Deciphering the distribution of the savanna biome

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SUMMARY

- We aimed to identify the limits of savanna across Africa, Australia and South America. We based our investigation on the rich history of hypotheses previously examined; that the limits of savanna are variously determined by rainfall, rainfall seasonality, soil fertility and disturbance.

- We categorized vegetation on all continents as "savanna" (open habitats with a C_4 grass layer) or "not savanna" (closed habitats with no C_4 grass layer) and used a combination of statistical approaches to examine how savanna presence varied as a function of five environmental correlates.

- Savanna presence is constrained by effective rainfall and rainfall seasonality. Soil fertility is regionally important, although the direction of its effect changes relative to rainfall. We identified three continental divergences in the limits of savanna that could not be explained by environment.

- Climate and soils do not have a deterministic effect on the distribution of savanna. Over the range of savanna, some proportion of the land is always "not savanna". We reconciled previous contradictory views of savanna limits by developing a new conceptual framework for understanding these limits by categorizing environmental factors into whether they have a positive or negative effect on woody growth and the frequency of disturbance.

INTRODUCTION

Understanding the factors that govern the distributions of biomes is a fundamental challenge for plant ecology. In the case of tropical savannas, the task is particularly difficult because of multiple interacting factors. Climate, hydrology, herbivory, fire, and soil characteristics can all influence the distribution of savanna (Tinley, 1982; Furley, 1992; Hopkins, 1992; Ruggiero *et al.*, 2002; Bond, 2008). However, we lack a conceptual framework for understanding how these interact to determine the limits of the savanna biome.

Tropical savannas are mixed tree – C_4 grass systems that occur across approximately 20% of the terrestrial surface (Scholes & Hall, 1996). Savannas and C_4 grasslands became prominent features of tropical landscapes approximately 6 to 8 mya as a result of a rapid global increase in the dominance of C_4 grasses (Cerling *et al.*, 1997). In some regions C_4 grasses replaced pre-existing C_3 grasslands (Strömberg, 2004). But C_4 grasslands also displaced forests, thickets and shrublands; biomes that coexist with savanna in modern landscapes, and define the modern limits of savannas (Keeley & Rundel, 2005). Inter-conversion between savanna and these other vegetation types occurs today, often in response to human activity (Bond & Parr, 2010). Large areas of tropical savanna and grasslands have been encroached by trees or shrubs (Asner *et al.*, 2004; Wigley *et al.*, 2009), while elsewhere transitional forests have been converted to grass-dominated ecosystems (Barlow & Peres, 2008).

Here we consider savanna to include any system with a continuous layer of C_4 grasses, regardless of whether trees are present. Shrublands, thickets, and forests will be referred to collectively as "closed-canopy ecosystems," even if they do not possess a truly closed canopy.

22 The defining characteristic of these systems is that the cover of woody plants is sufficiently
23 dense to shade out C_4 grasses.

24 In distinguishing between savanna and closed-canopy ecosystems, we emphasize the
25 presence or absence of C_4 grasses because of their unique biology, which has important
26 consequences for vegetation dynamics (Bond & Midgley, 2000; Sage & Kubien, 2003; Keeley &
27 Rundel, 2005; Bond, 2008; Leakey, 2009). C_4 grasses dominate in areas of high growing season
28 temperatures (Sage, 2004). In such climates, C_4 grasses are extremely productive if ample light is
29 available, permitting rapid accumulation of highly flammable fuels. However, C_4 grasses are
30 physiologically incapable of dominating the low-light environment of closed-canopy ecosystems
31 due to the metabolic costs of C_4 photosynthesis (Sage 2003). The combination of high
32 productivity, high flammability and shade intolerance causes C_4 grasses to play a critical role in
33 mediating the transition between savanna and closed-canopy ecosystems.

34 In savanna, the likelihood of fire is influenced by the traits of the vegetation. A high
35 density of grasses permits frequent fire, which in turn maintains an open canopy, thereby
36 promoting C_4 grasses, and initiating a positive feedback between savanna and fire (Beckage *et*
37 *al.*, 2009). In contrast, a closed-canopy state, where C_4 grasses are excluded, creates a humid
38 microclimate, and thus also greatly reduces the flammability of the vegetation (Ray *et al.*, 2005).
39 These closed-canopy habitats therefore resist burning, allowing them to persist in close
40 proximity to frequently-burned savanna (Bowman, 2000). The absence of grasses is critical for
41 the low flammability of these systems, so the canopy density at which grasses are excluded
42 represents a critical threshold in the transition from one state to another. Although we understand
43 the physical constraints to C_4 grass growth, we lack a sound theoretical framework of why mixed

44   tree - C$_4$ grass systems dominate across the tropical zone, and where and why they are replaced

45   by closed-canopy formations across the range of savanna.

46   There have been numerous attempts to identify the environmental limits of savanna. Nix

47   (1983), drawing on information from South America, identified a range of 1000 to 1500 mm

48   mean annual rainfall (MAP) within which savannas dominate. Stott (1988) identified a range of

49   800 to 2000 mm MAP and a dry season of 5 to 7 months within which savanna dominates in

50   South-East Asia. Scholes and Walker (1993) moved away from precise rainfall limits and

51   identified a monthly mean temperature > 10 degrees throughout the year, a wet season warmer

52   than the dry season, at least 60 days where there is enough moisture for plant growth, and at least

53   60 days where there is not enough moisture for plant growth. Schimper (1903) and Sarmiento et

54   al. (1983) considered that rainfall seasonality, via water limitations to forest plant growth,

55   prevented closed canopy formations from occurring. Lloyd et al. (2008) suggested that rainfall

56   seasonality is important in extending grass dominance into arid systems. Low soil fertility has

57   been considered by many as promoting savanna (Cole, 1960; Goodland & Pollard, 1973; Nix,

58   1983; Stott, 1988; Haridasan, 1992; Lloyd *et al.*, 2008). However, over much, if not all, of the

59   current extent of tropical savannas, the environmental conditions can also support forest,

60   thickets, and shrublands as evidenced by landscape patterns (Bowman, 2000; Russell-Smith *et

61   al.*, 2004), manipulation experiments (Woinarski *et al.*, 2004; Higgins *et al.*, 2007), model

62   experiments (Bond *et al.*, 2005) and palaeoclimate data. Similarly, large areas occupied by these

63   ecosystems have the potential to persist as savanna or closed-canopy formations once the shift

64   has occurred (Laws, 1970; Johnson, 2009). Most authors consider fire an important characteristic

65   of the savanna biome, but differ in the extent to which fire is perceived as a passive response to

66   the presence of flammable C_4 grasses and savannas or a major factor accounting for the existence

67   of savannas (Bond, 2008; Lloyd *et al.*, 2008).

68   Due to the largely stochastic nature of fire regimes, local correlative studies have limited

69   use in inferring environmental controls on the distribution of savanna and closed-canopy

70   vegetation. However, at sufficiently large scales patterns should be governed by the mean

71   behaviour of the dynamics between savanna and closed-canopy formations. It should then be

72   possible to identify the environmental limits where grass-dominated savanna vegetation gives

73   way to either mesic closed-canopy forest on one hand, or arid and semi-arid thicket or shrubland

74   on the other.

75   This study aims to identify the environmental limits of C_4 dominated savannas across

76   tropical Africa, Australia and South America. On all three continents C_4 grass-dominated

77   savannas are widespread, but the history and compositional makeup of the savannas are vastly

78   different. We used best available vegetation maps to classify each continent into savanna and

79   non-savanna vegetation. We assess the probability of a location being savanna along a

80   productivity gradient. We then determine where along this productivity gradient the savanna-

81   closed-canopy boundary exists on each continent, explore reasons for this and develop our

82   conceptual model of how these transitions occur. While the concepts we discuss here are relevant

83   to alternate stable states, and grass- and woody- dominated ecosystems worldwide, we focus on

84   tropical savanna systems dominated by C_4 grasses.

85

86   **METHODS**

87   The extent of savanna vegetation was determined via a composite of vegetation maps

88   covering Africa, Australia and South America. We used maps developed from ground

89   observations. Satellite-based products are subject to the influence of recent land-use change and

90   generally use arbitrary cut-offs for what constitutes 'forest' based on tree cover estimates

91   (Fairhead & Leach 1998). The distinctions used to assess whether a vegetation type was

92   classified as savanna were: 1) the presence of a dominant C_4 grass layer, and 2) discontinuous

93   tree cover. Hence, vegetation units classified as "closed-canopy" comprised shrubland, thicket,

94   heath, forest, dry forest, rainforest, evergreen tropical forest, moist tropical forest and closed

95   forest. We omitted from our analysis any vegetation units described as azonal vegetation, sand,

96   desert, waterlogged, seasonally inundated, riverine forest, alluvial or floodplain grasslands, sub-

97   montane, montane, afromontane, Highveld, agriculture, salt flat, or water. High-altitude tropical

98   grasslands were not sampled, as these systems represent a temperature constraint to woody

99   growth, and do not fit within our limits of "tropical or sub-tropical". Classification was based on

100   the metadata accompanying each vegetation map and consultation with regional experts.

101   **Vegetation maps**

102   *Africa*

103   White's 1983 vegetation map (White 1983) was used to define the limits of savanna in Africa.

104   Detailed maps are available for some countries in Africa, and several recent land-cover maps

105   have been created for Africa, but White's vegetation remains the only continent-wide vegetation

106   classification system. The major vegetation types in White's map are: grassland, grassy

107   shrubland, secondary wooded grassland, edaphic grassland mosaics, forest transitions and

108   mosaics, woodland, woodland mosaics and transitions, bushland and thicket, bushland and

109 thicket mosaics, Cape shrubland, forest, semi-desert vegetation, desert and transitional scrubland.

110 Areas not classified and excluded from the analysis were: altimontane vegetation, anthropic

111 landscapes, azonal vegetation, and Highveld grassland formations.

Australia

113 A composite of four vegetation maps were used. These were: 1) Northern Territory

114 Government 1: 1 million map; 2) Australian Tropical Savannas 1: 1 million (Fox et al. 2001), 3)

115 Queensland Regional Ecosystems; and, 4) Geosciences Australia 1: 2 million map covering the

116 Australian continent. We classified the biomass-accumulating *Triodia spp.* dominated grasslands

117 of Australia as "not savanna". Unlike other C_4 grasses, perennial *Triodia spp.* act functionally as

118 shrubs, accumulating above-ground biomass gradually over many years and with long-lived

119 evergreen leaves, and may carry fire when they are green (ie. not cured). This is unlike other C_4

120 grasses, which only carry fire once they have senesced and cured. Australia is unique in that

121 large tracts of the arid and semi-arid zones are covered by these hummock forming grass species.

122 Co-occurring woody species have life history traits characteristic of crown fire regimes, such as

123 fire stimulated recruitment and non-sprouting (=obligate seeder) fire responses which are absent

124 from the surface fire regimes of savannas (Allan & Southgate, 2002).

South America

126 Due to a lack of detailed vegetation maps for the entire continent, and that the vast

127 majority of South American savannas are contained within Brazil and Venezuela, we used two

128 vegetation maps representing these countries. For Brazil we used the 1:5,000,000 1993

129 Vegetation Map of the Instituto Brasileiro de Geografia e Estatistica (IBGE), digitized by the

130   USGS EROS Data Center. Based on the descriptions of the vegetation classes by the IBGE

131   (1992), we considered as savanna any vegetation classified as Cerrado, Campos, or tree-grass

132   Caatinga. For Venezuela we used the map developed by Huber & Alarcón (1988), where

133   savanna was considered as Llanos.

134

135   **Dataset**

136   We examined the vegetation maps 30º north and south of the equator on each continent,

137   which is the latitudinal band in which C_4 grasses dominate. We generated a random set of points

138   across each continent with the minimum enforceable distance between points 0.25 degrees, and

139   each point classified as "savanna" or "closed-canopy".

140   We collated information on four factors, *a priori*, that have been considered as important

141   regional and local determinants of savanna presence. These four factors are known to affect both

142   ecosystem productivity and fire return period.

143   We calculated effective rainfall as MAP-PET where MAP is mean annual precipitation

144   from the 0.5^o resolution WorldClim data and PET is potential evapotranspiration from the 0.5^o

145   resolution data set from the University of Delaware.

146   Soil fertility (SF) has been inferred by a number of studies as a determinant of savanna

147   presence (Goodland & Pollard, 1973; Cole, 1986; Stott, 1988; Haridasan, 1992; Lloyd *et al.*, 2008).

148   SF affects both the productivity of trees and grasses and, where there are mega-herbivores, the

149   extent of grazing and browsing. SF was determined as a product of Total Exchangeable Bases

150   extracted from the IGBP Harmonised World Soils Database where high values of TEB

9

151 correspond with high soil fertility. TEB is considered a particularly appropriate measure of

152 fertility for savanna systems (Nix, 1983).

153 Rainfall seasonality was first mooted as important for determining the distribution of

154 savannas by Schimper (1903) but this correlation has never been quantified across gradients of

155 seasonality and productivity. TRMM monthly rainfall data (Huffman *et al.*, 2007) was used to

156 calculate rainfall seasonality and was defined using an index which gives an indication of how

157 evenly dispersed rainfall is throughout the year. A value of 0 represents equal rain in all months,

158 a value of 100 means that all rain fell in one month and a value of 50 approximates a 5 month

159 dry season. Markam (1970) provides a definition of this index.

160 Topographic complexity affects fire spread, and thus also fire return times and the

161 probability of disturbance (Stambaugh & Guyette, 2008). Should frequent fires be important for

162 savanna presence, then topographic complexity is likely an important indicator of the likelihood

163 of fire spread. SRTM global topographic data were used to calculate topographic complexity,

164 which is defined as the standard deviation of 90 m resolution elevation values within a 1km cell

165 (about 100 values in each cell).

166 "Continent" was included as a fixed effect in our analyses. Millions of years of plant and

167 landscape evolution separate Africa, Australia and South America, and it has been suggested that

168 there is divergence in the limits of savannas amongst continents (Knapp *et al.*, 2004; Bond, 2008;

169 Lloyd *et al.*, 2008).

170 We were interested in understanding whether the distribution of fire is a driver of the

171 distribution of savanna, rather than a passive response. Fire occurrence and savanna presence are

172 closely related due to the flammability of C_4 grasses. Area burned can be used as an index of fire

173   return periods through space-for-time substitution, though it presents problems in systems that do

174   not burn uniformly. Moreover, a 9-year dataset is insufficient to describe systems such as the

175   *Triodia* dominated hummock grasslands of central Australia, and other semi-arid and arid

176   systems known to have long fire-return periods (Greenville *et al.*, 2009). Hence, directly

177   including information on fire in our analyses would have produced circularity in any arguments

178   of a dynamic relationship between climate, vegetation and fire. However, rainfall seasonality and

179   topographic complexity are two important correlates of fire (Archibald *et al.*, 2009). We used the

180   monthly MCD45A1 burnt area product to determine whether or not individual point locations

181   had burned in the last 9 years (9 years was the length of the MODIS data product).

182

183   **Analyses**

184   *Mapping the probability of savanna and fire occurrence*

185   The dataset generated for each continent was ordered in terms of MAP and binned

186   (ranging from 100 to 4000 mm) in 80 mm intervals. Within each interval the probability of

187   savanna presence was calculated as the mean of all points within that rainfall interval (0 = closed

188   canopy, 1 = savanna, thus the mean value is the probability of savanna presence). If a pixel

189   burned within the time period of the satellite data (9 years) fire occurrence was classified as 1,

190   and if it did not burn it was classified as 0. The probability of fire was calculated as the mean of

191   all the points within that rainfall interval. It is therefore an underestimate, as in systems with fire

192   return periods longer than 9 years a pixel may be incorrectly classified as "no fire" simply

193   because it had not burned. These two metrics were plotted against MAP to compare the limits of

194   savanna and fire (Figure 1).

195

The arid and mesic transitions

Processes driving the transition from savanna to forest on the mesic end of the continuum, and from savanna to arid shrubland/thicket/spinifex on the arid end of the continuum are unlikely to be similar. For the statistical analyses the datasets were therefore split into "arid" and "mesic" with the divider being the rainfall at which savanna occurrence is maximised for each continent. The environmental drivers were explored and explained separately for each transition.

203

Statistical modelling of savanna presence

We examined the ability of five environmental correlates to predict the distribution of savanna (Table 1: MAP-PET, SF, RS, TC, and Continent), and used these to develop 32 models, with a binomial response variable (savanna presence/absence). The 32 models were contrasted in an information theoretic framework described below.

For the statistical models, the presence/absence point data were area averaged at a 0.5 degree resolution. This means all points within a given 0.5 degree cell (up to 5 points) were summed and averaged to create a gridded dataset with values of savanna presence ranging from 0 and 1. Spatial analyses in R are limited by the inability to construct a distance matrix for more than 4000 points. Hence, the dataset was randomly subsampled for 4000 gridded values from each transition (4000 of 4247 arid transition; 4000 of 4125 mesic transition).

We used a method developed by Murphy *et al.,* (2010) to construct autoregressive error (ARerr) models that account for inherent and induced spatial autocorrelation in non-normal data. The autoregressive error models were constructed as generalised non-linear models using the

218   packages gnm and ncf in the freeware program R version 2.11.0. Particular to ARerr models is

219   that the spatial weights of the distance matrix are assigned according to the correlation structure

220   of the residuals for the model in question. The spatial correlation structure was determined by

221   constructing a non-spatial version of the global model. Using the residuals from the non-spatial

222   model a correlogram based on Moran's I was plotted and spatial autocorrelation modelled as a

223   function of distance. The modelled correlation between two points was then used to estimate the

224   spatial weights for the model in question.

225   Models were evaluated using $\Delta QAICc$ ($\Delta QAICc = QAICc_i - QAICc_{min}$), a robust form of

226   Akaike's Information Criterion, a model selection index favouring model parsimony that

227   accounts for overdispersion in data (Burnham & Andersen, 2002). Lower values of $\Delta QAICc$

228   indicate greater support for a model, relative to the best model in the candidate set. Values of

229    $\Delta QAICc < 2$ indicate that an alternate model performs almost as well as the best model and

230    $\Delta QAICc > 10$ suggests it is highly unlikely that the alternative model is appropriate. Based on

231    $QAICc$, Akaike weights (w_i) were calculated for each of the 32 models in the analysis. w_i is

232   equivalent to the probability of a given model being the most parsimonious in the candidate set.

233   From each model set representing each of the arid and mesic transitions, the global model was

234   used to estimate the predicted effects of each correlate on the probability of savanna presence.

235

236   *Regression tree modelling*

237   We also used a non-parametric approach to explore how the environmental data were

238   explicitly correlated with the distribution of savanna. A regression tree is a classification method

239   that predicts class membership by recursively partitioning data into more homogeneous subsets,

240   referred to as nodes (Breiman *et al.*, 1984). Regression trees provide a set of rules for classifying

13

241   data into categories (savanna or not-savanna) by identifying split conditions which decrease the

242   deviance at each node in the tree. Split conditions are explicit, and accommodate non-linear

243   relationships. The importance of different explanatory variables was assessed by randomly

244   permuting each variable in turn, running the model, and assessing the increase in Root Mean

245   Square Error (RMSE) that occurred; variables that are important for the final prediction would

246   result in a greater increase in RMSE when randomly permuted. Currently, there is no good way

247   of accounting for spatial autocorrelation with regression-tree modeling, which means the results

248   from this analysis need to be interpreted with caution, and in light of the statistical models

249   described above.

250

251   **RESULTS**

252   **Distribution of savanna and fire**

253   An initial assessment of the distribution of fire and savanna across a rainfall gradient

254   indicate marked differences between continents (Fig. 1). Savannas in South America occur up to

255   2500mm rainfall - 500mm above the limit of savanna in Australia, and 750mm above Africa's

256   wettest savannas. Similarly, a substantial proportion of the savannas of Australia and Africa

257   occur at rainfalls below 1000mm, which is not the case in South America (Fig 1). In Australia

258   and South America, fire occurrence is closely associated with the presence of savanna along this

259   rainfall gradient (Fig 1). In Africa, however, savanna extends far into areas of low rainfall where

260   burning is infrequent (Fig 1a).

261

Environmental drivers of the mesic savanna – forest transition

262 **Environmental drivers of the mesic savanna – forest transition**

263 In the gnm analysis of the mesic savanna-forest transition, all covariates had relevance in

264 determining the probability of savanna (Table 1). When the effect of each variable was examined

265 in isolation, MAP-PET and rainfall seasonality had the greatest influences (16.5% and 15.7% of

266 deviance explained, respectively), followed by continent (10.6% DE), soil fertility (5.3% DE)

267 and topographic complexity (1.1% DE). We found good agreement between our observed and

268 predicted distributions (Fig. 3)

269 When all variables were included in the model, the spatial global model explained

270 22.63% of the deviance in the data, and the non-spatial global model explained 34.36% of the

271 deviance, hence ~ 12% of the deviance could be attributed to the spatial structure of the data. The

272 response to MAP-PET was remarkably consistent across continents after accounting for all other

273 variables (Fig 2). On all continents, the probability of savanna occurrence was less than 20%

274 where MAP-PET exceeded 1200mm (Fig. 2). RS had a strong positive effect on savanna

275 presence, indicating that savanna is most extensive where rainfall is most seasonal. Africa

276 requires more seasonally-concentrated annual rainfall than either Australia or South America to

277 achieve the same probability of savanna occurrence (62 vs 49 and 52 respectively for a 50%

278 probability). Soil fertility explained 5% of the deviance in the data when examined in isolation,

279 however, this effect disappeared when all other variables were taken into account (Fig. 2).

280 Topographic complexity had a weak negative effect on savanna presence. Overall Australia had

281 a higher probability of savanna occurrence, albeit a small difference, relative to Africa and South

282 America (Fig 2). That is, accounting for other environmental correlates, savannas in Australia

283 extend into wetter habitats. Hence, when the envelope of Australian savannas was plotted onto

284 the environmental space of Africa and South America the extent of mesic closed-canopy

285 formations was much reduced (Fig. 4).

286   Regression tree results confirmed the importance of RS in the mesic savanna - forest

287 transition. Here RS was the most important correlate of savanna, reducing the RMSE by 50%

288 more than the next most important variable (MAP-PET). Across all continents areas with RS <

289 52 (equivalent to a dry season of less than 5 months) were highly unlikely to be classified as

290 savanna. The regression tree identified MAP-PET < 570 within which all continents have a high

291 probability of savanna - as long as they are also seasonal systems (Table 3A: split #4). It also

292 highlighted the existence of savanna on rare, but biogeographically important sites of very low

293 fertility and very high rainfall in South America (Table 2a, split #3). These low-fertility, high-

294 rainfall sites do not exist in Australia or Africa so it is not clear whether this is a true continental

295 distinction, or simply due to lack of representation on other continents. Continental scale

296 differences found across the mesic transition were not strong enough to justify splitting the data

297 by continent (Table 2a).

298

Environmental drivers of the arid savanna – shrubland/thicket transition

300   Continental differences in the limits of savanna were most apparent in the arid

301 continuum, where we found considerable variation in the breadth of the productivity gradient

302 occupied by savanna across Africa, Australia and South America (Fig. 2). Results from the gnm

303 analysis of the arid savanna – shrubland/thicket transition, found that all covariates had relevance

304 in determining the probability of savanna. When the effect of each variable was examined in

305 isolation "Continent" had the greatest explanatory power, explaining 17.5% of the deviance in

16

306 the data. Rainfall concentration explained 15.6 % of deviance in the data, followed by MAP-PET

307 (5.85% DE) and topographic roughness (1.25% DE). On its own, soil fertility explained virtually

308 none of the deviance in the data 0.02% DE. The global model explained 27% of the deviance

309 (Table 1), and the non-spatial global model explained 38% of the deviance in the data, hence

310 11% of the deviance in the data could be accounted for by the spatial structure of the data.

311   For a given MAP-PET, there was a 23 – 46% higher probability of savanna occurring in

312 Africa relative to Australia and South America (Fig. 2). Similarly, for a given RS, there was a 26

313 – 49% higher probability of savanna occurring in Africa and a 34 – 44% higher probability of

314 savanna presence for a given TC. From Figure 3 a 50% probability of savanna occurrence in

315 Africa corresponds to RS of 45, while in Australia and South America RS must exceed 71 and 74

316 respectively. Importantly, the environmental conditions of low rainfall and high seasonality do

317 not occur in arid South America, where seasonality does not exceed this value. TC explained

318 only 1.25% of the deviance in the data. In isolation soil fertility explained little of the deviance

319 in the data, but when examined in combination with all environmental correlates had high

320 relevance (Table 1, Fig. 2). This suggests the importance of a possible interaction between SF

321 and other factors as, across all continents, our analysis predicts that increasing soil fertility is

322 correlated with an increased probability of arid savanna occurrence (Fig. 2).

323   When we delve further into the role of "continent" via regression trees, there is strong

324 agreement between the statistical models and regression tree of divergence amongst continents in

325 the arid limits of savanna (Table 2). In contrast to the mesic transition there do seem to be

326 continental-level differences in savanna occurrence that cannot be explained by variation in

327 environmental drivers. In Africa and Australia sites with low MAR-PET can be savanna if they

328   have very high RS or high soil fertility (Table 3b, splits #7,#8), but savanna is never present in

329   South America for values of MAP-PET less than -760. (Table 3b, split #1). This is demonstrated

330   by plotting the limits of South American savannas onto Africa and Australia, which results in a

331   substantial reduction in the extent of savanna in semi-arid regions (Fig. 4c).

332

DISCUSSION

334   We found that across the tropics, the balance between savanna and closed-canopy

335   ecosystems is fundamentally similar because effective rainfall and rainfall seasonality constrain

336   their distribution (Fig. 2 - 3 and Table 1 - 2). Savannas are commonly perceived to occupy an

337   intermediate position in the continuum between grassland and forest. However, many tropical

338   landscapes contain mosaics of savanna and closed-canopy systems, and these mosaics have

339   persisted over millenia. That such strikingly different vegetation occurs as a mosaic hints that the

340   limit of savanna is not simply, and deterministically, defined by climate and soils. Our analysis

341   confirms this: over the entire range of environmental conditions where savannas occur, some

342   fraction of the land surface is "non-savanna" (Fig. 1).

343   We present evidence of globally-applicable environmental limits to mesic savanna as

344   there is consensus across regions in the direction and magnitude of the effects of effective

345   rainfall, rainfall seasonality, soil fertility and to a lesser extent, the topographic complexity of

346   landscapes. Our results corroborate previous studies showing that savanna presence correlates

347   with edaphic conditions and moisture availability (Cole, 1960; Stott, 1988; Furley, 1992;

348   Haridasan, 1992; Ruggiero *et al.*, 2002; Lloyd *et al.*, 2008), although we provide an alternative

349 interpretation for how these soil and climate constraints operate in a causal manner to limit

350 savanna. Lastly, "Continent" was an important correlate of savanna extent, primarily at the arid

351 limit of savanna, and we discuss divergences amongst continents in the limits of savanna and

352 present hypotheses and evidence for why these might exist.

353

354 *Does the counteraction between woody plant growth and disturbance govern the limits of*

355 *savanna?*

356 While quantifying these limits is useful, it fails to untangle the ecological mechanisms

357 that actually limit savanna. However, savanna-limiting mechanisms are not intuitive, primarily

358 because woody plants and C_4 grasses respond differently to the same climatic parameters. Total

359 effective rainfall, rainfall seasonality and soil fertility affect the growth rates of both woody

360 plants and C_4 grasses. Frequent fire reduces woody growth rates and tree density, but engenders

361 an environment more suitable for C_4 grasses (i.e., reduced competition from trees). If the

362 disturbance interval exceeds the time required for canopy closure, savanna will be replaced by

363 closed-canopy ("not savanna") vegetation (Fig. 5). Thus, understanding the rate of canopy

364 closure, relative to fire frequency is vital to understanding the limits and persistence of savannas.

365 We consider that the extent of savanna is determined by the counteraction between rates

366 of canopy closure - due to colonization and growth of trees; and the frequency of disturbance,

367 promoted by C_4 grass abundance - which results in canopy opening. If the environmental

368 conditions at which savannas dominate are determined this counteraction, then when factors

369 affecting these processes have been accounted for we should find convergence in the distribution

370   of savanna across the globe. On the other hand, if savannas in different parts of the world have

371   different environmental limits, then we need to search for alternative ecological explanations or

372   turn to historical differences to explain divergences.

373   Using the above framework we believe it possible to integrate previous and seemingly-

374   contradictory observations of the environmental limits of savanna. Importantly, the relevance of

375   local correlations between savanna presence, soil fertility and/or water-holding capacity can be

376   incorporated into our framework if they are understood as factors that increase woody growth

377   rates – thereby reducing the efficacy of fire in maintaining an open-canopy (Fig. 5a). From Fig.

378   5a we see that the exact boundary between savanna and closed-canopy vegetation should depend

379   on the shapes of relationships of potential tree and grass productivity to climate and disturbance

380   – for which there is little data available; the form of which may be influenced by phylogeny and

381   the traits of tree and grass species (Bond, 2008).

382   Concepts of climate-disturbance-vegetation interactions constraining the limits of

383   savanna can be contrasted with the hypothesis that the modern- and palaeo-extent of savanna

384   vegetation is attributable to the efficiencies of the C_4 photosynthetic system, as C_4 grasses are

385   superior competitors to woody plants under low but seasonal rainfall due to lower whole-plant

386   construction costs and high water-use-efficiency (Orians & Solbrig, 1977; Edwards et $al.$, 2010).

387   Hence, C_4 grasses colonise open habitats. However, decade-old fire exclusion and model

388   experiments show that 1) across many savanna systems, the competitive effect of C_4 grasses is

389   not strong enough to prevent tree recruitment in the absence of disturbance (Russell-Smith et $al.$,

390   2003; Higgins et $al.$, 2007; Asner et $al.$, 2009; Lehmann et $al.$, 2009) and 2) that an increase in

391   the density of woody stems often leads to co-incident reductions in grass biomass (Belsky, 1994;

392   Menaut *et al.*, 1995; Mordelet & Menaut, 1995; Scholes & Archer, 1997; Ludwig *et al.*, 2004;

393   Riginos, 2009). Our results, along with a recent study examining distribution of fire across

394   Africa (Archibald *et al.*, 2009), suggests that the limits of C_4 dominated systems are due to the

395   dynamic roles of succession and disturbance as described in Figure 5. Here effective rainfall and

396   rainfall seasonality are the ultimate drivers, while soil fertility locally modifies resource

397   availability, and topographic complexity locally modifies the probability of fire. However, the

398   remarkable divergence between continents in the arid limits of savanna is intriguing.

399

400   *Why is the role of rainfall seasonality paramount in limiting savanna?*

401   Rainfall seasonality was the most important predictor of savanna presence. Across the

402   mesic transition any area with rainfall seasonality < 52 (equivalent to a dry season less than 5

403   months) had <20% probability of being savanna across all three continents. Across the arid

404   transition seasonality in combination with adequate effective rainfall was necessary for savanna

405   presence. Rainfall seasonality may be particularly important because it acts both to <u>reduce</u> rates

406   of canopy closure (Sarmiento, 1984), and <u>increase</u> fire frequency (Archibald *et al.*, 2009).

407   Pronounced rainfall seasonality promotes fuel curing, affecting both the spatial connectivity of

408   fuels and the period over which fuels are available to burn (Bradstock, 2010). Rainfall

409   seasonality is also related to inter-annual rainfall variability and hence the probability of drought

410   which promotes both sapling tree death (Fensham *et al.*, 2009) and reduces adult woody growth

411   rates. Rainfall seasonality therefore has a strongly countervailing influence on woody growth and

412   the probability of disturbance. By referring to Figure 5b this alone might prove its importance in

413   explaining the limits of savanna.

414

Why does the role of soil fertility differ between the arid and mesic transitions?

416   We found a contrasting effect of soil fertility across the mesic and arid transitions (Fig. 2;

417   Table 2). In very wet areas low fertility sites were more likely to be savanna (Fig. 2 and Table 2;

418   split #3). These results conform to the notion that increased soil fertility lessens growth

419   constraints on woody plants thereby increasing woody growth rates and productivity. Hence, the

420   time required for a site to achieve a closed canopy that excludes C_4 grasses is increased,

421   simultaneously providing a greater opportunity for disturbance to occur (Fig. 5b).

422   In arid areas, high fertility sites were more likely to be savannas (Fig. 2; Table 2, Split

423   #7). There is less clarity about the role of soil fertility in arid areas. Across the African arid

424   transition browsing and large mammal disturbance are important mechanisms maintaining open

425   formations (Laws, 1970; Holdo *et al.*, 2009a; Staver *et al.*, 2009), in which case, this is likely to

426   be important in more fertile systems (Coe *et al.*, 1976; Fritz & Duncan, 1994; Asner *et al.*, 2009),

427   and low-rainfall systems (Staver *et al.*, 2009) which would explain why low-rainfall high fertility

428   systems are more likely to persist as savanna (Fig. 3). In Australia the distribution of biomass-

429   accumulating *Triodia* sp. ecosystems (that we consider "not-savanna") are well correlated with

430   sandy infertile soils (Nano & Clarke, 2008). Land systems with soils that have higher clay

431   contents and a low water-holding capacity, relative to the well-sorted sands of semi-arid

432   Australia, tend to support savanna (Fox *et al.*, 2001), as they favour shallow rooted grasses; akin

433   to the Walter hypothesis of tree-grass coexistence (Walter, 1971). In our analyses, arid sites of

434   extreme fertility represent a tiny percentage of combined land-masses. However these cases

435   provide information to explore processes promoting savanna.

22

436

What is the role of "continent"?

Some of the different patterns, with regard to precipitation, that we have observed (i.e. Fig. 1) can be explained by differing combinations of other factors. Low-fertility, high-rainfall savannas are only found in Brazil and Venezuela – but so too are the low-fertility and high-rainfall environments which promote these savannas. Similarly, savannas occur in the very low-rainfall areas of Africa and Australia because they are fertile, and these highly-fertile soils are not found in South America. However, there are three important examples where differences between continents cannot be explained by modern day environmental constraints.

Africa has a much higher probability of savanna presence across the arid transition than either Australia or South America (Fig. 2; Fig. 4a). Consequently, African savannas occupy a greater land area than would otherwise be anticipated were continent not factored into our analyses. Mega-herbivores and large predators were eradicated from South America and Australia over 20, 000 years ago, but not from Africa. Browse disturbance is critical in determining rates of woody plant growth in arid regions, while large mammal grazing and trampling reduces fuel loads and can prevent fire (Lehmann *et al.*, 2008; Asner *et al.*, 2009; Holdo *et al.*, 2009b). This is supported by the large discrepancy between the probability of savanna and fire occurrence where MAP < 1400mm across Africa (Fig. 1). There are numerous historical accounts and palaeo-ecological studies from Africa and elsewhere that demonstrate the addition or removal of large mammals induced radical changes to vegetation (Laws, 1970; Holdo *et al.*, 2009b; Johnson, 2009). Hence, according to our framework (Fig. 5), a disturbance other than fire, i.e., mammalian herbivory that reduces woody plant growth and prevents closed-

458   canopy formations would need to operate in these regions. From our analysis, the continent-level

459   differences in rainfall seasonality required to promote savanna across arid Africa and similarly

460   the correlation between soil fertility and the arid savanna-shrubland/thicket transition points to

461   the role of herbivores in extending the dominance of savanna across the African continent.

462   In Australia, savanna extends into wet habitats where rainfall is not as seasonally

463   concentrated as in either Africa or South America. Applying these Australian limits to Africa and

464   South America results in a reduction in the extent of the Amazon and Congo Basin forests (Fig.

465   4b). The Australian mesic transition is almost entirely confined to a small portion of the NE of

466   the continent (Fox *et al.*, 2001). Due to the small dataset pertaining to the Australian mesic

467   transition the power of this result is diminished, and to an extent an artifact of the differences in

468   range of rainfall seasonality found across the three continents. However, Australian mesic

469   savannas are dominated by tree species from the *Eucalyptus* genus (Fox *et al.*, 2001) and there is

470   much to suggest that *Eucalyptus* and fire are co-dependent (Gill *et al.*, 1981; Bradstock *et al.*,

471   2002), with species from the genus having adaptations to tolerate fire (bark thickness and

472   substantial resprouting potential), and in some species adaptations to promote fire (elevated fuels

473   and highly flammable leaf litter). Beckage et al (2009) shows how these characteristics can

474   promote fire and savanna in mesic environments. The phylogenetic peculiarities of eucalypts

475   might therefore be the explanation for the higher mesic limit of savanna in Australia.

476   Finally, there is a lack of savanna at low rainfalls in South America (Fig. 4c; Table 2,

477   split #1), although very similar environmental conditions correlate with a high probability of

478   savanna in Africa and Australia (Fig. 2, Fig. 4). This is puzzling; across the Neotropics the

479   distribution of savanna and adjacent fire-sensitive biomes is recognized as confounding or at the

480   very least as occupying similar environmental envelopes (Pennington *et al.*, 2000; Pennington *et*

481   *al.*, 2009). Simon et al. (2009) demonstrate that the fire sensistive arid thickets, semi-arid dry

482   forests and Amazonian forests of Brazil are the ancestral biomes for the lineages of tree species

483   that dominate the Brazilian savanna. Further, of the diverse array of tree species that dominate

484   the Cerrado many have congeners specific to either the gallery forests of the Cerrado or the

485   Amazon (Hoffmann *et al.*, 2009). Anecdotal reports suggest that differences in the soils between

486   the Caatinga and Cerrado not captured in this analysis are highly important in understanding the

487   transition between Caatinga and Cerrado vegetation (Lloyd *et al.*, 2008). Thicket vegetation

488   similar to Caatinga does occur in Africa under similar environmental conditions but is usually

489   not the dominant landscape type as it appears to be in South America.

490

491   *Summary*

492   The relationship between vegetation and climate is dynamic, and so too the relationship

493   between vegetation and disturbance. We provide a conceptual framework in which to consider

494   the limits of savannas and suggest that at global scales interactions between climate, disturbance

495   and vegetation underpin the limits of savannas due to the counteraction between factors

496   promoting woody plant growth and disturbance intervals. Of these drivers, rainfall seasonality

497   has a strongly contrasting effect on both. The mosaics of savanna and non-savanna are

498   compelling evidence that these are distinct, alternative ecosystem states as has been suggested in

499   the literature (Sternberg, 2001; Warman & Moles, 2009). In contrast, the mechanisms

500   maintaining the arid limits are less clear, although across Africa it appears that disturbance-

501   centered feedbacks involving mega-herbivores are crucial.

502

ACKNOWLEDGEMENTS

50% chance of closed canopy formations, regardless of whether these are tropical forest, tropical dry forest or semi-arid thickets and shrublands.

Figure 5. a) Graphical representation of the effect of soil resources on the time required to reach the non-flammability threshold. Resource availability determines the rate of canopy closure, so the time required to reach an alternate stable state is considerably shorter for the high-resource environment than for the low-resource environment and b) examples of the time required to reach canopy closure where different probabilities of fire operate. Fore example, 0.5 corresponds to the probability of a fire event occurring one in two years.

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Table 1. Model rankings from the gnm analyses of the arid and mesic transitions showing the top-ranked (*QAICc* < 10), uni-variate and null models.

Table 2. Split conditions identified by a regression tree run on points across the mesic and arid transitions (with continent included as a factor). "Total points" represents the total number of points in each split category. Also given is the percentage of points on each continent that were correctly classified by each split. Some sets of environmental conditions were not represented on all continents.
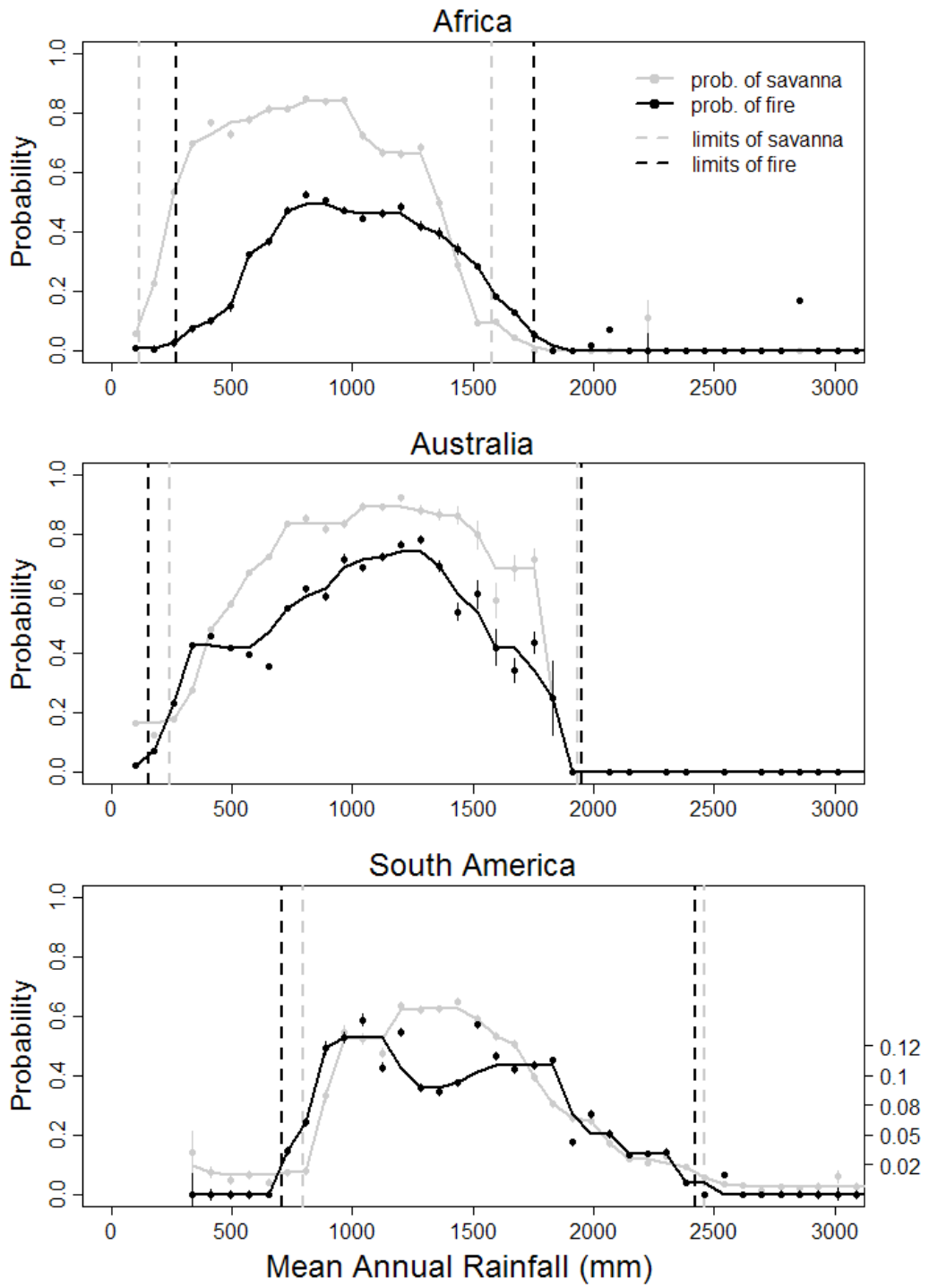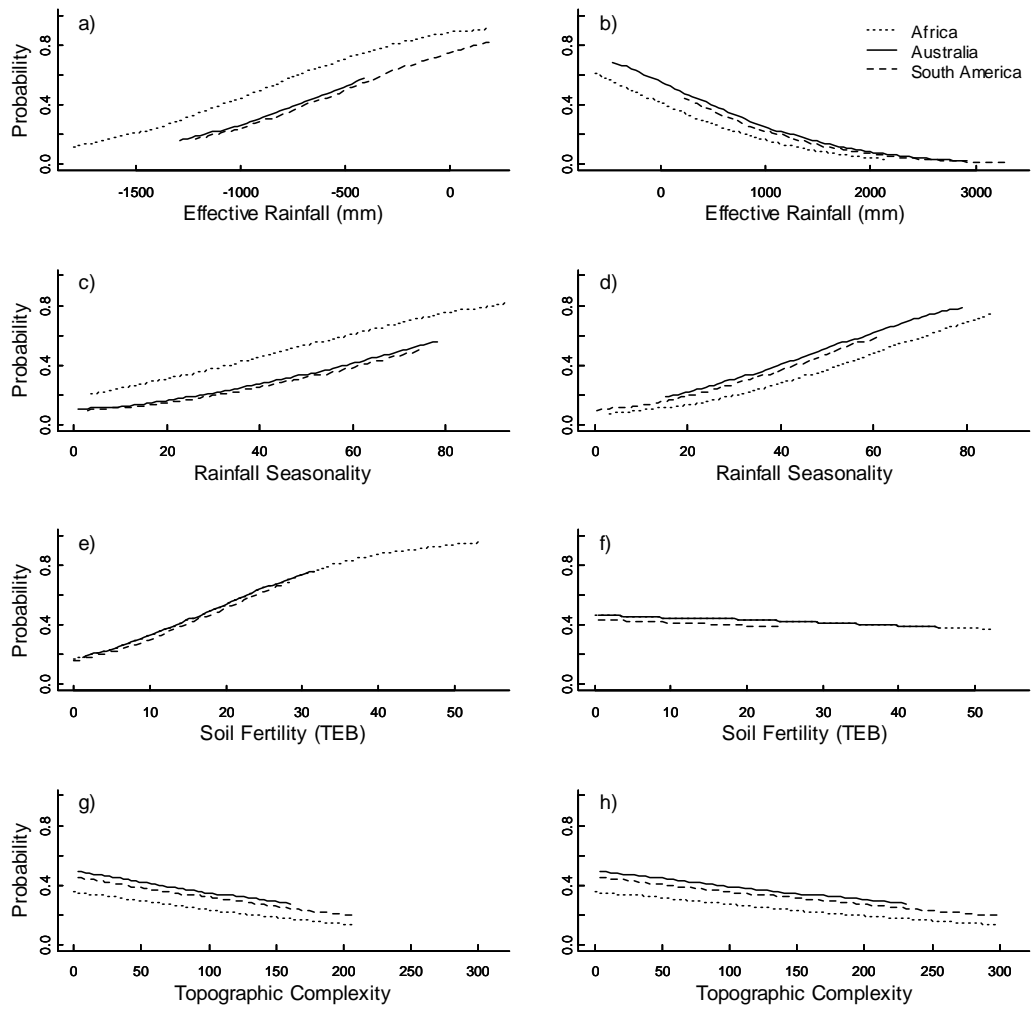
Figure 1.

Figure 2.

Figure 3.

a)

N

0 10 20   40 Decimal Degrees

b)

Probability of savanna
- 0.0- 0.2
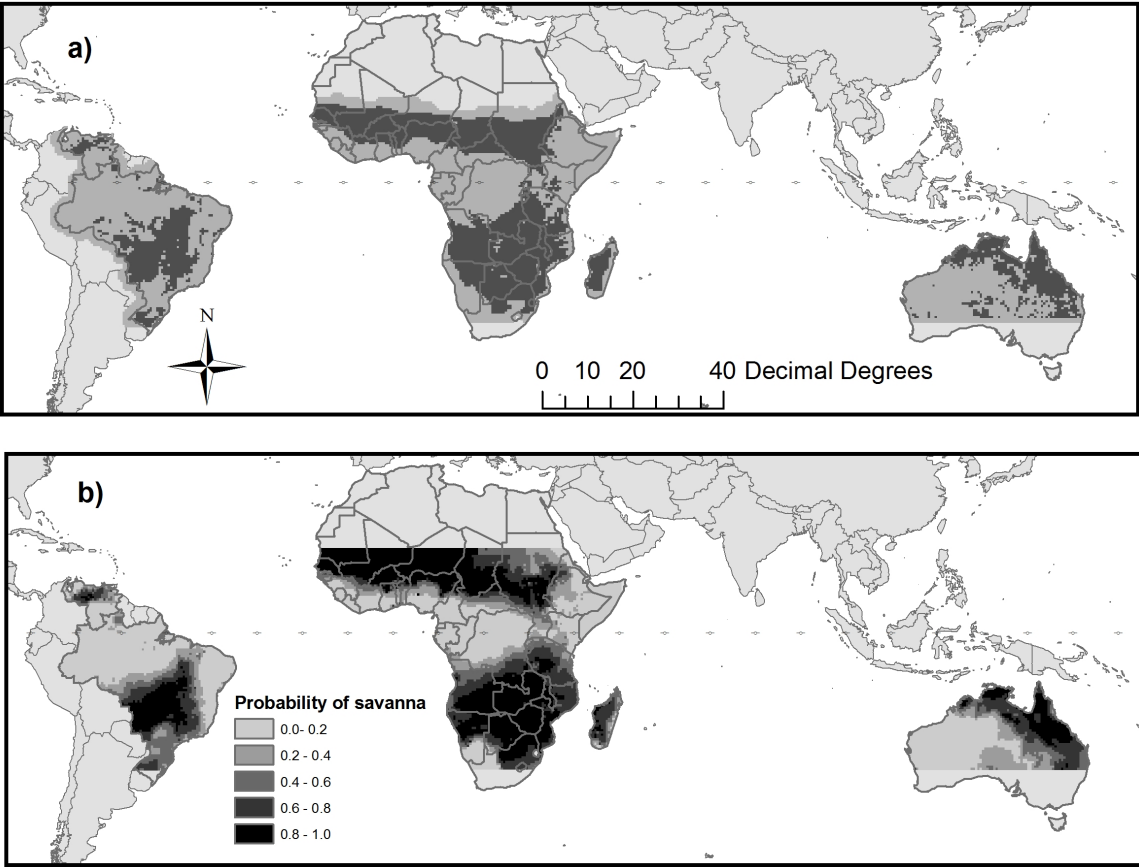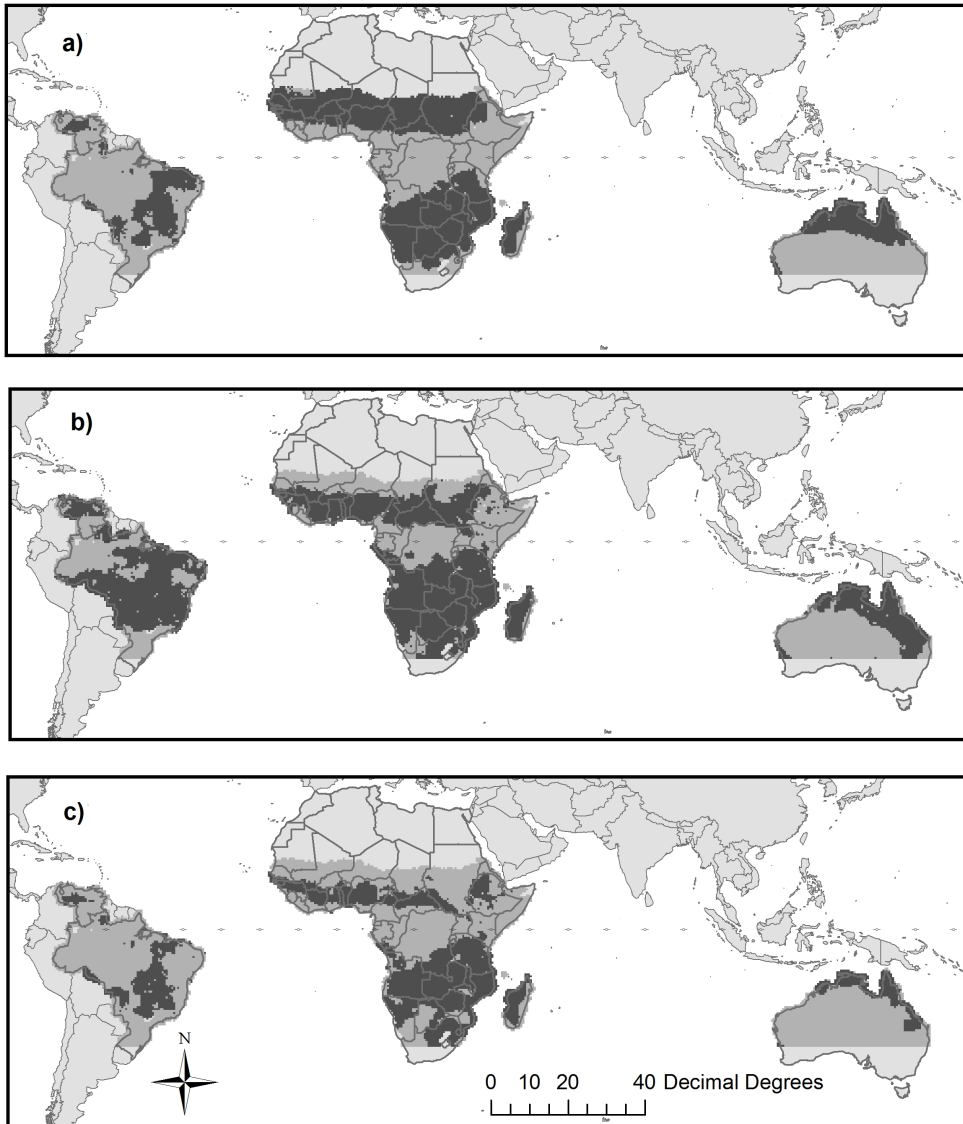- 0.2 - 0.4
- 0.4 - 0.6
- 0.6 - 0.8
- 0.8 - 1.0

Figure 4.

Figure 5.
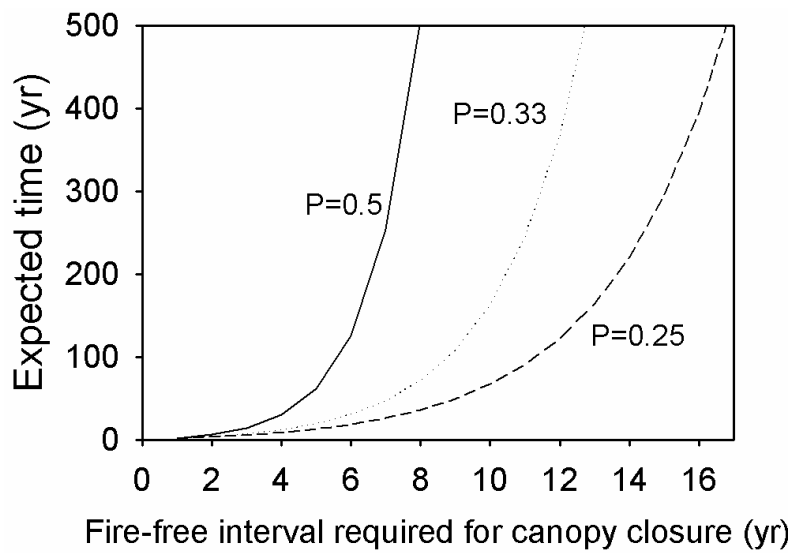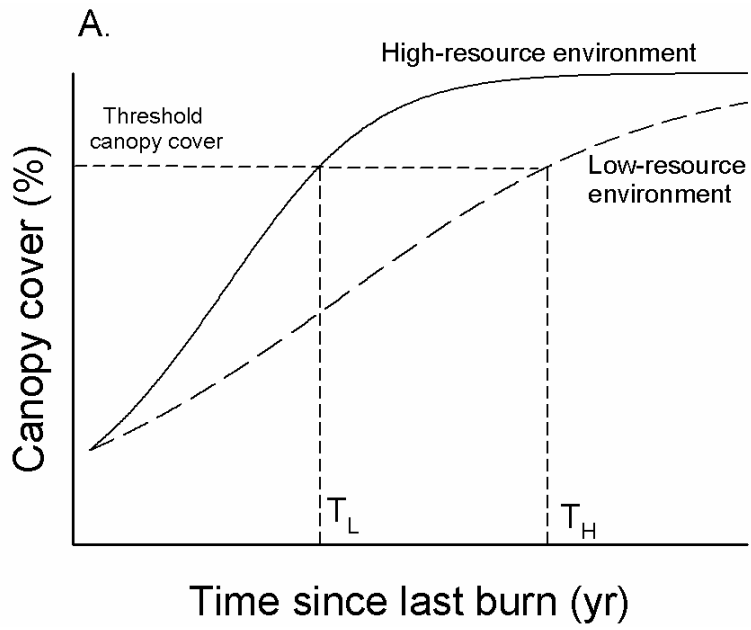
Table 1. ARerr model results for the arid and mesic transitions

Arid transition					Mesic transition				
Model	Rank	QAICc	DeltaQAICc	%DE	Model	Rank	QAICc	DeltaQAICc	%DE
RPET+SF+RC+TR+CONT	*1*	*4986.71*	*0.00*	*26.99*	*RPET+RC+TR+CONT*	*1*	*4526.78*	*0.00*	*22.60*
RPET+SF+RC+CONT	2	5019.38	32.67	26.36	*RPET+SF+RC+TR+CONT*	*2*	*4527.48*	*0.71*	*22.63*
CONT	18	5477.52	490.81	17.87	RPET	22	4832.28	305.50	16.53
RC	23	5600.38	613.67	15.58	RC	24	4875.19	348.41	15.70
RPET	28	6132.52	1145.81	5.85	CONT	28	5142.49	615.71	10.55
TR	29	6384.10	1397.39	1.25	SF	30	5414.30	887.52	5.25
Null	*31*	*6450.53*	*1463.82*	*0.00*	TR	31	5626.55	1099.77	1.13
SF	32	6451.17	1464.45	0.02	*Null*	*32*	*5683.04*	*1156.26*	*0.00*

Table 2.

MESIC TRANSITION:			Split	Total points	Veg class	% correctly classified		
Overall Accuracy = 0.34, Cohen's Kappa = 0.62 (p < 0.001)						AFR	AUS	S.AM
Rain concentration < 52			#1	1760	Not savanna	82	78	80
Rain concentration ≥ 52	Rain-PET ≥ 570	TEB ≥ 1.1	#2	66	Not savanna	69	100	78
		TEB < 1.1	#3	67	Savanna	–	–	76
Rain concentration ≥ 52	Rain-PET < 570		#4	509	Savanna	85	92	76

ARID TRANSITION:				Split	Total points	Veg class	% correctly classified		
Overall Accuracy = 0.64, Cohen's Kappa = 0.32 (p < 0.001)							AFR	AUS	S.AM
rain-PET < -760	continent = SAM			#5	52	Not savanna	–	–	98
	continent = AFR or AUS	Rain concentration < 72	TEB < 30	#6	2087	Not savanna	92	85	–
			TEB ≥ 30	#7	47	Savanna	50	74	–
		Rain concentration ≥ 72		#8	1484	Savanna	79	66	–
Rain-PET ≥ -760	Rain concentration < 38			#9	1727	Not savanna	94	52	78
	Rain concentration ≥ 38			#10	4483	Savanna	76	85	58

35

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