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Citation for published version:

Bueno, M, Pennington, RT, Dexter, K, Kamino, L, Pontara, V, Neves, D, Ratter, JA & Oliveira-Filho, A 2016, 'Effects of Quaternary Climatic Fluctuations on the Distribution of Neotropical Savanna Tree Species', *Ecography*. <https://doi.org/10.1111/ecog.01860>, <https://doi.org/10.1111/ecog.01860>

Digital Object Identifier (DOI):

[10.1111/ecog.01860](https://doi.org/10.1111/ecog.01860)

[10.1111/ecog.01860](https://doi.org/10.1111/ecog.01860)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Ecography

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1 **Effects of Quaternary Climatic Fluctuations on the Distribution of**
2 **Neotropical Savanna Tree Species**

3
4 Marcelo Leandro Bueno¹, R. Toby Pennington², Kyle G. Dexter^{2,3}, Luciana H. Yoshino
5 Kamino⁴, Vanessa Pontara¹, Danilo Rafael Mesquita Neves¹, James Alexander Ratter² and
6 Ary Teixeira de Oliveira-Filho¹

7
8 ¹ Programa de Pós-graduação em Biologia Vegetal, Universidade Federal de Minas Gerais –
9 UFMG, Campus Pampulha, Cep 31270-090, Belo Horizonte, Brazil.

10 ² Royal Botanic Garden Edinburgh, 20a Inverleith row, EH3 5LR, Edinburgh, UK.

11 ³ School of GeoSciences, University of Edinburgh, 201 Crew Building, King's Buildings, EH9
12 3JN, Edinburgh, UK.

13 ⁴ Instituto Prístino, Rua Santa Maria Goretti, 86, Cep 30642-020, Belo Horizonte, Brazil.

14
15 *e-mail: buenotanica@gmail.com

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23 **ABSTRACT**

24 In order to develop niche models for tree species characteristic of the cerrado
25 vegetation (woody savannas) of central South America, and to hindcast their distributions
26 during the Last Glacial Maximum and Last Inter-Glacial, we compiled a dataset of tree
27 species checklists for typical cerrado vegetation (n=282) and other geographically co-
28 occurring vegetation types, e.g. seasonally dry tropical forest (n=355). We then performed an
29 Indicator Species Analysis to select ten species that best characterize typical cerrado
30 vegetation and developed niche models for them using the Maxent algorithm. We used these
31 models to assess the probability of occurrence of each species across South America at the
32 following time slices: Current (0 ka pre-industrial), Holocene (6 ka BP), Last Glacial
33 Maximum (LGM - 21 ka BP), and Last Interglacial (LIG - 130 ka BP). The niche models
34 were robust for all species and showed the highest probability of occurrence in the core area
35 of the Cerrado Domain. The palaeomodels suggested changes in the distributions of cerrado
36 tree species throughout the Quaternary, with expansion during the LIG into the adjacent
37 Amazonian and Atlantic moist forests, as well as connections with other South American
38 savannas. The LGM models suggested a retraction of cerrado vegetation to inter-tableland
39 depressions and slopes of the Central Brazilian Highlands. Contrary to previous hypotheses,
40 such as the Pleistocene Refuge Theory, we found that the widest expansion of cerrado tree
41 species seems to have occurred during the LIG, most probably due to its warmer climate. On
42 the other hand, the postulated retractions during the LGM were likely related to both
43 decreased precipitation and temperature. These results are congruent with palynological and
44 phylogeographic studies in the Cerrado Domain.

45

46

47 **INTRODUCTION**

48 There is strong evidence that global climate fluctuations, and Pleistocene
49 glacial/interglacial cycles in particular, have played a key role in determining both the origin
50 and distribution of living organisms (Hewitt 2000). While at one time, tropical regions were
51 considered to have been more stable than temperate regions during Pleistocene climatic
52 cycles, a great number of studies have suggested otherwise (e.g. Haffer 1969, 1982, Prance
53 1982). Savanna is one of the main Neotropical biomes (Bourlière 1983), and it is thought to
54 have shifted its distribution significantly during the Pleistocene (Ledru 2002). The Cerrado
55 Phytogeographical Domain contains the largest expanse of the savanna in the Neotropics, and
56 there has been extensive research aimed at understanding its distribution during the
57 Pleistocene (e.g. Ledru 1993, Oliveira-Filho and Ratter 1995, Ledru et al. 1996, Salgado-
58 Labouriau 1997, Salgado-Labouriau et al. 1998, Ledru 2002, Oliveira-Filho and Ratter 2002,
59 Werneck et al. 2012). In addition to savannas, which are the main vegetation type, the
60 Cerrado Domain also contains grasslands, semideciduous and seasonally dry tropical forests.
61 The savannas, generally referred to as “cerrado” (note that throughout we use lower case to
62 refer to the vegetation type), are the subject of this study.

63 The Pleistocene refuge theory postulated that South American savannas, especially
64 cerrado vegetation, expanded into the Amazon during the Last Glacial Maximum (LGM;
65 20,000-13,000 years before present, 20 - 13 Ka), where it fragmented the distribution of rain
66 forest vegetation (Haffer 1969). However, paleoecological studies from the Amazon have
67 suggested continuous presence of rain forest there through the LGM (e.g. Colinvaux et al.
68 2000, Mayle et al. 2000, Colinvaux and De Oliveira 2001, Bush et al. 2002, Mayle and
69 Beerling 2004, Urrego et al. 2005, Bush and De Oliveira 2006, Bush et al. 2011).
70 Paleoecological studies focused on the Cerrado Domain itself have suggested a retraction of
71 the cerrado tree flora during the LGM, probably caused by considerable declines in both
72 precipitation and temperature (Salgado-Labouriau 1973, 1984, Ledru 1993, Behling 1995,

73 Ferraz-Vicentini and Salgado-Labouriau 1996, Ledru et al. 1996, Salgado-Labouriau et al.
74 1997, Barberi et al. 2000, Salgado-Labouriau 2001, Ledru 2002, Lima-Ribeiro et al. 2004).
75 Understanding the nature of any LGM retraction of cerrado vegetation in the Cerrado
76 Domain has important implications, because refugial areas may contain higher overall
77 species richness and higher genetic diversity within individual species (Collevatti et al. 2012,
78 Lima et al. 2014), and therefore should be priorities for conservation. Understanding whether
79 any refugial areas were numerous and scattered micro-refugia, or fewer, larger areas is
80 therefore of great relevance (Rull 2009, 2011, Vegas-Vilarrubia et al. 2011).

81 The key question of whether cerrado vegetation may have expanded into Amazonia or
82 contracted during the LGM can be addressed by modelling species distributions. Recent
83 investigations, based on modelling species distributions and patterns of species richness,
84 endemism and genetic variation, have provided increased evidence that climatically stable
85 areas could have played the role of refugia for moist forest species in the Neotropics during
86 Quaternary climatic fluctuations (Graham et al. 2006, Carnaval and Moritz 2008, Carnaval et
87 al. 2009, Keppel et al. 2012, Werneck et al. 2011, 2012, Carnaval et al. 2014, Montade et al.
88 2014). Most of these recent studies have focused on moist forests and the existence of such
89 refugia for cerrado vegetation has not been sufficiently tested using newer approaches, such
90 as species distribution modelling. In addition to this, there has been little investigation of the
91 distribution of savannas, and the cerrado in particular, before the LGM (although see
92 Werneck et al. 2012). During the Last Interglacial (LIG, which began ~130,000 to 116,000
93 BP (130 - 116 Ka), the climate was significantly warmer than during the Holocene
94 maximum, registering globally higher temperatures (ca. +2°C) and higher summer insolation
95 (Otto-Bliesner et al. 2006). Thus, expansion of the cerrado vegetation and contraction of
96 moist vegetation may have actually occurred during the LIG.

97 Species distribution modelling can be used to complement palynological studies and
98 enhance our capacity to hindcast and forecast changes in population and vegetation dynamics

99 (Scoble and Lowe 2010, Mellick et al. 2012). This study is the first to hindcast the
100 distributions of tree species characteristic of the cerrado vegetation to the Last Inter-Glacial
101 (LIG) and Last Glacial Maximum (LGM). Werneck et al. (2012) modelled the distribution of
102 cerrado vegetation based both on a map of the Cerrado Domain from Brazilian Institute of
103 Geography and Statistics (IBGE 1998) and a broader spatial definition, as geographically
104 defined by Olson et al. (2001). However, this approach is less realistic biologically than
105 studying the responses of individual species (Collevatti et al. 2013), which is the approach
106 that we use here.

107 Our main questions were: (a) was there an expansion or contraction of the cerrado
108 vegetation during the LGM and/or LIG; (b) if cerrado vegetation contracted during one of
109 these time periods, were there areas of higher environmental suitability that could have
110 operated as refugia; and (c) if and when cerrado vegetation expanded, was it extensive
111 enough to fragment Amazonian forest and/or establish connections between the cerrado and
112 the savannas of northern South America?

113

114 **METHODS**

115 **Study area**

116 The Cerrado Domain spreads across the Central Brazilian Highlands, which comprise
117 $\frac{1}{4}$ of Brazil's surface, and to smaller areas in northwestern Paraguay and eastern Bolivia
118 (Olson et al. 2001, Oliveira-Filho and Ratter 2002) (Fig. 1). It is the second largest
119 Phytogeographical Domain in South America, surpassed in area only by the Amazon (Ribeiro
120 and Walter 2008). The Cerrado Domain extends over 20 degrees of latitude and from
121 altitudes of 100 m in the Pantanal (western floodplains) to 1500 m in the highest tablelands of
122 the Central Brazilian Highlands (Ribeiro and Walter 2008). There is remarkable variation in
123 mean annual temperatures across the region, ranging from 18 to 28°C. Rainfall also varies

124 widely, from 800 to 2000 mm.yr⁻¹, with a long-lasting dry season during the austral winter
125 (approximately April–September) (Ab’Saber 2003).

126 The prevalent vegetation type of the Cerrado Domain bears the same name, cerrado. It
127 is a woody savanna that varies from fairly open grasslands to forests with a nearly closed
128 canopy called cerradão (Ribeiro and Walter 2008). The typical cerrado vegetation grows on
129 acidic, dystrophic soils and is one of the richest savanna floras of the world, with over 12,000
130 species of vascular plants (Mendonça et al. 2008).

131

132 **Dataset**

133 The floristic dataset was extracted from NeoTropTree (Oliveira-Filho 2014), a
134 database that consists of tree (defined as free-standing woody plants >3 m in height) species
135 checklists for >2000 geo-referenced sites compiled from the literature and herbarium
136 specimen records. We extracted all 638 sites and 2155 species matrix from the Cerrado
137 Domain, representing 288 sites of typical cerrado vegetation, 112 sites of semideciduous
138 forest, 116 of seasonally dry tropical forest and 122 of mesotrophic cerradão.

139 The cerrado vegetation is essentially a vegetation of poor dystrophic soils, and where
140 more fertile soils occur in the Cerrado Domain, they are occupied by seasonally dry tropical
141 forests or mesotrophic cerradão, which is transitional between seasonally dry tropical forests
142 and typical cerrado vegetation (Ratter *et al.* 1973, 1977, 1978a b, Oliveira-Filho and Ratter
143 2002, Ribeiro and Walter 2008, Bueno et al. 2013). Seasonally dry tropical forests are
144 notable for experiencing little fire and are thus occupied by a different set of plant lineages
145 (e.g. Cactaceae) than those in typical cerrado vegetation, which experiences frequent and
146 more intense fires (Pennington et al. 2000, 2009). Meanwhile, mesotrophic cerradão is an
147 almost closed forest with a canopy cover of 50-90%, with trees often growing to 8-12 m
148 (casting a considerable shade so that the ground layer is much reduced), and including a
149 blend of species from both typical cerrado vegetation and seasonally dry tropical forests

150 (Ratter *et al.* 1973, 1977, 1978a, Furley & Ratter 1988, Ratter 1992, Oliveira-Filho and
151 Fontes 2000, Oliveira-filho and Ratter 2002, Bueno et al. 2013). Semideciduous forests are
152 found in more humid areas than typical cerrado vegetation, such as along river courses (i.e.
153 gallery forest) or in transition zones with moist forests of the Amazon or the Mata Atlantica.
154 Semideciduous forests tend to be richer in species than the other vegetation types (Oliveira-
155 Filho and Ratter 1995, 2000, 2002).

156 We then performed an Indicator Species Analysis, ISA (Dufrene and Legendre 1997),
157 of the same matrix from the Cerrado Domain to extract the species that indicate typical
158 cerrado vegetation communities. The ISA produces an IV (indicator value) obtained by a
159 combination of a species' frequency within a group compared with other groups (specificity)
160 and the species' presence in most sites of that group (fidelity). We performed the analysis
161 using the labdsv package (Roberts 2013) in the R Statistical Software (R Core Team 2013).
162 We then selected the ten species with the top IVs in typical cerrado and extracted the
163 geographical coordinates of floristic lists in which the species were present from
164 NeoTropTree (see Table 1).

165

166 **Bioclimatic variables**

167 For all sites, we obtained the value, at 2.5 arc-min (approximately 5 km) resolution, of
168 the 19 standard BIOCLIM variables, which reflect various aspects of temperature,
169 precipitation, and seasonality and which are likely to be important in determining species
170 distributions (Hijmans et al. 2005). We cropped the bioclimatic layers to span from 12°47'N
171 to 34°46'S and from 78°31'W to 35°00'W, following Werneck et al. (2012) and which
172 represents a much larger spatial range than that of the Cerrado Domain. After assessing
173 correlations between the bioclimatic variables, we retained 10 of 19 variables, eliminating
174 those with less biological relevance from groups of strongly interrelated variables ($r > 0.9$).
175 This procedure was done to avoid over-parametrization of our modelling with redundant

176 variables. The final selected variables were: annual mean temperature, mean diurnal range,
177 isothermality, temperature annual range, mean temperature of wettest quarter, mean
178 temperature of the driest quarter, mean temperature of warmest quarter, annual precipitation,
179 precipitation of wettest month and precipitation of the driest month.

180

181 **Model construction**

182 We modelled the ecological niche of the ten selected indicator tree species (Table 1)
183 using Maxent v.3.3 (Phillips et al. 2006). It has been demonstrated that Maxent often
184 outperforms other modelling techniques to identify areas critical to the maintenance of
185 species populations (Elith et al. 2006, 2011, Pearson et al. 2007, Phillips and Dudík 2008,
186 Gogo-Prokurat 2011, Pena et al. 2014). In addition, an important reason for choosing Maxent
187 was that it allowed us to use presence-only species data, which is of great utility because the
188 vast majority of the biotic data available, including those used here, come in this form (Elith
189 et al. 2006, Phillips and Dudík 2008).

190 To calibrate and evaluate the quality of the models, we divided the data for each species
191 into a training set (75% of occurrences) and a test or validation set (25% of occurrences). We
192 constructed models five times and averaged the output to produce the final results used in
193 downstream analyses. Next, for each species, we defined a threshold value above which grid
194 cells were considered to have environmental characteristics suitable for the maintenance of
195 viable populations of the species (Pearson et al. 2007). We used the "Minimum Training
196 Presence" as the threshold selection method because it assumes that the species presence is
197 restricted to sites at least as suitable as those at which the species has been observed so far
198 (Pearson et al. 2007).

199 In order to produce models to infer the palaeodistribution of the cerrado indicator tree
200 species, we produced projections of the suitability of occurrence during the Current (0 ka pre-
201 industrial), Mid-Holocene (6 ka BP), Last Glacial Maximum (LGM - 21 ka BP), and Last

202 Interglacial (LIG - 130 ka BP) time periods based on climatic simulations (see
203 www.worldclim.org; Hijmans et al. 2005). [For the Last Glacial Maximum \(21 ka, LGM\),](#)
204 [Holocene \(6 ka\) and Current \(0 ka pre-industrial\), we employed the Community Climate](#)
205 [System Model – CCSM4 \(Gent et al. 2011\), and dates represent downscaled climate data](#)
206 [from simulations with Global Climate Models \(GCMs\) based on the Coupled Model](#)
207 [Intercomparison Project Phase 5 \(CMIP5; Taylor et al. 2012\). Paleo-climatic model for the](#)
208 [Last Interglacial \(120 ka, LIG\) used the approach of Otto-Bliesner et al. \(2006\).](#) We summed
209 the projections of the ten indicator tree species for each time period, which together represent
210 the probability of occurrence of typical cerrado vegetation during that time period. We
211 performed all geographic information system (GIS) analyses in ArcGIS v.10 (ESRI 2011).

212 To indicate potential areas of climatic stability for cerrado tree species during the whole
213 of the Quaternary, we adopted protocols similar to those used in recent studies for other
214 Neotropical Domains (Carnaval and Moritz 2008, Werneck et al. 2011, 2012). Spatial models
215 were converted from continuous outputs into presence/absence maps by applying the lowest
216 presence threshold for each model. This approach maximizes agreement between observed
217 and modelled distributions, balancing the cost arising from an incorrect prediction against the
218 benefit gained from a correct prediction (Pearson et al. 2007). By summing up the
219 presence/absence maps obtained under Current, Holocene (6 ka BP), LGM (21 ka BP) and
220 LIG (130 ka BP) projections, we generated a map of areas showing historical stability. This
221 combined map depicted areas that were potentially occupied by typical cerrado species
222 during the climatic oscillations of the Quaternary. These historically stable areas, which we
223 considered to be potential refugia, were defined as those grid cells for which the presence of
224 all indicator species was inferred across all time projections.

225

226 **Species distribution modelling validation**

227 We calculated the sensitivity (the proportion of observed presences in relation to those
228 that were predicted, which quantifies omission errors), the specificity (the proportion of
229 observed absences compared to those that were predicted, which quantifies commission
230 errors) and the TSS (true skill statistic), following Allouche et al. (2006). The TSS test
231 corrects the overall accuracy of the model prediction by the accuracy expected by chance.
232 This test provides a score between -1 and +1, with values >0.6 considered to be good, 0.2–0.6
233 to be fair to moderate and <0.2 to be poor (Jones et al. 2010). The TSS is a threshold-
234 dependent measure that is appropriate for evaluating predictive accuracy in cases where the
235 model prediction is formulated as a presence-absence map (Allouche et al. 2006, Jones et al.
236 2010). These analyses used the occurrence points of the ten indicator tree species and 202
237 occurrences of *Eugenia uruguayensis* Cambess. obtained from NeoTropTree (Oliveira-Filho
238 2014), which has a restricted niche that differs from the typical cerrado species and is ideal
239 for simulating absence points for typical cerrado vegetation.

240 We also used a threshold-independent method of model validation, the receiver
241 operating characteristic (ROC) curve analysis. The ROC curve is obtained by plotting
242 sensitivity values (the true positive fraction) on the y-axis against their equivalent specificity
243 values ($1 - \text{specificity}$, the false positive fraction) on the x-axis for all possible thresholds
244 (Fielding and Bell, 1997). The ROC analysis characterizes the predictive performance of a
245 model at all possible thresholds by a single number, the area under the curve (AUC) (Fawcett
246 2003, Phillips et al. 2006). A single AUC value was calculated for each species, representing
247 the average across the five iterations of model construction. The value of the AUC can fall
248 between 0.5 and 1.0. If the value is 0.5, the model is no better than random, while models
249 with values above 0.75 are generally considered potentially useful and models with a value
250 near one are considered to be strongly supported (Fielding and Bell 1997, Elith 2002,
251 Rushton et al. 2004, Phillips et al. 2006).

252

253 **RESULTS**

254 The ten tree species identified by our indicator species analyses as the most important
255 indicators of typical cerrado and therefore chosen to generate ecological niche models and
256 predict current and past distributions are given in Table 1. The quality of the models,
257 according to AUC and TSS values computed for the ten indicator tree species, showed that
258 sample and background predictions generated by Maxent were generally in agreement (Table
259 2). That is, the Maxent model performance in this study is much better than random. This was
260 confirmed by the correct assignment of the test data using the models, indicating that the
261 models showed a good performance in predicting species occurrences with bioclimatic
262 variables.

263 The palaeomodells suggest significant changes in the distributions of typical cerrado
264 tree species during the Quaternary (Fig. 2). The cerrado tree flora experienced its maximum
265 expansion during the Last Inter-Glacial (LIG), when the modelled species spread toward the
266 south and east of the Amazon basin as well as toward the Atlantic coast in both southeastern
267 and northeastern Brazil (Fig. 2A). All of these areas shelter current-day cerrado enclaves
268 within moist forests of both the Amazonian and Atlantic Forest Domains, as well as within
269 the semi-arid thorn-woodlands of the Caatinga Domain.

270 In contrast with the LIG, the models suggest a maximum retraction of the modelled
271 cerrado species during the Last Glacial Maximum (LGM), with an almost entire withdrawal
272 from both eastern Amazonia and Atlantic coastal areas coupled with a contraction toward
273 central Brazil and eastern Bolivia (Fig. 2B). Further, there was a notable retraction of typical
274 cerrado vegetation to inter-tableland depressions and the slopes of the Central Brazilian
275 Highlands, as well as a low suitability at higher altitudes (Fig. 3).

276 In the Mid-Holocene (Fig. 2C), the modelled species expanded their distributions to
277 approach those of the current distribution of the typical cerrado vegetation. Lastly, the results
278 obtained for the Current projection (Fig. 2D) showed a distribution similar to that of the

279 Cerrado Domain, as delimited by Olson et al. (2001). Indeed, a map of under vs. over-
280 prediction of cerrado vegetation with respect to the map of Olson et al. (2001) shows high
281 congruence, particularly in areas of the central Cerrado Domain. Meanwhile, we
282 overpredicted typical cerrado vegetation in ecotonal areas between the Cerrado Domain and
283 adjacent Domains, i.e. in semideciduous forests that transition to the Amazon and Mata
284 Atlantica moist forests (see Supplementary material Appendix 1, Fig. S1).

285 Some areas in the central region of the Cerrado Domain showed a high probability of
286 climatic stability throughout the Quaternary and are shown in yellow in Figure 4. These
287 postulated refugia for typical cerrado vegetation occur mainly in Minas Gerais and São Paulo
288 states and the Federal District, with smaller areas scattered across the Cerrado Domain in
289 other states, such as Tocantins, Goiás and Mato Grosso. The distribution of Brazilian
290 conservation units shows a low level of coincidence with these postulated refugia (Fig. 4).

291

292 **DISCUSSION**

293 **Modelling cerrado indicator species**

294 Our results demonstrated the greatest extent of typical cerrado tree species in the LIG,
295 the greatest contraction in the LGM, and a subsequent re-expansion in the Holocene. The
296 values obtained by TSS and AUC modelling suggest that the environmental variables used in
297 our models provided important information on the distribution of the tree species selected as
298 indicators of typical cerrado vegetation, and were higher than those obtained by other studies
299 modelling the climatic distribution of neotropical vegetation (Carnaval and Moritz 2008,
300 Werneck et al. 2011, 2012, Pena et al. 2014), but which did not model individual indicator
301 species. The indicator species method has been widely and effectively used to determine
302 ecological indicators of community types, habitat conditions, and environmental changes
303 (Dufrêne and Legendre 1997, Carignan and Villard 2002, Niemi and McDonald 2004, De
304 Cáceres and Legendre 2009, De Cáceres et al. 2010, 2012).

305 Our conclusions are based upon palaeoclimate simulations derived from GCMs, which
306 are known to be inaccurate, particularly in simulating precipitation (Stainforth et al. 2005,
307 2007a b, Woldemeskel et al. 2012). Because of this uncertainty, wherever possible we
308 discuss our results in light of palaeoclimatic reconstructions based upon other proxies,
309 including fossil pollen and speleotherms (e.g. Van der Hammen 1991, Ledru 1993, Van der
310 Hammen and Absy 1994, Ledru et al. 1996, Ferraz-Vicentini and Salgado-Labouriau 1996,
311 Salgado-Labouriau 1997, Salgado-Labouriau et al. 1997, 1998, Barberi et al. 2000, Saniotti et
312 al. 2002, Cruz et al. 2005, 2006, 2009, Cheng et al. 2013, Baker and Fritz 2015). One
313 important point that is clear from these studies is that climatic changes were probably not
314 synchronised across lowland tropical South America; rather, different parts of South America
315 may have experienced climatic change in different directions at the same time. Predicting the
316 exact history of dispersal, extinction and recolonization of any typical cerrado tree species
317 across lowland tropical South America is therefore challenging. Thus, here we try and focus
318 on general patterns that can be inferred from our multi-species, palaeodistribution modelling
319 approach.

320

321 **Cerrado distribution during the LIG, LGM and Holocene**

322 Climate models suggest a warmer and slightly drier climate during the LIG in those
323 areas of the present-day Atlantic and Amazon rain forests into which the cerrado tree species
324 modelled here are suggested to have expanded. Seasonal climates expanded toward the
325 Atlantic coast in southeastern Brazil, and the palaeomodel indicated suitable areas for typical
326 cerrado species as near the coast, e.g. in the Paraíba river valley, in Rio de Janeiro and São
327 Paulo. In fact, there were small remnants of cerrado in this region, most of which have
328 disappeared due to habitat alteration in the last century (Matsumoto and Bittencourt 2001).

329 The modelled expansion of typical cerrado tree species into the Amazon during the LIG
330 is particularly notable within the “Amazonian Dry Corridor”, a transverse zone with mean

331 annual precipitation below 1750 mm extending in a northwest-southeast direction near the
332 cities of Óbidos and Santarém (Haffer 1969, Figueroa and Nobre 1990, Van der Hammen and
333 Absy 1994). Although most of this region is forested, numerous isolated savannas are found
334 there, and it connects the savannas of central Venezuela with the savannas of central and
335 northeastern Brazil (Haffer 1969). Ab'Saber (2003) suggested the existence of savanna
336 corridors in Amazonia during the Quaternary, though he was not certain about the period
337 when such corridors may have existed. He also hypothesised that the corridors probably
338 linked present-day disjunct patches of Amazonian savannas. Our models provide some
339 corroboration for this idea, showing the expansion of cerrado species toward many of these
340 currently disjunct savannas (Sanaiotti et al. 2002), such as Alter do Chão, Amapá, Redenção,
341 Roraima, Humaitá and the Beni in Bolivia.

342 Our results are congruent with those of Werneck et al. (2012) who also suggested past
343 connections of the cerrado to other areas of savanna in South America during the LIG and a
344 lack of significant savanna areas or corridors across central Amazonia during the LGM.
345 Baker and Fritz (2015) discussed the importance of applying a salinity and temperature
346 correction to $\delta^{18}\text{O}$ isotopic records. When these corrections are applied to the mean value of
347 $\delta^{18}\text{O}$ during the LGM in Amazonia (Cheng et al. 2013), this substantially alters previous
348 climatic interpretations that the Amazon was “severely dry” during the LGM. These findings
349 all contrast with one assumption of the Pleistocene Refuge Theory (Haffer 1969, Prance
350 1982, Whitmore and Prance 1987), which implicated an LGM savanna expansion due to drier
351 climates.

352 Palaeoecological studies from localities across lowland tropical South America support
353 a decrease in temperature during the LGM, indicated by the expansion of cold-adapted taxa,
354 which are currently either relictual elements in Amazonia and the Central Brazilian
355 Highlands, such as *Podocarpus*, *Ilex*, *Myrsine* and *Hedyosmum* (Colinvaux et al. 1996,
356 Cardenas et al. 2011), or have vanished completely, like *Araucaria* (Ledru 1993). On the

357 other hand, during the LGM there was a drastic retraction in the occurrence of the tropical
358 palm *Mauritia*, which has been considered as an indicator of higher temperatures (Barberi et
359 al. 2000), as well as the disappearance of tree species characteristic of seasonally dry tropical
360 forest in eastern Bolivia (Whitney et al. 2013).

361 Many authors agree that climate in the central area of the Cerrado Domain during the
362 LGM was characterized by a decrease in both precipitation and temperature (Barberi et al.
363 2000, Ferraz-Vicentini and Salgado-Labouriau 1996, Lima-Ribeiro et al. 2004). However,
364 according to Salgado-Labouriau et al. (1998), there was no synchronicity of LGM climates
365 inferred from palynological studies in the Cerrado Domain, which they attributed to
366 differences in latitude and regional topography.

367 Our models emphasize low climatic suitability during the LGM for cerrado tree species
368 at high altitudes (above ~ 800 m) in the Cerrado Domain, particularly in the Central Brazilian
369 Highlands. For example, LGM palaeorecords of Barberi et al. (2000) and Salgado-Labouriau
370 et al. (1997) infer a prevalence of cold and semi-arid climates in those highlands, with strong
371 winds, partial soil exposure and concomitant increased erosion, based on the almost complete
372 absence of arboreal pollen elements. Our LGM models suggest that cerrado tree species
373 persisted at lower altitudes, probably favoured by a warmer climate, deeper soil and higher
374 ground water storage than at higher altitudes. Thus, the inter-tableland depressions and
375 highland slopes of central Brazil may have been refugia for cerrado species, rather than the
376 highlands where climates were too cold and dry, as suggested by Ab'Saber (2003) and
377 Werneck et al. (2012).

378 Our model, showing a retraction of major areas of typical cerrado vegetation during the
379 LGM, is also corroborated by recent studies of population genetics in cerrado tree species
380 (Ramos et al. 2007, Novaes et al. 2010, Lima et al. 2014). Phylogeographic studies of
381 *Hymenaea stignocarpa*, *Plathymenia reticulata*, *Tabebuia aurea* and *Mauritia flexuosa* found
382 greater genetic diversity in the central region of the Cerrado Domain, which is indicative that

383 this area could have been more stable during the LGM. A study of the phylogeography of the
384 tree species *Caryocar brasiliense* by Collevatti et al. (2003, 2012) showed that multiple
385 lineages may have contributed to the present-day populations of *Caryocar brasiliense* in the
386 Cerrado Domain, and that populations restricted to refugia in the central region during the
387 LGM may have spread and dispersed to favourable areas in the last 7,000 years. Moreover, in
388 his revision of Neotropical *Andira*, Pennington (2003) highlighted a north to south parapatric
389 distribution of *Andira cuyabensis* and *Andira cordata* across the centre of the Cerrado
390 Domain, perhaps related to a prior separation of the currently continuous typical cerrado
391 vegetation during the LGM, as also suggested by the palynological data of Ledru (1993).

392 At the end of the LGM, between 17,000 and 11,000 BP, the climate became
393 progressively more humid. However, permanent polar fronts remained at 10°S – 20°S
394 latitude (~ 8,500 BP), inferred from the presence of *Araucaria* forests (now confined to
395 southern and southeastern Brazil) and the association of temperate-adapted *Podocarpus* with
396 *Caryocar* in areas presently covered by typical cerrado (Ledru 1993, Ledru et al. 1996). With
397 increasing temperatures, the cold weather elements were probably confined to higher
398 altitudes, principally in gallery forests, a hypothesis supported by the presence of *Podocarpus*
399 in the higher plateaux of the Federal District and Chapada dos Veadeiros (Barbieri 2000).

400 The return of warmer, humid conditions in the Mid-Holocene would have favoured
401 the expansion of typical cerrado vegetation in the core area of the Cerrado Domain (Oliveira-
402 Filho and Ratter 2000). The appearance of *Mauritia* (Barbieri et al. 2000, Ledru 2002, Lima et
403 al. 2014) and the increasing concentration of charcoal particles, are both associated with
404 increasing temperatures and the re-expansion of cerrado vegetation (Salgado-Labouriau
405 1997). These changes are corroborated by palaeoecological studies from various localities
406 and supported by our palaeomodels for 6,000 BP. During this period, Behling (1995)
407 recorded an increase of species typical of cerrado vegetation, such as *Curatella americana*, in
408 the Lagoa do Pires between the Cerrado and Atlantic Forest Domains in Minas Gerais state.

409 In the state of Rondônia, there was an isotopic enrichment related to the replacement of forest
410 vegetation by typical cerrado vegetation (Pessenda et al. 1998a), as also observed in the
411 region of Humaitá, in the south of Amazonas state (Gouveia et al. 1997, Pessenda et al.
412 1998b, De Freitas et al. 2001). At the Bolivian border with Brazil, in an area now covered by
413 Amazonian forest, Mayle et al. (2000) and Mayle and Whitney (2012) also recorded the
414 presence of *Curatella* and *Mauritia* during the same period. This find is compatible with a
415 trend of continuously increasing pollen deposition of typical cerrado taxa in the period
416 (Barbieri 2000, Ledru 2002). The patterns may have been accentuated by soil leaching and
417 acidification, which would also have favoured the expansion of typical cerrado vegetation
418 (Oliveira-Filho and Ratter 2000).

419

420 **Current distribution of cerrado, stable areas and conservation**

421 Around 2,000 years BP, palaeoecological studies suggest the onset of present-day
422 climatic conditions. The establishment of a vegetation mosaic with a predominance of typical
423 cerrado species, interspersed with forest and wet grassland formations, is suggested by
424 numerous authors (Ab'Saber 2003, Oliveira-Filho and Ratter 1995, 2002, Ribeiro and Walter
425 2008). In the modelled current potential distribution, areas of the central Cerrado Domain are
426 maximally suitable for the occurrence of typical cerrado tree species, particularly on the
427 central Brazilian tablelands. This finding is corroborated by Ratter et al. (2003) and
428 Bridgewater et al. (2004), who demonstrated that areas of the central Cerrado Domain show
429 the highest species richness of cerrado tree species.

430 This high diversity may reflect the stability of the central Cerrado Domain throughout
431 the timespan of our climate models. Other studies have indicated that the stability of climate
432 through time facilitates the accumulation and maintenance of diversity in Neotropical
433 vegetation (Graham 2006, Carnaval et al. 2009, Werneck et al. 2012). The persistence of
434 some species in multiple refugia located throughout their present distribution indicates that

435 these species might have persisted through multiple climatic cycles in heterogeneous
436 environments (Keppel et al. 2012, Turchetto-Zolet et al. 2013). The microrefugia (yellow
437 areas in Figure 4) are small areas with favourable environmental features within which small
438 populations could have survived when their main distribution area contracted (Rull 2009,
439 2011, Vegas-Vilarrubia et al. 2011). These areas of historical climate stability likely allowed
440 a number species to persist through time, whereas extinction took place in areas that
441 experienced the most severe climate changes. This then likely resulted in greater diversity in
442 more stable areas (Rull 2008, 2011, Collevatti et al. 2012, Keppel et al. 2012).

443 There has been a great loss in species diversity and endemism in important areas of the
444 Cerrado, as a result of disturbance, and total clearance, by humans, especially due to the
445 expansion of agriculture, cattle ranching, and charcoal production (Ratter et al. 1997, Silva
446 and Bates 2002). There are estimates that less than 20% of the Cerrado Domain vegetation
447 remains undisturbed while only 7.44% is legally protected in conservation units. Meanwhile,
448 many threatened species remain outside any of the region's parks and reserves (MMA 2011)
449 contributing to the status of the Cerrado Domain as one of the world's biodiversity hotspots,
450 deserving urgent conservation intervention (Myers et al. 2000).

451 In our model, climatically stable areas are mostly outside the existing protected areas.
452 The few exceptions are those located in the Federal District and a number of Environmental
453 Protection Areas (APA; a lesser protection level) in Tocantins state (Figure 4). Larger
454 climatically stable areas in Minas Gerais and São Paulo states have no conservation units
455 (Figure 4). We suggest that the areas identified as climatically stable in our analyses should
456 be incorporated into systematic conservation planning to preserve the Cerrado tree flora, as
457 they represent probable refugial areas with potentially high species and genetic diversity.

458

459 **CONCLUSION**

460 Palaeodistribution modelling of tree species representative of typical cerrado vegetation

461 showed expansions and contractions related to the climatic fluctuations of the Quaternary,
462 with the widest expansion during the LIG, related to a warmer, more seasonal climate. The
463 inter-tableland depressions and the highland slopes in the central region of the Cerrado
464 Domain probably operated as refugia for the Cerrado flora during its major retraction in the
465 LGM, a conclusion that is highly congruent with palynological and phylogeographic studies.
466 This central region is indicated as the most species-rich and most stable throughout the
467 climate fluctuations of the Quaternary, and the conservation of such high-diversity and
468 climatically stable areas should be prioritized.

469

470 **ACKNOWLEDGEMENTS**

471 This study was in partial fulfilment of the Doctoral requirements of M.L. Bueno who
472 thanks CNPq for supporting a 12-month study period at the Royal Botanic Garden Edinburgh
473 (grant SWE - 202096/2011-4) and Postdoctoral scholarship in UFMG (151002/2014-2). M.L.
474 Bueno thanks the Royal Botanic Garden Edinburgh for support during the time this research
475 was conducted.

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736

737 Table 1. The ten tree species selected as indicators of typical cerrado vegetation. IV - indicator value; IV-*p* - the probability of obtaining as high an
 738 indicator value as that observed for typical cerrado vegetation.

Species	Species records	Relative frequency in main vegetation types				IV	IV- <i>p</i>
		Typical cerrado	Mesotrophic cerradão	Seasonally dry tropical forests	Semideciduous forests		
<i>Connarus suberosus</i> Planch.	296	0.85	0.59	0.02	0.00	0.50	0.001
<i>Erythroxylum suberosum</i> St. Hil.	234	0.84	0.58	0.01	0.00	0.50	0.001
<i>Palicourea rigida</i> Kunth	182	0.65	0.20	0.00	0.01	0.50	0.001
<i>Kielmeyera coriacea</i> Mart. & Zucc.	244	0.87	0.58	0.03	0.09	0.49	0.001
<i>Annona crassiflora</i> Mart.	194	0.69	0.26	0.02	0.04	0.48	0.001
<i>Caryocar brasiliense</i> Cambess.	263	0.75	0.40	0.03	0.06	0.47	0.001
<i>Couepia grandiflora</i> (Mart. & Zucc.) Benth.	242	0.70	0.33	0.02	0.02	0.46	0.001
<i>Qualea parviflora</i> Mart.	254	0.91	0.84	0.04	0.03	0.45	0.001
<i>Byrsonima coccolobifolia</i> Kunth	218	0.78	0.48	0.03	0.06	0.45	0.001
<i>Qualea grandiflora</i> Mart.	266	0.95	0.92	0.12	0.08	0.43	0.001

740 Table 2. Evaluation of the model performance for cerrado indicator tree species of cerrado vegetation by Maxent. True skill statistic (TSS)
 741 and area under the curve (AUC).

Species	Training samples	External test presence points	External test absence points	Sensitivity	Specificity	TSS	AUC
<i>Connarus suberosus</i> Planch.	237	59	202	0.95	1.00	0.95	0.92
<i>Erythroxylum suberosum</i> St.Hil.	176	58	202	0.78	1.00	0.78	0.92
<i>Palicourea rigida</i> Kunth	137	45	202	0.90	1.00	0.90	0.92
<i>Kielmeyera coriacea</i> Mart. & Zucc.	183	61	202	0.61	0.99	0.60	0.92
<i>Annona crassiflora</i> Mart.	146	48	202	0.95	1.00	0.94	0.93
<i>Caryocar brasiliensis</i> Cambess.	211	52	202	0.85	1.00	0.85	0.93
<i>Couepia grandiflora</i> (Mart. & Zucc.) Benth.	194	48	202	0.64	0.99	0.63	0.92
<i>Qualea parviflora</i> Mart.	191	63	202	0.93	1.00	0.93	0.91
<i>Byrsonima coccolobifolia</i> Kunth	164	54	202	0.75	1.00	0.75	0.93
<i>Qualea grandiflora</i> Mart.	200	66	202	0.93	1.00	0.93	0.91

742

743 **FIGURE LEGENDS**

744 **Figure 1.** Geographic distribution of the Cerrado Domain and savannas in South America
745 (Olson et al. 2001), with the location and vegetation type of floristic checklists used in this
746 study (typical cerrado vegetation: blue circles, mesotrophic cerradão: red circles, seasonally
747 dry tropical forest: orange circles, and semideciduous forests: green circles), following
748 (Oliveira-Filho 2009). Brazilian states are labelled as follows: Amazonas (AM), Bahia (BA),
749 Ceará (CE), Distrito Federal (DF), Espírito Santo (ES), Goiás (GO), Maranhão (MA), Minas
750 Gerais (MG), Mato Grosso (MT), Mato Grosso do Sul (MS), Pará (PA), Paraná (PR), Piauí
751 (PI), Rio de Janeiro (RJ), Rondônia (RO), São Paulo (SP), Tocantins (TO).

752

753 **Figure 2.** Predicted occupancy across northern South America of ten tree species that are
754 indicators of typical cerrado vegetation during: A – the Last Interglacial (LIG. 130 ka BP); B
755 – the Last Glacial Maximum (LGM. 21 ka BP); C – the Mid-Holocene (6 ka BP); and D-
756 under Current climate (0 ka pre-industrial). Predictions were based on ecological niche
757 models of climatic preference developed separately for each species using the MaxEnt
758 algorithm (Phillips et al. 2006). Predicted occupancy was then summed across all ten species.
759 Warmer colours (red/yellow) of the logistic output correspond to regions with a higher
760 probability of occurrence. Black lines represent the borders of Brazilian states and South
761 America countries.

762

763 **Figure 3.** Predicted occupancy of ten tree species that are indicators of typical cerrado
764 vegetation during the Last Glacial Maximum (LGM. 21 ka BP) showing the main highland
765 systems of Central Brazil and the low suitability of higher altitudes. Black lines are states
766 border. Warmer colours (red/yellow) correspond to regions with a higher probability of
767 occurrence for all ten species. See Fig. 2 and text for further details.

768 **Figure 4.** Predicted regions of historical stability for typical cerrado vegetation across the
769 Quaternary, based on summing the predicted occupancy of ten indicator tree species across
770 Current (0 ka pre-industrial), Mid-Holocene (6 ka BP), Last Glacial Maximum (LGM. 21 ka
771 BP) and Last Interglacial (LIG. 130 ka BP) climatic scenarios. Areas in yellow are those
772 where all ten species are predicted to occur at all four time periods, and represent postulated
773 refugial areas for typical cerrado vegetation. Areas outlined in red are Brazilian conservation
774 units, while black lines represent the limits of Brazilian states and South America countries.
775 Maps are given for (A) northern South America, (B) the central area of the Cerrado Domain,
776 and (C) the Federal District.

777

778

779 **SUPPLEMENTARY INFORMATION**

780 **Figure S1.** Geographic distribution of the Cerrado Domain and savannas in South America
781 (Olson et al. 2001). Dark red shading represents the overlap of current predicted typical
782 cerrado vegetation (based on this study) and the Cerrado Domain. Lighter red shading
783 indicates overprediction (areas where typical cerrado vegetation is predicted to occur at
784 present outside of the Cerrado Domain), while grey shading indicates underprediction (areas
785 within the Cerrado Domain where typical cerrado vegetation is not predicted to occur at
786 present). Brazilian states are labelled as follows: Amazonas (AM), Bahia (BA), Ceará (CE),
787 Distrito Federal (DF), Espírito Santo (ES), Goiás (GO), Maranhão (MA), Minas Gerais
788 (MG), Mato Grosso (MT), Mato Grosso do Sul (MS), Pará (PA), Paraná (PR), Piauí (PI), Rio
789 de Janeiro (RJ), Rondônia (RO), São Paulo (SP), Tocantins (TO).