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Implications of zero-deforestation palm oil for tropical grassy and dry forest biodiversity

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Abstract

Many companies have made zero-deforestation commitments (ZDCs) to reduce carbon emissions and biodiversity losses linked to tropical commodities. However, ZDCs conserve areas primarily based on tree cover and aboveground carbon, potentially leading to the unintended consequence that agricultural expansion could be encouraged in biomes outside tropical rainforest, which also support important biodiversity. We examine locations suitable for zero-deforestation expansion of commercial oil palm, which is increasingly expanding outside the tropical rainforest biome, by generating empirical models of global suitability for rainfed and irrigated oil palm. We find that tropical grassy and dry forest biomes contain >50% of the total area of land climatically-suitable for rainfed oil palm expansion in compliance with ZDCs (following the High Carbon Stock Approach; in locations outside urban areas and cropland), and that irrigation could double the area suitable for expansion in these biomes. Within these biomes, ZDCs fail to protect areas of high vertebrate richness from oil palm expansion. To prevent unintended consequences of ZDCs and minimise the environmental impacts of oil palm expansion, policies and governance for sustainable development and conservation must expand focus from rainforests to all tropical biomes.

Main article

Commercial agriculture drives one-quarter of tropical deforestation[1], causing substantial biodiversity loss[2] and carbon emissions[3]. Many companies have, therefore, made voluntary 'zero-deforestation commitments' (ZDCs) for tropical commodity supply chains[4,5]. ZDC-compliant commodities cannot be cultivated on recently-forested land, and ZDCs could effectively protect tropical rainforest from encroachment[6] if uptake of the commitments is widespread[7]. However, ZDCs could then displace agricultural expansion to other biomes: primarily tropical grassy biomes (grasslands, savannas and shrublands[8]) and dry forests (closed-canopy forests with highly seasonal rainfall[9])[10,11]. These habitats often lack protection, despite supporting distinct biota and potentially high carbon stocks[9,12–14]. Without robust guidance to identify and protect their biodiversity, agricultural expansion into these biomes in compliance with ZDCs could undermine benefits of ZDCs for global biodiversity and climate change mitigation.

Palm oil is a key deforestation-risk commodity[15], and ZDCs cover two-thirds of global palm oil production volume[4]. Palm oil ZDCs are chiefly implemented through Roundtable on Sustainable Palm Oil (RSPO) certification[4], which requires expansion to follow the combined High Conservation Value-High Carbon Stock Approach (HCV-HCSA) to determine habitat for protection[16], a methodology also applied to other commodities[17]. The HCV-HCSA conserves aboveground carbon and woody vegetation structure ('HCS'); biodiversity, ecosystem services and social/cultural values ('HCVs'); peat soils; and requires Free, Prior and Informed Consent before encroaching on community land[17,18]. However, national-level HCV guidance was originally developed for forestry, and the combined HCV-HCSA was largely developed in response to oil palm-driven deforestation in Southeast Asia[15], so guidance for other habitats is currently limited. Tropical grassy and dry forest biomes differ from rainforest in structure and function[9,12,13], which current HCV-HCSA guidance does not address, leading to inconsistent identification of their biodiversity values (Supplementary Information 1). Latin America and Africa support extensive grassy and dry forest biomes, where commercial oil palm is expanding rapidly[15,19–21], with irrigation in dry locations[22]. In Latin America, palm oil production has increased by 60% since 2011[23], and 80% of expansion prior to 2014 replaced cropland, pasture and savanna[19]. The largest RSPO-certified plantation in Africa was developed entirely in savanna[24], and sites of new certified plantations are frequently selected for their grassy habitat (Supplementary Information 1). Thus, we urgently need to understand the potential for zero-deforestation oil palm expansion in biomes outside tropical rainforest, and consequent biodiversity loss.

Here, we generate new maps of climatically-suitable areas for rainfed and irrigated oil palm expansion, based on locations of existing plantations[25] (an alternative approach to 'agro-ecological'[26] or crop growth[27] models), and accounting for water availability for irrigation (unlike existing models[27]). We assume that ZDCs protect all locations with ≥35 Mg ha^{-1} aboveground carbon and ≥30% canopy closure, and/or peat soils from expansion, following the HCSA[17]. We find that tropical grassy biomes and dry forests contain nearly 200 Mha climatically-suitable for rainfed or irrigated oil palm expansion in compliance with ZDCs, including locations of high vertebrate richness and overlapping with the ranges of 10% of all threatened vertebrate species. Thus, to minimise biodiversity loss, comprehensive guidelines to identify and manage 'high conservation values' specific to tropical grassy and dry forest biomes must be developed.

Results

Potential areas for rainfed oil palm expansion under ZDCs

Globally, we estimate that a total of 1.2 Bha of non-cultivated land (including primary vegetation, secondary vegetation, and both current and abandoned pasture, but excluding current cropland, tree plantations and urban areas), outside IUCN class I and II protected areas, are climatically-suitable for rainfed oil palm expansion (Fig. 1). If widely and effectively implemented, ZDCs would protect up to 86% of this 1.2 Bha, following our scenario of 'greater habitat protection' according to the HCSA (based on canopy closure and aboveground carbon, although in practice, protection depends on local context: see Methods). Thus, 167 Mha of climatically-suitable, non-cultivated land remains potentially available for expansion in compliance with ZDCs, which is six-fold greater than the current planted area of 27 Mha.

Current guidance for ZDCs protects a considerably higher percentage of the areas climatically-suitable for expansion in the moist forest biome (rainforest; 93%) than in grassy biomes (43%) or dry forest (51%) (Fig. 2a), because many areas of grassy and dry forest biomes have insufficient aboveground carbon and canopy closure to qualify for protection (Extended Data Fig. 1). Consequently, 95 Mha of the 167 Mha potentially available for expansion under ZDCs are in tropical grassy and dry forest biomes (~four-fold greater than the current planted area), the majority (87%) in the Neotropics and Afrotropics (Fig. 1). Just under half (69 Mha) of the potential area for expansion under ZDCs is in the tropical moist forest biome, which is likely to be highly degraded habitat, such as intensively-managed pasture, because of its low carbon stocks. The 95 Mha of climatically-suitable non-cultivated land in grassy and dry forest biomes includes both degraded pasture and also ancient habitats supporting high biodiversity, which cannot be distinguished by remote sensing, due to superficial similarity between the vegetation types. However, regional analyses in Brazil and Colombia suggest that a greater proportion of moist forest biome has been converted to pasture than other biomes (Supplementary Information 2). Consequently, our findings highlight the potential for zero-deforestation oil palm expansion into ancient, high-biodiversity grassy biome and dry forest habitats, emphasizing the need for sustainable development guidelines for identification and protection of biodiversity specific to these biomes, particularly in the Afrotropics and Neotropics.

Our estimates of the total area suitable for zero-deforestation expansion are sensitive to the thresholding of our models of suitability for cultivation (70-375 Mha for three thresholds tested), to the choice of suitability model (223 Mha according to an existing agro-ecological model[26], of which 110 Mha overlap with our model; Extended Data Fig. 2), and to habitat protection thresholds under ZDCs (358 Mha under a scenario of weaker habitat protection, compared to 167 Mha under greater habitat protection which we present in the Main Article). Nevertheless, this variation does not affect our conclusion that tropical grassy and dry forest biomes, especially in the Neotropics and Afrotropics, contain the largest areas suitable for expansion under ZDCs (Supplementary Information 3).

Potential for ecoregion-level habitat loss

If widespread, oil palm expansion under ZDCs could drive loss of unique habitats and biodiversity in tropical grassy and dry forest biomes, because large areas of certain individual ecoregions, which represent distinct habitats within biomes, are suitable for expansion. The percentage of individual ecoregions that is suitable for rainfed expansion under ZDCs is greater for ecoregions in the tropical dry forest biome (median 23% of ecoregions' remaining non-cultivated land is suitable for expansion) and grassy biomes (16%) than in the moist forest biome (6%) (Fig. 2b). Biodiversity of ecoregions such as the Llanos in Colombia (~80% of remaining non-cultivated land is suitable for expansion under ZDCs), Beni savanna in northern Bolivia (~70%), and Guinean savanna in West Africa (~53%), is particularly vulnerable (Table 1). However, these areas of non-cultivated land include both intact habitats and some degraded land, where oil palm could expand with lower immediate environmental costs (see Discussion). Our regional analyses suggest that extensive suitable areas in some ecoregions (particularly in the moist and dry forest biomes) have been converted to intensively-managed pasture, but if we assume that this pasture is unavailable for expansion, our estimates of the percentage of remaining untransformed habitat (outside cropland, tree plantations, urban areas, and here pasture too) that is suitable for expansion appear robust (Supplementary Table 3, Supplementary Fig. 2).

Yield in areas suitable for oil palm expansion under ZDCs

Overall, 97% of locations suitable for expansion under ZDCs are likely to have low yields under rainfed, high-fertiliser input cultivation (~10 $tha^{-1}yr^{-1}$ fresh fruit bunches; inter-quartile range 6.2-16.5 $tha^{-1}yr^{-1}$; Fig. 3a), based on recent yields in locations that we estimate as climatically-suitable (see Methods). These low yields of ~10 $t ha^{-1} yr^{-1}$ are roughly half of yields in existing industrial plantations (median 21 $t ha^{-1} yr^{-1}$), but are nevertheless likely to be viable for cultivation (see Discussion), although we are unable to account for net profitability. Low yields particularly apply to potential ZDC expansion in grassy biomes (in which 99.8% of climatically-suitable locations for expansion have low expected yield) and dry forests (99.1%), but also tropical moist forests (92.2%). Regardless of ZDCs, 87% of locations suitable for expansion have low expected yields overall (Supplementary Fig. 7; agro-ecological suitability model[26] results are similar: Supplementary Fig. 8), possibly because the most suitable locations for oil palm cultivation have already been converted to plantations or cropland (e.g. in Southeast Asia).

Opportunities for improved oil palm yield under irrigation

Our projections of climatically-suitable areas for expansion under ZDCs presented above are based on rainfed cultivation, but under irrigation up to 108 Mha could additionally become suitable (65% greater than rainfed cultivation alone, representing potential for a 10-fold expansion in the current planted area in total; Fig. 3b, Extended Data Figs. 3, 4). We assumed that surplus available water is used to irrigate the crop in dry months, calculated as the difference between monthly renewable water supply from freshwater lakes, rivers and renewable groundwater and current demand (see Methods). Irrigation could thus enable considerably greater expansion than rainfed cultivation alone, particularly in grassy biomes (up to an additional 79 Mha compared with rainfed cultivation) and dry forests (up to an additional 16 Mha; a two-fold increase compared with rainfed cultivation for both of these biomes) in the Neotropics and Afrotropics (Supplementary Information 4). Whilst we expect 97% of areas requiring irrigation to have low yield (Fig. 3b, pale colours), irrigation could improve yields in locations suitable for rainfed expansion, increasing the total climatically-suitable area with medium or high expected yield (17-18 $t ha^{-1} yr^{-1}$ median yield) more than five-fold compared with rainfed cultivation alone (Fig. 3).

Potential threats to vertebrate richness

We estimate that effective implementation of ZDCs would substantially reduce vertebrate (mammal, bird and amphibian) richness loss from oil palm expansion in rainforests, by protecting locations with the highest richness within the moist forest biome, and thus globally, from expansion (Fig. 4a). However, ZDCs fail to protect locations of high vertebrate richness within tropical grassy and dry forest biomes in Latin America and Africa, where the largest areas are suitable for zero-deforestation expansion (Fig. 4a). We estimated richness from vertebrate range maps refined by habitat type, and we estimated richness loss as the number of species that cannot persist in plantations, within 10-km grid-cells. Although this grid-cell resolution is likely to overestimate absolute values of richness, the broad patterns of richness loss among biomes and continents are likely to be robust (Supplementary Information 6). In Africa, where the contrast among biomes is greatest, expansion compliant with ZDCs within the moist forest biome would result in substantially less vertebrate richness loss (median 185 species lost per 10-km grid-cell on conversion to oil palm) than expansion in locations protected by ZDCs (median 224 species lost per 10-km grid-cell). By contrast, within grassy biomes in Africa, expansion under ZDCs would result in greater richness loss (median 200 species lost per 10-km grid-cell) than expansion in locations protected by ZDCs (median 169 species lost per 10-km grid-cell; fig 4a), so ZDCs could exacerbate vertebrate richness loss from oil palm expansion. All estimates of vertebrate richness loss assume that expansion is into intact habitat, and thus actual richness losses would be significantly lower if expansion also occurred in areas already converted to intensively-managed pasture (Supplementary Information 2). However, areas of intensively-managed pasture may not always be available for oil palm expansion (see Discussion), and our estimates of richness loss are robust if we assume that intensively-managed pasture is unavailable (Supplementary Fig. 3). Estimates of richness loss are similar for the agro-ecological suitability model[26], and when including suitability for irrigation (Supplementary Information 5). Thus, if widespread zero-deforestation oil palm expansion takes place, ZDCs could drive considerable biodiversity loss outside the tropical moist forest biome, despite substantially protecting rainforest biodiversity.

Range reduction of IUCN-threatened vertebrates

Under ZDCs, oil palm expansion in all biomes could decrease the range sizes of IUCN-threatened vertebrates, although reductions are generally small. In total, 28% (879 of 3,155 species) of threatened terrestrial vertebrates could undergo range reduction because these species' ranges overlap with potential rainfed expansion areas, and these species cannot persist in plantations (26% of threatened species according to the agro-ecological suitability model[26]). However, only a median 4.3% of species' total global range overlaps with potential rainfed expansion areas (Fig. 4b). When including locations requiring irrigation, 34% of threatened vertebrates (1,071 species) could undergo range reduction from oil palm expansion under ZDCs (Supplementary Fig. 18). As expected, the majority of these threatened species occur in tropical moist forest (817 species under rainfed expansion; 26% of threatened terrestrial vertebrates), although rainfed expansion in grassy biomes and dry forests could reduce the ranges of 189 threatened vertebrates (6% of all threatened vertebrates for both biomes combined; 10% when including locations requiring irrigation). Overall, there are likely opportunities for ongoing expansion under ZDCs without significant negative impacts on threatened vertebrates, provided that sufficient guidance is developed to identify and protect areas supporting such species.

Discussion

Suitable areas for oil palm expansion

We generated new empirical models of suitability for oil palm expansion under rainfed and irrigated conditions. Our rainfed suitability model is broadly similar to existing models that were generated using contrasting methods[26,28], but with slightly reduced area, suggesting that our estimated potential for expansion is conservative. We modelled suitability based on locations of commercial oil palm mills[25], representing areas most climatically similar to those already under commercial cultivation. Our model may therefore have excluded marginal areas that will become increasingly viable for commercial cultivation with the development of new varieties and practices to maintain high yields under climate change[26,28–30]. A few regions are predicted as suitable in our model but not in other models[26,28] (e.g. parts of the Caatinga in northern Brazil, Venezuelan Llanos; Extended Data Fig. 2), probably because we accounted for seasonality of water availability by calculating maximum cumulative water deficit in order to capture water stress experienced by growing oil palms[31] (Supplementary Information 7). Areas that we mapped as suitable for irrigated cultivation alone largely coincide with other models that assumed unlimited water availability[27,28], but are restricted to locations of sufficient surplus available water to remove the critical rainfed water deficit.

Even though we estimated that ZDCs would protect extensive areas, we found considerable potential for expansion under ZDCs. However, we could not account for availability of land (e.g. land ownership), nor exclude areas that should be protected for their biodiversity or local ecosystem service values, which depend on the rigour of local assessments (Supplementary Information 1)[18], suggesting that the actual area available for expansion is much lower than our estimates. Oil palm expansion could also occur in human-modified habitats (existing cropland or tree plantations[17], which we assumed were unavailable, or intensively-managed pasture[19], which we were unable to exclude from our analyses), which would drive less biodiversity loss than in areas of intact habitat (Supplementary Figs. 3, 15), but could in turn displace these land-uses to natural habitat[11,32]. Our main conclusions appear robust (Supplementary Information 2-5), but local information and mapping are needed to assess likely protection under ZDCs and potential impacts of expansion in detail (Supplementary Information 6).

We examine oil palm expansion if ZDCs were widely and effectively implemented. However, increasing numbers of ZDCs[4,5,33] have not necessarily resulted in action to reduce deforestation[5], and the impact of ZDCs has not yet been well-studied[5,34,35]. RSPO certification appears to reduce deforestation[36,37], although net benefits are minimal as deforestation increases concurrently elsewhere[38], and RSPO-certified palm oil has stagnated at ~19% of global production volume[39]. Thus, strong sector-wide regulation is imperative for reducing deforestation globally[33,37,38,40].

Potential for loss of tropical grassy and dry forest biodiversity

If oil palm production continues to expand rapidly[41,42], including under ZDCs, our findings demonstrate the potential for loss of unique biodiversity and habitats in tropical grassy and dry forest biomes in Latin America and Africa[12,43–46]. Widespread implementation of ZDCs would mitigate global biodiversity loss from oil palm expansion overall, by extensively protecting tropical moist forest, but could also drive conversion of distinct grassy biome and dry forest ecoregions[20], and increase expansion in locations of high vertebrate richness within these biomes. Recent soy expansion in the Cerrado has driven substantial habitat loss in a global biodiversity hotspot[47], possibly as an unintended consequence of the moratorium on expansion in the Brazilian Amazon[10,11,48,49], and we highlight the potential for a similar pattern in global oil palm expansion, before widespread conversion of grassy biomes and dry forests has occurred.

We estimate relatively small impacts of zero-deforestation oil palm expansion on IUCN-threatened vertebrates overall, but we have likely underestimated the impacts of expansion on biodiversity (Supplementary Information 6). We have not examined potential loss of plant or invertebrate biodiversity from expansion, yet grassy biomes often support high endemism and richness of these taxa[45], comparable to tropical rainforest in certain ecoregions[44] (e.g. the Cerrado[46]). Moreover, the locations suitable for expansion under ZDCs in the moist forest biome are likely to be highly degraded (and include large areas of intensively-managed pasture: Supplementary Information 2), whereas suitable areas in grassy biomes and dry forests include intact habitat, such as in the Guinea savanna, Northern Congolian Forest-savanna, and Cerrado[50,51] (among other ecoregions). Overall, widespread agricultural expansion under ZDCs could have substantial negative impacts on biodiversity, highlighting the need for robust guidance for sustainable agricultural development in all biomes.

Implications for greenhouse gas emissions

We were not able to quantify potential greenhouse gas emissions from zero-deforestation oil palm expansion in this study, because belowground carbon stocks are poorly understood in across the Tropics, particularly in grassy biomes[12,52], and aboveground carbon stocks are also poorly quantified outside rainforest[12,53]. Existing data suggest that belowground carbon stocks in grassy biomes are highly variable and can exceed those of moist forest[54–56], resulting in substantial carbon emissions upon conversion to cropland[50,55], and upon conversion of degraded pasture to oil palm[57]. Thus, the potential greenhouse gas emissions from conversion of tropical grassy and dry forest biomes to oil palm could be as high as those from rainforest conversion in many locations, but the lack of data on below- and aboveground carbon stocks, and the dynamics of belowground carbon following conversion to oil palm, highlights the need for more research on this topic.

Gaps in current guidance and key recommendations

While tropical conservation efforts have typically focused on rainforests, other biomes are also subject to multiple threats and are less well-protected[9,12,20,54,58–60], with ~50% of tropical dry forests already converted to other land-uses[61]. Therefore, there is an urgent need for policies and governance for sustainable tropical land-use in all biomes. Current guidance (HCV-HCSA and national interpretations[16–18], particularly "Annex 2. Grasslands in HCVs" in [18]) does not recognise important differences between tropical moist forest and grassy and dry forest biomes (e.g. importance of herbaceous vegetation; Supplementary Information 1, Box 1). Many recent oil palm concessions were developed on grassy or savanna habitat to comply with ZDCs, risking that these habitats could become rare through widespread conversion (e.g. savanna in Southern Gabon[24]; Supplementary Information 1), threatening biodiversity before guidance is comprehensive.

Nevertheless, the existing HCV-HCSA provides a framework for implementing comprehensive biodiversity protection in all biomes, like for tropical moist forest[17,18] (Fig. 2), with a current 'policy window' for development of detailed guidance beyond Southeast Asian rainforest. We provide recommendations for such guidance for grassy and dry forest biomes in Box 1. We also recommend that companies extend commitments to 'no conversion of natural habitat', to bolster protection for all biomes and support the development of comprehensive guidance for biodiversity protection. The RSPO should stipulate 'protection of biodiversity in *all biomes*' in its Principles and Criteria (which require new plantings to follow HCV-HCSA guidance[17,18])[16], to encourage rigorous HCV assessments, in line with the biodiversity identification and monitoring for all native vegetation types in the Round Table on Responsible Soy standard[62]. The RSPO should incorporate estimation of below-ground carbon storage of natural vegetation and soils into its greenhouse-gas emissions estimates, which are high in some tropical grassy biomes (and moist forests)[63], although we acknowledge that soil carbon stocks remain poorly understood[12,52], highlighting the need for further research on this topic. RSPO-certified oil palm is increasingly likely to expand in drier areas (Figs. 1, 3, Extended Data Figs. 3, 4), exacerbating water scarcity, particularly under irrigation[64], so detailed guidance for sustainable hydrological development (including irrigation) is also needed.

Sustainably increasing palm oil production

Oil palm expansion on highly-degraded pastures in the Llanos has limited negative impacts on biodiversity, and is carbon neutral six decades after conversion[57,65,66]. However, low-impact expansion in degraded habitat depends both on correct identification of grassy biomes and dry forests[9,12–14] and a better understanding of degradation and intactness, highlighting the urgent need for improved guidance (Box 1). Moreover, conversion of degraded areas prevents their regeneration, hindering progress towards global conservation and climate goals (e.g. Bonn Challenge)[20,67–69]. Therefore, key priorities are to understand and define degradation, and examine the impacts of agricultural expansion in degraded areas, in all biomes and biogeographic regions.

Given the potential negative impacts of ongoing expansion for biodiversity, improving yields of existing plantations could also reduce the environmental impacts of oil palm, through sustainable intensification[70,71]. The low yields we predict (10 $tha^{-1}yr^{-1}$ in most locations) are similar to yields of Southeast Asian smallholders[72]; and oil yields of ~2 $tha^{-1}yr^{-1}$ (assuming a conversion factor of 20%

from fresh fruit bunch yield to crude palm oil[31]), are equivalent to the maximum of other oil crops[27]. Thus, oil palm cultivation may be feasible in these locations. However, yield and economic viability depend on many factors, including costs of labour, seed material, inputs, transportation, and returns from competing land-uses; further research efforts could integrate these with considerations of climatic suitability for expansion. Global productivity could be increased by reducing labour shortages for harvesting[73], by implementing best management practices (potentially including irrigation), and/or planting oil palm varieties with broader climatic tolerances[73,74]. However, increasing yield does not necessarily remove economic incentives for expansion elsewhere[75]. Thus, there is strong need for internationally-coordinated governance to reduce yield gaps, better protect natural habitats, and reduce economic incentives for expansion[76].

Conclusion

Oil palm expansion that is compliant with ZDCs is most likely to occur in tropical grassy and dry forest biomes, where it has the potential to drive substantial habitat and biodiversity loss. New guidance is urgently needed to identify and protect areas of conservation priority in these biomes. Well-governed international policies that recognise and conserve natural habitat types are thus imperative for achieving sustainable tropical agriculture.

Methods

Overview

We mapped suitability for rainfed oil palm using the species distribution model Maxent, incorporating locations of current oil palm cultivation (a global dataset of oil palm mills[25]) and climate data[77], and selecting the best model from a range of permutations. We evaluated our models of climatic suitability for oil palm by comparing our estimates to current global oil palm plantations derived from the 'Spatial Database of Planted Trees'[78]. We mapped suitability for irrigated oil palm by supplementing monthly rainfall with a recent hydrological dataset of monthly surplus available freshwater[79]. We thereby produced new, up-to-date models of climatic suitability for both rainfed and irrigated oil palm. We conducted analyses for a recent agro-ecological model of suitability for rainfed oil palm[26] alongside our new rainfed model, as a sensitivity test. We mapped locations potentially available for oil palm cultivation (locations that have not been transformed to cropland[80,81], urban areas[80,81] or tree plantations[78], subsequently termed 'non-cultivated land'). We then quantified whether these areas would be protected under ZDCs, and identified their biome type, using four further global spatial datasets: aboveground biomass[82,83], canopy closure[84], peatlands[85], and terrestrial ecoregions[20]. To assess the impacts of oil palm expansion on vertebrates, we estimated the potential vertebrate richness of locations we deemed to be climatically-suitable for oil palm, by refining vertebrate range maps[86,87] according to habitat types suitable for each species. We conducted regional sensitivity analyses (for Brazil and Colombia) that explicitly included intensively-managed pasture as a land-use type, to assess whether our inclusion of intensively-managed pasture as 'non-cultivated land' potentially available for oil palm expansion in our global analyses (alongside primary and secondary vegetation) may have led to inaccuracies in our main findings. We ran all models and analyses at 5' grid-cell resolution (~10 km at the Equator), the finest possible from component datasets; where data were provided at finer resolution, we aggregated them before use. We ran all models and analyses of expansion across all tropical regions (between 23.5° N and 23.5° S, except for the regional analyses including intensively-managed pasture, and the refinement of global vertebrate range maps by habitat type), using R version 3.5.2[88] and ArcGIS Pro version 2.2.0.

Current occurrence of oil palm cultivation

To train our species distribution models of oil palm suitability, we used a global dataset of oil palm mills, collected from major palm oil supply chains and therefore representing occurrence of industrial oil palm cultivation[25] (and additionally smallholder cultivation where it is associated with industrial plantations, such as in Southeast Asia). Oil palm fresh fruit bunches require processing soon after harvest[31], so mills are generally adjacent to plantations[78]. We excluded mills in locations likely to be irrigated and thus cultivated under artificially-altered climatic conditions. We used a global dataset of water withdrawal for irrigation in 2014[79] to determine locations of potential irrigation, excluding all mills within 10 km of non-zero water withdrawal for irrigation. Additionally, we excluded mills in regions described as having widespread irrigation of oil palm[89]. Our final dataset for locations of current cultivation of rainfed oil palm therefore comprised N = 1021 oil palm mills occupying separate 5' grid-cells of the climate data. We assumed that each of these mills represented one known 'presence' datapoint for oil palm cultivation.

This dataset of rainfed oil palm occurrence exhibited spatial bias (88.4% of the mills were in Indonesia and Malaysia), that does not reflect the spatial extent of global suitability for oil palm, which includes large areas in all tropical regions, including Latin America and Africa[26,31]. To reduce concurrent spatial bias in our suitability model outputs, we systematically subsampled the mills to one mill per 1°-resolution grid-cell (111 km resolution at the Equator; n = 194 mills, 68.0% in Indonesia and Malaysia)[90], and found that this considerably improved model predictive performance, by reducing the dominance of the climate values at Asian mills in the overall distribution of climate values at mill locations (Supplementary Fig. 20; Supplementary Information 7). In comparison with models trained on the full mill dataset, models for the subsampled mills had consistently higher Boyce Index values and spatial cross-validation performance, indicating that they better predicted current plantations, including in novel spatial regions (see 'SDM evaluation' and Supplementary Information 7).

Climatic predictors of suitability for oil palm

We derived all climatic predictors from WorldClim v.2 global gridded climate data, averaged for 1970-2000, at 5' resolution[77]. We initially selected five climatic predictors known to correlate with oil palm growth and yield[31]: mean annual temperature (°C), minimum temperature of the coldest month (Tmin, °C), mean annual precipitation (mm), an annual moisture index, and maximum water deficit (MWD, mm) (see Supplementary Information 7 for details). Some of these predictors were inter-correlated (Supplementary Table 8), so we ran models with two uncorrelated predictors, Tmin and MWD, which represent the most strongly limiting climatic factors for oil palm growth and yield[31].

We did not include soil parameters as predictors of suitability for oil palm, because oil palm can be cultivated on the majority of tropical soil types, without substantial impacts on yield under appropriate management[31]. Previous estimates suggest that few locations in the tropics have unsuitable soil for oil palm cultivation[26]. However, we removed areas of mangrove from our predictions of climatically-suitable locations for planting (see below), to remove areas of saline soils, which limit oil palm yield[31], as well as to remove unsuitable saline flooded areas. We discuss the limitations of our approach in Supplementary Information 6.

Running species distribution models (SDMs)

SDMs have previously been used to model climatic suitability for crops at large spatial scales[91–93], and Maxent outputs have successfully predicted yield when trained on high-yield locations[93], such as the majority of oil palm mill locations (industrial mills supplying global traders)[25]. We ran SDMs of oil palm suitability using the R package *biomod2*[94], to provide up-to-date models of climatic suitability for oil palm. We used the SDM Maxent, because it is robust to incomplete datasets[95–97], and our oil palm mill locations do not represent all locations suitable for oil palm cultivation across the tropics. When running Maxent, we permitted linear and quadratic relationships with the climate variables[31] but otherwise maintained default settings. We projected all models across the entire tropics for the current climate.

Maxent requires randomly-sampled ‘background’ climate data to contrast with the distribution of climatic predictors at ‘presence’ (oil palm mill) locations. We randomly sampled eight sets of 50,000 background points (within seven buffer distances from the presence data, spanning 200-2000 km, and additionally with no buffer), weighted by latitude to account for variation in cell area in the unprojected climate grids, to find the optimal buffer size for model performance[98]. We therefore calibrated models with 16 combinations of presence and background locations (two presence datasets, full and subsampled oil palm mills; and eight background datasets). We selected the optimum combination of presence and background datasets based on model evaluation metrics[98], and found that an intermediate background buffer size was optimal (Supplementary Information 7).

We classified the continuous suitability projections (0-1) of the SDM outputs into suitable (which we further classified; see below) and unsuitable locations, using Minimal Predicted Area thresholding based on projected values at the oil palm mill locations[99,100] (Supplementary Information 7).

SDM evaluation

To examine the robustness of SDMs to spatial prediction, we conducted leave-one-out cross-validation for each model (continuous suitability output) on three spatially distinct portions of the data (Americas, Africa and Asia/Australasia), which we evaluated using the moving window Continuous Boyce Index[99]. We also used the moving window Continuous Boyce Index[99] to examine full model accuracy (accuracy of models trained with all of the data). We tested the continuous suitability projections of these full models on a largely-independent dataset of oil palm plantations (a map of global tree plantations compiled from mixed sources, largely from remote sensing, with a small subset of oil palm plantations verified against the oil palm mills dataset used to train the models)[78], with 50,000 randomly selected testing background points. We selected the single best model based on these full-model and cross-validation scores, alongside relative variable importance, for use in our analyses (Supplementary Information 7). Our best model included spatially-subsampled oil palm mills, and background points in a 500km-buffer, and was selected primarily for its high transferability to novel locations, suggesting robustness to spatial extrapolation.

To examine the sensitivity of our model outputs to the threshold determining oil palm suitability, we compared the performance of the best model classified into suitable and unsuitable locations (from the continuous suitability output of values 0-1) at three different Minimal Predicted Area thresholds (Supplementary Information 7). To compare these classifications, we tested our projections for each classification on the largely-independent dataset of oil palm plantations[78] (see above) using the True

Skill Statistic to measure predictive accuracy[101], and we compared our projections with an agro-ecological model of oil palm suitability[26]. We found that the mid-range suitability threshold of the three thresholds we tested (Minimal Predicted Area$_{99}$) gave high values for both of the evaluation metrics (Supplementary Fig. 24), so we present this classification in the results in the Main Article. Our final model of suitability for rainfed oil palm was therefore similar to the agro-ecological suitability model[26] (Extended Data Fig. 2), as well as to a recent low-resolution climatic envelope model[21]. As a sensitivity test to our reliance on our new model of oil palm suitability throughout the Results, we also conducted all key analyses for the agro-ecological suitability model[26], and for a conservative, 'high-confidence' model of areas of overlapping suitability between our final rainfed model and the agro-ecological model. We found that our conclusions are robust to the use of these alternative rainfed suitability models (Supplementary Information 3-5).

Classifying expected oil palm yield

We classified the continuous suitability outputs of the suitable locations from the best SDM (i.e. excluding unsuitable areas) into three suitability classes for oil palm cultivation (low, medium, high), using Minimal Predicted Area thresholding (as we used for classifying suitable and unsuitable areas). Each suitability class contained one-third of the oil palm mills used to train the model, excluding any that fell below the suitability threshold (Supplementary Information 7). We obtained expected yield values for these classes from global maps of oil palm yield in 2010[102], by comparing SDM outputs with all grid-cells where actual yield >0 tha^{-1} (Supplementary Information 7). For comparison with yield in current industrial plantations, we also extracted 2010 yield values[102] at the locations of oil palm mills used as 'presence' locations in the SDMs.

Modelling climatically-suitable locations under irrigation

To simulate locations suitable for oil palm under irrigation, we projected our best SDM to an altered climate, for which we simulated MWD under irrigation (Tmin was unaltered). To calculate potentially 'irrigated' MWD, we assumed that months with sufficient surplus available water to remove a critical annual MWD were ‘irrigated’. We calculated monthly surplus available water as the difference between monthly gross water demand (m^3, incorporating demand from households, industry, livestock and irrigation) and total renewable supply (m^3, incorporating unused desalinated water, renewable groundwater, and runoff from rivers, reservoirs and lakes), averaged for each month for 2005-2009[79,103], and we converted this to mm by dividing by grid-cell area (m^2). To simulate irrigation, we assumed a critical annual cumulative water deficit (at which oil palm begins to suffer water stress) of 100 mm, corresponding to empirical values of critical deficit[31], driving a ~10% decrease in yield[104], and to average monthly evapotranspiration for oil palm[105]. For locations requiring irrigation (i.e. with annual MWD >100 mm), we supplemented rainfall with surplus available water in the months with a moisture deficit (i.e. with rainfall < potential evapotranspiration, calculated according to the Hargreaves Equation[106,107]). Where monthly surplus available water was sufficient to reduce the annual MWD to <100 mm, we assumed that irrigation would be applied, because it could successfully remove the critical water deficit. Where monthly surplus available water was insufficient to reduce MWD to <100 mm, we used MWD based on rainfall alone. We tested the sensitivity of our estimates of suitability for irrigated oil palm cultivation to monthly surplus available water, and found that using 100% of surplus available water increases the area of non-cultivated land suitable for irrigated-only oil palm expansion by ~50% compared to using 50% of surplus available water (Supplementary Information 4). Our maps of suitability for irrigated oil palm contain some suitable zones of ~1° resolution, because Sutanudjaja *et al.* in [79] account for local water redistribution by pooling renewable water supply from desalinated and surface water across ~1° zones[79] (Extended Data Figs. 3, 4).

Mapping non-cultivated land

We determined terrestrial non-cultivated land using Copernicus 2015 high-accuracy global land-cover data[80,81], first excluding all permanent water bodies[80,81] and mangrove habitats[20]. We used the global land-cover data[80,81] to exclude locations of cropland and urban areas, and a comprehensive database of global tree plantations (including oil palm plantations: Spatial Database of Planted

Trees)[78] to exclude locations of existing tree plantations. Our areas of non-cultivated land therefore include all primary and secondary vegetation (including undisturbed natural habitat, degraded areas and intensively-managed pasture): habitats potentially available for conversion to oil palm. Nevertheless, we acknowledge the differing biodiversity values of these habitats (intact, disturbed and intensively-managed pasture), which we address in the Discussion and Supplementary Information 6, and in our sensitivity analyses including intensively-managed (improved) pasture (see below).

Mapping protected areas

We used the Protected Planet World Database on Protected Areas[108] to identify areas that are protected from conversion to agriculture. We included all terrestrial protected areas of IUCN classes I and II, which are most strictly protected (by law) and therefore least likely to undergo conversion[109]. For a subset of protected areas without a shapefile, we estimated protected area coverage as circles centred on point coordinates, corresponding to the reported protected area size (km^2)[110]. We considered a protected area to occupy a 5' grid-cell if its polygon covered the cell centre.

Determining protection under ZDCs

During impact assessments for development of zero-deforestation oil palm plantations, HCSA guidance designates locations for conservation based on their vegetation structure[17]. The vegetation stratification is designed to vary by location and habitat type, but has only been developed for moist forest in Southeast Asia to date[17]. We therefore applied the stratification thresholds generically across the tropics, regardless of continent or biome, although in practise they could vary during local application. Under the HCSA, all locations with vegetation dominated by trees >30cm diameter at breast height, with >50% canopy closure and aboveground carbon of approximately >75 Mg ha^{-1} ('low density forest') are designated for conservation. All locations dominated by trees 10-30cm diameter at breast height, with 30-40% canopy closure and aboveground carbon of ~35-75 Mg ha^{-1}

('young regenerating forest') are considered potential areas for conservation[17]. If these 'young regenerating forest' areas support additional conservation values identified in the 'High Conservation Value' assessment (conducted in tandem with the HCSA), or represent a significant habitat area in the landscape, they are designated for protection[17]. We therefore computed two scenarios to represent likely habitat protection under this scheme: in which all locations corresponding to (i) 'low density forest' are protected (weaker habitat protection), and (ii) all 'young regenerating forest' are additionally protected (greater habitat protection). We mapped these scenarios using global datasets of canopy closure[84] and aboveground biomass ('GlobBiomass')[82,83], assuming that 50% of biomass is carbon[111]. For both scenarios, we included all locations with peat soils as protected from cultivation[85]. We found that the two HCSA scenarios for habitat protection give similar patterns of potential availability for conversion across biomes and continents; therefore, we present the 'greater habitat protection' scenario (protection of 'young regenerating forest', ≥35 Mg ha^{-1} aboveground carbon and ≥30% canopy closure) in the Main Article, and 'weaker habitat protection' ('young regenerating forest', ≥75 Mg ha^{-1} aboveground carbon and ≥50% canopy closure) in Supplementary Information 2-5.

In addition to HCSA assessments, HCVs are also identified for protection prior to oil palm development[17]. However, we did not attempt to map these additional conservation values (e.g. presence of rare species in local habitat patch, conservation of socio-cultural values) because they cannot be captured reliably through global mapping, and require local case-by-case identification, based on on-the-ground data and stakeholder consultations. Furthermore, many of the national interpretations for HCVs were originally developed for forestry, and have not subsequently been developed for habitats other than tropical moist forest (Supplementary Information 1). Tropical grassy biomes are fundamentally different in biota and functioning to forests[12] and therefore require separate criteria to identify areas with HCVs, so the extent of habitat protection for these biomes varies depending on the approach taken by the assessor(s) (Supplementary Information 1). We discuss the limitations of this approach in Supplementary Information 6.

Biome and biogeographic realm classification

We based our biome classification on the most recent map of Terrestrial Ecoregions of the World[20]. We reclassified the biome assigned to 25 of 391 non-mangrove ecoregions, using ecological literature, expert knowledge of these habitats and the classification used in Murphy et al. 2016[44], mostly ensuring that grassland, savanna, shrubland and woodland ecoregions with a continuous grassy understorey were identified as 'tropical grassy biome'[8] (Extended Data Table 1). For our analyses, we then grouped 'tropical & subtropical moist broadleaf forest' ecoregions as tropical moist forest; 'tropical & subtropical dry broadleaf forest' ecoregions as tropical dry forest; ecoregions classified as 'tropical and subtropical grasslands, savannas and shrublands', 'montane grasslands and shrublands' and 'flooded grasslands and savannahs' as tropical grassy biomes; and ecoregions classified as 'deserts and xeric shrublands' and 'tropical and subtropical coniferous forests' as 'other' biomes.

We also used the map of global ecoregions[20] to classify locations by biogeographic realm. Because our region of interest is the tropics, we reclassified the realm of eight ecoregions in North Africa and the Arabian Peninsula, which had small suitable areas (median 161 km^2 under suitability threshold Minimal Predicted Area$_{100}$) to 'Afrotropic' from 'Palearctic'.

Impacts of oil palm expansion on vertebrates

Following references[112–114], we estimated potential vertebrate richness loss from oil palm expansion as the difference between richness (total number of species occurring in a grid-cell) of natural habitat, and richness of oil palm plantations (i.e. species that can persist in plantations). To estimate species' occurrence, we refined global range maps for three well-documented taxa (mammals, birds and amphibians)[86,87] according to Terrestrial Ecoregions of the World biome classification[20], and locations of cropland, urban areas[80,81] and tree plantations[78]. We considered a species as 'present' in a given grid-cell if its original range map contained the grid-cell centre, and if the biome or transformed habitat type (cropland, urban, tree plantation) of the grid-cell was listed as suitable for the species, following matching in Supplementary Table 7. Similarly, we considered that a species remained ‘present’ in a grid-cell following conversion to oil palm if its list of suitable habitats included ‘plantation’ (see Supplementary Fig. 15 for species richness maps). We also quantified threatened species’ (vulnerable, endangered or critically endangered in the IUCN Red List) potential range reduction from conversion to oil palm, by examining the overlap of locations suitable for oil palm expansion and threatened species’ refined range maps.

Sensitivity analyses including intensively-managed pasture

We were unable to account for locations of intensively-managed (improved) pasture globally, because there are no global datasets accurately distinguishing this land-use type from low-intensity natural or anthropogenic grazing[8]. We therefore used two recent, national landcover maps that distinguish intensively-managed pasture from natural grassy biome to conduct sensitivity analyses of our key results to the inclusion of pasture. We re-ran our main analyses for Colombia and tropical Brazil (i.e. North of -23.5°), incorporating intensively-managed pasture from IDEAM 2018 landcover for Colombia[115], and MapBiomas 2020 landcover for Brazil[116,117]. These datasets were developed by machine learning classification of satellite images with manual verification, incorporating local land-use statistics, biome type and expert knowledge (see Supplementary Information 6 for a discussion of their limitations). For both Brazil and Colombia, greater areas of forested biomes that we estimated as suitable for oil palm expansion had already been converted to pasture, in comparison to grassy biomes, suggesting that our conclusion that high-biodiversity habitats in grassy biomes are particularly vulnerable to oil palm expansion under ZDCs is robust (Supplementary Information 2). Our estimates of vertebrate richness loss from zero-deforestation oil palm expansion also appear robust, assuming that the areas already converted to intensively-managed pasture are unavailable for expansion. However, if pasture is available for expansion, we will have overestimated potential vertebrate richness loss in substantial areas of intensively-managed pasture (e.g. moist and dry forest in Brazil and Colombia: Supplementary Fig. 3).

Data Availability

Existing datasets analysed in the article are available at references given within the manuscript. The final models of climatic suitability for rainfed and irrigated oil palm cultivation, and summary data of suitability per ecoregion, are available at https://doi.org/10.17605/OSF.IO/2RH6N.

Code Availability

The code used to generate oil palm suitability models and conduct analyses is available at https://doi.org/10.17605/OSF.IO/2RH6N.

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Author Contributions

SF, JKH, CLP, JML and HK conceived the study; SF, CJM and PJP designed the models of oil palm suitability; CLP conducted the biome classification; RMB conducted refinements of species range maps; SF ran the suitability models, conducted the analyses and led the writing of the manuscript. All authors contributed critically to drafts of the paper and finalized the text.

Competing interests

The authors declare no competing interests.

Tables

Table 1. Areas of individual ecoregions suitable for oil palm expansion under ZDCs. Data are provided for the 20 ecoregions with the largest area suitable, for (a) rainfed, and (b) both rainfed and irrigated cultivation. Ecoregion names in **bold** are present in both (a) and (b), i.e. rank in the top 20 ecoregions with the largest suitable area for both rainfed-only (a) and rainfed and/or irrigated expansion (b) under ZDCs. Realms are coded as N: Neotropic; A: Afrotropic.

	(a) Rainfed cultivation				(b) Irrigated and rainfed cultivation			
	Ecoregion	**Biome**	**Realm**	**Suitable area for expansion under ZDCs: 1000 km^2 (% of total non-cultivated land)**	**Ecoregion**	**Biome**	**Realm**	**Suitable area for expansion under ZDCs: 1000 km^2 (% of total non-cultivated land)**
1	**Llanos**	Grassy	N	274 (79.7%)	**Llanos**	Grassy	N	279 (81.1%)
2	**Western Congolian forest-savanna**	Grassy	A	109 (29.3%)	Cerrado	Grassy	N	245 (16.1%)
3	**Guinean forest-savanna**	Grassy	A	93.7 (18.0%)	**Guinean forest-savanna**	Grassy	A	132 (25.4%)
4	**Beni savanna**	Grassy	N	77.1 (70.3%)	**Western Congolian forest-savanna**	Grassy	A	131 (35.2%)
5	**Southern Congolian forest-savanna**	Grassy	A	59.6 (10.6%)	**Southern Congolian forest-savanna**	Grassy	A	112 (19.8%)
6	**Guianan savanna**	Grassy	N	56.7 (53.2%)	Caatinga	Dry forest	N	82.3 (11.6%)
7	**Magdalena-Urabá moist forests**	Moist forest	N	45.7 (64.3%)	**Beni savanna**	Grassy	N	77.7 (70.9%)
8	**Eastern Guinean forests**	Moist forest	A	44.2 (24.7%)	**Mato Grosso tropical dry forests**	Dry forest	N	76.2 (20.2%)
9	**Tocantins/Pindaré moist forests**	Moist forest	N	41.3 (22.5%)	Northern Congolian Forest-Savanna	Grassy	A	72.0 (10.3%)
10	**Xingu-Tocantins-Araguaia moist forests**	Moist forest	N	40.9 (14.9%)	**Guianan savanna**	Grassy	N	56.7 (53.2%)
11	**Maranhão Babaçu forests**	Dry forest	N	36.2 26.3%)	Sudd flooded grasslands	Grassy	A	52.0 (27.5%)
12	Apure-Villavicencio dry forests	Dry forest	N	35.9 (64.0%)	**Madeira-Tapajós moist forests**	Moist forest	N	50.6 (7.1%)
13	**Madeira-Tapajós moist forests**	Moist forest	N	31.5 (4.4%)	**Xingu-Tocantins-Araguaia moist forests**	Moist forest	N	49.9 (18.2%)
14	Bahia coastal forests	Moist forest	N	30.4 (30.9%)	Sahelian Acacia savanna	Grassy	A	48.5 (1.4%)
15	**Mato Grosso tropical dry forests**	Dry forest	N	27.6 (7.3%)	**Magdalena-Urabá moist forests**	Moist forest	N	45.7 (64.3%)
16	Northeast Congolian lowland forests	Moist forest	A	26.6 (5.2%)	**Eastern Guinean forests**	Moist forest	A	44.7 (25.0%)
17	Western Guinean lowland forests	Moist forest	A	24.9 (12.3%)	East Sudanian savanna	Grassy	A	43.8 (4.9%)
18	Hispaniolan moist forests	Moist forest	N	22.6 (53.5%)	**Tocantins/Pindaré moist forests**	Moist forest	N	43.4 (23.7%)
19	Nigerian lowland forests	Moist forest	A	19.6 (31.4%)	**Maranhão Babaçu forests**	Dry forest	N	42.4 (30.7%)

20	Northern Swahili coastal forests	Moist forest	A	18.9 (14.6%)	Victoria Basin forest-savanna	Grassy	A	40.5 (54.4%)

Box

Box 1: Recommendations to improve the HCV-HCSA guidance for identifying 'High Conservation Value' biodiversity in tropical grassy and dry forest biomes

1. ***Issue:*** Tropical grassy and dry forest biomes are frequently misidentified as 'degraded', low-biodiversity habitat, because of superficial similarity of vegetation structure to degraded moist forest (e.g. lower stature trees and/or grassy understorey with shrubs and small trees) and a lack of understanding that ancient grassy biomes are not recently derived habitat[12,13,118]. However, some tropical dry forests are so fragmented that only degraded habitat is likely to remain[119]. Current guidance[17,18] does not clearly define these habitats and their intactness.

   Recommendations: Comprehensive definitions of different habitat types, recognising that certain degraded habitats may have unique conservation value. Crucially, guidance should include indicators to distinguish ancient, high-biodiversity grassy and dry forest biomes from degraded rainforest and recently-derived grassy biomes, such as fire-adapted flora in grassy biomes (with support for the ongoing development of these indicators)[13,14,118,120,121]. Floral biodiversity surveys require expert knowledge and are key in identifying habitat intactness[120], so building this capacity in all relevant locations is critical.

2. ***Issue:*** Tropical grassy biomes are characterised by frequent disturbance events (e.g. fire, grazing), and can vary temporally and spatially in vegetation type and cover, often comprising a mosaic of woody and open vegetation[12,13]. Without acknowledging this variation and ecological dynamism, impact assessments prior to plantation development could fail to identify the importance of these habitats (e.g. by omitting disturbance-dependent plant species from field inventories).

   Recommendations: Biodiversity survey design to reflect disturbance regimes (e.g. by conducting repeat plant surveys before and after disturbance events), and landscape-scale factors (e.g. habitat variation, large vertebrate migration routes).

3. ***Issue:*** Human livelihoods and ecological functioning of grassy biomes and dry forests are often tightly linked[8,12,14], so incorporating local community requirements into agricultural development is imperative for conservation of these biomes[122]. Human disturbance in grassy biomes (e.g. burning, grazing) does not always indicate habitat degradation, and is often fundamental for ecological functioning[8,12,14]. In turn, grassy biomes provide livelihoods for one fifth of the world's population (e.g. from grazing, firewood provisioning)[12], including many of the world's poorest people[123].

   Recommendations: Recognition of potential importance of anthropogenic disturbance for dynamism of grassy biomes: requiring identification of disturbance regimes and management which support these, ensuring that appropriate fire and grazing of grasslands is permitted, while recognising that some human disturbances can also drive biodiversity loss (e.g. over-grazing, use of inorganic fertilizers). This may require extensive discussion with local communities[12], and thus highlights the urgent need for improved practice of Free, Prior and Informed Consent[124,125].

Figure legends

Figure 1. Climatically-suitable locations for rainfed oil palm expansion under zero-deforestation commitments (ZDCs), by biome. (a) Neotropics, (b) tropical Africa, (c) tropical Asia and Australasia. Insets: (b) East coast of Africa and Madagascar, (c) South Pacific. Locations of 'other' biome are largely Neotropical 'xeric shrublands' with relatively high rainfall.

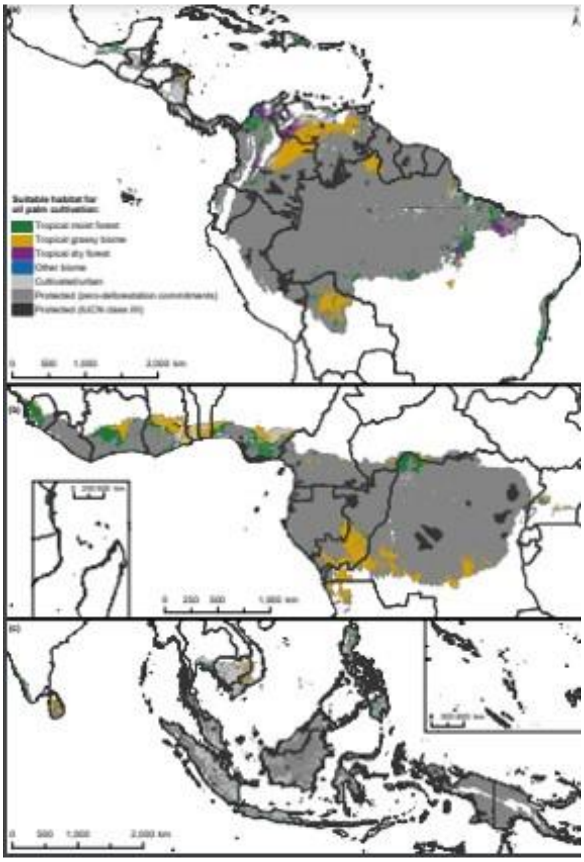


Figure 2. Comparison of potential for rainfed, zero-deforestation oil palm expansion among biomes. (a) Estimated protection of climatically-suitable areas for rainfed oil palm expansion under zero-deforestation commitments (ZDCs), according to the High Carbon Stock Approach (HCSA). Data are plotted as a percentage of the total climatically-suitable area of non-cultivated land by biome; this total suitable area is shown in brackets along the x axis. Locations that would be protected under ZDCs are shown in grey and locations potentially available for ZDC expansion are shown in colours (see Fig. 1). (b) Potential for loss of remaining non-cultivated land of individual ecoregions (i.e. percentage of remaining non-cultivated land per ecoregion that is climatically-suitable for expansion under ZDCs). Boxplot centre lines show the median, lower and upper

hinges show the first and third quartiles respectively, whiskers extend to the maximum and minimum values within 1.5*inter-quartile range, and outliers are plotted individually.

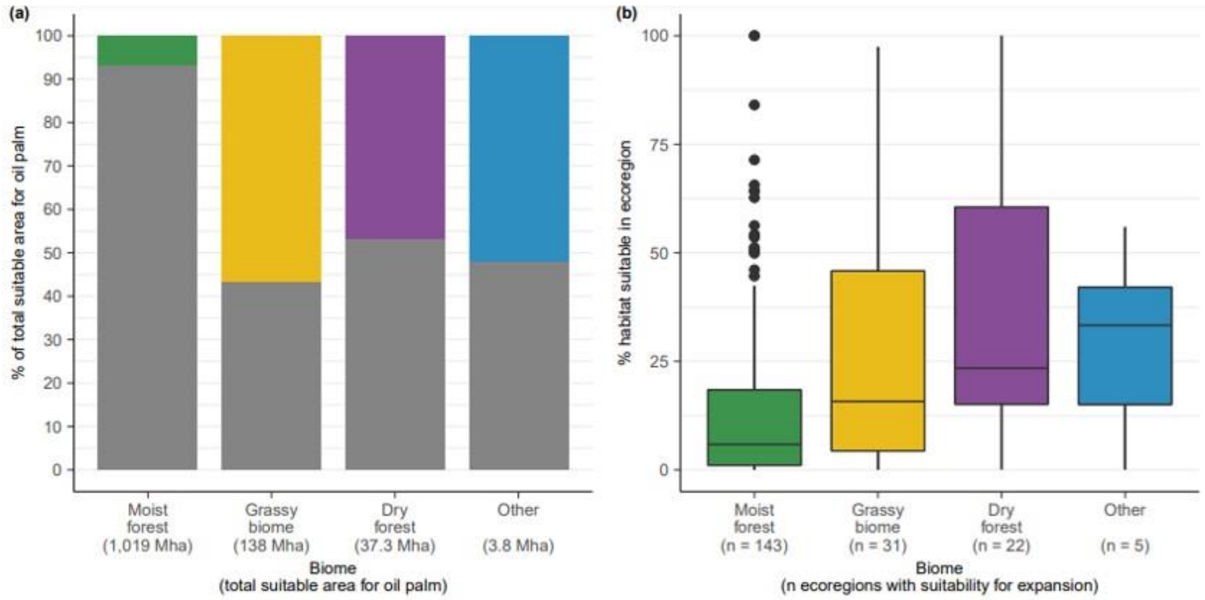


Figure 3. Expected annual fresh fruit bunch (FFB) yields in locations climatically-suitable for oil palm expansion under ZDCs, assuming high-fertiliser input cultivation. (a) Under rainfed cultivation; (b) under irrigation (assuming up to 100% of surplus available water is used for irrigation). In (b), dark colours show the expected yield in locations which are also suitable if rainfed, when under irrigation (i.e. the expected yield in locations shown in (a) when irrigation is applied, if required), and pale colours represent locations only suitable under irrigation. The difference between the distribution of expected yield values for dark colours in (a) and (b) thus represents the effect of applying irrigation to the locations suitable for rainfed cultivation. Note differences in y-axis values for the oil palm suitability classes. See Supplementary Information 4 for sensitivity analyses of predicted suitability for irrigated oil palm to model suitability thresholds, habitat protection under ZDCs, and water availability.

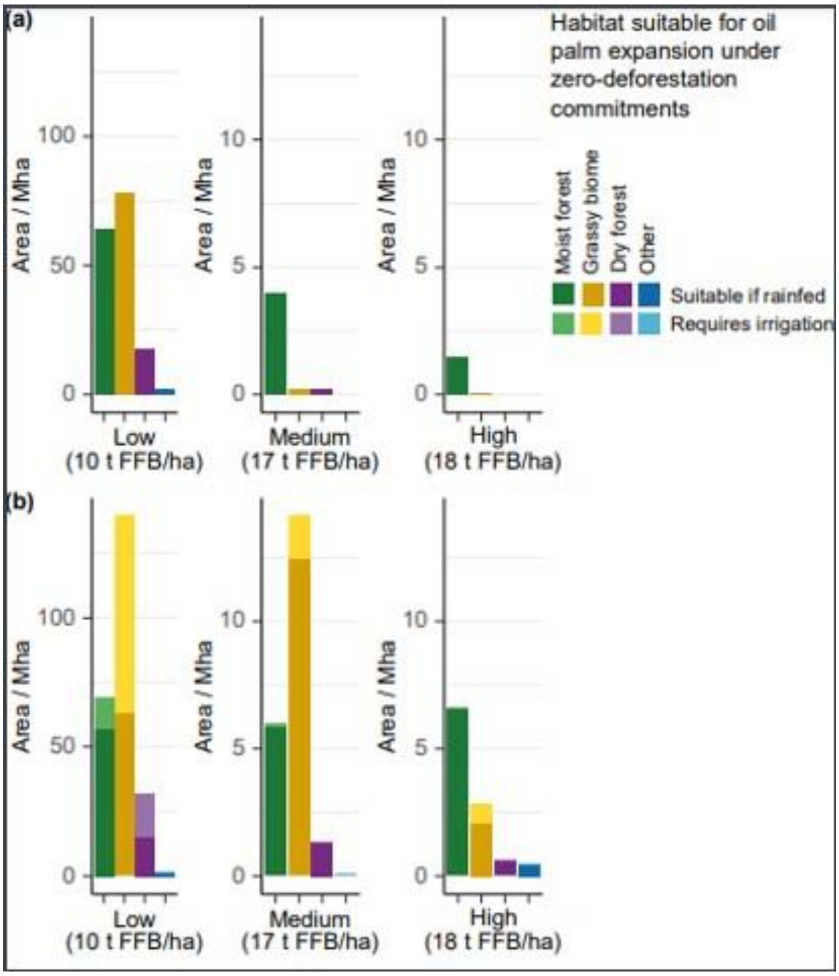
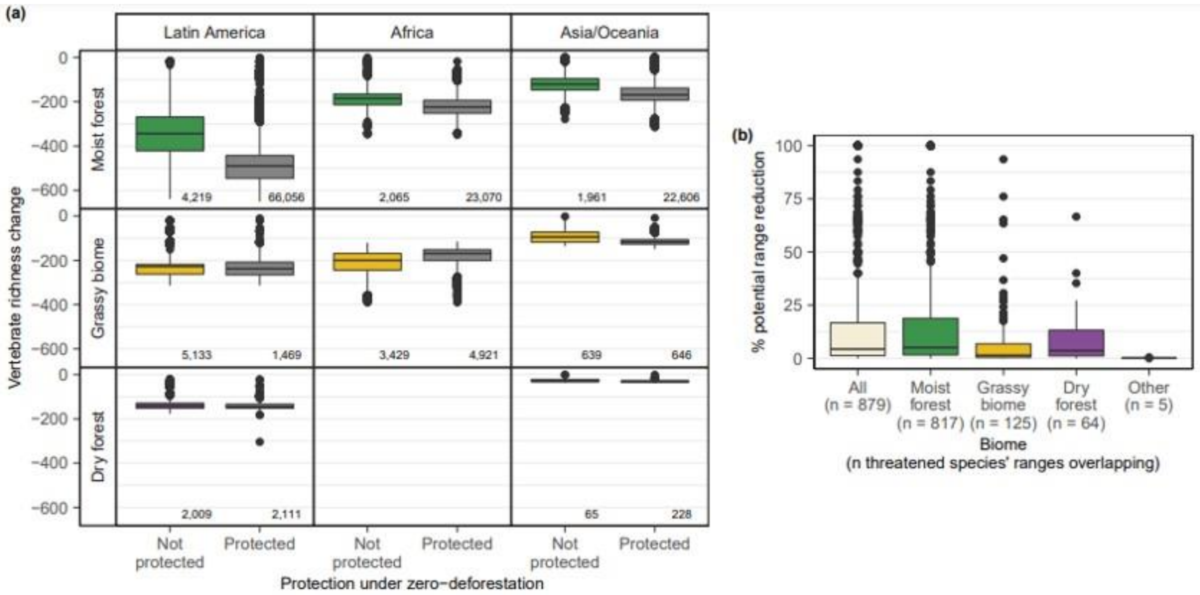


Figure 4. Potential impacts of rainfed, zero-deforestation oil palm expansion on vertebrates. (a) Vertebrate species richness change (mammals, birds and amphibians; negative values denote number of species lost), from conversion of natural habitat to oil palm, by expected protection under ZDCs, within each biome and continent. Boxplots show potential richness change of non-cultivated land climatically-suitable for oil palm expansion, where each datapoint is a 10-km grid-cell (sample sizes are given to the lower right of each boxplot). Richness loss in 'Other' biomes is negligible and shown in Supplementary Information 5. (b) Potential percentage range reduction of threatened vertebrates, from oil palm expansion under ZDCs (overlap between ranges of threatened vertebrates and locations climatically-suitable for expansion), for all species which could undergo range loss from expansion (i.e. species that have some range overlap with potential expansion locations and cannot persist in oil palm). Numbers of species overlapping with potential expansion locations

are given in x axis labels; note that a species can occur in more than one biome. For both (a) and (b), boxplot centre lines show the median, lower and upper hinges show the first and third quartiles respectively, whiskers extend to the maximum and minimum values within 1.5*inter-quartile range, and outliers are plotted individually.



References

1. Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A. & Hansen, M. C. Classifying drivers of global forest loss. *Science (80-.).* **361**, 1108–1111 (2018).

2. Laurance, W. F., Sayer, J. & Cassman, K. G. Agricultural expansion and its impacts on tropical nature. *Trends Ecol. Evol.* **29**, 107–116 (2014).

3. Pendrill, F. *et al.* Agricultural and forestry trade drives large share of tropical deforestation emissions. *Glob. Environ. Chang.* **56**, 1–10 (2019).

4. Haupt, F., Bakhtary, H., Schulte, I., Galt, H. & Streck, C. *Progress on Corporate Commitments and their Implementation*. (2018). Available at:

https://www.tropicalforestalliance.org/assets/Uploads/Progress-on-Corporate-Commitments-and-their-Implementation.pdf

5. Austin, K. G. *et al.* Mapping and Monitoring Zero-Deforestation Commitments. *Bioscience* **71**, 1079–1090 (2021).

6. Leijten, F. C., Sim, S., King, H. & Verburg, P. H. Which forests could be protected by corporate zero deforestation commitments? A spatial assessment. *Environ. Res. Lett.* (2020).

7. Garrett, R. D. *et al.* Criteria for effective zero-deforestation commitments. *Glob. Environ. Chang.* (2019). doi:10.1016/j.gloenvcha.2018.11.003

8. Lehmann, C. E. R. & Parr, C. L. Tropical grassy biomes: Linking ecology, human use and conservation. *Philos. Trans. R. Soc. B Biol. Sci.* (2016). doi:10.1098/rstb.2016.0329

9. Miles, L. *et al.* A global overview of the conservation status of tropical dry forests. *J. Biogeogr.* **33**, 491–505 (2006).

10. Gibbs, H. K. *et al.* Brazil's Soy Moratorium. *Science (80-.).* (2015). doi:10.1126/science.aaa0181

11. Jopke, P. & Schoneveld, G. C. *Corporate commitments to zero deforestation: An evaluation of externality problems and implementation gaps*. *CIFOR Occasional Paper* (2018). doi:10.17528/cifor/006827

12. Parr, C. L., Lehmann, C. E. R., Bond, W. J., Hoffmann, W. A. & Andersen, A. N. Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends in Ecology and Evolution* (2014). doi:10.1016/j.tree.2014.02.004

13. Ratnam, J. *et al.* When is a 'forest' a savanna, and why does it matter? *Glob. Ecol. Biogeogr.* (2011). doi:10.1111/j.1466-8238.2010.00634.x

14. Sanchez-Azofeifa, G. A. *et al.* Research Priorities for Neotropical Dry Forests. *Biotropica* **37**,

477–485 (2005).

15. Vijay, V., Pimm, S. L., Jenkins, C. N. & Smith, S. J. The Impacts of Oil Palm on Recent Deforestation and Biodiversity Loss. *PLoS One* **11**, (2016).

16. RSPO. Principles & Criteria for the Production of Sustainable Palm Oil. (2018).

17. Rosoman, G., Sheun, S. S., Opal, C., Anderson, P. & Trapshah, R., editors. The HCS Approach Toolkit. Singapore: HCS Approach Steering Group (2017).

18. Brown, E. & Senior, M.J.M., editors. *Common Guidance for the Identification of High Conservation Values*. HCV Resource Network (2017).

19. Furumo, P. R. & Aide, T. M. Characterizing commercial oil palm expansion in Latin America: land use change and trade. *Environ. Res. Lett.* **12**, 024008 (2017).

20. Dinerstein, E. *et al.* An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. *BioScience* (2017). doi:10.1093/biosci/bix014

21. Descals, A. *et al.* High-resolution global map of smallholder and industrial closed-canopy oil palm plantations. *Earth Syst. Sci. Data* **13**, 1211–1231 (2021).

22. Woittiez, L. S., van Wijk, M. T., Slingerland, M., van Noordwijk, M. & Giller, K. E. Yield gaps in oil palm: A quantitative review of contributing factors. *Eur. J. Agron.* **83**, 57–77 (2017).

23. Kuepper, B., Drost, S. & Piotrowski, M. *Latin American Palm Oil Linked to Social Risks, Local Deforestation*. Chain Reaction Research (2021). Available at: https://chainreactionresearch.com/wp-content/uploads/2021/12/Latin-American-Palm-Oil-Linked-to-Social-Issues-Local-Deforestation-1.pdf

24. Hoyle, D. *et al. RSPO NEW PLANTING PROCEDURES. Summary Report of ESIA, HCV Assessments and Management Plan. Mouila Lot 3 Extension, Olam Palm Gabon.* (2017).

25. World Resources Institute, Rainforest Alliance, Proforest & Daemeter. Universal Mill List.

(2018). Available at: https://data.globalforestwatch.org/documents/gfw::universal-mill-list/about

26. Pirker, J., Mosnier, A., Kraxner, F., Havlík, P. & Obersteiner, M. What are the limits to oil palm expansion? *Glob. Environ. Chang.* **40**, 73–81 (2016). doi:10.1016/j.gloenvcha.2016.06.007

27. Fischer, G. *et al. Global Agro-ecological Zones 4 (GAEZ v4) – Model documentation*. (FAO, 2021). doi:10.4060/cb4744en

28. FAO and IIASA. Global Agro-ecological Zones version 4 (GAEZ v4). (2021). Available at: http://www.fao.org/gaez/.

29. Tao, H. H. *et al.* Long-term crop residue application maintains oil palm yield and temporal stability of production. *Agron. Sustain. Dev.* (2017). doi:10.1007/s13593-017-0439-5

30. Wei, L., John Martin, J. J., Zhang, H., Zhang, R. & Cao, H. Problems and Prospects of Improving Abiotic Stress Tolerance and Pathogen Resistance of Oil Palm. *Plants* **10**, 2622 (2021).

31. Corley, R. H. & Tinker, P. B. . *The Oil Palm*. (Wiley-Blackwell, 2016).

32. Barona, E., Ramankutty, N., Hyman, G. & Coomes, O. T. The role of pasture and soybean in deforestation of the Brazilian Amazon. *Environ. Res. Lett.* **5**, 024002 (2010).

33. ten Kate, A., Kuepper, B. & Piotrowski, M. *NDPE Policies cover 83% of Palm Oil Refineries; Implementation at 78%*. Chain Reaction Research (2020). Available at: https://chainreactionresearch.com/wp-content/uploads/2020/04/NDPE-Policies-Cover-83-of-Palm-Oil-Refining-Market.pdf

34. Trase. The Trase Yearbook - The state of forest-risk supply chains. *Trase* (2020). Available at: https://insights.trase.earth/yearbook/summary

35. Austin, K. G. *et al.* Shifting patterns of oil palm driven deforestation in Indonesia and implications for zero-deforestation commitments. *Land use policy* **69**, 41–48 (2017).

36. Furumo, P. R., Rueda, X., Rodríguez, J. S. & Parés Ramos, I. K. Field evidence for positive certification outcomes on oil palm smallholder management practices in Colombia. *J. Clean. Prod.* **245**, 118891 (2020).

37. Carlson, K. M. *et al.* Effect of oil palm sustainability certification on deforestation and fire in Indonesia. *Proc. Natl. Acad. Sci.* **115**, 121–126 (2018).

38. Heilmayr, R., Carlson, K. M. & Benedict, J. J. Deforestation spillovers from oil palm sustainability certification. *Environ. Res. Lett.* **15**, 075002 (2020).

39. RSPO. Impact | RSPO - Roundtable on Sustainable Palm Oil. (2022). Available at: https://www.rspo.org/impact.

40. Bastos Lima, M. G., Persson, U. M. & Meyfroidt, P. Leakage and boosting effects in environmental governance: a framework for analysis. *Environ. Res. Lett.* **14**, 105006 (2019).

41. Corley, R. H. V. How much palm oil do we need? *Environ. Sci. Policy* (2009). doi:10.1016/j.envsci.2008.10.011

42. FAO. *FAOTSTAT Data for 2010-2018*. (2020). Available at: https://www.fao.org/faostat/en/

43. Olson, D. M. *et al.* Terrestrial Ecoregions of the World: A New Map of Life on Earth. A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* **51**, 933–938 (2001).

44. Murphy, B. P., Andersen, A. N. & Parr, C. L. The underestimated biodiversity of tropical grassy biomes. *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 20150319 (2016).

45. Smith, J. R., Hendershot, J. N., Nova, N. & Daily, G. C. The biogeography of ecoregions: Descriptive power across regions and taxa. *J. Biogeogr.* (2020). doi:10.1111/jbi.13871

46. Klink, C. A. & Machado, R. B. Conservation of the Brazilian Cerrado. *Conservation Biology* (2005). doi:10.1111/j.1523-1739.2005.00702.x

47. Strassburg, B. B. N. *et al.* Moment of truth for the Cerrado hotspot. *Nature Ecology and Evolution* (2017). doi:10.1038/s41559-017-0099

48. le Polain de Waroux, Y. *et al.* The Restructuring of South American Soy and Beef Production and Trade Under Changing Environmental Regulations. *World Dev.* **121**, 188–202 (2019).

49. Nepstad, L. S. *et al.* Pathways for recent Cerrado soybean expansion: extending the soy moratorium and implementing integrated crop livestock systems with soybeans. *Environ. Res. Lett.* **14**, 044029 (2019).

50. Searchinger, T. D. *et al.* High carbon and biodiversity costs from converting Africa's wet savannahs to cropland. *Nat. Clim. Chang.* (2015). doi:10.1038/nclimate2584

51. Cardoso Da Silva, J. M. & Bates, J. M. Biogeographic Patterns and Conservation in the South American Cerrado: A Tropical Savanna Hotspot. *Bioscience* (2002). doi:10.1641/0006-3568(2002)052[0225:bpacit]2.0.co;2

52. Poggio, L. *et al.* SoilGrids 2.0: Producing soil information for the globe with quantified spatial uncertainty. *SOIL* **7**, (2021).

53. Hill, T. C., Williams, M., Bloom, A. A., Mitchard, E. T. A. & Ryan, C. M. Are Inventory Based and Remotely Sensed Above-Ground Biomass Estimates Consistent? *PLoS One* (2013). doi:10.1371/journal.pone.0074170

54. Ryan, C. M. *et al.* Ecosystem services from southern African woodlands and their future under global change. *Philos. Trans. R. Soc. B Biol. Sci.* (2016). doi:10.1098/rstb.2015.0312

55. Grace, J., Jose, J. S., Meir, P., Miranda, H. S. & Montes, R. A. Productivity and carbon fluxes of tropical savannas. *J. Biogeogr.* **33**, 387–400 (2006).

56. Scharlemann, J. P., Tanner, E. V., Hiederer, R. & Kapos, V. Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon Manag.* **5**, 81–91 (2014).

57. Quezada, J. C., Etter, A., Ghazoul, J., Buttler, A. & Guillaume, T. Carbon neutral expansion of oil palm plantations in the Neotropics. *Sci. Adv.* **5**, eaaw4418 (2019).

58. Aleman, J. C., Blarquez, O. & Staver, C. A. Land-use change outweighs projected effects of changing rainfall on tree cover in sub-Saharan Africa. *Glob. Chang. Biol.* (2016). doi:10.1111/gcb.13299

59. Espírito-Santo, M. M. *et al.* Understanding patterns of land-cover change in the Brazilian Cerrado from 2000 to 2015. *Philos. Trans. R. Soc. B Biol. Sci.* (2016). doi:10.1098/rstb.2015.0435

60. Overbeck, G. E. *et al.* Conservation in Brazil needs to include non-forest ecosystems. *Diversity and Distributions* (2015). doi:10.1111/ddi.12380

61. Hoekstra, J. M., Boucher, T. M., Ricketts, T. H. & Roberts, C. Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecol. Lett.* (2005). doi:10.1111/j.1461-0248.2004.00686.x

62. RTRS. *RTRS Standard for Responsible Soy Production Version 3.1*. (2017). Available at: https://responsiblesoy.org/wp-content/uploads/2019/08/RTRS%20Standard%20Responsible%20Soy%20production%20V3.1%20ING-LOW.pdf

63. Batlle-Bayer, L., Batjes, N. H. & Bindraban, P. S. Changes in organic carbon stocks upon land use conversion in the Brazilian Cerrado: A review. *Agric. Ecosyst. Environ.* **137**, 47–58 (2010).

64. Rockström, J., Falkenmark, M., Lannerstad, M. & Karlberg, L. The planetary water drama: Dual task of feeding humanity and curbing climate change. *Geophys. Res. Lett.* **39**, (2012).

65. Ocampo-Peñuela, N., Garcia-Ulloa, J., Ghazoul, J. & Etter, A. Quantifying impacts of oil palm expansion on Colombia's threatened biodiversity. *Biol. Conserv.* (2018). doi:10.1016/j.biocon.2018.05.024

66. Gilroy, J. J. *et al.* Minimizing the biodiversity impact of Neotropical oil palm development. *Glob. Chang. Biol.* **21**, 1531–1540 (2015).

67. IUCN. *Bonn Challenge 2020 Report*. (2020). Available at: https://www.bonnchallenge.org/resources/bonn-challenge-2020-report

68. Gilroy, J. J. *et al.* Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism. *Nat. Clim. Chang.* **4**, 503–507 (2014).

69. Evans, M. C. *et al.* Carbon farming via assisted natural regeneration as a cost-effective mechanism for restoring biodiversity in agricultural landscapes. *Environ. Sci. Policy* **50**, 114–129 (2015).

70. Hunter, M. C., Smith, R. G., Schipanski, M. E., Atwood, L. W. & Mortensen, D. A. Agriculture in 2050: Recalibrating targets for sustainable intensification. *BioScience* (2017). doi:10.1093/biosci/bix010

71. Beyer, R. & Rademacher, T. Species Richness and Carbon Footprints of Vegetable Oils: Can High Yields Outweigh Palm Oil's Environmental Impact? *Sustainability* **13**, 1813 (2021).

72. Lee, J. S. H., Ghazoul, J., Obidzinski, K. & Koh, L. P. Oil palm smallholder yields and incomes constrained by harvesting practices and type of smallholder management in Indonesia. *Agron. Sustain. Dev.* **34**, 501–513 (2014).

73. Murphy, D. J. The future of oil palm as a major global crop: Opportunities and challenges. *J. Oil Palm Res.* **26**, 1–24 (2014).

74. Giam, X., Koh, L. P. & Wilcove, D. S. Tropical crops: Cautious optimism. *Science* (2014). doi:10.1126/science.346.6212.928-a

75. Villoria, N. B., Golub, A., Byerlee, D. & Stevenson, J. Will yield improvements on the forest frontier reduce greenhouse gas emissions? A global analysis of oil palm. *Am. J. Agric. Econ.*

95, 1301–1308 (2013).

76. Koh, L. P. & Lee, T. M. Sensible consumerism for environmental sustainability. *Biological Conservation* (2012). doi:10.1016/j.biocon.2011.10.029

77. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017). doi:10.1002/joc.5086

78. Harris, N., Goldman, E. & Gibbes, S. Spatial Database of Planted Trees (SDPT) Version 1.0. (2019). Available at: https://data.globalforestwatch.org/datasets/tree-plantations.

79. Sutanudjaja, E. H. *et al.* PCR-GLOBWB 2: A 5 arcmin global hydrological and water resources model. *Geosci. Model Dev.* (2018). doi:10.5194/gmd-11-2429-2018

80. Copernicus *et al.* Global Land Cover. (2019). Available at: https://lcviewer.vito.be/.

81. Buchhorn, M., Smets, B., Bertels, L., Lesiv, M. & Tsendbazar, N.-E. *Copernicus Global Land Operations 'Vegetation and Energy' "CGLOPS-1" Product User Manual. Moderate Dynamic Land Cover 100m version 2. Issue I2.10*. (2019). Available at: https://land.copernicus.eu/global/products/lc

82. Santoro, M. *et al.* GlobBiomass - global datasets of forest biomass. *PANGAEA* (2018). doi:https://doi.org/10.1594/PANGAEA.894711

83. Santoro, M. *et al.* A detailed portrait of the forest aboveground biomass pool for the year 2010 obtained from multiple remote sensing observations. *Geophys. Res. Abstr.* (2018). doi:10.1002/joc.5086

84. Hansen, M. C. *et al.* High-resolution global maps of 21st-century forest cover change. *Science (80-.).* (2013). doi:10.1126/science.1244693

85. Gumbricht, T. *et al. Tropical and Subtropical Wetlands Distribution version 2*. (2017). doi:https://doi.org/10.17528/CIFOR/DATA.00058

86. IUCN. The IUCN Red List of Threatened Species. Version 2018-1. *http://www.iucnredlist.org* (2018).

87. BirdLife International and Handbook of the Birds of the World. Bird species distribution maps of the world. Version 6.0. *Bird Species Distribution Maps of the World.* (2016). Available at: http://datazone.birdlife.org/species/requestdis.

88. R Core Team. R: A language and environment for statistical computing. (2018).

89. Silalertruksa, T. *et al.* Environmental sustainability of oil palm cultivation in different regions of Thailand: Greenhouse gases and water use impact. *J. Clean. Prod.* **167**, 1009–1019 (2017).

90. Fourcade, Y., Engler, J. O., Rödder, D. & Secondi, J. Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias. *PLoS One* **9**, e97122 (2014).

91. Liu, Z. *et al.* Shifts in the extent and location of rice cropping areas match the climate change pattern in China during 1980–2010. *Reg. Environ. Chang.* (2015). doi:10.1007/s10113-014-0677-x

92. Singh, K., McClean, C. J., Büker, P., Hartley, S. E. & Hill, J. K. Mapping regional risks from climate change for rainfed rice cultivation in India. *Agric. Syst.* **156**, 76–84 (2017).

93. Estes, L. D. *et al.* Comparing mechanistic and empirical model projections of crop suitability and productivity: Implications for ecological forecasting. *Glob. Ecol. Biogeogr.* (2013). doi:10.1111/geb.12034

94. Thuiller, W., Georges, D., Engler, R. & Breiner, F. biomod2: Ensemble Platform for Species Distribution Modelling. (2016).

95. Hernandez, P. A., Graham, C. H., Master, L. L. & Albert, D. L. The effect of sample size and species characteristics on performance of different species distribution modeling methods.

Ecography (Cop.). **29**, 773–785 (2006).

96. Merow, C., Smith, M. J., Silander, J. A., Merow, C. & Silander, J. A. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography (Cop.).* **36**, 1058–1069 (2013).

97. Phillips, S. J., Anderson, R. P. & Schapire, R. E. Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* (2006). doi:10.1016/j.ecolmodel.2005.03.026

98. VanDerWal, J., Shoo, L. P., Graham, C. & Williams, S. E. Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecol. Modell.* **220**, 589–594 (2009).

99. Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C. F. & Guisan, A. Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Modell.* **199**, 142–152 (2006).

100. Engler, R., Guisan, A. & Rechsteiner, L. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *J. Appl. Ecol.* (2004). doi:10.1111/j.0021-8901.2004.00881.x

101. Allouche, O., Tsoar, A. & Kadmon, R. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* (2006). doi:10.1111/j.1365-2664.2006.01214.x

102. International Food Policy Research Institute. *Global Spatially-Disaggregated Crop Production Statistics Data for 2010 Version 1.1*. (2019). doi:10.7910/DVN/PRFF8V/M2EMBN

103. Hofste, R. W. *et al. Aqueduct 3.0: Updated Decision-Relevant Global Water Risk Indicators*. (2019). Available at: https://www.wri.org/research/aqueduct-30-updated-decision-relevant-global-water-risk-indicators

104. Carr, M. K. V. The water relations and irrigation requirements of oil palm (Elaeis guineensis):

A review. *Experimental Agriculture* **47**, 629–652 (2011).

105. Yusop, Z., Hui, C. M., Garusu, G. J. & Katimon, A. Estimation of Evapotranspiration in Oil Palm Catchments By Short-Time Period Water-Budget Method. *Malaysian J. Civ. Eng.* (2008).

106. Hargreaves, G. H. & Allen, R. G. History and Evaluation of Hargreaves Evapotranspiration Equation. *J. Irrig. Drain. Eng.* **129**, 53–63 (2003).

107. Trabucco, A. & Zomer, R. J. Global Aridity Index and Potential Evapotranspiration (ET0) Climate Database v2. *Figshare fileset* (2019). doi:10.6084/m9.figshare.7504448.v3

108. UNEP-WCMC & IUCN. Protected Planet; The World Database on Protected Areas (WDPA). (2020). Available at: www.protectedplanet.net.

109. Dudley, N. (Editor). Guidelines for Applying Protected Area Management Categories. Gland, Switzerland: IUCN (2008). WITH Stolton, S., P. Shadie and N. Dudley. IUCN WCPA Best Practice Guidance on Recognising Protected Areas and Assigning Management Categories and Governance Types, Best Practice Protected Area Guidelines Series No. 21, Gland, Switzerland: IUCN (2013)

110. UNEP-WCMC. World Database on Protected Areas User Manual 1.5. (2017). Available at: https://www.protectedplanet.net/en/resources/wdpa-manual

111. Chave, J. J. *et al.* Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **145**, 87–99 (2005).

112. Jetz, W., Wilcove, D. S. & Dobson, A. P. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol.* (2007). doi:10.1371/journal.pbio.0050157

113. Beyer, R. M. & Manica, A. Historical and projected future range sizes of the world's mammals, birds, and amphibians. *Nat. Commun.* **11**, 5633 (2020).

114. Beyer, R. M. & Manica, A. Global and country-level data of the biodiversity footprints of 175

crops and pasture. *Data Br.* **36**, 106982 (2021).

115. IDEAM. Cobertura de la Tierra Metodología CORINE Land Cover Adaptada para Colombia Periodo 2018. República de Colombia. Escala 1:100.000. *Instituto de Hidrología, Meteorología y Estudios Ambientales* (2021). Available at: http://www.siac.gov.co/catalogo-de-mapas

116. Souza, C. M. *et al.* Reconstructing Three Decades of Land Use and Land Cover Changes in Brazilian Biomes with Landsat Archive and Earth Engine. *Remote Sens.* **12**, 2735 (2020).

117. MapBiomas. MapBiomas Project - Collection 6 of the Annual Series of Land Use and Land Cover Maps of Brazil. (2021). Available at: https://plataforma.brasil.mapbiomas.org/.

118. Veldman, J. W. & Putz, F. E. Grass-dominated vegetation, not species-diverse natural savanna, replaces degraded tropical forests on the southern edge of the Amazon Basin. *Biol. Conserv.* (2011). doi:10.1016/j.biocon.2011.01.011

119. Portillo-Quintero, C. A. & Sánchez-Azofeifa, G. A. Extent and conservation of tropical dry forests in the Americas. *Biol. Conserv.* (2010). doi:10.1016/j.biocon.2009.09.020

120. Veldman, J. W. *et al.* Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment* (2015). doi:10.1890/140270

121. Zaloumis, N. P. & Bond, W. J. Reforestation or conservation? The attributes of old growth grasslands in South Africa. *Philos. Trans. R. Soc. B Biol. Sci.* (2016). doi:10.1098/rstb.2015.0310

122. Garnett, S. T. *et al.* A spatial overview of the global importance of Indigenous lands for conservation. *Nat. Sustain.* (2018). doi:10.1038/s41893-018-0100-6

123. Djoudi, H., Vergles, E., Blackie, R. R., Koame, C. K. & Gautier, D. Dry forests, livelihoods and poverty alleviation: understanding current trends. *Int. For. Rev.* (2015). doi:10.1505/146554815815834868

124. Forest Peoples Programme. *Ground-truthing to improve due diligence on human rights in deforestation-risk supply chains*. (2020). Available at: https://www.forestpeoples.org/en/ground-truthing-to-improve-due-diligence

125. Drost, S., Rijk, G. & Piotrowski, M. *Oil Palm Growers Exposed to USD 0.4-5.9B in Social Compensation Risk*. Chain Reaction Research (2019). Available at: https://chainreactionresearch.com/wp-content/uploads/2019/12/Social-compensation-risks-for-palm-growers-4.pdf