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1 **Tropical grassy biomes: linking ecology, human use and conservation**

2

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11 **Abstract**

12

13 Tropical grassy biomes are changing rapidly the world over through a coalescence of
14 high rates of land use change, global change and altered disturbance regimes that
15 maintain the ecosystem structure and function of these biomes. Our theme issue
16 brings together the latest research examining the characterisation, complex ecology,
17 drivers of change, and human use and ecosystem services of tropical grassy biomes.
18 Recent advances in ecology and evolution have facilitated a new perspective on these
19 biomes. However, there continue to be controversies over their classification and
20 state dynamics that demonstrate critical data and knowledge gaps in our quantitative
21 understanding of these geographically dispersed regions. We highlight an urgent need
22 to improve ecological understanding in order to effectively predict the sensitivity and
23 resilience of tropical grassy biomes under future scenarios of global change. With
24 human reliance on tropical grassy biomes increasing and their propensity for change,
25 ecological and evolutionary understanding of these biomes is central to the dual goals
26 of sustaining their ecological integrity and the diverse services these landscapes
27 provide to millions of people.

28 **1. Introduction**

29 Historically extensive across the global tropics, tropical grassy biomes (TGBs)
30 are now changing rapidly through high rates of land clearance (1), increasing land use
31 intensity (2, 3), woody encroachment (4) and disruption of the disturbance regimes
32 (5, 6) that maintain ecosystem function. These biomes were the cradle of human
33 evolution (7), and in our contemporary world, they support the livelihoods and
34 wellbeing of over one billion people (8). With the population of Africa alone set to
35 treble by 2050 (3), the continuing pace of climate change (9), increasing atmospheric
36 CO₂ concentrations (9), and the increasing agricultural development of TGBs (3, and
37 Estes et al., in this issue (10)), there is an urgent need to understand the unique
38 ecology of these systems. TGBs, like tropical forests, are subject to a complex set of
39 pressures as a result of human actions. However, unlike other biomes, the contrasting
40 life forms and physiologies of the dominant C₃ woody plant species and grass species
41 utilising the C₄ photosynthetic pathway sees the future of this biome linked, in a
42 profound way, to the ever-rising atmospheric CO₂ concentration and the global
43 political agenda to reduce these emissions. Further, TGBs have generally few policy
44 and legislative mechanisms in place for their protection (11, see also the example
45 provided by do Espirito Santo et al. (12)).

46 TGBs contribute 30% of global terrestrial net primary productivity and store
47 15% of the world's carbon (13). While TGBs are less carbon dense than forests (by an
48 order of magnitude or more), their productivity is such that large proportions of the
49 carbon gained in a single year, are rapidly released back to the environment via fire,
50 herbivory and human use (14, 15 and see analysis of this in Archibald and Hempson
51 (16)). Indeed, the disequilibrium nature of TGB vegetation dynamics means that these
52 biomes are highly sensitive to annual and decadal changes in environmental controls
53 (14). The degree to which this dynamism will influence trajectories of vegetation
54 change in grassy biomes into the future is unresolved. However, it is apparent that
55 many intact savannas are now on a trajectory of increasing woody biomass, although
56 the degree of gain varies regionally, with Australian savannas most stable over time
57 (4).

58 Tropical grassy biomes first arose approximately 10 million years ago and
59 expanded such that by two million years ago, tropical savannas and grasslands were a

60 dominant biome covering the tropics (17). Today, these biomes, cover in excess of
61 20% of the global land surface. At the last glacial maximum, TGBs extended more
62 widely throughout Asia, Africa and the Americas than today (18-20). The extent of
63 these vast biomes has shifted with glacial - inter-glacial cycles in response to changing
64 atmospheric CO₂ concentrations, rainfall, rainfall seasonality, temperature and fire
65 (19, 21). Given that all of these aspects of our environment are now changing at
66 unprecedented rates, extensive alterations in the distribution and dynamics of TGBs
67 over the coming century will be inevitable and are likely already being observed (1, 4,
68 22, see the analysis provided by Stevens et al. (23)).

69 The last decade has seen a revolution in our understanding of the evolution
70 (17, 24, 25), antiquity (26-28), distribution (29, 30) and ecosystem dynamics of TGBs
71 (14, 31), as well as their role in the global carbon cycle (32). Some of these advances
72 have sparked controversies that are now active debates in the literature (e.g. ancient
73 grasslands and afforestation policies (33-35); the existence or not of alternative
74 vegetation states (29, 36, 37)). Indeed, insights and theory from savanna ecology have
75 challenged long standing ecological assumptions of climate determinism in defining
76 the limits of biomes (38).

77 Over the coming decade, we anticipate important in-roads will be made in
78 reconciling the complex ecology and biogeochemical cycling of these geographically
79 dispersed biomes via integration of remote sensing, modelling, ecology and evolution.
80 However, it will be critical to incorporate the role of people in shaping and responding
81 to changing ecosystem dynamics and function across this global region, as in the
82 Anthropocene people will be increasingly important agents of landscape change,
83 directly and indirectly influencing the environmental controls and ecological processes
84 that structure TGBs from global to local scales.

85

86 **2. This Issue**

87 Tropical Grassy Biomes are expansive and changing rapidly, yet our capacity to
88 predict trajectories of change in these biomes is limited, despite their importance to
89 human livelihoods, biodiversity and biogeochemical cycling. In this issue, we highlight
90 the need for integration among research related to the ecology and dynamics of these
91 biomes: characterization and definition of tropical grassy biomes; complex ecology;

92 patterns and drivers of change; and, human use and ecosystem services. For the first
93 time, analyses are presented on the biogeography and potential distributions of Asian
94 savannas (39). Other significant steps forward in our understanding include: methods
95 for characterizing ancient versus derived grassy biomes (40, 41), comparative data on
96 the species diversity of TGB regions across the globe (42), an improved understanding
97 of the complex ecology of herbivory and fire (16, 43) and the context dependent
98 response of vegetation to global change (44), and finally, tools to examine tradeoffs
99 in biodiversity, carbon and agriculture to aid land use planning and policy (10).

100

101 **3. Defining Tropical Grassy Biomes**

102 Tropical grassy biomes include C₄ grass dominated savannas and grasslands
103 (following the definitions of (30, 45)). Definitions of tropical grassy biomes have
104 historically been varied and fraught with problems. Functionally, TGBs are
105 characterized by a grassy ground layer (generally dominated by grasses using the C₄
106 photosynthetic pathway - with a noted exception in Brazil (46) and Indochina (39)) and
107 an overstorey varying from 0% up to 60 - 80% woody cover (45). The biota, depending
108 on its biogeographic and environmental settings, is tolerant of any, or all of, fire,
109 grazing and browsing (31). However, universally, the flora is shade intolerant, at least
110 at the establishment phase, due to the open canopy overstorey (45). While the
111 biodiversity value of these systems to-date has been typically overshadowed by that
112 of tropical forests (26), Murphy et al. (2016) in this issue (42), illustrate the biodiversity
113 value of TGBs, particularly of vertebrates and range-restricted species, and emphasize
114 variation in diversity among the TGB regions (the South American region generally
115 being the richest).

116 The disequilibrium nature of tropical grassy biome vegetation dynamics, with
117 varying levels of woody cover, has consistently posed problems for the categorization
118 of these ecosystems (8). This problem has been compounded by a focus on trees,
119 rather than ground layer composition and function; for example, the Millennium
120 Ecosystem Assessment focuses on drylands and forests (47, 48), but does not explicitly
121 consider tropical savannas. While tropical rainforests have been mapped globally, no
122 accurate global map of the tropical grassy biomes exists. The most widely used general
123 vegetation map and classification scheme is Olson et al.'s (2001) ecoregions (49),

124 although this biome classification is problematic because it does not recognize some
125 of the world's major savannas and grasslands, including those in Asia (e.g. India,
126 Thailand, Burma) and Madagascar. Wide use of such maps for research, policy and
127 conservation has the potential to have adverse impacts on landscape management
128 and the perceived conservation value of these regions (e.g. conversion of TGBs,
129 perceived as degraded land, for agriculture, see (50)). For the first time, Ratnam et al.
130 (2016) focus on this issue in Asia (39) by reviewing the scattered literature on the
131 distribution of Asian savannas and evidence for the antiquity and diversity of TGBs
132 across this continent.

133 In many regions, including Madagascar, south east Asia and South America,
134 grassy biomes have historically been considered either to be a degraded form of forest
135 of anthropogenic origin created via tree clearing, burning and grazing, or a subclimax
136 or secondary successional stage (28, 39). While true in some locations (see Veldman
137 2016, this issue (40)), in the majority of areas this perspective is misplaced (34). A
138 wealth of new information including dated phylogenetic analyses demonstrates the
139 antiquity of both tree and grass species (and lineages) specialised to these biomes (25,
140 27, 28). The presence of endemic plant lineages and species, as well as species with
141 unique life histories and architectures, including forbs with large underground storage
142 organs, are strong indicators of the antiquity of TGBs (35, 41).

143 The fauna of these regions also contains numerous endemic species
144 specialized to open and grassy environments providing additional evidence for the
145 origin and age of the tropical grassy systems. Fauna include species of granivorous
146 birds (e.g. the Madagascan mannikin, *Lonchura nana*), a suite of grazing ungulates
147 (e.g. the critically endangered Kouprey, *Bos sauveli*, from Cambodia, and the chital
148 deer, *Axis axis*, from India) and a high diversity of small marsupials in Australia (42).
149 Many of these species are endangered and threatened with imminent extinction (51).
150 Fire is a frequent disturbance in the TGBs and has been part of these systems for
151 millions of years (17, 21); consequently the plants and animals they contain are
152 generally adapted to its occurrence (25).

153 To date it has been difficult to distinguish ancient, old-growth grasslands and
154 savannas from secondary systems given superficial similarities in structure. Here,
155 Veldman (2016) and Zaloumis & Bond (2016), examining the Neotropics and South

156 Africa respectively, differentiate ancient and secondary systems, noting differences in
157 species composition with the former particularly rich in forbs, many with well-
158 developed underground storage organs that facilitate survival in seasonally dry
159 climates with frequent fire. The challenge is to test the generality of these
160 compositional characteristics across TGB regions.

161

162 **4. Ecology**

163 The ecology of TGBs is complex by virtue of the numerous environmental controls,
164 acting across different scales of influence, both directly and indirectly to structure
165 these ecosystems (Figure 1). The last decade has seen a shift from a long-standing
166 view of deterministic relationships among vegetation, climate and soils, focused on
167 niche separation between trees and grasses for water use, to one that integrates niche
168 separation (e.g., phenological, water use) with the controls of fire and mammal
169 herbivory structuring vegetation via the restriction of woody plant growth (31).
170 Archibald and Hempson (16) explore trade-offs in fire and mammalian herbivory
171 across the African continent where realms of influence can change through space and
172 time. Complementing this research is that of Anderson et al. (43) who examine spatial
173 associations of African mammalian herbivores relative to body size and influences on
174 ecosystem function relative to species composition. Both of these studies raise
175 important questions about the function or dysfunction of TGBs in the context of
176 changing disturbance regimes.

177 Integration of bottom up (e.g., climate and soils) and top down (e.g., fire and
178 mammalian herbivory) controls in structuring TGB vegetation has significantly
179 improved our process understanding of the dynamics and limits of these systems (14,
180 52). But, it has also highlighted the degree to which contemporary dynamics of TGBs,
181 from local to continental scales, are a function of historical contingencies (44, 53). In
182 assessment of regional patterns and dynamics of vegetation, emergent patterns of
183 woody cover can appear almost stochastic, due to the array of structural states
184 possible for a given set of environmental conditions (29). At the heart of the current
185 disagreement around alternate vegetation states prevalent in the tropical savanna
186 and forest literature (all of state shifts between savanna and forest, grassland and
187 savanna, and variation in tree cover within savannas) may be a lack of recognition of

188 both the role of contingency in influencing contemporary dynamics of TGBs, and that
189 the relative role of environmental controls in structuring vegetation varies across
190 savanna systems: i.e., some savannas likely exist due to soil barriers to woody plant
191 growth, while others exist because of controls, such as prevalent fire, that also act to
192 limit woody plant recruitment and growth. That is, the similarities in structure among
193 TGBs (open canopied vegetation with a predominantly C₄ grassy ground layer) have
194 led to an unfounded assumption in the literature that the processes regulating
195 vegetation structure across these varied and geographically dispersed ecosystems are
196 directly equivalent. Finally, the presence of numerous, well-documented, feedbacks
197 structuring TGBs where the species composition can influence the strength and
198 direction of effects (Figure 1; tree cover - fire; fire - grazing; grazing - browsing),
199 combined with the importance of historical contingencies means that multiple states
200 influencing both the limits and structure of TGBs are highly likely. In this issue, Oliveras
201 and Malhi (54) examine the shades of green in our understanding of the processes
202 structuring the limits of TGBs highlighting how biotic and abiotic processes operate at
203 different scales and that nature of vegetation dynamics is context dependent.

204 Savanna vegetation dynamics have been shown to vary as a function of plant traits
205 that aggregate from the individual to ecosystem level (14, 55). However, current
206 model simulations generally represent TGBs as functionally identical, in contrast to
207 ecological knowledge (although see Moncrieff et al. in this issue (44)). TGBs constitute
208 a geographically dispersed set of regions, where the flora and fauna representing
209 unique evolutionary and environmental histories (14). The relative importance of
210 environmental controls in structuring these systems varies across these geographic
211 regions, and relative to the environmental niche of each region (14). For example, the
212 high rainfall Australian savannas dominated by tall, fast growing, narrow canopied
213 evergreen *Eucalyptus* species are less sensitive to fire than the wide canopied
214 deciduous *Brachystegia* and *Julbernardia* species that dominate a savanna region
215 equivalent in area across southern Africa (56, 57). Thus, for a given set of
216 environmental conditions, similar fire frequencies and intensities could produce
217 different vegetation structures, and the difference in sensitivity to fire of these floras
218 is highly likely underpinned by the functional traits of the plant species themselves
219 (55). It is increasingly appreciated that the functional biogeography of TGBs has critical

220 implications for our capacity to determine the sensitivity and resilience of TGB regions
221 to global change (e.g., Moncrieff et al., this issue (44)), and yet, our quantitative
222 understanding of functional biogeography of TGBs remains limited. This information
223 is needed as our capacity to predict future change will rely on a quantitative
224 representation of the aggregation the traits that characterize these floras in
225 influencing ecosystem dynamics and responding to environmental variation.

226 Across tropical grassy biomes, vegetation composition, woody cover and grass
227 biomass are considered key determinants of ecosystem function. However,
228 quantitative links between structure and function, ultimately, remain poor and there
229 is no consensus of these relationships among TGB regions (8). Despite, the
230 antagonistic dynamics between tree and grass dominance being central to savanna
231 ecology, we retain a limited predictive capacity of vegetation structure. It could be
232 argued that our current lack of knowledge about the physio-ecological responses of
233 TGBs to global change is hindered by both the functional differences among the TGB
234 regions and our weak quantitative understanding of the processes that structure
235 vegetation due to the complexity of interactions and scales of feedbacks in operation
236 (Figure 1). To aid the management of global change impacts for both people and
237 biodiversity, we need to determine the relative sensitivities of savanna vegetation
238 types to key environmental controls – CO₂, water availability, and disturbance
239 dynamics – and identify structural thresholds where critical ecosystem functions
240 change.

241

242 **5. Drivers of Change**

243 Tropical vegetation is changing at broad spatial scales but there is a limited
244 understanding of current trends. On one hand, rates of land use change are increasing
245 (3, 11), and on the other, woody encroachment is widespread across savannas
246 especially in Brazil and South Africa (in this issue, see Honda & Durigan, 2016 and
247 Stevens et al. 2016). The extent to which drivers that enhance tree growth (e.g.,
248 increasing atmospheric CO₂ concentrations [CO₂]_a), reduced disturbance, improved
249 plant water use efficiencies), prevail over drivers of enhanced tree mortality (e.g.,
250 reduced rainfall, increasing intensity of El Niño, increased temperature, increased
251 harvesting) is unknown, but this is the key to the future management and integrity of

252 the biome.

253 Rising $[\text{CO}_2]_a$ has long been hypothesised to be a key driver in the re-organisation of
254 tropical vegetation, specifically in savannas where the contrasting life forms and
255 physiologies of the dominant C_3 trees and C_4 grasses are expected to respond
256 differently (58). While modelling of the proposed mechanisms underpinning shifts in
257 the competitive interactions between C_3 trees and C_4 grasses is improving (i.e.
258 increased plant water use efficiencies of C_3 plant species, specifically woody plant
259 species; carbon allocation and storage patterns that vary between life forms; reduced
260 photorespiration in C_3 grasses), demonstrating the potential for regional shifts in
261 biome extent and woody biomass (59), there is a major gap in the experimental
262 evidence of the responses of tropical plant species to altered CO_2 concentrations,
263 especially with regards to interactions with other environmental controls (8). In
264 particular, dominant woody taxa in each savanna region have different life histories,
265 allocation strategies, and architectures (14, 55, 60). Increasingly, functional traits are
266 recognised as phylogenetically conserved (61), and differential responses to CO_2
267 would likely be expected relative to both ecological and environmental settings.
268 Looking across a rainfall gradient and landuse types in South Africa, Stevens et al.
269 (2016) report large increases in woody cover in just a few decades providing support
270 for a global driver (23), while also noting the interaction with megaherbivores
271 (elephants). Woody encroachment may provide carbon benefits, but will undoubtedly
272 come at a biodiversity cost (62).

273 Tropical grassy biomes are characterised by seasonally dry and hot climates (30).
274 While climates across this swath of the world are changing, particularly in terms of the
275 frequency and intensity of El Niño drought events, disagreement among model
276 predictions contributes to the lack of certainty for climate change predictions across
277 tropical regions (63). Novel climates, in combination with rising CO_2 will generate
278 novel interactions among organisms, where small shifts in the season and timing of
279 rainfall may have large consequences for the phenological cycles of plants and
280 animals, and stark consequences for crop production (3). In contrast, small changes in
281 total rainfall may be of limited consequence, where increasing $[\text{CO}_2]_a$ will drive
282 improvements in plant water use efficiencies (64). Temperature is assumed important
283 in determining plant distributions and function primarily based on assumptions from

284 the Northern Hemisphere. Yet the importance of temperature in the dynamics of TGBs
285 is poorly understood. The small body of research suggests if there is sufficient water,
286 a warming climate may enhance plant success through improved germination (65, 66)
287 and sapling growth rates (67), and an extended growing season (68).

288 Yet, across TGBs, rates of land use and cover change appear to exceed the effects
289 of climate change (1, 11). With increasing global scarcity of lands for agriculture and
290 increasing food demands (69), land use intensity is only likely to increase. There are a
291 multitude of land use types across TGBs, many of which are context dependent, from
292 shifting cultivation and grazing lands to commercial agriculture (see Ryan et al., in this
293 issue). However, all affect the continuity of ecosystems and, some land use types more
294 so than others (see Estes et al., in this issue). Increasing land use intensity and
295 fragmentation disrupts disturbance regimes and vegetation dynamics (70), potentially
296 amplifying encroachment by further reducing tree mortality. To date, 50% of the
297 Brazilian cerrado has been transformed for agriculture, a rate of land use change
298 roughly double that of the Amazon forest (71, 72). Land has historically been
299 perceived as being of marginal agricultural value across TGBs (see Estes et al. and Ryan
300 et al. in this issue). However, technical innovations in managing highly weathered
301 tropical red soils and the breeding of suitable crop varieties have transformed
302 agriculture in Brazil (3). This tropical agricultural revolution has been proposed as a
303 viable development model for wetter African savannas (Estes et al. 2016 and (3)). do
304 Espírito Santo et al. (this issue) document land abandonment and encroachment in
305 secondary savannas of the cerrado (12), where this development policy has been to
306 the detriment of the integrity of the system and where, globally, rates of
307 encroachment are highest (4).

308 Finally, people also directly influence disturbance regimes at broad scales (6, 70).
309 Active suppression of fire in the savanna regions of Asia and Brazil in particular has
310 facilitated woody or weed encroachment (see Honda & Durigan, 2016 and (73)). The
311 increasing extent of roads and fences act as fire breaks and also prohibit large scale
312 animal movements (6). These changes to the major savanna processes of fire and
313 herbivory, combined the effects of the poaching crisis of Africa and Asia, are likely to
314 have profound consequences for ecosystem function (Archibald and Hempson;
315 Anderson et al. in this issue).

316

317 **6. Human use and value**

318 Quantifying and understanding the value of TGBs to humans is challenging
319 because in many regions, particularly in Asia, data on the value of TGBs to human
320 livelihoods are limited. TGBs are sometimes described as “unused” or “degraded”,
321 although these systems provide fundamental resources and ecosystem services
322 supporting the livelihoods of the millions of people living in these regions. Further, the
323 people of these regions are among the worlds poorest and most vulnerable (74), and
324 global change will inevitably affect ecosystem services and resource availability.
325 Perhaps more so than any other TGB region, direct use by local communities is
326 greatest in Africa and Asia (see Ryan et al. 2016, this issue), given the urbanization of
327 Latin America and the sparse population densities of Australia. Ryan et al. (2016, this
328 issue) highlight the diversity and number of ecosystem services (supporting,
329 regulating and cultural services) provided by TGBs (specifically in relation to southern
330 Africa) that, to-date, have typically been either overlooked or considered at small
331 spatial scales. Critical resources provided include food (wild fruits, tubers, nuts, edible
332 insects, bushmeat), NTFPs for sale (e.g. honey, beeswax, insects), fuel (fire wood and
333 charcoal), construction materials (e.g. thatching grass, timber), water, nutrient cycling
334 and medicinal plants (Ryan et al. this issue).

335 Across Africa, Asia and even South America, fuel wood harvesting is a significant
336 activity (see Woollen et al. and do Espirito-Santo et al. in this issue). Although the fuel
337 wood crisis predicted in the 1970s has not materialized, projections surrounding levels
338 of fuel wood sustainability are varied (75). In some regions (e.g. South Africa) fuel
339 wood harvesting is considered sustainable due to regeneration after coppicing (76),
340 possibly facilitated by CO₂ fertilization (e.g. (77)). Elsewhere, wood demand is
341 anticipated to increase due to increasing populations and a switch to charcoal, which
342 has an increasing international market (75). The implications of changing wood
343 demands are raised by Woollen et al. (2016, in this issue (78)): wood for construction
344 material is now traded off against wood for charcoal. How changes in wood resources
345 in the context of global change will influence the integrity and functioning of TGBs
346 needs urgent attention.

347 Water availability will change with growing populations, altered landscapes and

348 global change, and in the seasonally dry climates of these regions water availability is
349 critical to both ecosystem dynamics and human use of landscapes, yet understanding
350 of the nature of this change and the implications is restricted to a few regions (75).
351 Honda and Durigan (2016, this issue (79)) provide, for the first time, estimates of
352 rainfall partitioning in the cerrado and demonstrate how fire suppression, indirectly
353 via woody encroachment, can reduce rain interception. Given many TGB regions are
354 experiencing woody encroachment, this is a reminder of the functional role of
355 disturbance in the provision of water resources. Across TGBs, afforestation (often of
356 exotic species) is common (8), in part, to meet fuel wood needs; improved
357 examination of the trade-offs between fuel wood and woody encroachment with
358 water are desperately required. Further, much needed are examinations of the
359 biophysical and biogeochemical consequences of woody encroachment and land
360 cover change, such as albedo and nutrient cycling.

361 People and institutional structures can strongly influence and affect TGBs - their
362 biodiversity, functioning and services (8). For example, in many areas declines in
363 mammal species have been reported due to bushmeat hunting and poaching,
364 savannas have become degraded through overgrazing, land abandonment, and
365 afforested monocultures (80-82). The economic importance of the wildlife across
366 TGBs, particularly in African and some Asian regions (and to a lesser extent Australia),
367 is a unique economic advantage that contributes to the tourism industries of these
368 regions. Major ecological changes driven by the global changes set out above,
369 combined with human pressures could threaten these economic benefits. Human
370 usage needs to be reconciled with ecological values in these areas, including
371 biodiversity; human activity has already reduced the richest botanical savanna region,
372 the Brazilian cerrado, to a series of, arguably, dysfunctional fragments. Finally, the
373 climate change mitigation agenda could represent a threat to TGBs, as there is
374 increasing talk of the need for “negative emissions” to meet the emissions targets set
375 out at the Paris climate conference (COP21) in 2015 where inappropriate application
376 of these targets could lead to afforestation of TGBs (34).

377

378 **7. Conclusions**

379 The pace and scale of change in TGBs is astonishing and will affect human livelihoods,

380 biodiversity, carbon and biogeochemical cycling. Yet, our capacity to predict the
381 direction and extent of change, as well as the consequences, is currently limited.
382 Research will improve our ecological understanding of TGBs, and it is clear that our
383 capacity to effectively predict the sensitivity and resilience of each TGB region is
384 dependent upon understanding the cascading and interacting effects of ecological,
385 socioeconomic and global drivers across contrasting contexts. This is no easy task even
386 from a purely ecological perspective as these systems are complex, ecosystem
387 dynamics are context dependent and uncertainty surrounds the influence of global
388 change drivers.

389 In order to better conserve and manage TGBs for the future, we must look
390 beyond a simplified view considering only the tree layer, to a perspective that
391 embraces the grassy ground layer and the unique functions associated with this. Only
392 with this broader perspective will we be in a position to consider the range of
393 trajectories and possible states that are likely across the different regions and how the
394 influence of key drivers may vary. To apply the most appropriate conservation and
395 management efforts in the right place, field studies are needed to characterize and
396 determine the antiquity and value of TGBs more broadly. Additionally, field studies
397 will help us understand how the multiple pathways for structural (and compositional)
398 change links to the functioning of these biomes.

399 Experiments manipulating global change drivers (e.g. water availability,
400 temperature, and CO₂) will help unravel the complexities of savanna process and
401 dynamics so we are in a stronger position to understand how different TGB regions
402 may respond to future change. We need to work with land managers and politicians
403 to ensure that processes critical to the healthy functioning of TGBs (i.e. fire, herbivory)
404 are maintained. This will mean revisiting carbon mitigation initiatives, taking a more
405 nuanced approach to applying REDD+ in TGBs, and ultimately recognizing TGBs are
406 wholly different to forests in terms of ecosystem function. Many of the world's
407 poorest live in the TGBs; it is therefore essential that the dual goals of sustaining the
408 ecological integrity of this biome and supporting the people who live in these
409 landscapes must not be viewed as competing demands.

410

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417 **References**

418

- 419 1. Mitchard ETA, Flintrop CM. Woody encroachment and forest degradation in
420 sub-Saharan Africa's woodlands and savannas 1982–2006. *Philosophical*
421 *Transactions of the Royal Society B* 2013;371(1696):20150346.
- 422 2. Lambin EF, Geist HJ, Lepers E. Dynamics of land-use and land-cover change in
423 tropical regions. *Annual review of environment and resources*. 2003;28(1):205-41.
- 424 3. Searchinger TD, Estes L, Thornton PK, Beringer T, Notenbaert A, Rubenstein
425 D, et al. High carbon and biodiversity costs from converting Africa's wet savannas
426 to cropland. *Nature Clim Change*. 2015;5(5):481-6.
- 427 4. Stevens N, Lehmann CER, Murphy BP, Durigan G. Savanna woody
428 encroachment is widespread across three continents. *Global Change Biology*. In
429 press; XXX(XXX):XXX.
- 430 5. Archibald S. Managing the human component of fire regimes: lessons from
431 Africa. *Phil Trans R Soc B*. 2016;371(1696):20150346.
- 432 6. Archibald S, Lehmann CER, Gomez-Dans J, Bradstock RA. Defining pyromes
433 and global syndromes of fire. *Proceedings of the National Academy of Sciences*.
434 2013;10(16):6442 - 7.
- 435 7. Cerling TE, Wynn JG, Andanje SA, Bird MI, Korir DK, Levin NE, et al. Woody
436 cover and hominin environments in the past 6[thinsp]million years. *Nature*.
437 2011;476(7358):51-6.
- 438 8. Parr CL, Lehmann CER, Bond WJ, Hoffmann WA, Andersen AN. Tropical grassy
439 biomes: misunderstood, neglected, and under threat. *Trends in Ecology & Evolution*.
440 2014;29(4):205-13.
- 441 9. Climate change 2013: the physical science basis: Working Group I
442 contribution to the Fifth assessment report of the Intergovernmental Panel on
443 Climate Change: Cambridge University Press; 2014.
- 444 10. Estes L, Searchinger T, Spiegel M, Tian D, Sickinga S, Mwale M, et al.
445 Reconciling agriculture, carbon, and biodiversity in a savanna transformation frontier
446 *Phil Trans R Soc B*. 2016;7103(XXX):XXX.

- 447 11. Aleman JC, Blarquez O, Staver CA. Land-use change outweighs projected
448 effects of changing rainfall on tree cover in sub-Saharan Africa. *Global Change*
449 *Biology*. 2016.
- 450 12. do Espírito Santo M, Leite M, Silva J, Barbosa R, Rocha A, Anaya F, et al.
451 Patterns of land-cover change in the Brazilian Cerrado from 2000 to 2015 *Phil Trans*
452 *R Soc B*. 2016;7103(XXX):XXX.
- 453 13. Grace J, José JS, Meir P, Miranda HS, Montes RA. Productivity and carbon
454 fluxes of tropical savannas. *J Biogeog*. 2006;33(3):387-400.
- 455 14. Lehmann CER, Anderson TM, Sankaran M, Higgins SI, Archibald S, Hoffmann
456 WA, et al. Savanna Vegetation-Fire-Climate Relationships Differ Among Continents.
457 *Science*. 2014;343(6170):548-52.
- 458 15. Tredennick AT, Hanan NP. Effects of Tree Harvest on the Stable-State
459 Dynamics of Savanna and Forest. *The American Naturalist*. 2015;185(5):E153-E65.
- 460 16. Archibald S, Hempson GP. Competing consumers: contrasting the patterns
461 and impacts of fire and mammalian herbivory in Africa *Phil Trans R Soc B*.
462 2016;7103(XXX):XXX.
- 463 17. Edwards EJ, Osborne CP, Stromberg CAE, Smith SA, C4 Grasses Consortium.
464 The Origins of C4 Grasslands: Integrating Evolutionary and Ecosystem Science.
465 *Science*. 2010;328(5978):587-91.
- 466 18. Bird MI, Taylor D, Hunt C. Palaeoenvironments of insular Southeast Asia
467 during the Last Glacial Period: a savanna corridor in Sundaland? *Quaternary Science*
468 *Reviews*. 2005;24(20):2228-42.
- 469 19. Harrison SP, Prentice CI. Climate and CO2 controls on global vegetation
470 distribution at the last glacial maximum: analysis based on palaeovegetation data,
471 biome modelling and palaeoclimate simulations
472 doi:10.1046/j.1365-2486.2003.00640.x. *Global Change Biology*. 2003;9(7):983-1004.
- 473 20. Werneck FP, Nogueira C, Colli GR, Sites JW, Costa GC. Climatic stability in the
474 Brazilian Cerrado: implications for biogeographical connections of South American
475 savannas, species richness and conservation in a biodiversity hotspot. *J Biogeog*.
476 2012;39(9):1695-706.

- 477 21. Daniau A-L, Goñi MFS, Martinez P, Urrego DH, Bout-Roumazeilles V, Desprat
478 S, et al. Orbital-scale climate forcing of grassland burning in southern Africa.
479 Proceedings of the National Academy of Sciences. 2013;110(13):5069-73.
- 480 22. Buitenwerf R, Bond WJ, Stevens N, Trollope WSW. Increased tree densities in
481 South African savannas: >50 years of data suggests CO₂ as a driver. Global Change
482 Biology. 2012;18(2):675-84.
- 483 23. Stevens N, Eramasmus B, Archibald S, Bond WJ. Woody encroachment over 70
484 years in South African savannas: overgrazing, global change or extinction aftershock?
485 . Phil Trans R Soc B. 2016;7103(XXX):XXX.
- 486 24. Scheiter S, Higgins SI, Osborne CP, Bradshaw C, Lunt D, Ripley BS, et al. Fire
487 and fire-adapted vegetation promoted C₄ expansion in the late Miocene. New
488 Phytologist. 2012;195(3):653-66.
- 489 25. Simon MF, Grether R, de Queiroz LP, Skema C, Pennington RT, Hughes CE.
490 Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ
491 evolution of adaptations to fire. Proceedings of the National Academy of Sciences.
492 2009;106(48):20359-64.
- 493 26. Pennington RT, Hughes CE. The remarkable congruence of New and Old
494 World savanna origins. New Phytologist. 2014;204(1):4-6.
- 495 27. Maurin O, Davies TJ, Burrows JE, Daru BH, Yessoufou K, Muasya AM, et al.
496 Savanna fire and the origins of the 'underground forests' of Africa. New Phytologist.
497 2014;204(1):201-14.
- 498 28. Vorontsova MS, Besnard G, Forest F, Malakasi P, Moat J, Clayton WD, et al.,
499 editors. Madagascar's grasses and grasslands: anthropogenic or natural? Proc R Soc
500 B; 2016: The Royal Society.
- 501 29. Staver AC, Archibald S, Levin SA. The Global Extent and Determinants of
502 Savanna and Forest as Alternative Biome States. Science. 2011;334(6053):230-2.
- 503 30. Lehmann CER, Archibald SA, Hoffmann WA, Bond WJ. Deciphering the
504 distribution of the savanna biome. New Phytologist. 2011;191(1):197-209.
- 505 31. Bond WJ. What Limits Trees in C₄ Grasslands and Savannas? Annual Review
506 of Ecology, Evolution, and Systematics. 2008;39(1):641-59.

- 507 32. Poulter B, Frank D, Ciais P, Myneni RB, Andela N, Bi J, et al. Contribution of
508 semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature*.
509 2014;509(7502):600-3.
- 510 33. Veldman JW, Overbeck GE, Negreiros D, Mahy G, Le Stradic S, Fernandes GW,
511 et al. Tyranny of trees in grassy biomes. *Science (New York, NY)*.
512 2015;347(6221):484.
- 513 34. Veldman JW, Overbeck GE, Negreiros D, Mahy G, Le Stradic S, Fernandes GW,
514 et al. Where Tree Planting and Forest Expansion are Bad for Biodiversity and
515 Ecosystem Services. *BioScience*. 2015:biv118.
- 516 35. Bond WJ. Ancient grasslands at risk. *Science*. 2016;351(6269):120-2.
- 517 36. Hirota M, Holmgren M, Van Nes EH, Scheffer M. Global Resilience of Tropical
518 Forest and Savanna to Critical Transitions. *Science*. 2011;334(6053):232-5.
- 519 37. Ratajczak Z, Nippert JB. Comment on “Global Resilience of Tropical Forest
520 and Savanna to Critical Transitions”. *Science*. 2012;336(6081):541.
- 521 38. Bond WJ, Woodward FI, Midgley GF. The global distributiou of ecosystems
522 in a world without fire. *New Phytologist*. 2005;165:525-38.
- 523 39. Ratnam J, Tomlinson K, Rasquinha D, Sankaran M. Savannas of Asia: evidence
524 for antiquity, biogeography, and an uncertain future *Phil Trans R Soc B*.
525 2016;7103:XXX.
- 526 40. Veldman J. Clarifying the confusion: old-growth savannas and tropical
527 ecosystem degradation *Phil Trans R Soc B*. 2016;7103(XXX):XXX.
- 528 41. Zaloumis N, Bond WJ. The deforestation story: testing for anthropogenic
529 origins of Africa’s flammable biomes. . *Phil Trans R Soc B*. 2016;7103(XXX):XXX.
- 530 42. Murphy BP, Andersen AN, Parr CL. The underestimated biodiversity of
531 tropical grassy biomes *Phil Trans R Soc B*. 2016;7103(XXX):XXX.
- 532 43. Anderson TM, White S, Davis B, Erhardt R, Palmer M, Packer C. The spatial
533 distribution of African savannah herbivores: species associations and habitat
534 occupancy in a landscape context *Phil Trans R Soc B*. 2016;7103(XXX):XXX.
- 535 44. Moncrieff GR, Scheiter S, Langan L, Trabucco A, Higgins S. The future
536 distribution of the savanna biome: model-based and biogeographic contingency *Phil*
537 *Trans R Soc B*. 2016;7103(XXX):XXX.

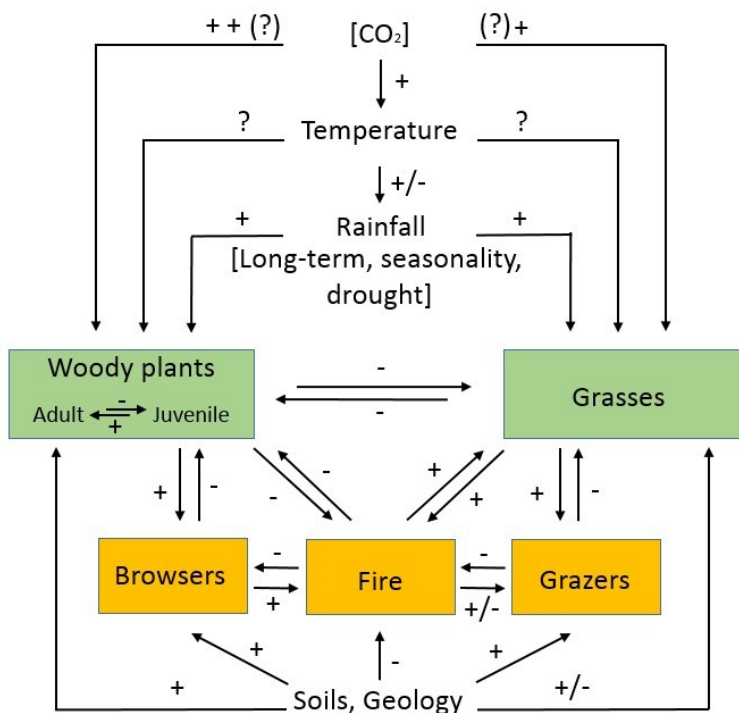
- 538 45. Ratnam J, Bond WJ, Fensham RJ, Hoffmann WA, Archibald S, Lehmann CER,
539 et al. When is a 'forest' a savanna, and why does it matter? *Global Ecology and*
540 *Biogeography*. 2011;20(5):653-60.
- 541 46. Oliveira PS, Marquis RJ. *The cerrados of Brazil: ecology and natural history of*
542 *a neotropical savanna*: Columbia University Press; 2002.
- 543 47. Assessment ME. *Forest and woodland systems. Ecosystems and Human Well-*
544 *being: Current State and Trends* World Resources Institute, Washington, DC. 2005.
- 545 48. Assessment ME. *Drylands Systems. Chapter 22. Ecosystems and Human*
546 *Wellbeing: Current State and Trends*. 2005;1.
- 547 49. Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GV,
548 Underwood EC, et al. *Terrestrial Ecoregions of the World: A New Map of Life on*
549 *Earth A new global map of terrestrial ecoregions provides an innovative tool for*
550 *conserving biodiversity*. *BioScience*. 2001;51(11):933-8.
- 551 50. Dinerstein E, Baccini A, Anderson M, Fiske G, Wikramanayake E, McLaughlin
552 D, et al. *Guiding agricultural expansion to spare tropical forests*. *Conservation*
553 *Letters*. 2015;8(4):262-71.
- 554 51. Woinarski JC, Legge S, Fitzsimons JA, Traill BJ, Burbidge AA, Fisher A, et al.
555 *The disappearing mammal fauna of northern Australia: context, cause, and*
556 *response*. *Conservation Letters*. 2011;4(3):192-201.
- 557 52. Sankaran M, Ratnam J, Hanan NP. *Tree-grass coexistence in savannas*
558 *revisited- insights from an examination of assumptions and mechanisms invoked in*
559 *existing models*. *Ecology Letters*. 2004;7:480-90.
- 560 53. Moncrieff GR, Scheiter S, Bond WJ, Higgins SI. *Increasing atmospheric CO2*
561 *overrides the historical legacy of multiple stable biome states in Africa*. *New*
562 *Phytologist*. 2014;201(3):908-15.
- 563 54. Oliveras I, Malhi Y. *Many shades of green: the dynamic tropical forest-*
564 *savanna transition zones* *Phil Trans R Soc B*. 2016;7103(XXX):XXX.
- 565 55. Moncrieff GR, Lehmann CER, Schnitzler J, Gambiza J, Hiernaux P, Ryan CM, et
566 al. *Contrasting architecture of key African and Australian savanna tree taxa drives*
567 *intercontinental structural divergence*. *Global Ecology and Biogeography*. 2014:n/a-
568 n/a.

- 569 56. Murphy BP, Lehmann CE, Russell-Smith J, Lawes MJ. Fire regimes and woody
570 biomass dynamics in Australian savannas. *J Biogeog.* 2014.
- 571 57. Ryan CM, Williams M. How does fire intensity and frequency affect miombo
572 woodland tree populations and biomass? *Ecological Applications.* 2010;21(1):48-60.
- 573 58. Bond WJ, Midgley GF. A proposed CO₂-controlled mechanism of woody plant
574 invasion in grasslands and savannas. *Global Change Biology.* 2000;6(8):865-9.
- 575 59. Higgins SI, Scheiter S. Atmospheric CO₂ forces abrupt vegetation shifts
576 locally, but not globally. *Nature.* 2012;488(7410):209-12.
- 577 60. Bowman DMJS, Prior LD. TURNER REVIEW No. 10 Why do evergreen trees
578 dominate the Australian seasonal tropics?
579 doi:10.1071/BT05022. *Australian Journal of Botany.* 2005;53(5):379-99
- 580 61. Donoghue MJ. A phylogenetic perspective on the distribution of plant
581 diversity. *Proceedings of the National Academy of Sciences.* 2008;105(Supplement
582 1):11549-55.
- 583 62. Pellegrini AFA, Socolar JB, Elsen PR. Trade-offs between savanna woody plant
584 diversity and carbon storage in the Brazilian cerrado. *Global Change Biology.* 2016.
- 585 63. Seth A, Rauscher SA, Biasutti M, Giannini A, Camargo SJ, Rojas M. CMIP5
586 projected changes in the annual cycle of precipitation in monsoon regions. *Journal of*
587 *Climate.* 2013;26(19):7328-51.
- 588 64. Eamus D. The interaction of rising CO₂ and temperatures with water use
589 efficiency. *Plant, Cell & Environment.* 1991;14(8):843-52.
- 590 65. Stevens N, Seal CE, Archibald S, Bond W. Increasing temperatures can
591 improve seedling establishment in arid-adapted savanna trees. *Oecologia.*
592 2014;175(3):1029-40.
- 593 66. Faria AP, Fernandes GW, França MGC. Predicting the impact of increasing
594 carbon dioxide concentration and temperature on seed germination and seedling
595 establishment of African grasses in Brazilian Cerrado. *Austral Ecology.*
596 2015;40(8):962-73.
- 597 67. Wakeling JL, Cramer MD, Bond WJ. The savanna-grassland 'treeline': why
598 don't savanna trees occur in upland grasslands? *Journal of Ecology.* 2012;100(2):381-
599 91.

- 600 68. Prior LD, Eamus D, Duff GA. Seasonal and diurnal patterns of carbon
601 assimilation, stomatal conductance and leaf water potential in *Eucalyptus tetradonta*
602 saplings in a wet-dry savanna in northern Australia. *Aust J Bot.* 1997;45:241-58.
- 603 69. Tilman D, Balzer C, Hill J, Befort BL. Global food demand and the sustainable
604 intensification of agriculture. *Proceedings of the National Academy of Sciences.*
605 2011;108(50):20260-4.
- 606 70. Andela N, van der Werf GR. Recent trends in African fires driven by cropland
607 expansion and El Nino to La Nina transition. *Nature Clim Change.* 2014;4(9):791-5.
- 608 71. Sano EE, Rosa R, Brito JL, Ferreira LG. Land cover mapping of the tropical
609 savanna region in Brazil. *Environmental monitoring and assessment.* 2010;166(1-
610 4):113-24.
- 611 72. Brannstrom C, Jepson W, Filippi AM, Redo D, Xu Z, Ganesh S. Land change in
612 the Brazilian Savanna (Cerrado), 1986–2002: comparative analysis and implications
613 for land-use policy. *Land Use Policy.* 2008;25(4):579-95.
- 614 73. Durigan G, Ratter JA. The need for a consistent fire policy for Cerrado
615 conservation. *Journal of Applied Ecology.* 2016;53(1):11-5.
- 616 74. Djoudi H, Vergles E, Blackie R, Koame CK, Gautier D. Dry forests, livelihoods
617 and poverty alleviation: understanding current trends. *International Forestry Review.*
618 2015;17(S2):54-69.
- 619 75. Ryan CM, Pritchard R, McNicol I, Owen M, Fisher J, Lehmann CER. Ecosystem
620 services from Southern African woodlands and their future under global change *Phil*
621 *Trans R Soc B.* 2016;7103(XXX):XXX.
- 622 76. Twine WC, Holdo RM. Fuelwood sustainability revisited: integrating size
623 structure and resprouting into a spatially realistic fuelshed model. *Journal of Applied*
624 *Ecology.* 2016.
- 625 77. Wigley BJ, Bond WJ, Hoffman MT. Thicket expansion in a South African
626 savanna under divergent land use: local vs. global drivers? *Global Change Biology.*
627 2010;16(3):964-76.
- 628 78. Woollen E, Ryan CM, Grundy I, Baumert S, Vollmer F, Fernando J, et al.
629 Charcoal production in the Mopane woodlands of Mozambique: what are the
630 tradeoffs with other ecosystem services? *Phil Trans R Soc B.* 2016;7103(XXX):XXX.

- 631 79. Honda E, Durigan G. Woody encroachment and its consequences on
632 hydrological processes in the savanna *Phil Trans R Soc B*. 2016;7103(XXX):XXX.
- 633 80. Craigie ID, Baillie JE, Balmford A, Carbone C, Collen B, Green RE, et al. Large
634 mammal population declines in Africa's protected areas. *Biological Conservation*.
635 2010;143(9):2221-8.
- 636 81. Conant RT. Challenges and opportunities for carbon sequestration in
637 grassland systems: *FAO*; 2010.
- 638 82. Zaloumis NP, Bond WJ. Grassland restoration after afforestation: No direction
639 home? *Austral Ecology*. 2011;36(4):357-66.
- 640 83. Hanan NP, Lehmann CER. Tree-grass interactions in savannas : paradigms,
641 contradictions and conceptual models. In: Hill M, J., Hanan NP, editors. *Ecosystem
642 Function in Savannas: Measurement and Modeling at Landscape to Global Scales*
643 *CRC Press*; 2011. p. 39 - 56.

644 Figure 1: *The complex ecology of tropical grassy biomes*. The network of interactions
 645 governing the structure of tropical grass biomes, adapted and expanded from (83) and
 646 of particular relevance is the extent of consumer centred feedbacks in structuring
 647 these ecosystems. Direction of effects are indicated as positive (+) or negative (-)
 648 based on literature (summarised in 14 and throughout this issue), and where the
 649 literature is sparse or poorly reconciled, uncertainty of effects are indicated with (?).
 650 With respect to interactions between CO₂ and plants, estimated effects are positive,
 651 but there is uncertainty associated with the strength of interactions due to a lack of
 652 experimental evidence and the potentially hysteretic effects of consumer centred
 653 feedbacks. It must be noted that in some instances, species and their traits can modify
 654 the direction and strength of effects, as is the case with interactions between fire and
 655 grazing as outlined in (16) and relative to the ecological and environmental setting.
 656 Hence, not all interactions are present across all TGBs and not all interactions are of
 657 equal relative influence across ecological and environmental settings.
 658



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