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Savanna woody encroachment is widespread across three continents

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1   **Savanna woody encroachment is widespread across three continents**

2   Running head: Global savanna encroachment

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18

19   **Abstract**

20   Tropical savannas are a globally extensive biome prone to rapid vegetation change in response

21   to changing environmental conditions. Via a meta-analysis, we quantified savanna woody vegetation

22   change spanning the last century. We found a global trend of woody encroachment that was

23   established prior the 1980s. However, there is critical regional variation in the magnitude of

24   encroachment. Woody cover is increasing most rapidly in the remaining uncleared savannas of South

25   America, most likely due to fire suppression and land fragmentation. In contrast, Australia has

26   experienced low rates of encroachment. When accounting for land-use, African savannas have a mean

27   rate annual woody cover increase two and a half times that of Australian savannas. In Africa,

28   encroachment occurs across multiple land uses and is accelerating over time. In Africa and Australia,

29   rising atmospheric CO_2, changing land management and rainfall are likely causes. We argue that the

30   functional traits of each woody flora, specifically the N-fixing ability and architecture of woody plants,

31   are critical to predicting encroachment over the next century and that African savannas are at high

32   risk of widespread vegetation change.

33

Introduction

34

35 The savanna biome covers around 20% of the Earth's surface, contributing 30% of terrestrial net

36 primary production (NPP) (Grace *et al.*, 2006), and is increasingly considered critical to the regulation

37 of the terrestrial carbon cycle (Poulter *et al.*, 2014; Liu *et al.*, 2015). However, savannas are also

38 home to 20% of the Earth's population and the majority of rangelands and livestock (Scholes &

39 Archer, 1997). Understanding current trends in vegetation change across the biome is critical to

40 predicting the future of this ecologically, economically and culturally important biome.

41

42 Global change is increasingly understood to be affecting tropical vegetation at large spatial

43 scales. A poorly resolved global driver of vegetation change is the exponential increase of

44 atmospheric CO_2 concentration, henceforth denoted as $[CO_2]$. Rising $[CO_2]$ affects plant growth and

45 vegetation both directly, and indirectly via $[CO_2]$-driven climate change (Leakey *et al.*, 2009).

46 Concurrently, humans have caused extensive change in the spatial processes of fire and mega-

47 herbivory that maintain savanna ecosystem function, via land clearing for agriculture, building of

48 roads and fences, hunting, and deliberate lighting or suppression of fire (Lamprey & Reid, 2004;

49 Archibald *et al.*, 2013). Combined, the degree of human-induced land use and land cover change,

50 increases in $[CO_2]$ and future climate change mean change in savanna vegetation structure and

51 function must be anticipated. However, estimates of future savanna vegetation change vary

52 considerably; some modelling studies predict that elevated $[CO_2]$ will drive large increases in

53 savanna woody cover (Higgins & Scheiter, 2012; Donohue *et al.*, 2013), while other models that only

54 consider climate changes produce variable predictions ranging from savannas remaining stable

55 (Bergengren *et al.*, 2011) to savannas invading forests (Anadon *et al.*, 2014) and forests invading

56 savannas (Zelazowski *et al.*, 2011).

57 Woody encroachment, the increase in woody biomass, stem densities or woody cover, is a

58 symptom of an alteration in ecosystem processes; it has been documented across continents and

59   biomes (Myers-Smith *et al.*, 2011; Murphy *et al.*, 2014; O'Connor *et al.*, 2014). However, as an open-

60   canopied tropical biome, savannas appear particularly vulnerable to woody encroachment (Parr *et*

61   *al.*, 2014), where encroachment can have negative consequences for soil carbon storage (Berthrong

62   *et al.*, 2012), ground water recharge, tourism (Gray & Bond, 2013), grazing potential (Angassa &

63   Baars, 2000) and biodiversity (Ratajczak *et al.*, 2012).

64   Predicting woody encroachment across savannas is hampered by their ecological complexity

65   as a wide range of drivers can act to release constraints on woody plant growth and recruitment –

66   including browsing, grazing, fire, climate, and $[CO_2]$. Combinations of local (e.g. land use), regional

67   (e.g. changing temperature, rainfall, evaporative demands) and global drivers (e.g. rising $[CO_2]$) are

68   all recognised as potential causes of increasing woody cover in savannas (Bond & Midgley, 2012).

69   Local land use such as heavy grazing and consequent reductions in fire frequency and intensity

70   promotes encroachment by releasing woody plants from grass competition (O'Connor *et al.*, 2014).

71   Rising $[CO_2]$ can accelerate woody plant growth through increasing available soil water through

72   improving plant water-use efficiencies (Polley *et al.*, 1997; Leakey *et al.*, 2009), potentially extending

73   the growing season, increasing maximum growth rates for individual woody plants while also

74   increasing potential tree cover (where potential tree cover is not limited by other factors, e.g. soil

75   fertility). Increased $[CO_2]$ will also directly increase the rate of carbon uptake by plants, potentially

76   increasing growth rates and the recruitment of woody plants (Bond & Midgley, 2000; Hoffmann *et*

77   *al.*, 2000; Kgope *et al.*, 2010). The vulnerability of a region to encroachment will therefore depend on

78   both the prevailing land use history, the environmental setting, as well as the functional traits of

79   woody plants that likely govern their responsiveness to both local (e.g. sensitivity to fire) and global

80   drivers (e.g. growth response to elevated $[CO_2]$). However, there are remarkably few experimental

81   data examining the effect of increased $[CO_2]$ on seasonally dry tropical vegetation and the plant

82   functional types within them (but see (Hoffmann *et al.*, 2000; Stokes *et al.*, 2005; Kgope *et al.*, 2010).

83   These gaps in understanding highlight that there has been no systematic review of recent

84   changes in woody cover that have occurred across savannas. While, the number of continental- and

85   global-scale satellite studies of vegetation greenness are increasing, these studies cover only the

86   short time-scale of the satellite record and record measures of greenness (e.g. NDVI) that

87   incorporate the signal of both trees and grasses (Buitenwerf *et al.*, 2015; Liu *et al.*, 2015). We

88   undertake a meta-analysis of studies documenting change in woody cover, with specific attention to

89   studies of woody cover increase, across the tropical and sub-tropical savanna ecosystems of Africa,

90   Australia and Brazil to assess the extent, magnitude and type of encroachment.

91

92   **Materials and Methods**

93   *Data compilation*

94   We conducted a meta-analysis of woody vegetation change in natural tropical and sub-tropical C4

95   grass-dominated savannas in Africa, Australia and South America. We defined savannas as C4

96   grasslands with a significant tree component following the definitions provided by Lehmann *et al.*,

97   (2011) and Ratnam *et al.*, (2011).Sites were untransformed by large-scale agriculture, but could have

98   been subject to livestock grazing. Studies documenting land clearing were excluded. We searched

99   the literature using a combination of the following terms: "bush"; "woody", "woody cover" "shrub";

100   "tree"; plus "thickening"; "encroachment"; "invasion"; "increase"; "change"; "dynamics", "loss",

101   "mortality", "decline", "death", "elephant damage", "elephant impact", "drought", "wind fall",

102   "cyclone" and "storm". Studies were included where woody cover, biomass or tree basal area was

103   recorded at two or more points in time. These data were used to derive an annual increment of

104   woody cover change, i.e. (final cover – initial cover) / time in years. Seven studies from the Brazilian

105   cerrado were used where biomass or basal area was recorded. These values were converted to

106   percent cover using a linear regression based on data from (Pinheiro, 2008). In Australia we used

107   converted measures of basal area to canopy cover using data presented by Lehmann *et al.* (2009). In

108   Africa, similar conversion formulae were not available so only studies considering changes in woody

109   cover were considered.

110

111   We also compiled studies documenting change in the extent of forest and savanna

112   vegetation. Sites were included if they were untransformed by large-scale agriculture and human-

113   induced afforestation or deforestation. The literature was searched using the terms, "forest",

114   "savanna", "expansion", "shift", "increase", "decrease", "biome switch". Similarly, these studies

115   required two time points. However, across publications there was far less consistency in the metric

116   of change quantifying changes in the extent of savanna. Change was recorded as both change in

117   forest patch size (where the extent of an entire forest patch was measured) or the proportion of

118   ground area covered by forest versus savanna over a given area. We therefore recorded changes as

119   the proportional change of forest relative to savanna but did not use this in the statistical analyses

120   described later.

121

122   From each study, we compiled site latitude and longitude, and used this information to

123   compile climatic information from WorldClim (Hijmans *et al.*, 2005). Where possible, for each study

124   by site combination we extracted information on the dominant land use at the site, the identity and

125   basic traits of the encroaching woody plant species.

126

127   Uncleared savannas are dominated by three land uses; conservation and commercial and

128   communal grazing land (predominately cattle grazing) (McAlpine *et al.*, 2009). Conservation lands

129   represent the best control situation where natural disturbances caused by regular fires and

130   moderate herbivory (grazers and browser) are mostly maintained. In some areas, elephants are

131 present, which can interact strongly with woody cover, by extensively damaging woody plants

132 (Guldemond & Aarde, 2008). Commercial grazing is primarily centred around livestock production

133 resulting in a grazer-dominated system (Scholes, 2009). In Africa, the other predominant land use is

134 communally-owned subsistence farming (communal rangelands) (Scholes, 2009). In communal

135 rangelands, communities rely on the land for natural resources and grazing. Where there was

136 sufficient information provided, we assigned the site one of these predominant four land use types:

137 conservation (without elephants); conservation (with elephants); commercial grazing; communal

138 grazing. If the land was not used for any particular purpose it was termed remnant land. Where

139 possible, we documented the main encroaching woody species at each site. If plants belonged to the

140 family Fabaceae we recorded if the plants had the potential to fix atmospheric nitrogen (Sprent &

141 Platzmann, 2001) (Appendix S4).

142

143 *Statistical Analysis*

144 Our database consisted of studies documenting both increases and decreases in woody cover over

145 time (Figure 1). We found that studies that documented woody cover declines were often

146 accompanied by direct evidence of the environmental driver of vegetation change (e.g. drought,

147 elephant damage), and that these changes were generally observed over short time periods. Of the

148 110 sites in the database documenting savanna woody change, 13 sites documented declines in

149 woody cover (Appendix S4). Of those sites, only two did not provide direct evidence for the cause of

150 the decline. Therefore, we performed an analysis which aimed to investigate correlates of woody

151 cover increase.

152

153 Data were analysed using a generalised linear model (Gaussian error family) framework in R

154 (version 3.1.1) (R Core Team, 2014). We included initial woody cover as a covariate representing site

155 level variation. Initial cover (IC) has an important bearing on the potential for a site to increase in

156   woody cover. We expect that sites low in woody cover are more likely to experience higher rates of

157   woody cover increase simply because these sites are less limited by tree-tree competition, and

158   where suppression of disturbance may facilitate rapid increases in woody cover closer to the

159   potential (Roques *et al.*, 2001; Lehmann *et al.*, 2009). Continent was included as a factor given the

160   observed regional differences in the functional relationships between woody vegetation and climate

161   (Lehmann *et al.*, 2014). Further, based on the literature, it is clear that different human interventions

162   have had more or less impact in different regions. Hence, continent could infer differences in both

163   human management and ecological setting. Mean annual precipitation (MAP) was a covariate given

164   that both mean woody cover and potential woody cover increase with MAP (Jolly *et al.*, 2005;

165   Sankaran *et al.*, 2005; Lehmann *et al.*, 2014). Finally, we included the first year of a study to examine

166   whether rates of cover change were constant through time. This could help infer whether global

167   change drivers (i.e. [CO_2]) have relevance in interpretation of these data. We included an interaction

168   between initial cover and continent as patterns of woody cover are also known to vary among

169   continents. Unfortunately, we could not include other site level factors such as fire return time or

170   herbivore abundance as these data were inconsistently recorded across studies. Given the variable

171   time periods over which these studies were undertaken, it would be inappropriate to estimate a

172   mean fire return time based on the more recent remotely sensed data.

173

174   Candidate models to describe rate of woody cover increase were compared using Akaike's

175   information criterion, corrected for small sample sizes (AICc) to rank the models. As models with a

176   ΔAICc < 2 are considered well supported, we used model averaging on the models with a ΔAICc < 2.

177   We used the averaged final parameter estimates, standard errors and confidence intervals to

178   demonstrate the effect size of the different parameters. All analysis was performed using the software

179   R (version 3.1.1) (R Core Team, 2014) with the packages 'stats' and 'AICmodavg' version 2.0.3 for

180   model selection and averaging. Following the full factorial model including continent we performed

181   the same analysis for each continent separately. We did this to test the effect of variables, specifically

182   MAP, without confounding MAP and continent as the available rainfall range varies strongly between

183   ccontinent (Lehmann *et al.*, 2011).

184

185   We tested for differences in the rate of woody encroachment between comparable land

186   uses within Australia and Africa using a one-way ANOVA. To test for differences in the rates of

187   woody cover between different land uses within Africa we used a two-way ANOVA. Post-hoc analysis

188   was performed using a TukeyHSD test in R (version 3.1.1) (R Core Team, 2014).

189

190   **Results**

191   *Global patterns of woody cover change in C4 grassy ecosystems*

192   Of 94 studies covering 110 savanna sites, woody encroachment was apparent in 84% of sites (Figures

193   1–2). Woody encroachment within savannas has occurred across the rainfall gradient in all three

194   regions (Figure 2a). Australia had the lowest average rate of woody cover change of 0.1% per year

195   (1% per decade) (Table 1), where only small net increases in woody cover were recorded (Figure 2b).

196   In Australia, 4 sites recording declines in tree cover were consistently attributed to inter-decadal

197   drought (Appendix 1, 4). Brazil had the highest mean rate of woody cover increase of 0.7% per year

198   (7% per decade) (Table 1, Figure 2b) with only 2 sites recording decreases in untransformed

199   savannas (Appendix 1,4). The average rate of increase in African savannas was 0.25% per year (2.5%

200   per decade) (Table 1, Figure 2b). Africa had the highest number of sites (14) documenting declines in

201   woody cover (Figure 2b), which were directly attributed to either elephants or inter-decadal

202   drought.

203   Twelve studies, covering 82 sites, examined forest expansion into savanna. Forest expansion

204   was recorded at 85% of sites examined (Figure 1, Table 1). In Australia, where the majority of sites

205 and studies occurred, forest expansion occurred at a rate of 0.7% per year (7% increase in forest

206 area into savanna matrix, per decade) (72 sites). Here, forest expansion into savanna was usually

207 attributed to fire suppression. There were significantly fewer studies of forest–savanna boundary

208 shifts in Africa (5 studies) and Brazil (5 studies), forest expansion was still apparent across all sites. In

209 Africa, a mean annual increase of 0.3% of forest area per year within the savanna matrix was

210 observed, and in Brazil a larger mean annual increase of 1.1% forest area per year was recorded

211 (Table 1).

212   We examined the relevance of continent, mean annual precipitation, start year and initial

213 cover on rates of woody cover increase and identified two plausible models (Table 2a). Model

214 averaged coefficients indicated that continent, mean annual precipitation, start year and initial cover

215 had relevance in these data. Rates of woody cover increase were higher in studies which started

216 later in the 1900s and early 2000s. We found a strong interaction between initial cover and

217 continent, particularly in South America (Table 2b). There, annual rates of increase were highest with

218 low initial woody cover, and thereafter the rate of annual increase in woody cover decreased as

219 initial woody cover increased. We repeated this analysis separately for each continent. In Africa the

220 start year was positively correlated with the rate of encroachment. In South America, observed rates

221 increase were positively correlated with increasing the initial cover. Mean annual precipitation was

222 not an important predictor of rates of woody cover increases in any of the continents.

223   African savannas can be classified into four land management types (Table 1 and methods).

224 When comparing rates of woody cover increase among land management types, significant woody

225 cover increases occurred across all of these management types except in conservation areas where

226 elephants were present (0.1% per year) ($F_{3,49}$=2.75, $p<0.033$) (Table 1). A post-hoc Tukey test

227 confirms that the presence of elephants is associated with significantly lower rates of increase in

228 comparison to communal rangelands and grazed lands.

229 *Contrasting patterns between continents*

230   Cattle grazing is a land use common across Australia and Africa, enabling a comparison of woody

231   cover changes across these comparable regions. We found that average rates of change in Africa

232   were two and a half times of Australian savannas (2.5% vs. 1.1% per decade; Table 1), and the

233   patterns of woody cover increase were significantly higher in African grazing land when compared to

234   Australian grazing land ($F_{(1, 27)}$ =16.04, p<0.000).

235   The biology of the encroaching species differed between continents. In Africa, 94% of sites

236   (from the 71% of studies reporting such information) were characterised by species with the

237   potential to fix nitrogen (Appendix S4). In South American savannas only 10% of sites were recorded

238   as being characterised by N-fixing species (from the 85% of studies reporting such information). In

239   Australia, none of the encroachment was caused by N-fixing species (from the 30% of studies

240   reporting the dominant woody encroaching species).

241

242   **Discussion**

243   We demonstrate that woody encroachment – both within savannas and forest expansion into

244   savannas – is widespread across the savanna biome. Woody encroachment, albeit with varying

245   regional magnitude, occurred across regions and land uses. Our meta-analysis of historical records

246   demonstrates a widespread trend of increasing woody cover, which was already apparent in the

247   1970s.

248   We found that initial cover was an important correlate of the rate of encroachment, where a

249   high initial cover was associated with a lower subsequent rate of encroachment. This could

250   potentially be attributed to density dependence (Roques *et al.*, 2001; Lehmann *et al.*, 2009). Mean

251   annual precipitation was not correlated with the rate of encroachment in any region and

252   encroachment occurred across the available rainfall gradient. Water availability is however a key

253   constraint on savanna net primary productivity and maximum woody cover (Sankaran *et al.*, 2005;

254   Staver *et al.*, 2011). It is therefore possible that unquantified site-level variation outweighed the role

255   of rainfall, or that this metric was insensitive to other water-related factors, such as duration of the

256   dry season. Precipitation has been previously found to be an important correlate of encroachment,

257   where in high versus low rainfall comparisons of encroachment, sites at high rainfall are more likely

258   to fluctuate in woody cover over time (Lehmann *et al.*, 2009). Continent was an important correlate

259   of the rate of encroachment where Brazilian savannas have experienced, on average three times the

260   rate of encroachment of African savannas and seven times the rate of Australian savannas. Local

261   differences in fire and browse history, soil nutrient status and physical structure could not be

262   consistently quantified in this analysis as this information was not consistently reported.

263

264   Extensive encroachment across savannas could suggest a uniform global driver of change,

265   specifically elevated [CO_2] that has been variously hypothesised to drive a re-organisation of tropical

266   vegetation. However, our correlative analyses do not preclude regional and local drivers of change

267   generating similar net effects. Therefore, a more compelling approach to test for evidence of a

268   global driver is to examine encroachment across land uses which are expected to have different

269   trends in woody cover over time. In Africa, three land uses are common to untransformed savannas;

270   commercial cattle ranches, communal rangelands and conservation areas. Commercial cattle

271   farming causes a grazer (cattle) dominated system characterised by a moderate but constant

272   stocking rate with an infrequent fire return period (Higgins *et al.*, 1999; Roques *et al.*, 2001).

273   Encroachment is often predicted for this land use type (Wigley *et al.*, 2010). In contrast communal

274   rangelands, subsistence agriculture around rural villages, are predicted to experience declines in

275   woody cover due to wood harvesting for building, energy and income (e.g. charcoal). Rates of woody

276   cover decline are predicted to increase as human densities increase (Banks *et al.*, 1996; Ryan *et al.*,

277   2014). The third land use is conservation, where little change in woody cover is predicted due to

278   regular fires and moderate herbivory (grazers and browsers) maintaining savanna ecosystems. A

279   common distinction within conservation areas is the presence or absence of elephant, the presence

280   of which is predicted to cause declines in woody cover (Guldemond & Aarde, 2008). Our analysis

281 demonstrates that within Africa encroachment has occurred across all these land uses, except in the

282 presence of elephants. This is a powerful indicator that in Africa a global driver is a likely cause of

283 woody encroachment and also highlights the role of mega-herbivory in slowing encroachment.

284 Indeed, the contrast between areas with and without elephants (Table 1) highlights that the removal

285 of elephants is also a likely significant cause of encroachment across Africa (Guldemond & Aarde,

286 2008), as free-roaming elephants have disappeared from many parts of Africa and are now largely

287 confined to conservation areas (Owen-Smith, 1992). In contrast, the mega-herbivore fauna of

288 Australia and Brazil have been extinct for millennia, such that the legacy will not be evident in

289 contemporary trends of vegetation change.

290

291   A second indicator for a global process is how rates of encroachment vary with time. We

292 found that in Africa, the later the start year the higher the rate of encroachment. For example, a 10-

293 year study starting in 1960 ending in 1970 was likely to have a lower rate of encroachment than a

294 study starting in 1995. Accelerating encroachment rates have been noted in other African studies

295 (Buitenwerf *et al.*, 2012; O'Connor *et al.*, 2014). This is congruent with the encroachment rates

296 responding to an increasing intensity of a global driver, most likely increasing atmospheric [CO_2],

297 increasing land-use intensity and increasing disruption of fire and mega-herbivory (Ramankutty &

298 Foley, 1999; Archibald *et al.*, 2013).

299

300 *What is the role of continent?*

301 Encroachment is occurring across all savannas, however the regional context appears linked to

302 observed rates of encroachment. This highlights that regional specific characteristics such as land

303 use and the biology of flora is required to contextualise our findings. For example, human

304 intervention in the contiguity of savannas has been severe in the Brazilian cerrado (Klink & Machado,

305 2005) and the extraordinary rates of encroachment across Brazil appear a direct consequence of a

306 legislated policy of fire suppression (Klink & Machado, 2005). Fire extent and frequency are further

307   reduced by landscape fragmentation and transformation with only a few savanna patches larger

308   than 1000 ha remaining (Durigan *et al.*, 2003; Klink & Machado, 2005; Silva *et al.*, 2008). Therefore,

309   in Brazil the net impact of local processes is likely causing encroachment at a regional scale across

310   remaining Brazilian savannas.

311

312   In Africa, savanna encroachment is significantly higher than that observed in Australia. These

313   differences are more pronounced (2.5 times higher) when comparing similar land uses (commercial

314   cattle ranching). Our findings point to a global driver, most likely elevated $[CO_2]$, in African savannas

315   even though this region also has the most records of woody cover declines. Elephant impacts and

316   low soil nutrients, harvesting pressures by humans were instrumental in causing these observed

317   reductions in woody cover particularly in the nutrient poor *Brachystegia* dominated savannas

318   (Mapaure & Campbell, 2002; Ryan *et al.*, 2014). These observations raise the question, what makes

319   Australian savannas relatively resistant to woody encroachment, particularly when no regional land

320   use or policy can explain the changes?

321

322   Australian savannas are characterised by low nutrient soils, highly connected landscapes

323   with little topographic barriers that generate fire regimes of frequent, intense and large fires

324   (Archibald *et al.*, 2013). Frequent fire retards tree growth, biomass and establishment (Murphy *et*

325   *al.*, 2014) and could buffer encroachment in landscape that has densities of less than 1 person per

326   km^2(Australian Burea of Statistics, 2012). Whilst there are regional differences within Australia in

327   both rainfall seasonality and fire regimes (Archibald *et al.*, 2013), Australian savannas generally have

328   extreme seasonality and longer dry seasons than either Africa or Australia (Lehmann *et al.*, 2011;

329   Staver *et al.*, 2011). Although reduced evaporation and improved water use efficiencies from $[CO_2]$

330   fertilisation could act to increase the duration of the growing season (Donohue *et al.*, 2013), the

331   effect is potentially small, relative to other savanna regions as the dry season remains in excess of six

332   months and will still result in seasonal drought and fire.

333

334   In contrast with Australia and Brazil, African savannas contain a high abundance of nitrogen-

335   fixing woody plant species from the family Fabaceae (Appendix S3). Their dominance could enhance

336   ecosystem level responses to elevated $[CO_2]$ (Leakey *et al.*, 2009) as nitrogen-fixing species can

337   match the elevated rates of photosynthesis with increased nitrogen-fixation (Rogers *et al.*, 2009a) by

338   producing more nitrogen-fixing tissues (Leakey *et al.*, 2009; Rogers *et al.*, 2009a), or a greater

339   nitrogenase activity. Additionally, improved water use efficiencies associated with elevated $[CO_2]$

340   could lower drought inhibition of nitrogen-fixers (Polley *et al.*, 1997; Rogers *et al.*, 2009b). The role

341   of nitrogen-fixing species in savanna ecology has generally been ignored despite the dominance of

342   these taxa in African savannas. With elevated $[CO_2]$ and/or reduced drought stress, communities

343   with a high proportion of nitrogen-fixing woody species may display rapid increases in biomass over

344   time.

345

346   Regional variation in plant architecture occurs between savannas of Africa, Australia and

347   South America (Dantas & Pausas, 2013; Moncrieff *et al.*, 2014). Regional differences in stem

348   diameter to canopy diameter ratios must change the rate at which tree cover increases per unit of

349   carbon gain. For example, Australian savanna trees are characterised by tall narrow canopies when

350   compared to African savanna trees which have, on average, canopy widths twice that of Australian

351   trees for a given stem diameter (Moncrieff *et al.*, 2014). These architectural differences are likely to

352   result in different rates of encroachment, for example an increase in woody cover from 20% to 40%

353   would require more than twice the carbon gain in Australia as Africa (Moncrieff et al 2014).

354   Therefore, all else being equal, the architectural traits of African savanna trees will promote higher

355   rates of woody cover increase in African than Australian savannas.

356   Finally, African savannas are dominated by deciduous woody species (Chidumayo, 2001;

357   Bowman & Prior, 2005). In deciduous savanna systems $[CO_2]$ mediated increases in water use

358   efficiency could extend the growing season by alleviating moisture limitation at the beginning or the

359 end of the growing season. An extended growing season, where leaves are retained for longer

360 periods, has already been recorded in some semi-arid African savannas (Buitenwerf *et al.*, 2015). A

361 delay in leaf fall in the early dry season, when average daily temperatures remain moderate, would

362 extend the photosynthetically active period for plants (Stevens *et al.*, 2015). In contrast, both

363 Australian and Brazilian savannas are dominated by evergreen woody plant species and changes may

364 be relatively less pronounced (Bowman & Prior, 2005; Buitenwerf *et al.*, 2015).

365

366 *Gaps and bias in the literature*

367 This review highlighted notable gaps in information. Across Africa, the *Brachystegia* dominated

368 savannas cover 2.7 million km^2 (Pienaar *et al.*, 2015) (similar expanse to all Australian savannas) yet

369 there is a paucity of studies in this region. In South America, we could find only 2 studies

370 documenting woody cover across Venezuelan savannas. On the other hand, other regions were over

371 represented, generating a spatial bias within the dataset, most notably in South Africa. Additionally a

372 publication bias almost certainly exists where studies which do not document either positive or

373 negative change are less likely to be published.

374 *Conclusions*

375 Encroachment is occurring across the savanna biome. Our results demonstrate that these patterns

376 and their potential causes are not easily extrapolated across savanna regions and that regional

377 context is key to interpretation of these trends. Savannas regions are dominated by different plant

378 families with different suites of biological traits (Lehmann et al 2014). We argue that the biology of

379 regional floras will influence the susceptibility of a region to encroachment.

380 While, our study allows us to chart trajectories of woody cover change it does not allow us to

381 determine the underlying causes of encroachment. However, this comparison enables us to

382 establish testable hypothesis to explain regional variation in encroachment, highlighting the need for

383 experimentation that to date has been lacking in savanna ecology.

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Author contributions

NS and CL conceived the study, analysed the data and wrote the paper. NS, CL, GD and BM compiled

the data, and GD and BM provided comments on a draft of the manuscript.

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Table 1: Summary of woody cover change studies across savannas and forest–savanna boundaries

551 separated by continent and land use.

	No. data points	Mean duration (years)	Mean starting year	Mean change in woody cover (%)	Mean rate of change (% year^{-1})	Mean initial woody cover (%) or % forest cover
African forest–savanna	**5**	**34**	**1962**	**8.5**	**0.3**	**14.3**
African savanna	**68**	**68**	**1948**	**10.8**	**0.25**	**20.1**
Subsistence grazing land (communal)	25	62	1941	10.6	0.13	20.4
Conservation (without elephants)	6	46	1953	16.5	0.4	23.4
Conservation (with elephants)	19	33	1962	3.2	0.3	33.6
Grazing	17	58.4	1941	17.2	0.3	13.1
Australian forest–savanna	**72**	**42**	**1961**	**27.3**	**0.7**	**Not reported**
Australian savanna	**18**	**45**	**1951**	**4.7**	**0.1**	**20.3**
Conservation	1	40	1964	4.9	0.1	62.7
Grazing	17	45	1951	4.7	0.1	17.0
S. American forest–savanna	**5**	**10**	**2002**	**7.5**	**1.04**	**59.8**
S. American savanna	**19**	**18**	**1984**	**16.3**	**0.74**	**42.4**
Conservation	10	13	1994	4.8	0.43	60.3
Grazed	9	23	1973	29.2	1.1	20.0

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560　**Table 2a**: Best models (where ΔAICc <2) assessing the relationship between variables and the annual

561　rate of woody cover increase (% yr^{-1}). Models are ranked based on differences in the corrected

562　Akaike's Information Criterion (ΔAICc). K is the number of estimated parameters, Akaike weight

563　(AICcWt) is the weight of each model. AC = annual rate of change; CONT = continent; SY= starting year,

564　IC = initial cover; T = duration; MAP = mean annual precipitation.

Model	K	ΔAICc	AIC$_c$ Wt	% deviance explained
AC ~ CONT +MAP+SY+ IC + IC:CONT	9	0.00	0.51	17.7
AC ~ CONT+MAP+IC+IC:CONT	8	0.67	0.36	18.32

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566　**Table 2b** .Final parameter estimates (β), standard errors (SE) and confidence intervals of model

567　averaging based on top models (see Table 2). Significant parameters i.e. where confidence intervals

568　do not overlap zero, are show in bold. SY = Starting year, AC = annual rate of change; CONT = continent;

569　IC = initial cover; MAP = mean annual precipitation.

Predictors	β	Lower CI (2.5%)	Upper CI (97.5%)	SE
Intercept	-5.1246	-16.6910	6.4417	5.8590
SY	0.0027	-0.0007	0.0099	0.0030
IC	0.0035	-0.0021	0.0091	0.0028
MAP	0.0004	0.0000	0.0008	0.2639
CONT (Aus)	-0.2190	-0.7443	0.3064	0.3122
CONT (S Am)	**0.8764**	**0.2549**	**1.4978**	**0.0002**
CONT (Aus): IC	-0.0032	-0.0135	0.0070	0.0051
CONT (S Am):IC	**-0.0182**	**-0.0286**	**-0.0079**	**0.0052**

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574 **Table 3** .Final parameter estimates (β) and standard errors (SE) from a GLM performed separately for

575 each continent. Significant parameters are in bold.

	Africa	Australia	South America
Intercept	**-12.83/5.930**	-1.703/2.483	23.97/20.42
Start Year	**0.006/0.003**	0.0009/0.0013	-0.0113/0.011
Start cover	--0.0004/0.0002	-0.0009/0.0005	**-0.0132/0.0056**
MAP	-0.000/0.0001	0.0000/0.0001	0.0000/0.0012

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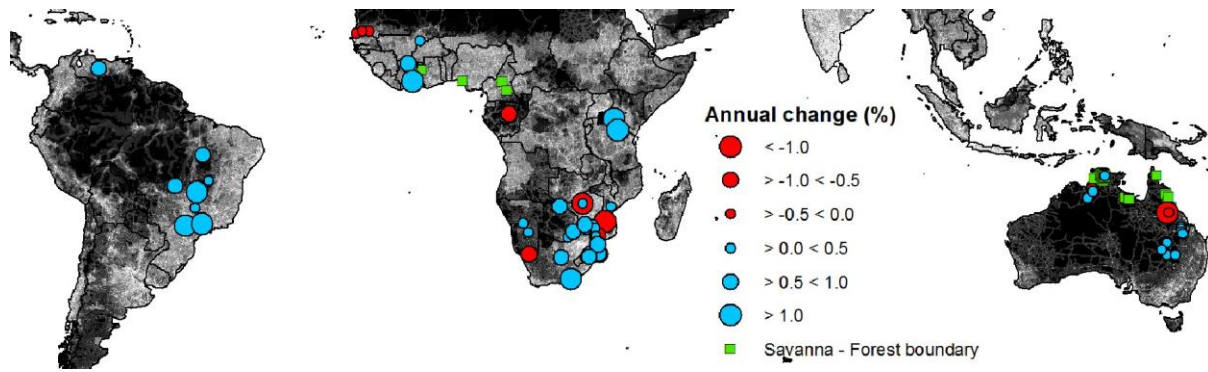586

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Figure 1: Sites with reported change in woody cover in tropical C4 grassy ecosystems. Blue circles indicate savanna woody encroachment. Red circles indicate a decline in savanna woody cover. The size of the circle reflects the magnitude of the rate of change in woody cover relative to the duration of the study. Green squares indicate locations where forest expansion into savannas has been reported. Due to the variability in the methods of measurement for change in forest–savanna boundaries, we only denote change without showing the magnitude of change. The background map shading represents the human impact index (HII), where darker shading represents less intervention in the landscape, and lighter shading a higher human impact. The scores provided by the HII range from 0 to 100, and combines socio-economic, roads, land tenure and data on land transformation (Sanderson *et al.*, 2002). Due to the nature of the symbols not all symbols are visible (e.g. forest-savanna boundary change in South America). Please see published database for all records (Appendix S1 & S2).

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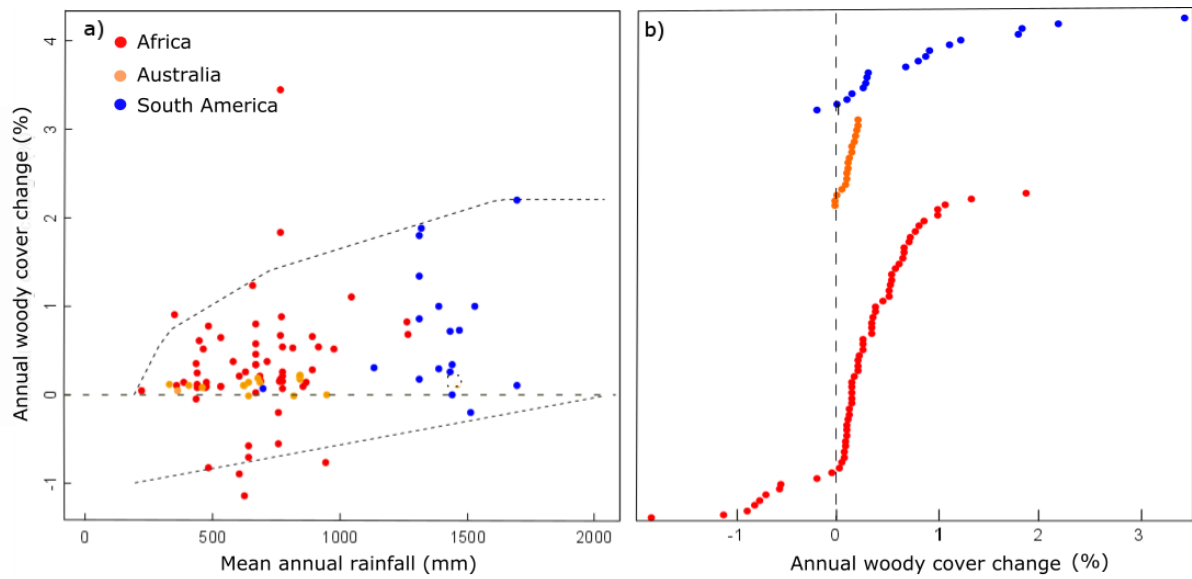
Figure 2a: Annual rate of woody cover change plotted against mean annual rainfall. Upper and lower

dashed lines represent the 5_{th} and 95_{th} percentiles. Positive values indicate woody cover increases

whilst negative values indicate decreases **b)** Annual rate of woody cover change for each site, shown

in rank order. Points are separated by continent in Africa (red), Australia (orange) and South America

(blue).The dashed vertical line marks the divide between increases and decreases.