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

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19 **Abstract**

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

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41 **Main article**

42 Commercial agriculture drives one-quarter of tropical deforestation¹, causing substantial biodiversity
43 loss² and carbon emissions³. Many companies have, therefore, made voluntary ‘zero-deforestation
44 commitments’ (ZDCs) for tropical commodity supply chains^{4,5}. ZDC-compliant commodities cannot
45 be cultivated on recently-forested land, and ZDCs could effectively protect tropical rainforest from
46 encroachment⁶ if uptake of the commitments is widespread⁷. However, ZDCs could then displace
47 agricultural expansion to other biomes: primarily tropical grassy biomes (grasslands, savannas and
48 shrublands⁸) and dry forests (closed-canopy forests with highly seasonal rainfall⁹)^{10,11}. These habitats
49 often lack protection, despite supporting distinct biota and potentially high carbon stocks^{9,12–14}.
50 Without robust guidance to identify and protect their biodiversity, agricultural expansion into these
51 biomes in compliance with ZDCs could undermine benefits of ZDCs for global biodiversity and
52 climate change mitigation.

53 Palm oil is a key deforestation-risk commodity¹⁵, and ZDCs cover two-thirds of global palm oil
54 production volume⁴. Palm oil ZDCs are chiefly implemented through Roundtable on Sustainable Palm
55 Oil (RSPO) certification⁴, which requires expansion to follow the combined High Conservation Value-
56 High Carbon Stock Approach (HCV-HCSA) to determine habitat for protection¹⁶, a methodology also
57 applied to other commodities¹⁷. The HCV-HCSA conserves aboveground carbon and woody
58 vegetation structure (‘HCS’); biodiversity, ecosystem services and social/cultural values (‘HCVs’);
59 peat soils; and requires Free, Prior and Informed Consent before encroaching on community
60 land^{17,18}. However, national-level HCV guidance was originally developed for forestry, and the
61 combined HCV-HCSA was largely developed in response to oil palm-driven deforestation in
62 Southeast Asia¹⁵, so guidance for other habitats is currently limited. Tropical grassy and dry forest
63 biomes differ from rainforest in structure and function^{9,12,13}, which current HCV-HCSA guidance does
64 not address, leading to inconsistent identification of their biodiversity values (Supplementary
65 Information 1). Latin America and Africa support extensive grassy and dry forest biomes, where
66 commercial oil palm is expanding rapidly^{15,19–21}, with irrigation in dry locations²². In Latin America,
67 palm oil production has increased by 60% since 2011²³, and 80% of expansion prior to 2014 replaced

68 cropland, pasture and savanna¹⁹. The largest RSPO-certified plantation in Africa was developed
69 entirely in savanna²⁴, and sites of new certified plantations are frequently selected for their grassy
70 habitat (Supplementary Information 1). Thus, we urgently need to understand the potential for zero-
71 deforestation oil palm expansion in biomes outside tropical rainforest, and consequent biodiversity
72 loss.

73 Here, we generate new maps of climatically-suitable areas for rainfed and irrigated oil palm
74 expansion, based on locations of existing plantations²⁵ (an alternative approach to ‘agro-ecological’²⁶
75 or crop growth²⁷ models), and accounting for water availability for irrigation (unlike existing
76 models²⁷). We assume that ZDCs protect all locations with ≥ 35 Mg ha⁻¹ aboveground carbon and
77 $\geq 30\%$ canopy closure, and/or peat soils from expansion, following the HCSA¹⁷. We find that tropical
78 grassy biomes and dry forests contain nearly 200 Mha climatically-suitable for rainfed or irrigated oil
79 palm expansion in compliance with ZDCs, including locations of high vertebrate richness and
80 overlapping with the ranges of 10% of all threatened vertebrate species. Thus, to minimise
81 biodiversity loss, comprehensive guidelines to identify and manage ‘high conservation values’
82 specific to tropical grassy and dry forest biomes must be developed.

83 **Results**

84 **Potential areas for rainfed oil palm expansion under ZDCs**

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

92 remains potentially available for expansion in compliance with ZDCs, which is six-fold greater than
93 the current planted area of 27 Mha.

94 Current guidance for ZDCs protects a considerably higher percentage of the areas climatically-
95 suitable for expansion in the moist forest biome (rainforest; 93%) than in grassy biomes (43%) or dry
96 forest (51%) (Fig. 2a), because many areas of grassy and dry forest biomes have insufficient
97 aboveground carbon and canopy closure to qualify for protection (Extended Data Fig. 1).

98 Consequently, 95 Mha of the 167 Mha potentially available for expansion under ZDCs are in tropical
99 grassy and dry forest biomes (~four-fold greater than the current planted area), the majority (87%)
100 in the Neotropics and Afrotropics (Fig. 1). Just under half (69 Mha) of the potential area for
101 expansion under ZDCs is in the tropical moist forest biome, which is likely to be highly degraded
102 habitat, such as intensively-managed pasture, because of its low carbon stocks. The 95 Mha of
103 climatically-suitable non-cultivated land in grassy and dry forest biomes includes both degraded
104 pasture and also ancient habitats supporting high biodiversity, which cannot be distinguished by
105 remote sensing, due to superficial similarity between the vegetation types. However, regional
106 analyses in Brazil and Colombia suggest that a greater proportion of moist forest biome has been
107 converted to pasture than other biomes (Supplementary Information 2). Consequently, our findings
108 highlight the potential for zero-deforestation oil palm expansion into ancient, high-biodiversity
109 grassy biome and dry forest habitats, emphasizing the need for sustainable development guidelines
110 for identification and protection of biodiversity specific to these biomes, particularly in the
111 Afrotropics and Neotropics.

112 Our estimates of the total area suitable for zero-deforestation expansion are sensitive to the
113 thresholding of our models of suitability for cultivation (70-375 Mha for three thresholds tested), to
114 the choice of suitability model (223 Mha according to an existing agro-ecological model²⁶, of which
115 110 Mha overlap with our model; Extended Data Fig. 2), and to habitat protection thresholds under
116 ZDCs (358 Mha under a scenario of weaker habitat protection, compared to 167 Mha under greater

117 habitat protection which we present in the Main Article). Nevertheless, this variation does not affect
118 our conclusion that tropical grassy and dry forest biomes, especially in the Neotropics and
119 Afrotropics, contain the largest areas suitable for expansion under ZDCs (Supplementary Information
120 3).

121 **Potential for ecoregion-level habitat loss**

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

138 **Yield in areas suitable for oil palm expansion under ZDCs**

139 Overall, 97% of locations suitable for expansion under ZDCs are likely to have low yields under
140 rainfed, high-fertiliser input cultivation (~10 $\text{tha}^{-1}\text{yr}^{-1}$ fresh fruit bunches; inter-quartile range 6.2-
141 16.5 $\text{tha}^{-1}\text{yr}^{-1}$; Fig. 3a), based on recent yields in locations that we estimate as climatically-suitable

142 (see Methods). These low yields of $\sim 10 \text{ tha}^{-1}\text{yr}^{-1}$ are roughly half of yields in existing industrial
143 plantations (median $21 \text{ tha}^{-1}\text{yr}^{-1}$), but are nevertheless likely to be viable for cultivation (see
144 Discussion), although we are unable to account for net profitability. Low yields particularly apply to
145 potential ZDC expansion in grassy biomes (in which 99.8% of climatically-suitable locations for
146 expansion have low expected yield) and dry forests (99.1%), but also tropical moist forests (92.2%).
147 Regardless of ZDCs, 87% of locations suitable for expansion have low expected yields overall
148 (Supplementary Fig. 7; agro-ecological suitability model²⁶ results are similar: Supplementary Fig. 8),
149 possibly because the most suitable locations for oil palm cultivation have already been converted to
150 plantations or cropland (e.g. in Southeast Asia).

151 **Opportunities for improved oil palm yield under irrigation**

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

166 **Potential threats to vertebrate richness**

167 We estimate that effective implementation of ZDCs would substantially reduce vertebrate (mammal,
168 bird and amphibian) richness loss from oil palm expansion in rainforests, by protecting locations with
169 the highest richness within the moist forest biome, and thus globally, from expansion (Fig. 4a).
170 However, ZDCs fail to protect locations of high vertebrate richness within tropical grassy and dry
171 forest biomes in Latin America and Africa, where the largest areas are suitable for zero-deforestation
172 expansion (Fig. 4a). We estimated richness from vertebrate range maps refined by habitat type, and
173 we estimated richness loss as the number of species that cannot persist in plantations, within 10-km
174 grid-cells. Although this grid-cell resolution is likely to overestimate absolute values of richness, the
175 broad patterns of richness loss among biomes and continents are likely to be robust (Supplementary
176 Information 6). In Africa, where the contrast among biomes is greatest, expansion compliant with
177 ZDCs within the moist forest biome would result in substantially less vertebrate richness loss
178 (median 185 species lost per 10-km grid-cell on conversion to oil palm) than expansion in locations
179 protected by ZDCs (median 224 species lost per 10-km grid-cell). By contrast, within grassy biomes in
180 Africa, expansion under ZDCs would result in greater richness loss (median 200 species lost per 10-
181 km grid-cell) than expansion in locations protected by ZDCs (median 169 species lost per 10-km grid-
182 cell; fig 4a), so ZDCs could exacerbate vertebrate richness loss from oil palm expansion. All estimates
183 of vertebrate richness loss assume that expansion is into intact habitat, and thus actual richness
184 losses would be significantly lower if expansion also occurred in areas already converted to
185 intensively-managed pasture (Supplementary Information 2). However, areas of intensively-
186 managed pasture may not always be available for oil palm expansion (see Discussion), and our
187 estimates of richness loss are robust if we assume that intensively-managed pasture is unavailable
188 (Supplementary Fig. 3). Estimates of richness loss are similar for the agro-ecological suitability
189 model²⁶, and when including suitability for irrigation (Supplementary Information 5). Thus, if
190 widespread zero-deforestation oil palm expansion takes place, ZDCs could drive considerable
191 biodiversity loss outside the tropical moist forest biome, despite substantially protecting rainforest
192 biodiversity.

193 **Range reduction of IUCN-threatened vertebrates**

194 Under ZDCs, oil palm expansion in all biomes could decrease the range sizes of IUCN-threatened
195 vertebrates, although reductions are generally small. In total, 28% (879 of 3,155 species) of
196 threatened terrestrial vertebrates could undergo range reduction because these species' ranges
197 overlap with potential rainfed expansion areas, and these species cannot persist in plantations (26%
198 of threatened species according to the agro-ecological suitability model²⁶). However, only a median
199 4.3% of species' total global range overlaps with potential rainfed expansion areas (Fig. 4b). When
200 including locations requiring irrigation, 34% of threatened vertebrates (1,071 species) could undergo
201 range reduction from oil palm expansion under ZDCs (Supplementary Fig. 18). As expected, the
202 majority of these threatened species occur in tropical moist forest (817 species under rainfed
203 expansion; 26% of threatened terrestrial vertebrates), although rainfed expansion in grassy biomes
204 and dry forests could reduce the ranges of 189 threatened vertebrates (6% of all threatened
205 vertebrates for both biomes combined; 10% when including locations requiring irrigation). Overall,
206 there are likely opportunities for ongoing expansion under ZDCs without significant negative impacts
207 on threatened vertebrates, provided that sufficient guidance is developed to identify and protect
208 areas supporting such species.

209 **Discussion**

210 **Suitable areas for oil palm expansion**

211 We generated new empirical models of suitability for oil palm expansion under rainfed and irrigated
212 conditions. Our rainfed suitability model is broadly similar to existing models that were generated
213 using contrasting methods^{26,28}, but with slightly reduced area, suggesting that our estimated
214 potential for expansion is conservative. We modelled suitability based on locations of commercial oil
215 palm mills²⁵, representing areas most climatically similar to those already under commercial
216 cultivation. Our model may therefore have excluded marginal areas that will become increasingly
217 viable for commercial cultivation with the development of new varieties and practices to maintain

218 high yields under climate change^{26,28-30}. A few regions are predicted as suitable in our model but not
219 in other models^{26,28} (e.g. parts of the Caatinga in northern Brazil, Venezuelan Llanos; Extended Data
220 Fig. 2), probably because we accounted for seasonality of water availability by calculating maximum
221 cumulative water deficit in order to capture water stress experienced by growing oil palms³¹
222 (Supplementary Information 7). Areas that we mapped as suitable for irrigated cultivation alone
223 largely coincide with other models that assumed unlimited water availability^{27,28}, but are restricted
224 to locations of sufficient surplus available water to remove the critical rainfed water deficit.

225 Even though we estimated that ZDCs would protect extensive areas, we found considerable
226 potential for expansion under ZDCs. However, we could not account for availability of land (e.g. land
227 ownership), nor exclude areas that should be protected for their biodiversity or local ecosystem
228 service values, which depend on the rigour of local assessments (Supplementary Information 1)¹⁸,
229 suggesting that the actual area available for expansion is much lower than our estimates. Oil palm
230 expansion could also occur in human-modified habitats (existing cropland or tree plantations¹⁷,
231 which we assumed were unavailable, or intensively-managed pasture¹⁹, which we were unable to
232 exclude from our analyses), which would drive less biodiversity loss than in areas of intact habitat
233 (Supplementary Figs. 3, 15), but could in turn displace these land-uses to natural habitat^{11,32}. Our
234 main conclusions appear robust (Supplementary Information 2-5), but local information and
235 mapping are needed to assess likely protection under ZDCs and potential impacts of expansion in
236 detail (Supplementary Information 6).

237 We examine oil palm expansion if ZDCs were widely and effectively implemented. However,
238 increasing numbers of ZDCs^{4,5,33} have not necessarily resulted in action to reduce deforestation⁵, and
239 the impact of ZDCs has not yet been well-studied^{5,34,35}. RSPO certification appears to reduce
240 deforestation^{36,37}, although net benefits are minimal as deforestation increases concurrently
241 elsewhere³⁸, and RSPO-certified palm oil has stagnated at ~19% of global production volume³⁹. Thus,
242 strong sector-wide regulation is imperative for reducing deforestation globally^{33,37,38,40}.

243 **Potential for loss of tropical grassy and dry forest biodiversity**

244 If oil palm production continues to expand rapidly^{41,42}, including under ZDCs, our findings
245 demonstrate the potential for loss of unique biodiversity and habitats in tropical grassy and dry
246 forest biomes in Latin America and Africa^{12,43–46}. Widespread implementation of ZDCs would mitigate
247 global biodiversity loss from oil palm expansion overall, by extensively protecting tropical moist
248 forest, but could also drive conversion of distinct grassy biome and dry forest ecoregions²⁰, and
249 increase expansion in locations of high vertebrate richness within these biomes. Recent soy
250 expansion in the Cerrado has driven substantial habitat loss in a global biodiversity hotspot⁴⁷,
251 possibly as an unintended consequence of the moratorium on expansion in the Brazilian
252 Amazon^{10,11,48,49}, and we highlight the potential for a similar pattern in global oil palm expansion,
253 before widespread conversion of grassy biomes and dry forests has occurred.

254 We estimate relatively small impacts of zero-deforestation oil palm expansion on IUCN-threatened
255 vertebrates overall, but we have likely underestimated the impacts of expansion on biodiversity
256 (Supplementary Information 6). We have not examined potential loss of plant or invertebrate
257 biodiversity from expansion, yet grassy biomes often support high endemism and richness of these
258 taxa⁴⁵, comparable to tropical rainforest in certain ecoregions⁴⁴ (e.g. the Cerrado⁴⁶). Moreover, the
259 locations suitable for expansion under ZDCs in the moist forest biome are likely to be highly
260 degraded (and include large areas of intensively-managed pasture: Supplementary Information 2),
261 whereas suitable areas in grassy biomes and dry forests include intact habitat, such as in the Guinea
262 savanna, Northern Congolian Forest-savanna, and Cerrado^{50,51} (among other ecoregions). Overall,
263 widespread agricultural expansion under ZDCs could have substantial negative impacts on
264 biodiversity, highlighting the need for robust guidance for sustainable agricultural development in all
265 biomes.

266 **Implications for greenhouse gas emissions**

267 We were not able to quantify potential greenhouse gas emissions from zero-deforestation oil palm
268 expansion in this study, because belowground carbon stocks are poorly understood in across the
269 Tropics, particularly in grassy biomes^{12,52}, and aboveground carbon stocks are also poorly quantified
270 outside rainforest^{12,53}. Existing data suggest that belowground carbon stocks in grassy biomes are
271 highly variable and can exceed those of moist forest^{54–56}, resulting in substantial carbon emissions
272 upon conversion to cropland^{50,55}, and upon conversion of degraded pasture to oil palm⁵⁷. Thus, the
273 potential greenhouse gas emissions from conversion of tropical grassy and dry forest biomes to oil
274 palm could be as high as those from rainforest conversion in many locations, but the lack of data on
275 below- and aboveground carbon stocks, and the dynamics of belowground carbon following
276 conversion to oil palm, highlights the need for more research on this topic.

277 **Gaps in current guidance and key recommendations**

278 While tropical conservation efforts have typically focused on rainforests, other biomes are also
279 subject to multiple threats and are less well-protected^{19,12,20,54,58–60}, with ~50% of tropical dry forests
280 already converted to other land-uses⁶¹. Therefore, there is an urgent need for policies and
281 governance for sustainable tropical land-use in all biomes. Current guidance (HCV-HCSA and national
282 interpretations^{16–18}, particularly “Annex 2. Grasslands in HCVs” in ¹⁸) does not recognise important
283 differences between tropical moist forest and grassy and dry forest biomes (e.g. importance of
284 herbaceous vegetation; Supplementary Information 1, Box 1). Many recent oil palm concessions
285 were developed on grassy or savanna habitat to comply with ZDCs, risking that these habitats could
286 become rare through widespread conversion (e.g. savanna in Southern Gabon²⁴; Supplementary
287 Information 1), threatening biodiversity before guidance is comprehensive.

288 Nevertheless, the existing HCV-HCSA provides a framework for implementing comprehensive
289 biodiversity protection in all biomes, like for tropical moist forest^{17,18} (Fig. 2), with a current ‘policy
290 window’ for development of detailed guidance beyond Southeast Asian rainforest. We provide
291 recommendations for such guidance for grassy and dry forest biomes in Box 1. We also recommend

292 that companies extend commitments to ‘no conversion of natural habitat’, to bolster protection for
293 all biomes and support the development of comprehensive guidance for biodiversity protection. The
294 RSPO should stipulate ‘protection of biodiversity in *all biomes*’ in its Principles and Criteria (which
295 require new plantings to follow HCV-HCSA guidance^{17,18})¹⁶, to encourage rigorous HCV assessments,
296 in line with the biodiversity identification and monitoring for all native vegetation types in the Round
297 Table on Responsible Soy standard⁶². The RSPO should incorporate estimation of below-ground
298 carbon storage of natural vegetation and soils into its greenhouse-gas emissions estimates, which
299 are high in some tropical grassy biomes (and moist forests)⁶³, although we acknowledge that soil
300 carbon stocks remain poorly understood^{12,52}, highlighting the need for further research on this topic.
301 RSPO-certified oil palm is increasingly likely to expand in drier areas (Figs. 1, 3, Extended Data Figs. 3,
302 4), exacerbating water scarcity, particularly under irrigation⁶⁴, so detailed guidance for sustainable
303 hydrological development (including irrigation) is also needed.

304 **Sustainably increasing palm oil production**

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

313 Given the potential negative impacts of ongoing expansion for biodiversity, improving yields of
314 existing plantations could also reduce the environmental impacts of oil palm, through sustainable
315 intensification^{70,71}. The low yields we predict (10 tha⁻¹yr⁻¹ in most locations) are similar to yields of
316 Southeast Asian smallholders⁷²; and oil yields of ~2 tha⁻¹yr⁻¹ (assuming a conversion factor of 20%

317 from fresh fruit bunch yield to crude palm oil³¹), are equivalent to the maximum of other oil crops²⁷.
318 Thus, oil palm cultivation may be feasible in these locations. However, yield and economic viability
319 depend on many factors, including costs of labour, seed material, inputs, transportation, and returns
320 from competing land-uses; further research efforts could integrate these with considerations of
321 climatic suitability for expansion. Global productivity could be increased by reducing labour
322 shortages for harvesting⁷³, by implementing best management practices (potentially including
323 irrigation), and/or planting oil palm varieties with broader climatic tolerances^{73,74}. However,
324 increasing yield does not necessarily remove economic incentives for expansion elsewhere⁷⁵. Thus,
325 there is strong need for internationally-coordinated governance to reduce yield gaps, better protect
326 natural habitats, and reduce economic incentives for expansion⁷⁶.

327 **Conclusion**

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

333 **Methods**

334 **Overview**

335 We mapped suitability for rainfed oil palm using the species distribution model Maxent,
336 incorporating locations of current oil palm cultivation (a global dataset of oil palm mills²⁵) and
337 climate data⁷⁷, and selecting the best model from a range of permutations. We evaluated our
338 models of climatic suitability for oil palm by comparing our estimates to current global oil palm
339 plantations derived from the 'Spatial Database of Planted Trees'⁷⁸. We mapped suitability for
340 irrigated oil palm by supplementing monthly rainfall with a recent hydrological dataset of monthly
341 surplus available freshwater⁷⁹. We thereby produced new, up-to-date models of climatic suitability

342 for both rainfed and irrigated oil palm. We conducted analyses for a recent agro-ecological model of
343 suitability for rainfed oil palm²⁶ alongside our new rainfed model, as a sensitivity test. We mapped
344 locations potentially available for oil palm cultivation (locations that have not been transformed to
345 cropland^{80,81}, urban areas^{80,81} or tree plantations⁷⁸, subsequently termed 'non-cultivated land'). We
346 then quantified whether these areas would be protected under ZDCs, and identified their biome
347 type, using four further global spatial datasets: aboveground biomass^{82,83}, canopy closure⁸⁴,
348 peatlands⁸⁵, and terrestrial ecoregions²⁰. To assess the impacts of oil palm expansion on vertebrates,
349 we estimated the potential vertebrate richness of locations we deemed to be climatically-suitable
350 for oil palm, by refining vertebrate range maps^{86,87} according to habitat types suitable for each
351 species. We conducted regional sensitivity analyses (for Brazil and Colombia) that explicitly included
352 intensively-managed pasture as a land-use type, to assess whether our inclusion of intensively-
353 managed pasture as 'non-cultivated land' potentially available for oil palm expansion in our global
354 analyses (alongside primary and secondary vegetation) may have led to inaccuracies in our main
355 findings. We ran all models and analyses at 5' grid-cell resolution (~10 km at the Equator), the finest
356 possible from component datasets; where data were provided at finer resolution, we aggregated
357 them before use. We ran all models and analyses of expansion across all tropical regions (between
358 23.5° N and 23.5° S, except for the regional analyses including intensively-managed pasture, and the
359 refinement of global vertebrate range maps by habitat type), using R version 3.5.2⁸⁸ and ArcGIS Pro
360 version 2.2.0.

361 **Current occurrence of oil palm cultivation**

362 To train our species distribution models of oil palm suitability, we used a global dataset of oil palm
363 mills, collected from major palm oil supply chains and therefore representing occurrence of
364 industrial oil palm cultivation²⁵ (and additionally smallholder cultivation where it is associated with
365 industrial plantations, such as in Southeast Asia). Oil palm fresh fruit bunches require processing
366 soon after harvest³¹, so mills are generally adjacent to plantations⁷⁸. We excluded mills in locations
367 likely to be irrigated and thus cultivated under artificially-altered climatic conditions. We used a

368 global dataset of water withdrawal for irrigation in 2014⁷⁹ to determine locations of potential
369 irrigation, excluding all mills within 10 km of non-zero water withdrawal for irrigation. Additionally,
370 we excluded mills in regions described as having widespread irrigation of oil palm⁸⁹. Our final dataset
371 for locations of current cultivation of rainfed oil palm therefore comprised N = 1021 oil palm mills
372 occupying separate 5' grid-cells of the climate data. We assumed that each of these mills
373 represented one known 'presence' datapoint for oil palm cultivation.

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

386 **Climatic predictors of suitability for oil palm**

387 We derived all climatic predictors from WorldClim v.2 global gridded climate data, averaged for
388 1970-2000, at 5' resolution⁷⁷. We initially selected five climatic predictors known to correlate with oil
389 palm growth and yield³¹: mean annual temperature (°C), minimum temperature of the coldest
390 month (Tmin, °C), mean annual precipitation (mm), an annual moisture index, and maximum water
391 deficit (MWD, mm) (see Supplementary Information 7 for details). Some of these predictors were
392 inter-correlated (Supplementary Table 8), so we ran models with two uncorrelated predictors, Tmin

393 and MWD, which represent the most strongly limiting climatic factors for oil palm growth and
394 yield³¹.

395 We did not include soil parameters as predictors of suitability for oil palm, because oil palm can be
396 cultivated on the majority of tropical soil types, without substantial impacts on yield under
397 appropriate management³¹. Previous estimates suggest that few locations in the tropics have
398 unsuitable soil for oil palm cultivation²⁶. However, we removed areas of mangrove from our
399 predictions of climatically-suitable locations for planting (see below), to remove areas of saline soils,
400 which limit oil palm yield³¹, as well as to remove unsuitable saline flooded areas. We discuss the
401 limitations of our approach in Supplementary Information 6.

402 **Running species distribution models (SDMs)**

403 SDMs have previously been used to model climatic suitability for crops at large spatial scales^{91–93},
404 and Maxent outputs have successfully predicted yield when trained on high-yield locations⁹³, such as
405 the majority of oil palm mill locations (industrial mills supplying global traders)²⁵. We ran SDMs of oil
406 palm suitability using the R package *biomod2*⁹⁴, to provide up-to-date models of climatic suitability
407 for oil palm. We used the SDM Maxent, because it is robust to incomplete datasets^{95–97}, and our oil
408 palm mill locations do not represent all locations suitable for oil palm cultivation across the tropics.
409 When running Maxent, we permitted linear and quadratic relationships with the climate variables³¹
410 but otherwise maintained default settings. We projected all models across the entire tropics for the
411 current climate.

412 Maxent requires randomly-sampled ‘background’ climate data to contrast with the distribution of
413 climatic predictors at ‘presence’ (oil palm mill) locations. We randomly sampled eight sets of 50,000
414 background points (within seven buffer distances from the presence data, spanning 200–2000 km,
415 and additionally with no buffer), weighted by latitude to account for variation in cell area in the
416 unprojected climate grids, to find the optimal buffer size for model performance⁹⁸. We therefore
417 calibrated models with 16 combinations of presence and background locations (two presence

418 datasets, full and subsampled oil palm mills; and eight background datasets). We selected the
419 optimum combination of presence and background datasets based on model evaluation metrics⁹⁸,
420 and found that an intermediate background buffer size was optimal (Supplementary Information 7).
421 We classified the continuous suitability projections (0-1) of the SDM outputs into suitable (which we
422 further classified; see below) and unsuitable locations, using Minimal Predicted Area thresholding
423 based on projected values at the oil palm mill locations^{99,100} (Supplementary Information 7).

424 **SDM evaluation**

425 To examine the robustness of SDMs to spatial prediction, we conducted leave-one-out cross-
426 validation for each model (continuous suitability output) on three spatially distinct portions of the
427 data (Americas, Africa and Asia/Australasia), which we evaluated using the moving window
428 Continuous Boyce Index⁹⁹. We also used the moving window Continuous Boyce Index⁹⁹ to examine
429 full model accuracy (accuracy of models trained with all of the data). We tested the continuous
430 suitability projections of these full models on a largely-independent dataset of oil palm plantations
431 (a map of global tree plantations compiled from mixed sources, largely from remote sensing, with a
432 small subset of oil palm plantations verified against the oil palm mills dataset used to train the
433 models)⁷⁸, with 50,000 randomly selected testing background points. We selected the single best
434 model based on these full-model and cross-validation scores, alongside relative variable importance,
435 for use in our analyses (Supplementary Information 7). Our best model included spatially-
436 subsampled oil palm mills, and background points in a 500km-buffer, and was selected primarily for
437 its high transferability to novel locations, suggesting robustness to spatial extrapolation.

438 To examine the sensitivity of our model outputs to the threshold determining oil palm suitability, we
439 compared the performance of the best model classified into suitable and unsuitable locations (from
440 the continuous suitability output of values 0-1) at three different Minimal Predicted Area thresholds
441 (Supplementary Information 7). To compare these classifications, we tested our projections for each
442 classification on the largely-independent dataset of oil palm plantations⁷⁸ (see above) using the True

443 Skill Statistic to measure predictive accuracy¹⁰¹, and we compared our projections with an agro-
444 ecological model of oil palm suitability²⁶. We found that the mid-range suitability threshold of the
445 three thresholds we tested (Minimal Predicted Area₉₉) gave high values for both of the evaluation
446 metrics (Supplementary Fig. 24), so we present this classification in the results in the Main Article.
447 Our final model of suitability for rainfed oil palm was therefore similar to the agro-ecological
448 suitability model²⁶ (Extended Data Fig. 2), as well as to a recent low-resolution climatic envelope
449 model²¹. As a sensitivity test to our reliance on our new model of oil palm suitability throughout the
450 Results, we also conducted all key analyses for the agro-ecological suitability model²⁶, and for a
451 conservative, ‘high-confidence’ model of areas of overlapping suitability between our final rainfed
452 model and the agro-ecological model. We found that our conclusions are robust to the use of these
453 alternative rainfed suitability models (Supplementary Information 3-5).

454 **Classifying expected oil palm yield**

455 We classified the continuous suitability outputs of the suitable locations from the best SDM (i.e.
456 excluding unsuitable areas) into three suitability classes for oil palm cultivation (low, medium, high),
457 using Minimal Predicted Area thresholding (as we used for classifying suitable and unsuitable areas).
458 Each suitability class contained one-third of the oil palm mills used to train the model, excluding any
459 that fell below the suitability threshold (Supplementary Information 7). We obtained expected yield
460 values for these classes from global maps of oil palm yield in 2010¹⁰², by comparing SDM outputs
461 with all grid-cells where actual yield >0 tha⁻¹ (Supplementary Information 7). For comparison with
462 yield in current industrial plantations, we also extracted 2010 yield values¹⁰² at the locations of oil
463 palm mills used as ‘presence’ locations in the SDMs.

464 **Modelling climatically-suitable locations under irrigation**

465 To simulate locations suitable for oil palm under irrigation, we projected our best SDM to an altered
466 climate, for which we simulated MWD under irrigation (Tmin was unaltered). To calculate potentially
467 ‘irrigated’ MWD, we assumed that months with sufficient surplus available water to remove a critical

468 annual MWD were 'irrigated'. We calculated monthly surplus available water as the difference
469 between monthly gross water demand (m^3 , incorporating demand from households, industry,
470 livestock and irrigation) and total renewable supply (m^3 , incorporating unused desalinated water,
471 renewable groundwater, and runoff from rivers, reservoirs and lakes), averaged for each month for
472 2005-2009^{79,103}, and we converted this to mm by dividing by grid-cell area (m^2). To simulate
473 irrigation, we assumed a critical annual cumulative water deficit (at which oil palm begins to suffer
474 water stress) of 100 mm, corresponding to empirical values of critical deficit³¹, driving a ~10%
475 decrease in yield¹⁰⁴, and to average monthly evapotranspiration for oil palm¹⁰⁵. For locations
476 requiring irrigation (i.e. with annual MWD >100 mm), we supplemented rainfall with surplus
477 available water in the months with a moisture deficit (i.e. with rainfall < potential
478 evapotranspiration, calculated according to the Hargreaves Equation^{106,107}). Where monthly surplus
479 available water was sufficient to reduce the annual MWD to <100 mm, we assumed that irrigation
480 would be applied, because it could successfully remove the critical water deficit. Where monthly
481 surplus available water was insufficient to reduce MWD to <100 mm, we used MWD based on
482 rainfall alone. We tested the sensitivity of our estimates of suitability for irrigated oil palm
483 cultivation to monthly surplus available water, and found that using 100% of surplus available water
484 increases the area of non-cultivated land suitable for irrigated-only oil palm expansion by ~50%
485 compared to using 50% of surplus available water (Supplementary Information 4). Our maps of
486 suitability for irrigated oil palm contain some suitable zones of ~1° resolution, because Sutanudjaja
487 *et al.* in ⁷⁹ account for local water redistribution by pooling renewable water supply from desalinated
488 and surface water across ~1° zones⁷⁹ (Extended Data Figs. 3, 4).

489 **Mapping non-cultivated land**

490 We determined terrestrial non-cultivated land using Copernicus 2015 high-accuracy global land-
491 cover data^{80,81}, first excluding all permanent water bodies^{80,81} and mangrove habitats²⁰. We used the
492 global land-cover data^{80,81} to exclude locations of cropland and urban areas, and a comprehensive
493 database of global tree plantations (including oil palm plantations: Spatial Database of Planted

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

501 **Mapping protected areas**

502 We used the Protected Planet World Database on Protected Areas¹⁰⁸ to identify areas that are
503 protected from conversion to agriculture. We included all terrestrial protected areas of IUCN classes
504 I and II, which are most strictly protected (by law) and therefore least likely to undergo
505 conversion¹⁰⁹. For a subset of protected areas without a shapefile, we estimated protected area
506 coverage as circles centred on point coordinates, corresponding to the reported protected area size
507 (km²)¹¹⁰. We considered a protected area to occupy a 5' grid-cell if its polygon covered the cell
508 centre.

509 **Determining protection under ZDCs**

510 During impact assessments for development of zero-deforestation oil palm plantations, HCSA
511 guidance designates locations for conservation based on their vegetation structure¹⁷. The vegetation
512 stratification is designed to vary by location and habitat type, but has only been developed for moist
513 forest in Southeast Asia to date¹⁷. We therefore applied the stratification thresholds generically
514 across the tropics, regardless of continent or biome, although in practise they could vary during local
515 application. Under the HCSA, all locations with vegetation dominated by trees >30cm diameter at
516 breast height, with >50% canopy closure and aboveground carbon of approximately >75 Mg ha⁻¹
517 ('low density forest') are designated for conservation. All locations dominated by trees 10-30cm
518 diameter at breast height, with 30-40% canopy closure and aboveground carbon of ~35-75 Mg ha⁻¹

519 ('young regenerating forest') are considered potential areas for conservation¹⁷. If these 'young
520 regenerating forest' areas support additional conservation values identified in the 'High
521 Conservation Value' assessment (conducted in tandem with the HCSA), or represent a significant
522 habitat area in the landscape, they are designated for protection¹⁷. We therefore computed two
523 scenarios to represent likely habitat protection under this scheme: in which all locations
524 corresponding to (i) 'low density forest' are protected (weaker habitat protection), and (ii) all 'young
525 regenerating forest' are additionally protected (greater habitat protection). We mapped these
526 scenarios using global datasets of canopy closure⁸⁴ and aboveground biomass ('GlobBiomass')^{82,83},
527 assuming that 50% of biomass is carbon¹¹¹. For both scenarios, we included all locations with peat
528 soils as protected from cultivation⁸⁵. We found that the two HCSA scenarios for habitat protection
529 give similar patterns of potential availability for conversion across biomes and continents; therefore,
530 we present the 'greater habitat protection' scenario (protection of 'young regenerating forest', ≥ 35
531 Mg ha^{-1} aboveground carbon and $\geq 30\%$ canopy closure) in the Main Article, and 'weaker habitat
532 protection' ('young regenerating forest', $\geq 75 \text{ Mg ha}^{-1}$ aboveground carbon and $\geq 50\%$ canopy closure)
533 in Supplementary Information 2-5.

534 In addition to HCSA assessments, HCVs are also identified for protection prior to oil palm
535 development¹⁷. However, we did not attempt to map these additional conservation values (e.g.
536 presence of rare species in local habitat patch, conservation of socio-cultural values) because they
537 cannot be captured reliably through global mapping, and require local case-by-case identification,
538 based on on-the-ground data and stakeholder consultations. Furthermore, many of the national
539 interpretations for HCVs were originally developed for forestry, and have not subsequently been
540 developed for habitats other than tropical moist forest (Supplementary Information 1). Tropical
541 grassy biomes are fundamentally different in biota and functioning to forests¹² and therefore require
542 separate criteria to identify areas with HCVs, so the extent of habitat protection for these biomes
543 varies depending on the approach taken by the assessor(s) (Supplementary Information 1). We
544 discuss the limitations of this approach in Supplementary Information 6.

545 **Biome and biogeographic realm classification**

546 We based our biome classification on the most recent map of Terrestrial Ecoregions of the World²⁰.

547 We reclassified the biome assigned to 25 of 391 non-mangrove ecoregions, using ecological
548 literature, expert knowledge of these habitats and the classification used in Murphy et al. 2016⁴⁴,
549 mostly ensuring that grassland, savanna, shrubland and woodland ecoregions with a continuous
550 grassy understorey were identified as 'tropical grassy biome'⁸ (Extended Data Table 1). For our
551 analyses, we then grouped 'tropical & subtropical moist broadleaf forest' ecoregions as tropical
552 moist forest; 'tropical & subtropical dry broadleaf forest' ecoregions as tropical dry forest;
553 ecoregions classified as 'tropical and subtropical grasslands, savannas and shrublands', 'montane
554 grasslands and shrublands' and 'flooded grasslands and savannahs' as tropical grassy biomes; and
555 ecoregions classified as 'deserts and xeric shrublands' and 'tropical and subtropical coniferous
556 forests' as 'other' biomes.

557 We also used the map of global ecoregions²⁰ to classify locations by biogeographic realm. Because
558 our region of interest is the tropics, we reclassified the realm of eight ecoregions in North Africa and
559 the Arabian Peninsula, which had small suitable areas (median 161 km² under suitability threshold
560 Minimal Predicted Area₁₀₀) to 'Afrotropic' from 'Palearctic'.

561 **Impacts of oil palm expansion on vertebrates**

562 Following references^{112–114}, we estimated potential vertebrate richness loss from oil palm expansion
563 as the difference between richness (total number of species occurring in a grid-cell) of natural
564 habitat, and richness of oil palm plantations (i.e. species that can persist in plantations). To estimate
565 species' occurrence, we refined global range maps for three well-documented taxa (mammals, birds
566 and amphibians)^{86,87} according to Terrestrial Ecoregions of the World biome classification²⁰, and
567 locations of cropland, urban areas^{80,81} and tree plantations⁷⁸. We considered a species as 'present' in
568 a given grid-cell if its original range map contained the grid-cell centre, and if the biome or
569 transformed habitat type (cropland, urban, tree plantation) of the grid-cell was listed as suitable for

570 the species, following matching in Supplementary Table 7. Similarly, we considered that a species
571 remained 'present' in a grid-cell following conversion to oil palm if its list of suitable habitats
572 included 'plantation' (see Supplementary Fig. 15 for species richness maps). We also quantified
573 threatened species' (vulnerable, endangered or critically endangered in the IUCN Red List) potential
574 range reduction from conversion to oil palm, by examining the overlap of locations suitable for oil
575 palm expansion and threatened species' refined range maps.

576 **Sensitivity analyses including intensively-managed pasture**

577 We were unable to account for locations of intensively-managed (improved) pasture globally,
578 because there are no global datasets accurately distinguishing this land-use type from low-intensity
579 natural or anthropogenic grazing⁸. We therefore used two recent, national landcover maps that
580 distinguish intensively-managed pasture from natural grassy biome to conduct sensitivity analyses of
581 our key results to the inclusion of pasture. We re-ran our main analyses for Colombia and tropical
582 Brazil (i.e. North of -23.5°), incorporating intensively-managed pasture from IDEAM 2018 landcover
583 for Colombia¹¹⁵, and MapBiomias 2020 landcover for Brazil^{116,117}. These datasets were developed by
584 machine learning classification of satellite images with manual verification, incorporating local land-
585 use statistics, biome type and expert knowledge (see Supplementary Information 6 for a discussion
586 of their limitations). For both Brazil and Colombia, greater areas of forested biomes that we
587 estimated as suitable for oil palm expansion had already been converted to pasture, in comparison
588 to grassy biomes, suggesting that our conclusion that high-biodiversity habitats in grassy biomes are
589 particularly vulnerable to oil palm expansion under ZDCs is robust (Supplementary Information 2).
590 Our estimates of vertebrate richness loss from zero-deforestation oil palm expansion also appear
591 robust, assuming that the areas already converted to intensively-managed pasture are unavailable
592 for expansion. However, if pasture is available for expansion, we will have overestimated potential
593 vertebrate richness loss in substantial areas of intensively-managed pasture (e.g. moist and dry
594 forest in Brazil and Colombia: Supplementary Fig. 3).

595 **Data Availability**

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

599 **Code Availability**

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

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605 5 arc-minute resolution. We thank Christopher Wheatley and Colin Beale for assistance in running oil
606 palm suitability models and analysing results, and Daisy Dent, Angela Hodge and Chris Thomas
607 helpful comments during development of the article.

608 **Author Contributions**

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

613 **Competing interests**

614 The authors declare no competing interests.

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616

617 **Tables**

618 **Table 1. Areas of individual ecoregions suitable for oil palm expansion under ZDCs.** Data are provided for the
 619 20 ecoregions with the largest area suitable, for (a) rainfed, and (b) both rainfed and irrigated cultivation.
 620 Ecoregion names in **bold** are present in both (a) and (b), i.e. rank in the top 20 ecoregions with the largest
 621 suitable area for both rainfed-only (a) and rainfed and/or irrigated expansion (b) under ZDCs. Realms are
 622 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%)
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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 remain¹¹⁹. 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 intactness¹²⁰, 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).

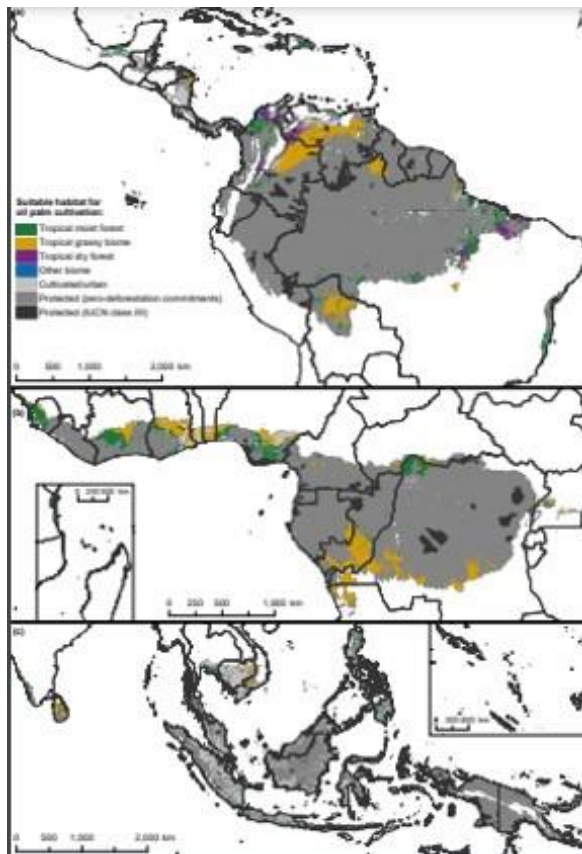
Recommendations: Biodiversity survey design to reflect disturbance regimes (e.g. by conducting repeat plant surveys before and after disturbance events), and landscape-scale factors (e.g. habitat variation, large vertebrate migration routes).

- 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 biomes¹²². 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 people¹²³.

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 communities¹², and thus highlights the urgent need for improved practice of Free, Prior and Informed Consent^{124,125}.

642 **Figure legends**

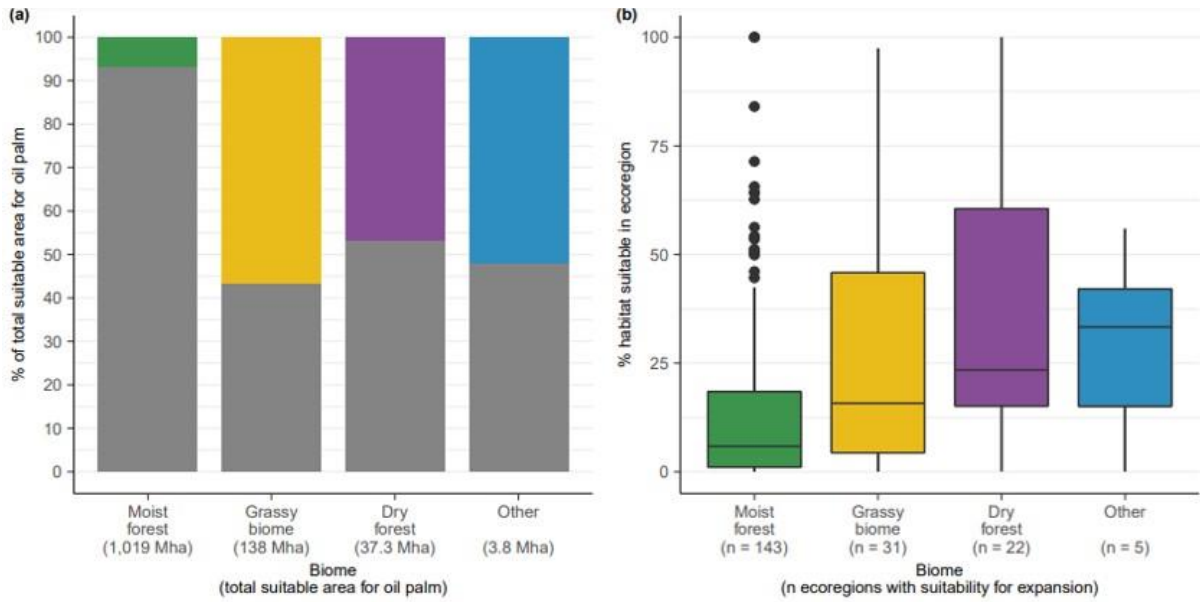
643 **Figure 1. Climatically-suitable locations for rainfed oil palm expansion under zero-deforestation**
644 **commitments (ZDCs), by biome.** (a) Neotropics, (b) tropical Africa, (c) tropical Asia and Australasia. Insets: (b)
645 East coast of Africa and Madagascar, (c) South Pacific. Locations of 'other' biome are largely Neotropical 'xeric
646 shrublands' with relatively high rainfall.
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650 **Figure 2. Comparison of potential for rainfed, zero-deforestation oil palm expansion among biomes.** (a)
651 Estimated protection of climatically-suitable areas for rainfed oil palm expansion under zero-deforestation
652 commitments (ZDCs), according to the High Carbon Stock Approach (HCSA). Data are plotted as a percentage
653 of the total climatically-suitable area of non-cultivated land by biome; this total suitable area is shown in
654 brackets along the x axis. Locations that would be protected under ZDCs are shown in grey and locations
655 potentially available for ZDC expansion are shown in colours (see Fig. 1). (b) Potential for loss of remaining
656 non-cultivated land of individual ecoregions (i.e. percentage of remaining non-cultivated land per ecoregion
657 that is climatically-suitable for expansion under ZDCs). Boxplot centre lines show the median, lower and upper

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

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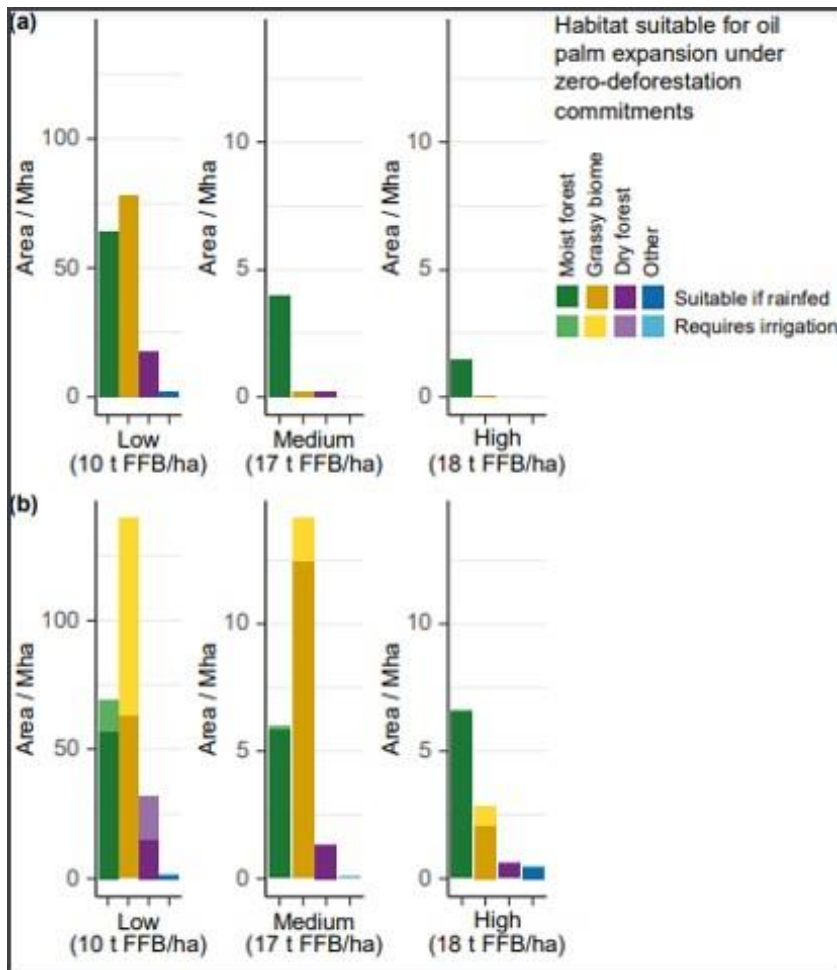
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663 **Figure 3. Expected annual fresh fruit bunch (FFB) yields in locations climatically-suitable for oil palm**

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

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677 **Figure 4. Potential impacts of rainfed, zero-deforestation oil palm expansion on vertebrates.** (a) Vertebrate

678 species richness change (mammals, birds and amphibians; negative values denote number of species lost),

679 from conversion of natural habitat to oil palm, by expected protection under ZDCs, within each biome and

680 continent. Boxplots show potential richness change of non-cultivated land climatically-suitable for oil palm

681 expansion, where each datapoint is a 10-km grid-cell (sample sizes are given to the lower right of each

682 boxplot). Richness loss in 'Other' biomes is negligible and shown in Supplementary Information 5. (b) Potential

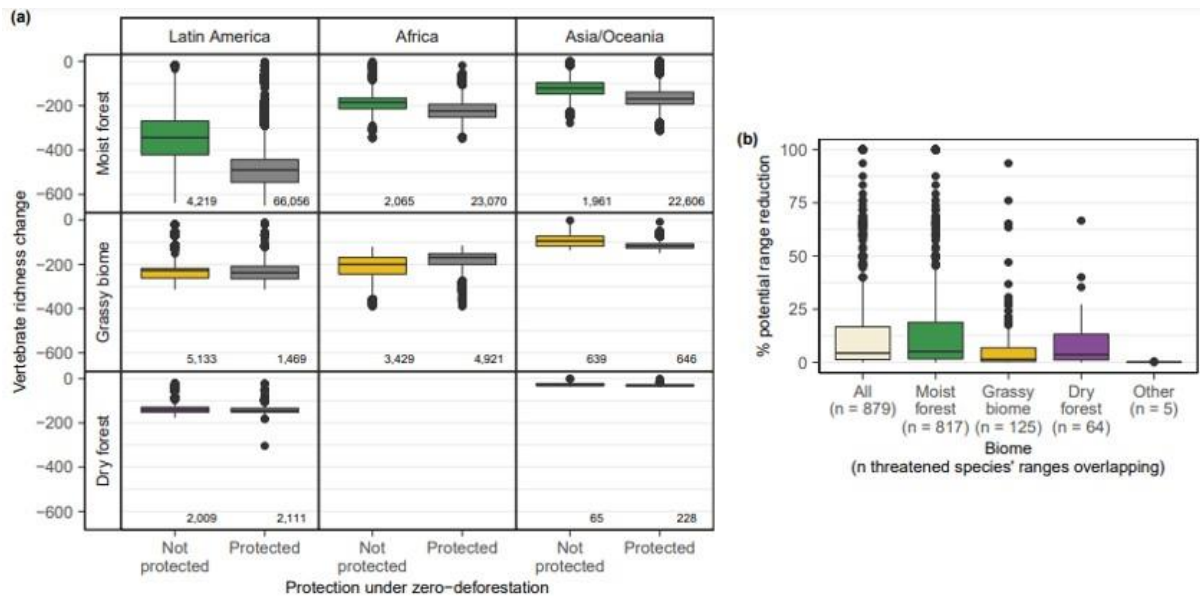
683 percentage range reduction of threatened vertebrates, from oil palm expansion under ZDCs (overlap between

684 ranges of threatened vertebrates and locations climatically-suitable for expansion), for all species which could

685 undergo range loss from expansion (i.e. species that have some range overlap with potential expansion

686 locations and cannot persist in oil palm). Numbers of species overlapping with potential expansion locations

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