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The effect of fire on tree-grass coexistence in savannas: a simulation study

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1 **The effect of fire on tree-grass coexistence in savannas:**
2 **a simulation study**

3

4 Running head: **Fire effects on tree-grass coexistence in savannas**

5

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22 **Additional keywords:** tree to grass ratio; wildfires; African biome distribution; LPJ-GUESS;

23 dynamic vegetation models; demographic bottleneck hypothesis

24

25

26

27

28 **ABSTRACT**

29 The savanna biome has the highest amount of burned area globally. While the global distribution of
30 most biomes can be predicted successfully from climatic variables, savannas are an exception.

31 Attempts to dynamically model the distribution of savannas, including a realistically varying tree to
32 grass ratio are fraught with difficulties. In a simulation study using the dynamic vegetation model LPJ-
33 GUESS we investigate the effect of fire on the tree-grass ratios as well as the biome distribution on the
34 African continent. We performed simulations at three spatial scales: locally, at four sites inside Kruger
35 National Park (SA); regionally, along a precipitation gradient; and for the African continent.

36 We evaluated the model using results of a fire experiment and found that the model underestimates the
37 effect of fires on tree cover partially.

38 On regional scale, high frequencies were able to prevent trees from out-competing grasses in mesic
39 regions between ca. 700 to 900 mm MAP. Across the African continent incorporation of fire improved
40 notably the simulated distribution of the savanna biome. Our model results confirm the role of fire in
41 determining savanna distributions, a notion that has been challenged by competing theories of tree-
42 grass coexistence.

43

44 **Abstract for TOC (50 words for a more general audience)**

45 A dynamic vegetation model is used to assess the effect of fire on tree to grass ratios and the African
46 savanna biome distribution. High fire frequencies were found to maintain tree grass co-existence under
47 mesic conditions (700 to 900 mm MAP) and the incorporation of fire substantially improved
48 continental simulations of biomes.

49 **INTRODUCTION**

50 Savannas cover about one eighth of the global land surface (Scholes and Archer 1997) and have
51 important functions for terrestrial carbon cycling (Grace *et al.* 2006), biodiversity, and food production
52 (Hirota *et al.* 2011). On the African continent, 90 percent of the population are estimated to depend on
53 rain-fed crop production and pastoralism within the savanna biome to meet its basic food supplies
54 (Patt *et al.* 2007).

55 Given its importance for supply of numerous ecosystem services, the projection of the distribution of
56 the savanna biome, as well as related properties such as standing biomass are of high interest (Scheiter
57 and Higgins 2009), especially when considering that climate simulations for the next century project
58 pronounced changes to the spatiotemporal distribution of precipitation across the African continent
59 (Schreck and Semazzi 2004; Boko *et al.* 2007). Simulations of vegetation distribution and carbon
60 stocks are done using dynamic vegetation models (DVMs) for both current as well as projected
61 climate. However, most DVMs (Bonan *et al.* 2003; Hickler *et al.* 2006) are known to only poorly
62 represent processes in tree-grass systems, including resource competition and interactions with fire
63 (Scheiter and Higgins 2009). This leads to poor performance in simulating the contemporary
64 distribution and structure of the savanna biome in some DVM studies, which casts doubts on the
65 ability to accurately simulate the vegetation and carbon cycle response to future climate change in the
66 tropics.

67 Savannas are characterized by the co-dominance of the two life forms trees and grasses, although large
68 savanna regions are located within a climate space warm and wet enough to support closed forests
69 (Bond 2008). While Bond and Keeley (2005) concluded that this mismatch between actual and
70 (climatically) potential vegetation could be explained by fire, the co-existence of trees and grasses has
71 also been hypothesised from a number of alternative mechanisms (for a review see: Sankaran *et al.*
72 2004; Murphy and Bowman 2012). These can be broadly separated into competition-based and
73 demographic hypotheses. The first suite proposes a classic niche separation, resulting in co-existence
74 by differences in resource acquisition. Niche separation can, for example, be achieved by differences
75 in rooting depths (the so-called 'rooting niche model', Walter 1971) and according to this theory the
76 co-existence of trees and grasses is maintained independent of disturbances. Here trees and grasses

77 compete for water in the first soil layer where grasses outcompete trees. Trees are able to persist in the
78 system because of exclusive access to deeper water (Sankaran *et al.* 2004; but see also February and
79 Higgins 2010 who found instances where grasses also accessed deeper water).

80 The second suite of hypotheses ('demographic bottleneck models') relies on recurring disturbance
81 events to prevent trees from dominating over grasses. Grasses are considered to be favoured by fires
82 since the fires occur in the dry season when the above ground biomass of the grasses is already
83 desiccated leading to minor damage only. Contrary to the grasses, tree susceptibility to these
84 disturbances is assumed to differ depending on life-history stages. Savannas can thus be viewed as
85 transitional 'disequilibrium' systems where frequent disturbance (i.e. fire or grazing) prevents
86 reaching the stable state of tree dominance (Sankaran *et al.* 2004).

87 Apart from analyses relating vegetation and fire to each other, many studies investigated properties of
88 savanna fires (see for example Hoffmann *et al.* 2003 for the effect of fires on above ground biomass
89 and Govender *et al.* 2006 for the effect of fuel on fire intensity).

90 Definitive testing of these explanatory models can only be conducted using large field manipulation
91 experiments. But such multi-factorial experiments, comparing the effects of different mechanisms, are
92 currently lacking, although experiments have been performed testing whether a single mechanism is
93 acting (e.g. for a review of root partitioning between woody and herbaceous species see Schenk and
94 Jackson 2002).

95 Despite the attempts to explain the co-occurrence of trees and grasses in the past by single
96 mechanisms, Murphy and Bowman (2012) concluded in a review that savannas are complex systems
97 in which forest and grassland dominated vegetation can be viewed as fire mediated alternative stable
98 states. They developed a conceptual model of savanna occurrence which included fire activity, water
99 and nutrient availability and suggested that the ability of dynamic vegetation models to accurately
100 reproduce vegetation pattern should be used to validate the underlying conceptual models.

101 In this study, we aim at providing improved understanding of savanna vegetation dynamics focussing
102 at the effects of wildfires. We use a dynamic vegetation model for the African continent to assess the
103 potential effect of wildfires on the tree to grass ratio. We also investigate under which environmental
104 conditions (i.e. mean annual precipitation) wildfires are able to maintain tree grass coexistence. We

105 simulate vegetation dynamically along a precipitation gradient, vary the relative extent of the
106 investigated factor, using foliar cover as diagnostic parameter for competitive ability and evaluate the
107 performance of the model with site data from burn plots of the Kruger National Park in South Africa.
108 To see whether the incorporation of wildfires is of relevance for the biome distribution at a continental
109 scale, we simulate African potential vegetation with and without and wildfires using fire fractions
110 derived from the remotely sensed MODIS MCD45 (Roy *et al.* 2008) burned area dataset.

111 **Methods**

112 *Simulation model*

113 We used the dynamic vegetation model LPJ-GUESS (Smith *et al.* 2001; Sitch *et al.* 2003), coupled to
114 an extended version of the fire model SPITFIRE (Thonicke *et al.* 2010) with the modifications
115 described in Lehsten *et al.* (2009). LPJ-GUESS is applied as a gap-model (Smith *et al.* 2001),
116 simulating the competition of different age cohorts of a number of plant functional types (PFTs) for
117 light and water within a number of repeatedly simulated patches. Stomatal conductance which is
118 linked to photosynthesis and availability of water and light is calculated separately for each age cohort.
119 The age cohorts differ in growth characteristics as well as in their susceptibility to fire. This allows
120 simulating size-specific fire effects on vegetation since the fire effect is estimated by the ratio between
121 the flame height and the tree height, which can lead to a dynamic, fire-dependent age distribution of
122 trees. Fire effects on vegetation also depend on the susceptibility of the plant type to fire and on the
123 fireline intensity.

124 Fireline intensity is calculated based on the equation developed by Byram (1959) which
125 multiplies the caloric heat content (reduced depending on the fuel moisture), the weight of the
126 fuel consumed and the rate of spread (which depends on the wind speed reduced by the
127 roughness of the vegetation following the equations by Rothermel (1972)). These fire
128 equations are in use in a large number of contemporary fire behavior models. Flame height is
129 calculated following Peterson and Ryan (1986) as the product of a plant functional type
130 parameter multiplied with the fireline intensity to the power of 0.667. Details on this
131 calculation are given in Thonicke *et al.*(2010).

132 Fire properties are calculated depending on the fuel quality (type, moisture), fuel quantity (calculated
133 by LPJ-GUESS-SPITFIRE) and the climate (which is read in). Trees can either be damaged by the
134 fire, resulting in a loss of biomass (esp. leaves), or they can be killed. If a tree is killed by a fire, all
135 biomass which has not been burned (above and below ground) is transferred to the litter carbon pool.
136 All individuals establish from seeds, re-sprouting is not implemented in the model. For each simulated
137 grid cell a number of replicate patches are simulated (see below) and the results are averaged to
138 account for stochastic effects of senescence and establishment or fire events. Re-establishment of trees
139 can occur once per year and depends only on the amount of light reaching the ground.
140 For the simulation experiments performed in this study we additionally include a modified water
141 uptake routine for trees which scales root water uptake exponentially with an exponent of 0.6
142 compared to the exponent of unity in the standard water uptake routine of LPJ-GUESS (Sitch *et al.*
143 2003). This increases water uptake under dry conditions, since initial runs (data not shown) have
144 shown that the standard water uptake routine as in Sitch *et al.* (2003), and Gerten *et al.* (2004)
145 underestimated tree biomass in seasonally dry areas. Grasses retain the original linear water uptake
146 scheme. All parameter settings of the plant functional types in the simulations are similar to Lehsten *et*
147 *al.* (2009), except for the additional plant functional type 'shrub'. This PFT retains all plant specific
148 parameters from the tropical broad leaved raingreen tree PFT (Sitch *et al.* 2003) but with changes in
149 two allometric parameters: the linear factor in the height – diameter relationship (Sitch *et al.*, 2003)
150 was set to one eighth of the value used for trees and the maximum crown diameter was set to 10 m²
151 (compared to 27 m² used for trees; Sitch *et al.*, 2003). These settings result in a PFT with considerably
152 lower total height and stem diameter compared to the PFT tropical broadleaved raingreen tree, but
153 retains all other characteristics such as phenology or root distribution from this PFT. This plant type
154 has a considerably higher chance of being killed by a fire, caused by its lower height, though moist
155 fuels or low fuel loads can lead to flame heights below the height of the shrub and hence allow the
156 shrub to survive a low intensity fire. Additionally to the changes mentioned above, phenology has
157 been adapted to assure that the leaves are shed in the beginning of the dry season and not at the end of
158 the calendar year as in the original LPJ-GUESS version (for details see Lehsten *et al.* 2009).
159

160 *Climate data*

161 All simulations were performed at a 1 degree grid scale applying daily values for temperature and
162 precipitation from NCEP (Kalnay *et al.* 1996) for the period 1980 to 2007 with precipitation values
163 corrected using precipitation data from TRMM (re-gridded to one degree resolution). The ratio
164 between the annual precipitations recorded by TRMM and NCEP was calculated from the period in
165 which the respective series overlapped, and this was used to correct the precipitation values from
166 NCEP for the whole time span (for details on data generation see Weber *et al.*, 2009). Model spin up
167 (i.e. simulation time to allow stabilising the carbon pools and vegetation) was performed for a period
168 of 1000 years repeating the available 27 years of climate data, at a constant atmospheric CO₂
169 concentration of 341 ppm. Soil texture data were similar to the one used in Sitch *et al.* (2003), based
170 on the FAO dataset (FAO 1991), atmospheric CO₂ concentration in the transient simulation increased
171 up to 384 ppm according to the measurements at (www.esrl.noaa.gov/gmd/ccgg/trends/).

172

173 *Patch scale general model setup*

174 We simulated a number of replicates for each grid cell, accounting for the stochastic elements in some
175 process-descriptions in LPJ-GUESS-SPITFIRE, especially in the simulation of growth dynamics and
176 wildfires. At continental scale, 200 replicates were calculated for each simulated location (each
177 replicate is equivalent to a size of approximately 1000 m² Smith *et al.*(2001)). The number of
178 simulated patches was increased to 500 for the detailed study of changes in tree to grass ratio along the
179 latitudinal and precipitation gradient. Since we aimed to elucidate the influence of fire frequency on
180 the tree to grass ratio, the application region, chosen to follow the eastern 20 degree meridian from 5
181 to 15 degrees north, covered a transect with pronounced environmental differences. Along this
182 transect, mean annual precipitation decreases approximately linearly. Fractional cover for trees and
183 grasses was simulated in response to artificially prescribed fire return intervals.

184

185 *Patch scale simulations*

186 We artificially prescribed fire frequency along a precipitation gradient from 100 to 1400 mm annually
187 (MAP), spaced over approximately 1100 km (Fig. 1). This allows assessing the main effects of fire on

188 vegetation, without it being confounded by other factors. We prescribed a burning probability
189 corresponding to a fire return interval of 1, 2, 4, 8, 16 and ∞ years. While the average fire return
190 interval of evergreen tropical forest was estimated to be around 500 years, the fire regime in African
191 savannas may cover the full range from more than 1000 years (virtually no fire) to annual fire
192 according to Scholes *et al.* (1996). For our simulation experiment, fire is simulated to occur on
193 December 15, coinciding with the peak of the seasonal distribution of burned area in northern
194 hemisphere sub-Saharan Africa (Fig. 2) identified from MODIS MCD45A1 data (Roy, *et al.* 2008;
195 <http://modis-fire.umd.edu/MCD45A1.asp>).

196

197 *Tree cover data from experimental plots*

198 Data were collected in the Kruger National Park (KNP), South Africa between February and March
199 2010. The park is situated in the savannas of north-eastern South Africa, and covers an area of
200 $\sim 19,633 \text{ km}^2$. The vegetation in the park is mainly characterized by dense savanna dominated by
201 Acacia and Combretum species. Within the park there are long-term Experimental Burning Plots
202 (EBPs) where fire is manipulated as a treatment since more than 50 years and thus KNP is an ideal
203 environment for comparing fire effects on vegetation (Govender *et al.* 2006; Higgins *et al.* 2007).
204 Each replicate plot consists of different experimental burning treatments as well as a control treatment
205 (no fire) and each treatment is implemented in a 7-ha plot in a split-plot randomized design (see Fig.
206 2a in Moustakas 2015). The burning treatments include several experiments manipulating fire return
207 interval (burning every 1, 2, 3, 4, and 6 year) as well as fire seasonality. We have used annual burning
208 every August which is the dry season and the control treatment that excludes fire. We have decided
209 against using the 3, 4, and 6 year burning treatments since we were not able to obtain tree cover
210 estimates for the 4 year burning and our simulations did not contain burning every 3 or every 6 years.
211 Tree cover data were collected in 2009 at the sites: Mopani (496 mm MAP), Satara (544 mm MAP),
212 Skukuza (550 mm MAP) and Pretoriuskop (737mm MAP). The fractional tree cover was estimated
213 using the Kendall-Moran algorithm (KM2P; Kendal and Moran 1963). The KM2P algorithm estimates
214 tree cover based upon the distance to the second nearest neighbours of each tree. The KM2P was
215 ranked amongst the best estimating methods of plant cover when sample size was around 25 focal

216 trees (White *et al.* 2008) which was the case in each plot. These data were not intended to be used as a
217 quantitative model evaluation at site scale, but as a visualisation of how well the model performs
218 compared to site data. The reasons why we did not perform a proper model evaluation are that this
219 would have required site specific climate data over several decades to configure its spin-up and
220 transient simulations which were not available.

221

222 *Continental scale simulations*

223 We simulated vegetation at the African continent in response to presence and absence of wildfires. In
224 the first simulation, burnt area was prescribed from the MODIS burned area product MCD45A1 (Roy,
225 *et al.* 2008), which lists the fire date using 500*500m pixels, while the fire effects on vegetation were
226 dynamically calculated by LPJ-GUESS-SPITFIRE (depending on fuel load, dryness, and total height
227 and fire susceptibility of the plant type). The proportion of burned area per one-degree grid cell was
228 prescribed, using an average daily probability of burning derived from the MODIS data. This was
229 done under the assumption that MODIS pixels that could not be classified, e.g. due to cloud cover, had
230 a similar burning frequency as the remaining pixels within the one degree cell. Since the burned area is
231 likely to be underestimated by current remote sensing products (Roy, *et al.* 2008) we chose quality
232 level four which represent the highest detection rate, noting that this quality level also has highest rate
233 of commission errors (i.e. rate of areas being erroneously detected as burned). The daily varying
234 proportion of burned area was subsequently transformed into a daily varying burning probability for
235 each simulated patch. Further details on the implementation and effects of fire on the vegetation are
236 provided in Lehsten *et al.* (2009).

237

238 **Vegetation data**

239 We compared simulated vegetation distribution with and without wildfires to the map of potential
240 vegetation by Ramankutty and Foley (1999) that was derived on the basis of the 1km global satellite
241 based DISCover land cover dataset (Loveland and Belward 1997). In contrast to Ramankutty and
242 Foley (1999) who differentiated between savannas and tropical deciduous forest, we combined these
243 classes into a single class 'savanna' because both classes seem to have a similar relationship to

244 wildfires (i.e. do not differ in their typical fire frequency) which leads to a fine-scaled mixture of both
245 biomes in the southern hemisphere of Africa (Ratnam *et al.* 2011). After re-gridding the potential
246 vegetation map to a one degree scale, the distribution of savanna and tropical deciduous forest exert a
247 more or less random rather than an environmentally determined pattern. We therefore differentiate
248 only rainforest, savanna, open shrubland, dense shrubland, grassland and desert (Fig. 5).
249 The simulated mixture of plant functional types per grid-cell was converted into biome types applying
250 the classification scheme of Hickler *et al.*(2006), adopted to match the potential vegetation classes for
251 the African continent (Tab. 1). Comparison between our simulated and the mapped potential
252 vegetation of Ramankutty and Foley (1999) was performed using the Kappa statistic, developed
253 especially for the purpose of comparing vegetation maps (Monserud and Leemans 1992). Kappa
254 values range between zero and one. Values below 0.05 indicate no; 0.05 – 0.20 very poor; 0.2 –0.4
255 poor; 0.4 – 0.55 fair; 0.55 – 0.7 good; and 0.7 – 0.85 very good agreement (Monserud and Leemans
256 1992). We calculated the Kappa statistic for each vegetation class as well as a global Kappa statistic
257 combining all vegetation types.

258

259 **Results**

260

261 *Effects of fire on tree to grass ratio*

262 Prescribing fire along the precipitation gradient did not affect the dominance of trees at the wet, and
263 grasses at the dry end (Fig. 3). However, in regions between MAP of around 600 to 900 mm, fire
264 prevented trees and shrubs from out-competing grasses, but only when the prescribed fire return
265 interval was around eight years, or less. In these ‘mid-mesic’ regions, trees and grasses co-dominated
266 at variable ratios depending on fire return interval. When fire was excluded, grasses reached a
267 maximum cover of 0.4; while at frequent fire return intervals (e.g. annual fires) the maximum grass
268 cover simulated by LPJ-GUESS-SPITFIRE was up to 0.7 (Fig. 3).

269

270 *Experimental tree cover data versus simulated tree cover data*

271 To confront model outputs with observed data we plotted the tree cover percentage under annual
272 burning, biennial burning and no burning aside the field data derived from the experimental burning
273 plots from the Kruger National Park (Fig. 4). Results show that tree cover for the burned plots is
274 underestimated by the model, while at unburned plots the simulated tree cover is in the range indicated
275 by the experimental data. They also show that fire is having an clear effect on tree cover starting at ca
276 540 mm MAP (Mopani, Satara and Skukuza) while at Pretoriuskop the tree cover values are in a
277 relatively small range (though the highest value is found in the unburned plot and the lowest in the
278 annually burned plot in Pretoriuskop).

279

280 **Vegetation-fire interactions on continental scale**

281 Excluding fire in an African-continental scale simulation resulted in a notable expansion of the
282 equatorial rainforest belt towards the northern and southern direction, emergence of tropical evergreen
283 plant functional types along the continent's south-east coastal regions and across the island of
284 Madagascar (Fig. 5), compared to simulations that had fire prescribed. While the expansion of tropical
285 rainforest vegetation was at the expense of savannas, the extension and location of shrublands was
286 unaffected by the presence of fire. The Kappa-statistic for the comparison of the potential vegetation
287 of Ramankutty and Foley (1999) to our simulations (Table 2) improved notably for the 'fire present'
288 case, both for the vegetation classes 'tropical evergreen forest' and 'deciduous forest / savanna', as
289 well as for the overall total.

290

291 **Discussion**

292 The predominant factors controlling the co-existence of trees and grasses in savanna ecosystems have
293 been of longstanding interest to ecological research (for a reiview see: Sankaran *et al.* 2004; Murphy
294 and Bowman 2012). A number of hypotheses, including resources acquisition and demographic
295 bottleneck models, have been put forward to explain observed vegetation patterns in savannas but as
296 yet, no conclusive multi-factorial model that applies to all savanna environments has emerged. Our
297 simulation study aims to contribute to efforts to develop such a general model, by investigating the
298 role of wildfires in savanna vegetation dynamics.

299 A synthesis of tree cover for 854 savanna locations in Africa identified a strong effect of MAP on the
300 tree to grass ratio (Sankaran *et al.* 2005). Soil physical properties that determine the water storage
301 capacity are an additional key factor closely related to rainfall and that needs to be considered for a
302 more process-based interpretation of a relationship between canopy structure and MAP (Sankaran *et*
303 *al.* 2005). This data can be interpreted in terms of envelope functions that set an upper limit (*sensu*
304 Sankaran *et al.*, 2005) or in terms of a sigmoidal function through the bulk of the data (Bucini and
305 Hanan 2007). For both analyses it was argued that disturbance may play an important additional role
306 to determine savanna vegetation structure atop the climatic effects, although Sankaran *et al.* (2005)
307 could not detect a consistent response to herbivory. Regarding the role of soil and nutrients, in a meta-
308 analysis of several datasets examining tree-grass interactions across precipitation gradients in savannas
309 it was found that soil and plant nutrient ratios did not change along with precipitation (Dohn *et al.*
310 2013). Further, soil properties were not notably influential in determining tree-grass interactions at the
311 Kruger National Park sites where our field data were collected in the absence of fire (Moustakas *et al.*
312 2013).

313 Based on extensive empirical data, Sankaran *et al.* (2004) predicted that a sigmoidal increasing woody
314 cover with increasing MAP in the absence of fire or other disturbances should be transformed into a
315 more linear (i.e. gradual) increase of woody cover with MAP if disturbances like fire are taken into
316 account as per the ‘demographic bottleneck model’. Driving LPJ-GUESS-SPITFIRE with typically
317 observed fire frequencies of between 3 to 8 years (Tansey *et al.* 2008), our simulations resulted in a
318 fractional tree cover along the precipitation gradient that more closely resembles a linear relationship
319 between tree cover and MAP, lending further support to the ‘demographic bottleneck model’.

320 The main assumption of the ‘demographic bottleneck model’ is that different species groups and age
321 classes of trees differ in their susceptibility to disturbances such as fire. Fire mortality of mature trees
322 in savannas and tropical forests is generally determined by bark thickness, which in turn is related to
323 stem diameter and species groups (Hoffmann *et al.* 2012). The long history of fires in tropical
324 savannas has led to a variety of adaptations to fire (Bond and Keeley 2005) resulting in high resistance
325 against cambial damage of typical savanna trees, while evergreen trees are known to have a very low
326 resistance against cambial damage, resulting in a strong disadvantage in fire prone sites. However,

327 top-kill still results in a high mortality regardless of the tree type. This determines the land use practice
328 of frequent burns of at least every 2-3 years in national parks and tree plantations to minimize the risk
329 of intensive fire by preventing fuel accumulation (Saarnak 2001).

330 Rainforest trees have comparatively thinner bark compared with savannah trees. Seedlings, having low
331 stem height are most susceptible to fire damage since their crowns are located within the flame height.
332 Older, tall tropical broad-leaved raingreen trees have low direct or post-fire mortality, which depends
333 mainly on the amount of crown scorching. These fire effects are especially pronounced in the mid-
334 mesic range. At sites with high precipitation, fire intensity is very low due to the wet conditions, and
335 any effect of fires on established trees is compensated by rapid post-fire tree re-growth in our
336 simulations. By contrast, at very dry sites, establishment of trees is prevented by soil water shortage,
337 rather than by fire disturbance. At these sites, the effect of fire disturbance is already comparably low
338 due to low grass productivity and thereby low fuel loads. Recently, several empirical-based studies
339 have demonstrated that tree cover-fire feedbacks are critical for maintaining forest and savannah
340 boundaries (Sankaran *et al.* 2004; Lehmann *et al.* 2011; Hoffmann *et al.* 2012; Murphy and Bowman
341 2012). In essence, the interaction between tree growth rates and fire frequency limits forest
342 development. Hence, canopy closure will be favoured by any factor that increases growth (e.g.
343 elevated availability of water or in some cases also nutrients), or decreases fire frequency.

344 In an analysis by Scheiter and Higgins (2009) the combination of a simplified DVM with a dynamic
345 fire model that relied solely on fuel load, fuel moisture and wind speed yielded a much larger area
346 influenced by fires compared to studies based on remote sensing data. While the knowledge and
347 understanding of the drivers of fire is improving (Archibald *et al.* 2009, 2010) these drivers are
348 complex and far from well understood. Saarnak (2001) estimates the number of natural ignitions to be
349 currently below one percent. Several studies have linked fire occurrence and climatic variables (e.g.
350 Lehsten *et al.* 2010; Lehmann *et al.* 2011) demonstrating that the human decision process leading to
351 the fire application is driven at least partially by climatically determined factors. Regions differ in their
352 culture of how to apply fires. To cover these variances, a complex model of human application of fires
353 would be required which would introduce a considerable amount of additional uncertainty.

354 Hence we decided to prescribe remotely-sensed fire as an input to the LPJ-GUESS-SPITFIRE model
355 in this study, which allowed us to focus on the influence of fire on recent vegetation without
356 potentially confounding effects of simulated fire activity uncertainties.

357 When comparing the experimental data and the simulation results, local-scale heterogeneity (all plots
358 cover around 7 ha) induced by local conditions such as soils and grazing will not be covered at DVM-
359 scales. Based on the model results with annual fire frequency, Skukuza and Satara would be classified
360 as grasslands, having a woody leaf area index of below 0.5. Vegetation at the third experimental site
361 would be classified as savanna, since tropical broadleaf raingreen trees dominate in the simulations.

362 Our simulations in which annual burning led to tree cover being too low compared to experimental
363 data indicates that the post-fire survival rates of young trees is too low in the model where one year
364 old trees are not above the flame escape height and hence are killed with a high probability. At higher
365 precipitation levels, fires are less intense due to higher fuel moistures, thereby allowing more trees to
366 survive due to less intense fires (which result in lower flame height). The experimental results suggest
367 a possible improvement to the model, while for the purpose of classifying biomes at continental scale
368 this seems not to be important because an annual fire frequency is rarely detected at a spatial
369 resolution of one degree.

370 Though our simulation results were strongly improved by the incorporation of fire in the model, our
371 results (notably at the patch scale) are contradicting the result of Staver *et al.* (2011) who show that
372 fire only influences tree cover above a precipitation level of 1000mm MAP while in our simulation
373 significant effects are starting at 400mm MAP. When plotting continental scale tree cover and MAP in
374 burned and unburned conditions many other factors might be influencing the fire regime, for example
375 grazing, differences in seasonality or soil conditions. This has potentially led to the large variability in
376 the tree cover of the analysis of (Staver *et al.* 2011). Since the experimental data shows a significant
377 effect even at the lowest MAP level of 550 mm this shows that more research is needed to identify
378 how fires and vegetation are linked to other factors (e.g. grazing and soils). Another continental scale
379 analysis (Lehmann *et al.* 2011) showed that savannas are present up to precipitations well above the
380 precipitation level which prevents grasses from persisting even at high fire frequencies. The reason
381 for the underestimation of the effect of fires at high precipitations in our simulation is that we

382 use a daily average burning probability and even slight differences in the timing of the
383 seasons can lead to fires occurring at wet days which will have only limited effects on the
384 vegetation. While climate data is currently available for a century, only slightly more than a
385 decade of remotely sensed burned area has been recorded (at sufficiently high resolution).
386 Since it is necessary to use the full time series of climate data to meaningfully run LPJ-
387 GUESS-SPITFIRE we decided to transform the burned area data into a probability of burning
388 only related to the day of the year to be able to prescribe fire over the whole simulation.
389 Although not included here, effects similar to fire may also be caused by herbivory which also acts as
390 size-selective population harvesting. In the Eastern Cape region (South Africa), Trollope (1974)
391 showed experimentally that a combination of fire and grazing is required to keep the landscape open,
392 since the burned bushes suffered a severe damage of the stems, but coppiced from the base of the
393 system. Only light grazing by goats prevented a fast shrub encroachment in the area. Staver *et al.*
394 (2012) also showed that grazing and fire and herbivory can form a single trait off axis. Acacia saplings
395 showed a continuum of adaptations responding to herbivory and fire and the species occurrence
396 depended upon both. Our study aimed to show that the simulation of biome distributions are markedly
397 improved by incorporating wildfire which was achieved even without the incorporation of herbivory.
398 The incorporation of additional processes such as re-sprouting and herbivory might improve the
399 models ability to predict vegetation, especially if applied at a fine scale. Yet, it also requires the
400 parameterisation of the additional processes and in the case of the incorporation of herbivory a reliable
401 spatio-temporal dataset of grazing pressure including both wild animals as well as livestock. Such a
402 dataset is, to the knowledge of the authors, currently not available for simulations at continental scale.
403 Additional anecdotal evidence that fire is crucial to maintain an open landscape even in the presence
404 of large densities of herbivores comes from most national parks in African savannas where artificially
405 maintained burning regimes are necessary to prevent shrub encroachment and to support grass growth
406 for livestock herbivory (Saarnak 2001). Browsing densities can be considered relatively high in these
407 parks since the visibility of game for tourists is the economic basis of most parks, thus herbivory alone
408 seems not sufficient to maintain the *status quo*.

409 All simulations performed in this study include differences in phenology between trees and grasses.
410 Some models suggest that these differences alone can maintain co-existence of trees and grasses
411 ('phenological niche separation model' *verso* Sala *et al.*, 1997). However, since the simulations without
412 wildfires resulted in a poor agreement between simulated and observed biome distribution for the
413 savanna biome, we have no indication that this is the case.

414 A strong sensitivity of African biome distribution in response to fire (similarly to our study) was also
415 demonstrated by Bond *et al.* (2005) applying the Sheffield Dynamic Vegetation Model without fire
416 and comparing it to satellite derived vegetation data.

417 Still, considerable differences remain between the simulated and mapped potential vegetation in case
418 of open and dense shrublands and grasslands. These vegetation classes occur at a very narrow range of
419 low MAP, limited to a thin band along the Mediterranean, the southern and northern edge of the
420 Sahara desert, next to the Kalahari Desert, and at the horn of Africa. For these biomes, successful
421 representation by vegetation models has to rely not only on the correct representation of growth
422 processes but equally so on the availability of high resolution rainfall data and soil physical parameters
423 to match the exact geographic location. Our simulations were based on adjusted NCEP reanalysis data
424 (Kalnay *et al.*, 1996; for details see Weber *et al.*, 2009). Although this climate input data had a spatial
425 resolution of one degree, it was generated in parts from coarser resolution raw data that requires
426 spatial interpolation for the reanalysis. Visual inspection of the vegetation maps shown in Figure 4
427 indicates the presence of simulated shrublands and grasslands in regions close (but not identical) to
428 those identified by Ramankutty and Foley (1999). This spatial mismatch may, at least in parts, result
429 from imprecision in the precipitation input. The Kappa statistic only provides a measure of how many
430 cells of similar vegetation type are exactly at the same position in different maps. Similar cells in close
431 proximity are identified as mismatch, which leads to the low values for the simulated grasslands and
432 shrublands.

433 **Conclusion**

434 Through incorporation of fire into a dynamic vegetation model the simulation of the distribution of
435 biomes on the African continent was markedly improved. Our work supports data-based predictions
436 that the tree to grass ratio in tropical savannas depends strongly on the fire frequency (following the

437 ‘demographic bottleneck model’) especially in the mid-mesic climate space. Though there is abundant
438 evidence that a multitude of disturbances including grazing and climatic variability influences
439 vegetation structure, we have shown that the sole application of typical fire frequencies to drive
440 vegetation simulations was sufficient to generate realistic vegetation pattern at a continental scale.
441 Further improvement of simulation results will require higher resolved climate and soil data,
442 especially for the precise simulation of locations of grassland and shrubland biomes, as well as
443 accounting for landscape management, for example, grazing and agriculture.

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595 Table 1. Classification scheme for the simulated maps of plant functional types, adopted from Hickler
 596 *et al.* (2006), all values are maximum annual LAI values.

597

Biome	Classification	Dominant PFT
Tropical rain forest	Tree LAI >2.5	Tropical broadleaved raingreen
Savanna / trop. deciduous forest	0.5 < Tree LAI >2.5	Tropical broadleaved raingreen tree or shrub
Grassland / steppe	Tree LAI <0.5 and Grass LAI >0.2	
Dense shrubland	Shrub LAI > 1.5	Shrub
Open shrubland	Shrub LAI < 1.5	Shrub
Desert	Total LAI < 0.2	

598

599 Table 2. Kappa statistic of agreement between the simulated biomes to the biomes mapped by
600 Ramankutty and Foley (1999).

Biome	Kappa	Kappa
	without fire	with fire
Tropical rain forest	0.49	0.67
Savanna / tropical deciduous forest	0.46	0.71
Grassland / Steppe	0.15	0.15
Dense Shrubland	0.23	0.23
Open Shrubland	0.12	0.11
Desert	0.86	0.86
Total	0.53	0.64

601
602

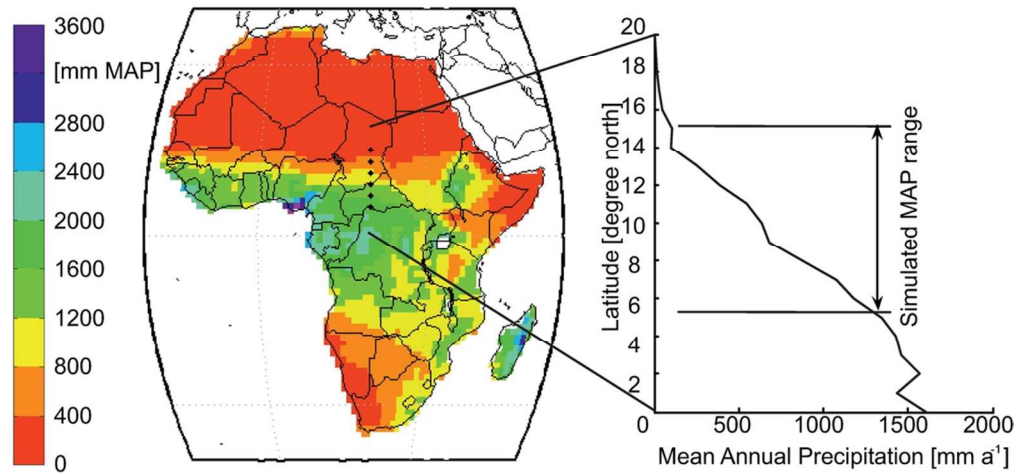


Figure 1. Continental and latitudinal mean annual precipitation.
Left panel: mean annual precipitation, derived from adjusted NCEP and locations of the simulated latitudinal gradient. Right panel: mean annual precipitation over the simulated latitudinal gradient.
96x55mm (300 x 300 DPI)

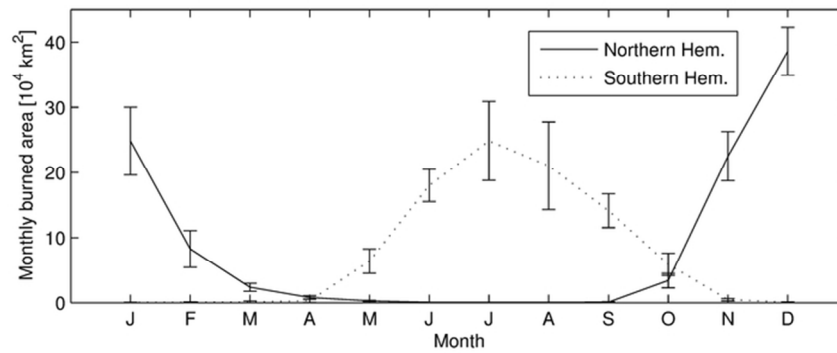


Figure 2. Average monthly burned area over the years 2000–2007 of the African continent derived from the MODIS MCD45 remotely sensed data. The error bars indicate one standard deviation.
70x26mm (300 x 300 DPI)

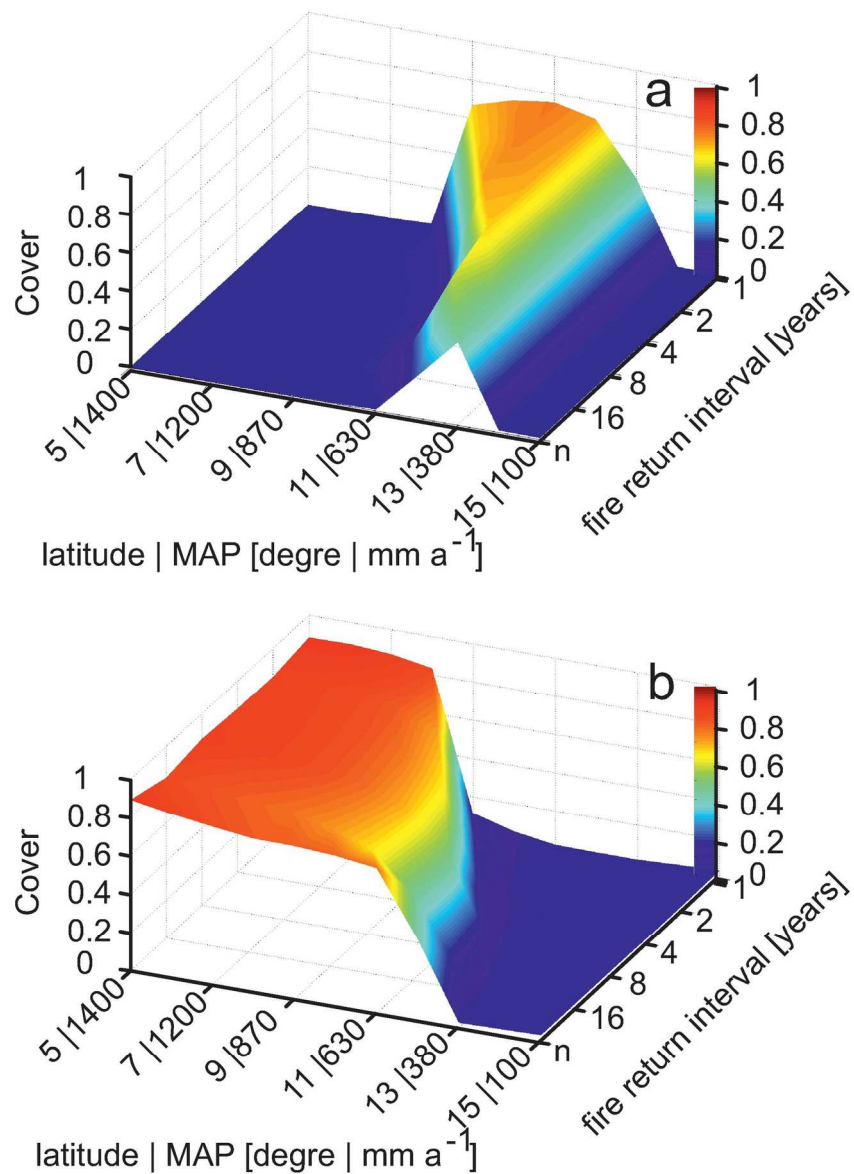


Figure 3. Stand scale analysis: Cover ratio of grasses (panel a) and trees (panel b) along the 20° meridian from 5° to 15° north. The precipitation decreases along the gradient linearly from 1400 to 100 mm mean annual precipitation (see Fig. 1). Simulation results with varying fire return interval. The cover is shown as absolute ratio ranging from 0 to 1.

131x188mm (300 x 300 DPI)

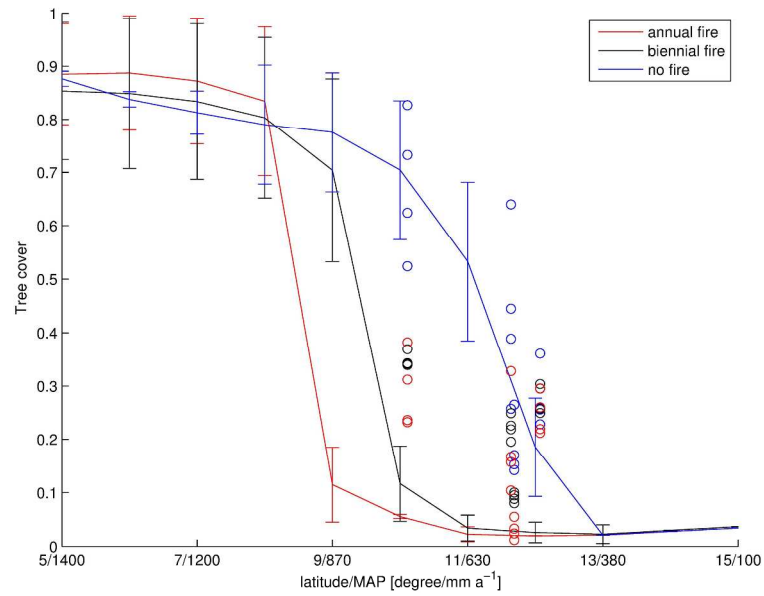
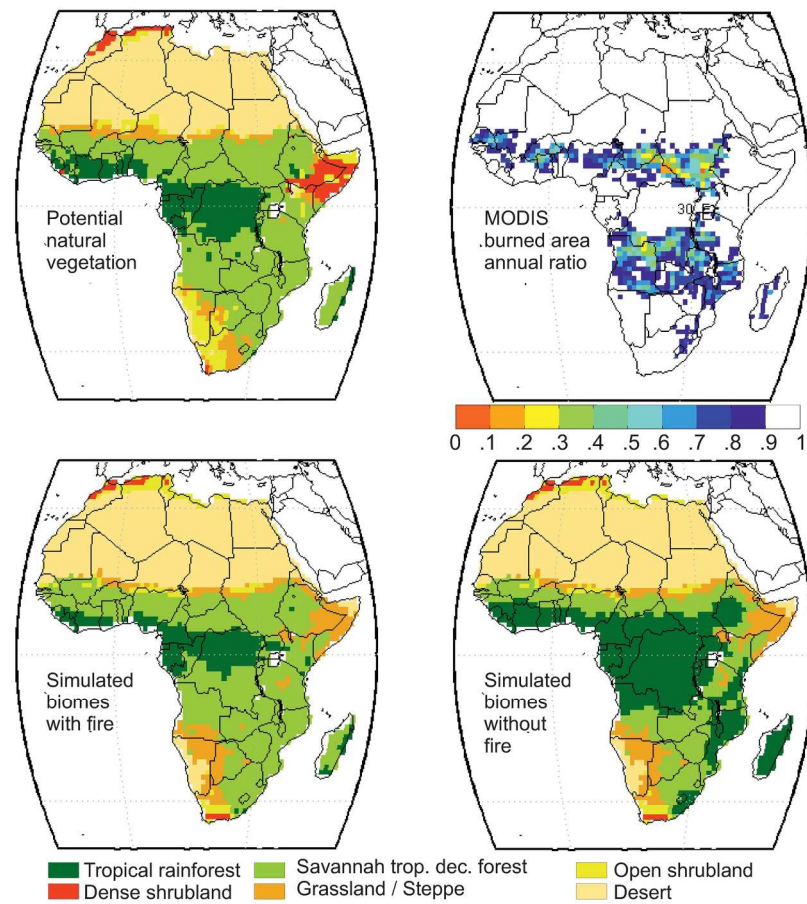


Figure 4. Simulated experimental and tree cover
 The circles are the experimental data collected at Kruger National Park (4 plots per site and fire frequency)
 and the lines with error bars show the simulated results. The error bars indicate one standard deviation.
 Different colours indicate different fire frequencies.
 279x361mm (300 x 300 DPI)



Upper right panel: Annual ratio of burned area at a one degree spatial resolution as detected by MODIS MCD 45. Remaining panels: biome classification: Upper left: biome distribution according to Ramankutty and Foley (2006). The lower panels displays the biome distribution as simulated with LPJ-GUESS SPITFIRE, lower left panel with fire and lower right panel without fire.
185x173mm (300 x 300 DPI)