

# Primates in peril: the significance of Brazil, Madagascar, Indonesia and the Democratic Republic of the Congo for global primate conservation

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Primates occur in 90 countries, but four—Brazil, Madagascar, Indonesia, and the Democratic Republic of the Congo (DRC)—harbor 65% of the world's primate species (439) and 60% of these primates are Threatened, Endangered, or Critically Endangered (IUCN Red List of Threatened Species 2017-3). Considering their importance for global primate

conservation, we examine the anthropogenic pressures each country is facing that place their primate populations at risk. Habitat loss and fragmentation are main threats to primates in Brazil, Madagascar and Indonesia. However, in DRC hunting for the commercial bushmeat trade is the primary threat. Encroachment on primate habitats driven by local and global market demands for food and non-food commodities hunting, illegal trade, the proliferation of invasive species, and human and domestic-animal borne infectious diseases cause habitat loss, population declines, and extirpation. Modeling agricultural expansion in the 21st century for the four countries under a worst-case-scenario, showed a primate range contraction of 78% for Brazil, 72% for Indonesia 62% for Madagascar and 32% for DRC. These pressures unfold in the context of expanding human populations with low levels of development. Weak governance across these four countries may limit effective primate conservation planning. We examine landscape and local approaches to effective primate conservation policies and assess the distribution of protected areas and primates in each country. Primates in Brazil and Madagascar have 38% of their range inside protected areas, 17% in Indonesia and 14% in DRC, suggesting that the great majority of primate populations remain vulnerable. We list the key challenges faced by the four countries to avert primate extinctions now and in the future. In the short term, effective law enforcement to stop illegal hunting and illegal forest destruction is absolutely key. Long-term success can only be achieved by focusing local and global public awareness, actively engaging with international organizations, multinational businesses and consumer nations to reduce unsustainable demands on the environment. Finally, the four primate range states need to ensure that integrated, sustainable land-use planning for economic development includes the maintenance of biodiversity and intact, functional natural ecosystems.

## 1 Review Article

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81

82 **ABSTRACT**

83 Primates occur in 90 countries, but four—Brazil, Madagascar, Indonesia, and the Democratic  
84 Republic of the Congo (DRC)—harbor 65% of the world’s primate species (439) and 60% of  
85 these primates are Threatened, Endangered, or Critically Endangered (IUCN Red List of  
86 Threatened Species 2017-3). Considering their importance for global primate conservation, we  
87 examine the anthropogenic pressures each country is facing that place their primate populations  
88 at risk. Habitat loss and fragmentation are main threats to primates in Brazil, Madagascar and  
89 Indonesia. However, in DRC hunting for the commercial bushmeat trade is the primary threat.  
90 Encroachment on primate habitats driven by local and global market demands for food and non-  
91 food commodities hunting, illegal trade, the proliferation of invasive species, and human and  
92 domestic-animal borne infectious diseases cause habitat loss, population declines, and  
93 extirpation. Modeling agricultural expansion in the 21st century for the four countries under a  
94 worst-case-scenario, showed a primate range contraction of 78% for Brazil, 72% for Indonesia  
95 62% for Madagascar and 32% for DRC. These pressures unfold in the context of expanding  
96 human populations with low levels of development. Weak governance across these four  
97 countries may limit effective primate conservation planning. We examine landscape and local  
98 approaches to effective primate conservation policies and assess the distribution of protected  
99 areas and primates in each country. Primates in Brazil and Madagascar have 38% of their range  
100 inside protected areas, 17% in Indonesia and 14% in DRC, suggesting that the great majority of  
101 primate populations remain vulnerable. We list the key challenges faced by the four countries to  
102 avert primate extinctions now and in the future. In the short term, effective law enforcement to  
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104 be achieved by focusing local and global public awareness, actively engaging with international  
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106 on the environment. Finally, the four primate range states need to ensure that integrated,  
107 sustainable land-use planning for economic development includes the maintenance of  
108 biodiversity and intact, functional natural ecosystems.

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## 113 INTRODUCTION

114 A recent evaluation of primate species worldwide indicated that more than half are facing near-  
115 term extinction due to unsustainable human activities (*Estrada et al., 2017*). According to the  
116 IUCN Red List, wild primates occur in 90 countries across the Neotropics, Africa, and Asia.  
117 Sixty-five per cent of primate species (286 of 439 species), however, are found in only four  
118 countries, —Brazil, Madagascar, Indonesia, and the Democratic Republic of the Congo (DRC)  
119 (*IUCN, 2017*). Based on a comprehensive literature review, we compare the anthropogenic  
120 pressures faced by each of these four countries that place primate populations at risk, analyzing  
121 differences and similarities affecting land cover changes caused by agricultural expansion,  
122 mining and fossil fuel extraction, and local and international trade demands for food and nonfood  
123 commodities. We discuss the impact of bushmeat hunting, illegal trade and zoonotic, human and  
124 domestic-animal borne infectious diseases on primate population persistence. This information is  
125 analyzed within the context of an increasing human population with low levels of human  
126 development, income inequality, political instability, and weak governance. We model the  
127 expansion of agricultural during the 21<sup>st</sup> century and identify areas of expected spatial conflict  
128 between new crop production and primate distributions in each country. We provide an  
129 examination of the conservation value of protected areas, of habitat restoration, and forest  
130 connectivity at the landscape level, and stress the importance of community managed forests,  
131 where appropriate, for primate conservation at the local level. We further discuss socially  
132 oriented conservation actions by NGOs and governments for averting local primate extinction. In  
133 our conclusion, we discuss the multiple challenges faced by Brazil, Madagascar,  
134 Indonesia and DRC, as well as the global community to ensure the conservation of their unique  
135 primate fauna.

## 136 Survey methodology

137 We conducted a thorough (at the time of writing) review of the peer-reviewed scientific  
138 literature. We integrated the most recent evaluation for primate species conservation status in  
139 each country from the **International Union for the Conservation of Nature** (*IUCN, 2017*) and  
140 information from **Global Forest Watch**, along with the published literature, to evaluate trends in  
141 forest loss between 2001 and 2016 in each country and its effect as a major threat to primate  
142 survivorship. Information from **FAO** (Food and Agriculture Organization of the UN) was used to  
143 profile industrial agriculture expansion in the four countries for the same period. We complement  
144 these results with a summary of spatial conflict between primate species' distributions and  
145 predicted agricultural expansion during the 21<sup>st</sup> century for each country. Species distributions  
146 were obtained from the **IUCN** range maps (*IUCN, 2017*). Agricultural expansion is derived from  
147 remote sensing data from **IMAGE** (Integrated Model to Assess the Global Environment;  
148 [http://themasites.pbl.nl/models/image/index.php/Agricultural\\_economy](http://themasites.pbl.nl/models/image/index.php/Agricultural_economy)) and represents the  
149 predicted presence (irrespective of the intensity) of agricultural production at each grid cell (0.5°  
150 of spatial resolution; see *Dobrovolski et al., 2014*). We document the pressures exerted by  
151 international commodities trade on primate habitat loss and degradation using information from  
152 the **International Trade Centre** (<http://www.intracen.org/>). Legal and illegal primate trade was  
153 documented from the **CITES** (Convention on International Trade in Endangered Species of Wild  
154 Fauna and Flora) trade database and from published reports. Information on human population  
155 growth and socioeconomic metrics in each country was profiled with information from FAO and  
156 the World Bank. Civil conflict and quality of governance indicators for each country were

157 obtained from the **2017 Global Peace Index of the Institute for Economics and Peace**  
158 (<http://economicsandpeace.org/>) and from the **World Bank**. We assessed the distribution of  
159 protected areas and primate ranges in the four countries using information from the **Protected**  
160 **Planet** of the UN Environmental Program *UNEP-WCMC (2017)*, the **IUCN Red List**, and forest  
161 cover data from *Hansen et al., 2013*. We included 2190 protected areas in the Brazil dataset, 49  
162 in DRC, 147 in Madagascar and 646 in Indonesia (*Text S1*). We gather information on the **2016**  
163 **Corruption Perceptions Index (CPI)** of Transparency International  
164 (<https://www.transparency.org>) for each country and obtained, from the World Bank, average  
165 values for the four countries of four indicators of governance quality in 2016  
166 (<http://info.worldbank.org/governance/wgi/index.aspx#reports>). We compared these to the  
167 average values for 35 high-income countries

168 We are aware that some of the datasets we consulted vary in their level of reliability an  
169 objectivity. For example, some data from **FAO** and the **World Bank** are based on information  
170 provided directly by host governments, and therefore may be incomplete or reflect broad  
171 estimates. Similarly, data from the **IUCN** on the population size, distribution, and conservation  
172 status of certain rare, cryptic, or highly inaccessible primate species are based on surveys or  
173 census methods that may vary in completeness, and therefore final determinations are subject to  
174 a consensus based on “expert opinion”. In other cases, the data are obtained through careful  
175 monitoring by an agency (e.g. **International Trade Centre, Transparency International**) or  
176 were independently corroborated using remote sensing to add increased reliability (e.g., **Global**  
177 **Forest Watch, IMAGE, Protected Planet**). Each of the agencies we used as sources of  
178 information stipulate in their portals the limitation of the data they presented (see *Text S1* for a  
179 list and the relevant URLs). We note that although the numbers reported may vary in their level  
180 of accuracy, the trends within and between each country are consistent with high confidence.

181

### 182 **Richness of primate species and IUCN threatened status and population status**

183 While Brazil, Madagascar, Indonesia and DRC differ significantly in their human population  
184 demography, culture, history, and economy, they are important reservoirs for the world’s  
185 biodiversity, with each considered a megadiverse country (*Mittermeier, Robles Gil &*  
186 *Mittermeier, 1997; Table S1, Text S1*). They also harbor a nonoverlapping and significant share  
187 (65%; n = 286 species) of the world’s nonhuman primate species (n = 439 species): Brazil – 102  
188 primate species, 17 genera; Madagascar – 100, 15 genera; Indonesia – 48, 8 genera; and DRC –  
189 36, 15 genera. This includes 55 genera and all 16 recognized nonhuman primate families (*IUCN,*  
190 *2017; Table S2, Fig. 1*). Each country’s primate population is imperiled by the expanding  
191 pressures of human activities and, as a group, 62% of their primate species are Threatened (i.e.  
192 assessed as either Vulnerable, Endangered or Critically Endangered on the IUCN Red List) and  
193 60% are declining (*IUCN, 2017; Fig. 1*). The two countries with the greatest number of  
194 Threatened and declining primate species are Madagascar and Indonesia followed by Brazil and  
195 DRC (*Fig. 1*).

### 196 **Large-scale encroachment and loss of primate habitats**

#### 197 **Trends in forest loss**

198 Habitat loss is a major driver of local extirpation of primate species. Using information from the  
199 Global Forest Watch database (*GFW, 2018; Hansen et al., 2013*) we found a general increase in

200 loss of forest (defined as >30% canopy cover), for the period 2001 to 2016 in all four countries  
201 (Fig. 2A). Total forest loss for the period was 46.43 M ha for Brazil, 23.08 M ha for Indonesia,  
202 10.52 M ha for DRC and 2.75 M ha for Madagascar (Fig. 2B; Table S3). Brazil's initiatives to  
203 combat deforestation resulted in important reductions in forest loss (80%) from 2005 to 2012  
204 (Fig. 2; *Nepstad et al., 2014*; *PRODES, 2018*), although in biomes such as the dry forests of the  
205 *Cerrado*, deforestation continued at high rates (*Strassburg et al., 2017*). Unfortunately,  
206 deforestation in Brazil increased sharply in 2016 (Fig. 2 A, B), probably the result of a shift in  
207 government policies that have relaxed conservation laws (*Brançalion et al., 2016*).

208

209 Importantly, between 2000 and 2013 each of the four countries experienced losses in their  
210 remaining area of Intact Forest Landscapes (IFL; *Potapov et al., 2017*). The largest percent of  
211 IFL losses occurred in Madagascar and Indonesia, followed by Brazil and DRC (Table 1). These  
212 trends highlight important reductions in primate habitats that are exacerbated by increases in  
213 low-density, small-scale deforestation, which is more difficult to identify and track  
214 (*Kalamandeen et al., 2018*). For example, in Amazonia, the number of new small clearings (<1  
215 ha) increased by 34% between 2001–2007 and small-scale low-density forest loss (km<sup>2</sup> forest  
216 loss per 100 km<sup>2</sup>) expanded markedly between 2008–2014. Overall, cleared forest patches less  
217 than 6.25 ha accounted for ~34% of the total Brazilian Amazon forest lost between 2001 and  
218 2014, including in forest loss in reserves that are described as protected areas (*Kalamandeen et*  
219 *al., 2018*). In 2000, DRC was reported to have almost 2 M km<sup>2</sup> of forest (>30% canopy cover)  
220 (*GFW, 2018*). Of this, 32% was classified as Intact Forest Landscape (*Potapov et al., 2017*) and  
221 (36%) as hinterland forests (minimally disturbed forests, *Tyukavina et al., 2013*). Between 2000  
222 and 2013, 4.2% of DRC's intact forests were lost (Table 1; *Potapov et al., 2017*), and in total  
223 5.3% of the country's total forest was lost between 2001 and 2016 (*GFW, 2018*). Over the past 5  
224 years, DRC has experienced a mean annual forest loss of approximately 0.5%, the lowest of the  
225 four countries in this analysis.

226

227 Wide range tropical deforestation also results in forest fragmentation, leading to higher  
228 extinction rates in local populations (*Hanski et al., 2013*). A recent study predicts that additional  
229 forest loss will result in a large increase in the total number of forest fragments in the Neotropics,  
230 Africa and Asia, accompanied by a decrease in their size (*Taubert et al., 2018*). In general,  
231 extinction risk increases with decreasing fragment size (*Hanski et al., 2013*).

232

### 233 Trends in expansion of agricultural land

234 Keeping in mind the limitations of statistics reported by the Food and Agriculture Organization  
235 of the United Nations (information provided to the FAO comes directly from host governments  
236 who may provide incomplete data), from 2001 to 2015 the combined estimated increase of  
237 agricultural land in Brazil, Madagascar, Indonesia, and DRC totaled some 29.5 M ha (see Text  
238 S1, Fig S1, Table S4), with Brazil having the largest increase (19.1 M ha) followed by Indonesia  
239 (9.3 M ha), DRC (650 K ha), and Madagascar (572 K ha) (Table S4) (for estimates of trends in  
240 the production of key crops in each country for the period 2001-2015 see Fig. S2 to S5 and Text  
241 S1). The agricultural footprint (increase of agricultural area as percent of land area, based on data  
242 from FAO and the World Bank; Table S4) for this period was 4.89% for Indonesia, 2.25% for  
243 Brazil, 0.97% for Madagascar, and 0.28% for DRC. In the case of DRC, a higher footprint  
244 estimate of 1.20% has been reported for rural areas (period from 2000-2010) resulting in the  
245 addition of 2.77 M ha of rural roads, villages, and active and abandoned fields and gardens. This

246 rural complex accounted for 13.1% of DRC's total land area in 2015 (*Molinario et al., 2015*).  
247 Between 2000-2010, the overall loss of "core forest" (which made up 36.6% of the 2010 land  
248 area) to perforated forest, patch forest, fragmented forest or edge was estimated at 3.8%  
249 (*Molinario et al. 2017*). The main cause of forest loss in DRC (92%) was shifting cultivation  
250 (*Molinario et al., 2017*).

251

### 252 **Projected agricultural expansion and primate range contraction in the 21<sup>st</sup> century**

253 Increases in species extinction risk are typically related to the loss of individual populations and  
254 associated declines in their geographical range (*Ceballos & Ehrlich, 2002; Wolf & Ripple, 2017*).  
255 A global study modeling conflict between agricultural expansion and primate species'  
256 distributions predicted that during the 21<sup>st</sup> century, regions expected to be converted from forest  
257 to agricultural production account for 68% of the area currently used by primates, and that  
258 worldwide this will lead to unsustainable spatial conflict for 75% of primate species (*Estrada et*  
259 *al., 2017*). Modeling agricultural expansion in the 21<sup>st</sup> century for the four countries under a  
260 worst-case-scenario, shows a primate range contraction of 78% for Brazil, 72% for Indonesia,  
261 62% for Madagascar and 32% for DRC (*Figs. 3, 4*). A business-as-usual scenario also predicts  
262 high spatial conflict while an optimistic scenario predicts significantly lower spatial conflict (*Fig.*  
263 *S6*). This suggests that targeted policies designed to shift agricultural expansion to already  
264 altered landscapes in order to minimize habitat fragmentation and loss of existing forest is  
265 critical in limiting spatial conflicts in each country (*Dobrovolski et al., 2013, 2014*). Global  
266 dietary changes, towards eating more meat, greater dependence on vegetable oils, and, to a lesser  
267 extent, more coffee, tea, among others. as countries develop, will require these primate-rich  
268 countries to convert additional forested land into monocultures to meet local and global market  
269 demands (*Kastner et al. 2012; Tilman & Clark, 2014*). Other threats such as hunting, logging,  
270 mining, fossil fuel extraction, anthropogenic infectious diseases, and climate change also are  
271 expected to result in primate range contraction (see below).

272

### 273 **Other large-scale stressors**

#### 274 **Logging, mining and fossil fuel extraction and primate habitat loss and degradation**

275 Since the 1980s, the extraction of hardwoods has increased in the four countries in response to an  
276 ever-expanding worldwide demand for tropical timber (*Estrada, 2012*). This has resulted in  
277 deforestation and new economic incentives to construct roads in forested areas (*Alamgir et al.,*  
278 *2017*). Although some primate species can survive temporarily in logged forests, both legal and  
279 illegal logging result in a decrease of canopy cover, reduced humidity in the subcanopy and  
280 undergrowth that increases tree mortality, the incidence of ground fires, a decline in forest  
281 undergrowth, and negatively impacts the regeneration of large tree species that provide food,  
282 resting sites, and refuge for primates (*Alisjahbana & Busch, 2017; Lewis, Edwards & Galbraith,*  
283 *2015; Peres, 1999, 2001; World Bank, 2016*) (*Text S1*).

284

285 Mining is a persistent threat to primates and their habitats. The mining of precious gems and  
286 minerals contributes to habitat destruction, fragmentation, deforestation, and the poisoning and  
287 pollution of soil and ground water (*Alvarez-Berríos & Aide, 2015*). In addition, mining (and  
288 fossil fuel extraction, see below) stimulates human migration, the illegal logging and  
289 colonization of forested areas, hunting, and the construction of roads and railways (*Alamgir et*  
290 *al., 2017; Butt et al., 2013; Laurance et al., 2015*). In eastern DRC, there is an unfortunate  
291 overlap of unprotected areas of high animal and plant biodiversity with areas that are rich in

292 minerals (*Edwards et al., 2014*). Increased global demand for easily-mined surface deposits of  
293 tantalum, a rare earth metal used in electronics including cell phones, has resulted in the  
294 expansion of illegal mining camps in several national parks in DRC. Bushmeat hunting in this  
295 area has decimated several primate populations (e.g., Grauer's gorillas, and eastern chimpanzees;  
296 *Plumptre et al., 2015; Spira et al., 2017*). Of the existing 1249 mining prospecting permits in  
297 DRC, 952 (76%) have their centers in the rural complex (areas that have been in the cycle of  
298 slash-and-burn agriculture for at least 18 years). Permits in the rural complex cover 143,316 km<sup>2</sup>,  
299 which is 78% of the total permitted area. The mean area of mining permits is 150 km<sup>2</sup> (and there  
300 is no difference between the size of permitted area in the rural complex and in forests more  
301 distant from human settlement). Approximately one quarter of the mining prospecting permits  
302 are located inside the forest and, if these are opened up for mineral extraction, they will pose a  
303 grave threat to primates (see [Text S1](#)).

304  
305 In Madagascar, the illegal mining of nickel, cobalt, gold, and precious gems (sapphire) has  
306 affected many forests, including protected areas with an important negative impact on  
307 populations of Malagasy primates including the iconic ring-tailed lemur (*Lemur catta*) (*Gould &*  
308 *Sauther, 2016*). In Brazil, between 2001 and 2013 approximately 1,680 km<sup>2</sup> of tropical moist  
309 forest was lost across 1600 gold mining sites, including significant forest loss inside 13 protected  
310 areas (*Alvarez-Berrios & Aide, 2015*). A more recent study showed that between 2005 and 2015  
311 mining in Brazil significantly increased Amazon forest loss up to 70 km beyond mining lease  
312 boundaries, causing 11,670 km<sup>2</sup> of deforestation (9% of all Amazon forest loss during this  
313 period) (*Sonter et al., 2017*). The disposal of mining waste is a significant threat to the local  
314 biota, including primates. In Brazil, for example, 126 mining dams are currently at risk of failing.  
315 In one such case, dam failure poisoned hundreds of kilometers of the Doce River with toxic mud  
316 (*Garcia et al., 2017*). In Kalimantan, Indonesia, gold mining is a major threat to the proboscis  
317 monkey (*Nasalis larvatus*) (*Meijaard & Nijman, 2000*) and to Bornean orangutans and Bornean  
318 gibbons (*Hylobates muelleri*) (*Lanjouw, 2014*). From 2000–2010, some 3,000 km<sup>2</sup> of, mostly  
319 lowland, forest in Indonesia was lost due to logging and as of 2011, over 40,000 km<sup>2</sup> of  
320 additional land was allocated to mining concessions (*Abood et al., 2015*). Most of these  
321 concessions are located on the islands of Sumatra and Borneo, where it directly impedes with  
322 conservation efforts to protect arboreal primates such as the slow loris (*Nycticebus* spp.), langurs  
323 (*Presbytis* spp. and *Trachypithecus* spp.), gibbons (*Hylobates* spp.), siamangs (*Symphalangus*  
324 *syndactylus*) and orangutans (*Pongo* spp.). For some species such as the western tarsier (*Tarsius*  
325 *bancanus*) and Sody's slow loris (*Nycticebus bancanus*) on the island of Belitung (*Yustian,*  
326 *2007*), finding a way to manage tin mines using environmentally friendly approaches is crucial  
327 for the survival of these nocturnal primates. In addition, traditional methods of gold mining and  
328 limestone karst mining now threaten the habitat of the agile gibbon (*Hylobates agilis*), the  
329 siamang, the black-crested Sumatran langur (*Presbytis melalophos*) and the silvered langur  
330 (*Trachypithecus cristatus*) in the province of Jambi in West Sumatra. Miners living in these areas  
331 also exploit primates and other wildlife for meat and capture live primates for pets that are sold  
332 in local towns (see hunting and illegal trade below; *Agustin et al., 2016; Yanuar, 2009*).

333  
334 Fossil fuel extraction negatively impacts primate survivorship. For example, over the next 20  
335 years, the global demand for oil is expected to increase by over 30% and the expected increase in  
336 natural gas by 53% from 2014 levels (*Butt et al., 2013; Finer et al., 2015*). This peak oil  
337 production it is projected to fall to present day levels (due to the changeover to electric vehicles)

338 by the year 2040 (*Longley 2018*). Brazil, Indonesia, and Madagascar are already expanding  
339 concessions and exporting this commodity (The International Trade Center - [www.intracen.org](http://www.intracen.org)).  
340 In the western Amazon of Brazil, for example, such concessions include national parks and  
341 territories of indigenous peoples (*Finer et al., 2015*). In DRC, oil concessions now cover almost  
342 all of the Albertine Rift and much of the central basin, where a concentration of endemic primate  
343 taxa is found (*Ministère Hydrocarbures DRC, 2013*).

344

#### 345 **International commodities trade and loss and degradation of primate habitat**

346 International trade commodity-driven deforestation is increasingly caused by global demand for  
347 agricultural and nonfood commodities (e.g., soy, beef, palm oil, timber, ores, fossil fuel)  
348 negatively impacting tropical biodiversity (*Henders et al., 2015; Henders et al., 2018*) and  
349 primate range and population persistence (*Estrada et al 2017*). While the growing human  
350 populations in Brazil, Madagascar, Indonesia and DRC (see “Human population” below) have  
351 resulted in increased internal demands for food and non-food commodities, global market  
352 pressures from highly industrialized nations are significant drivers of rapid and widespread  
353 habitat loss. According to the International Trade Centre, these four primate-rich countries sell at  
354 least 50% of all exports of raw materials to China, the US, Canada, India, and several European  
355 countries (*Table 2*). Commodities such as frozen beef, soy, sugar cane, hardwoods, and ores are  
356 principal exports of Brazil; in DRC minerals are the primary global export commodity, followed  
357 by smaller amounts of hardwoods, natural rubber, coffee, and cacao; for Madagascar, major  
358 exports are minerals, coffee, tea, spices, hardwood, and vegetable and roots/tubers; and for  
359 Indonesia, rice, natural rubber, oilseeds, and wood (*Text S1*). In Brazil, 30% of deforestation  
360 between 2000 and 2010 was driven by global demands for beef and soy exports (*Karstensen,*  
361 *Peters & Andrew, 2013*). Given that segments of the human population in each of these countries  
362 are undernourished (see “Human population” below), the exportation of food may threaten local  
363 food security, human safety and political stability (*FAO, IFAD & WFP, 2015*). The growing and  
364 unsustainable global demand for food and non-food crops, wood, fossil fuel, minerals, and gems  
365 by a small number of consumer nations has resulted in a rapid increase in agricultural  
366 production, wood extraction, itinerant miners, and oil/gas extraction. This also has led to an  
367 expansion of road networks and hydropower development in all four countries (*Alamgir et al.,*  
368 *2017*), ensuing increased forest loss, illegal colonization and logging, increases in itinerant  
369 mining and increases in primate hunting and trade (*Estrada et al., 2017; Latrubesse et al., 2017;*  
370 *Plumptre et al 2015; Spira et al., 2017; Timpe & Kaplan, 2017; Winemiller et al., 2016*).  
371 Importing nations process the raw materials and the final product is commercialized for local and  
372 global consumption. A particularly unfortunate example of this is the growing global demand for  
373 products produced by industrialized nations such as cell phones, laptops and other electronic  
374 devices using conflict minerals such as coltan, mined in DRC (*Hayes & Burge, 2003; Mancheri*  
375 *et al., 2018; Spira et al., 2017*). To balance global market demands with the needs of the four  
376 primate-rich countries to develop their internal economies, ensure food security, and improve the  
377 standard of living for their expanding human populations, the ‘greening’ of trade can promote  
378 environmental protection (*Neumayer, 2001; Henders et al., 2018*). International corporations  
379 should add these costs to products so that there is a continuous regeneration of funds to  
380 sustainably promote conservation (*Butler & Laurance, 2008*). Alternatively, the World Bank or  
381 UN could require that corporations and consumer nations pay into a sustainability/conservation  
382 fund based on their levels of consumption and environmental damage (e.g., like a carbon tax;  
383 Carbon Tax Center <https://www.carbontax.org>; consulted August 2017). In countries in which

384 the rural poor depend on forest products, community forest management could bridge or  
385 integrate the needs of conservation and commodity production, sustainably safeguarding the  
386 continued integrity of complex ecological systems (*Sharif & Saha, 2017*). The recent  
387 environmentally-oriented, demand-side policies regarding illegal timber imports by the EU (*EU,*  
388 *2010*), the EU resolution on oil palm production and deforestation (*EP, 2017*), and the  
389 Amsterdam Declaration to eliminate deforestation from agricultural commodity chains  
390 (*Amsterdam, 2015*) represent important and positive ‘green’ changes that need to be adopted by  
391 the U.S., China, and other consume nations. However, the continued growth of the global  
392 demand for forest-risk agricultural and nonfood commodities requires additional legislation and  
393 a stronger global effort at regulating the negative impact of unsustainable commodity trade  
394 (*Henders et al., 2018*).

395

## 396 **Local-scale anthropogenic threats to primate populations**

### 397 **Hunting**

398 Hunting (for meat and culturally valued body parts) negatively impacts 54% to 90% of primate  
399 species in the Neotropics, Africa, Madagascar, and Asia (*Estrada et al., 2017*). According to  
400 IUCN, about 85% of primate species in Indonesia are hunted, 64% in Madagascar, 51% in DRC  
401 and 35% in Brazil (*IUCN, 2017*) but we need to recognise that the IUCN primate assessments  
402 are now ten years old and many do not mention hunting specifically. The new assessments of the  
403 African primates (which will come online in 2018) are in general much clearer regarding  
404 individual threats and a much higher percentage – at least in Africa- will list hunting as a primary  
405 threat than in previous assessments. In reality, for example, almost all primates in DRC are  
406 hunted- even the smallest monkey, the talapoin has now been recorded at bushmeat markets  
407 (*Bersacola et al., 2014*). An exception is the nocturnal strepsirrhines, which are so small and so  
408 hard to catch that they are rarely taken unless for traditional medicine). Commercialized  
409 bushmeat hunting is a primary driver of primate population reduction and, in the case of the  
410 Brazilian Amazon, has led to the extirpation of highly endangered taxa such as spider monkeys  
411 (*Ateles* spp.) and woolly monkeys (*Lagothrix* spp.) (*Effiom et al., 2013; Peres et al., 2016;*  
412 *Stevenson & Aldana, 2008*). Hunting has contributed to extirpation of smaller and threatened  
413 primates in the Atlantic Forest such as the yellow-breasted capuchin monkey (*Sapajus*  
414 *xanthosternos*), Coimbra-Filho’s titi monkey (*Callicebus coimbrai*) (*Canale et al., 2012; Hilário*  
415 *et al., 2017*) and the largest Neotropical primate species, the southern muriquis (*Brachyteles*  
416 *arachnoides*) (*Talebi et al., 2011*). In DRC hunting has significantly reduced the numbers of  
417 gorillas and bonobos (*Hickey et al., 2013; Plumptre et al., 2016c*). In a wild meat market in  
418 Kisangani (DRC) about 65 primates were traded per day over a 131-day period (about 8, 515  
419 primates/131 days) (*Van Vliet et al., 2012*). In Basankusu (DRC), the rate was 17 primates traded  
420 per visit (*Dupain et al., 2012*). The primates present in these markets included species of the  
421 genera *Chlorocebus*, *Cercocebus*, *Colobus*, as well as chimpanzees and bonobos (*Text S1*). In  
422 DRC, the Endangered or Critically Endangered l’Hoest’s Monkey (*Allochrocebus lhoesti*), Dryas  
423 monkey (*Cercopithecus dryas*) (*Fa et al., 2014*), Grauer’s gorilla (*Gorilla beringei graueri*) and  
424 the eastern chimpanzee (*Pan troglodytes schweinfurthii*) experience high levels of poaching and  
425 are part of the commercial bushmeat trade (*Fig. 4, Plumptre et al., 2015, 2016a,b,c; Spira et al.,*  
426 *2017*). In DRC, hunting has resulted in emptying of all but the smallest bodied faunal species  
427 across large swathes of forest. For example, a large area of the Sankuru Natural Reserve has  
428 almost no bonobos remaining (*Liengola et al., 2009*); in a survey of the corridor area between the  
429 two sectors of the largest national park in the country (Salonga), bonobos were never found

430 closer than 10 kilometers from the nearest village (*Maisels et al., 2009*; see *Text 1*). Given that  
431 only 21-27.5% of bonobos live in protected areas (*Hickey et al., 2013*), their survival into the  
432 next century remains in doubt. However, primates living in protected areas also face significant  
433 challenges. Most of the remaining 3,800 Grauer's gorillas and all mountain gorillas *Gorilla*  
434 *beringei beringei* (estimated population size 880) are restricted to protected areas (*Plumptre et*  
435 *al., 2016b*). Because the population density of lemurs, monkeys, and apes living outside of  
436 protected areas has decreased rapidly, this has resulted in an increase in the price or value of  
437 primate bushmeat, making it profitable for hunters to risk prosecution by entering into protected  
438 areas (*Rovero et al., 2012*).

439  
440 Poorer households in the forested northwestern Makira landscape of Madagascar rely more on  
441 wildlife than richer households (*Golden et al., 2016*). Widespread hunting of black-and-white  
442 ruffed lemurs (*Varecia varecia*), diademed sifakas (*P. diadema*) and the brown lemur (*Eulemur*  
443 *fulvus*) in eastern Madagascar, has put these primates at increased risk (*Jenkins et al., 2011*). In  
444 periods following political crisis and instability in Madagascar, lemurs were traded as a prized  
445 source of meat (*Barrett & Ratsimbazafy, 2009*). Larger diurnal species such as the black-and-  
446 white ruffed lemur, indri (*Indri indri*), and sifaka (*Propithecus* spp.) are targeted because  
447 traditional taboos protecting lemurs have eroded rapidly (*Golden, 2009; Jenkins et al., 2011*).  
448 Even small species such as mouse lemurs (*Microcebus* spp.) are eaten, with hunters capable of  
449 capturing up to 50 a night; the impact on wild populations is considerable (*Gardner & Davies,*  
450 *2014*) (*Text S1*). Primate bushmeat consumption and trade in southern Sumatra results in  
451 hundreds of macaques killed monthly to meet the demand from wild meat restaurants (*KSBK,*  
452 *2002*). Other primates eaten are the Sangihe Island tarsiers (*Tarsius sangirensis; Shekelle &*  
453 *Salim, 2009*) and Bornean orangutans (*Pongo pygmaeus; Meijaard et al., 2011*). In Borneo,  
454 between 1,950 to 3,100 orangutans are killed annually for consumption (including 375 to 1550  
455 females), significantly impacting the viability of many small isolated populations (*Ancrenaz et*  
456 *al., 2016; Meijaard et al., 2011; Santika et al., 2017a*). In Indonesia, even subsistence hunting  
457 can have major effects on primate populations already decimated by land conversion and habitat  
458 loss (orangutans in Sumatra, Kloss' gibbons, pig-tailed langurs, Mentawai Island langurs and  
459 populations of *Trachypithecus* spp. and *Presbytis* spp. on others Indonesian islands) (*Fuentes,*  
460 *1998, 2002; Paciulli, 2004*).

461  
462 Numerous primates in each of the four countries consume ripe fruits and serve as important  
463 agents of seed, dispersal promoting forest regeneration (*Chapman et al., 2013*). The extirpation  
464 of primates due to hunting results in a change in dispersal dynamics, the size and distribution of  
465 seed shadows, a reduction in plant genetic diversity and seedling recruitment (*Caughlin et.,*  
466 *2015; Pacheco & Simonetti, 2000; Brodie et al., 2009*). There also is evidence that lemur  
467 population decline has resulted in the reduced viability of several species of Malagasy trees  
468 (*Federman et al., 2016*). Similarly, the population collapse of larger-bodied primates in response  
469 to over-hunting in the Brazilian Amazon has impacted the regeneration of long-lived and  
470 hardwood tree species and this is likely to reduce the ability of these forests to store carbon  
471 (*Peres et al., 2016; Stevenson & Aldana, 2016*). The overhunting of primates reduces the  
472 recruitment of trees whose seeds they disperse which also reduces food sources available to the  
473 local mammalian and avian communities (*Abernethy et al., 2013; Nuñez-Iturri, Olsson & Howe,*  
474 *2008*).

475

#### 476 **Legal and illegal primate live trade**

477 Many primate species are impacted by unsustainable live trade, often organized by criminal  
478 networks or sanctioned by local and national governments (Fig. 4, *Alves, Souto & Barboza,*  
479 *2010; Nijman et al., 2011; Alamgir et al., 2017; Nekaris et al. 2013; Shanee, Mendoza &*  
480 *Shanee, 2015; UNODC, 2013*). According to the CITES trade database, Indonesia is the leading  
481 exporter of live primates, with 98% being either captive-bred or captive-born long-tailed  
482 macaques (*Macaca fascicularis*) and the remainder principally wild-caught animals from a  
483 number of other species (Table 3). Most of the international trade from Indonesia is for scientific  
484 or biomedical research (*V. Nijman, unpublished data based on CITES trade data*). In DRC, over  
485 the last decade a much smaller number (N = 581) of primates, mostly guenons (*Cercopithecus*  
486 spp.), were exported for purposes of commercial trade, and almost all were wild-caught. (*V.*  
487 *Nijman, unpublished data based on CITES trade data*). However, there appear to be wide  
488 discrepancies between the numbers reported by the importing countries (N = 561) and the  
489 numbers reported as exported by DRC (N = 347) (other items, such as skin, bones, “specimens”  
490 total 16,202 reported by importers; DRC reported 5,364 exports over the same period). In  
491 contrast, the live primate trade out of Madagascar and Brazil appears to be better controlled, with  
492 only 24 to 51 individuals, bodies and skins reported. All primates exported from Madagascar  
493 were wild-caught (Table 3).

494

495 In general, the illegal trade in primates is for pets, meat, and medicinal or mystical purposes. In  
496 Brazil, legal international trade in live primates appears to be limited (*Svensson et al., 2016*).  
497 However, surveys of animal markets in Brazil and in the tri-country border of Peru-Colombia-  
498 Brazil showed that capuchin and brown woolly monkey (*Lagothrix lagothricha*) body parts were  
499 important trade items (*Ferreira et al., 2013; Van Vliet et al. 2014*) (Text S1). The pet trade in  
500 primates in Indonesia occurs openly in dozens of markets, and is prevalent in Sumatra, Java, and  
501 Bali, as well as in Indonesian Borneo and on Sulawesi. For example, during 66 visits to bird  
502 markets in North Sumatra, 10 species of primates totaling 1953 individuals were available for  
503 sale (*Shepherd, 2010*). Some 1,300 primates were recorded during 51 surveys to six markets on  
504 Java and Bali (*Nijman et al., 2017*). This included individuals of eight species. The most  
505 common primates traded were macaques and the greater slow loris (*Nycticebus coucang*, Text  
506 S1). Slow lorises are locally traded for medicinal purposes throughout Indonesia (*Nekaris et al.,*  
507 *2010*) (Text S1). In Madagascar, a study reported the presence of ~30,000 pet lemurs of at least  
508 16 species over a three-year period (*Reuter et al., 2016*).

509

#### 510 **Harvesting (capture and killing) to extinction**

511 Range contraction, combined with unsustainable bushmeat hunting and capture for the trade of  
512 selected species, suggests that high prices for rare or difficult to acquire species can, over time,  
513 drive even large populations to local extirpation. The Anthropogenic Allee Effect (AAE)  
514 (*Courchamp et al., 2006*) proposes that such extinctions are caused when prices for wildlife  
515 products increase with species rarity and that this price-rarity relationship creates financial  
516 incentives to extract the last remaining individuals of a population, despite higher search and  
517 harvest costs (*Holden & McDonald-Madden, 2017*). Another study suggests that while range  
518 contraction (habitat loss and fragmentation) causes population declines, local densities may  
519 remain relatively stable, especially in the case of animals like primates in which individuals can  
520 live for 20, 30, or > 40 years, facilitating harvesting to extinction of selected species (*Burgess et*  
521 *al., 2017*). The authors also showed that opportunistic exploitation, where harvesters hunt or

522 capture rare species while chasing target species, can significantly reduce population number.  
523 Clearly, current and predicted range contraction and abundance declines increase the extinction  
524 risk to harvested primate species in the four countries. This deserves greater consideration in  
525 research, conservation management, and protection plans.

526

## 527 **Other emerging threats**

### 528 **Infectious diseases**

529 Across anthropogenically impacted landscapes, the threat to primates of exposure to emerging  
530 infectious diseases resulting from increased contact with human and domesticated animals or  
531 periodic epizootic outbreaks across a broad region can result in local primate population declines  
532 or extirpations from otherwise suitable habitat (Nunn & Altizer, 2006; Nunn & Gillespie, 2016).  
533 Between October 2002 and January 2004, outbreaks of EVD (Ebola Virus Disease) killed over  
534 90% of the western gorillas (*Gorilla gorilla*) and possibly 80% of chimpanzees inhabiting the  
535 Lossi Sanctuary in northwest Republic of Congo (Bermejo et al., 2006). To date, however, there  
536 has not been an Ebola outbreak associated with any species of wildlife in DRC (Pigott et al  
537 2014; 2016). Developing vaccines that can be administered safely and effectively to free-ranging  
538 populations of great apes may help mitigate the impact of EVD outbreaks although this would be  
539 extremely challenging since these primates are hunted and hence are not habituated to humans  
540 (Leendertz et al., 2016). In most cases, these vaccines are not yet available even to local human  
541 populations, which presents an ethical dilemma regarding whether or not to provide these  
542 vaccines to endangered apes. In Brazil, 80% of isolated populations of black-and-gold (*Alouatta*  
543 *caraya*) and brown (*Alouatta guariba clamitans*) howler monkeys in two areas in the state of Rio  
544 Grande do Sul were lost after a Yellow Fever (YF) epizootic event in 2008 and 2009 (Freitas &  
545 Bicca-Marques, 2011; Veiga et al. 2014), including populations inhabiting protected areas  
546 (Fialho et al., 2012). Since 2016, an ongoing YF outbreak in Southeast Brazil has caused the  
547 death of thousands of primates, including threatened species such as the northern masked titi  
548 monkey (*Callicebus personatus*) and the brown howler monkey. In many instances,  
549 misinformation regarding vectors of YF disease transmission has resulted in members of the  
550 local human population exterminating nearby monkey populations (Bicca-Marques et al., 2017)  
551 (Text S1).

552

553 Susceptible primate populations inhabiting protected areas also are vulnerable to the introduction  
554 of exotic (non-native or alien) pathogenic agents into the naïve population, a process known as  
555 pathogen pollution (Daszak, Cunningham & Hyatt, 2000). The death of introduced marmosets  
556 (*Callithrix* spp.) infected with human herpesvirus 1 in a Brazilian nature reserve illustrates how  
557 proximity to humans can risk the survival of wild primate populations (Longa et al., 2011). The  
558 risk of epizootic disease transmission is particularly serious for those primates living near or  
559 within regions inhabited by dense human populations, such as in most of Indonesia, where  
560 *Streptococcus equi* caused high mortality among long-tailed macaques in 1994 (Soedarmanto et  
561 al., 1996). In Indonesia, outbreaks of measles, rubella, and parainfluenza has affected the  
562 survivorship of long-tailed macaque *M. fascicularis* groups living in close contact with humans  
563 (Schillaci et al., 2006). In Madagascar, lemurs inhabiting forests near human settlements are  
564 exposed to pathogenic enterobacteria (*Escherichia coli*, *Shigella* spp., *Salmonella enterica*,  
565 *Vibrio cholera* and *Yersinia* spp.; Bublitz et al., 2015), protists (*Cryptosporidium* sp.;  
566 *Rasambainarivo et al., 2013*; *Toxoplasmosis gondii*) and viruses (*Herpesvirus hominis* and West  
567 Nile *Flavivirus*; Junge & Sauter, 2006) found in humans, livestock, pets and peridomestic

568 rodents. Likely or proven cases of transmission of human diseases to great apes include  
569 enterobacteria, human herpes simplex virus, a measles-like disease, a polio-like disease,  
570 respiratory diseases scabies (*Gilardi et al. 2015*).

571

## 572 **Climate change**

573 Evidence for the impact of local and global climate change on primate populations is limited.  
574 However, current assessments indicate the expected extremes in temperature and rainfall will put  
575 primates at significant risk (see Fig. 2 of *Graham et al., 2016*). Climate change projections  
576 suggest that Brazil's four endemic species of Atlantic forest lion tamarins (*Leontopithecus* spp.)  
577 will experience major shifts and/or reductions in habitat suitability in the coming decades  
578 (*Meyer, Pie & Passos, 2014*). Similarly, the distribution of the northern muriqui (*Brachyteles*  
579 *hypoxanthus*) is expected to be reduced by more than half of its original area, with a large decline  
580 in the future suitability of currently protected reserves due to climate change (*Melo et al., 2016*).  
581 In Madagascar, in response to climate change most lemur species are expected to experience  
582 marked reductions in population number and distributions, even in the absence of future  
583 anthropogenic deforestation, with predicted declines of ~60% for lemurs' habitats (*Brown and*  
584 *Yoder, 2015*).

585

586 Climate change will likely increase primate exposure to potentially harmful human-borne  
587 parasites, triggered, for example, by increases in temperature and rainfall leading to faster  
588 parasite reproduction or longer periods of parasite transmissibility in primate rich regions  
589 (*Barrett et al., 2013*). Although certain species may be successful in shifting their range into  
590 newly created or expanded environments, this is likely to have negative consequences for other  
591 species that are displaced or out competed (*Schloss, Nuñez & Lawler, 2012*). For example, forest  
592 fragmentation resulting from changing climates is expected to limit the availability of dispersal  
593 routes used by titis (*Callicebus* spp.) in eastern Brazil (*Gouveia, et al., 2016*). Moreover in the  
594 future, protected areas and parks created to sustain threatened species may no longer be suitable  
595 due to changes in vegetative cover in response to climate change, or individuals may migrate into  
596 neighboring and unprotected forests where they are exposed to hunters or local residents (*Araújo*  
597 *et al. 2004*,; *Malhi et al., 2008*; *Struebig et al., 2015*; *Wiederholt & Post, 2010*). Projections of  
598 climate change in Central Africa are less clear (*Abernethy et al., 2016*). However, rainfall decline  
599 may occur, leading to a reduction in forest cover in DRC (*Beyene et al., 2013*); other work  
600 suggests the opposite may be true (*Zelazowski et al., 2011*). Regardless, clearing of additional  
601 forest for agriculture results in land desiccation which when combined with droughts and El  
602 Niño episodes result in extensive wildfires (*Laurance et al., 2014*; *World Bank, 2017*), impacting  
603 primate populations (*Graham et al., 2016*.) The most forceful example of this is human-made  
604 fires that resulted in the burning of 2.6 M ha of land in Indonesia between June and October of  
605 2015. These fires were fed by drought and the effects of a prolonged El Niño. Degraded  
606 peatlands, most of them found in Sumatra, Kalimantan and Papua Province, Indonesia are  
607 particularly sensitive to fires that easily spread to adjacent forests. For example, the 2015 fires  
608 burned some 700 K ha of natural forest, swamp forest and forestry concessions plus 505.8 K ha  
609 of palm oil concessions (*World Bank, 2017*). Therefore, mitigating climate change impacts on  
610 the potential for mass fires is critical for primate survivorship in Indonesia.

611

## 612 **Human population**

### 613 **Trends and projections in human population growth**

614 Environmental pressures exerted by a growing human population are a major driver of primate  
615 habitat and population decline in each country (*Crist, Mora & Engelman, 2017*). In 2016,  
616 Indonesia was the most populous of the four countries with slightly over 263 million people,  
617 followed by Brazil (about 211 million), DRC (about 80 million) and Madagascar (about 26  
618 million). Human population density is highest in Indonesia (145 people/km<sup>2</sup>) and lowest in  
619 Brazil (25 people/km<sup>2</sup>) (*Table 4, Text S1*). Population growth rates for 2016 were highest in  
620 DRC (3.09%/yr) and Madagascar (2.75%/yr), lower in Indonesia (1.07%/yr) and lowest in Brazil  
621 (0.77%/yr) (*Table 4*). Human population projections for the year 2050 indicate continued growth  
622 in all four countries with DRC showing the steepest increase, followed by Madagascar,  
623 Indonesia, and Brazil. In Brazil and Indonesia, much of this population growth is expected to  
624 occur in urban areas (*Fig. 5*). And although in the short term rural populations are expected to  
625 expand rapidly in DRC and Madagascar, projections suggest that by 2050 their urban population  
626 (69% of the population of DRC and 55% of the population in Madagascar) will surpass their  
627 rural population (*Fig. 5*). The large size and projected increase of the population in all four  
628 countries in the first half of this century is expected to exponentially extend the human and urban  
629 footprint on primate habitats, near and beyond cities. These negative impacts will result from  
630 increasing demands for energy, space, food, water, minerals, oil, construction material, forest  
631 products, and transportation, as well as from environmental damage caused by pollution and by  
632 the expansion of road and rail networks to satisfy food and non-food urban needs (*Estrada 2013*;  
633 *Estrada et al., 2017*). And, although cities concentrate poverty, they also are places of  
634 innovation, knowledge, technical expertise, and leadership (*van Ginkel, 2008*) offering important  
635 decision-making tools for primate conservation. For example, green (environmentally friendly)  
636 policy initiatives such as recycling, desalination and water treatment, a commitment to re-useable  
637 energy, and others can limit a cities ecological footprint (*Butler & Laurance, 2008*). These policy  
638 changes offer the opportunity for these four countries to take advantage of the movement of  
639 people from rural to urban areas to reinvest in forest recovery and habitat restoration in these  
640 newly vacant spaces (*Ashraf et al., 2016*), and thereby promote conservation policies favouring  
641 primate population recovery and expansion.

642

## 643 **Socioeconomic indicators and human development**

### 644 **Gross Domestic Product per Capita (GDPPC)**

645 Effective and long-term primate conservation requires economic resources, adequate  
646 conservation policies, effective law enforcement, conservation-oriented research and public  
647 interest. If high levels of poverty are predominant, country-wide primate conservation will be a  
648 low national priority. The 2015 GDPPC of Brazil, Madagascar, Indonesia and DRC, was, on  
649 average, lower than the world's average (\$10,130) and significantly lower than the average  
650 GDPPC for the top 25 most developed nations (\$57,509). Among the four countries, DRC and  
651 Madagascar have the lowest 2015 GDPPC values (\$452 and \$402, respectively; Indonesia  
652 \$3,346; Brazil \$8,678) (*Table S5*). Changes in the GDPPC from 1990 to 2015 for these four  
653 primate-richest countries indicate major gains for Indonesia and Brazil whereas the GDPPC has  
654 remained very low in DRC and Madagascar (*Fig. 6*). This is consistent with levels of child  
655 malnutrition. The percent of children who are underweight in Brazil is 3.7% (2002), in Indonesia  
656 19.9% (2013), in DRC 23.4% (2013) and in Madagascar 36.8% (2004). In contrast the values for  
657 high income countries is 0.9% (2016) (*The World Bank, 2017*).

658

### 659 **Human Development**

660 The 2015 UN Human Development Index (HDI; a combination of life expectancy, school  
661 enrollment, literacy, and income, with the Lowest human development = 0; Highest = 1.0;  
662 *UNDP, 2016*) indicates that DRC and Madagascar have the lowest values among the four  
663 countries, while the HDI values for Brazil and Indonesia approach the world's average (*Fig. 7*).  
664 In general, the HDI increased in all four countries from 1990 to 2015, but while the HDI increase  
665 in Brazil and Indonesia paralleled increases in the world's average, human development  
666 remained relatively stagnant for Madagascar and DRC (*Fig. 7*). Values of the HDI for these four  
667 countries are, nonetheless, quite low compared to those highest ranking 25 countries worldwide  
668 (*Fig. 7, Table S5*). Low levels of HDI are commonly associated with political instability, extreme  
669 income inequality, and limited environmental protection (*Alsamawi et al., 2014; Neumayer,*  
670 *2017*). While these four primate-rich countries have much to achieve in human development  
671 compared to the top 25 developed nations, it also is clear that the economic standing and human  
672 development of Brazil and Indonesia are following a trajectory that is different from that of DRC  
673 and Madagascar (*Fig. 7*). These latter two countries face more serious challenges in securing  
674 resources for their human population and for primate conservation.

675

### 676 **Civil conflict**

677 Civil unrest and conflict also affect primate survivorship due to indiscriminate bombing, the  
678 spread of toxic chemicals (*Douglas & Alie, 2014; Loucks et al., 2009*), increases in the  
679 availability of firearms, and the increase in bushmeat hunting by soldiers and displaced civilians.  
680 Poaching of many primates including grey-cheeked mangabeys (*Lophocebus albigena*), bonobos  
681 and Grauer's gorillas, for example, has increased markedly in DRC because of ongoing civil  
682 wars (*Douglas & Alie 2014; IUCN & ICCN 2014; McNeely, 2003; Plumptre et al., 2016a*).  
683 Landmines, the legacy of wars in the 1960's, 1970's, and 1990's, and numerous militia groups  
684 continue to jeopardize monkeys and apes in DRC, where civil conflict has interrupted wildlife  
685 protection by guards in national parks (e.g., Virunga; *Kalpers et al., 2003; McNeely, 2003*).  
686 Currently, heavily armed militias in the Kasai, North Kivu and South Kivu in DRC fight for  
687 ethnic and political control and, together with illegal miners, prospect for "conflict minerals"  
688 (e.g., coltan, tin, tantalum, tungsten, and gold) and diamonds, and hunt primates as bushmeat  
689 (*Gavin, 2017; Nelleman, Redmond, Refisch, 2010*). Similarly, border conflicts between Indonesia  
690 and Malaysia on the island of Borneo have caused damage to the forest and wildlife. In the  
691 1990s, however, business and military leaders colluded to suspend conflict in order to cut down  
692 and burn millions of hectares of forest to plant cash crops (*McNeely, 2003*), impacting the  
693 survival of entire primate communities. Civil conflict also alters land use patterns and can lead to  
694 increased unregulated forest conversion. In the north Sumatran region of Aceh, for example,  
695 human conflicts combined with forest fires and legal and illegal logging led to a reduction in  
696 forest cover of greater than 30% from 1990 to 2010 (*Margono et al., 2012*). Disputes over land  
697 rights, private corporate actions, and governmental regulations also have led to forest burning  
698 and land-clearing across the island of Sumatra, directly threatening the Sumatran langur, banded  
699 langur (*P. femoralis*), and Thomas's langur (*P. thomasi*), as well as Bornean orangutans and  
700 Müller's gibbons in Indonesian Borneo (*Lanjouw, 2014; Meijaard & Nijman, 2000; Supriatna et*  
701 *al., 2017*).

702

703 Civil unrest, inter-country wars and continued militarization contribute to the displacement of the  
704 local human population, increasing poverty, social insecurity, and environmental damage. The  
705 2017 Global Peace Index (GPI; <http://economicsandpeace.org/>), which measures ongoing

706 domestic and international conflict (ODIC), societal safety and security (SSS) and militarization  
707 (MILIT) (*IEP, 2017*) rank DRC as having the highest values among the four countries ([Table 5](#)).  
708 Madagascar and Indonesia have lower GPI values for all three insecurity measures, and Brazil  
709 has a low value for just one measure ODIC). When a country's economic, political and human  
710 resources are drained to deal with ongoing civil and ethnic conflicts and societal safety, primate  
711 conservation is not a priority. Insecurity and lack of personal safety in these countries are  
712 enhanced by prevailing corruption and low-quality governance (see below).

713

### 714 **Corruption, governance quality and primate conservation**

715 Corruption is a major threat to primates because it distorts environmental laws, giving way to  
716 deforestation and land speculation and promoting poverty and illegal activities, including  
717 mining, poaching, logging, and the primate trade. Corruption and inequality interact by  
718 generating a vicious circle of greed, the unequal distribution of power in society, and the unequal  
719 distribution of wealth. The 2016 Transparency International Corruption Perceptions Index (0:  
720 highly corrupt to 100: very clean) profiling 176 countries (*CPI, 2016*) places Brazil with a score  
721 of 40 (rank 79), Indonesia a score 37 (rank 90), Madagascar a score 26 (rank 145), and DRC  
722 with a score of 21 (rank 156), consistent with the high levels of corruption present in all four  
723 countries, but especially in Madagascar, DRC (*CPI, 2016*), and most recently in Brazil.

724 Corruption hampers efforts directed at wildlife conservation and weakens protected area capacity  
725 to prevent drivers of primate habitat loss and local species extirpation (see [Text S1](#) for the case  
726 of Brazil). In the four countries laws are often skirted or ignored through bribery and extortion.  
727 For example, trading orangutans in Indonesia is a crime but 440 confiscations in the last 25 years  
728 have led to only seven convictions and sentencing was lenient (*Nijman, 2017*). DRC has a  
729 patronage system in which the profits of “unofficial economic activities” or “predation” flow  
730 upwards to the top of the chain of command hampering the way forward with environmental  
731 issues (*Baaz & Olssen, 2011*; see [Text 1](#)). In Madagascar, illegal exploitation and export of  
732 rosewood in protected areas, with associated negative effects on wildlife populations, has been  
733 facilitated by political instability and corruption (*Randriamalala & Liu, 2010*). Complicity  
734 between businesses and politicians had led to the theft of billions of dollars in revenue from  
735 national economies, benefitting the very few at the expense of the many and preventing  
736 sustainable development (*Baaz & Olsson, 2011*; *CPI, 2016*). Profiling four key World Bank  
737 indicators of governance quality in 2016 indicates that these primate-richest countries all rank  
738 significantly lower than the average values for 35 high-income countries ([Fig. 8](#)). Overall, weak  
739 governance appears to be characteristic of these four countries, with DRC (coded in the World  
740 Bank database as Congo Dem. Rep.) and Madagascar ranking lowest (see *Freudenberger 2010*).  
741 Given high levels of corruption and prevalent low human development, country-wide  
742 conservation of primate habitats and populations in these four countries remains a complex  
743 challenge. Moreover, measurements of the effectiveness of governance require a thorough causal  
744 analysis (with counterfactuals) to determine the degree to which the current status of individual  
745 primate species is best attributed to good policies that are poorly implemented, the continuation  
746 of ineffective policies, or the result of strong and effectively managed policies (see *Baylis et al.,*  
747 [2016](#))

748

### 749 **Landscape approaches to primate conservation**

#### 750 **Protected areas**

751 Protected areas represent an effective conservation tool in which local, state and national  
752 governments can act to protect ecosystems and provide resources to conserve animal  
753 populations, provided that these areas also contribute to alleviate rural poverty (*Adams & Hutton,*  
754 *2017*). An Africa-wide assessment of which factors were most effective in maintaining great ape  
755 populations concluded, after examining 120 areas, that effective law enforcement was the most  
756 important (*Tranquilli et al., 2012*) followed by long-term conservation NGO involvement.  
757 Similarly, a recent rangewide assessment of the two great ape taxa in Western Equatorial Africa  
758 shows that the presence of wildlife guards was one of the most effective predictors of great ape  
759 density (*Strindberg et al., 2018*), and that intact forest and low human pressure metrics were also  
760 key – both of which are generally characteristic of the protected areas and selectively-logged  
761 Forest Stewardship Council (FSC)-certified concessions of Central Africa. Globally, protected  
762 area networks are located in ecological zones that have low value and low demand for land  
763 conversion, are inexpensive to protect, and, some, but by no means all, are, located far from  
764 areas of high biodiversity (*Joppa & Pfaff, 2009*). As a result, this discrepancy or this mode of  
765 selection has placed primate-rich lowland forests at risk because lowland forests offer profitable  
766 opportunities to obtain land well-suited to industrial agriculture (*Venter et al., 2014*) or clear-  
767 cutting for timber. In this regard, governments need to partner with the scientific community and  
768 the expertise of local, regional, national and international NGOs to design extensive networks of  
769 protected areas and private reserves that have as their goal the creation of ecological zones and  
770 land use policies that collectively sustain both biodiversity and human communities (*Hill et al.,*  
771 *2015*). There is evidence that protected areas provide sustainable core habitat for primates. They  
772 represent a keystone tool for the conservation of threatened primates in Brazil's Atlantic forest.  
773 For example, almost 80% of the total localities of Atlantic Forest where muriquis (*Brachyteles*  
774 spp.) presently inhabit are protected areas (private or governmental - state and federal units,  
775 *Strier et al., 2017*). In Central Africa, a long-term study (2007–2014) in which camera traps were  
776 used to census terrestrial mammals found strong evidence of stability in several threatened  
777 African primates such as the l'Hoest's monkey, mandrills (*Mandrillus sphinx*) and chimpanzees  
778 (*Beaudrot et al., 2016*).

779  
780 Conservation efforts targeted to deliberately increase positive human influences, including  
781 veterinary care and close monitoring of individual animals succeeded in doubling the Virunga  
782 mountain gorilla population over 40 years (*Robbins et al., 2011*). These gorillas occur in  
783 protected areas, including in DRC. Protected areas are effective in minimizing population decline  
784 as has been reported for the pale-thighed langur (*Presbytis siamensis*) in Sumatra and the red-  
785 fronted brown lemur (*Eulemur rufifrons*) in Madagascar (*Beaudrot et al., 2016*). From 1990 to  
786 2000, protected areas in Sumatra experienced lower deforestation rates than nearby unprotected  
787 areas (*Gaveau et al., 2009; Gaveau, Wich & Marshall, 2016*). In Zanzibar, Tanzania, mean  
788 group sizes of the Zanzibar red colobus *Piliocolobus kirkii* were significantly higher in protected  
789 areas (21 individuals) than outside protected areas (13 individuals). Clearly, individuals outside  
790 of protected areas are at greatest risk (*Davenport et al., 2017*). In this regard, Brazil has 29% of  
791 its land under protection, DRC 13%, Madagascar 12%, and Indonesia 12% (*Table 6*; see *Text S1*  
792 for additional information).

793

#### 794 **Assessing the overlap between protected areas and primate distributions**

795 Modeling the distribution of protected areas and primate distributions in the four countries  
796 showed that, on average, primates in Brazil have 38% of their range included within protected

797 areas; 38% in Madagascar, 17% in Indonesia and 14% in DRC, suggesting that the great  
798 majority of primate populations exist outside of protected areas (Fig. 9, Fig. S7; see [Strindberg](#)  
799 [et al.](#), 2018 for the case of central African chimpanzees and western lowland gorillas in Western  
800 Equatorial Africa where 80% of both primates occur outside of protected areas). Regrettably, the  
801 distribution of protected areas in each of the four countries is extremely patchy, and in many  
802 cases subpopulations of the same species are isolated from each other and inhabit areas that are  
803 experiencing considerable deforestation and fragmentation as they are increasingly impacted by  
804 agricultural expansion, logging and illegal hunting as well as an ever-growing urban footprint  
805 (Fig. 3, Fig. 9) ([Mascia et al.](#), 2014; [Rovero et al.](#), 2015; [Spracklen et al.](#), 2015). Due to illegal  
806 activity in the Brazilian Amazon, natural resource reduction is pervasive. Most transgressions  
807 were related to habitat degradation (37%), illegal fishing (27%) and the game hunting (18%)  
808 ([Kauano, Silva & Michalskil](#), 2017). Increasing human population density within 50 km of a  
809 protected area is a crucial factor that promotes illegal activities. Meeting global goals for  
810 protected-area coverage will be insufficient to protect biodiversity unless these areas are well  
811 managed and properly located ([Butchart et al.](#), 2015). Analysis of the distribution of protected  
812 areas and primate distributions is critical for diagnosing areas in need of protection. For example,  
813 whereas 22% of the distribution of the Bornean orangutan is in protected areas and 29% occurs  
814 in forest concessions, the remaining 49% is in unprotected and commercially developed forests  
815 ([Wich et al.](#), 2012). A similar pattern emerged in an earlier analysis of all primate species in  
816 Indonesian Borneo ([Meijaard & Nijman](#), 2003).

817

### 818 **Community forest management (CFM), habitat restoration and landscape connectivity**

819 Community forest management (CFM) aims to reduce deforestation and maintain biodiversity  
820 while also improving local human welfare (alleviate poverty). In general, there is evidence of  
821 CFM being associated with greater tree density and basal area ([Bowler et al.](#), 2012). A review of  
822 33 community forests (all but one in Latin America, the other in India) showed that a  
823 commitment to land-sharing (combining forms of agroforestry along with forest managed by  
824 local communities in which resources are extracted sustainably) can lead to reduced rates of  
825 deforestation compared to protected forests ([Porter-Bolland et al.](#), 2012). In another study of  
826 CFM certification of timber, based on 318 comparisons from 50 studies distributed across  
827 Africa, Asia and South and Central America, CFM performed better than open access areas in  
828 56% of 185 comparisons, equally in 25% and worse in 19% (comparisons focused on economic,  
829 social and environmental variables) ([Burivalova et al.](#), 2017). Similarly, a nation-wide survey in  
830 Madagascar of CFM impacts on household living standards (as measured by per capita  
831 consumption expenditures) showed that well-being was stronger for households closer to forests  
832 and households with more years of education ([Rasolofson et al.](#), 2017). In another study in  
833 Madagascar, CMF was shown to reduce deforestation in CFM localities that do not permit  
834 commercial uses of wood compared to areas that lack CFM or in CFM areas that allow  
835 commercial uses ([Rasolofson et al.](#), 2015). In Indonesia, the total area of CFM forests (Hutan  
836 Desa, or village forest, is an approach that stresses local village governance and autonomy in  
837 forest protection and in controlling resource extraction by outside groups) increased from  
838 750 km<sup>2</sup> in 2012 to 2500 km<sup>2</sup> in 2016. A spatial matching approach showed that under a Hutan  
839 Desa management scheme, deforestation was avoided compared to the expected likelihood of  
840 deforestation in the absence of Hutan Desa management ([Santika et al.](#), 2017b).

841

842 Forests are one of the few resources accessible to local communities in primate range countries,  
843 and participating in their ownership, stewardship, and restoration can provide food, economic

844 opportunity, and income to poor people (*Porter-Bolland et al., 2012*). Reforestation is an  
845 important conservation tool to help both rural communities and to mitigate species extinction due  
846 to habitat loss, fragmentation, and isolation, especially if it involves protecting large forest areas  
847 (*Taubert et al., 2018*). An expansion in available habitat via restoration can facilitate an increase  
848 in species' population size and connect fragments and protected areas, if strategically located  
849 restored forest can promote immigration and gene flow from previously isolated but now source  
850 populations (*Hylander, 2013*). Targeting habitat restoration to areas of once contiguous forest  
851 using corridors 1-km wide between the most extensive, intact, and closest forest fragments can  
852 have a positive effect on wildlife population expansion (*Newark et al., 2017*). A study in the  
853 Atlantic Forest of Brazil that modeled the use of forest corridors as a conservation tool found that  
854 regenerating corridors totaling 6.4 K ha would result in a continuous forested area measuring  
855 251.9 K ha. Although full regeneration of these corridors is likely to take 10 to 40 years  
856 (*Newmark et al. 2017*), extinction-prone primate species such as golden lion tamarins  
857 (*Leontopithecus rosalia*) and golden-headed lion tamarins (*Leontopithecus chrysomelas*) can  
858 disperse through linked forests that are <10 years old (*Dosen, Raboy & Fortib, 2017; Newmark et al. 2017*).  
859 Landscape connectivity also can include community managed forests in which  
860 agroecosystems such as shade-grown coffee (*Coffea spp.*), cacao (*Theobroma cacao*), and  
861 cardamom (*Elettaria cardamomum*), as well as small shaded mixed plantations of natural rubber  
862 (*Hevea brasiliensis*) and oil palm, among other arboreal crops, provide income for farmers and  
863 temporary habitat, food resources, and dispersal routes for isolated segments of primate  
864 subpopulations (*Estrada, Raboy & Oliveira, 2012; McLennan, Spagnoletti & Hockings, 2017*).  
865 Still, the persistence of primates in agroecosystems in Brazil, Madagascar, Indonesia and DRC  
866 may not be a long-term sustainable conservation solution ([Text S1](#))

867

### 868 **Primate rewilding**

869 Where primate species are locally extirpated, reintroductions may be a feasible conservation  
870 strategy if there is long-term protection of forests and monitoring of population changes (*Baker,*  
871 *2002; Beck et al., 2007; Wilson et al., 2014*). In general, guidelines for most species, including  
872 great apes, underline the importance of ensuring that the threat that caused the animals to become  
873 locally extinct (such as poaching) has ceased before attempting reintroduction (*Beck et al., 2007,*  
874 *IUCN/SSG, 2013*). Reintroduction and translocation programs also serve to intensify public  
875 interest on conservation issues, especially when combined with social media (*Kierulff et al.,*  
876 *2012*). Reintroduced primates include orangutans and slow lorises in Indonesia (*Moore et al.,*  
877 *2014; Wilson et al., 2014*), and golden lion tamarins, pygmy marmosets (*Cebuella pygmaea*) and  
878 northern muriquis in Brazil (*Car, Queirogas & Pedersoli, 2015; Kierulff et al., 2001; Melo,*  
879 *2016*). Some of these releases, e.g. golden lion tamarins, led to the establishment of self-  
880 sustaining populations, whereas in others, for example, Javan slow lorises (*Nycticebus*  
881 *javanicus*), high mortality in the first few months, questions the viability of these programs  
882 (*Moore et al., 2014*). In Madagascar, there have been reintroductions and translocations of  
883 captive-born and wild-born lemurs (*Schwitzer, 2013*). This has resulted in successful population  
884 establishment in the cases of released aye-ayes (*Daubentonia madagascariensis*), captive-bred  
885 black-and-white ruffed and collared-brown lemurs (*Eulemur collaris*), but in several instances,  
886 there was high mortality due to natural predation (*Britt, Welch & Katz, 2004; Donati et al., 2007;*  
887 *Mittermeier et al., 2010*). In contrast, the translocation of black-and-white ruffed lemurs and  
888 diademed sifakas from forests from a forest selected for clearing by a mining company to the  
889 nearby Analamazaotra Special Reserve (ASR), was successful (*Day et al., 2009*). After several

890 years of rehabilitation, bonobos rescued from the illegal trade also have been successfully  
891 reintroduced in the “Ekolo Ya Bonobo” release site in DRC  
892 (<http://www.lolayabonobo.org/ekolo-ya-bonobo>; accessed 30th November 2017). Nevertheless,  
893 extreme caution must be taken in evaluating areas for reintroduction, as in many cases humans  
894 and primates favor the same ecological zones, and primates may face severe competition from  
895 human, as is the case for the Bornean orangutan (*Santika et al., 2017a*) and the population of  
896 black-and-white ruffed lemur currently living in the ASR (*Rasoamanarivo et al., 2015*). These  
897 two studies may guide future attempts (Text S1). Finally, reintroductions are costly relative to  
898 other options (e.g. long-term protection of forested land) and therefore are often best used as a  
899 last resort (*Wilson et al., 2014*).

900

### 901 **Socially-oriented conservation actions for averting local extinction threats to primates**

902 The development of community-based local education programs, action groups, and  
903 NGOs/Associations that focus on primate conservation initiatives are key instruments that can  
904 successfully result in local and long-term conservation of primate species. The involvement of  
905 NGOs (International Committees for Conservation and Management – ICCM and the Pro-  
906 Muriqui Institute (Text S1) has been crucial in Brazil for the conservation of threatened species  
907 such as the golden lion tamarin and the muriqui (Text S1). The Critically Endangered Javan slow  
908 loris is one of the focal species of the Little Fireface Project (<http://www.nocturama.org>).  
909 Implemented in 2011, this project has involved a wide range of audiences and stakeholders,  
910 providing annual training sessions for law enforcement officers and coordinated biannual events  
911 in villages close to where wild slow lorises occur, to increase protection and pride in this  
912 endemic species. A population of these slow lorises has been monitored on Mt Papandayan,  
913 West Java, for seven years, revealing vital information on their biology and conservation  
914 (*Nekaris, 2016; Nekaris et al., 2018; Text S1*). In DRC, international conservation NGOs are  
915 working in and around most conservation landscapes, with coordination offices in the capital;  
916 some of these NGOs have been working in DRC for over 30 years. NGOs support the wildlife  
917 authority of the ICCN (Congolese Institute for Nature Conservation), and provide technical  
918 assistance (training, equipment) to government antipoaching patrols, that plays a critical  
919 conservation role inside national parks, including the development of a system for rapid  
920 collection of both patrol and survey data in the field (SMART,  
921 <http://smartconservationtools.org/>) (Text S1).

922

923 Literacy is another critical factor in developing effective conservation education programs  
924 (*Clayton & Myers, 2009; Oboh & Tsue, 2010*). Youth (15-24 years) literacy rates are 76.8%  
925 (2012 data) in Madagascar, 85.0% in the DRC (2016), 98.8% in Brazil (2014) and 99.7% in  
926 Indonesia (2016) (<http://data.uis.unesco.org/#>). In addition, in rural parts of DRC and  
927 Madagascar, adult literacy is some 25% lower than in urban populations (*UNESCO, 2006*).  
928 Educational programs targeted at less literate populations are more effective when environmental  
929 messages are presented using simply written phrases, radio and television programs, music,  
930 images, live performances, and other non-written forms of communication.

931 In Madagascar, the NGO Reniala acts to protect forests, rehabilitate lemurs from the pet trade,  
932 provide incentives to discourage hunting, and has developed alternative livelihood projects for  
933 local residents, such as beekeeping (<https://association-reniala.jimdo.com/>). Centre Valbio is a  
934 research center with an integrated conservation program, that works directly with the Malagasy

935 government in the Ranomafana National Park—41,500 hectares of rainforest that includes the  
936 golden bamboo lemur (*Haplemur aureus*), discovered at this site in 1986  
937 (<http://www.stonybrook.edu/commcms/centre-valbio/conservation.html>). The Maromizaha forest  
938 Conservation and Community Project in Madagascar protects a large forest tract with 13 species  
939 of lemurs, using forest-friendly alternative agricultural practices and promoting the development  
940 of ecotourism (*Gamba et al., 2013*). Because of the recent growth in trained primatologists in the  
941 four countries, their conservation concerns have led to the creation of professional societies that  
942 can more effectively articulate conservation concerns with local governments, NGOs, rural  
943 communities and international societies (*Text 1*). In Madagascar, conservation education,  
944 especially of young children, also has made important strides in protecting primates (*Dolins et al.,*  
945 *2010*).

946  
947

### 948 **Conclusions and key challenges ahead**

949 Primate conservation is a global, multilayered, biological, ecological and social issue. There are  
950 over 500 primate species in the wild and these taxa differ in ecological requirements, behavioral  
951 flexibility, reproductive capacity, social systems, and are long-lived (*Fig. 10*). As a result, their  
952 responses to conservation initiatives are often difficult to assess in both the short and long term.  
953 There is no single blueprint or best course of action for advancing primate conservation in Brazil,  
954 Madagascar, Indonesia and DRC. Each country differs in its history, societal and economic  
955 needs, and current environmental and governmental policies that are driving primate habitat loss  
956 and population decline. These four countries face unprecedented environmental and social  
957 challenges in implementing effective primate conservation (*Fig. 11*). They have rapidly growing  
958 human populations and low human development indices compared with more developed nations.  
959 Each has also experienced large-scale losses of native vegetation and other natural resources plus  
960 high levels of corruption and weak governance. Each country's desire to move its economy  
961 forward to meet the needs of its population remains a priority but this seems difficult to achieve  
962 in a global system in which international trade led by the demands for food and non-food  
963 products by a small set of developed and consumer nations distract attention from the needs of  
964 their local populations. Despite significant increases in revenues derived from agricultural  
965 exports in these four countries, millions of their citizens remain undernourished, undereducated,  
966 and poor (*World Bank, 2017*). While Brazil has made important strides in reducing deforestation,  
967 decreasing poverty, and fostering science and education with direct positive impacts on primate  
968 conservation, a change in government policies in 2012 reduced the protection of natural  
969 vegetation on private lands (*Brancaion et al., 2016*) and laws governing protected areas were  
970 reduced and weakened (*Bernard et al., 2016*). Funding for science also was reduced (*Overberch*  
971 *et al., 2018*). This has resulted in a sharp increase in deforestation rates (*Fig. 2*), with expected  
972 negative effects on biodiversity, primates, people's livelihood's and conservation.

973

974 Given the rapid pace and large scale at which native forests have been cleared in Latin America  
975 and Indonesia to expand agriculture to satisfy global and local demands (*Tilman et al., 2017*),  
976 critically evaluated approaches are needed to ensure primate survival. For example, it is argued  
977 that promoting "sustainable intensification" of agriculture on already cleared lands could readily  
978 supply production that might otherwise be expected to come at the cost of future land conversion  
979 (*Carlson et al., 2018*). This requires linking smallholders (farmers) with commercial  
980 international agriculture (*Goldsmith & Cohn, 2017*). This, however, does not mitigate the already

981 high environmental costs of cleared land. Moreover, global dietary changes, promoted in large  
982 part by multinational businesses and designed to expand corporate profit margins, will require  
983 these primate-rich countries to convert additional forested land into monocultures (*Kastner et al.*  
984 *2012; Tilman & Clark 2014*). This is likely to happen more slowly in DRC, as civil war, political  
985 instability, governance issues and continued poverty (according to the internationally recognized  
986 metrics used by the World Bank / UNDP) limit international investment (*Kastner et al. 2012*).  
987 Based on a range of global factors, agribusiness corporations may switch to different crops and  
988 land-use patterns to maximize profit or may increase or decrease investments in other countries  
989 leading to increased environmental damage and poverty (*Carrasco et al., 2014; Lim et al., 2016;*  
990 *Villoria et al., 2013; Weng et al., 2013*). Intensification of agriculture to increase yields does not  
991 necessarily contribute to global hunger reduction, as an unequal amount of food and nonfood  
992 products are used by already well-fed people in a small number of consumer nations. Rather,  
993 food security needs to increase in areas of the world where the hungry live using eco-efficient  
994 approaches that encourage sustainable productivity and incorporates natural biodiversity, and  
995 clean and reusable forms of energy, while sustaining multiple ecosystem services (*Keating et al.,*  
996 *2010*). Using an eco-friendly approach, agriculture practiced by small landholders and sensitive  
997 to local markets and conditions rather than large-scale industrial farming, is the key to food  
998 security in the developing world (*Tscharntke et al., 2012*).

999

1000 Clearly, additional research is needed to examine the role of local and global market demands on  
1001 primate conservation (*Larrosa, Carrasco & Milner-Gulland, 2016*), including studies to evaluate  
1002 the extent to which the reduction of land for purposes of agricultural conversion benefits the  
1003 local human and nonhuman primate communities. Within this framework, economic instruments  
1004 targeted to consumer nations such as taxes on agricultural inputs and taxes on consumption as  
1005 well as investment in sustainable agri-environmental production that guarantees the persistence  
1006 of multiple ecosystem services may be, in some countries, viable alternatives to mitigate the  
1007 negative impacts of agricultural expansion (*Nepstad et al., 2014; Tanenzap et al., 2015*).

1008

1009 Worldwide, policies targeting consumer nations that reduce their ecological footprint in primate  
1010 range regions are needed. Green tagging and certification, greater controls on fair trade,  
1011 corporate responsibility in recycling, and pollution and carbon emissions control, the  
1012 elimination of excessive packaging, and the sustainable purchasing of goods and services are  
1013 critical tools for lowering worldwide demand for processed materials (*Moran, Peterson &*  
1014 *Verones, 2016*) and would help alleviate pressures on primate habitats (*Dalerum, 2014*). As part  
1015 of the ‘greening’ of trade, international corporations should add ‘environmental’ costs to  
1016 products so that there is a continuous regeneration of funds to sustainably promote conservation  
1017 (*Butler & Laurance, 2008*). Alternatively, the World Bank or UN could require that corporations  
1018 and consumer nations pay into a sustainability/conservation fund based on their levels of  
1019 consumption and environmental damage (e.g., like a carbon tax; Carbon Tax Center  
1020 <https://www.carbontax.org>; consulted August 2017). In countries in which the rural poor depend  
1021 on forest products, community forest management could bridge or integrate the needs of  
1022 conservation and commodity production, sustainably safeguarding the continued integrity of  
1023 complex ecological systems (*Sharif & Saha, 2017*). The recent environmentally-oriented,  
1024 demand-side policies regarding illegal timber imports by the EU (*EU, 2010*), the EU resolution  
1025 on oil palm production and deforestation (*EP, 2017*), and the Amsterdam Declaration to  
1026 eliminate deforestation from agricultural commodity chains (*Amsterdam, 2015*) represent

1027 important and positive ‘green’ changes that need to be adopted by the U.S., China, and other  
1028 consume nations. However, the continued growth of the global demand for forest-risk  
1029 agricultural and nonfood commodities requires additional legislation and a stronger global effort  
1030 at regulating the negative impact of unsustainable commodity trade (*Henders et al., 2018*).

1031  
1032 In the context of large-scale deforestation, Brazil, Madagascar, Indonesia, and DRC face  
1033 additional challenges that require cost-effective policies designed to maintain intact areas of  
1034 forest and biodiversity (*Busch & Engelmann, 2018*) (Fig. 11). One approach to achieve this goal  
1035 is the REDD+ program where funds are provided by consumer nations to forest-rich countries to  
1036 offset emissions from deforestation, forest fragmentation, and other forms of environmental  
1037 degradation (*Venter & Koh, 2012*). These funds could be targeted to expand forested habitats and  
1038 connect forest fragments, as well as provide security for local populations by increasing the  
1039 economic and ecological value of maintaining forested land. These programs are just beginning  
1040 but are showing some promising results in DRC (*Fobissie, 2015*), in Makira, Madagascar (see.  
1041 <https://madagascar.wcs.org/Makira-Carbon.aspx>) and in the Atlantic Forest of Brazil  
1042 (*Branca et al., 2013*).

1043  
1044 The forecasted future human population and economic growth of Brazil, Indonesia, DRC, and  
1045 Madagascar along with increased global and local demands for food and non-food products will  
1046 heighten pressures on primate populations in these four countries. The Brazilian ability to  
1047 combat deforestation by 80% between 2005 and 2013 is an example that could be followed by  
1048 the other three countries (*Dobrovolski & Rattis, 2014; Nepstad et al., 2014*). Countries that rely  
1049 on agricultural and natural resource exports from these four primate-rich countries must become  
1050 major contributors to conservation efforts that take place beyond their borders. The safeguarding  
1051 of the primate fauna in each country will require an increase in suitable land devoted to protected  
1052 areas and improved conservation management, as many species lack adequate protection (*Joppa  
1053 et al., 2009*). In addition, given that the unprecedented globalized demand for illegal wildlife, the  
1054 bushmeat trade, and the use of body part in traditional medicine and as trophies, is rapidly  
1055 depleting natural primate populations (*UNODC, 2016*), an international agency, such as Interpol,  
1056 that has the capacity to conduct and coordinate counter intelligence investigations worldwide is  
1057 critically needed. These international investigations can identify criminal organizations involved  
1058 in the illegal trade, which should be considered a form of bioterrorism (Fig. 4, Fig. 11). Given  
1059 the severity of this problem, stopping the supply chain of illegal primate hunting and primate  
1060 trade in the four countries needs to be included in integrated conservation models (*Brashares et  
1061 al., 2014*) that also addresses government corruption (*Estrada et al., 2017*). This also requires a  
1062 focused effort to promote a positive attitude, both in primate range countries and in consumer  
1063 nations towards environmental protection and conservation education, and interventions need to  
1064 provide resources and access to information to encourage members of local communities to  
1065 protect wildlife (*Challender and MacMillan, 2014*).

1066  
1067 Our review has shown that local and global social, economic and political factors imperil the  
1068 persistence of primate populations in Brazil, Madagascar, Indonesia and DRC, and that more  
1069 needs to be done by local governments and international bodies to ensure that primates, a critical  
1070 component of each nation’s natural heritage and biodiversity, do not become rare, locally  
1071 extirpated, or in the case of endemic species, extinct. If this is allowed, these countries risk losing  
1072 complex ecosystem services and social, historical, and cultural relationships that have persisted

1073 between human primates and nonhuman primates over many thousands of years (*Fuentes, 2012*).  
1074 These countries also risk the destabilizing consequences of habitat degradation, pollution,  
1075 climate change, and food insecurity for their human populations. Because Brazil, Madagascar,  
1076 Indonesia and the Democratic Republic of the Congo harbor 65% of the world's primate species,  
1077 these countries are of critical significance for global primate conservation. Consequently, urgent  
1078 local and global action must be taken to reverse the current situation of impending primate  
1079 extinctions.

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1086

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2259

**Table 1** (on next page)

Tree cover loss (30% canopy cover) in Intact Forested Landscapes in Brazil, DRC, Indonesia and Madagascar for the period 2001-2016.

Source of data: *Potapov et al., 2017*.

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	Forest cover (>30% canopy, 2000; km <sup>2</sup> x 10 <sup>3</sup> )	IFL area 2000 (km <sup>2</sup> x 10 <sup>3</sup> )	% of IFL of country's forest cover in 2000	Reduction 2000- 2013 (%) not attributed to fire
Madagascar	170	17.2	10	18.5
Indonesia	1610	359.2	22	10.8
Brazil	5190	2476.1	48	6.2
DRC	1992	643.9	32	4.2

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**Table 2** (on next page)

Major importing countries (50% of exports) of trade commodities (99 categories and their subcategories e.g., frozen beef, arboreal and non-arboreal food and non-food crops, ores, oil, wood and others) produced by Brazil, DRC, Madagascar, and Indonesia.

Source of data: (<http://www.trademap.org/> (accessed 10 December 2017)). International trade maps for the four countries for all exports and for specific commodities see Text S1.

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	Brazil		DRC		Madagascar		Indonesia
	% volume imported by		% volume imported by		% volume imported by		% volume imported by
China	19	China	46	France	24	China	19
USA	13	S. Arabia	11	USA	13	USA	11
Argentina	7			Germany	9	Japan	11
The Netherlands	6			China	7	India	8
Germany	3						
Japan	3						
Total %	<b>50</b>		<b>57</b>		<b>53</b>		<b>50</b>

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**Table 3** (on next page)

CITES trade from Indonesia, Brazil, DRC and Madagascar over the period 2006-2016 (data from 2016 incomplete).

Percentage of wild-caught in brackets. Importer refers to data as reported by the various importing countries; exporter refers to data reported by the exporting countries, here Indonesia, Brazil, DRC, and Madagascar. Source: <https://trade.cites.org/> (accessed 15 August 2017). See Text S1.

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Country	Indonesia	Brazil	DRC	Madagascar
<b>Live animals</b>				
Importer	15,579 (0.06)	166 (0)	561 (100)	13 (7.69)
Exporter	19,009 (0.67)	154 (0)	217 (97.24)	4 (25.00)
<b>Bodies, skeletons, skins</b>				
Importer	40 (100)	0 (0)	20 (90.00)	11 (100)
Exporter	3 (0)	153 (60.13)	9 (100)	47 (100)
<b>Specimens</b>				
Importer	51,743 (12.65)	385 (82.60)	4,876 (92.99)	17,695 (100)
Exporter	73,780 (33.06)	2,449 (60.76)	4,184 (93.40)	10,805 (99.96)

**Table 4**(on next page)

Land area, 2016 human population size, population density, and population growth rates in Brazil, Madagascar, Indonesia, and DRC.

Source: FAOStats <http://www.fao.org/faostat/en>; The World Bank.

<http://data.worldbank.org/data-catalog/world-development-indicators> (accessed 5 February 2018).

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	<b>Brazil</b>	<b>Madagascar</b>	<b>Indonesia</b>	<b>DRC</b>
Land area km <sup>2</sup>	8,515,767	587,041	1,904,569	2,344,858
2016 Population	207,852,865	25,566,097	263,354,770	80,071,935
2016 Population in urban areas	82%	34%	52%	39%
2016 Density (persons/km <sup>2</sup> )	25	44	145	36
2016 Population growth rate (%) FAO	0.77	2.75	1.07	3.09
2016 Population growth rate (%) World Bank	0.82	2.69	1.14	3.28

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**Table 5** (on next page)

The Global Peace Index ranking.

Ranking based on the values of the GPI of 163 countries. High values = A higher ranking represents a more unfavorable condition for the three dimensions of the GPI. Sources: Global Peace Index <http://economicsandpeace.org> (accessed 10 October 2017); economic ranking: World Economic Outlook Database (<https://www.imf.org/external/pubs/ft/weo/2017/01/weodata/index.aspx>) (accessed 11 October 2017).

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Country	ODIC rank	SSS	MILIT
Brazil (8th economy)	17	116	109
DRC (90th economy)	153	127	107
Madagascar (134th economy)	68	42	23
Indonesia (15th economy)	92	44	14

5 ODIC Ongoing Domestic and International Conflict, SSS Societal Safety  
6 and Security, MILIT Militarization

**Table 6** (on next page)

The number and accumulated extent of protected areas in Brazil, Madagascar, Indonesia and DRC.

According to the Protected Planet Database of the UNEP-WCMC - WCPA , Brazil has approximately 29% of its land area protected and therefore has exceeded the United Nations Environmental Program's global goal for countries to set aside and protect 17% of their land as protected areas. The other three countries have not reached the 17% goal

(<https://www.protectedplanet.net/country/ID>; <http://www.drcprotectedareas.org/en/parap>; [i] Waeber et al., 2016[i]).

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	Brazil	Madagascar	Indonesia	DRC
Protected areas	2,190	221	646	90
km <sup>2</sup> protected	2,468,479	71,000	226,249	260,000
Land area km <sup>2</sup>	8,515,767	587,041	1,904,569	2,344,858
% of land area protected	29	12	12	13

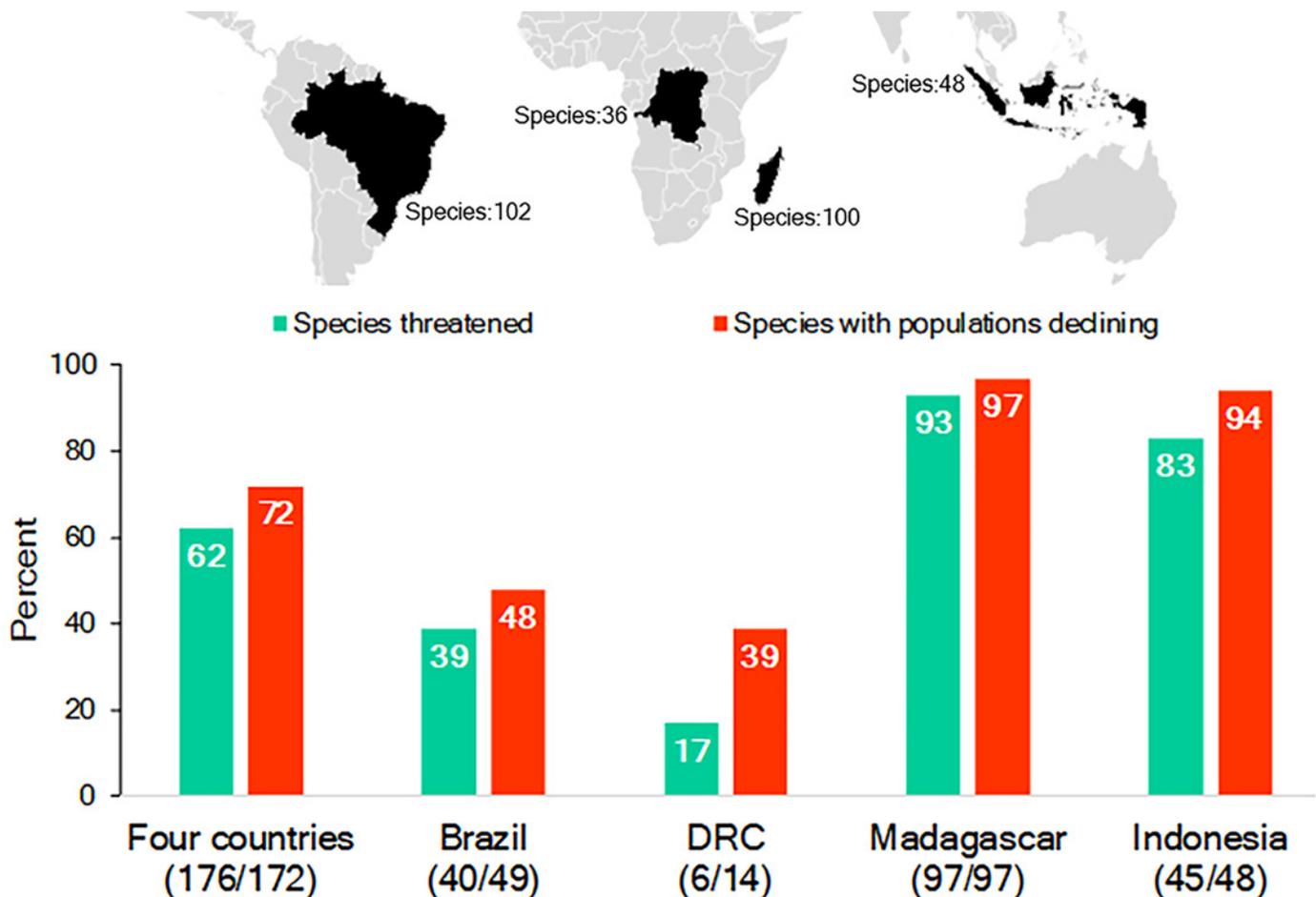
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## Figure 1

The richness of species and IUCN species conservation and population status of primates in Brazil, the Democratic Republic of the Congo (DRC), Madagascar and Indonesia.

In the graph, the numbers below the names of the countries refer to the number of species used to calculate the percentages for species threatened and declining populations. Because population assessments are not available for all species, we focused on those for which recent information is available (Table S2). Source of data: IUCN Red List 2017-3

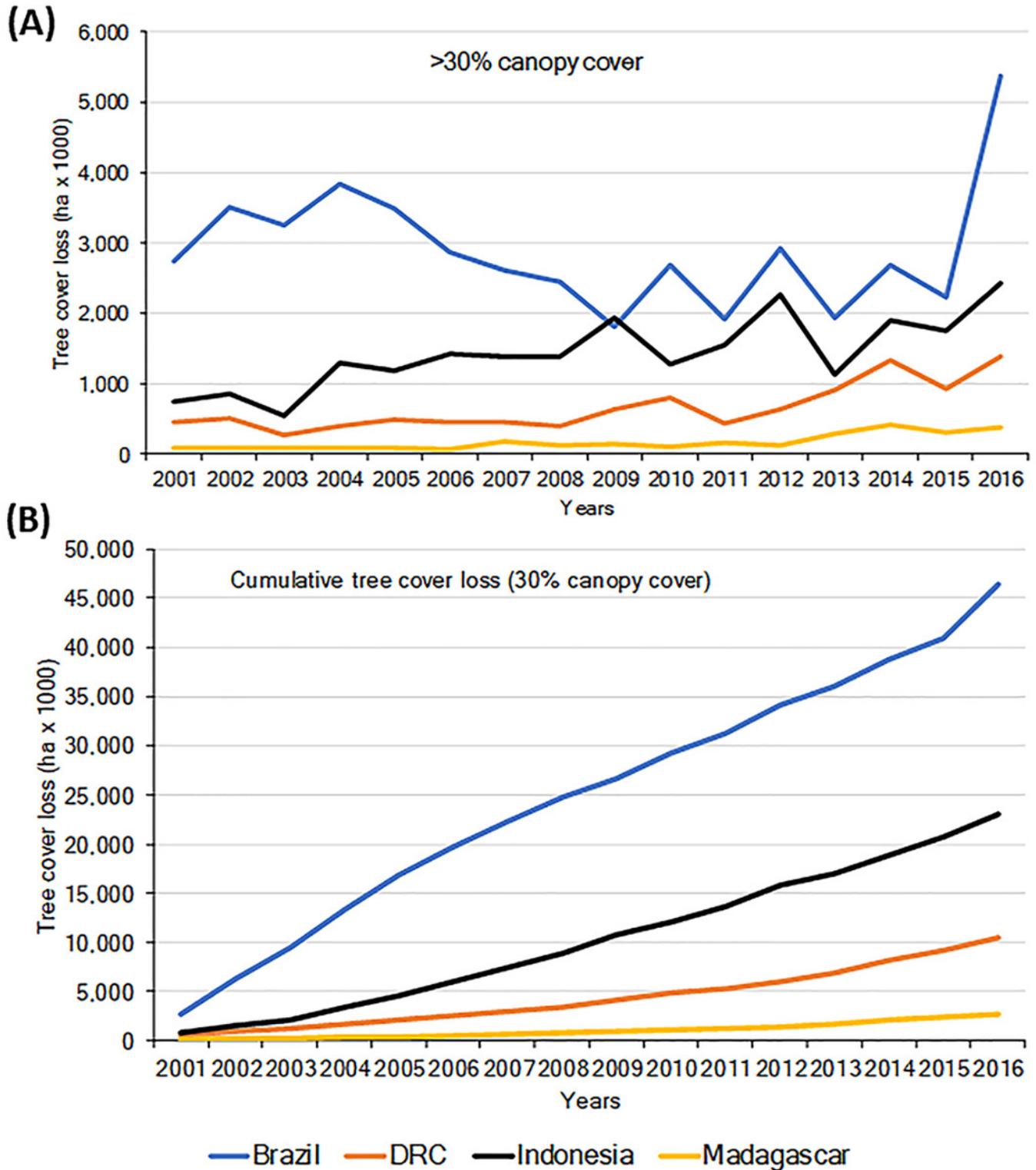
<http://www.iucnredlist.org> (accessed 5 February 2018).



## Figure 2

(A) Trends in tree cover loss (>30% canopy cover) in Brazil, DRC, Indonesia, and Madagascar for the period 2001-2016. (B) Cumulative tree cover (in Intact Forest Landscapes IFL) loss in each country for the same period.

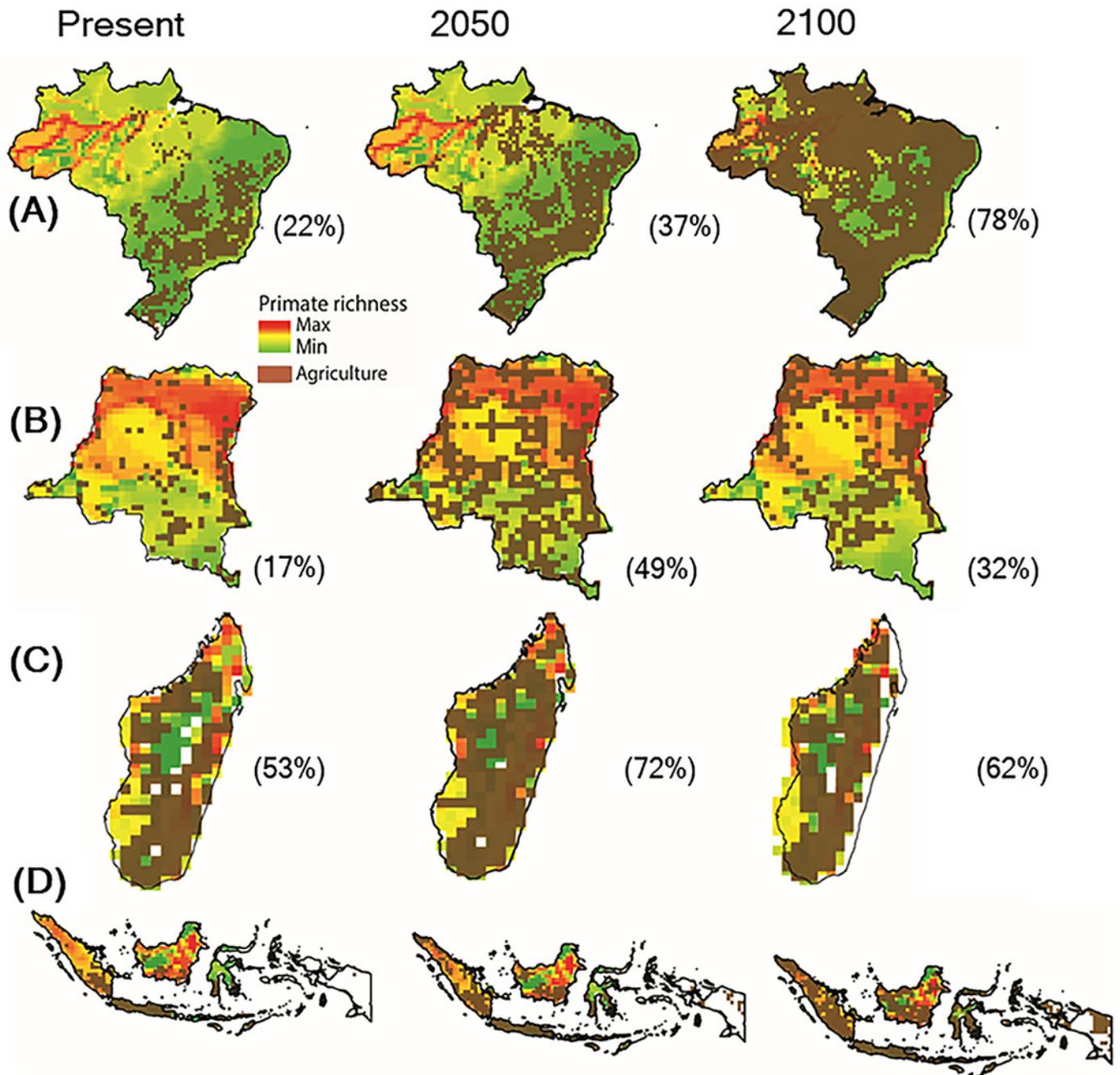
Source of data Global Forest Watch <http://www.globalforestwatch.org> (accessed 5<sup>th</sup> February 2018) IFL: an unbroken expanse of natural ecosystems of at least 500 km<sup>2</sup>, forested, and without signs of significant human activity (*Potapov et al., 2008*). Forest loss ranged in Brazil from 2.74 M ha in 2001 to 5.37 M ha in 2016; in Indonesia from 745.43 K ha to 2.42 M ha; in DRC from 455.43 K ha to 1.38 M ha, and in Madagascar from 86.95 K ha to 383.55 K ha.



## Figure 3

The projected expansion of agriculture and pastures in (A) Brazil, (B) the Democratic Republic of the Congo, (C) Madagascar and (D) Indonesia for 2050 and 2100, under a worst-case scenario of land use from native vegetation to agricultural fields and past

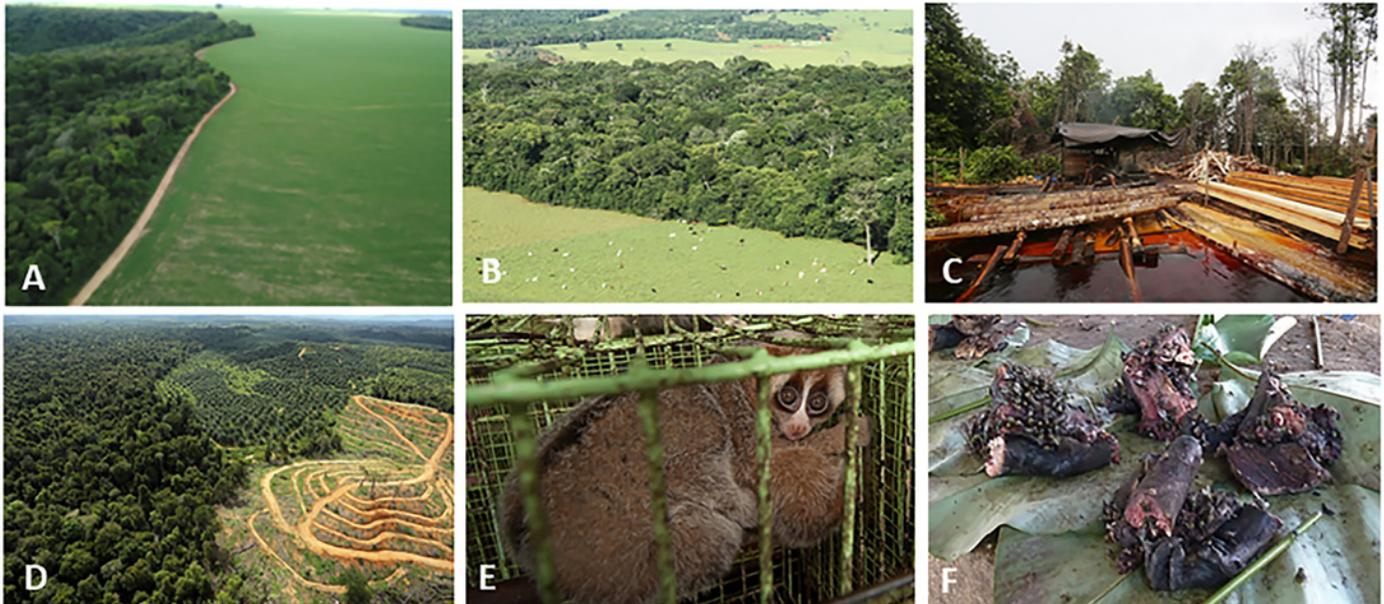
See Text S1 for a description of the methods used. Data on species geographic distribution are derived from *IUCN (2017)* and the scenarios of agricultural expansion from the Integrated Model to Assess the Global Environment (IMAGE, version 2.2) (IMAGE Team, 2001) (see *Dobrovolski et al., 2013*). Notice the spatial shift of conservation conflicts, including the abandonment of some agricultural areas by 2100 in DRC and Madagascar. This condition, however, may not imply an immediate benefit for primate species, as local populations would have been extirpated, areas would have been dramatically altered prior to abandonment, and would likely require decades to regenerate to closed-canopy, old secondary forest. See Fig. S6 for a model based on an optimistic scenario and on a business-as-usual scenario.



## Figure 4

Photos of selected land cover changes in primate range countries, illegal primate trade, and the primate bushmeat trade.

Photo credits include the following: (A) Soybean plantation and recent deforestation of forest patches in the *Cerrado* Biome, Jataí, Goiás State, Brazil (Photo credit: Fabiano R. de Melo), (B) Pastures for cattle ranching surrounding Atlantic Forest patches inside the *Cerrado* Biome, Rio Verde, Goiás State, Brazil. (Photo credit: Izaltino Guimarães Jr.), (C) Indonesia, illegal logging Central Kalimantan (Photo credit: R. Butler), (D) Indonesia, deforestation (Photo credit: R. Butler), (E) Indonesia, Sunda slow loris (*Nycticebus coucang*), sold in Jakarta (Photo credit: A. Walmsley and Little Fireface Project), (F) DRC, smoked bonobo (*Pan paniscus*) meat at a rural meat market (Photo credit: J. Head).

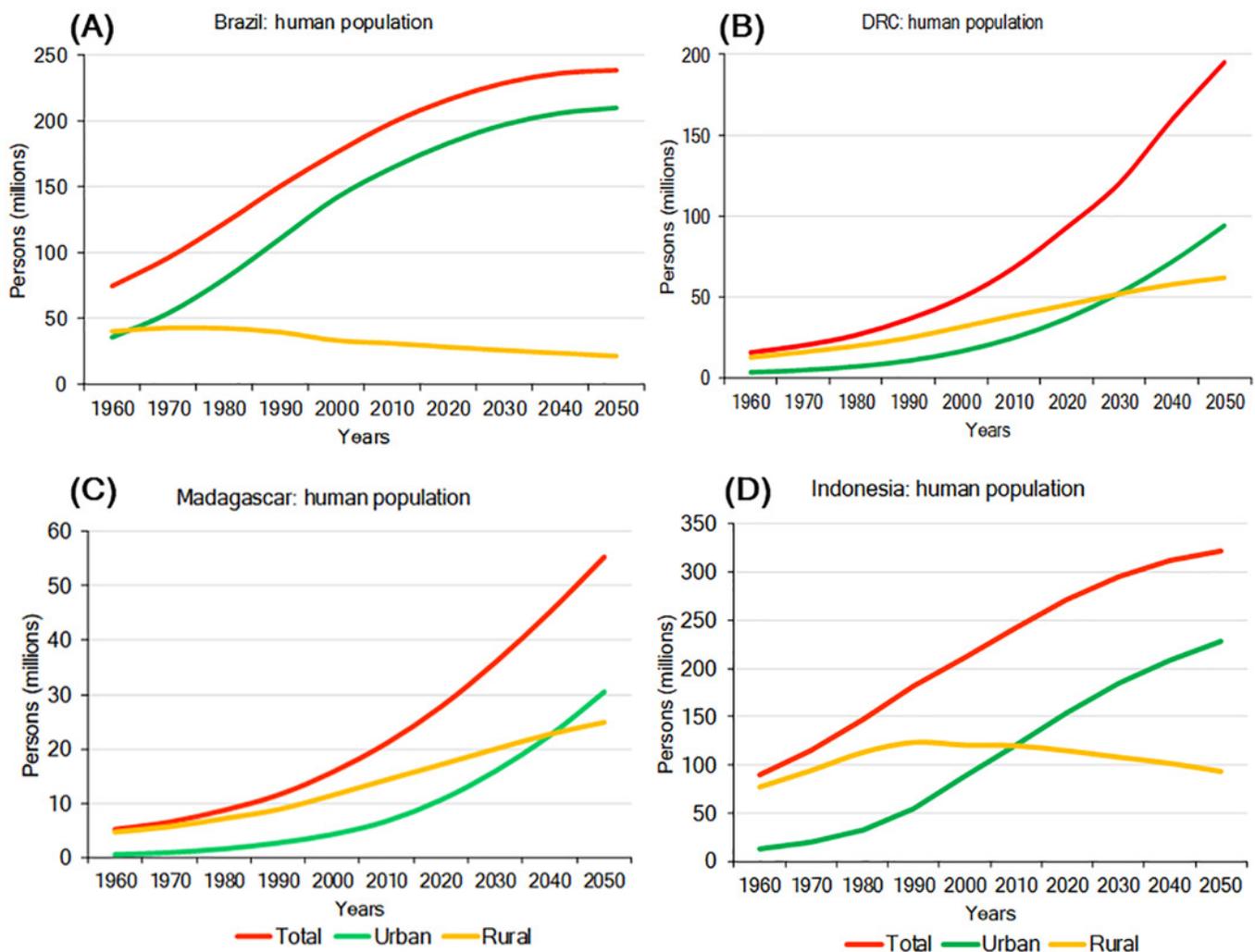


## Figure 5

Total urban and rural population growth and projections for (A) Brazil, (B) DRC, (C) Madagascar, and (D) Indonesia.

Steep growth is forecasted for the next few decades with urban populations significantly increasing, while rural populations are expected to decline. Source:

<http://www.fao.org/faostat/en/#data> (accessed 15 August 2017).

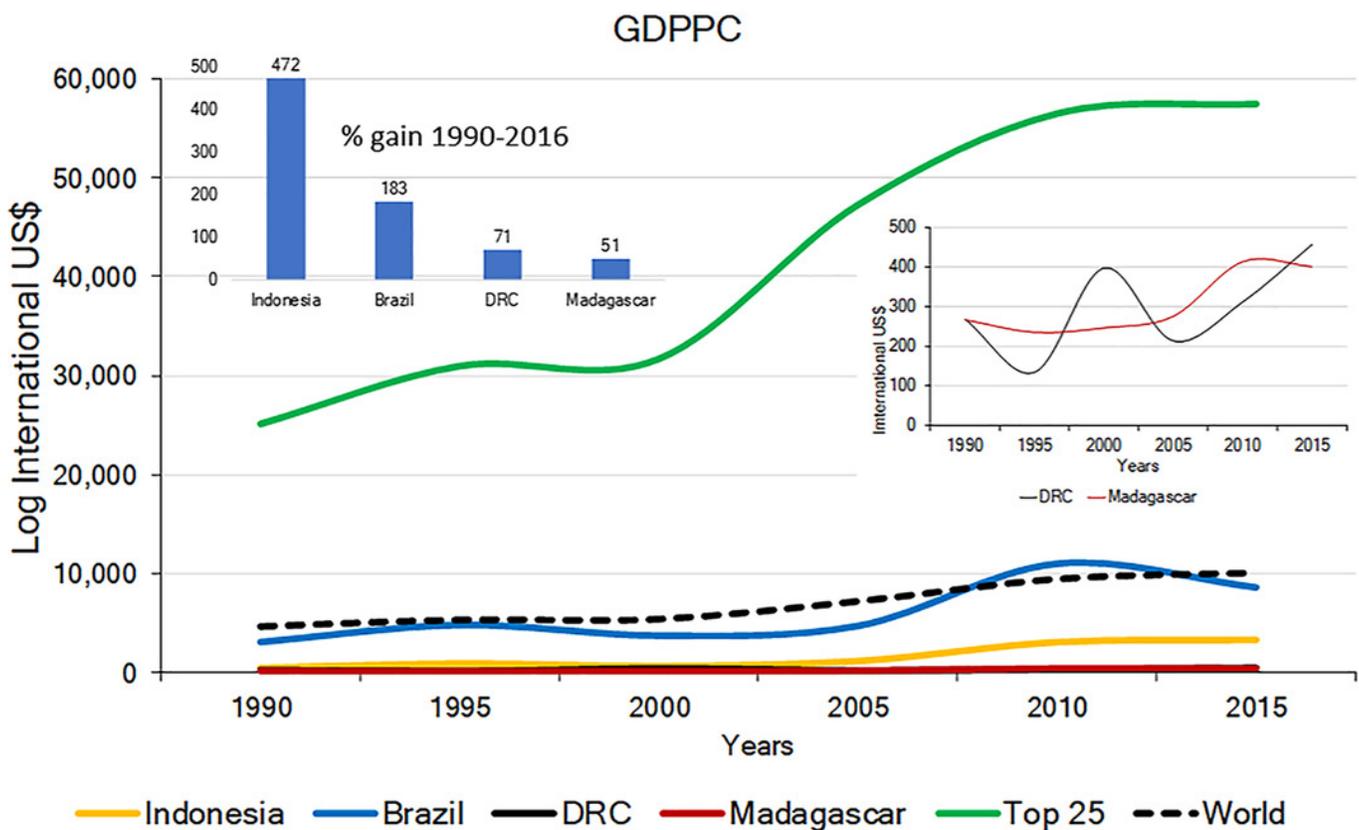


## Figure 6

Gross Domestic Product per capita (GDPPC International USD) in the four countries for the period 1990 to 2015.

Included for comparison are the world's average and the average for the top 25 most developed nations. The trends for DRC and Madagascar are shown in the small line graph on the right. Available at

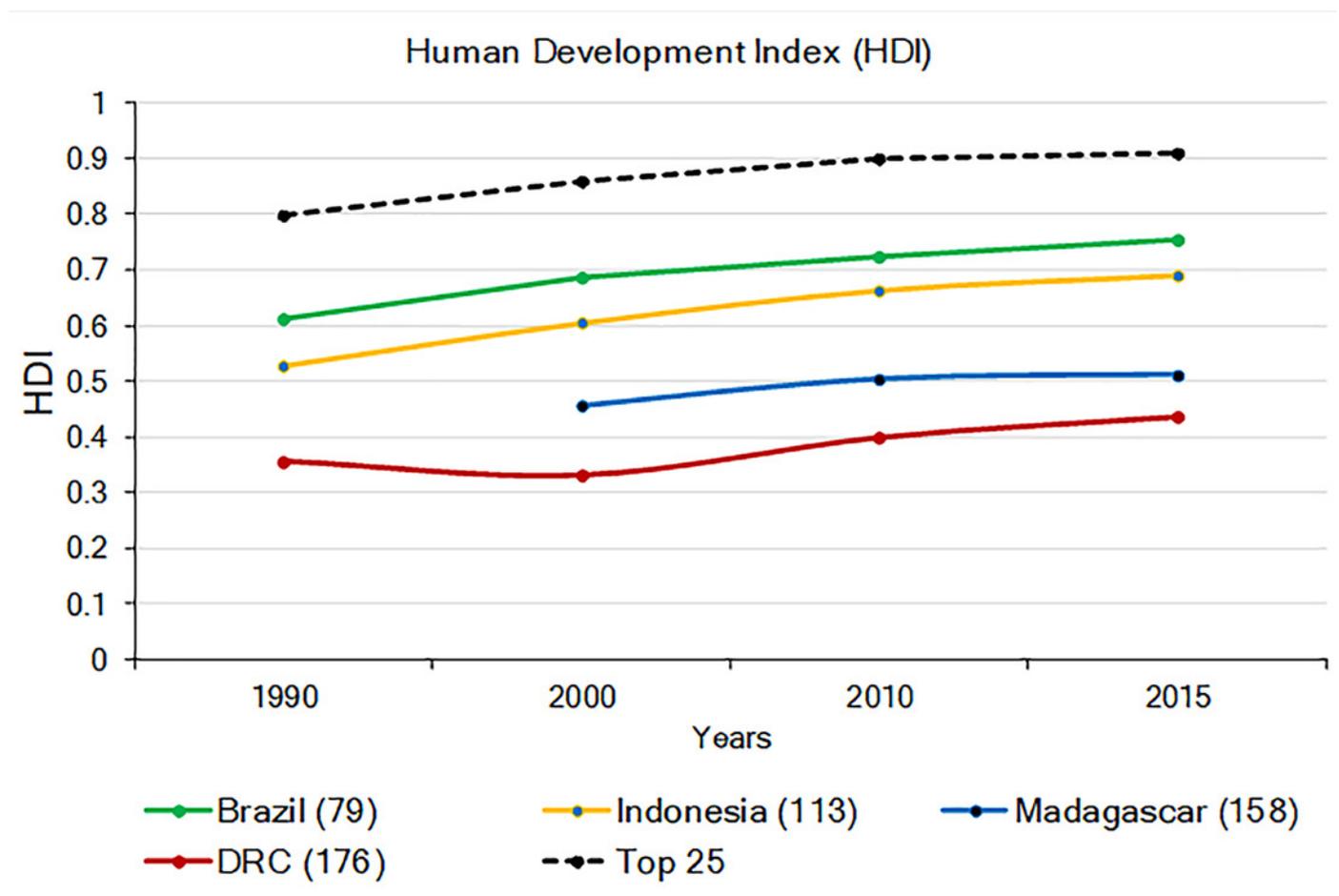
[http://data.worldbank.org/indicator/NY.GDP.PCAP.CD?contextual=max&locations=BR&year\\_high\\_desc=false](http://data.worldbank.org/indicator/NY.GDP.PCAP.CD?contextual=max&locations=BR&year_high_desc=false); <http://data.worldbank.org/indicator/NY.GDP.PCAP.CD> (accessed November 2017).



## Figure 7

The 1990 to 2015 Human Development Index (HDI) in Brazil, Indonesia, Madagascar and DRC (Lowest human development = 0; highest = 1.0). Also shown is the average HDI for the world and for the top 25 most developed nations.

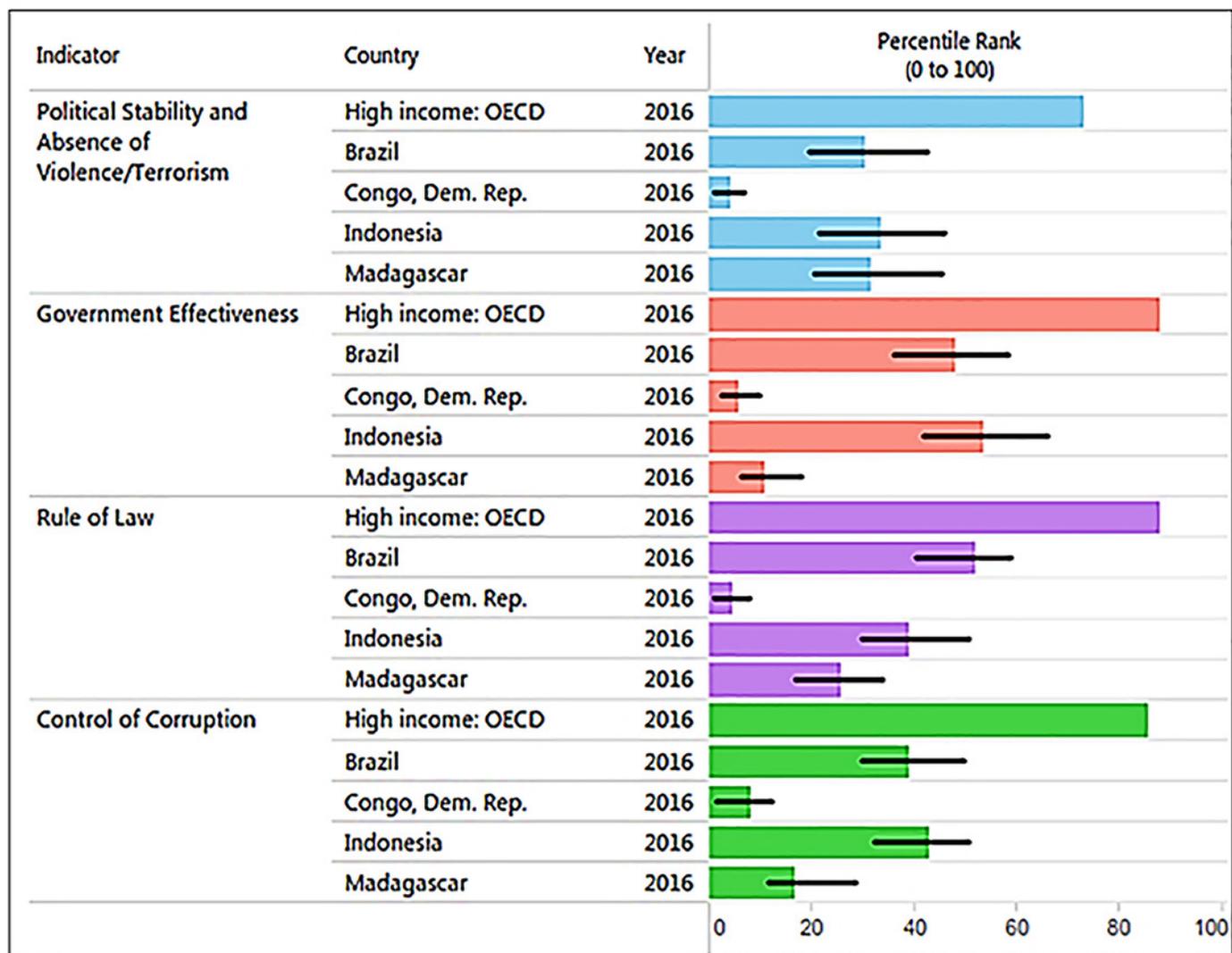
The number in parentheses after each country indicates their HDI world rank. The number in parenthesis after the name of each country indicates its HDI ranking compared to 188 countries. No data are available for Madagascar for 1990. Source: United Nations Development Program (<http://hdr.undp.org/en/composite/trend> (accessed 11 January 2018)).



## Figure 8

The graph, produced using the World Bank database, shows the percentile rank of four key World Bank governance indicators for Brazil, DRC, Madagascar, and Indonesia. Percentile rank: the percentage of countries that rate below the selected country.

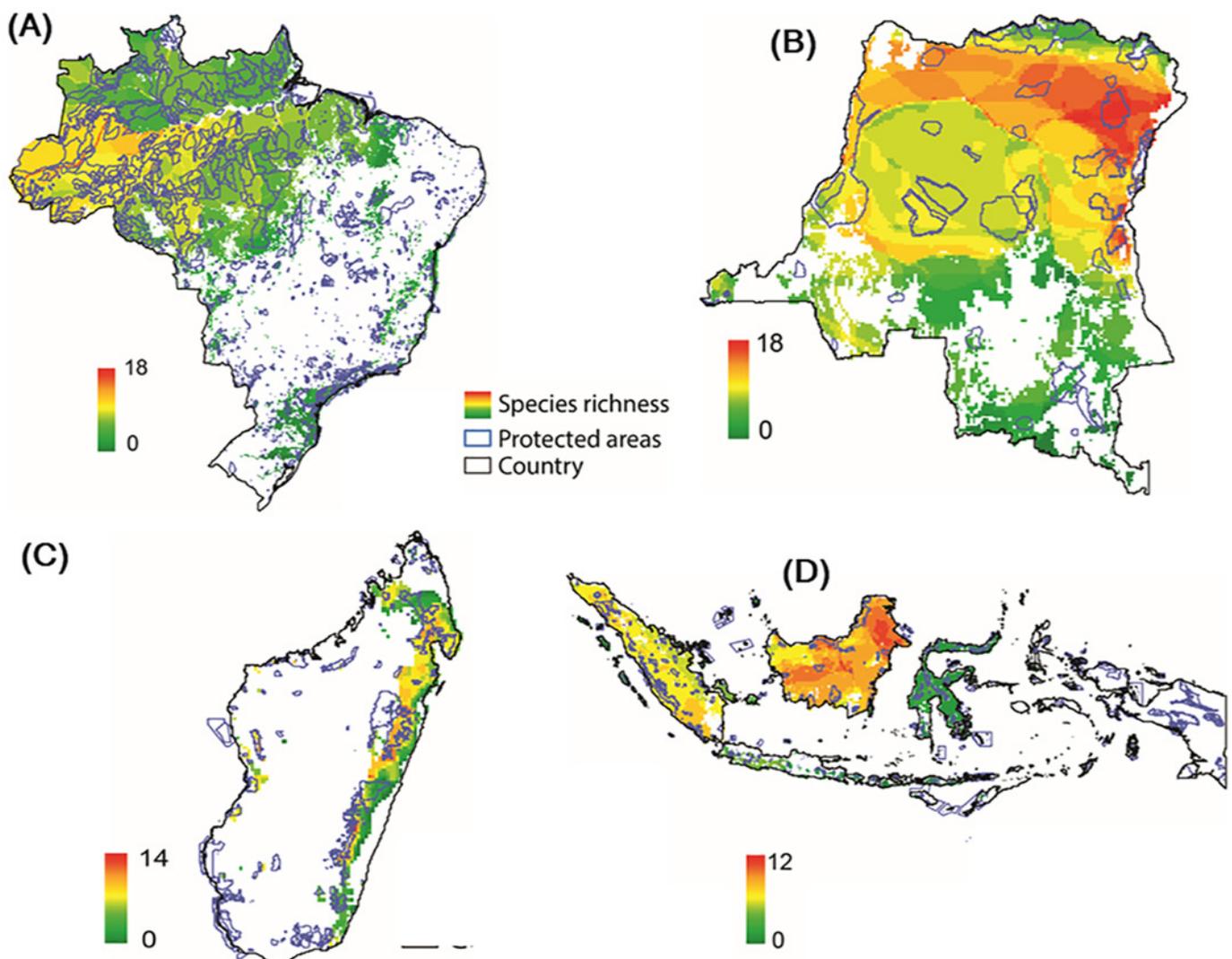
Higher values indicate better governance ratings. Shown for comparison is the percentile rank for high-income OECD countries ( $n = 35$ ; Organization for Economic Co-operation and Development). Percentile ranks have been adjusted to account for changes over time in the set of countries covered by the governance indicators. The statistically likely range of the governance indicator is shown as a thin black line. For instance, a bar of length 75% with the thin black lines extending from 60% to 85% has the following interpretation: an estimated 75% of the countries rate worse and an estimated 25% of the countries rate better than the country of choice. Source: <http://info.worldbank.org/governance/wgi/index.aspx#reports> (accessed 17 November 2017).



## Figure 9

Distribution of protected areas and primate distributions in (A) Brazil, (B) DRC, (C) Madagascar and (D) Indonesia.

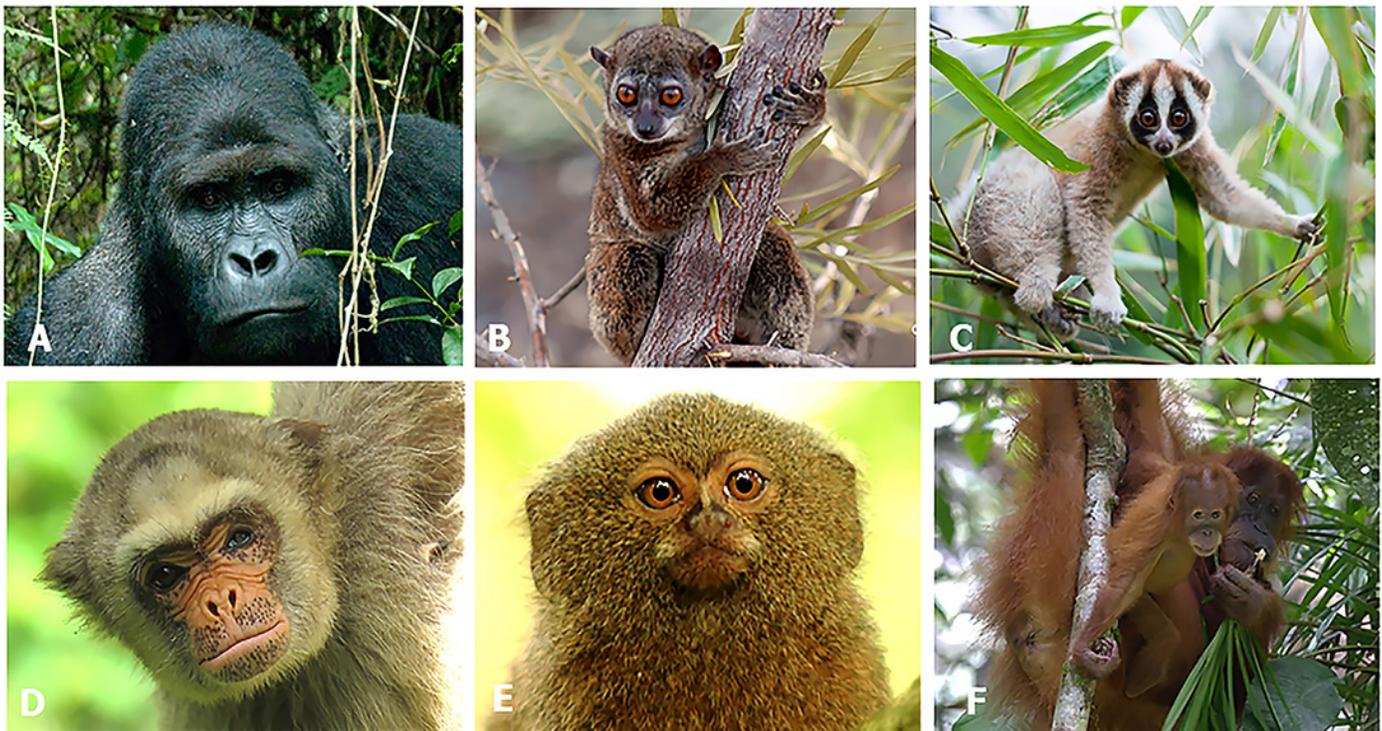
In this model, primate species distributions are based on data from the IUCN Red List (consulted May 2017), protected areas distributions from UNEP-WCMC (2017) and forest cover from *Hansen et al., 2013*. Images are scaled to ca. 300 m of spatial resolution. We included 2190 protected areas in the Brazil dataset, 49 in DRC, 147 in Madagascar and 646 in Indonesia (Text S1).



## Figure 10

Photos of selected primates from each country.

Conservation status and photo credits include the following: A) DRC, Grauer's gorilla (*Gorilla beringei graueri*), Critically Endangered, (Photo credit: J. Martin), B) Madagascar, Sahafary sportive lemur (*Lepilemur septentrionalis*) Critically Endangered (Photo credit: R. A. Mittermeier), C) Indonesia, Javan slow loris (*Nycticebus javanicus*), Critically Endangered (Photo Credit: Andrew Walmsley/Little Fireface Project), D) Brazil, northern muriqui (*Brachyteles hypoxanthus*), Critically Endangered (Photo credit: Raphaella Coutinho), E) Brazil, pygmy marmoset (*Cebuella pygmaea*), Vulnerable, (Photo credit: Pablo Yépez), F) Sumatran orangutan (*Pongo abelii*), Critically Endangered (Photo Credit: Perry van Duijnhoven).



## Figure 11

Diagram summarizing key environmental challenges common to Brazil, DRC, Madagascar, and Indonesia that affect conservation of their primate fauna.

The relative importance of some pressures and population aspects vary from country to country. For example, hunting in DRC is a large-scale pressure because the local human population has little or no access to domestic meat. Because of their large size and low population density relative to the size of the country, Brazil and DRC are in a better position to anticipate the direction of these pressures and prevent primate declines and extirpation. However, in contrast to Brazil, DRC is particularly poor, its human population is rapidly growing, and human development is very low, whereas civil unrest is predominant and corruption and weak governance are an ever-present condition. Madagascar differs from these two countries, and from Indonesia in having a very small percentage of its original forest left. A rapidly expanding human population and high levels of poverty and weak governance are predominant. Indonesia is a developing country with a large human population that has embarked on a policy of rapidly replacing its forests with commercial plantations and expanding industrial logging at the expense of biodiversity.

