



Charles Darwin University

Savanna woody encroachment is widespread across three continents

Stevens, Nicola; Lehmann, Caroline E R; Murphy, Brett P.; Durigan, Giselda

Published in:
Global Change Biology

DOI:
[10.1111/gcb.13409](https://doi.org/10.1111/gcb.13409)

Published: 01/01/2017

Document Version
Peer reviewed version

[Link to publication](#)

Citation for published version (APA):

Stevens, N., Lehmann, C. E. R., Murphy, B. P., & Durigan, G. (2017). Savanna woody encroachment is widespread across three continents. *Global Change Biology*, 23(1), 235-244. <https://doi.org/10.1111/gcb.13409>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

"This is the peer reviewed version of the following article: Stevens, N. , Lehmann, C. E., Murphy, B. P. and Durigan, G. (2017), Savanna woody encroachment is widespread across three continents. *Glob Change Biol*, 23: 235-244. doi:10.1111/gcb.13409, which has been published in final form at <https://doi.org/10.1111/gcb.13409> . This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions."

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

2 Running head: Global savanna encroachment

3

4 Nicola Stevens^{1,2*}, Caroline E.R. Lehmann³, Brett P. Murphy⁴ and Giselda Durigan⁵

5

6 1 South African Environmental Observation Network (SAEON), Fynbos Node, Cape Town, South Africa.

7 2 University of Stellenbosch, Department of Botany and Zoology, Private Bag X1, Matieland, 7602,

8 Stellenbosch, South Africa. nicolastvns@gmail.com. Tel:+27 21 808 3236; Fax: +27 21 808 2405

9 3 School of GeoSciences, University of Edinburgh, Edinburgh EH9 3FF, United Kingdom

10 4 Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin NT 0909,

11 Australia

12 5 Floresta Estadual de Assis, Instituto Florestal, 19807-270 Assis, SP, Brasil

13 * *Corresponding author*

14

15 Keywords: Woody encroachment; woody vegetation change; CO₂; forest expansion; fire suppression,

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 CO₂, 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 CO₂ concentration, henceforth denoted as [CO₂]. Rising [CO₂] affects plant growth and
45 vegetation both directly, and indirectly via [CO₂]-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 [CO₂] 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 [CO₂] 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 [CO₂]. Combinations of local (e.g. land use), regional
67 (e.g. changing temperature, rainfall, evaporative demands) and global drivers (e.g. rising [CO₂]) 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 [CO₂] 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 [CO₂] 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 [CO₂]). However, there are remarkably few experimental
81 data examining the effect of increased [CO₂] 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. [CO₂]) 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 [CO₂] 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 [CO₂],
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 [CO₂], 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 km²(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 [CO₂]
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 [CO₂] (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 [CO₂]
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 [CO₂] 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 [CO₂] 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 km² (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

385 **Acknowledgements**

386 BM was supported by a grant from the Australian Research Council (DE130100434). GD thanks the
387 Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq, for the productivity grant
388 (≠303402/2012-1).

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

393 **References**

- 394 Anadon JD, Sala OE, Maestre FT (2014) Climate change will increase savannas at the expense of
395 forests and treeless vegetation in tropical and subtropical Americas. *Journal of Ecology*, **102**,
396 1363–1373.
- 397 Angassa A, Baars RM (2000) Ecological condition of encroached and non-encroached rangelands in
398 Borana, Ethiopia. *African Journal of Ecology*, **38**, 321–328.
- 399 Archibald S, Lehmann CE, Gómez-Dans JL, Bradstock RA (2013) Defining pyromes and global
400 syndromes of fire regimes. *Proceedings of the National Academy of Sciences*, **110**, 6442–
401 6447.
- 402 Australian Bureau of Statistics (2012) Year Book Australia. *Year Book Australia*, 2012.
- 403 Banks DI, Griffin NJ, Shackleton CM, Shackleton SE, Mavrandonis JM (1996) Wood supply and
404 demand around two rural settlements in a semi-arid savanna, South Africa. *Biomass and
405 Bioenergy*, **11**, 319–331.

406 Bergengren JC, Waliser DE, Yung YL (2011) Ecological sensitivity: a biospheric view of climate change.
407 *Climatic Change*, **107**, 433–457.

408 Berthrong ST, Plneiro G, Jobbágy EG, Jackson RB (2012) Soil C and N changes with afforestation of
409 grasslands across gradients of precipitation and plantation age. *Ecological Applications*, **22**,
410 76–86.

411 Bond WJ, Midgley GF (2000) A proposed CO₂-controlled mechanism of woody plant invasion in
412 grasslands and savannas. *Global Change Biology*, **6**, 865–869.

413 Bond WJ, Midgley GF (2012) Carbon dioxide and the uneasy interactions of trees and savannah
414 grasses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 601–612.

415 Bowman D, Prior LD (2005) TURNER REVIEW No. 10. Why do evergreen trees dominate the
416 Australian seasonal tropics? *Australian Journal of Botany*, **53**, 379–399.

417 Buitenwerf R, Bond WJ, Stevens N, Trollope WSW (2012) Increased tree densities in South African
418 savannas:> 50 years of data suggests CO₂ as a driver. *Global Change Biology*, **18**, 675–684.

419 Buitenwerf R, Rose L, Higgins SI (2015) Three decades of multi-dimensional change in global leaf
420 phenology. *Nature Climate Change*.

421 Chidumayo EN (2001) Climate and phenology of savanna vegetation in southern Africa. *Journal of*
422 *Vegetation Science*, 347–354.

423 Dantas V de L, Pausas JG (2013) The lanky and the corky: fire-escape strategies in savanna woody
424 species. *Journal of Ecology*, **101**, 1265–1272.

425 Donohue RJ, Roderick ML, McVicar TR, Farquhar GD (2013) Impact of CO₂ fertilization on maximum
426 foliage cover across the globe's warm, arid environments. *Geophysical Research Letters*, **40**,
427 3031–3035.

428 Durigan G, De Siqueira MF, Franco G, Bridgewater S, Ratter JA (2003) The vegetation of priority areas
429 for cerrado conservation in São Paulo State, Brazil. *Edinburgh Journal of Botany*, **60**, 217–
430 241.

431 Grace J, José JS, Meir P, Miranda HS, Montes RA (2006) Productivity and carbon fluxes of tropical
432 savannas. *Journal of Biogeography*, **33**, 387–400.

433 Gray EF, Bond WJ (2013) Will woody plant encroachment impact the visitor experience and economy
434 of conservation areas? *Koedoe*, **55**, 00–00.

435 Guldemond R, Aarde R (2008) A Meta-Analysis of the Impact of African Elephants on Savanna
436 Vegetation. *The Journal of Wildlife Management*, **72**, 892–899.

437 Higgins SI, Scheiter S (2012) Atmospheric CO₂ forces abrupt vegetation shifts locally, but not
438 globally. *Nature*, **488**, 209–212.

439 Higgins SI, Shackleton CM, Robinson ER (1999) Changes in woody community structure and
440 composition under contrasting landuse systems in a semi-arid savanna, South Africa.
441 *Journal of Biogeography*, **26**, 619–627.

442 Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate
443 surfaces for global land areas. *International journal of climatology*, **25**, 1965–1978.

444 Hoffmann WA, Bazzaz FA, Chatterton NJ, Harrison PA, Jackson RB (2000) Elevated CO₂ enhances
445 resprouting of a tropical savanna tree. *Oecologia*, **123**, 312–317.

446 Jolly WM, Nemani R, Running SW (2005) A generalized, bioclimatic index to predict foliar phenology
447 in response to climate. *Global Change Biology*, **11**, 619–632.

448 Kgope BS, Bond WJ, Midgley GF (2010) Growth responses of African savanna trees implicate
449 atmospheric [CO₂] as a driver of past and current changes in savanna tree cover. *Austral
450 Ecology*, **35**, 451–463.

451 Klink CA, Machado RB (2005) Conservation of the Brazilian cerrado. *Conservation biology*, **19**, 707–
452 713.

453 Lamprey RH, Reid RS (2004) Expansion of human settlement in Kenya's Maasai Mara: what future for
454 pastoralism and wildlife? *Journal of Biogeography*, **31**, 997–1032.

455 Leakey AD, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, Ort DR (2009) Elevated CO₂ effects on
456 plant carbon, nitrogen, and water relations: six important lessons from FACE. *Journal of*
457 *Experimental Botany*, **60**, 2859–2876.

458 Lehmann CE, Prior LD, Bowman DM (2009) Decadal dynamics of tree cover in an Australian tropical
459 savanna. *Austral Ecology*, **34**, 601–612.

460 Lehmann CE, Sally A. Archibald, Hoffmann WA, Bond WJ (2011) Deciphering the distribution of the
461 savanna biome. *New Phytologist*, **191**, 197–209.

462 Lehmann CE, Anderson TM, Sankaran M et al. (2014) Savanna vegetation-fire-climate relationships
463 differ among continents. *Science*, **343**, 548–552.

464 Liu YY, van Dijk AI, de Jeu RA, Canadell JG, McCabe MF, Evans JP, Wang G (2015) Recent reversal in
465 loss of global terrestrial biomass. *Nature Climate Change*.

466 Mapaure IN, Campbell BM (2002) Changes in miombo woodland cover in and around Sengwa
467 Wildlife Research Area, Zimbabwe, in relation to elephants and fire. *African Journal of*
468 *Ecology*, **40**, 212–219.

469 McAlpine CA, Etter A, Fearnside PM, Seabrook L, Laurance WF (2009) Increasing world consumption
470 of beef as a driver of regional and global change: A call for policy action based on evidence
471 from Queensland (Australia), Colombia and Brazil. *Global Environmental Change*, **19**, 21–33.

472 Moncrieff GR, Lehmann CER, Schnitzler J et al. (2014) Contrasting architecture of key African and
473 Australian savanna tree taxa drives intercontinental structural divergence. *Global Ecology*
474 *and Biogeography*, n/a–n/a.

475 Murphy BP, Lehmann CE, Russell-Smith J, Lawes MJ (2014) Fire regimes and woody biomass
476 dynamics in Australian savannas. *Journal of Biogeography*, **41**, 133–144.

477 Myers-Smith IH, Forbes BC, Wilmking M et al. (2011) Shrub expansion in tundra ecosystems:
478 dynamics, impacts and research priorities. *Environmental Research Letters*, **6**, 045509.

479 O'Connor TG, Puttick JR, Hoffman MT (2014) Bush encroachment in southern Africa: changes and
480 causes. *African Journal of Range & Forage Science*, **31**, 67–88.

481 Owen-Smith RN (1992) *Megaherbivores: the influence of very large body size on ecology*. Cambridge
482 university press.

483 Parr CL, Gray EF, Bond WJ (2012) Cascading biodiversity and functional consequences of a global
484 change-induced biome switch. *Diversity and Distributions*, **18**, 493–503.

485 Parr CL, Lehmann CE, Bond WJ, Hoffmann WA, Andersen AN (2014) Tropical grassy biomes:
486 misunderstood, neglected, and under threat. *Trends in ecology & evolution*, **29**, 205–213.

487 Pienaar B, Thompson DI, Erasmus BF, Hill TR, Witkowski ET (2015) Evidence for climate-induced
488 range shift in *Brachystegia* (miombo) woodland. *South African Journal of Science*, **111**, 1–9.

489 Pinheiro E da S (2008) *Análises ecológicas e sensoriamento remoto aplicados à estimativa de*
490 *fitomassa de Cerrado na estação ecológica de Assis, SP*. Universidade de São Paulo.

491 Polley HW, Mayeux HS, Johnson HB, Tischler CR (1997) Viewpoint: Atmospheric CO₂, soil water, and
492 shrub/grass ratios on rangelands. *Journal of Range Management*, 278–284.

493 Poulter B, Frank D, Ciais P et al. (2014) Contribution of semi-arid ecosystems to interannual
494 variability of the global carbon cycle. *Nature*, **509**, 600–603.

495 Ramankutty N, Foley JA (1999) Estimating historical changes in global land cover: Croplands from
496 1700 to 1992. *Global biogeochemical cycles*, **13**, 997–1027.

497 Ratajczak Z, Nippert JB, Collins SL (2012) Woody encroachment decreases diversity across North
498 American grasslands and savannas. *Ecology*, **93**, 697–703.

499 Ratnam J, Bond WJ, Fensham RJ et al. (2011) When is a “forest” a savanna, and why does it matter?
500 *Global Ecology and Biogeography*, **20**, 653–660.

501 Rogers A, Ainsworth EA, Leakey AD (2009a) Will elevated carbon dioxide concentration amplify the
502 benefits of nitrogen fixation in legumes? *Plant Physiology*, **151**, 1009–1016.

503 Rogers A, Ainsworth EA, Leakey AD (2009b) Will elevated carbon dioxide concentration amplify the
504 benefits of nitrogen fixation in legumes? *Plant Physiology*, **151**, 1009–1016.

505 Roques KG, O'connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African
506 savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of*
507 *Applied Ecology*, **38**, 268–280.

508 Ryan CM, Berry NJ, Joshi N (2014) Quantifying the causes of deforestation and degradation and
509 creating transparent REDD+ baselines: a method and case study from central Mozambique.
510 *Applied Geography*, **53**, 45–54.

511 Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The Human
512 Footprint and the Last of the Wild The human footprint is a global map of human influence
513 on the land surface, which suggests that human beings are stewards of nature, whether we
514 like it or not. *BioScience*, **52**, 891–904.

515 Sankaran M, Hanan NP, Scholes RJ et al. (2005) Determinants of woody cover in African savannas.
516 *Nature*, **438**, 846–849.

517 Scholes RJ (2009) Syndromes of dryland degradation in southern Africa. *African Journal of Range &*
518 *Forage Science*, **26**, 113–125.

519 Silva LC, Sternberg L, Haridasan M, Hoffmann WA, MIRALLES-WILHELM F, Franco AC (2008)
520 Expansion of gallery forests into central Brazilian savannas. *Global Change Biology*, **14**,
521 2108–2118.

522 Sprent JI, Platzmann J (2001) *Nodulation in legumes*. Royal Botanic Gardens Kew.

523 Staver AC, Archibald S, Levin SA (2011) The global extent and determinants of savanna and forest as
524 alternative biome states. *Science*, **334**, 230–232.

525 Stevens N, Archibald SA, Nickless A, Swemmer A, Scholes RJ (2015) Evidence for facultative
526 deciduousness in *Colophospermum mopane* in semi-arid African savannas. *Austral Ecology*.

527 Stokes C, Ash A, Tibbett M, Holtum J (2005) OzFACE: the Australian savanna free air CO₂ enrichment
528 facility and its relevance to carbon-cycling issues in a tropical savanna. *Australian Journal of*
529 *Botany*, **53**, 677–687.

530 Wigley BJ, Bond WJ, Hoffman M (2010) Thicket expansion in a South African savanna under
531 divergent land use: local vs. global drivers? *Global Change Biology*, **16**, 964–976.

532 Zelazowski P, Malhi Y, Huntingford C, Sitch S, Fisher JB (2011) Changes in the potential distribution of
533 humid tropical forests on a warmer planet. *Philosophical Transactions of the Royal Society of*
534 *London A: Mathematical, Physical and Engineering Sciences*, **369**, 137–160.

535

536

537

538

539

540

541

542

543

544

545

546

547

548

549

550 **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

552

553

554

555

556

557

558

559

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⁻¹). Models are ranked based on differences in the corrected
 562 Akaike's Information Criterion (ΔAIC_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	ΔAIC_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

565

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

570

571

572

573

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

576

577

578

579

580

581

582

583

584

585

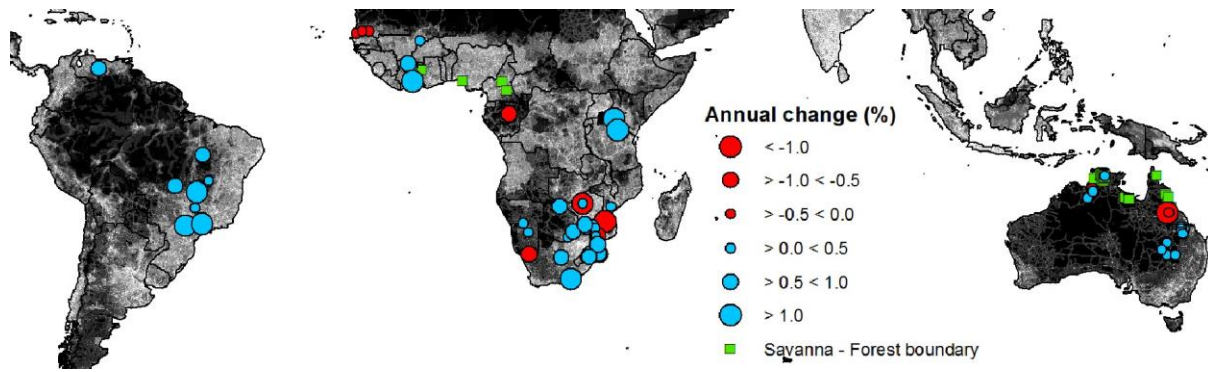
586

587

588

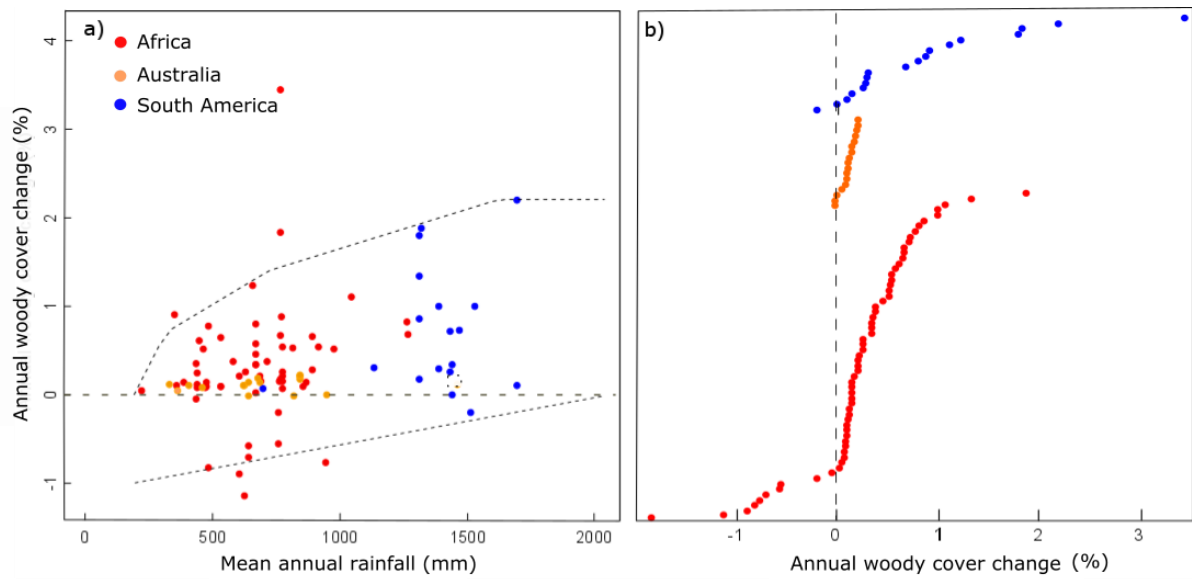
589

590



591

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).



604

605 **Figure 2a:** Annual rate of woody cover change plotted against mean annual rainfall. Upper and lower
 606 dashed lines represent the 5th and 95th 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.