

14. Primate Responses to Changing Environments in the Anthropocene

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Abstract

Most primate habitats are undergoing intense and rapid changes due to anthropogenic influences resulting in many primate populations being threatened. Habitat loss and fragmentation are already extensive, thus dispersal to unoccupied habitats is an unlikely adaptive response to these changes. Furthermore, most primates have slow life-histories and long generation times, and because environmental change is occurring at an unprecedented rate, gene-based adaptations are also unlikely to evolve fast enough to offer successful responses to these changes. However, long primate life-histories are linked to well-developed brains, which may allow primates to respond to environmental change through behavioural flexibility. Here we ask; what are the most common challenges of changing environments for primates and what do we know about their behavioural abilities to respond to such changes? To answer this question, we first review the most common types of habitat/landscape alterations, the extent of human-primate interactions, and the impact of climate change. Next, we evaluate how primates respond to these changes via behavioural flexibility and using different approaches and datasets, we discuss how to investigate if these responses are beneficial with regard to population persistence. Finally, we discuss how comparisons across species, space, and time can be used to draw generalizations about primate responses to environmental change while considering their behavioural flexibility and the data derived from case studies. We demonstrate how understanding behavioural flexibility as a response to environmental change will be crucial to optimize conservation efforts by constructing informed management plans.

33 Keywords: Conservation, Comparative Studies, Behavioural Ecology, Behavioural Flexibility,
34 Habitat Change

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36 **14.1 Introduction**

37 *14.1.1 The Anthropocene*

38 Humans are dramatically changing the world. Our population has increased from 2.5 billion
39 in 1950 to 7.4 billion in 2015 and is predicted to go up to 9.8 billion by 2050 (Fig. 14.1a; FAO
40 2017). This growth is associated with increasing resource use, including a dramatic increase in
41 the number of livestock (Fig. 14.1b) and in the use of large areas for agriculture (Fig. 14.1c).
42 Conversely, the proportion of areas with forest, including primary forest, is decreasing globally
43 (Fig. 14.1d and Fig. 14.1e; FAO 2016).

44 Furthermore, the concentration of “greenhouse gases” has dramatically increased since the
45 mid-19th century and these contribute significantly to increasing global temperature and
46 associated changes in climate (IPCC 2014). It is well documented that over the last 130 years the
47 global climate has already warmed by approximately 0.85° C and the temperature increase is
48 likely to exceed 2° C by the end of the century (IPCC 2014; Raftery et al. 2017).

49 Finally, the current species extinction rate is much faster than the estimated evolutionary
50 “background” extinction rate (Barnosky et al. 2011; Ceballos et al. 2015), and has been referred
51 to as the “sixth mass extinction” (Ceballos et al. 2015). For example, conservative estimates
52 suggest that the average rate of loss of vertebrate species over the last century is 100 times
53 higher than the background rate (Ceballos et al. 2015). Beyond the extinction of entire species,
54 populations of many species are in considerable decline (Ceballos et al. 2017).

55 Given the magnitude and range of anthropogenic impacts, Crutzen and Stoermer (2000)
56 suggested that we label the current geological epoch as the “Anthropocene”. While the starting
57 point of this epoch, and whether the Anthropocene even qualifies as a geological epoch, is hotly
58 debated (Carey 2016), the term is commonly used to summarize humanity’s profound impact on
59 the environment.

60 *14.1.2 Primates in the Anthropocene*

61 As a result of the increasing human population, anthropogenic landscape changes, and
62 climate change, about 60% of the ~500 species of non-human primates (hereafter primates) are
63 estimated to be threatened by extinction (Estrada et al. 2017). However, the impact of different
64 human activities on primates varies across regions (Estrada et al. 2017; Almeida-Rocha et al.
65 2017), and within the same region different species may exhibit different population dynamics in
66 response to the same changes (Chapman et al. 2000, 2010, 2017; Fedigan and Jack 2012).

67 The ability to make accurate and repeatedly reliable predictions about the population
68 dynamics of species in response to current and anticipated environmental change will be central
69 to creating effective conservation strategies. This will require a detailed understanding of
70 environmental changes, their causes and cascading effects, and the biology of the species
71 impacted by these changes. However, given the ongoing alterations to primate habitats and the
72 bleak outlook for most primates (Estrada et al. 2017), there will not be enough time to evaluate
73 comprehensively the ability of all primate species to respond. This will make extrapolations from
74 existing datasets, or those quickly gathered from lesser-known species and/or populations a
75 necessity.

76 In this chapter, we review what we know about the ability of primates to respond to
77 changing environments by addressing four questions: 1) What are the most common changes
78 that occur in primate environments? 2) How do primates respond to environmental changes? 3)
79 How can we best investigate the vulnerability of different primates to environmental changes
80 considering that responses appear flexible? 4) How can long-term datasets be used to improve
81 our understanding of primate vulnerability and, therefore, our ability to conserve primate
82 populations? We then discuss the applicability and benefits of comparisons across species, space,
83 and time and give an outlook for the integration of behavioural ecological studies into primate
84 conservation.

85 **14.2 What are the most common changes that occur in primate environments?**

86 *14.2.1 Landscape alterations in primate habitats*

87 With very few exceptions, primates occur in tropical or subtropical regions (Fig. 14.2), and
88 the human population is currently expanding faster in primate-range countries than in countries
89 without primates (Fig. 14.1a). Associated with this greater human population increase in primate-
90 range countries is the faster increase in the number of livestock (Fig. 14.1b) and expansion of
91 agricultural land (Fig. 14.1c) compared to countries without primates. Furthermore, logging,
92 mining, and construction of transportation networks, such as new roads is rising in many tropical
93 countries (Laurance et al. 2009, 2014; Weng et al. 2013). These landscape alterations often lead
94 to disturbances, degradations, fragmentations, or the entire loss of forest areas, which is the
95 primary habitat of primates (Reed and Fleagle 1995; Chapman et al. 2006; Lovett and Marshall
96 2006). For example, cropland in tropical countries expanded by 48,000 km² per year between
97 1999 and 2008, largely at the expense of forest (Phalan et al. 2013). One estimate suggests that
98 approximately 1 billion ha of additional agricultural land, primarily in developing countries, will
99 be needed by 2050 to meet the demands of the growing human populations - an area larger than
100 Canada (Laurance et al. 2014). As a result, forest cover is in considerable decline in primate-range
101 countries, where, according to FAO data, 3.37% (or 72 of 2138 million ha) of forest cover has
102 been lost between 2000 and 2014 (Fig. 14.1d). Primary forest, which is more important for many
103 primates than disturbed forest (Gouveia et al. 2014; Chapman et al. 2017), only represented

104 32.33% of the total forest area in primate-range countries in 2014, and has decreased by 4.22%
105 between 2010 and 2014 (Fig. 14.1e; see also Emrich et al. 2000; Wright and Muller-Landau 2006).
106 In their most recent Global Forest Resources Assessment, the FAO (2016) estimated that the *rate*
107 of global annual forest loss has decreased. However, in some important primate regions, such as
108 Southeast Asia, the Congo basin, or the Brazilian Amazon, deforestation rates have increased in
109 recent years (FAO 2017; Rigby and White 2017).

110 14.2.2 Primate interactions with humans

111 Increases in human population size is likely to lead to more frequent interactions between
112 primates and people in both natural and anthropogenic habitats (McLennan et al. 2017). For
113 example, monkey temples in Asia, which are important refuges for primates in human dominated
114 landscapes, are visited by millions of people annually and bring people and primates in close, and
115 largely peaceful, contact (e.g. (Jones-Engel et al. 2005; Conly and Johnston 2008). However,
116 greater human population density can also lead to an increase in the hunting of ‘bushmeat’ for
117 local and commercial uses (Fa and Brown 2009). Primates are especially vulnerable to bushmeat
118 hunting because they commonly have slow life-histories, and many primates are relatively large-
119 bodies, which makes them a preferred target for hunters (Linder and Oates 2011; Chapman and
120 Gogarten 2012; Wilkie et al. 2016). The encroachment of human settlements to remote areas is
121 also leading to increasing conflicts between humans and primates, including “crop raiding” (Hill
122 2000; Marchal and Hill 2009; see below).

123 Furthermore, more frequent encounters between primates and humans can lead to an
124 increase in parasite and disease transmission from humans and domestic animals to primates
125 and vice versa (Woodford et al. 2002; Chapman et al. 2005b). Documented cases include the
126 transmission of human respiratory paramyxoviruses, *Streptococcus pneumoniae*, and the cold
127 (human rhinovirus C) to chimpanzees (*Pan troglodytes*; Köndgen et al. 2008, 2017; Boesch 2008;
128 Scully et al. 2018), or the transmission of human measles to rhesus macaques (*Macaca mulatta*;
129 Jones-Engel et al. 2006b). In Kenya, an emergence of bovine tuberculosis in baboons (*Papio* spp.)
130 was caused by infected meat consumed by the monkeys from the dump at a tourist lodge
131 (Sapolsky and Share 2004).

132 There are also numerous examples for the transmission of diseases from primates to
133 humans, such as the transmission of Simian Foamy virus from macaques (*Macaca* spp.), or Ebola
134 from gorillas (*Gorilla gorilla*) and chimpanzees to humans (Leroy et al. 2004; Jones-Engel et al.
135 2005, 2008; Bermejo et al. 2006). Perhaps, the most prominent case is the spread of Simian
136 Immunodeficiency Viruses (SIV) from different African primates to humans, which gave rise to
137 the global AIDS pandemic (Hahn et al. 2000).

138 An example of transmission in both direction is the virus causing yellow fever, which can be
139 transmitted by mosquitos between humans and primates (Fernandes et al. 2017). The most

140 recent outbreak of yellow fever in Brazil has resulted in the death of several hundred humans
141 and thousands of monkeys (Bicca-Marques et al. 2017; Fernandes et al. 2017). Diseases that can
142 be transmitted from primates to humans bear an additional risk for primates: during the recent
143 outbreak of yellow fever outbreak in Brazil, some people afraid of yellow fever harassed and
144 killed primates (Bicca-Marques et al. 2017).

145 *14.2.3 Effect of climate change on primate habitats*

146 In comparison to the extensive effects of logging, agricultural clearing, and hunting, the
147 impact of climate change has been previously considered to be minor, but this view has been
148 replaced by the recognition that current climate change is having significant impacts on tropical
149 ecosystems, primates, and biota in general, and this impact is likely to increase in the near future
150 (Parmesan 2006; Brook et al. 2008; Dunham et al. 2011; Corlett 2012; Pacifici et al. 2017).
151 Generally, the increase of temperature in primate habitats is predicted to be higher than the
152 average increase in global temperature, while the predicted change in rainfall patterns depends
153 on the region (Graham et al. 2016). For example, East Africa is predicted to receive more rainfall,
154 while rainfall is predicted to decline in Mesoamerica (Altmann et al. 2002; Chapman et al. 2005a;
155 Graham et al. 2016). Even today, some long-term primate studies have already documented
156 temperature changes of over 4° C in the last 40 to 50 years and change in annual rainfall of as
157 much as 300 mm (Altmann et al. 2002; Chapman et al. 2005a).

158 The frequency and intensity of extreme weather events, such as floods, heavy precipitation,
159 hurricanes (also called typhoons or cyclones), heat waves, droughts, and fires are expected to
160 become more frequent and intense in many regions (IPCC 2013; Diffenbaugh et al. 2017).
161 Furthermore, much of the inter-annual climatic variation in the tropics is driven by El Niño
162 Southern Oscillations (ENSOs; Campos, this Volume; Dunham et al. 2011; Corlett 2012; Campos
163 et al. 2015), and extreme “El Niños” (the warm phases of ENSOs) are expected to become more
164 frequent, resulting in severe droughts in some areas, large amounts of rainfall in other areas, and
165 more intense hurricanes in the Pacific (Cai et al. 2014, 2015).

166 Such changes in climate can have significant impacts on primate populations. For example,
167 on Barro Colorado Island, Panama, fruiting, flowering, and leaf set were disrupted on six
168 occasions between 1929 and 1994 when seasonal rains deviated from their typical pattern. In
169 1970, one such unusual rainfall event led to severe fruit crop failure and the mass mortality of
170 howler monkeys (*Alouatta palliata*) and other animals (Foster 1982; Milton 1982; Wright et al.
171 1999; Wright and Calderón 2006). Additional extensive long-term monitoring of primate
172 populations, climate, and phenology are needed to understand the future effect of climate
173 change. For example, regression modeling of annual fruiting revealed solar irradiance and ENSO
174 as the strongest predictors of fruiting in Kibale National Park, Uganda (Chapman et al. In Press).
175 The projected changes in rainfall associated with climate change, and coincident variation in
176 cloud cover suggest that phenophase dynamics may be affected by climate change. As of yet,

177 however, there is no clear signal as to how primate populations in Kibale will change, despite
178 over 40 years of monitoring (Chapman et al. 2010, 2017).

179 *14.2.4 Indirect, synergistic, and cascading effects of anthropogenic changes on primates*

180 Perhaps the most significant changes in the future will be the result of various indirect,
181 cascading, and synergistic effects on primate habitats that have not been anticipated. For
182 example, climate change, habitat loss, and fragmentation, can all affect plant phenology
183 (Parmesan 2006; Morellato et al. 2016). This means that temporal and spatial variation in food
184 abundance can change, potentially leading to the immigration of new competitors, predators, or
185 pathogens into primate habitats. For example, Rothman et al. (2015) showed a general decline
186 in the nutritional value of leaves in Kibale, Uganda, over as little as 15 years, and such changes
187 have the potential to decrease habitat suitability for local populations of leaf-eating red colobus
188 (*Procolobus rufomitratu*s) and Black-and-White Colobus (*Colobus guereza*). Some environmental
189 changes also have the potential to lead to other perturbations (i.e. cascading effects) and to
190 amplify one another (i.e. synergistic effects; (Brook et al. 2008). For example, logging can affect
191 primates by (1) decreasing food availability, (2) creating roads that fragment primate habitats
192 and facilitate (3) bushmeat hunting, and serve to (4) increase the opportunities for disease
193 transmission (Chapman et al. 2005b; Goldberg et al. 2008; Remis and Jost Robinson 2012).

194 *14.2.5 Protection and restoration of primate habitats*

195 Some disturbed primate habitats are changing because humans undertake efforts to protect
196 and/or restore them and such efforts can have significant benefits to primate populations
197 (Fedigan and Jack 2001; Robbins et al. 2011; Strier and Ives 2012; Wheeler et al. 2016; Omeja et
198 al. 2016). Ideally, these efforts will provide new protected areas or improve existing habitats and
199 lead to viable populations of primates and other organisms. Since the 1990s, protected areas
200 have increased in size globally, primate regions included (Butchart et al. 2010; Rands et al. 2010;
201 Estrada et al. 2017). However, these positive developments need to be viewed realistically (Joppa
202 et al. 2008; Andam et al. 2008; Joppa and Pfaff 2009, 2010). For example, many primates do not
203 live inside protected areas (Meijaard et al. 2010; Estrada et al. 2017). Also, although protected
204 areas are normally effective at protecting land from being cleared, they are less effective at
205 eliminating logging, human-created fire, and bushmeat hunting (Oates 1996; Chapman and Peres
206 2001; Bruner et al. 2001; Hartter et al. 2011; Gaveau et al. 2016). Researching how to make the
207 largest conservation gains for primates from existing and new conservation areas is a clear
208 priority that will necessitate working closely with the local communities.

209 In primate-range countries, human population growth is much greater in urban than in rural
210 areas as people move from the farms to the cities, and populations in rural areas are predicted
211 to be on a general decline in the next few years (Fig. 14.3). With these trends, abandoned areas
212 that were occupied by primates prior to being converted to human uses are increasing (Jacob et

213 al. 2008). There are a variety of trajectories for these lands: they could be converted into huge
214 agricultural monocultures, like palm oil plantations (Linder 2013), or to agroecosystems where
215 some form of primate conservation is possible (Estrada et al. 2012), or to agricultural land with
216 fragments and corridors (Pozo-Montuy et al. 2013; see also Meijaard et al. 2010). Alternatively,
217 the land could be allowed to regenerate to natural forest, which offers greater potential for the
218 persistence of primates (Chapman In Press). For example, Baya and Storch (2010) surveyed a
219 village site in Korup National Park, Cameroon that was abandoned 7-8 years previously and they
220 found that all 8 species of endemic primates had repopulated the area; in addition, sighting
221 frequency was not significantly different from other sectors of the park surveyed in 2004-2005
222 (Linder 2008). In Kibale National Park, Uganda, 7 years after an area of grassland was replanted
223 with trees as part of a carbon offset program, all species of diurnal primates were present in high
224 numbers, including the endangered red colobus and chimpanzee (Omeja et al. 2012, 2016;
225 Chapman et al. 2017).

226 The outcome of such conservation efforts is, however, not always predictable because other
227 factors, such as climate and the immigration of competitors (e.g., elephants; (Omeja et al. 2014,
228 2016), can change and different species of primates respond in different ways to habitat
229 regeneration (Fedigan and Jack 2001, 2012; Chapman et al. 2017).

230 **14.3 How do primates respond to environmental changes?**

231 *14.3.1 General ways to respond to changing environments*

232 Animals possess three key possible ways to responding to changing environments (Wong
233 and Candolin 2015): 1) moving to other areas that fit their requirements i.e., **dispersal**, 2) evolving
234 adaptations to the new conditions, i.e., **evolutionary (or genetic) change**, or 3) exhibiting
235 behavioural responses that are already in their repertoire (or reaction norms) to cope with new
236 conditions, i.e., **phenotypic plasticity**.

237 Habitat loss is already a major concern for the survival of primates (Estrada et al. 2017) and,
238 therefore, unoccupied habitat with the same characteristics as the current habitat is typically
239 nonexistent. Furthermore, fragmentation results in physical barriers between suitable patches,
240 which increases the risks for dispersing individuals (Arroyo-Rodríguez et al. 2013). Thus, *dispersal*
241 is an unlikely suitable response to the Anthropocene.

242 Mammalian species with slow life-histories, such as many even-toed ungulates and
243 carnivores, are assumed to be even more vulnerable to extinction than mammals with fast life-
244 histories, like most rodents (Purvis et al. 2000; Gonzalez-Voyer et al. 2016). Of course, many
245 primates have very slow life-histories: on average, females give birth for the first time around 4
246 years of age (ranging from 256 days to 13.9 years), inter-birth intervals are commonly longer than
247 a year (mean = 1.5 years, range = 0.4-5.5 years), and, with the exception of very few species,
248 females give birth to only a single infant per birth (values based on data from the PanTHERIA

249 database¹; Jones et al. 2009). Most anthropogenic changes, however, occur very rapidly and for
250 primates and other long-lived animals it is very unlikely that *evolutionary changes* are able to
251 keep pace with these changes (Wong and Candolin 2015).

252 However, primates have relatively large brains and it has been suggested that large brains
253 are associated with higher behavioural flexibility, conferring advantages in dealing with both
254 social and ecological challenges (Strier, this Volume; Reader and Laland 2002; Sol et al. 2008).
255 Thus, given the constraints on dispersal and evolutionary change as a response to environmental
256 change, behavioural adjustments appear to be the most likely possibility with which primates
257 might respond to the Anthropocene. What kind of flexible, behavioural responses can primates
258 exhibit to cope with the anthropogenic environmental changes thus becomes a critical question
259 that must be answered to inform conservation strategies.

260 14.3.2 Primate behavioural responses to landscape alterations

261 In response to habitat fragmentations, disturbances, or degradations, primates can change
262 their ranging patterns, activity budgets, and diet (Wong et al. 2006; Wong and Sicotte 2007;
263 Pebsworth et al. 2012; Mekonnen et al. 2017; McLennan et al. 2017). Furthermore, the spatial
264 and temporal distribution of food resources is considered to be one of the most important factors
265 affecting social behaviour and mating patterns (i.e., primate socio-ecological theory; (Wrangham
266 1980; Isbell 1991; Sterck et al. 1997; Snaith and Chapman 2007; Koenig et al. 2013). Thus, if
267 human impact on primate habitats affects the abundance and distribution of their food resources
268 changes in group size and composition, reproductive patterns, or social relationships may occur
269 (langurs: Sterck 1999; tana river colobus, *Cercocebus galeritus*: Mbora et al. 2009; red colobus:
270 Gogarten et al. 2015; Muriquis, *Brachyteles hypoxanthus*: Strier and Mendes 2012).

271 Some of these behavioural responses allow primates to survive in human modified
272 landscapes (Schwitzer et al. 2011; Bonilla-Sánchez et al. 2012; Chapman et al. 2016; McLennan
273 et al. 2017), such as tree plantations or suburban settings (Moore et al. 2010; Hoffman and
274 O’Riain 2011). In some cases, primates even thrive in human modified landscapes by
275 supplementing their natural diet with human cultivated resources via crop feeding (Hill 2000;
276 Marchal and Hill 2009; Chapman et al. 2016), feeding on garbage, food items in houses, or fruit
277 trees in gardens (Hoffman and O’Riain 2012), or being voluntarily provisioned with food from
278 humans. For example, some primates obtain large parts of their diet from local people and
279 tourists at monkey temples in Asia (Jones-Engel et al. 2005; Fuentes and Gamerl 2005).

¹The calculation of age of first birth includes data from 102 primate species, and the calculation of inter-birth intervals included data from 108 primate species. These averages are not corrected for phylogenetic relatedness and might be biased depending on the inclusion of varying number of primates from different taxonomic groups.

280 14.3.3 *Primate behavioural responses to interactions with humans*

281 Where humans do not pose a threat to them, primates can easily habituate to humans. For
282 example, the ursine colobus (*Colobus vellerosus*) at the Boabeng-Fiema Monkey Sanctuary in
283 Ghana (Wong et al. 2006), different macaque species at monkey temples in Asia (Fuentes and
284 Gamerl 2005; Jones-Engel et al. 2006a), and baboons close to tourist lodges and human
285 settlements in Senegal or Botswana (UK, personal observation) are all examples where primates
286 peacefully co-exist with humans and, in some cases, this co-existence can even result in economic
287 benefits to local human populations (Fuentes and Gamerl 2005). However, if encounters are less
288 peaceful, such as occurs in the context of bushmeat hunting, primates can become more cryptic,
289 vigilant, try to avoid risky areas, and become more aggressive towards humans and dogs (Remis
290 and Jost Robinson 2012; McLennan et al. 2017). For example, vervets (*Chlorocebus tantalus*) in
291 areas of Cameroon where they were heavily hunted by humans with dogs suppress loud,
292 conspicuous alarm calls directed at dogs, possibly to avoid detection (Kavanagh 1980).

293 14.3.4 *Primate behavioural responses to climate change*

294 In response to increasing temperatures, which can make metabolic costs of moving or
295 foraging unsustainable during the hottest time of the day, primates can change their daily activity
296 patterns. For example, they may rest or socialize in the shade during the middle of the day and
297 spend more time foraging during cooler periods (Hill 2005). Primates also show a high degree of
298 variability in birth seasonality, ranging from strictly seasonal breeding species, such as macaques,
299 to species in which females can give birth throughout the year, such as baboons (*Papio* spp.;
300 Janson and Verdolin 2005). In such flexible species, females may adjust their breeding behaviour
301 by only reproducing during favorable times. For example, yellow baboons in Kenya (*P.*
302 *cynocephalus*) breed throughout the year, but females are less likely to cycle or to conceive after
303 periods of extreme heat (Beehner et al. 2006). However, how quickly a population modifies their
304 seasonal reproductive patterns remains to be determined.

305 While some primates rarely drink water, other species need year-round access to water
306 sources (Hill 2005; McDougall et al. 2010; Fedigan and Jack 2012). If the habitat of these obligate
307 drinkers receives less rainfall, water sources can become rare and widely dispersed, requiring
308 changes in ranging patterns in order to maintain access to drinking water, as has been
309 documented for vervet monkeys (*Chlorocebus aethiops*; (McDougall et al. 2010). Such shifts
310 could become permanent if previously favorable areas become unsuitable year-round. This may
311 increase encounters between groups, leading to higher energy expenditures, increased stress,
312 and even elevated mortality levels. In contrast, more rainfall and shorter dry periods may have
313 no direct, but rather indirect effects on primates, such as causing temporal shifts of food
314 availability, or fruit crop failure, which has been documented to cause increased mortality (Milton
315 1982; Wright et al. 1999; Wright and Calderón 2006).

316 Hurricanes represent another extreme weather event with potentially severe impact on
317 primates and their habitats that may increase in frequency and intensity with climate change
318 (Erhart and Overdorff 2008; Dunham et al. 2011; Johnson et al. 2011; Schaffner et al. 2012).
319 Primates respond in various ways to the impact of hurricanes. For example, black howlers
320 (*Alouatta pigra*) and spider monkeys (*Ateles geoffroyi*) in Belize and toque macaques (*Macaca*
321 *sinica*) in Sri Lanka responded to the habitat destruction following hurricanes by changes in
322 activity budgets, diet, and social behaviour (Behie et al. In Press; Dittus 1988; Behie and Pavelka
323 2005, 2013).

324 14.3.5 Primate behavioural responses to indirect and synergistic effects of changing 325 environments

326 Changes in plant phenology may represent one of the most important indirect effects of
327 anthropogenic activities on primates because it can lead to a change in temporal and spatial
328 distribution of food resources. As discussed above, primates can respond to such alterations by
329 adjusting group size, social structure, and mating patterns. Furthermore, they can shift their diets
330 and rely on fallback food when their preferred resources become scarce during some (or all)
331 periods of the year (Hanya and Chapman 2012). Temporal variation in food abundance is also
332 one of the main factors suspected to determine timing of reproduction (Janson and Verdolin
333 2005; Carnegie et al. 2011). For example, capuchin monkeys in Santa Rosa can give birth
334 throughout the year, but do so mostly during the period of highest fruit abundance (Carnegie et
335 al. 2011). Thus, if temporal variation in food availability changes, some primates may shift their
336 birth peak. Cascading and synergistic effects describe processes rather than specific types of
337 environmental change; thus, primate responses will depend on the nature of the changes
338 involved in such processes (e.g., habitat fragmentation, hunting), which, to a large extent, are
339 unknown.

340 14.4 How can we best investigate the vulnerability of different primates to environmental 341 changes considering that responses appear flexible?

342 Primates show highly flexible behaviour which they can adjust to various types of
343 environmental change, but are these behavioural responses beneficial and sufficient to ensure
344 their survival? And why are some species doing well in human-dominated landscapes, while other
345 species already have gone extinct² or are threatened by extinction?

346 There are three general approaches to investigating the vulnerability of primates to
347 anthropogenic change: 1) *comparative studies* of different populations and species, 2) *niche*
348 *modelling studies*, and 3) *behavioural ecological studies* based on the behaviour of individuals.

²It seems almost a certainty that with the disappearance of Miss Waldron's red colobus (*Procolobus waldroni*) the first primate species has been driven to extinction in modern times (McGraw 2005; Oates et al. 2016).

349 *14.4.1 Comparative Studies*

350 Studies using the comparative method commonly aim to investigate the relationships
351 among morphological, life history, behavioural, and ecological variables across species while
352 controlling for the effects associated with phylogenetic relatedness (Harvey and Pagel 1991;
353 Nunn and Barton 2001). With regard to species or population persistence, such analyses aspire
354 to understand the relationships among biological variables (e.g., body weight, age at first
355 reproduction) and variables reflecting the vulnerability of species to extinction. Using this
356 approach, Purvis et al. (2000) showed that primates with small geographic distributions, large
357 body mass, and low population density are at higher risk of extinction than are species with large
358 distribution, small body mass, and high population density. Furthermore, mammalian species
359 that are highly specialized with regard to diet or habitat are more threatened by habitat changes,
360 while species with slow life-histories, such as primates, are more threatened by hunting and
361 other direct effects (González-Suárez et al. 2013).

362 The notion that behavioural flexibility may be beneficial for coping with environmental
363 change has received support from a comparative study showing that within-species variability in
364 life-history (e.g., age at first reproduction) and population density appears to reduce the
365 vulnerability of mammals to extinction (González-Suárez and Revilla 2013). Furthermore,
366 mammals with relatively large brains (and therefore presumably greater behavioural flexibility)
367 are more successful in novel environments than mammals with relatively small brains (Sol et al.
368 2008). However, a different study indicated that larger brains in primates and other mammals
369 are associated with increased vulnerability to extinction (Gonzalez-Voyer et al. 2016). Thus, the
370 behavioural flexibility resulting from large brains in primates may not outweigh the costs of slow
371 life-histories and the higher energy demands that large brains necessitate and, therefore, may
372 even represent a disadvantage in this heavily human-dominated world.

373 Phylogenetic comparative studies require large data sets (e.g., PanTHERIA or AnAge; Jones
374 et al. 2009; Tacutu et al. 2013), but there are often problems related to accuracy and
375 comparability (Borries et al. 2016). Furthermore, animals are constantly making behavioural
376 adjustments to environmental conditions, and, therefore, species parameters, such as group size,
377 vary considerably depending on the study location, the provisioning of the group, or the study
378 period (Strier 2009, 2017; Borries et al. 2016). To address this concern, some studies include the
379 Coefficient of Variation (CV) of a variable to explicitly assess the effect of within-species variation
380 (González-Suárez and Revilla 2013; Kamilar and Baden 2014). However, to observe a large
381 proportion of the possible variation within a species, samples from long periods of time and
382 different locations are necessary (Chapman et al., this Volume; Hogan and Melin, this Volume)
383 and for most species this is simply not available. In such analyses it is also important to consider
384 that variation assessed by CVs is positively related to the number of data points and the duration
385 of the study (Strier, this Volume; González-Suárez and Revilla 2013; Strier et al. 2014). Finally,

386 comparative studies are limited to the variables included in comparative databases and these
387 may not necessarily be the variables of interest with regard to the survival of a population.

388 Thus, while comparative studies can lead to important insights and generalizations as to how
389 different species or populations of primates may or may not respond to anthropogenic changes,
390 these limitations should be kept in mind and it will remain important to investigate single species
391 as this information is “essential to understand the species-specific aspects of vulnerability and
392 potential for recovery” (Fedigan and Jack 2012, p. 181).

393 14.4.2 Niche Modelling Studies

394 One approach to assessing vulnerability at the species level is through niche modelling (e.g.,
395 Johnson and Brown, this Volume) which investigates broader factors (e.g., rainfall patterns,
396 elevation, temperature) that affect the geographical distribution of a species. By extrapolating
397 from the results of such studies, it is possible to predict which unoccupied habitats might be
398 suitable for a specific species (Vidal-García and Serio-Silva 2011) and how this species might be
399 able to cope with anticipated environmental change in their current habitats.

400 For example, Vidal-Garcia and Serio-Silva (2011) used a niche modelling approach to develop
401 a distribution model for the primates of southern Mexico. Using records of the presence of the
402 three endemic primates and 19 potential environmental predictors of their distribution, they
403 found strong relationships (e.g., *Alouatta palliata* was strongly associated with precipitation
404 during the coldest quarter of the year). By using this modeling approach these authors located
405 areas with a high probability of the presence of the target primate; information that is now being
406 used in conservation planning. However, such studies do not typically have the data required to
407 investigate the proximate causes limiting population distributions, such as daily access to drinking
408 water sources or required plant resources.

409 14.4.3 Behavioural Ecological Approach

410 Investigating the mechanisms underlying the persistence or extinction of populations on the
411 individual level can be achieved by combining behavioural ecology with conservation biology.
412 This behavioral ecological approach to conservation has also been labeled as “Conservation
413 Behaviour” (Caro and Durant 1995; Blumstein and Fernández-Juricic 2010; Blumstein 2012) and
414 it can contribute to many critical aspects of conservation, including predictions of population
415 persistence, design of protected reserves, and management of populations (Caro and Durant
416 1995).

417 The idea behind conservation behaviour is that individual behavioural responses to
418 environmental changes determine individual survival, reproduction, and migration, which
419 ultimately determines population dynamics (Blumstein 2012; Wong and Candolin 2015). In other
420 words, the focus on individual survival and reproduction of behavioural ecological studies is
421 shifted to a focus on the broader survival of populations in conservation behaviour. Blumstein

422 (2012) stressed the importance of social and mating behaviour in such investigations, as the link
423 from environmental variation to demographic success often goes through social structure and
424 breeding system. For example, environmental factors affect dispersal and mating patterns, which
425 determine effective, and, therefore, minimal viable population sizes (Caro and Durant 1995).
426 Knowing these parameters is important when designing protected areas of the appropriate size,
427 shape, and connectivity. Anthropogenic changes can also affect the occurrence of sexually
428 selected behaviours, such as male infanticide in primates, which can impede population growth
429 (Jack and Fedigan, this Volume; Sterck 1999). Thus, environmental conditions, such as the
430 distribution and abundance of resources, predator density, cover from predators, and pathogens
431 are linked to demographic structure through individual behaviour. Investigating this link can
432 reveal insights into the adaptiveness of primate behavioural flexibility, uncover key-factors that
433 determine population persistence, and predict population responses to anthropogenic change,
434 all of which can help improve conservation efforts.

435 **14.5 How can long-term datasets be used to improve our understanding of primate** 436 **vulnerability and, therefore, our ability to conserve primate populations?**

437 As a result of the slow life histories of primates, long-term datasets spanning several
438 generations are often necessary to observe the relationship between environmental change and
439 population dynamics (Strier 2009; Fedigan and Jack 2012; Campos et al. 2015; Chapman et al.
440 2017). Such datasets require a lot of effort and dedication to collect, thus only a few primate
441 populations have now been continuously observed for the needed duration (e.g., the seven
442 populations of different primate species that are part of the “Primate Life History Database, see
443 (Strier et al. 2010; Campos et al. 2017). The collection of such long-term data also requires
444 substantial continuous funding, a requirement that is getting harder to achieve despite a very
445 apparent need.

446 Long-term data can be supplemented from other sources to generate more comprehensive
447 datasets with which to investigate the impact of environmental change on population dynamics.
448 To assess *environmental change*, questionnaires can be used to assess human activity and its
449 impact on primates and their habitats (McKinney 2015). Aerial photographs and historic and
450 contemporary satellite imagery can reveal information about changes in forest structure and
451 coverage (Harper et al. 2007). Satellite imagery can also be used to estimate human-primate
452 interactions by assessing human population density and the distance between human
453 settlements or roads (e.g., logging routes) to primate habitats (Espinosa et al. 2014). Long-term
454 data on past, current, and predicted temperature or rainfall are available from online resources,
455 such as WorldClim (<http://www.worldclim.org/>) or from the Data Distribution Centre of the
456 Intergovernmental Panel on Climate Change (IPCC DDC; <http://www.ipcc-data.org/>). Some long-
457 term datasets also include plant phenology data (e.g., Santa Rosa, Costa Rica: Hogan and Melin,
458 this Volume; Kibale, Uganda: Chapman et al. In Press; Cabang Panti Research Station, Borneo:

459 Dillis et al. 2015), which, in combination with plant transects and food lists, can be used to assess
460 temporal variation in food availability over space and time.

461 Data on *individual behaviour* is often the central piece of long-term primate behavioural
462 ecological studies and can be used to assess changes in both activity budgets and more specific
463 patterns of social, feeding, and ranging behaviour in response to environmental change.
464 Furthermore, long-term studies also put a great deal of effort into collecting data on life-history
465 events, such as emigration, death, or birth of individuals. These data are essential to assess the
466 effect of individual behaviour on *survival and reproduction*, which is of central interest to
467 behavioural ecologists. The same long-term life-history data can also be used to assess the effects
468 of environmental change on survival and fertility rates (Campos et al. 2017). However, to assess
469 changes in *demographic structure* of an entire population, regular area wide censuses are
470 necessary (e.g., Barro Colorado Island, Panama: Milton and Giacalone 2014; Beza Mahafaly:
471 Sussman et al. 2012; Hacienda La Pacifica, Costa Rica: Clarke and Glander 2010; Hato Masaguaral,
472 Venezuela: Rudran and Fernandez-Duque 2003; Kibale, Uganda: Chapman et al. 2017; Kinkazan,
473 Japan: Yamagiwa 2010; Santa Rosa, Costa Rica: Fedigan and Jack 2012), ideally including
474 knowledge about sex and age composition of individuals in the encountered groups. Ultimately,
475 changes in demographic structure can be used to make predictions about the *survival of*
476 *populations*.

477 Such comprehensive datasets can be used to investigate how primates respond to changing
478 environments, to make predictions about the viability of populations, and to implement
479 conservation measures. For example, if females can breed throughout the year, how does this
480 affect individual fitness and the dynamics within the population? Such questions can be
481 addressed by using a comprehensive, longitudinal dataset to: 1) assess fluctuation in food
482 availability, temperature, and rainfall patterns; 2) determine the timing of life history events with
483 regard to environmental conditions for the entire populations; 3) investigate whether individuals
484 have greater reproductive success, better health, and longer life expectancy if they adjust the
485 timing of life history events from year to year according to environmental conditions; and finally,
486 4) assess how this individual flexibility affects the demographic structures of the entire
487 population and improves the population viability in comparison to non-flexible species (see also
488 (Campos et al. 2017; Strier, this Volume). If flexibility is adaptive, these populations should be
489 less affected by periods of unfavourable conditions, such as periods of resource scarcity. The
490 knowledge acquired could be used to either provision susceptible populations with water or food
491 during crucial periods (but this creates issues as well; e.g., Asquith 1989), or to specifically design
492 protected areas that ensure sufficient resources and protection during these periods.

493 Building comprehensive and meaningful species models that are generalizable to a variety
494 of habitats that link environmental change to population persistence through individual
495 behaviour is challenging and currently only possible for very few primate species. Nevertheless,

496 investigating the link between only some of the factors at a time, for example the consequence
497 of changes in temperature and rainfall on demography (Campos et al. 2015), or the fluctuation
498 in resources availability or logging on population abundance (Chapman et al. 2017) can also be
499 informative with regard to understand primate adaptations to changing environments.
500 Importantly, based on such studies, researchers could go back to their datasets and ask more
501 specific questions about the behavioural mechanisms underlying the observed link (Fedigan and
502 Jack 2001, 2012).

503 **14.6 Comparisons across species, space, and time**

504 While a single-species approach is necessary to identify the mechanism underlying primate
505 population responses to environmental change, or responding to major issues like climate
506 change, deforestation, or bushmeat requires generalizations that are applicable to sets of species
507 (phylogenetic and functional groups), times, and locations. Environmental factors, individual
508 behaviour, and the demographic structure of populations can be compared along three different
509 dimensions to disentangle flexibility and phylogenetic constraints in primate responses to
510 changing environments (Chapman and Rothman 2009). First, long-term studies on a single
511 population can be considered to be a comparative study over time (**temporal dimension**)
512 because a population at one given time is compared with the same population at another time
513 when conditions have changed. Second, populations of the same species can be compared across
514 different habitats (**spatial dimension**). Third, different species can be compared within the same
515 habitat (**phylogenetic dimension**). Furthermore, these three dimensions can be combined, for
516 example by comparing different species across different habitats (i.e. *spatial* and *phylogenetic*
517 *dimension*). When investigating responses to environmental change, we think that the following
518 three types of comparisons as especially useful: 1) *Spatial comparisons*; 2) *Phylogenetic and*
519 *temporal comparisons*; and 3) *Phylogenetic, spatial, and temporal comparisons*

520 *14.6.1 Spatial comparisons*

521 Comparisons within the same species across different habitats that have experienced different
522 types and degrees of modification can advance our understanding of the potential of within-
523 species flexibility (Struhsaker 1999; Chapman and Peres 2001; Chapman et al. 2010). For
524 example, Meijard et al. (2010) found that population densities of Bornean orangutans between
525 conservation areas and pulp and paper plantations were similar, and suggested that behavioural
526 flexibility facilitated these apes surviving in modified landscapes. Such contrasts can be
527 considered natural experiments that allow us study animal adaptations (Schroeder et al. 2011; but
528 see Caro and Sherman 2011 for limitations of this approach).

529 *14.6.2 Phylogenetic and temporal comparisons*

530 By comparing different species in the same habitat over time, it is possible to directly
531 compare responses across species towards the same environmental changes. For example,

532 howler and capuchin monkeys (*Cebus capucinus imitator*) in Santa Rosa, Costa Rica, showed
533 differences in population growth in the same regenerating forest. In this case, both species faced
534 the same changes in the environment and differences in population dynamics can probably be
535 attributed to differences in diet, life-history pace, dispersal patterns, and behavioural flexibility
536 (Fedigan and Jack 2001, 2012). Additionally, studying several species within the same habitat
537 enables the investigation of interactive effects at the community level, such as density
538 compensation (Peres and Dolman 2000).

539 *14.6.3 Phylogenetic, spatial, and temporal comparisons*

540 Comparisons of different species across different locations over time can be insightful if the
541 locations are undergoing similar changes. For example, Campos et al. (2017) analyzed long-term
542 data to investigate the impact of climate variability on fertility and survival rates in seven species
543 of primates and found out that highly seasonal species appear to be more vulnerable to climate
544 change than non-seasonally breeding species. The challenge of such comparisons is to control for
545 ecological and demographic differences between locations that potentially affect the observed
546 response (Strier 2009), such as the number of receptive females when comparing male behaviour
547 across species and habitats (e.g., Kalbitzer et al. 2015).

548 **14.7 Integrating behavioural ecological studies into primate conservation**

549 The integration of conservation biology and behavioural ecology faces many challenges
550 (Caro and Sherman 2013), yet a better incorporation of these two theoretical frameworks could
551 help to improve efforts to protect primates. Primate behavioural ecologists can help to improve
552 this integration by specifically considering 1) the effects of anthropogenic changes on behaviour
553 and 2) the effects of specific behavioural responses, for example the alteration of breeding
554 seasonality, on population dynamics (McLennan et al. 2017). It is also important to make relevant
555 data more easily available to other conservation biologists, managers, and the public. Similar to
556 some conservation-oriented journals (e.g. *Biological Conservation*), behavioural ecological
557 journals could include a dedicated space at the end of their published articles in which authors
558 are asked to include information on the relevance, if any, of their findings to conservation. This
559 could include information on predicted changes in population size as a result of environmental
560 change or a description of the size and quality of habitat necessary to preserve the future
561 populations. Furthermore, determining and communicating possible key-factors that limit
562 population growth or increase mortality in its current habitat, such as a lack of drinking water or
563 protein-rich food (Milton and Giacalone 2014), may be critical to the implementation of
564 measures, such as the artificial provisioning of these resources, or to guide regeneration projects
565 that ensure the viability of these populations despite anticipated environmental change.

566 **14.8 Conclusion**

567 Our world is undergoing anthropogenic changes at an unprecedented pace and scale, thus
568 it is crucial to understand how primates respond to these changes to prevent further extinctions.

569 Behavioural flexibility will be vital for many primates to survive, and careful comparative
570 investigations using data spanning generations of primates are required to determine whether
571 this flexibility is sufficient to prevent population decline and to improve conservation efforts.
572 Fortunately, some ongoing long-term studies have already collected data over a few decades,
573 which can be supplemented with available data on environmental change to conduct analyses as
574 to how primates are able to respond to the Anthropocene. However, based on the finding of the
575 current long-term studies that are just now emerging, we highlight the need for more long-term
576 studies that are explicitly designed to quantify change in behaviours and identify potential drivers
577 of changes. For the many primate species without longitudinal data, extrapolating from other
578 long-term studies offer the potential to obtain valuable conservation insights.

579 While it is important and often exciting to investigate questions about the ability of
580 organisms to respond to environmental change, we should also make use of our own potential
581 for flexibility and modify our own behaviour to preserve the exciting diversity of primates and
582 biodiversity that we find in this world.

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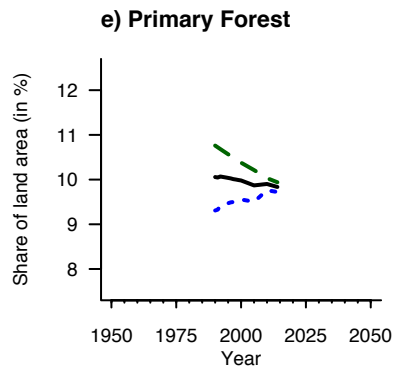
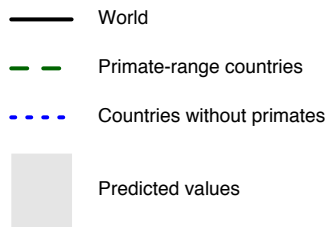
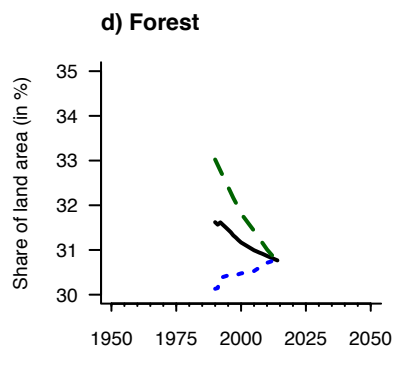
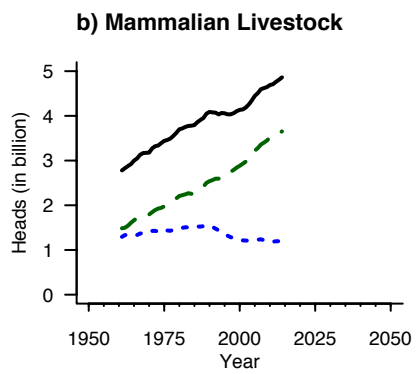
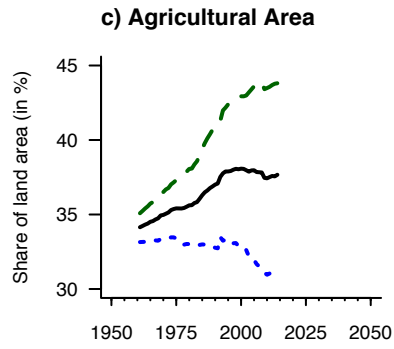
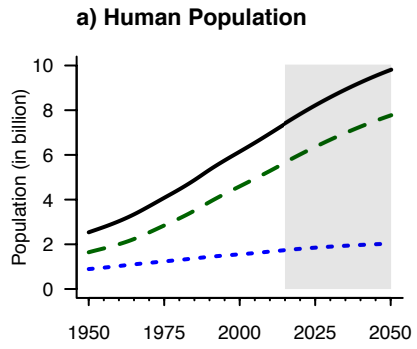
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1024 **Figure Captions**

1025 *Figure 14. 1*

1026 Indicators of the human impact on the world, globally and summarized for countries with
1027 and without primates. a) Human population size with predicted growth until 2050. b) Number of
1028 livestock including the most important mammalian breeds (cattle, sheep, pigs, goats, and
1029 buffaloes). C) Percentage of agricultural area per total land area. D) Percentage of forest area per
1030 total land area. E) Percentage of primary forest area per total land area. Note that the scale for
1031 d) and e) differs from the scale of c). Data from the FAOSTAT Database (FAO 2017). A country
1032 was considered a primate-range country if its boundaries were spatially intersecting with the
1033 global distribution of primates, which was determined using the “Terrestrial Mammals” shapefile

1034 from the IUCN Red List of Threatened Species (IUCN 2016).

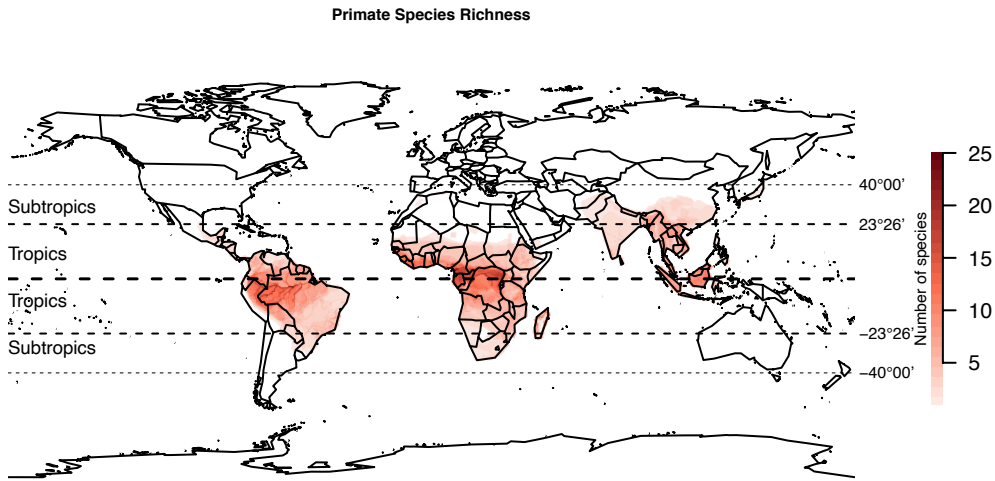


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1036

1037 *Figure 14.2*

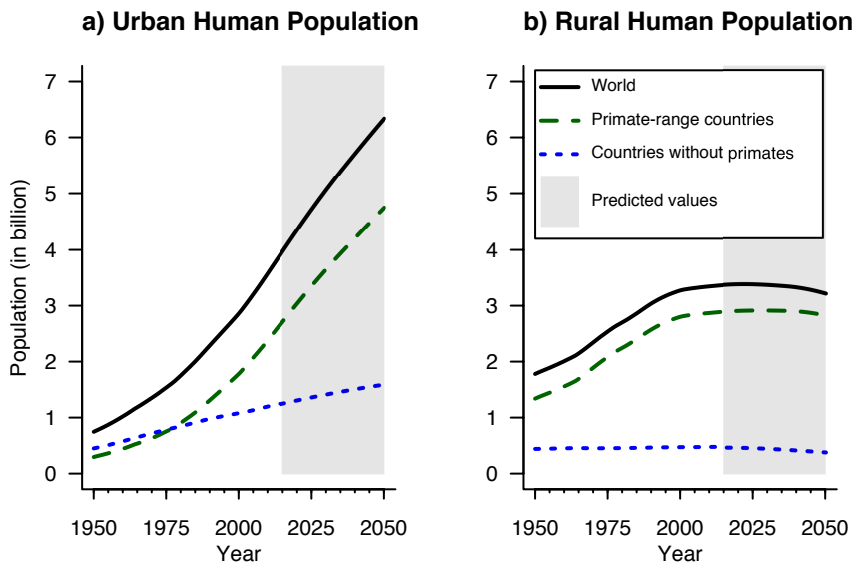
1038 Global distribution and species richness of primates. Distribution data are taken from the
1039 IUCN Red List of Threatened Species (IUCN 2016) and the map was created with the function
1040 lets.presabs from the letsR package (Vilela and Villalobos 2015) in R ver. 3.3.2 (R Core Team
1041 2016).



1042

1043 *Figure 14.3*

1044 Human population size with predicted growth until 2050 for a) urban and for b) rural areas.
1045 Data sources are the same as for Fig. 14.1.



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1047