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

2 Running head: Global savanna encroachment

3

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5

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14

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16 land use change, N-fixation, allometry, deciduousness.

17 To be considered for: Primary research articles

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<sub>2</sub>, 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

## 34 **Introduction**

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<sub>2</sub> concentration, henceforth denoted as [CO<sub>2</sub>]. Rising [CO<sub>2</sub>] affects plant growth and  
45 vegetation both directly, and indirectly via [CO<sub>2</sub>]-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<sub>2</sub>] 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<sub>2</sub>] 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<sub>2</sub>]. Combinations of local (e.g. land use), regional  
67 (e.g. changing temperature, rainfall, evaporative demands) and global drivers (e.g. rising [CO<sub>2</sub>]) 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<sub>2</sub>] 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<sub>2</sub>] 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<sub>2</sub>]). However, there are remarkably few experimental  
81 data examining the effect of increased [CO<sub>2</sub>] 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 (Pineiro, 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 (Guldmond & 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<sub>2</sub>]) 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  $\Delta AICc < 2$  are considered well supported, we used model averaging on the models with a  $\Delta AICc < 2$ .  
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<sub>2</sub>] 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 (Guldmond & 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<sub>2</sub>],  
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<sub>2</sub>], 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 al.*  
325 *et al.*, 2014) and could buffer encroachment in landscape that has densities of less than 1 person per  
326 km<sup>2</sup>(Australian Bureau 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<sub>2</sub>]  
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<sub>2</sub>] (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<sub>2</sub>]  
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<sub>2</sub>] 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<sub>2</sub>] 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<sup>2</sup> (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.

384

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389 **Author contributions**

390 NS and CL conceived the study, analysed the data and wrote the paper. NS, CL, GD and BM compiled  
391 the data, and GD and BM provided comments on a draft of the manuscript.

392

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550 **Table 1:** Summary of woody cover change studies across savannas and forest–savanna boundaries  
 551 separated by continent and land use.

	<b>No. data points</b>	<b>Mean duration (years)</b>	<b>Mean starting year</b>	<b>Mean change in woody cover (%)</b>	<b>Mean rate of change (% year<sup>-1</sup>)</b>	<b>Mean initial woody cover (%) or % forest cover</b>
<b>African forest–savanna</b>	<b>5</b>	<b>34</b>	<b>1962</b>	<b>8.5</b>	<b>0.3</b>	<b>14.3</b>
<b>African savanna</b>	<b>68</b>	<b>68</b>	<b>1948</b>	<b>10.8</b>	<b>0.25</b>	<b>20.1</b>
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
<b>Australian forest– savanna</b>	<b>72</b>	<b>42</b>	<b>1961</b>	<b>27.3</b>	<b>0.7</b>	<b>Not reported</b>
<b>Australian savanna</b>	<b>18</b>	<b>45</b>	<b>1951</b>	<b>4.7</b>	<b>0.1</b>	<b>20.3</b>
Conservation	1	40	1964	4.9	0.1	62.7
Grazing	17	45	1951	4.7	0.1	17.0
<b>S. American forest– savanna</b>	<b>5</b>	<b>10</b>	<b>2002</b>	<b>7.5</b>	<b>1.04</b>	<b>59.8</b>
<b>S. American savanna</b>	<b>19</b>	<b>18</b>	<b>1984</b>	<b>16.3</b>	<b>0.74</b>	<b>42.4</b>
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  $\Delta AIC_c < 2$ ) assessing the relationship between variables and the annual  
 561 rate of woody cover increase (% yr<sup>-1</sup>). Models are ranked based on differences in the corrected  
 562 Akaike's Information Criterion ( $\Delta AIC_c$ ). K is the number of estimated parameters, Akaike weight  
 563 ( $AIC_c Wt$ ) 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	$\Delta AIC_c$	$AIC_c Wt$	% 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 ( $\beta$ ), 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	$\beta$	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
<b>CONT (S Am)</b>	<b>0.8764</b>	<b>0.2549</b>	<b>1.4978</b>	<b>0.0002</b>
CONT (Aus): IC	-0.0032	-0.0135	0.0070	0.0051
<b>CONT (S Am):IC</b>	<b>-0.0182</b>	<b>-0.0286</b>	<b>-0.0079</b>	<b>0.0052</b>

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574 **Table 3** .Final parameter estimates ( $\beta$ ) and standard errors (SE) from a GLM performed separately for  
575 each continent. Significant parameters are in bold.

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

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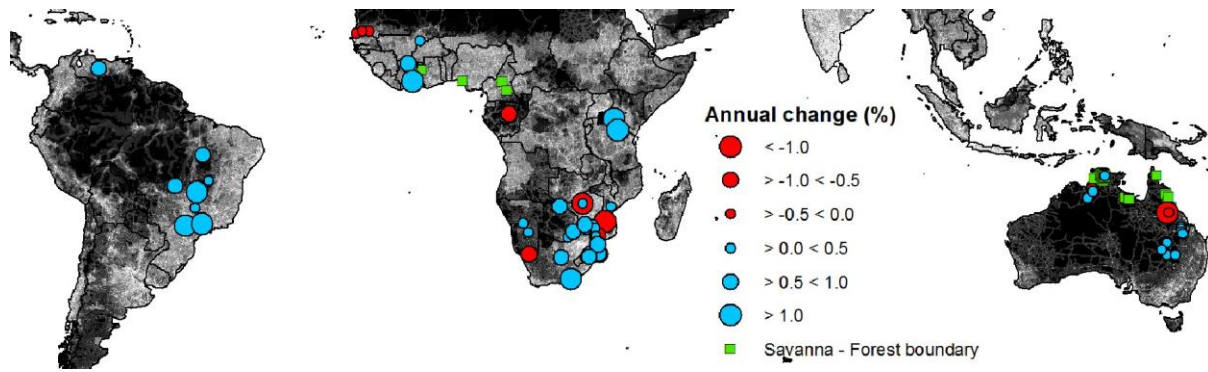
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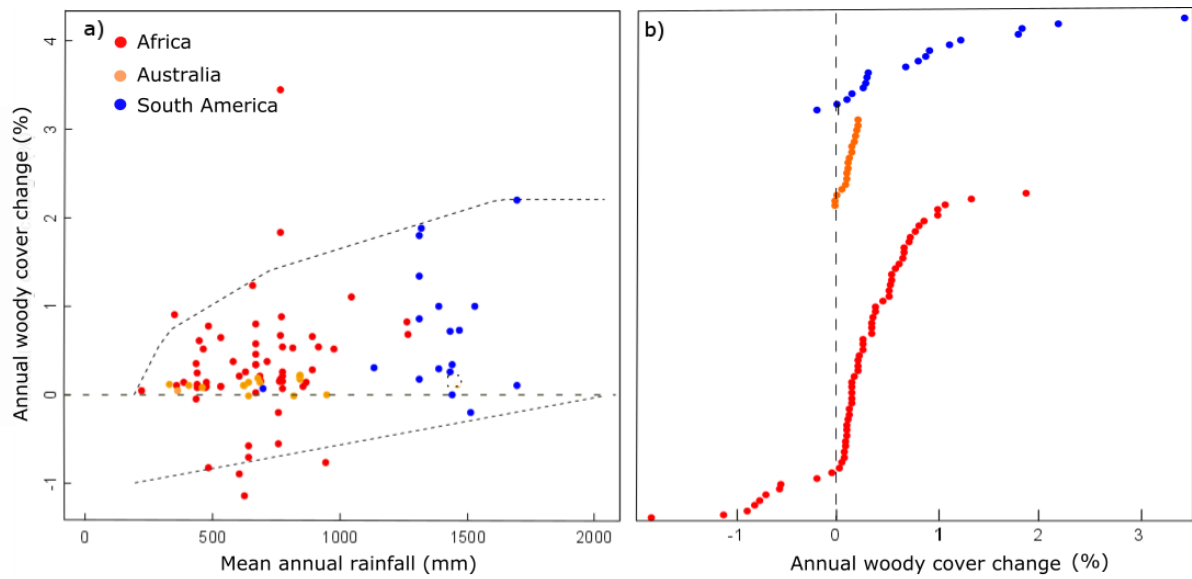
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592 **Figure 1:** Sites with reported change in woody cover in tropical C4 grassy ecosystems. Blue circles  
 593 indicate savanna woody encroachment. Red circles indicate a decline in savanna woody cover. The  
 594 size of the circle reflects the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



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605 **Figure 2a:** Annual rate of woody cover change plotted against mean annual rainfall. Upper and lower  
 606 dashed lines represent the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Positive values indicate woody cover increases  
 607 whilst negative values indicate decreases **b)** Annual rate of woody cover change for each site, shown  
 608 in rank order. Points are separated by continent in Africa (red), Australia (orange) and South America  
 609 (blue). The dashed vertical line marks the divide between increases and decreases.