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Climate change will increase savannas at the expense of forests and treeless vegetation in

tropical and subtropical Americas

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23 **SUMMARY**
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25 **1.** Transition areas between biomes are particularly sensitive to environmental changes. Our
26 understanding of the impacts of ongoing climate change on terrestrial ecosystems has
27 significantly increased during the last years. However, it is largely unknown how climatic
28 change will affect transitions among major vegetation types.

29 **2.** We modeled the distribution of three alternative states (forest, savanna and treeless areas) in
30 the tropical and subtropical Americas by means of climate-niche modeling. We studied how such
31 distribution will change by the year 2070 by using 17 downscaled and calibrated global-climate
32 models from the Coupled Model Intercomparison Project Phase 5 and the latest scenarios
33 provided by the 5th Assessment Report of the IPCC.

34 **3.** Our results support the savannization of the tropical and subtropical Americas because of
35 climate change, with an increase of savannas mainly at the expense of forests.

36 **4.** Our models predict an important geographical shift in the current distribution of transition
37 areas between forest and savannas, which is much less pronounced in the case of those between
38 savannas and treeless areas. Largest shifts, up to 600 km northward, are predicted in the forest-
39 savanna transitions located in the eastern Amazon.

40 **5.** Our findings indicate that climate change will promote a shift towards more unstable states:
41 the extent of the transition areas will notably increase, and largely stable forest areas are
42 predicted to shrink dramatically.

43 **6.** *Synthesis.* Our work explores dimensions of the impact of climate change on biomes that have
44 received little attention so far. Our results indicate that climate change will not only affect the
45 extent of savanna, forest and treeless areas in the tropical and subtropical Americas, but also
46 will: i) promote a significant geographical shift and an increase of the extent of transition areas
47 between biomes, and ii) decrease the stability of the equilibrium between forest, savanna and
48 treeless areas, yielding a more unpredictable system.

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INTRODUCTION

The Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)

provides unequivocal evidence of ongoing climate change, which is characterized by an increase

in temperature globally and important modifications in rainfall patterns (IPCC, 2013). Climate

change will have major impacts on the structure and functioning of terrestrial ecosystems

(Peñuelas *et al.,* 2013), and is already promoting important changes in the spatial extent and

distribution of vegetation types worldwide (Gang et al., 2013). Our understanding of the impacts

of ongoing climate change on terrestrial ecosystems has significantly increased in recent years

(see Parmesan (2006); Parmesan & Yohe (2003); Paruelo et al. (1995); Walther (2010) and

Peñuelas et al. (2013) for reviews). In tropical areas, forests might retreat yielding more open

savanna-like systems, a pattern particularly well identified for the Amazonian region (Franchito,

Rao & Fernandez, 2012; Salazar, Nobre & Oyama, 2007; Zelazowski et al., 2011).

Climate-induced changes in vegetation types will have direct effects on the provisioning of

ecosystem services for humans (MEA, 2003). Shifts from grasslands into woodlands results in a

significant reduction in livestock production (Anadón et al., 2014), which can be offset by an

increase in carbon sequestration (Havstad et al., 2007) and soil fertility (Eldridge et al., 2011).

The shift from forest to grassland can also have impacts on ecosystem services other than the

provisioning of timber or food, such as a decrease in carbon sequestration and regulation of

climate (MEA, 2003).

Biome transitions are areas of high socio-ecological interest for many reasons. These

areas have a unique and high biological diversity at multiple levels (from genes to communities;

see Kark & Van Rensburg (2006) for a review), and are areas of high conservation interest

(Smith et al., 2001; Smith et al., 1997). These areas are also particularly sensitive to human

74 activities such as grazing (Hudak, 1999), and to important components of climate change such as

75 the increase in precipitation intensity and rainfall variability predicted for many terrestrial

76 ecosystems worldwide (IPCC, 2013; Meehl, Arblaster & Tebaldi, 2005). In this direction, rapid

77 vegetation shifts in responses to recent changes in climatic conditions are already being detected

78 in areas such as the Arctic tundra (Sturm, Racine & Tape, 2001), the Alps (Gehrig-Fasel, Guisan

79 & Zimmermann, 2007) and the drylands of the Southwestern U.S. (Van Auken, 2009). Recent

80 studies have highlighted how climate change drivers, such as an intensification of the rainfall

81 regime, may favor the recruitment and expansion of woody plants in savannah ecosystems

82 (Holmgren et al., 2013; Kulmatiski & Beard, 2013), a vegetation transition with major ecological

83 effects on biodiversity, nutrient cycling and carbon sequestration in drylands worldwide

84 (Eldridge et al., 2011). As such, forecasting how vegetation in transitional areas will respond to

85 climate change is an urgent ecological question that has been poorly studied to date.

86   Understanding how climatic variables such as rainfall and temperature determine woody

87 vegetation cover in grassland-woodland transition areas has been an area of active research in the

88 last decades (Hirota et al., 2011; Sankaran et al., 2005; Staver, Archibald & Levin, 2011;

89 Williams et al., 1996). Continental-scale analyses of tree cover in African savannas have found

90 that mean annual precipitation largely limits the maximum cover of woody species, and that

91 disturbance dynamics control savanna structure below this maximum (Sankaran et al., 2005).

92 More recent analyses have reported the presence of three alternative stable states (forest,

93 savanna, and treeless) in the world´s savannas (Hirota et al., 2011). These authors found that the

94 tree cover values characterizing savannas (~20%) and forests (~80%) were found over multiple

95 rainfall conditions, suggesting that woody cover is not controlled by gradual increases in

96 precipitation, and that there is a shifting probability of being in either of the three stable states

97   identified. The reverse side of this multiple stable state equilibrium is the existence of highly

98   unstable tree cover values (~5% and ~60%) that can be then identified as transition areas

99   between biomes. A key property of the findings reported by Hirota *et al.* (2011) is that any given

100 locality will have a probability of being forest, savanna and desert according to their climatic

101 characteristics, and thus they allow us to quantify how likely transitions between vegetation

102 types are likely to occur. For example, in a locality with very high probability of being forest and

103 low of being savanna or treeless, the probability of transition between vegetation states in very

104 low. As a consequence, the uncertainty of the locality is very low since it is highly probable that

105 it will be a forest. On the contrary, the uncertainty of a locality with similar and high

106 probabilities of being forest and savanna (and low probability of being treeless) is very high,

107 since it is very difficult to predict whether this locality will be a forest or a savanna. In localities

108 of high uncertainty, small changes in tree cover due to human activities (e.g. fires, selective

109 logging) might have a large effect on the system and promote the transition from one state to

110 another. On the contrary, localities with low uncertainty are likely to be more resilient to human-

111 induced changes to tree cover (Hirota et al., 2011).

112   While research conducted over the last decades has provided key insights to advance our

113 understanding of the mechanisms driving grass/woody vegetation coexistence in savanna

114 systems, and has improve our ability to predict their responses to climate change, no previous

115 studies so far have explicitly evaluated how forest-savanna-treeless transitions will change under

116 future climatic conditions at regional to continental scales (but see Hutyra et al. (2005); Salazar,

117 Nobre & Oyama (2007); Salazar & Nobre (2010) for forest-savanna transitions). We aimed to

118 assess forest-savanna-treeless transitions under climate change for the tropical and subtropical

119 Americas; a region that is crucial for preserving global biodiversity (Myers et al., 2000),

120   regulating the Earth´s climate (Gedney & Valdes, 2000), and that directly supports the livelihood

121   of more than 700 million people. Our objectives were to: i) assess the climatic determinants of

122   the occurrence of treeless vegetation, savannas and forest in the tropical and subtropical

123   Americas, ii) predict the future extent and distribution under climate change scenarios of treeless

124   vegetation, savannas and forest in that region, iii) evaluate how climate change will affect the

125   distribution of the transition areas among them, and iv) assess how climate change will affect the

126   uncertainty of the occurrence of different vegetation types. To achieve these objectives, we

127   modeled the spatial distribution of grasslands and woodlands and their transition areas in the

128   studied region using the alternative stable state framework provided by Hirota et al. (2011) and

129   large-scale remote sensing and climate data, and employed the latest climate change scenarios

130   provided by the 5th Assessment Report of the IPCC (Taylor, Stouffer & Meehl, 2012) to forecast

131   how such distribution will change by the year 2070.

132

133   **MATERIALS AND METHODS**

134   **Modeling the distribution of forest, savanna and treeless areas**

135   Our study area comprises the tropical and subtropical Americas, here defined as those areas

136   between latitude 35°N and 35°S. Hirota *et al.* (2011) suggested that the different vegetation types

137   in tropical areas, as described by tree cover, are actually alternative states, exhibiting sharp

138   transitions between them at so-called tipping points. These authors identified three alternative

139   states in the tropical areas of the Americas (forest, savanna and treeless areas) that were defined

140   by the cutting levels of 5 and 60% of tree cover (i.e., treeless=0-5%, savanna=5-60%, forest=60-

141   100%).

142 We modeled the distribution of the three states (forest, savanna or treeless) according to climatic

143 variables by means of generalized linear models with a binomial distribution of errors, with the

144 presence/absence of the state as independent variables, and with climatic descriptors (Mean

145 annual temperature [T], Mean annual precipitation [P], T + P, P/T ratio and Aridity index

146 [P/Potential evapotranspiration]) as independent variables. Our models rely on the understanding

147 that climate governs the broadest outlines of distributions of species and biomes. This statement

148 is well supported by current knowledge (see Araújo & Peterson (2012) for a review). In this

149 sense, our models capture the main controls of biome distribution at a continental scale (i.e.,

150 climate), as shown by the high values of explained deviance obtained (see Results section).

151 Models were fitted to a random sample of 3000 2.5' x 2.5' (aprox. 4.5 x 4.5 km) cells from the

152 study area. Tree cover percentage was assessed from the MOD44B Collection 3 product from

153 MODIS (Hansen et al., 2003) originally at a 500 m resolution. 2.5 arc-minute resolution values

154 were obtained by averaging the 500 m side cells within each 2.5 arc-minute side cell. Average

155 tree-cover values were then transformed to a categorical map describing the three alternative

156 states in the present time, using the 5% and 60% cutting levels described above. Mean annual

157 precipitation, temperature and evapotranspiration were also assessed for each 2.5 arc-minute side

158 cell. Precipitation and temperature were obtained from Worldclim database

159 (www.worldclim.org; Hijmans et al. 2005). Evapotranspiration was obtained from the Global

160 Potential Evapo-Transpiration (Global-PET) dataset (*http://www.cgiar-csi.org/*). Both databases

161 describe climatic average values of the period 1950-2000 and are available at a 2.5 arc-minute

162 resolution.

163 Eleven candidate models were fitted to the MOD44B data, including linear and quadratic

164 responses to the different climatic descriptors (Table 1). Models for each state were ranked

165   according to the Akaike Information criterion (Burnham & Anderson, 2002). In accordance with

166   previous works showing that tree cover and climate relationships at the continental scale are

167   insensitive to the spatial resolution (Staver, Archibald & Levin, 2011), our results at 2.5 arc-

168   minutes resolution were very similar to those obtained using a 30 second (aprox. 1 km)

169   resolution (data not shown). We used the Global Land Cover 2000 (GLC2000) map to filter out

170   areas undergoing human activities (categories 16-18 and 22; (Bartholome & Belward, 2005)

171   from our analyses. These areas cover 5.1 x 10^6 km^2, comprising 23% of our study area (Fig. S1).

172   By only using natural areas, we maximize the decoupling of climate and land-use controls on the

173   dynamics of biomes and their transitions areas. As such, our predictions are based solely on

174   climatic controls and are largely independent of land-use change.

175   As it will be detailed in the Results section, a global model (i.e. including all the study

176   area) for forest and treeless states presented high explanatory power (D^2>40%; Table 1). For the

177   savanna state, however, the best global model according to the Akaike Information criterion

178   performed poorly (D^2=12%; Table 1), suggesting spatial non-stationarity (i.e. the response of the

179   savanna state to climatic condition changes within our study area). To obtain a more robust

180   model, and starting from the best global model (P^2+T^2; Table 1), we developed models with a

181   spatial factor describing different subareas within our study area. This factor was included as an

182   interaction term in the models. Because of the latitudinal organization of macroclimatic control

183   and major biomes on the Earth (Bailey & Ropes, 1998), this factor divided our study area

184   latitudinally in two or three areas. Since we did not know which areas were a priori responsible

185   for the presence of non-stationarity in our data, we fitted models with different spatial factors

186   describing all possible two and three latitudinal subareas within our study area. To make the

187   number of latitudinal subareas tractable, the minimum latitudinal width of the subareas were 5°

188   (for example from 15°N to 20°N, see Table S1 in Supporting Information for examples of factors

189   including different latitudinal subareas). In total we fitted 91 models, each one including the best

190   global model and a spatial factor. As detailed in the Results section below, a large number of

191   models had a very similar explanatory power (Table S1, Supplementary Information). Hence, the

192   model for the savanna state was built using a weighted average consensus approach (Marmion et

193   al., 2009). For doing so, we first selected a subset of models with the highest accuracy, and then

194   calculated a weighted average according to a model performance metric (Hartley, Harris &

195   Lester, 2006; Marmion et al., 2009). In our case, and given the differences in the explanatory

196   power of the models, we selected the 20% best models according to their explained variance (n =

197   18 models, range of explained variance of these models = 27.6-33.6%). Models were weighted

198   according also to their explained deviance (Araujo et al. 2007). We did not use the Akaike

199   weights (Burnham & Anderson, 2002) for model averaging because this approach led us to the

200   selection of only one best model (i.e. weight of the first ranked model = 0.996).

201   Our distribution models for forest, savanna and treeless areas were projected to the study

202   area using present conditions (1950-2000) and climate change scenarios. For the scenarios, we

203   used 17 downscaled and calibrated global climate models from the Coupled Model

204   Intercomparison Project Phase 5 (CMIP5) (Taylor, Stouffer & Meehl, 2012) (See Table S2,

205   Supplementary Information). We selected for our projections the Representative Concentration

206   Pathway 8.5 (RCP8.5) for the year 2070. Within the Fifth IPCC Assessment Report, RCP8.5

207   represents the scenario with the highest concentration of greenhouse gases, and with a predictive

208   radiative forcing of + 8.5W/m^2 (IPCC, 2013). Our rationale behind the selection of the worst (but

209   possible) scenario is that we are more interested in capturing the overall directions of the changes

210   than in quantifying exactly the extent of the changes. To describe the extent of forest, savanna

211   and treeless areas in the present time and for the year 2070, each cell was assigned to the state

212   with largest probability of occurrence.

213

214   **Modeling transitions**

215   Our study system is comprised by three states (forest, savanna and treeless areas) and two

216   possible transitions (forest-savanna and savanna-treeless). To model these two transitions, we

217   first divided our study area in the forest-savanna and savanna-treeless systems. These two

218   subareas are mutually exclusive. The forest-savanna system is defined as those areas where the

219   probability in the present time of being savanna or forest is larger than the probability of being

220   treeless. Conversely, the savanna-treeless system is defined as those areas where the probability

221   of being savanna or treeless in the present time is larger than the probability of being forest (Figs.

222   2 and 3). Starting from the distribution maps of the three alternative states for the present time

223   and the climate-change scenario of the 17 CMIP5 global climate models, we calculated transition

224   maps between forest and savanna, and between savanna and treeless areas for these two periods.

225   In the transition maps, we calculated for each cell a transition index ($Trans_{AB}$) calculated as

226    $Trans_{AB}= p(A) - P(B)$, where $P(A)$ and $P(B)$ are the probability of being in state A and B, as

227   described by the distribution maps. The transition index ranges between 1 and -1, with 1 being

228   those cells with the largest probability of being in state A and least probability of being in state

229   B, and -1 the other way around (maximum probability of being in state B and least of being in

230   state A). Values close to 0 indicate high uncertainty, being difficult to predict whether the cell

231   will be in state A or B, and cells with $Trans_{AB}=0$ are those that have exactly the same probability

232   of being in state A or B, according to their climatic conditions. From the transition maps we

233   identified transition areas, i.e. areas with the highest uncertainty, which were defined as those

234   with $Trans_{AB}$ absolute values below 0.2. In the same vein, we defined the core areas of the

235   biomes, i.e. areas with the lowest uncertainity, as those with $Trans_{AB}$ absolute values above 0.5.

236   The modeling approach described above was performed for each one of the 17 CMIP5 global

237   climate models. Final projection maps for biome distribution, transition areas and their changes

238   were built from the ensemble mean of the projections provided by the 17 models (Araújo &

239   New, 2007).

240

241   **RESULTS**

242   For the three states considered, the models with the largest values of explained deviance were

243   those including temperature and precipitation (Table 1). The best models for forests and

244   savannas included both variables with their quadratic terms, whereas for treeless areas the best

245   model included the linear term of precipitation and the quadratic term of temperature. For forest

246   and treeless states, a global model (i.e. including all the study area) presented high explanatory

247   power (D^2=45 and 60% for forest and treeless areas, respectively). As noted in the Methods, the

248   global model performed poorly for savanna (D^2=12%). Models considering a spatial factor with

249   multiple subareas had larger explanatory power for this area (D^2 values ranging from 15.4% to

250   33.7%; Table S1). The consensus model for this state resulting from the ensemble modeling

251   presented an averaged explained deviance of 30.3% (Table 1).

252   Our results indicate that forests will decrease in area in favor of savannas by the year

253   2070 under the RCP8.5 climate change scenario (Table 2 and Fig. 1). Forest areas are predicted

254   to lose $1.5\pm0.9 \times 10^6$ km^2. This biome is expected to cover $22 \pm 4\%$ of our study area in year

255   2070, which means a 24% (range 9-39%) reduction in comparison to its current distribution.

256   Results from the 16 out of 17 CMIP5 global climate models indicated a reduction of forest area

257   (Table S3). The general agreement shown by the projections of each one of the 17 CMIP5 global

258   climate models in relation to changes in forest area indicates that our predictions are robust

259   regarding uncertainties of the global climate models (Table 2). Changes in extent of treeless

260   areas are predicted to be of small extent (-24 ±178 x 10^3 km^2). Results from 8 CMIP5 climate

261   models predicted a reduction, whereas 9 models show an increase in treeless areas. This limited

262   change actually means that the percentage of the tropical and subtropical Americas covered by

263   treeless areas might not vary significantly due to climate change. As it will be discussed below,

264   this result does not mean that treeless areas might remain stable, but that the extension of some

265   treeless areas might be compensated by the contraction of others.

266   For the forest-savanna system, the largest transition area is located in the southern portion

267   of the Amazonian rainforest (Figure 2). Comparatively, minor transition areas are located north

268   of the Amazonian forest and along Central America. Within the savanna-treeless system, main

269   transition areas are located in the southern border of the North American deserts and along

270   Pacific coast in South America (Fig. 3). Our predictions indicate that, within the forest-savanna

271   system, changes in the multistate equilibrium toward savanna occur mainly in the East Amazonia

272   and North Matto Grosso regions (Fig. 4). Within the savanna-treeless transition realm, changes

273   towards savanna occur in the Peruvian and Bolivian slopes of the Andes facing west, north of the

274   Atacama Desert. Despite the overall reduction of the total forest area, our models predict an

275   increase in the probability of forest in the southern Atlantic Forest region. Shifts towards treeless

276   areas are of much lesser extent and intensity (i.e. amount of change in the transition index) than

277   those towards forest or savanna. Main areas where our models predict a shift towards treeless

278   areas are Northeastern Brazil and part of the Chaco, between Paraguay and Bolivia.

279   Our models predict an important geographical shift in the current distribution of the

280   forest–savanna transition, which is less pronounced in the case of the savanna-treeless transition

281   (Fig. 5). The largest move in forest–savanna transitions (up to 600 km westward) occurs in the

282   eastern part of the Amazon, affecting the contact areas of the Amazon with three different

283   savanna systems present in the region (Llanos, Roraima and Cerrado). Lesser shifts (up to 100

284   km northward) occur in the southern limit of the Amazonia. Regarding the savanna-treeless

285   transition line, our models predict minor shifts (up to 50 km westward) in the arid and semiarid

286   areas of West South America (i.e., Atacama, Chaco, Monte Desert). Our models suggest that the

287   shift in the transition line in this area increases towards the South, being maximal in the

288   Argentinean Monte Desert. Transition areas located in the North American deserts (i.e. Mojave,

289   Sonoran, Chihuahuan) are not expected to shift (Fig. 5).

290   Changes in the extent and geographical location of the transition areas occur

291   simultaneously with an increase of the uncertainty of the system state (Fig. 6). In the forest-

292   savanna system, the reduction of forest areas is at the expense of those areas with current lowest

293   uncertainty of being forest. A large fraction (58%) of these areas, which can be considered the

294   core of the forest biome, shift towards areas with higher uncertainty levels (Fig. 6). As a result,

295   core forest areas, which nowadays occupy $3.1 \times 10^6 \, km^2$, are projected to cover $1.3 \times 10^6 \, km^2$

296   (range: $0.3 – 2.4 \times 10^6 \, km^2$, Table S4). The different projections resulting from the 17 CMIP

297   global climate models show consistent patterns in the changes in uncertainty of the forest-

298   savanna system, as shown by the reduced standard deviation of the predictions (Fig. 6). All 17

299   CIMP5 climate models predict a reduction in the areas of low uncertainty of being forest (Table

300   S4). Forest-savanna transition areas (i.e. those where the difference in the probability of being

301   forest and savanna is <0.2) increased on average by 32%, from $2 \times 10^6 \, km^2$ to $2.7 \times 10^6 \, km^2$

302 (range= 2.2 – 3.6 x10^6 km^2, Table S4). A similar pattern, but much less pronounced, occurs in the

303 savanna-treeless system, with a decrease in areas with high certainty of being treeless that shift

304 towards areas of higher uncertainty (Fig. 6 and Table S5). The largest increases in uncertainty of

305 the system state, projected to occur on the forest-savanna system, are located around two areas:

306 the Amazon forest, particularly in the west, and the southern portion of the Atlantic Forest,

307 because of their shifts towards savanna and forest, respectively (Fig. 7). The largest decreases in

308 uncertainty are located in those savanna areas on the West of South America (Llanos, Roraima,

309 Northern Cerrado), which are clearly expected to shift towards savanna.

310

311 **DISCUSSION**

312 Transitions between forests, savannas and treeless are of utmost importance for understanding

313 major environmental issues such as desertification (Maestre et al., 2009; Schlesinger et al., 1990)

314 and the global carbon cycle (Pacala et al., 2001), and have important socio-economical and

315 management implications at large scales (Gifford & Howden, 2001; Hudak, 1999; Van Auken,

316 2009). Despite the importance of this topic, no previous study has evaluated how climate change

317 will affect these transitions areas at regional to continental scales. Our results indicate that

318 climate change according to the RCP8.5 scenario of the IPCC will promote the savannization of

319 the tropical and subtropical Americas, with an increase of savannas mostly at the expense of

320 forests. Such change will also increase the extent of transition areas between savannas and

321 forests, and will promote a dramatic reduction of stable forest areas. According to current

322 knowledge, the shifts predicted in the distribution and stability of transitions areas are expected

323 to bring important changes to the biota and the provision of ecosystem services such as C

324 sequestration, climate regulation and food production in one of the most important regions

325 worldwide for biodiversity and human wellbeing (MEA, 2005).

326   Our modeling approach, which relies on niche modeling theory and focuses exclusively

327   on the climatic controls of transitions, does not take into account other factors that have been

328   identified as interacting with climate drivers, such as feedbacks between tree cover and climate,

329   particularly in the rainforest (Coe et al., 2013; Malhi et al., 2008), sea surface temperature

330   (Pereira, Costa & Malhado, 2013), CO_2 fertilization (Lapola, Oyama & Nobre, 2009) and land

331   uses (Nepstad et al., 2008). In the same vein, our models use average annual values, and do not

332   consider intra- and inter-annual variability in rainfall and temperature, which have been

333   described to have significant effects in driving tree cover (Holmgren et al., 2013; Malhi et al.,

334   2008). Notwithstanding, the overall agreement (discussed below) between our projections and

335   those obtained by previous studies using more complex models regarding the direction, spatial

336   location and order of magnitude of the vegetation changes observed at a regional scale makes us

337   confident on the results reported here. ~~Furthermore, the relatively reduced variability of the~~

338   ~~projections obtained from each one of the 17 CMIP5 global climate models used also indicates~~

339   ~~that our predictions are robust regarding the uncertainty of the models using the Representative~~

340   ~~Concentration Pathway 8.5 for the year 2070.~~

341

342   CLIMATE-CHANGE IMPACTS ON THE EXTENT OF SAVANNA, FOREST AND

343   TREELESS AREAS

344   Our models predict that climate change will increase the extent of savannas in the Americas by

345   12% (range=5-19%, average increase=1.5 x10^6 km^2) at the expense mostly of forests, which will

346   decrease by 24% (range= 9-38%, average decrease= 1.5 x10^6 km^2) and in much less extent of

347   treeless areas. Overall this result matches the process of savannization predicted for the area for

348   the 21st century because of climate change (Franchito, Rao & Fernandez, 2012; Hutyra et al.,

349   2005; Cook & Vizy, 2008; Salazar & Nobre, 2010). In agreement with previous results (Cook,

350   Zeng & Yoon, 2012; Franchito, Rao & Fernandez, 2012; Hutyra et al., 2005; Salazar & Nobre,

351   2010), our projections indicate that major increases of savanna will occur at the expense of the

352   Amazon rainforest, particularly at its south and southeastern portions. The amount of predicted

353   reduction of forest, ranging from 9% to 38%, falls within the range predicted by other authors for

354   South America (Cook & Vizy, 2008; Hutyra et al., 2005; Salazar, Nobre & Oyama, 2007;

355   Zelazowski et al., 2011). Previous studies have indicated that a larger stability of the forest in the

356   Mata Atlantica in comparison with the Amazon under a climate-change scenario (Cook, Zeng &

357   Yoon, 2012). Our results go one step further and predict a strong increase of the probability of

358   being forest in this area. The forest of the Mata Atlantica is strongly fragmented, and only around

359   10% of its original area actually remains (Saatchi et al., 2001). Our findings indicate that in this

360   region management actions designed to increase tree cover could take advantage of this positive

361   inertia towards the forest.

362   In comparison with the transitions between forest and savanna, our prediction of

363   transitions between savanna and treeless areas are overall small in extent, with a decrease of <1%

364   of the treeless areas ($2.4 \times 10^4 \, km^2$). The impacts of climate change on the extent of drylands have

365   been much less explored than those on forests, particularly in the Amazon region. Existing work

366   indicates an overall increase in aridity and the extent of drylands in most the arid areas of

367   tropical and subtropical Americas (Feng & Fu, 2013; Seager et al., 2007). Our results partially

368   match these patterns, since they predict a general increase in the extent of the Caatinga (NE

369   Brazil) and Chaco Seco (Argentina and Paraguay), and a patchy increase in the extent in North

370   American deserts. However, against current knowledge (Feng & Fu, 2013), our models predict a

371   savannization of the Atacama Desert and particularly, of the Sechura Desert, along the Peruvian

372   Pacific coast.

373   Changes in vegetation type from forest into savanna and treeless groups are expected to

374   have major effects on climate (Oyama & Nobre, 2003; Shukla, Nobre & Sellers, 1990).

375   Vegetation changes affect climate directly via changes in albedo and transpiration, the later

376   mediated through changes in rooting depth. Vegetation changes also affect climate indirectly

377   through changes in carbon cycling. Albedo increases along the gradient from forest, savanna to

378   treeless vegetation therefore increasing the amount of radiation reflected back to the atmosphere

379   and reducing surface temperature (Balling Jr, 1988). Rooting depth decreases from forest to

380   treeless vegetation, reducing the depth of the soil explored by roots and functionally reducing the

381   soil water-holding capacity (Jackson et al., 1996). A reduced soil-water capacity may decrease

382   the latent heat therefore reducing the cooling capacity of the ecosystem. Finally, carbon storage

383   is much larger in forest than in savannas and treeless vegetation in tropical areas (Saatchi et al.,

384   2011), so the transition from forest into savanna may results in a net carbon emission into the

385   atmosphere that will enhance climate warming.

386

387   CLIMATE CHANGE EFFECTS ON TRANSITION AREAS AND THE STABILITY OF THE

388   SYSTEM

389   Using the framework of alternative stable states provided by Hirota *et al.* (2011), we were able to

390   project how the transition areas between biomes and the stability of the system are expected to

391   change under climate change. These two related aspects have been much less explored than the

392   changes in the extent of the biomes themselves. As with the projected changes in the extent of

393   biomes, shifts in the transitions between forests and savannas were much more pronounced than

394   those between savannas and treeless areas.

395   Our models predict that climate change will promote a shift towards more unstable states,

396   yielding more uncertainty in system state. Two aspects of this result deserve particular attention.

397   On the one hand, the extent of the transition areas will increase by 32% on average (range=10-

398   80%), and forest-savanna transition areas, now restricted to a thin belt between both biomes

399   might become the dominant biome in large areas, particularly in the South and Eastern part of

400   Brazil. On the contrary, large stable forest areas are predicted to decrease by 58% on average

401   (range=23-90%). The climate control of vegetation types is strongest in the core (i.e. ecological

402   optimum) of their distribution and weakens towards the edges (Sala, Lauenroth & Golluscio,

403   1997). It is in the edges of the distribution of vegetation types where other factors such as

404   grazing intensity, fire, and logging become more important. The increase in uncertainty of large

405   areas of the Amazon rainforest means that these areas will likely be less resilient to

406   perturbations, and thus that they might be more sensitive to human management (Hirota et al.,

407   2011). In these areas of high uncertainty, positive feedbacks might make that small changes in

408   tree cover might induce a self-propagating shift to the alternative state (i.e. from forest to

409   savanna or from savanna to forest). In this way, fragmented landscapes with a patchy distribution

410   of forest and savanna might be more likely to turn into solely savanna landscapes, due to, for

411   example, an increase in fire frequency and extent (Malhi et al., 2008). Interestingly, and as

412   pointed out for the Mata Atlantica above, these feedbacks can also work in the opposite direction

413   and, in areas of high uncertainty, tree cover increases due to habitat management are more likely

414   to trigger the conversion of savanna to forest. Land-use changes are at present the main driver of

415   the transition between states in the study area, particularly the conversion of forest to savanna

416 and treeless areas due to deforestation (Malhi et al., 2008). Overall, our results indicate that

417 climate change will increase the importance of land use in shaping the extent of biomes during

418 the next century.

419

420 PREDICTED IMPACTS OF CLIMATE CHANGE ON BIODIVERSITY AND ECOSYSTEM

421 SERVICES

422 The Amazon rainforest is a major component of the Earth's system, regulating Earth's climate

423 (Malhi et al., 2008), and hosts up to a quarter of the world's terrestrial species (Barthlott &

424 Winiger, 1998). Rapid transition from one vegetation type to another will certainly result in

425 major biodiversity losses (Sala et al., 2005). Our models predict a shift of the forest-savanna

426 transition area of up to 600 km in the eastern Amazon for year 2070. Given the magnitude and

427 speed of this change, a pertinent question here is to what extent species will be able to keep pace

428 with climatic changes to reach the equilibrium (Loarie et al., 2009). Although our understanding

429 of colonization processes under climate change is still limited, current models indicate that

430 species will lag behind projected climate shifts (Nathan et al., 2011; Prasad et al., 2013). The

431 mismatch between climatic change velocity and colonization rates is expected to be exacerbated

432 in flat reliefs (Loarie et al., 2009), which are dominant in the Amazonian Basin. In this area, our

433 models predict the largest shifts from forest to savanna suggesting a high risk for species

434 extinctions. However, as it has been described for tree species colonization after the ice caps

435 retreated during the Holocene, isolated habitat patches outside the core distribution range of the

436 biome could play key role in tracking climate change (Anderson et al., 2006; McLachlan, Clark

437 & Manos, 2005; Parducci et al., 2012). In our case, for example, small savanna patches currently

438   embedded in a forest matrix, could serve as colonizing source for the surrounding landscape

439   when climate potentially in the area change from forest to savanna.

440   The portfolio of ecosystem services provided by forest, savannas and treeless vegetation

441   types are drastically different. For example, savanna and grasslands in tropical and subtropical

442   America constitute one of the main providers of food, particularly protein, of the world (FAO,

443   2007). As the reverse side of the ecosystem services linked to rainforest, predicted changes might

444   have a positive impact on the provisioning of food (MEA, 2005). We predicted an increase in the

445   extent of transition areas and in the uncertainty of the system. This means that alternative states

446   (i.e. forest, savanna, treeless) are likely to be more evenly distributed at a small scale (i.e. a finer

447   grain distribution) and that localities are expected to tip from one state to another more easily. As

448   a result, ecosystem services provided at a local scale are likely to be more diversified but also

449   more unpredictable, since larger portions of our study area might contain a combination of

450   different biomes that will change more frequently. Food, timber, climate amelioration, clean

451   water, recreation and conservation are ecosystem services that will affected by vegetation

452   transitions. These changes in the portfolio of ecosystem services resulting from vegetation

453   transitions will affect different groups of stakeholders because they value ecosystem services

454   differently.

455

468
469   **REFERENCES**

470   Anadón, J. D., Sala, O. E., Turner, B. L. & Bennett, E. M. (2014) Effect of woody plant encroachment on
471   livestock production: A comparison of North and South America. *Proceedings of National*
472   *Academy of Sciences,* **in press**.
473   Anderson, L. L., Hu, F. S., Nelson, D. M., Petit, R. J. & Paige, K. N. (2006) Ice-age endurance: DNA
474   evidence of a white spruce refugium in Alaska. *Proceedings of the National Academy of Sciences,*
475   **103,** 12447-12450.
476   Araújo, M. B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology &*
477   *Evolution,* **22,** 42-47.
478   Araújo, M. B. & Peterson, A. T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology,* **93,**
479   1527-1539.
480   Bailey, R. G. & Ropes, L. (1998) *Ecoregions: the ecosystem geography of the oceans and continents.*
481   Springer New York.
482   Balling Jr, R. C. (1988) The climatic impact of a Sonoran vegetation discontinuity. *Climatic Change,* **13,**
483   99-109.
484   Barthlott, W. & Winiger, M. (1998) *Biodiversity: a challenge for development research and policy.*
485   Springer.
486   Bartholome, E. & Belward, A. S. (2005) GLC2000: a new approach to global land cover mapping from
487   Earth observation data. *International Journal of Remote Sensing,* **26,** 1959-1977.
488   Burnham, K. P. & Anderson, D. R. (2002) *Model selection and multimodel inference: a practical*
489   *information-theoretic approach.* Springer.
490   Coe, M. T., Marthews, T. R., Costa, M. H., Galbraith, D. R., Greenglass, N. L., Imbuzeiro, H. M., Levine,
491   N. M., Malhi, Y., Moorcroft, P. R. & Muza, M. N. (2013) Deforestation and climate feedbacks
492   threaten the ecological integrity of south–southeastern Amazonia. *Philosophical Transactions of*
493   *the Royal Society B: Biological Sciences,* **368**.
494   Cook, B., Zeng, N. & Yoon, J.-H. (2012) Will Amazonia Dry Out? Magnitude and Causes of Change from
495   IPCC Climate Model Projections. *Earth Interactions,* **16**.
496   Cook, K. H. & Vizy, E. K. (2008) Effects of Twenty-First-Century Climate Change on the Amazon Rain
497   Forest. *Journal of Climate,* **21**.

498 Eldridge, D. J., Bowker, M. A., Maestre, F. T., Roger, E., Reynolds, J. F. & Whitford, W. G. (2011)
499   Impacts of shrub encroachment on ecosystem structure and functioning: towards a global
500   synthesis. *Ecology Letters,* **14,** 709-722.
501 FAO (2007) *Gridded livestock of the world 2007, by G.R.W. Wint and T.P. Robinson.* Food and Agriculture
502   Organization of the United Nations, Rome.
503 Feng, S. & Fu, Q. (2013) Expansion of global drylands under a warming climate. *Atmospheric Chemistry &*
504   *Physics,* **13**.
505 Franchito, S. H., Rao, V. B. & Fernandez, J. P. R. (2012) Tropical land savannization: impact of global
506   warming. *Theoretical and applied climatology,* **109,** 73-79.
507 Gang, C. C., Zhou, W., Li, J. L., Chen, Y. Z., Mu, S. J., Ren, J. Z., Chen, J. M. & Groisman, P. Y. (2013)
508   Assessing the Spatiotemporal Variation in Distribution, Extent and NPP of Terrestrial Ecosystems
509   in Response to Climate Change from 1911 to 2000. *Plos One,* **8**.
510 Gedney, N. & Valdes, P. J. (2000) The effect of Amazonian deforestation on the northern hemisphere
511   circulation and climate. *Geophysical Research Letters,* **27,** 3053-3056.
512 Gehrig-Fasel, J., Guisan, A. & Zimmermann, N. E. (2007) Tree line shifts in the Swiss Alps: Climate
513   change or land abandonment? *Journal of vegetation science,* **18,** 571-582.
514 Gifford, R. M. & Howden, M. (2001) Vegetation thickening in an ecological perspective: significance to
515   national greenhouse gas inventories. *Environmental Science & Policy,* **4,** 59-72.
516 Hansen, M. C., DeFries, R. S., Townshend, J. R. G., Carroll, M., Dimiceli, C. & Sohlberg, R. A. (2003)
517   Global percent tree cover at a spatial resolution of 500 meters: First results of the MODIS
518   vegetation continuous fields algorithm. *Earth Interactions,* **7,** 1-15.
519 Hartley, S., Harris, R. & Lester, P. J. (2006) Quantifying uncertainty in the potential distribution of an
520   invasive species: climate and the Argentine ant. *Ecology Letters,* **9,** 1068-1079.
521 Havstad, K. M., Peters, D. P. C., Skaggs, R., Brown, J., Bestelmeyer, B. T., Fedrickson, E., Herrick, J. E. &
522   Wright, J. (2007) Ecological services to and from rangelands of the United States. *Ecological*
523   *Economics,* **64,** 261-268.
524 Hirota, M., Holmgren, M., Van Nes, E. H. & Scheffer, M. (2011) Global Resilience of Tropical Forest and
525   Savanna to Critical Transitions. *Science,* **334,** 232-235.
526 Holmgren, M., Hirota, M., van Nes, E. H. & Scheffer, M. (2013) Effects of interannual climate variability
527   on tropical tree cover. *Nature Climate Change*.
528 Hudak, A. T. (1999) Rangeland mismanagement in South Africa: failure to apply ecological knowledge.
529   *Human Ecology,* **27,** 55-78.
530 Hutyra, L., Munger, J., Nobre, C., Saleska, S., Vieira, S. u. & Wofsy, S. (2005) Climatic variability and
531   vegetation vulnerability in Amazonia. *Geophysical Research Letters,* **32**.
532 IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the*
533   *Fifth Assessment Report of the Intergovernmental Panel on Climate Change* Cambridge
534   University Press, Cambridge, United Kingdom and New York, NT, USA.
535 Jackson, R., Canadell, J., Ehleringer, J., Mooney, H., Sala, O. & Schulze, E. (1996) A global analysis of
536   root distributions for terrestrial biomes. *Oecologia,* **108,** 389-411.
537 Kark, S. & Van Rensburg, B. J. (2006) Ecotones: marginal or central areas of transition? *Israel Journal of*
538   *Ecology & Evolution,* **52,** 29-53.
539 Kulmatiski, A. & Beard, K. H. (2013) Woody plant encroachment facilitated by increased precipitation
540   intensity. *Nature Climate Change,* **3,** 833-837.
541 Lapola, D. M., Oyama, M. D. & Nobre, C. A. (2009) Exploring the range of climate biome projections for
542   tropical South America: The role of CO2 fertilization and seasonality. *Global Biogeochemical*
543   *Cycles,* **23**.
544 Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B. & Ackerly, D. D. (2009) The velocity of
545   climate change. *Nature,* **462,** 1052-1055.

546 Maestre, F. T., Bowker, M. A., Puche, M. D., Belén Hinojosa, M., Martínez, I., García-Palacios, P.,
547   Castillo, A. P., Soliveres, S., Luzuriaga, A. L. & Sánchez, A. M. (2009) Shrub encroachment can
548   reverse desertification in semi-arid Mediterranean grasslands. *Ecology Letters,* **12,** 930-941.
549 Malhi, Y., Roberts, J. T., Betts, R. A., Killeen, T. J., Li, W. & Nobre, C. A. (2008) Climate change,
550   deforestation, and the fate of the Amazon. *Science,* **319,** 169-172.
551 Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K. & Thuiller, W. (2009) Evaluation of consensus
552   methods in predictive species distribution modelling. *Diversity and Distributions,* **15,** 59-69.
553 McLachlan, J. S., Clark, J. S. & Manos, P. S. (2005) Molecular indicators of tree migration capacity under
554   rapid climate change. *Ecology,* **86,** 2088-2098.
555 MEA (2003) *Ecosystems and human well-being: A framework for assessment.* Island Press, Washington,
556   DC.
557 MEA (2005) *Ecosystems and Human Well-being: Synthesis.* Island Press, Washington, DC.
558 Meehl, G. A., Arblaster, J. M. & Tebaldi, C. (2005) Understanding future patterns of increased
559   precipitation intensity in climate model simulations. *Geophysical Research Letters,* **32**.
560 Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. & Kent, J. (2000) Biodiversity
561   hotspots for conservation priorities. *Nature,* **403,** 853-858.
562 Nathan, R., Horvitz, N., He, Y., Kuparinen, A., Schurr, F. M. & Katul, G. G. (2011) Spread of North
563   American wind-dispersed trees in future environments. *Ecology Letters,* **14,** 211-219.
564 Nepstad, D. C., Stickler, C. M., Soares-Filho, B. & Merry, F. (2008) Interactions among Amazon land use,
565   forests and climate: prospects for a near-term forest tipping point. *Philosophical Transactions of*
566   *the Royal Society B: Biological Sciences,* **363,** 1737-1746.
567 Oyama, M. D. & Nobre, C. A. (2003) A new climate-vegetation equilibrium state for tropical South
568   America. *Geophysical Research Letters,* **30**.
569 Pacala, S. W., Hurtt, G. C., Baker, D., Peylin, P., Houghton, R. A., Birdsey, R. A., Heath, L., Sundquist, E.
570   T., Stallard, R. & Ciais, P. (2001) Consistent land-and atmosphere-based US carbon sink
571   estimates. *Science,* **292,** 2316-2320.
572 Parducci, L., Jørgensen, T., Tollefsrud, M. M., Elverland, E., Alm, T., Fontana, S. L., Bennett, K. D.,
573   Haile, J., Matetovici, I. & Suyama, Y. (2012) Glacial survival of boreal trees in northern
574   Scandinavia. *Science,* **335,** 1083-1086.
575 Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol.*
576   *Evol. Syst.,* **37,** 637-669.
577 Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural
578   systems. *Nature,* **421,** 37-42.
579 Paruelo, J. M., Lauenroth, W. K., Epstein, H. E., Burke, I. C., Aguiar, M. R. & Sala, O. E. (1995) Regional
580   climatic similarities in the temperate zones of North and South America. *Journal of*
581   *Biogeography,* **22,** 915-925.
582 Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., Barbeta, A., Rivas-Ubach, A.,
583   Llusià, J. & Garbulsky, M. (2013) Evidence of current impact of climate change on life: a walk
584   from genes to the biosphere. *Global Change Biology,* **19,** 2303-2338.
585 Pereira, M. P. S., Costa, M. H. & Malhado, A. C. M. (2013) Vegetation patterns in South America
586   associated with rising CO2: uncertainties related to sea surface temperatures. *Theoretical and*
587   *applied climatology,* **111,** 569-576.
588 Prasad, A. M., Gardiner, J. D., Iverson, L. R., Matthews, S. N. & Peters, M. (2013) Exploring tree species
589   colonization potentials using a spatially explicit simulation model: implications for four oaks
590   under climate change. *Global Change Biology,* **19,** 2196-2208.
591 Saatchi, S., Agosti, D., Alger, K., Delabie, J. & Musinsky, J. (2001) Examining fragmentation and loss of
592   primary forest in the southern Bahian Atlantic forest of Brazil with radar imagery. *Conservation*
593   *Biology,* **15,** 867-875.

594 Saatchi, S. S., Harris, N. L., Brown, S., Lefsky, M., Mitchard, E. T., Salas, W., Zutta, B. R., Buermann,
595   W., Lewis, S. L., Hagen, S., Petrova, S., White, L., Silman, M. & Morel, A. (2011) Benchmark
596   map of forest carbon stocks in tropical regions across three continents. *Proc Natl Acad Sci U S A,*
597   **108,** 9899-904.
598 Sala, O. E., Lauenroth, W. K. & Golluscio, R. A. (1997) Plant functional types in temperate semi-arid
599   regions. *Plant functional types* (eds T. M. Smith, H. H. Shugart & F. I. Woodward). Cambridge
600   University Press, Cambridge.
601 Sala, O. E., van Vuuren, D., Pereira, H., Lodge, D., J, A., S, C. G., A, D., V, W. & M, X. (2005)
602   Biodiversity across scenarios. *Ecosystems and Human Well-Being: Scenarios: Scenarios* (eds C. S.
603   R, P. P. L, B. E. M & Z. M), pp. 375-408. Island press, Washington DC.
604 Salazar, L. F. & Nobre, C. A. (2010) Climate change and thresholds of biome shifts in Amazonia.
605   *Geophysical Research Letters,* **37**.
606 Salazar, L. F., Nobre, C. A. & Oyama, M. D. (2007) Climate change consequences on the biome
607   distribution in tropical South America. *Geophysical Research Letters,* **34**.
608 Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux, J.,
609   Higgins, S. I., Le Roux, X. & Ludwig, F. (2005) Determinants of woody cover in African savannas.
610   *Nature,* **438,** 846-849.
611 Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Huenneke, L. F., Jarrell, W. M., Virginia, R. A. &
612   Whitford, W. G. (1990) Biological feedbacks in global desertification. *Science(Washington),* **247,**
613   1043-1048.
614 Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.-P., Harnik, N., Leetmaa, A. &
615   Lau, N.-C. (2007) Model projections of an imminent transition to a more arid climate in
616   southwestern North America. *Science,* **316,** 1181-1184.
617 Shukla, J., Nobre, C. & Sellers, P. (1990) Amazon deforestation and climate change.
618   *Science(Washington),* **247,** 1322-1325.
619 Smith, T. B., Kark, S., Schneider, C. J., Wayne, R. K. & Moritz, C. (2001) Biodiversity hotspots and
620   beyond: the need for preserving environmental transitions. *Trends in Ecology & Evolution,* **16,**
621   431.
622 Smith, T. B., Wayne, R. K., Girman, D. J. & Bruford, M. W. (1997) A role for ecotones in generating
623   rainforest biodiversity. *Science,* **276,** 1855-1857.
624 Staver, A. C., Archibald, S. & Levin, S. A. (2011) The global extent and determinants of savanna and
625   forest as alternative biome states. *Science,* **334,** 230-232.
626 Sturm, M., Racine, C. & Tape, K. (2001) Climate change: Increasing shrub abundance in the Arctic.
627   *Nature,* **411,** 546-547.
628 Taylor, K. E., Stouffer, R. J. & Meehl, G. A. (2012) An Overview of CMIP5 and the Experiment Design.
629   *Bulletin of the American Meteorological Society,* **93**.
630 Van Auken, O. (2009) Causes and consequences of woody plant encroachment into western North
631   American grasslands. *Journal of Environmental Management,* **90,** 2931-2942.
632 Walther, G.-R. (2010) Community and ecosystem responses to recent climate change. *Philosophical*
633   *Transactions of the Royal Society B: Biological Sciences,* **365,** 2019-2024.
634 Williams, R., Duff, G., Bowman, D. & Cook, G. (1996) Variation in the composition and structure of
635   tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in
636   the Northern Territory, Australia. *Journal of Biogeography,* **23,** 747-756.
637 Zelazowski, P., Malhi, Y., Huntingford, C., Sitch, S. & Fisher, J. B. (2011) Changes in the potential
638   distribution of humid tropical forests on a warmer planet. *Philos Trans A Math Phys Eng Sci,* **369,**
639   137-60.

640

641

642

643   **Figure Legends**

644

645   **Fig 1.** Spatial projection of the three alternative states (forest, savanna and treeless areas) for the

646   present time (1950-2000) and for the year 2070 under the RCP8.5 scenario in the tropical and

647   subtropical Americas.

648

649   **Fig 2.** Transition map for the forest-savanna system for the present time (1950-2000) and for the

650   year 2070 under the RCP8.5 scenario in the tropical and subtropical Americas. For the year

651   2070, the mean value of the 17 transition maps resulting from the 17 CMIP5 global climate

652   models is shown. A histogram with the total amount of area of each class can be found in Fig. 6

653   (Top). The total area of each class for each one of the 17 transition maps resulting from the 17

654   CMIP5 global climate models can be found in Table S4.

655

656   **Fig 3.** Transition map for savanna-treeless system for the present time (1950-2000) and for the

657   year 2070 under the RCP8.5 scenario in the tropical and subtropical Americas. For the year

658   2070, the mean value of the 17 transition maps resulting from the 17 CMIP5 global climate

659   models is shown. A histogram with the total amount of area of each class can be found in Fig. 6

660   (Bottom). Rest of legend as in Fig. 2.

661

662   **Fig 4.** Projected shift towards forest, savanna or treeless states for the year 2070 under the

663   RCP8.5 scenario in the tropical and subtropical Americas. Shifts are estimated as the difference

664   between the transition index in the present time and the year 2070 for the forest-savanna and the

665   savanna-treeless systems. The mean value of the projected shifts for the 17 transition maps

666   resulting from the 17 CMIP5 global climate models is shown. Beige area indicates those cells

667   where the change in the probability transition is below 0.1. Darker tones of green, red and blue

668   indicate stronger shifts toward forest, savanna and treeless areas respectively.

669

670   **Fig 5.** Transition areas for the forest-savanna (left) and the savanna-treeless systems (right) in the

671   present time and the year 2070 under the RCP8.5 scenario. For a given transition (i.e. forest-

672   savanna), transition areas are defined as those cells in which the difference between the two

673   alternative systems is less than 0.2. The mean value of the 17 transition maps for the year 2070

674   resulting from the 17 CMIP5 global climate models was used as base transition map.

675

676   **Fig 6.** Projected area under different classes of the transition index for the present (1950-2000)

677   and under the RCP8.5 scenario for the year 2070 for the forest-savanna (Top) and the savanna-

678   treeless transitions (Bottom). Forest-savanna transition index is calculated as p(forest) –

679   p(savanna). Savanna transition index is calculated as p(savanna) – p(treeles). Values closer to 1

680   and -1 indicates lower uncertainty whereas values closer to 0 indicates higher uncertainty. Mean

681   values and standard deviation of the 17 CMIP5 global climate models are shown. Results for

682   each CMIP5 global climate model are shown in Figs. S4 and S5. Area in 10^3 km^2. Note that the

683   total area of savanna is the sum of the savanna areas in both transition systems. The spatial

684   representation of this histogram can be found in Figs. 2 and 3.

685

686   **Fig 7.** Changes in the uncertainty of the forest-savanna transition between the present (1950-

687   2000) and the RCP8.5 scenario (2070) in the tropical and subtropical Americas. The change in

688   uncertainty is calculated as the change in the transition index between the two projections (i.e.

689   1950-2000 and 2070). The mean value resulting from analysis of the 17 CMIP5 global climate

690   models is shown. Positive values of uncertainty indicate areas where the probability of tipping

691   between forest and savanna will increase due to climate change.

692

693 **Table 1.** Candidate climatic models fitted to the distribution of forest, savanna and treeless areas

694 in the tropical and subtropical Americas. For each model, the explained deviance (D^2) and

695 Akaike Information Criterion (AIC) value are shown. For each state, the selected model is in

696 bold. For the Savanna, the best global model (i.e, that with $D^2 = 12.29\%$) was not used and the

697 value in brackets represents the explained deviance of the model finally employed. In this case,

698 the D^2 value represents weighted mean of the D^2 values of the 20% best multi-zone models (see

699 Methods and Table S1 in Supporting Information). P=Mean annual precipitation; T=Mean

700 annual temperature, ARIDITY=Aridity index (P/Potential evapotranspiration)

701

702

Model	Forest D^2	AIC	Savanna D^2	AIC	Treeless D^2	AIC
P	39.30	2230.60	1.69	4029.92	65.02	946.43
P^2	44.52	2041.20	10.35	3677.38	56.97	1165.07
T	24.79	2762.85	0.01	4098.74	28.05	1942.20
T^2	24.81	2764.23	4.29	3925.37	29.37	1908.62
P^2+T	45.64	2002.16	10.35	3679.19	56.79	1172.06
T^2+P	41.76	2144.44	5.35	3884.16	**66.84**	**901.23**
P^2+T^2	**45.88**	**1995.36**	**12.29 (30.34)**	**3601.67**	56.97	1169.33
ARIDITY	32.38	2484.60	0.99	4058.49	58.97	1109.37
ARIDITY^2	38.65	2256.38	4.02	3936.52	59.50	1096.95
P/T	15.30	3111.09	0.32	4086.00	27.80	1948.89
$(P/T)^2$	33.02	2462.86	0.43	4083.42	-	-

703

704

705 **Table 2.** Projected representation of forest, savanna and treeless areas in our study area for the

706 present time (1950-2000) and for 2070 under the RCP8.5 scenario. For the 1950-2000 period,

707 real values (i.e. observed from the data, not modeled) are shown in brackets. Mean values and

708 standard deviation from the 17 downscaled and calibrated CMIP5 global climate models are

709 indicated. Results for each CMIP5 global climate model are shown in Fig. S3

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	1950-2000		2070 RCP8.5		Change	
	Area ($\times 10^3$ km^2)	**%**	**Area** ($\times 10^3$ km^2)	**%**	**Area** ($\times 10^3$ km^2)	**Change (%)**
Forest	6235	29 (31)	4760 ±896	22 ±4	-1474 ±896	-24 (-38 - -9)
Savanna	12765	58 (52)	14263 ±921	65 ±4	1498 ±921	12 (5 - 19)
Treeless	2847	13 (17)	2823 ±178	13 ±1	-24 ±178	-1 (-7 - 5)

712

713 **Fig 1.**

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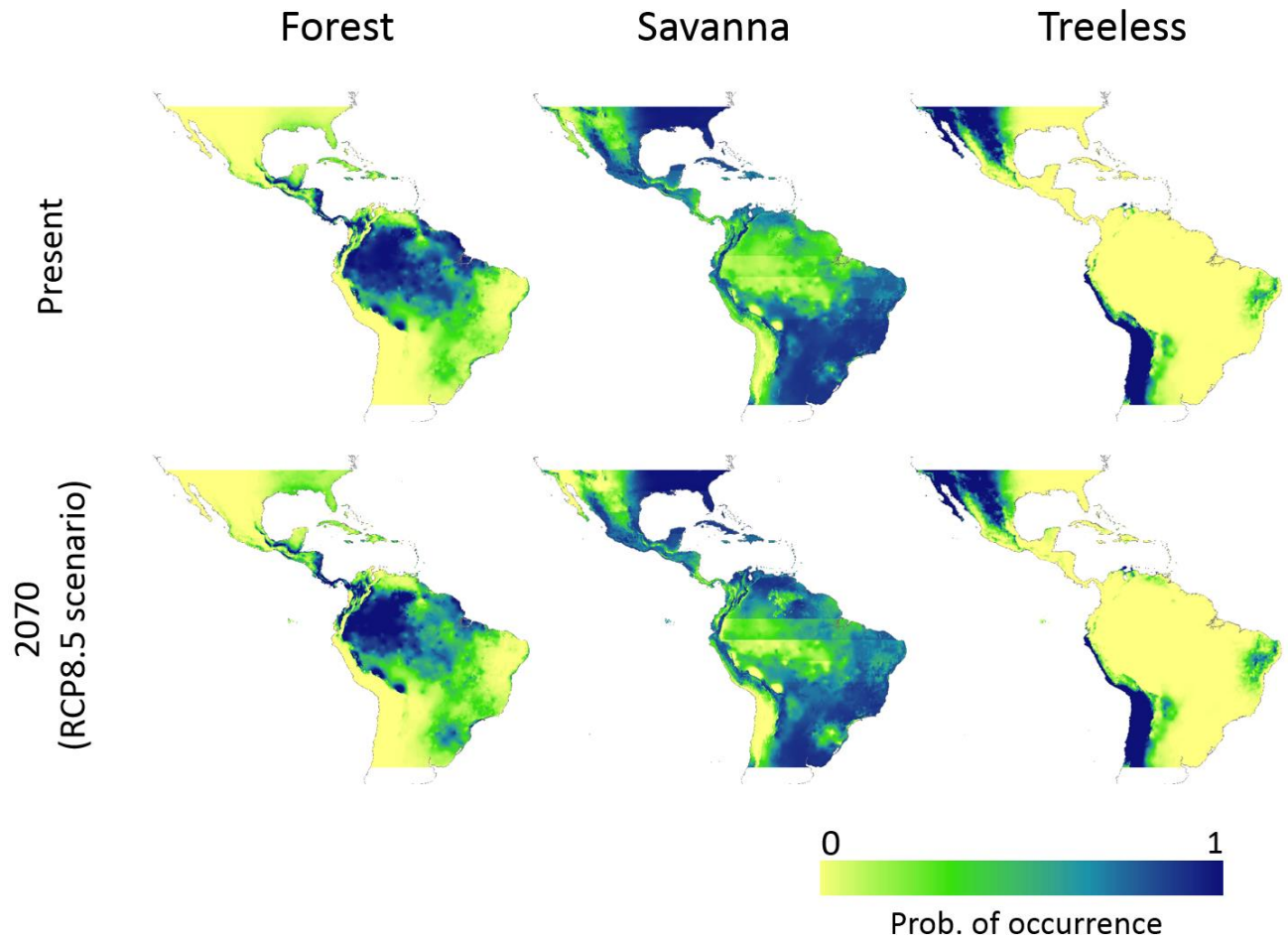
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717

718   **Fig 2**

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Forest-savanna transition

Present   2070 (RCP8.5 scenario)

| 1 | 0.5 | 0.3 | 0.1 | -0.1 | -0.3 | -0.5 | -1 |

p(forest) − p(savanna)
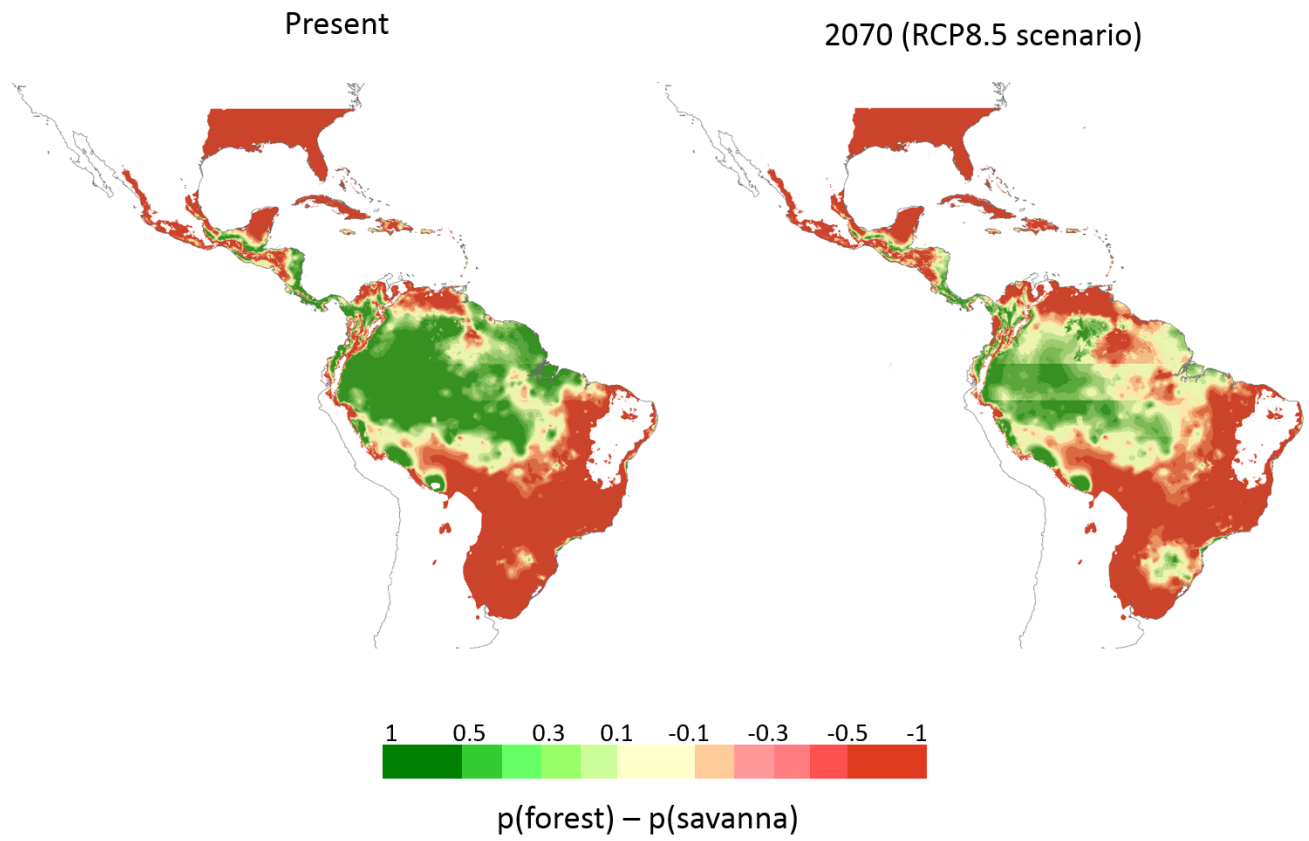
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724

725   **Fig 3.**

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Savanna-treeless transition

Present   2070 (RCP8.5 scenario)

1   0.5   0.3   0.1   -0.1   -0.3   -0.5   -1

p(savanna) − p(treeless)
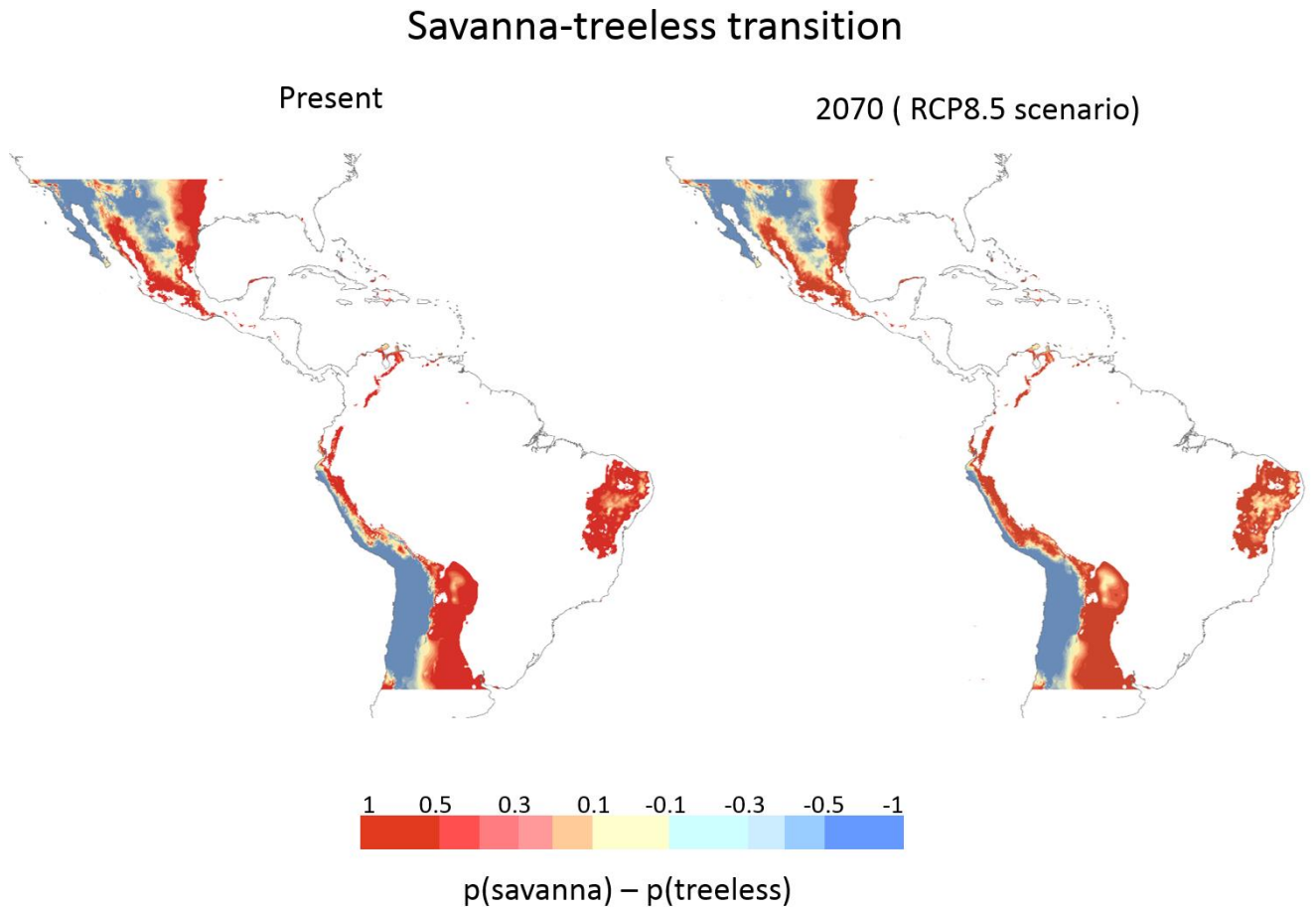
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732   **Fig 4.**

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Shift towards forest

Shift towards savanna

Shift towards treeless

734

735

736   **Fig 5.**

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Forest-savanna transition areas   Savanna-treeless transition areas

■ Transition area (only present)

■ Transition area (only 2070)

■ Transition area (overlap present-2070)
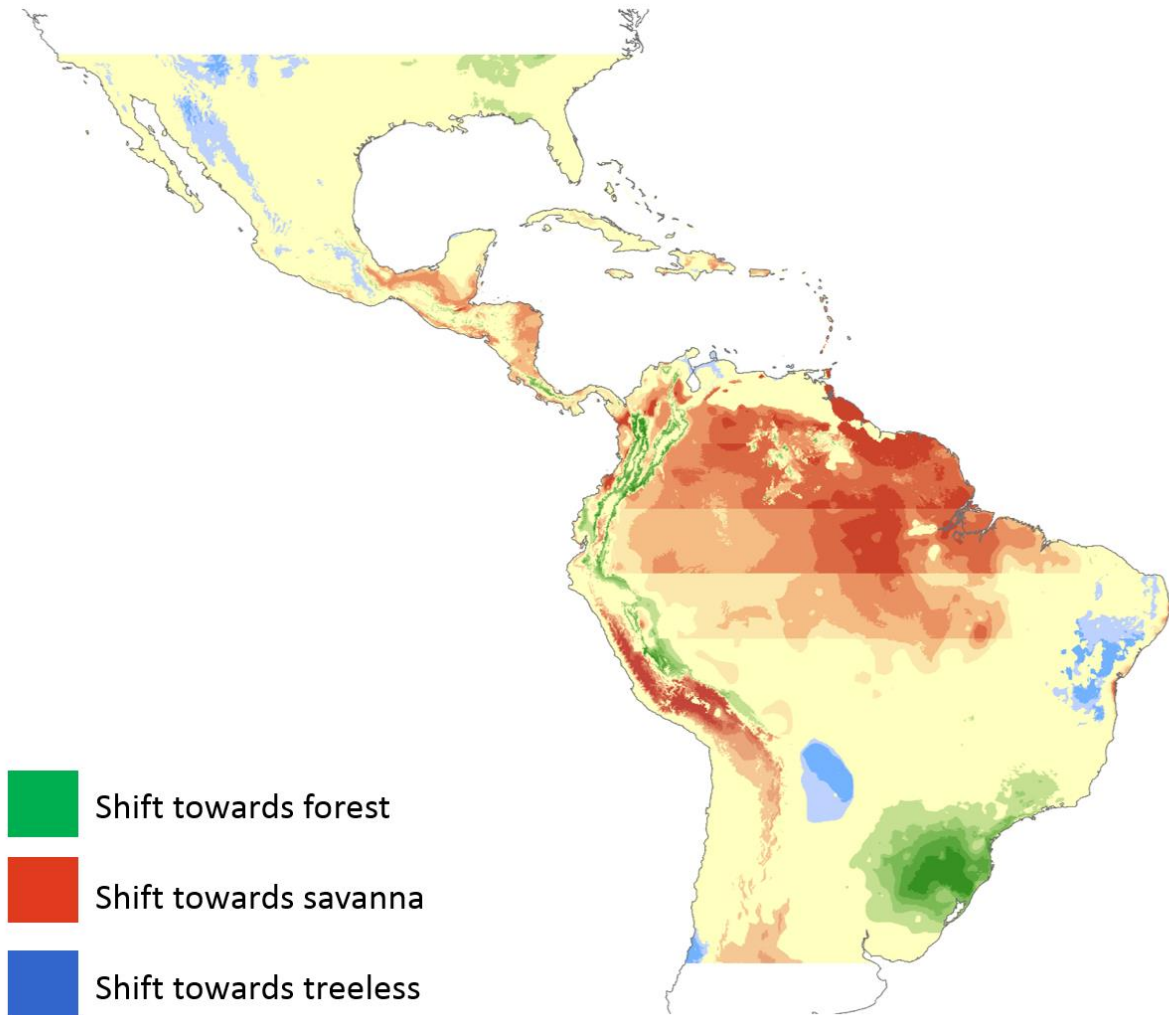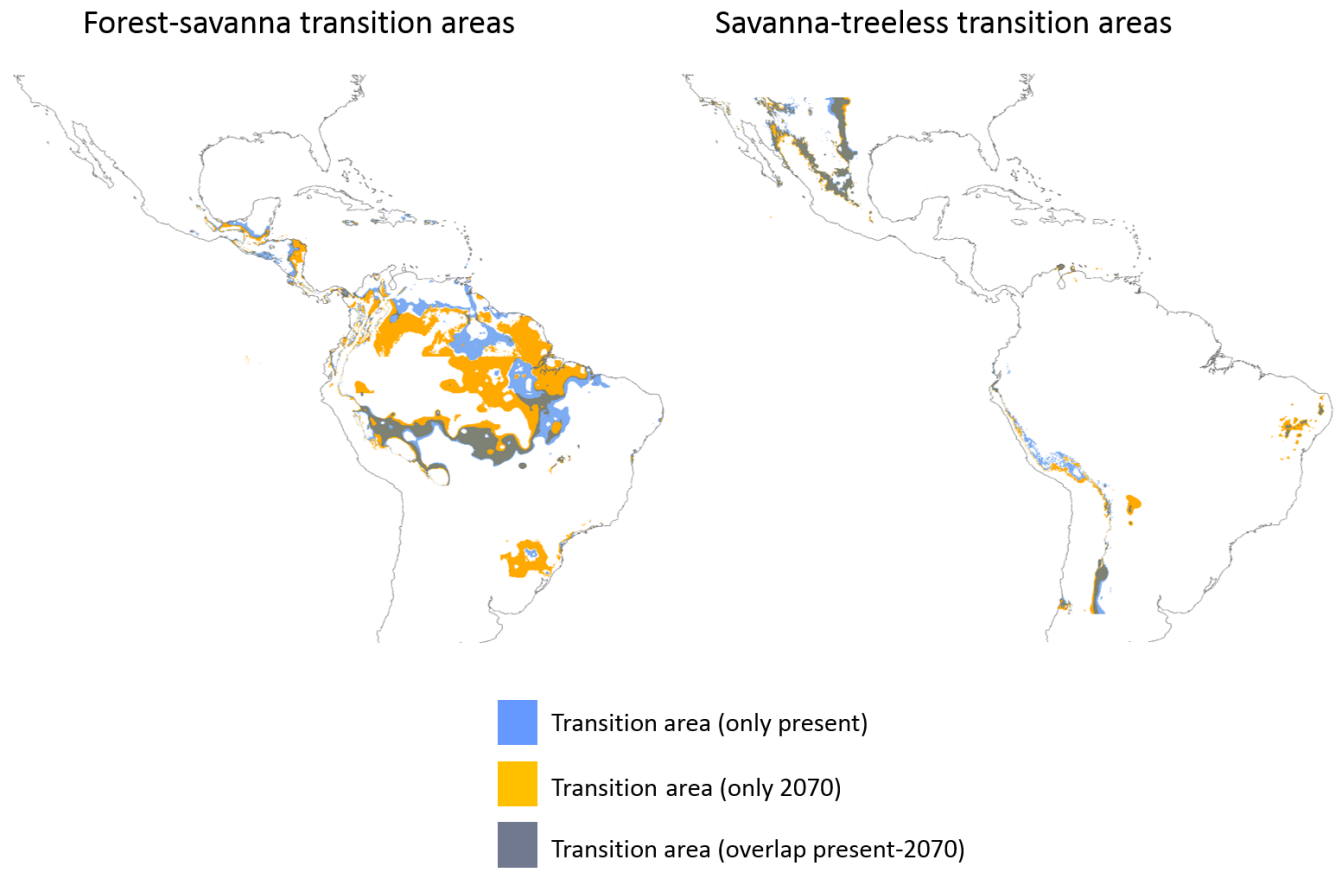
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742   **Fig 6.**
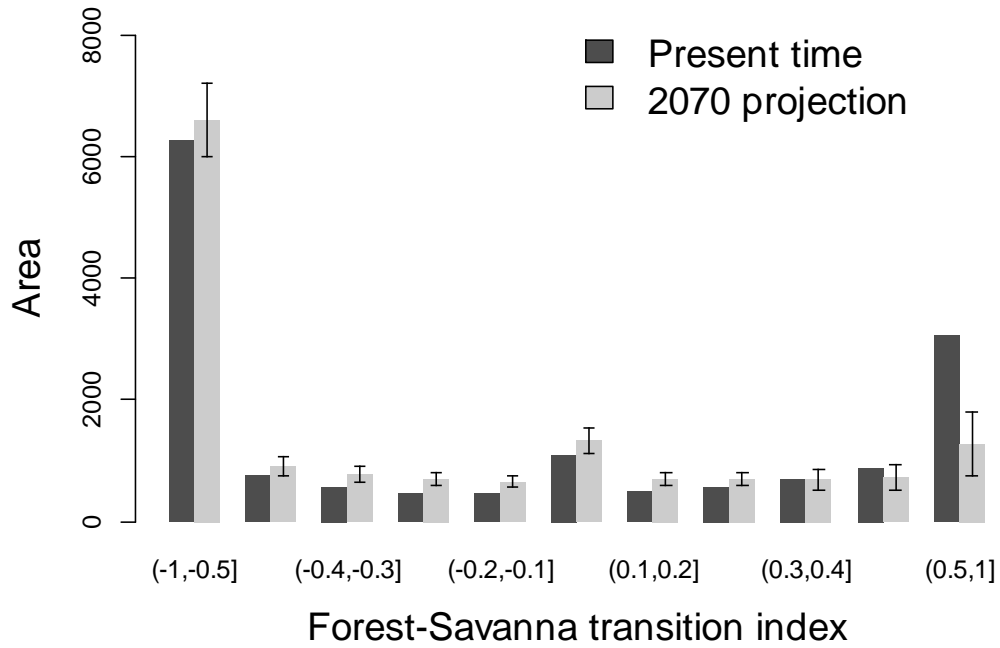
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747 **Fig 7.**

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Maximum increase in uncertainty   No change   Maximum decrease in uncertainty

1   0.5   0.3   0.1   -0.1   -0.3   -0.5   -1

Change in uncertainty
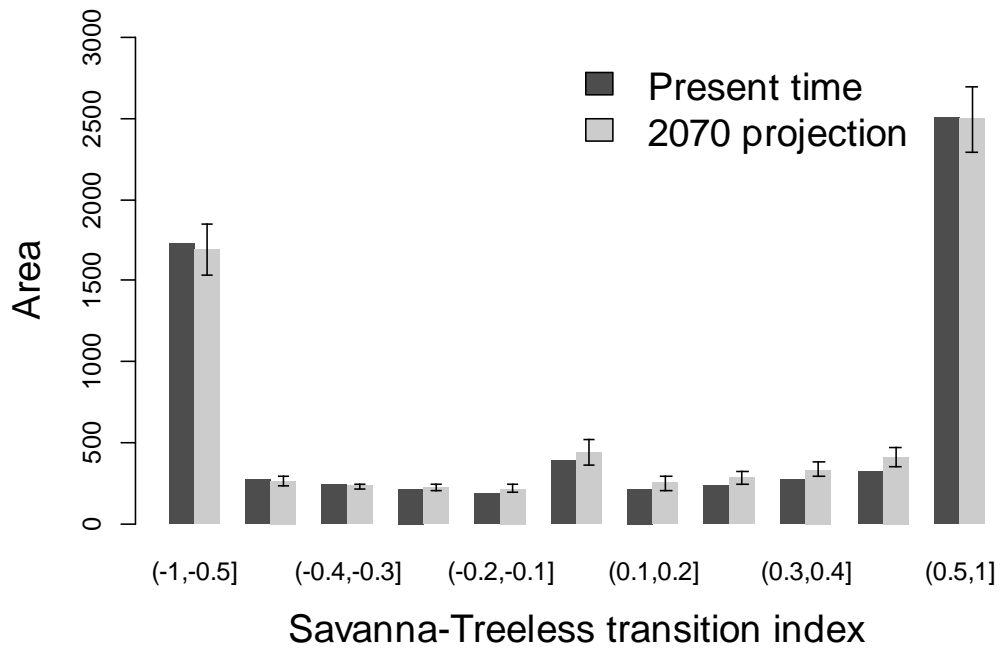
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753   **SUPPORTING INFORMATION**
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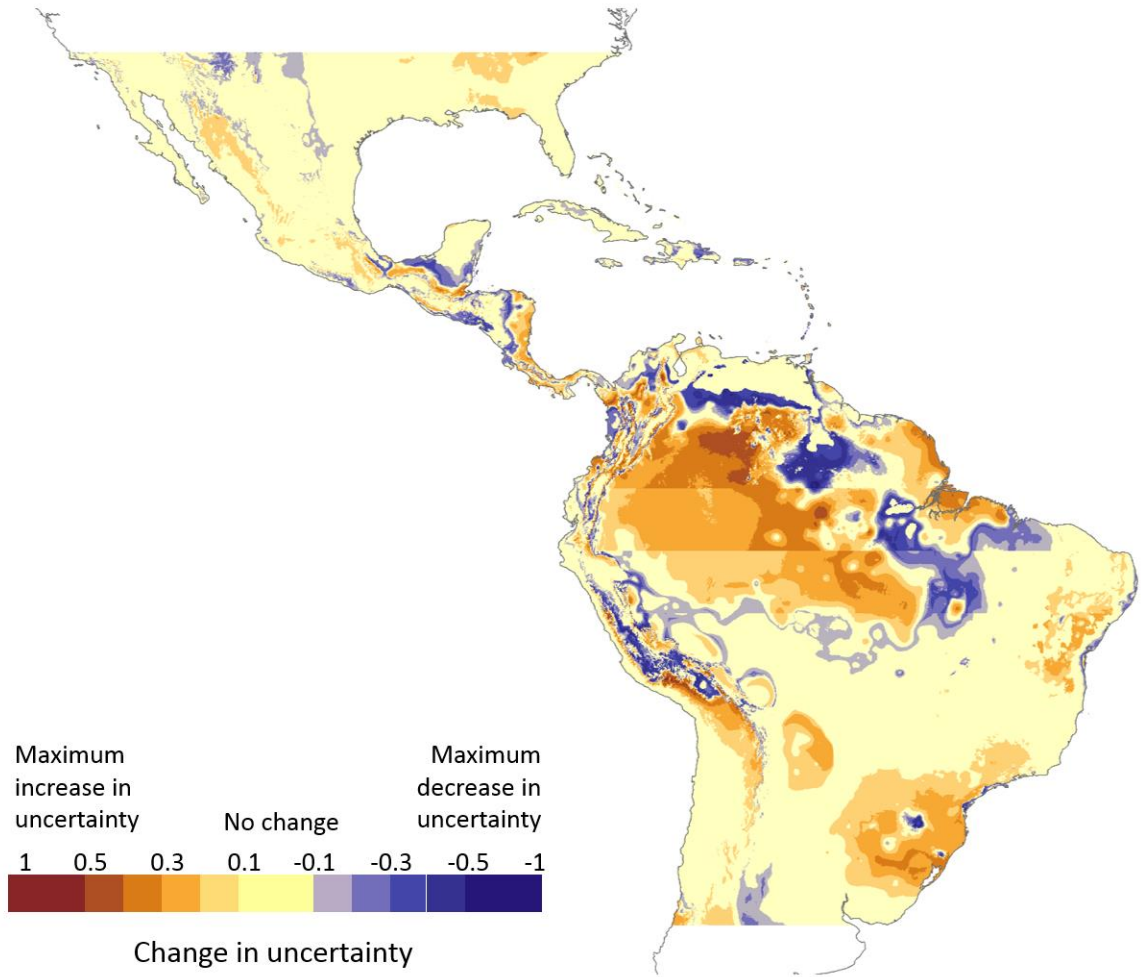755   **Table S1.** 20% best models fitted to the distribution of savanna. In all cases, the models include

756   the same climatic variables (i.e. best global model P^2+T^2, see Table 1) plus a spatial factor**.** All

757   best models included the spatial factor describing three subareas, defined by the latitudinal limits

758   Lim1 and Lim2. Latitudinal limits for the entire study area are 35°N and -35N. The minimum

759   latitudinal width of a subarea was 5°. For example, the model ranked first included a spatial

760   factor with three subareas with limits: 35°N - 20°N, 20°N - -5°N and 5°N - -35°N

Rank	N subareas	Lim1	Lim2	D2	AIC
1	3	20°	-5°	33.55	2751.08
2	3	10°	-5°	33.28	2762.37
3	3	25°	-5°	31.63	2830.00
4	3	15°	-5°	32.81	2781.58
5	3	20°	0°	31.15	2849.34
6	3	10°	0°	30.26	2885.90
7	3	15°	0°	30.11	2891.87
8	3	25	0°	29.56	2914.77
9	3	5°	-5°	32.40	2798.09
10	3	20°	-10°	30.58	2872.94
11	3	30°	-5°	27.97	2979.52
12	3	25°	-10°	28.83	2944.51
13	3	20°	-15°	29.19	2929.69
14	3	5°	0°	28.99	2937.92
15	3	30°	0°	26.50	3040.08
16	3	15°	-10°	29.65	2910.80
17	3	10°	-10°	29.89	2901.21
18	3	25°	-15°	27.63	2993.68

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763 **Table S2.** List of the 17 Coupled Model Intercomparison Project Phase 5 (CMIP5) general

764 circulation models used in this study

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Model Name	Institution ID	Modeling Center
ACCESS1-0	CSIRO-BOM	Commonwealth Scientific and Industrial Research Organization (CSIRO) and Bureau of Meteorology (BOM), Australia
BCC-CSM1-1	BCC	Beijing Climate Center, China Meteorological Administration
CCSM4	NCAR	National Center for Atmospheric Research
CNRM-CM5	CNRM - CERFACS	Centre National de Recherches Météorologiques / Centre Européen de Recherche et Formation Avancée en Calcul Scientifique
GFDL-CM3	NOAA GFDL	NOAA Geophysical Fluid Dynamics Laboratory
GISS-E2-R	NASA GISS	NASA Goddard Institute for Space Studies
HadGEM2-AO	NIMR/KMA	National Institute of Meteorological Research/Korea Meteorological Administration
HadGEM2-CC	MOHC (additional realizations by INPE)	Met Office Hadley Centre (additional HadGEM2-ES realizations contributed by Instituto Nacional de Pesquisas Espaciais)
HadGEM2-ES	MOHC (additional realizations by INPE)	Met Office Hadley Centre (additional HadGEM2-ES realizations contributed by Instituto Nacional de Pesquisas Espaciais)
INM-CM4	INM	Institute for Numerical Mathematics
IPSL-CM5A-LR	IPSL	Institut Pierre-Simon Laplace
MIROC-ESM-CHEM	MIROC	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies
MIROC-ESM	MIROC	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies
MIROC5	MIROC	Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology
MPI-ESM-LR	MPI-M	Max-Planck-Institut für Meteorologie (Max Planck Institute for Meteorology)
MRI-CGCM3	MRI	Meteorological Research Institute
NorESM1-M	NCC	Norwegian Climate Centre

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769 **Table S3.** Predicted extent of forest, savanna and treeless areas in the tropical and subtropical

770 Americas for 2070 under the RCP8.5 scenario for the 17 downscaled and calibrated CMIP5

771 global climate models (GCM). Area in 10^3 km^2. See description of climatic models in Table S2

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GCM	Forest	% Forest	Savanna	%Savanna	Treeless	% Treeless
ACCESS1-0	4562	21	14568	67	2717	12
BCC-CSM1-1	4942	23	14108	65	2797	13
CCSM4	4735	22	14343	66	2769	13
CNRM-CM5	4886	22	14384	66	2577	12
GFDL-CM3	3091	14	15707	72	3049	14
GISS-E2-R	4544	21	14313	66	2990	14
HadGEM2-AO	4011	18	15292	70	2543	12
HadGEM2-CC	3882	18	15289	70	2676	12
HadGEM2-ES	4127	19	14980	69	2740	13
INM-CM4	6107	28	12848	59	2891	13
IPSL-CM5A-LR	5668	26	13010	60	3168	15
MIROC-ESM-CHEM	5493	25	13551	62	2803	13
MIROC-ESM	6397	29	12632	58	2818	13
MIROC5	5057	23	13949	64	2841	13
MPI-ESM-LR	3355	15	15569	71	2923	13
MRI-CGCM3	5306	24	13928	64	2613	12
NorESM1-M	4767	22	14001	64	3079	14

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781 **Table S4.** Predicted extent of the classes of the Forest-savanna transition index in the tropical

782 and subtropical Americas for 2070 under the RCP8.5 scenario for the 17 downscaled and

783 calibrated CMIP5 global climate models (GCM). This index is calculated as p(forest) –

784 p(savanna). Values closer to 1 indicates cells with low uncertainty of being savanna, values

785 closer to -1 indicates cells with low uncertainty of being forest and values closer to 0 indicates

786 high uncertainty. Mean values are shown in Figure 6 (top). See description of climatic models in

787 Table S2. Area in $10^3 \, km^2$

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GCM	(.5,1]	(.5,.4]	(.4,.3]	(.3,.2]	(.2,.1]	(.1,-.1]	(-.1,-.2]	(-.2,-.3]	(-.3,-.4]	(-.4,-.5]	(-.5,-1]
ACCESS1-0	6965	993	876	690	650	1288	663	657	716	721	1146
BCC-CSM1-1	6025	1000	962	840	678	1427	763	754	744	650	1286
CCSM4	6285	849	800	721	637	1388	661	709	620	737	1307
CNRM-CM5	6378	965	975	883	776	1598	773	681	643	797	1218
GFDL-CM3	6992	893	835	936	935	1928	760	616	291	157	331
GISS-E2-R	6890	883	854	729	635	1088	534	631	720	797	1347
HadGEM2-AO	7555	982	648	540	577	1171	554	540	623	707	997
HadGEM2-CC	7303	1099	795	653	666	1204	631	696	684	606	687
HadGEM2-ES	7364	1064	831	668	559	1239	680	689	673	739	717
INM-CM4	5940	771	651	538	488	1048	674	704	797	949	2440
IPSL-CM5A-LR	6514	689	532	540	551	1331	872	689	834	1111	1467
MIROC-ESM-CHEM	6252	933	766	629	609	1362	690	718	619	750	2014
MIROC-ESM	5423	880	759	725	723	1400	850	945	1065	1075	1744
MIROC5	6242	712	673	632	722	1401	821	822	744	697	1278
MPI-ESM-LR	7536	1288	1022	748	650	1121	579	531	459	582	643
MRI-CGCM3	6542	647	642	652	627	1366	807	906	816	726	1289
NorESM1-M	6191	859	801	680	646	1211	600	597	665	622	1692

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791 **Table S5.** Predicted extent of the classes of the Savanna-Treeless transition index in the tropical

792 and subtropical Americas for 2070 under the RCP8.5 scenario for the 17 downscaled and

793 calibrated CMIP5 global climate models (GCM). This index is calculated as p(savanna) −

794 p(treeless).Values closer to 1 indicates cells with low uncertainty of being treeless, values closer

795 to -1 indicates cells with low uncertainty of being savanna and values closer to 0 indicates high

796 uncertainty. Mean values are shown in Figure 6 (bottom). See description of climatic models in

797 Table S2. Area in $10^3 \, km^2$

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GCM	(.5,1]	(.5,.4]	(.4,.3]	(.3,.2]	(.2,.1]	(.1,-.1]	(-.1,-.2]	(-.2,-.3]	(-.3,-.4]	(-.4,-.5]	(-.5,-1]
ACCESS1-0	1694	217	225	205	198	350	197	248	276	354	2573
BCC-CSM1-1	1628	278	248	218	205	491	275	293	325	389	2440
CCSM4	1537	257	226	234	262	539	273	291	348	444	2788
CNRM-CM5	1483	268	230	218	203	362	206	255	292	347	2348
GFDL-CM3	1746	309	235	250	240	587	349	354	374	419	2369
GISS-E2-R	1856	254	207	207	226	497	233	230	276	333	2474
HadGEM2-AO	1495	238	213	196	192	446	268	301	356	430	2878
HadGEM2-CC	1547	269	240	240	203	381	242	278	345	405	2740
HadGEM2-ES	1692	258	246	214	171	336	205	253	273	396	2648
INM-CM4	1737	269	218	218	233	471	276	297	355	448	2373
IPSL-CM5A-LR	1990	290	260	236	206	402	221	251	326	375	2223
MIROC-ESM-CHEM	1791	245	220	206	184	357	223	248	300	348	2453
MIROC-ESM	1777	256	219	205	185	378	227	254	317	381	2130
MIROC5	1586	293	251	251	232	529	330	354	413	521	2404
MPI-ESM-LR	1846	262	220	197	211	366	185	250	369	411	2445
MRI-CGCM3	1475	211	222	255	235	468	289	356	407	531	2432
NorESM1-M	1856	272	227	231	257	485	243	293	324	435	2738

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801 **Fig S1.** Distribution of areas undergoing human activities (categories 16-18 and 22 in the Global

802 Land Cover 2000 (GLC2000; Bartholome & Belward, 2005) in the Tropical and Subtropical

803 Americas (dark grey). These areas were filtered out from our analyses.

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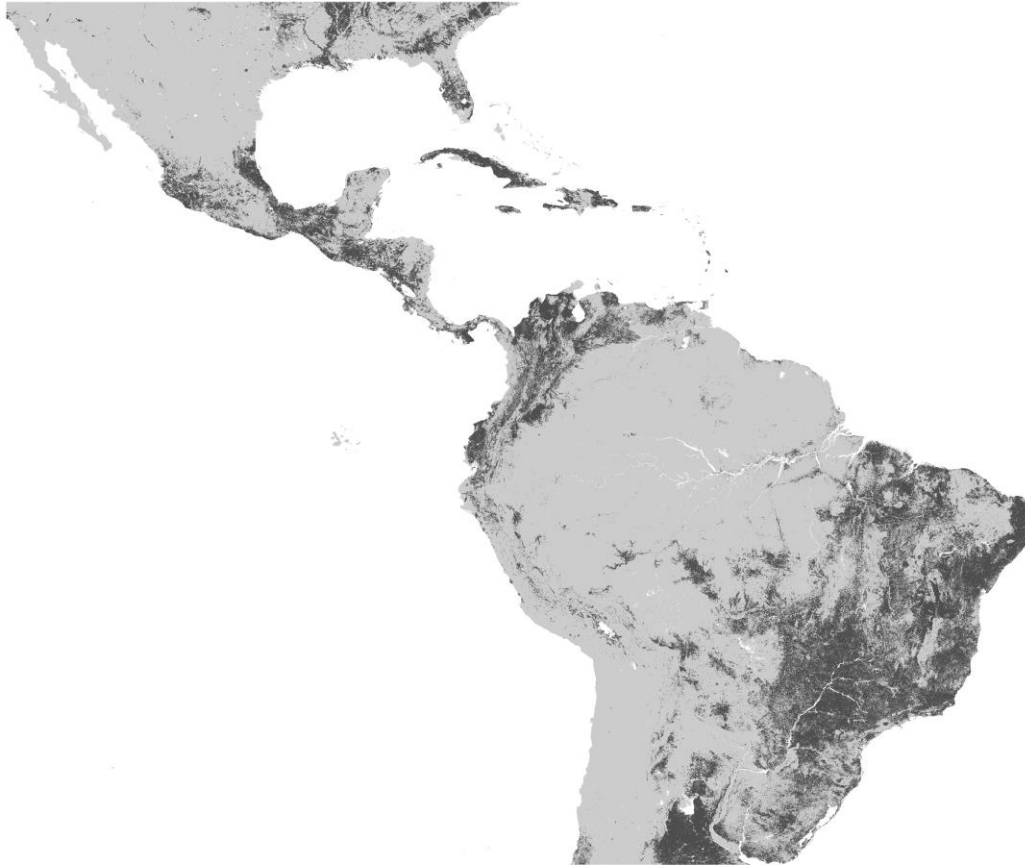
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807 **REFERENCES**

808 Bartholome, E. & Belward, A. S. (2005) GLC2000: a new approach to global land cover mapping from
809 Earth observation data. *International Journal of Remote Sensing,* **26,** 1959-1977

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