (corresponding to 3.3 Mha) could be available in Africa with limited conservation concern. Such a percentage drops to 0.2% (corresponding to 0.13 Mha) when focusing only on areas of compromise defined by low primate vulnerability and high oil palm suitability.

A potential strategy to mitigate detrimental effects of oil palm development on primate diversity would be to identify alternative trajectories of agricultural expansion based on "smart" criteria delaying, as much as possible, primate range loss. The real world applicability of such criteria is not straightforward, because the areas where agricultural expansion would have the least effect on primate diversity are often the least suitable for oil palm cultivation, as shown by our main results. Intuitively, this implies that an expansion trajectory that minimizes impacts on biodiversity might be much less profitable (and hence less likely to happen) than a trajectory based on yield maximization and/or production cost reduction. To explore this issue, we compared two income-driven oil palm expansion scenarios, based on either suitability (areas more suitable to oil palm are converted first) or accessibility (areas more accessible are converted first) (29), against two conservation-driven scenarios based on either minimizing CO_2 emissions (30) (areas with low carbon stocks are converted first) (31) or impacts on primates (areas with low primate vulnerability, measured as in Fig. 1*A*, are converted first). This approach is conceptually similar to that used by Koh and Ghazoul (32) to model oil palm expansion in Indonesia by 2020, with the main difference that our conservation-driven scenarios account explicitly for primate species vulnerability in addition to carbon stocks.

To assign boundaries and reference points to scenarios of land conversion, we referred to the figures detailed above, and focused on four different estimates for future oil palm demand (in 2050), namely, demand for edible use only, assuming that 50% of oil palm expansion will happen in Africa (22 Mha); combined demand for edible use and biofuel, assuming that 50% of oil palm expansion will happen in Africa (26.5 Mha); demand for edible use only, assuming that 100% of oil palm expansion will happen in Africa (44 Mha); and combined demand for edible use and biofuel, assuming that 100% of oil palm expansion will happen in Africa (53 Mha).

The scenario maximizing suitability led to the highest cumulative loss of primate habitat (i.e., the sum of range reduction for all primate species) at any step of land conversion to oil palm (Fig. 4*A*). This result stems naturally from the high overlap between oil palm suitability and primate vulnerability (Fig. 2). The accessibility scenario led to a lower primate habitat loss, slightly less detrimental to primate range than a scenario of random land conversion. A possible explanation for this pattern is that accessible lands are likely to be more degraded (33) and less suitable for hosting a high number of primate species than remote areas. The

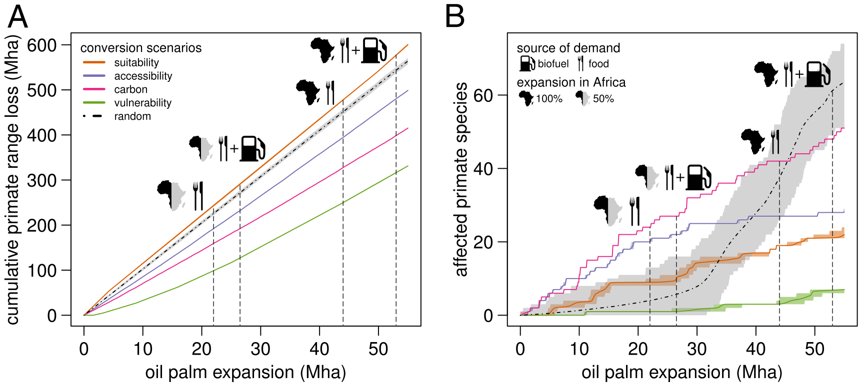

Fig. 4. Comparing production-driven and conservation-driven oil palm expansion scenarios. We computed (*A*) the cumulative range loss (in megahectares) for all primate species and (*B*) the cumulative number of primate species expected to lose more than 10% of their range, under different oil palm expansion scenarios where land is converted (*i*) in decreasing order of oil palm suitability (as in Fig. 1*B*); (*ii*) in decreasing order of accessibility (blue lines); (*iii*) in decreasing order of carbon stock (magenta lines); and (*iv*) in decreasing order of cumulative primate vulnerability (as in Fig. 1*B*) (gold lines). The *x* axis quantifies oil palm expansion in terms of area. Solid lines represent the average values obtained in 1,000 simulations, while the shaded areas represent the minimum and maximum values (in most cases, those are hardly visible, since all simulations produced very similar results). An additional scenario (dash-dotted black lines) with random expansion of oil palm is also included for reference purposes. Vertical dashed lines indicate different estimates of the land required to cope with future oil palm demand (in 2050), either considering or not the demand for palm oil destined to biofuel production, and under the alternative, simplified assumptions that either 50% or 100% of the future expansion will happen in Africa.

two conservation-driven scenarios showed similar trajectories, and led to the lowest primate range losses of all scenarios. This result suggests that carbon stocks are correlated with primate species richness (34), likely due to primates' high dependence on forest habitat (35).

All four scenarios showed distinctive effects on the cumulative number of primate species "affected" by land conversion. We conservatively considered a species affected if expected to lose at least 10% of its current range to land conversion (Fig. 4*B*). While the cumulative loss of habitat provides an overall view on the potential impact of oil palm expansion on African primates, this second measure assesses species-specific effects, being dependent on the extent and location of individual primate ranges. The scenario based on carbon stocks depicted the worst trajectory, with a higher number of species affected than in the other scenarios throughout most of the land conversion process, surpassed only by the random scenario toward the end of the simulation. In the accessibility scenario, a large number of species (similar to that of the carbon stock scenario) was affected at the initial stages of conversion (Fig. 4*B*), with the trend becoming less dramatic at latter stages. These counterintuitive results suggest that many areas suitable to oil palm near human-populated centers (hence highly accessible and with poor carbon stocks) host small-ranged, vulnerable primate species, and that their conversion can therefore have a strong detrimental effect on primate conservation. By contrast, the primate vulnerability scenario showed the best trajectory (i.e., least affecting primate ranges) at any stage of land conversion. In this scenario, the number of species significantly affected by oil palm expansion can be kept relatively low even assuming that all future oil palm expansion will happen in Africa (Fig. 4*B*). This seems to suggest the existence of considerable room for compromise. Nevertheless, such compromise is negated by the fairly linear trends observed in Fig. 4*A*, which reveals how, even in the scenario driven by primate vulnerability, at any stage of oil palm expansion, for every 1,000 ha of land conversion, on average, more than five primate species will lose 1,000 ha of range land. Such a scenario, however, has much less impact on primates than an expansion scenario based oil palm suitability, for which the average number of primate species losing 1,000 ha for each 1,000 ha of converted land rises to 11 (see also *SI Appendix*, Table S1). However, the expansion trajectory prioritizing primate conservation for primate vulnerability would result in the cultivation of oil palm in areas with medium to low suitability (Fig. 1).

More-complex scenarios combining the previous criteria in different hierarchical order led to equivalent results (*SI Appendix*, Figs. S3 and S4). A scenario in which we tried to synthesize profit and conservation targets into a single optimization criterion of land conversion (see *Materials and Methods* for details) led to an intermediate impact on primates, with trajectories lying in between those depicted by the suitability and the vulnerability scenarios (*SI Appendix*, Fig. S5). This reinforces the idea that, even with a smart land management plan for oil palm expansion, consequences on African primates will be significant.

Conclusions

The substantial lack of land where oil palm can be grown without negatively affecting habitat of African primates (3.3 Mha at the scale of our study, if we include all areas with at least minimum suitability to grow oil palm; 0.13 Mha if we focus only on areas of high oil palm suitability) highlights how reconciling future oil palm development and primate conservation in Africa will be very challenging. Furthermore, considering the positive association between primate diversity and overall species richness [particularly that of forest-dependent frugivores and insectivores (26)], our worrisome results might extend to African biodiversity in general. These findings are reinforced by our scenario simulations. If projections materialize, with global demand of oil palm for alimentary use doubling over the period 2005–2050 (16), the effects on primate diversity could be dramatic, possibly leading to over 400 Mha of cumulative habitat loss and to more than 40 species severely affected in the worst-case scenario. Noteworthy is that the magnitude of those effects is significantly increased by accounting also for the estimated future demand for palm oil for biofuel (with the cumulative range loss and the number of affected primates rising to almost 600 Mha and 60 species, respectively). This highlights how future policies about transport emission will play a leading role in determining the fate of African biodiversity, especially considering that we have based our analyses on very conservative projections for future demand of oil palm for biodiesel. Less conservative estimates predict that coping with demand for biofuel in 2050 would require a conversion of land to oil palm cultivation threefold (36) to almost 10-fold (16) the one we assumed in our simulations [9 Mha (17)].

Adopting conservation-driven criteria of land conversion based on primate vulnerability would be ideally key to minimize the species-specific impact of oil palm expansion, by limiting the number of primate species expected to lose significant fractions of their range (Fig. 4*B*). However, the practical applicability of these criteria is put in question both by their lesser profitability compared with alternative (less sustainable) expansion trajectories accounting, for example, for land suitability and/or accessibility and by the complexity of political and economic factors controlling the processes of land conversion and agricultural expansion in the real world. Paradoxically, such complexity would likely lead to trajectories depicting the effects of oil palm expansion on African primates not too distant from those produced by the random land conversion criterion we took as a frame of reference in our simulations.

In this context, achieving success in biodiversity conservation will mainly depend on realistic mitigation strategies. Among them, an important one could be yield intensification through the adoption of high-quality seeds and the advancement of breeding technologies, which might sensibly reduce the amount of land needed to cope with the increasing demand (3, 6, 19, 37). Policy initiatives at both national and international levels, as well as voluntary initiatives from producing companies, have also the potential to mitigate large-scale deforestation (7). Much of the oil palm industry is striving to meet the progressive socioenvironmental regulation set forth by the Round Table on Sustainable Palm Oil (38), but there is still a long way to go (39). Recent examples show that the certification, despite not being that successful in limiting fire or peatland clearance, can significantly reduce deforestation in participating plantations. However, such encouraging results could be partially biased by the fact that, to date, most adopters have been old plantations having little forest remaining (40).

Retailer-led initiatives could be important steps to tackle the problem at its roots, by modifying consumption patterns to reduce global demand for palm oil. Achieving this ultimate goal, however, would require additional actions. Among them, increasing consumers' awareness of the environmental consequences of their daily choices is a promising one, having already created momentum for change (41). We hope that our findings will help keep the momentum going.

Materials and Methods

Range data (georeferenced polygons) for all African primate species (n = 193) were obtained from the International Union of Conservation of Nature (IUCN) dataset "Terrestrial Mammals" (42) and rasterized on a regular 10 × 10-km grid in Africa Albers Equal Area Conic projection. As a criterion for rasterization, primate occurrences were attributed only to 10 × 10-km cells whose center was included within the corresponding primate polygon(s). This choice (more conservative than that of attributing occurrences to all cells intersecting a primate's range) led to the exclusion of seven very small-ranged species from the IUCN dataset (namely *Cheirogaleus minusculus*, *Cheirogaleus sibreei*, *Lepilemur jamesorum*, *Microcebus gerpi*, *Microcebus mamiratra*, *Microcebus marohita*, and *Propithecus perrieri*). The rest of the analyses focused, therefore, on the remaining 186 species.

We used this 10 × 10-km grid as a reference for all of our analyses. Oil palm suitability data layers (at a resolution of 5 arc minutes, i.e., ∼10 km at the equator) were obtained from The International Institute for Applied Systems and The Food and Agriculture Organization of the United Nations Global Agro-Ecological Zones database (43), and harmonized to the 100-km^2 grid using a nearest-neighborhood algorithm.

We used the map corresponding to a rainfed, intermediate-level inputs/improved management model as the most representative of the current global oil palm agricultural practices (14). Under the intermediate input scenario, the farming system is partly market-oriented, with production based on improved varieties, and moderate levels of mechanization, fertilization, and pest control (27). We renumbered suitability categories from 1 (low suitability) to 7 (high suitability), to indicate attainable yields respectively larger than 0%, 5%, 25%, 40%, 55%, 70%, and 85%.

Then, we generated a map of cumulative primate vulnerability. For this, we first converted the IUCN threat status of each species into a numerical value using a geometric progression (44), such as LC = 2, NT = 4, VU = 8, EN = 16, and CR = 32. We conservatively set the category DD (i.e., data deficient) to 2, to retain the species' contribution to diversity without overestimating its vulnerability. We summed the converted threat values of all species having a range intersecting the target 10-km^2 cell in our reference grid. Finally, we computed vulnerability for each cell as the natural logarithm of this sum plus 1. This measure offers a good compromise to focusing either on species richness or individual species vulnerability: A locality will be considered of highest primate vulnerability only when rich in primate species of high average vulnerability. However, high values of cumulative vulnerability will be attributed also to areas having either very high richness or very high average vulnerability (*SI Appendix*, Fig. S2).

We excluded protected areas and all areas falling in nonnatural habitat from both the oil palm suitability and the vulnerability maps. Protected areas where obtained (in the form of georeferenced polygons) from the World Database on Protected Areas (45) and rasterized on the 100-km^2 reference grid. To identify nonnatural habitats, we used the Copernicus Global Land Monitoring Service's African land cover map that is based on Project for On-Board Autonomy-Vegetation imagery for 2015 (46). The Copernicus land cover map has an original resolution of 100 m and was resampled on the 100-km^2 grid using a mode algorithm. We considered as nonnatural habitats all of the areas falling in one of the following categories: permanent and temporary water bodies, cropland, urban, bare or sparse vegetation. In addition, we conservatively excluded current "oil palm concessions" from areas of potential expansion, i.e., areas already allocated for industrial-scale oil palm plantations, using data from Global Forest Watch (47), also rasterized on the 100-km^2 grid.

Excluding nonnatural habitats from primate ranges permitted us to sensibly reduce the well-known problem of overestimation of species' areas of occupancy associated with IUCN range data (48). We report, in *SI Appendix*, Fig. S6, some examples of how the level of detail of IUCN ranges is improved by the application of the land use filter, while, in *SI Appendix*, Table S2, we report the descriptive statistics of the comparison between the original IUCN ranges of all African primates and their "filtered" counterparts. We also explored potential issues stemming from limitations of IUCN data possibly affecting our cumulative vulnerability index. For this, we performed a sensitivity analysis where we progressively removed an increasing percentage of area of occupancy (by randomly selecting cells in the 100-km^2 grid) from all primate species. The degree of removal varied from 1 to 50%, with incremental steps of 1%. At each removal step, we recomputed the cumulative primate vulnerability within the area focus of our analyses (that is, all of the African land with at least minimum suitability to growing oil palm) and then we computed the percentage of 100-km^2 cells experiencing a shift in their vulnerability class (Fig. 1*A*) in respect to that obtained using the full IUCN ranges. In *SI Appendix*, Fig. S7, we show how large reductions in all primate ranges have a comparatively small effect on our categorization, providing evidence of a high robustness of the cumulative vulnerability metric. The filtering step led to the exclusion of another small-ranged species, *Lepilemur tymerlachsoni*.

We overlapped the oil palm suitability map with the primate vulnerability map, assigning each 100-km^2 cell to one of nine different categories obtained from combining three levels of increasing primate vulnerability (lower than 2; equal to or higher than 2 and lower than 4; equal to or higher than 4) with three levels of increasing oil palm suitability (lower than 3; equal to or higher than 3 and lower than 5; equal to or higher than 5). For each combination of primate vulnerability and oil palm suitability, we also computed the total area in square kilometers.

To explore the sensitivity of our analyses to the choice of the input level, we replicated the above analyses using oil palm suitability maps for low and high input level models. The low input model assumes that the farming system is mainly subsistence-based and not necessarily market-oriented, with production based on traditional cultivars, labor-intensive techniques, and no use of additional nutrients and/or pesticides. By contrast, the high input model assumes that the farming system is mainly market-oriented, with a fully mechanized production relying on high-yielding varieties, nutrient enrichment, and chemical pest control (27).

We computed the additional land area that would have to be converted to oil palm in the period 2015–2050 to meet future demand for palm oil. For edible palm oil (16), the additional demand in 2050 should be for +53 Mha with respect to 2005, where oil palm covered an area of 11 Mh. In 2015, ref. 5 reports an area of 20 Mha for oil palm. This would lead to an increase of +44 Mha of oil palm on the period 2015–2050. For biofuel, +47.9 Mt of additional vegetable oil would be necessary with respect to 2014 (hence +46.6 Mt with respect to 2015) to meet the global demand in 2050 (17). Assuming that oil palm will retain the same market share as 2014 for vegetable oils used for biofuel (77%), the additional demand for palm oil in 2050 will be +36.1 Mt with respect to 2015. Considering an average yield of 4 t/ha (16), this corresponds to 9 Mha of land. This last number is very conservative compared with other estimates from other studies [+30 Mha (36) or +63 Mha to 82 Mha (16)]. Consequently, a minimum area of +53 Mha of land would have to be converted to oil palm in the period 2015–2050 to meet global demand for palm oil in 2050 for both edible consumption and biofuel.

Finally, we explored the effects of different scenarios of oil palm expansion on African primates. In each scenario, we simulated the progressive conversion (one 100-km^2 grid cell at a time) of natural land to oil palm plantation, until 55 Mha of land with a minimum oil palm suitability (≥ 1) had been converted. At each step, we kept track of the cumulative converted area, of the corresponding primate range loss (averaged over all species), and of the cumulative number of primate species expected to lose more than 10% of their range. We assumed the 10% threshold as an estimator of significant range loss effect. In the various scenarios, we explored different sequences of land conversion driven by different criteria.

We considered two income-driven scenarios based on oil palm suitability and land accessibility. We first simulated a scenario where expansion was driven by oil palm suitability, and where cells with higher suitability were converted first (as in Fig. 1*B*). Cells within the same suitability category were converted in random order. We simulated a second scenario taking into account human accessibility. Data on accessibility, measured in terms of minimum travel time to the closest major city, were obtained at a resolution of ∼100 km^2 from ref. 29, and resampled on our 100-km^2 reference grid using a bilinear interpolation. In this second scenario, cells with higher accessibility were converted first. Cells having identical values of accessibility were converted in random order.

We compared these two first income-driven scenarios with two additional conservation-driven scenarios. We thus simulated a third expansion scenario minimizing the impact on available carbon stocks. We obtained data on carbon stock from the 100-km^2 global map by ref. 31. The carbon data were resampled on our 100-km^2 reference grid using a bilinear interpolation. For this scenario, cells with lower carbon stock were converted first. Cells having identical values of carbon stock were converted in random order. We simulated a fourth scenario minimizing the impact on primate species. In this fourth scenario, cells with lower primate vulnerability (Fig. 1*A*) were converted first. Finally, these four scenarios were compared with a random scenario where land cells were converted to oil palm plantations at random. Because simulations included random steps, they were replicated 1,000 times for each scenario, and the results were averaged over all of the replicates.

We also explored more-complex scenarios combining the different income and conservation criteria. We first combined the suitability, accessibility, and carbon criteria in all possible hierarchical orders to see if this had an effect on the results. We also identified a scenario integrating all criteria (maximizing accessibility A and oil palm suitability S, while minimizing carbon stocks C and primate vulnerability V). To do so, we first standardized A, S, C, and V between 0 and 1. Then, we computed a spatial optimization index I at 1-km^2 resolution on our reference grid, as $I = A + S + (1 - C) + (1 - V)$. In the simulations, cells with the highest optimization index were the first to be converted to oil palm. Cells with identical I values were randomized in random order. As for the other scenarios, we

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ran conversion simulations 1,000 times, and then we averaged the results over all of the replicates.

To ensure full reproducibility and transparency of our research, we provide all of the data and scripts used in our analysis (49).

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