Pathways of savannization in a mesic African savanna-forest mosaic following an extreme fire

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22 Abstract

23 1. Fires in savannas limit tree cover, thereby promoting flammable grass accumulation and
24 fuelling further frequent fires. Meanwhile, forests and thickets form dense canopies that
25 reduce C4-grass fuel loads and creating a humid microclimate, thereby excluding fires under
26 typical climatic conditions.

27 2. However, extreme fires occasionally burn into these closed-canopy systems. Although
28 these rare fires cause substantial tree mortality and can make repeat fires more likely, the
29 long-term consequences of an extreme fire for closed canopy vegetation structure and
30 potential to convert to savanna (hereafter "savannization") remain largely unknown.

31 3. Here, we analysed whether an extreme fire could, alone, alter species composition,
32 vegetation structure, and fire regimes of closed-canopy ecosystems in an intact savanna-
33 forest-thicket mosaic, or whether successive fires after an initial extreme fire were
34 necessary to trigger a biome transition between from forest to savanna.

35 4. We found that forests that only burned once recovered, whereas those that burned again
36 following an initial extreme fire transitioned from closed-canopy forests towards open,
37 grassy savannas.

38 5. While thickets had less tree mortality in fires than forests, repeat fires nonetheless
39 precipitated a transition towards savannas.

40 6. Colonization of the savanna tree community lagged behind the grass community, but also
41 began to transition.

Synthesis. Our results suggest that rare extreme fires, followed by repeated burning can indeed result in savannization in places where savanna and forest represent alternative stable states.

Introduction

Fires are becoming more frequent and severe in forested ecosystems globally (Andela *et al.*, 2019, Jolly *et al.*, 2015). In tropical forests, extreme fires associated with droughts and agriculture are expanding into forests that historically burnt only once every few hundred years (Chen *et al.*, 2014, Morton *et al.*, 2013, Sanford *et al*, 1985). Some authors have hypothesized that these tropical forest understory fires may result in runaway feedbacks, leading to more frequent fires and to savannization of forests, resulting in eventual forest collapse (Cochrane, 1999, Barlow & Peres, 2004, Barlow & Peres, 2008, Silverio et al, 2013, Flores *et al*, 2016, van Nes et al, 2018). However, although we know that the occurrence of one forest understory fire can increase the likelihood of subsequent fires, direct evidence of forest savannization by runaway feedbacks is sparse. Invasive exotic grasses have been shown to invade the forest understory only locally (Silverio *et al.*, 2013), limited by dispersal (although accelerated by human activity (see Veldman and Putz, 2010)) and possible biogeochemical feedbacks. As a result, the question of whether fires alone can convert an intact tropical forest to a savanna remains open.

Historically and today, fires burn frequently in most savannas, at a rate of several per decade, but rarely penetrate beyond intact forest margins (Kellman & Meave, 1997, Biddulph & Kellman, 1998, Hennenberg *et al.*, 2008). In some places, this can allow the persistence of a forest-savanna mosaic, despite the potentially destructive impact of fire on forest trees (Cochrane & Laurance, 2002, Brando *et al*, 2011, Brando *et al*, 2014), by feedbacks that are spatially localized (Favier *et al.*, 2004, Beckett & Bond, 2019). Mechanistically, C4-grass-fuelled fires maintain an open canopy by preventing fire-sensitive forest saplings from establishing, but fires stop readily at savanna-forest boundaries,

because shade in the forest understory prevents shade-intolerant C4 grasses from accumulating within meters of the boundary (Charles-Dominique *et al.*, 2018, Hennenberg *et al.*, 2008, Hoffmann *et al.*, 2012a). Forest microclimates also reduce wind speeds and increase fuel moisture (Biddulph & Kellman, 1998, Hoffmann *et al.*, 2012b, Little *et al.*, 2012), further hampering fire spread. These feedbacks provide support for the idea that savanna and forest are alternate stable states (Staver *et al.*, 2011a). However, the impact of extreme events (especially extreme fires, see Keeley & Pausas, 2019) on the dynamics of these mosaics is largely unknown.

One possibility is that mosaics are mostly stable, with distinct distributions and stable edges, not just on short to medium time scales (ten to several hundred years), but also on longer time scales (Killeen *et al,* 2006, Breman et al, 2012, Rull *et* al, 2013, Cardoso *et al,* 2020). This might be the case if savanna-fire feedbacks are very strong (Beckage et al, 2009, Dantas et al, 2016), or if some other process besides fire – e.g., oligotrophy, seasonal flooding – play a strong role in stabilizing savanna-forest distributions within a mosaic (Veenendaal et al, 2015, Murphy and Bowman, 2012). If this is the case, extreme fires in forests may have minor medium-term effects on forest structure, acting as a stand-replacing disturbance from which forests recover via succession (Fearnside, 1990, Kennard, 2002, Brando et al, 2020) rather than as a trigger of a catastrophic transition.

An alternative possibility is that savanna-forest boundaries may be highly dynamic over longer time-scales (Schwartz *et al.*, 1986, West *et al.*, 2000, Staver *et* al, 2017, Aleman et al 2019) and in response to changing climate or climate events (Hirota *el al,* 2010, Breman et al, 2012, Beckett & Bond, 2019, Wright et al, 2021, Sato *et al,* 2021). Spatially explicit modelling work suggests that fires at the savanna-forest boundary can influence the

biogeographic distribution of biomes (Staver *et al,* 2011b, van de Leemput *et al,* 2015, Goel *et al,* 2020a, Goel *et al,* 2020b, Wuyts *et al,* 2019). Meanwhile, local observations confirm that boundaries can be dynamic through time (Brook & Bowman, 2006, Silva *et* al, 2008, Ibanez *et al,* 2013, Beckett & Bond, 2019), from Africa (Baccini et al., 2017; Aleman et al., 2018), to South America, to Australia (Marimon et al., 2014; Ondei et al., 2017; Stevens et al., 2017; Rosan et al., 2019).

Modern evaluations of invasions of forests by savannas have predominantly focused on the Neotropics (Cavelier et al, 1998, Veldman and Putz, 2011, Silverio *et al.*, 2013, Flores et al 2016), typically in the context of invasive exotic grasses, El Niño-fuelled droughts, and deforestation (Nepstad *et* al. 1996, Barlow and Peres, 2004, Barlow and Peres, 2008, Veldman and Putz, 2011, Silverio *et al.*, 2013). This work provides invaluable insights into the potential processes of savannization, which includes the susceptibility of forest trees to fire induced mortality (Barlow and Peres, 2008, Staver *et al,* 2020), the invasion of grassy fuels following repeat fires (Veldman and Putz, 2011, Silverio *et al,* 2013), and finally the formation of no-analogue grassy systems that differ from old-growth savannas (Veldman and Putz, 2011). However, these transitions involve exotic grass species, which lead to novel fire regimes, and deforestation-derived boundaries (Alencar *et al.* 2015), with ambiguous historical and palaeoecological precedents.

From its conception in the 1940's (Aubreville, 1949, Budowski, 1956), the term savannization has been used to refer to fire-induced degradation of tropical forests via anthropogenic deforestation and agriculture (Nyerges, 1990, Uhl *et al,* 1982, Cochrane, 1999, Nepstad *et al,* 1999). The term re-emerged following predictions of large-scale Amazonian Forest collapse under elevated CO_2 (Cox *et al,* 2004) and is widely used in the

115 contemporary literature to refer to a reduction of forest tree biomass and species. In doing
116 so, forest ecologists – unintentionally but incorrectly – have maligned savannas as
117 degraded, species-poor forests or as an early successional stage of forest vegetation
118 (Veldman, 2016, Bond, 2016, Schmidt *et al*, 2019). The term savannization should be used to
119 refer to the conversion of one vegetation state (typically forest) into a savanna, a system
120 subject to the ecological processes that determine savanna vegetation dynamics. This
121 replacement of forest with savanna (true 'savannization') could, in theory, be possible in
122 regions where savannas and forests represent alternative stable states (Staver & Levin,
123 2012, Archibald *et al*, 2019, Aleman *et al*, 2020). However, the question of whether extreme
124 fires can cause a biome switch from intact forests to old-growth savannas has not yet been
125 settled.

126 This question has both theoretical and practical importance. From the perspective of
127 understanding ecological processes, we have no clear understanding of the possible role of
128 extreme fires in biogeographic transitions between savanna and forest (*e.g.*, Aleman et al
129 2019) and in shaping transitions in response to changing climate (Beckett & Bond 2019).
130 From a practical perspective, recent decades have seen significant increases in deforestation
131 and fragmentation of intact tropical forests (Watson et al, 2018; Taubert et al, 2018). The
132 most commonly proposed solution to this is to plant trees in order to restore fragmented
133 landscapes (e.g., the Bonn Challenge, REDD+; Veldman et al, 2015b), but this can be harmful
134 to the natural, biodiverse, open systems found in savanna-forest mosaics (Bond and Parr,
135 2010, Veldman et al, 2015b, Ratnam et al, 2011). Understanding the stability and dynamics
136 of mosaics would help to justify and inform their management as mosaics, with a focus on
137 the preservation of savannas as well as forests (Bond & Parr, 2010).

Here, we have examined vegetation trajectories after extreme fires empirically, focusing on a mesic savanna-forest-thicket mosaic in Hluhluwe iMfolozi Park, South Africa. Extreme fires burned into forests and thickets in 2004 and 2008, some of which have burned again subsequently and others of which have not. These events offer a natural experiment in which to observe, *in situ*, the ecological trajectories of closed-canopy vegetation following extreme fires. On the one hand, a forest or thicket experiencing fire might recover its original state. If so, we expect 1) a reduction in tree cover and biomass that is only temporary, 2) the inhibition of a regular fire regime (e.g. by suppression of grassy fuels), and 3) a transient shift to early-successional forest trees species (light-loving but not as fire tolerant as savanna species) that eventually transitions back to the original forest state. On the other hand, a forest or thicket might transition to savanna. If so, we instead expect 1) a reduction in tree cover and biomass that persists through time, 2) the establishment of a regular fire regime (or at least of sufficient grassy biomass to support one), and 3) a shift in tree species composition, from shade-tolerant but fire-sensitive species that compete for light, to shade-intolerant species that invest in fire protection. Differentiating between these possibilities provides us the rare opportunity to test the forest savannization hypothesis developed for the Amazon (Cochrane et al 1999), allowing us to investigate what happens in the aftermath of extreme disturbances in forests and thickets.

Materials and Methods

The northern section of Hluhluwe-iMfolozi Park (HiP) receives sufficient annual rainfall (approx. 1000mm per annum) (Balfour & Howison, 2002) to support a closed-canopy forest, with vegetation dynamics that are driven by fire compared to the more arid (approx. 600mm per annum), herbivore-driven system in the iMfolozi section (Staver *et al.*, 2012).

Closed-canopy vegetation types in HiP are differentiated into scarp forests (which we refer to as forests here onwards) and thicket (*sensu* Charles-Dominique et al 2015a). Forest, thicket, and savanna definitions are based on the classification scheme used in Charles-Dominique et al (2015a), using vegetation structure and associated growth forms (Woodward et al, 2004; Ratnam et al, 2011). In HiP, forests are classified as tall (>10m) woody vegetation with a shade-tolerant intermediate tree layer, lacking a C4 grass layer but occasionally containing patches of C3 grasses and herbaceous plants among the litter layer (Charles-Dominique *et al,* 2015). Thickets are instead classified as having dense shrub and treelet vegetation, a canopy that is generally 4 to 6m tall, and a variable understory with dense patches of herbaceous sub-shrubs, shrubs and occasional patches of C4 grass subtypes that are shade-tolerant (Charles-Dominique *et al,* 2015, Charles-Dominique *et al,* 2018); thicket in the HiP context is entirely distinct from and not to be confused with subtropical Albany thicket, whose distribution is centered in the Eastern Cape of South Africa. Finally, savannas are classified as having discontinuous tree cover with a continuous layer of C4 grasses. Forest and thicket patches coexist with savanna patches in a mosaicked landscape, which is home to a full complement of savanna herbivores, including elephant and black rhino.

As in most of southern Africa, fires are usually lit by people, pre-empting lightning fires which generally occur near the end of the dry season (Archibald *et al.*, 2017). Humans have been burning fires in the region for at least 150 ka with Iron Age farmers arriving in the area ~ 2 ka (Hall, 1980, Staver *et al.*, 2017). The Hluhluwe section of HiP experiences relatively frequent fires, with mean and median fire return intervals of 2.9 and 1.3 years, respectively (Balfour and Midgley, 2008).

On the 14th and 15th of September 2008, an extreme fire occurred in the Hluhluwe section of HiP that, unlike typical savanna fires, burned into large tracts of thicket and forest. These extreme fires resulted from a combination of air temperatures above 30 °C, relative humidity below 30%, and wind speeds averaging more than 25 $km.hr^{-1}$ with gusts to 30 $km.h^{-1}$ or more (Bradstock et al 2009; Browne & Bond, 2011). In this region, such conditions are exceedingly rare: over the period 2001-2008, a total of only 69.6 hours (~ 3 days) of extreme fire weather conditions occurred, with the longest consecutive period (11 hours) occurring on the day of the extreme fire in 2008 (Browne & Bond, 2011). Aerial photography of the region from 1937 to 2013 shows that, from 1937 to 1992, closed canopy patch sizes gradually increased in extent (Beckett & Bond, 2019). However, between 1992 to 2013, when this extreme fire occurred, forest and thicket patches were lost from the landscape. Some areas that experienced this extreme fire burned subsequently, whereas others did not (see below for further detail, Appendix S1).

Vegetation sampling

We used a set of plots in which the structure and species composition of woody plants were recorded in forest, thicket and savanna vegetation types. A total of 131 plots were sampled (Fig. 1), 51 of which were first sampled in 2007 by Staver *et al (2012)* and resampled in 2014 by Case and Staver (2017), 31 of which were sampled once in 2014 by Charles-Dominique *et al* (2015a), and an additional 49 which were established specifically for this study between 2009 and 2015. Staver et al (2012) sampled 253 plots across HiP, 51 of which were chosen as the savanna baselines as they burnt in the 2008 fire and were near forest and thicket patches. Intact forest and thicket plots were established and sampled in 2014 and 2015 in mature unburnt vegetation patches (Fig. 1), as mapped by Whateley and Porter (1983) and

by aerial-photograph-derived vegetation maps (Beckett & Bond, 2019). These represent our pre-fire baselines for forest and thicket communities and, along with the 2007 savanna plots, are referred to from here on as our 'before' dataset, while burnt plots represent the 'after' dataset.

To determine vegetation change trajectories after the extreme fires, in 2013, we identified regions within the 2008 fire scar that were known to have burnt subsequently, and established plots in these areas. These plots were sampled repeatedly, supplemented with some additional, once-sampled plots allowing a space-for-time chronosequence to evaluate vegetation change. Three additional plots were laid out in a forest that burned in a separate fire in 2004 and sampled nine and 11 years after the fire. These three plots (with 20 m buffers on all sides) covered approximately 80 % of the burnt forest area. One of these plots was burnt again in 2012 and was excluded from the 11-year resampling as it had no analogues. The data from nine years after the fire are included in the analyses, while the repeat sample at 11 years are only included in figures in the Supplementary Materials for interest. Plot sampling dates, repeat sample dates, and vegetation history are summarized in Appendix S1.

Each plot measured 40 m x 10 m, within which area we identified every woody plant (including lianas) above 50cm in height and recorded its height as one of four size classes (0.5-2 m, 2-5 m, 5-10 m, and >10 m). In 103 of the 134 sites, the grass layer was evaluated at 20 points along the plot midline; grass biomass was measured via disk pasture meter (DPM) and the dominant grass species beneath the disk was recorded. A DPM is a weighted metal disk of a known diameter, which is dropped on a grass sward from a standard height. The resting height is a measure of the grass biomass under the disk (Bransby and Tainton, 1977),

230 which can be calibrated locally (grass biomass = 1.26 + 26.1*[DPM], R2 = 0.73, N = 1745;
231 Waldram et al, 2007).

232 Fire occurrence

233 Fire frequency of each plot from 2001 to 2016 was derived from a combination of the
234 Ezemvelo KwaZulu Natal Wildlife fire records for HiP and personal observations. The EKZNW
235 fire records are hand drawn maps from rangers responsible for sections of the park. These
236 indicate the general location of the fire, but do not include information on fine-scale fire
237 refugia and unburnt vegetation patches within the burned area (see Fig. 1). Where EKZNW
238 fire records indicated fires burned into large forest patches, we verified these records
239 against MODIS Active Fire Detections (MCD14DL, Collection 6). MODIS Active Fires maps
240 thermal anomalies within 1km pixels using the MODIS MOD14/MYD14 Fire and Thermal
241 Anomalies algorithm (Giglio *et al.*, 2003). MODIS Active Fires increases the probability that
242 fires within forests are detected, since forest canopies can interfere with detection of burn
243 scars.

244 Data analysis and statistics

245 Aerial photography and vegetation maps were analysed using Quantum GIS 3.0.0 (Quantum
246 GIS Development Team, 2018). Statistical analyses were performed in R (version 3.4.0, R.
247 Core Team, 2017), using the packages *vegan* (Oksanen *et al.*, 2013) and *tidyverse* (Wickham,
248 2017). Fire frequency before and after extreme fire was compared using a Wilcoxon signed-
249 rank test for non-parametric paired data. Grass biomass was compared between vegetation
250 types and time periods using a one-way analysis of variance with Tukey's HSD contrasts to
251 identify significant differences in mean values. We used a multivariate analysis of variance
252 (MANOVA) to test for differences in the total mean cumulative length of the vegetation

253 types at different time periods and followed this with a series of ANOVA models to test for
254 significant differences between vegetation types within the size classes. Cumulative length
255 is a composite measure of species importance, similar to basal area, which combines stem
256 density (reported in Appendix S2) and tree height into a single value (Fei *et al.*, 2005). This is
257 done by summing the heights of all individuals of a species, thereby allowing large trees to
258 contribute more to the overall score than small trees. We performed an NMDS Ordination
259 on a Bray-Curtis species dissimilarity matrix of the cumulative length of each tree species for
260 the 'before' plots, representing vegetation communities that had not experienced the
261 extreme fire (the intact forest, intact thicket, and 2007 savanna plots). Data were
262 transformed using a Hellinger transformation (Legendre & Legendre, 2012). Species were
263 assigned to a biome (forest, thicket, or savanna) based on their association with sites in the
264 NMDS ordination; species not found before the extreme fire were classified as pioneers. We
265 then performed a Principal Coordinates Analysis (PCoA) and a pairwise permutational
266 MANOVA on a Bray-Curtis dissimilarity matrix of the total cumulative length in each plot, as
267 well as within the size classes to identify changes in the composition of species types.

268 Results

269 Establishment of a savanna fire regime

270 Forests and thickets rarely burned, with intact forest and thicket sites experiencing no fires
271 between 2000 and 2016 (Fig. 2). Savanna sites, in contrast, burned several times in a
272 decade. In fact, fire frequency (FF) increased from approximately one fire every four years
273 (FF = 0.24 yr^{-1} (SD = 0.11)) before the 2008 extreme fire to one fire every three years (FF =
274 0.36 yr^{-1} (SD = 0.13); t = -11.8, df = 43, $p < 0.05$) after 2008. Thicket patches that burned in
275 the 2008 extreme fire quickly established a savanna fire regime, with sites burning on

276 average once every three years (FF = 0.34 yr^{-1} (SD = 0.07)) , up from no fires between 2000
277 and 2007.

278 Some forests that burned in extreme fires burned again, whereas others did not. To
279 investigate how contrasting fire returns affected their post-extreme-fire trajectories, we
280 split plots into two groups, those that burned only once (hereafter "once-burnt forests")
281 versus those that burned in an extreme fire and at least once subsequently (hereafter
282 "frequently-burnt forests"). Frequently-burnt forests burned on average once every four
283 years after the extreme fire (FF = 0.26 yr^{-1} (SD = 0.04) , Fig. 2).

284 Colonisation by savanna grasses

285 Intact thicket and forest plots differed from savanna plots in having closed canopies and
286 little or no grass in the understory (Fig. 3). Savanna plots had on average 233 gm^{-2} (SD = 87)
287 of grass biomass whereas intact thicket and forest patches had 148 gm^{-2} (SD = 84) and 10
288 gm^{-2} (SD = 2.8) respectively (Fig. 3). Frequently-burnt thicket and frequently-burnt forest
289 plots showed an increase in grass biomass following successive fires, with grass biomass
290 four and 22 times higher than intact thicket and forest plots respectively (Fig. 3). Once-burnt
291 forest plots had relatively high, but variable, grass biomass (130 gm^{-2} (SD = 114)) in the first
292 year after the extreme fires. By the end of the study, 9 years later, grass biomass was less
293 variable (33 gm^{-2} (SD = 11)), approaching the levels of intact forest grass biomass. In terms
294 of grass species, *Panicum maximum* colonised forests and thickets immediately after fire,
295 whereas *Themeda triandra* increased in abundance only where fires occurred repeatedly
296 (Fig. 3).

297 Trajectories in woody structure

298 Forest, thicket, and savanna plots displayed distinct woody size-class distributions (See
299 Appendix S3), with most savanna trees in the smallest size class, most forest trees in the
300 largest size class, and an even spread between the two intermediate size classes in thicket
301 (Fig. 4, Appendix S3). Savanna plots showed little change in structure between 2007 and
302 2014, despite an increase in fire frequency (Pillai's Trace = 0.039, approx F(3,91) = 1.24, p =
303 0.301, Appendix S3).

304 Thicket plots that burned frequently were structurally distinct from intact thicket plots
305 (Pillai's Trace = 0.76, approx F(4,30) = 23.41, p < 0.001, Appendix S3), converging to savanna
306 woody size class structure 7 years after the extreme fire (Pillai's Trace = 0.15, approx F(4,51)
307 = 2.24, p = 0.077, Appendix S3), with most trees in the smallest size class. Similarly, forests
308 that burned multiple times were different to intact forests (Pillai's Trace = 0.89, approx
309 F(4,28) = 58.73, p < 0.001) and also converged to a savanna-like vegetation structure (Pillai's
310 Trace = 0.20, approx F(4,53) = 3.37, p = 0.016) 7 years after the extreme fire, with
311 comparable numbers of trees in the smaller two size classes but differences in the larger
312 two size classes (Appendix S3).

313 Six years after the 2008 extreme fire, once-burnt forests were structurally distinct from
314 both intact forests (Pillai's Trace = 0.902, approx F(4,17) = 38.90, p < 0.001) and savannas
315 (Pillai's Trace = 0.77, approx F(3,43) = 46.72, p < 0.001). The six year once-burnt and the
316 frequently-burnt forests were also different (Pillai's Trace = 0.61, approx F(4,12) = 4.72, p =
317 0.016), with the second largest size class contributing to the majority of the difference
318 between the two (F(1,15) = 21.96, p < 0.001). Nine years after an extreme fire, statistical
319 differences between once-burnt forests and intact forests (Pillai's Trace = 0.761, approx
320 F(4,17) = 13.50, p < 0.001), savannas (Pillai's Trace = 0.767, approx F(3,43) = 47.30, p <

0.001), and frequently-burnt forests (Pillai's Trace = 0.716, approx $F(4,12) = 7.57$, $p < 0.05$) were qualitatively similar to those of the six-year once-burnt forests (Appendix S3, Appendix Fig. S1), except that the cumulative length of the second largest size class of once-burnt forests began to approach that of the intact forests ($F(1,20) = 3.64$, $p = 0.071$).

Trajectories in woody species composition

Forest, thicket, and savanna plots were characterized by distinct woody species assemblages (Fig. 5, Appendix Table S4 & Table S5). The overall (Appendix Table S4) and size class specific (Appendix Table S5) abundance of species types within savannas did not differ between 2007 and 2014 (Fig. 6).

Compositionally, frequently-burnt thickets differed from savannas 7 years after the extreme fire (Fig. 6, Appendix Table S4 & S5), despite both vegetation types experiencing similar disturbance regimes. This was most evident in the smallest size class, in which frequently-burnt thickets were dominated by basally resprouting thicket species, *e.g.*, *Euclea racemosa, Euclea divinorum* and *Berchemia zeyheri,* mixed in with some savanna species, including *Acacia karroo (=Vachellia karoo), Acacia nilotica (=V. nilotica), Dichrostachys cinerea, Cordia caffra, Combretum molle* and *Rhus (= Searsia) pentheri* (Fig. 5), whereas savannas rarely featured thicket species.

By contrast, while frequently-burnt forests also differed from savannas (Appendix Table S4 & S5) 7 years after the extreme fire, their composition had changed more dramatically. Forests, when frequently burned, completely switched to being dominated by thicket species, including *Euclea natalensis* and *Euclea racemosa,* and savanna species (see Fig. 5 & 6), and closely resembled the frequently-burnt thickets.

Once-burnt forests were dominated by pioneer forest species seldom found in intact forests (including *Trema orientalis, Croton sylvaticus,* and *Dombeya burgessiae*). These trees apparently grew from seed banks, which contrasts with trees in frequently-burnt thicket plots, which may have resprouted basally. After 6 years, these once-burnt forests recovered some species characteristic of mature forest, including *Englerophytum natalense* and *Chaetacme aristata*, in smaller size classes, although the larger size classes remained dominated by the unique pioneer forest assemblage (Fig. 6). The once-burnt forests (after six years) were not different to the frequently-burnt forests in overall abundance of species types (Appendix Table S4), but they were different when considering size-class-specific species-type abundances (Appendix Table S5). Nine years after fire, once-burnt forests were dominated by mature forest species in the two smaller size classes and by pioneer forest species in the second largest size class (Appendix Fig. S2). These plots differed from frequently-burnt forests in overall and size-class-specific species-type abundances (Appendix Table S4 & S5, Fig. S3.).

Discussion

Extreme fires differ from typical savanna fires in penetrating beyond the biome boundaries, often opening up the canopy of closed forest or thicket. Here, we found that forests that burned only once recovered via secondary successional pathways, whereas forests and thickets that burned again following the initial extreme fire underwent a persistent transition from closed-canopy vegetation states to open-canopy grassy systems. Among grasses, *Panicum maximum* invaded first but was gradually replaced by *Themeda triandra*, a more flammable species (Simpson et al, 2016). Woody species composition was the slowest to respond to woody structural change, and we observed only minimal colonization of

366 woody savanna species into the new grass layer of repeatedly burned thicket and forests
367 over a decade of post-burn observations.

368 Together, these results suggest that extreme fires, when followed by subsequent fires, can
369 trigger a biome switch from closed, fire-suppressing vegetation state to open, fire-
370 dependent vegetation, structurally resembling savannas. This transition occurred on the
371 time scale of a decade, which suggests that savanna-forest-thicket mosaics are likely
372 dynamic even on the short-to-medium term (Rull *et al*, 2013, Beckett and Bond, 2019, but
373 see Killeen et al, 2006). Repeated fire was crucial for maintaining an open canopy and
374 allowing flammable grasses to colonise (see also Balch *et al.*, 2009, Silverio *et al.*, 2013),
375 ultimately determining whether a biome shift from forest or thicket to savanna occurred.

376 In the transition from closed canopy vegetation states to savanna, initial grass colonization
377 was dominated by *Panicum maximum*, which accumulated biomass rapidly. However, with 7
378 years of repeated fires, *Themeda triandra* gained in dominance in open-canopy systems.
379 This replacement is consistent with the ecology of these two species: *Panicum maximum*
380 (Paniceae) is often observed in relatively shaded savanna environments and is known to
381 retain moisture longer into the dry season (Simpson et al, 2016), whereas *Themeda triandra*
382 (Andropogoneae) prefers open, full-sun environments (Downing & Marshall, 1980,
383 Kinyamario *et al.*, 1995) and is highly flammable (Simpson et al., 2016) but slower to
384 colonise new environments (O'Connor & Everson, 1998).

385 On the time scale of a decade, however, novel savannas differed from old-growth savannas
386 in their woody-layer composition (see also Veldman, 2016), and colonization of open
387 habitats by savanna trees was slower than grass colonization. While forest canopies opened
388 up readily, allowing grasses to colonise, the woody community remained depauperate of

389 savanna trees (see also Veldman & Putz, 2011). Thickets differed from forests in that, even
390 when burned repeatedly, they retained a tree community dominated by thicket species
391 (probably resprouts). Meanwhile, forests that only burned once were colonised mostly by a
392 unique pioneer assemblage. However, in novel savannas, frequent fires gradually depleted
393 thicket and forest remnants, and we hypothesize that savanna woody species will eventually
394 colonise (see also Charles-Dominique et al, 2015b). Further observation of previously
395 closed-canopy areas that continue to experience frequent fires would allow this hypothesis
396 to be tested.

397 Notably, we also found that forests could recover readily from a single extreme fire after a
398 decade allowed the canopy to close and shade out grass fuels, thereby regaining its previous
399 state. Forests likely recovered primarily from a seed bank, with an early-successional forest
400 composed of rapidly growing pioneers (*i.e., Trema orientalis, Croton sylvaticus, Celtis*
401 *africana*) and the clonally spreading liana *Dalbergia armata*. These species excluded light-
402 demanding grasses, likely by shading and microclimate effects that also make the
403 environment suitable for the establishment of climax forest species (see also Pammenter et
404 al. 1985). Further work exploring a range of fire severities on the capability of a forest to
405 recover would allow one to separate out the effects of an extreme fire with subsequent fires
406 versus an extreme fire alone.

407 Thickets also recovered from a single fire readily but differed from forest in their post-fire
408 recovery trajectory. While forests recovered via pioneer species germination, resulting in
409 complete species turnover, thickets instead recovered via basal resprouting. Fire-driven tree
410 mortality in thickets was low, as in savannas, contrasting with much higher tree mortality in
411 forests (see also Ryan & Williams, 2011, Staver *et al.*, 2020). We predict that, on longer time

scales, thickets and, by extension, other dry forests may be more resilient or tolerant of fires than wetter forests (see also Staal et al, 2020, Staver *et al*, 2020).

Our study documents a novel example of invasion of grass-fuelled fires into closed forest and thicket communities in an intact, ancient African savanna-forest-thicket mosaic. Our results offer a few key insights. Firstly, we show that extreme fires can allow savannas to invade forests even in the absence of invasive exotic grasses. Fires have been implicated in the expansion of the savanna biome from the late Miocene (Bond *et al.*, 2003, Keeley & Rundel, 2005, Scheiter *et al*, 2012, Behrensmeyer & Freeman, 2018), perhaps by gradually opening up forests and allowing shade-intolerant savanna grasses to spread at the forest edge (Schertzer & Staver,2018). Fires have also been implicated in constricting forest distributions in response to millennial scale changes in climate (Aleman *et al.*, 2019, Sato *et al*, 2021) – probably by increasing forest canopy openness, thereby facilitating grass invasion and eventually colonization by savanna trees. However, on-the-ground observations of this savannization process in action in intact landscapes are very few.

Secondly, we provide rare direct support for the longstanding hypothesis that runaway fire feedbacks, following an initial extreme fire, can result in the savannization of tropical forests (Cochrane, 1999) without additional anthropogenic drivers. In HiP, as in the Amazon, these extreme fires present a real problem. Their rarity makes them difficult to predict with any accuracy; however, we can be confident that extreme fire weather conditions are increasing in frequency as temperatures rise and aridity increases, making extreme fires an accelerating concern in savanna-forest mosaics, as they are elsewhere (Jolly *et al.*, 2015, Flannigan et al, 2013). Transitions from forest to savanna are indeed possible and likely to increase in potential extent in future.

435 The key difference between this study and work published under the savannization
436 umbrella in the Neotropics revolves around the level of anthropogenic influence in these
437 systems. Contemporary savannization in the Amazon is recorded in areas where exotic
438 pasture grasses have invaded degraded forests, thereby increasing fuel loads and promoting
439 subsequent fires (Silverio *et al*, 2013). However, paleoecological evidence suggests that
440 savannization did occur in the Neotropics predating European colonization, probably as a
441 results of fire in combination with low CO_2 (Rull *et al*, 2013, Sato *et al*, 2021). It is interesting
442 to note the potential impact the disappearance of Neotropical megafauna may have had on
443 the probability of savannization occurring under non-anthropogenic conditions (Owen-
444 Smith, 1987, Johnson, 2009). Recent work suggests that Neotropical grassy systems
445 experienced a large increase in fire activity following the late-Quaternary collapse of large
446 herbivore populations (Karp *et al*. 2021). Conversely, in African systems, the presence of
447 herbivores (especially elephants) may open up the forest and thicket canopies along biome
448 boundaries, allowing grass and therefore fire invasion and precipitating forest conversion to
449 savanna . The role of megafauna in savannization processes has not been sufficiently
450 investigated and offers an interesting avenue for future research.

451 Preventing or suppressing extreme fires is challenging in savannas, where fires are used as a
452 management tool under less extreme conditions. In savannas, woody encroachment has
453 long been a conservation concern, with widespread observations of increases in the woody
454 component of savannas (Stevens *et al.*, 2017), particularly where fire is suppressed instead
455 of being actively managed (Silva et al, 2008, Durigan, 2020). This trend is predicted to
456 intensify as increasing CO_2 favours C3 trees over C4 grasses (Higgins & Scheiter, 2012; Bond
457 & Midgley, 2000, Moncrieff et al, 2014) – suggesting that, while forests are at increased risk
458 of savannization, savannas are also at increased risk of forest expansion and woody

459 encroachment. Widespread fire suppression is clearly not the solution for preventing
460 extreme fires. Rather, we should aim instead for a rationalized fire management policy,
461 allowing and encouraging fires in fire-dependent savannas but minimizing fires under
462 extreme conditions, especially near fire-sensitive forests. Most crucially, we show that
463 forests can recover readily from the effects of extreme fires, especially when an extreme
464 event is not followed by subsequent fires, which may be easier to prevent.

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468 References

469 Aleman JC, Blarquez O, Elenga H et al. (2019) Palaeo-trajectories of forest savannization in
470 the southern Congo. Biology letters, 15, 20190284.

471 Aleman, J. C., & Staver, A. C. (2018). Spatial patterns in the global distributions of savanna
472 and forest. Global Ecology and Biogeography, 27(7), 792-803.

473 Aleman, J. C., Fayolle, A., Favier, C., Staver, A. C., Dexter, K. G., Ryan, C. M., ... & Swaine, M.
474 D. (2020). Floristic evidence for alternative biome states in tropical Africa. Proceedings of
475 the National Academy of Sciences, 117(45), 28183-28190.

476 Alencar, A. A., Brando, P. M., Asner, G. P., & Putz, F. E. (2015). Landscape fragmentation,
477 severe drought, and the new Amazon forest fire regime. Ecological applications, 25(6), 1493-
478 1505.

479 Andela N, Morton DC, Giglio L et al. (2019) The Global Fire Atlas of individual fire size,
480 duration, speed and direction. Earth System Science Data, 11, 529-552.

481 Archibald S, Beckett H, Bond WJ, Coetsee C, Druce DJ, Staver AC (2017) Interactions
482 between Fire and Ecosystem Processes. In: Conserving Africa's Mega-Diversity in the
483 Anthropocene: The Hluhluwe-iMfolozi Park Story. (eds Cromsigt JP, Archibald S, Owen-Smith
484 N) pp Page.

485 Archibald, S., Bond, W. J., Hoffmann, W., Lehmann, C., Staver, C., & Stevens, N. (2019).
486 Distribution and determinants of savannas. Savanna woody plants and large herbivores, 1-
487 24.

488 Aubréville, A. (1949). Climats, forêts et désertification de l'Afrique tropicale.

489 Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D., & Houghton, R. A.
490 (2017). Tropical forests are a net carbon source based on aboveground measurements of
491 gain and loss. Science, 358(6360), 230-234.

492 Balch JK, Nepstad DC, Curran LM (2009) Pattern and process: fire-initiated grass invasion at
493 Amazon transitional forest edges. In: Tropical fire ecology. pp Page., Springer.

494 Balfour DA, Howison OE (2002) Spatial and temporal variation in a mesic savanna fire
495 regime: responses to variation in annual rainfall. African Journal of Range & Forage Science,
496 19, 45-53.

497 Balfour, D. A., & Midgley, J. J. (2008). A demographic perspective on bush encroachment by
498 Acacia karroo in Hluhluwe-Imfolozi Park, South Africa. African Journal of Range and Forage
499 Science, 25(3), 147-151.

500 Barlow, J., & Peres, C. A. (2004). Ecological responses to El Niño–induced surface fires in
501 central Brazilian Amazonia: management implications for flammable tropical
502 forests. Philosophical Transactions of the Royal Society of London. Series B: Biological
503 Sciences, 359(1443), 367-380.

504 Barlow, J., & Peres, C. A. (2008). Fire-mediated dieback and compositional cascade in an
505 Amazonian forest. Philosophical Transactions of the Royal Society B: Biological
506 Sciences, 363(1498), 1787-1794.

507 Beckage, B., Platt, W. J., & Gross, L. J. (2009). Vegetation, fire, and feedbacks: a disturbance-
508 mediated model of savannas. The American Naturalist, 174(6), 805-818.

509 Beckett H, Bond WJ (2019) Fire refugia facilitate forest and savanna co-existence as
510 alternative stable states. Journal of Biogeography, 46(12), 2800-2810

511 Behrensmeyer, A. K., & Freeman, K. H. (2018) Grassland fire ecology has roots in the late
512 Miocene. Proceedings of the National Academy of Sciences, 115(48), 12130-12135.

513 Biddulph J, Kellman M (1998) Fuels and fire at savanna-gallery forest boundaries in
514 southeastern Venezuela. Journal of Tropical Ecology, 14, 445-461.

515 Bond WJ, Midgley GF, Woodward FI (2003) The importance of low atmospheric CO2 and fire
516 in promoting the spread of grasslands and savannas. Global Change Biology, 9, 973-982.

517 Bond, W. J. (2008). What limits trees in C4 grasslands and savannas?. Annual review of
518 ecology, evolution, and systematics, 39, 641-659.

519 Bond, W. J. (2016). Ancient grasslands at risk. Science, 351(6269), 120-122.

520 Bond, W. J., & Midgley, G. F. (2000). A proposed CO2-controlled mechanism of woody plant
521 invasion in grasslands and savannas. Global Change Biology, 6(8), 865-869.

522 Bond, W. J., & Parr, C. L. (2010). Beyond the forest edge: ecology, diversity and conservation
523 of the grassy biomes. Biological conservation, 143(10), 2395-2404.

524 Bradstock RA, Hammill KA, Collins L, Price O (2009) Effects of weather, fuel and terrain on
525 fire severity in topographically diverse landscapes of south-eastern Australia. Landscape
526 Ecology, 25, 607-619.

527 Brando, P. M., Balch, J. K., Nepstad, D. C., Morton, D. C., Putz, F. E., Coe, M. T., et al. (2014).
528 Abrupt increases in Amazonian tree mortality due to drought-fire interactions. PNAS,
529 111(17), 6347–6352.

530 Brando, P. M., Nepstad, D. C., Balch, J. K., Bolker, B., Christman, M. C., Coe, M., & Putz, F. E.
531 (2011). Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size,
532 wood density and fire behavior. Global Change Biology, 18(2), 630–641.

533 Brando, P. M., Soares-Filho, B., Rodrigues, L., Assunção, A., Morton, D., Tuchschneider, D., ...
534 & Coe, M. T. (2020). The gathering firestorm in southern Amazonia. Science advances, 6(2),
535 eaay1632.

536 Bransby, D. I., & Tainton, N. M. (1977). The disc pasture meter: possible applications in
537 grazing management. Proceedings of the annual congresses of the Grassland Society of
538 Southern Africa, 12(1), 115-118.

539 Breman, E., Gillson, L., & Willis, K. (2012). How fire and climate shaped grass-dominated
540 vegetation and forest mosaics in northern South Africa during past millennia. The Holocene,
541 22(12), 1427-1439.

542 Brook, B. W., & Bowman, D. M. (2006). Postcards from the past: charting the landscape-
543 scale conversion of tropical Australian savanna to closed forest during the 20th century.
544 Landscape Ecology, 21(8), 1253.

545 Browne C, Bond W (2011) Firestorms in savanna and forest ecosystems: curse or cure? Veld
546 & Flora, 97, 62-63.

547 Budowski, G. 1956. Tropical savannas, a sequence of forest felling and repeated burnings.
548 Turrialba 6(1-2) :23-33

549 Cardoso, A. W., Oliveras, I., Abernethy, K. A., Jeffery, K. J., Glover, S., Lehmann, D., ... &
550 Malhi, Y. (2020). A distinct ecotonal tree community exists at central African forest–savanna
551 transitions. Journal of Ecology.

552 Case MF, Staver AC (2017) Fire prevents woody encroachment only at higher-than-historical
553 frequencies in a South African savanna. Journal of Applied Ecology, 54, 955-962.

554 Cavelier, J., Aide, T., Santos, C., Eusse, A., & Dupuy, J. (1998). The savannization of moist
555 forests in the Sierra Nevada de Santa Marta, Colombia. Journal of Biogeography, 25(5), 901-
556 912.

557 Charles-Dominique T, Staver AC, Midgley GF, Bond WJ (2015a) Functional differentiation of
558 biomes in an African savanna/forest mosaic. South African Journal of Botany, 101, 82-90.

559 Charles-Dominique T, Beckett H, Midgley GF, Bond WJ (2015b) Bud protection: a key trait
560 for species sorting in a forest-savanna mosaic. New Phytol, 207, 1052-1060.

561 Charles-Dominique T, Midgley GF, Tomlinson KW, Bond WJ (2018) Steal the light: shade vs
562 fire adapted vegetation in forest–savanna mosaics. New Phytologist, 218, 1419-1429.

563 Chen Y, Morton D, Jin Y et al. (2014) Erratum: Long-term trends and interannual variability
564 of forest, savanna and agricultural fires in South America (Carbon Management (2013) 4: 6
565 (617-638)).

566 Cochrane MA (1999) Positive Feedbacks in the Fire Dynamic of Closed Canopy Tropical
567 Forests. Science, 284, 1832-1835.

568 Cochrane MA, Laurance WF (2002) Fire as a large-scale edge effect in Amazonian forests.
569 Journal of Tropical Ecology, 18, 311-325.

570 Cox, P. M., Betts, R. A., Collins, M., Harris, P. P., Huntingford, C., & Jones, C. D. (2004).
571 Amazonian forest dieback under climate-carbon cycle projections for the 21st
572 century. Theoretical and applied climatology, 78(1), 137-156.

573 Dantas, V. D. L., Hirota, M., Oliveira, R. S., & Pausas, J. G. (2016). Disturbance maintains
574 alternative biome states. Ecology Letters, 19(1), 12-19.

575 Downing B, Marshall D (1980) Complementary dominance of Themeda triandra and
576 Panicum maximum examined through shoot production. Proceedings of the Annual
577 Congresses of the Grassland Society of Southern Africa, 15, 163-166.

578 Durigan, G (2020) Zero-fire: not possible nor desirable in the Cerrado of Brazil. Flora,
579 151612.

580 Favier C, Chave J, Fabing A, Schwartz D, Dubois MA (2004) Modelling forest–savanna mosaic
581 dynamics in man-influenced environments: effects of fire, climate and soil heterogeneity.
582 Ecological Modelling, 171, 85-102.

583 Fearnside, P. M. (1990). Fire in the tropical rain forest of the Amazon basin. In Fire in the
584 tropical biota (pp. 106-116). Springer, Berlin, Heidelberg.

585 Fei S, Gould PJ, Steiner KC, Finley JC, Mcdill ME (2005) Forest regeneration composition and
586 development in upland, mixed-oak forests. Tree physiology, 25, 1495-1500.

587 Flannigan M, Cantin AS, De Groot WJ, Wotton M, Newbery A, Gowman LM (2013) Global
588 wildland fire season severity in the 21st century. Forest Ecology and Management, 294, 54-
589 61.

590 Flores, B. M., Fagoaga, R., Nelson, B. W., & Holmgren, M. (2016). Repeated fires trap
591 Amazonian blackwater floodplains in an open vegetation state. Journal of Applied
592 Ecology, 53(5), 1597-1603.

593 Giglio L, Kendall J, Mack R (2003) A multi-year active fire dataset for the tropics derived from
594 the TRMM VIRS. International Journal of Remote Sensing, 24, 4505-4525.

595 Goel, N., Guttal, V., Levin, S. A., & Staver, A. C. (2020a). Dispersal increases the resilience of
596 tropical savanna and forest distributions. The American Naturalist, 195(5), 833–850.

597 Goel, N., Van Vleck, E. S., Aleman, J. C., & Staver, A. C. (2020b). Dispersal limitation and fire
598 feedbacks maintain mesic savannas in Madagascar. Ecology, 12(1), 145–12.

599 Hall M (1980) An iron-smelting site in the Hluhluwe Game Reserve, Zululand. Annals of the
600 Natal Museum, 24, 165-175.

601 Hennenberg KJ, Goetze D, Szarzynski J, Orthmann B, Reineking B, Steinke I, Porembski S
602 (2008) Detection of seasonal variability in microclimatic borders and ecotones between
603 forest and savanna. Basic and Applied Ecology, 9, 275-285.

604 Higgins, SI, & Scheiter, S (2012). Atmospheric CO 2 forces abrupt vegetation shifts locally,
605 but not globally. Nature, 488(7410), 209-212.

606 Hirota, M., Nobre, C., Oyama, M. D., & Bustamante, M. M. (2010). The climatic sensitivity of
607 the forest, savanna and forest–savanna transition in tropical South America. New
608 Phytologist, 187(3), 707-719.

609 Hoffmann WA, Geiger EL, Gotsch SG et al. (2012a) Ecological thresholds at the savanna-
610 forest boundary: how plant traits, resources and fire govern the distribution of tropical
611 biomes. Ecol Lett, 15, 759-768.

612 Hoffmann WA, Jaconis SY, Mckinley KL, Geiger EL, Gotsch SG, Franco AC (2012b) Fuels or
613 microclimate? Understanding the drivers of fire feedbacks at savanna-forest boundaries.
614 Austral Ecology, 37, 634-643.

615 Ibanez, T., Borgniet, L., Mangeas, M., Gaucherel, C., Géraux, H., & Hély, C. (2013). Rainforest
616 and savanna landscape dynamics in New Caledonia: towards a mosaic of stable rainforest
617 and savanna states? Austral Ecology, 38(1), 33-45.

618 Johnson, C. N. (2009). Ecological consequences of Late Quaternary extinctions of
619 megafauna. Proceedings of the Royal Society B: Biological Sciences, 276(1667), 2509-2519.

620 Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DM
621 (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. Nat
622 Commun, 6, 7537.

623 Karp, A. T., Faith, J. T., Marlon, J. R., & Staver, A. C. (2021). Global response of fire activity to
624 late Quaternary grazer extinctions. Science, 374(6571), 1145-1148.

625 Keeley JE, Pausas JG (2019) Distinguishing disturbance from perturbations in fire-prone
626 ecosystems. International Journal of Wildland Fire, 28, 282-287.

627 Keeley JE, Rundel PW (2005) Fire and the Miocene expansion of C4 grasslands. Ecology
628 Letters, 8, 683-690.

629 Kellman, M., & Meave, J. (1997). Fire in the tropical gallery forests of Belize. Journal of
630 Biogeography, 24(1), 23-34.

631 Kennard, D. K. (2002). Secondary forest succession in a tropical dry forest: patterns of
632 development across a 50-year chronosequence in lowland Bolivia. Journal of tropical
633 ecology, 18(1), 53-66.

634 Killeen, T. J., Chavez, E., Peña-Claros, M., Toledo, M., Arroyo, L., Caballero, J., ... & Steininger,
635 M. (2006). The Chiquitano dry forest, the transition between humid and dry forest in
636 eastern lowland Bolivia. In Neotropical savannas and seasonally dry forests (pp. 214-233).
637 CRC Press.

638 Kinyamario J, Trlica M, Njoka T (1995) Influence of tree shade on plant water status, gas
639 exchange, and water use efficiency of Panicum maximum Jacq. and Themeda triandra Forsk.
640 in a Kenya savanna. African Journal of Ecology, 33, 114-123.

641 Legendre P, Legendre LF (2012) Numerical ecology, Elsevier.

642 Little JK, Prior LD, Williamson GJ, Williams SE, Bowman DMJS (2012) Fire weather risk differs
643 across rain forest-savanna boundaries in the humid tropics of north-eastern Australia.
644 Austral Ecology, 37, 915-925.

645 Moncrieff GR, Scheiter S, Bond WJ, Higgins SI (2014) Increasing atmospheric CO2 overrides
646 the historical legacy of multiple stable biome states in Africa. New Phytol, 201, 908-915.

647 Morton D, Le Page Y, Defries R, Collatz G, Hurtt G (2013) Understorey fire frequency and the
648 fate of burned forests in southern Amazonia. Philosophical Transactions of the Royal Society
649 B: Biological Sciences, 368, 20120163.

650 Murphy, B. P., & Bowman, D. M. (2012). What controls the distribution of tropical forest and
651 savanna?. Ecology letters, 15(7), 748-758.

652 Nepstad, D. C., Uhl, C., Pereira, C. A., & Da Silva, J. M. C. (1996). A comparative study of tree
653 establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos, 25-39.

654 Nepstad, D. C., Verssimo, A., Alencar, A., Nobre, C., Lima, E., Lefebvre, P., ... & Brooks, V.
655 (1999). Large-scale impoverishment of Amazonian forests by logging and
656 fire. Nature, 398(6727), 505-508.

657 Nyerges, A. E. (1992). Swidden agriculture and the savannization of forests in Sierra
658 Leone (Doctoral dissertation, Ann Arbor: UMI).

659 O'Connor T, Everson T (1998) Population dynamics of perennial grasses in African savanna
660 and grassland. Population biology of grasses, 399.

661 Oksanen J, Blanchet FG, Kindt R et al. (2013) Package 'vegan'. Community ecology package,
662 version, 2.

663 Ondei, S., Prior, L. D., Vigilante, T., & Bowman, D. M. (2017). Fire and cattle disturbance
664 affects vegetation structure and rain forest expansion into savanna in the Australian
665 monsoon tropics. Journal of biogeography, 44(10), 2331-2342.

666 Owen-Smith, N. (1987). Pleistocene extinctions: the pivotal role of
667 megaherbivores. Paleobiology, 13(3), 351-362.

668 Pammenter N, Berjak M, Macdonald I (1985) Regeneration of a Natal coastal dune forest
669 after fire. South African Journal of Botany, 51, 453-459.

670 Ratnam J, Bond WJ, Fensham RJ et al. (2011) When is a 'forest' a savanna, and why does it
671 matter? Global Ecology and Biogeography, 20, 653-660.

672 Rosan, T. M., Aragão, L. E., Oliveras, I., Phillips, O. L., Malhi, Y., Gloor, E., & Wagner, F. H.
673 (2019). Extensive 21st-century woody encroachment in South America's
674 savanna. Geophysical Research Letters, 46(12), 6594-6603.

675 Rull, V., Montoya, E., Nogue, S., Vegas-Vilarrubia, T., & Safont, E. (2013). Ecological
676 palaeoecology in the neotropical Gran Sabana region: long-term records of vegetation
677 dynamics as a basis for ecological hypothesis testing. Perspectives in Plant Ecology,
678 Evolution and Systematics, 15(6), 338-359.

679 Ryan CM, Williams M (2011) How does fire intensity and frequency affect miombo
680 woodland tree populations and biomass? Ecological Applications, 21, 48-60.

681 Sato, H., Kelley, D. I., Mayor, S. J., Martin Calvo, M., Cowling, S. A., & Prentice, I. C. (2021).
682 Dry corridors opened by fire and low CO2 in Amazonian rainforest during the Last Glacial
683 Maximum. Nature Geoscience, 1-8.

684 Sanford, R. L., Saldarriaga, J., Clark, K. E., Uhl, C., & Herrera, R. (1985). Amazon rain-forest
685 fires. Science, 227(4682), 53-55.

686 Scheiter S, Higgins SI, Osborne CP, Bradshaw C, Lunt D, Ripley BS, Taylor LL, and Beerling DJ
687 (2012) Fire and fire-adapted vegetation promoted C4 expansion in the late Miocene. New
688 Phytologist 195, no. 3: 653-666.Schwartz D, Mariotti A, Lanfranchi R, Guillet B (1986)

13C/12C ratios of soil organic matter as indicators of vegetation changes in the Congo. Geoderma, 39, 97-103.

Schertzer, E., & Staver, A. C. (2018). Fire spread and the issue of community-level selection in the evolution of flammability. Journal of The Royal Society Interface, 15(147), 20180444.

Schwartz, D., Mariotti, A., Lanfranchi, R., & Guillet, B. (1986). 13C/12C ratios of soil organic matter as indicators of vegetation changes in the Congo. Geoderma, 39(2), 97-103.

Silva, LCR, Sternberg L, Haridasan M, Hoffmann WA, Miralles-Wilhelm F, and Franco AC.(2008) Expansion of gallery forests into central Brazilian savannas. Global Change Biology 14, no. 9: 2108-2118.

Silverio DV, Brando PM, Balch JK, Putz FE, Nepstad DC, Oliveira-Santos C, Bustamante MM (2013) Testing the Amazon savannization hypothesis: fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. Philos Trans R Soc Lond B Biol Sci, 368, 20120427.

Simpson KJ, Ripley BS, Christin PA, Belcher CM, Lehmann CE, Thomas GH, and Osborne CP. (2016) Determinants of flammability in savanna grass species. Journal of Ecology, 104(1), 138-148.

Schmidt, I. B., Ferreira, M. C., Sampaio, A. B., Walter, B. M., Vieira, D. L., & Holl, K. D. (2019). Tailoring restoration interventions to the grassland-savanna-forest complex in central Brazil. Restoration Ecology, 27(5), 942-948.

Staal, A., Fetzer, I., Wang-Erlandsson, L., Bosmans, J. H., Dekker, S. C., van Nes, E. H., ... & Tuinenburg, O. A. (2020). Hysteresis of tropical forests in the 21st century. Nature communications, 11(1), 1-8.

711 Staver AC, Archibald S, Levin SA (2011a) The global extent and determinants of savanna and
712 forest as alternative biome states. Science, 334, 230-232.

713 Staver AC, Beckett H, Graf J (2017) 3 r Long-Term Vegetation Dynamics within the Hluhluwe
714 iMfolozi Park. Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-
715 iMfolozi Park Story, 56.

716 Staver AC, Bond WJ, Cramer MD, Wakeling JL (2012) Top-down determinants of niche
717 structure and adaptation among African Acacias. Ecol Lett, 15, 673-679.

718 Staver, A. C., & Levin, S. A. (2012). Integrating theoretical climate and fire effects on savanna
719 and forest systems. The American Naturalist, 180(2), 211-224.

720 Staver, A. C., Archibald, S., & Levin, S. (2011b). Tree cover in sub-Saharan Africa: rainfall and
721 fire constrain forest and savanna as alternative stable states. Ecology, 92(5), 1063-1072.

722 Staver, A. C., Brando, P. M., Barlow, J., Morton, D. C., Paine, C. T., Malhi, Y., ... & del Aguila
723 Pasquel, J. (2020). Thinner bark increases sensitivity of wetter Amazonian tropical forests to
724 fire. Ecology Letters, 23(1), 99-106.

725 Stevens N, Lehmann CE, Murphy BP, Durigan G (2017) Savanna woody encroachment is
726 widespread across three continents. Glob Chang Biol, 23, 235-244.

727 Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M. S., Rödig, E., ... & Huth, A.
728 (2018). Global patterns of tropical forest fragmentation. Nature, 554(7693), 519-522.

729 Uhl, C., Clark, H., Clark, K., & Maquirino, P. (1982). Successional patterns associated with
730 slash-and-burn agriculture in the upper Rio Negro region of the Amazon basin. Biotropica,
731 249-254.

van de Leemput, I. A., van Nes, E. H., & Scheffer, M. (2015). Resilience of Alternative States in Spatially Extended Ecosystems. PLoS ONE, 10(2), e0116859. http://doi.org/10.1371/journal.pone.0116859.s012

Van Nes, E. H., Staal, A., Hantson, S., Holmgren, M., Pueyo, S., Bernardi, R. E., ... & Scheffer, M. (2018). Fire forbids fifty-fifty forest. PloS one, 13(1), e0191027.

Veenendaal, E. M., Torello-Raventos, M., Feldpausch, T. R., Domingues, T. F., Gerard, F., Schrodt, F., ... & Kemp, J. (2015). Structural, physiognomic and above-ground biomass variation in savanna-forest transition zones on three continents-how different are co-occurring savanna and forest formations?. Biogeosciences, 12(10), 2927-2951.

Veldman JW, Buisson E, Durigan G et al. (2015a) Toward an old-growth concept for grasslands, savannas, and woodlands. Frontiers in Ecology and the Environment, 13, 154-162.

Veldman, J. W., & Putz, F. E. (2010). Long-distance dispersal of invasive grasses by logging vehicles in a tropical dry forest. Biotropica, 42(6), 697-703.

Veldman JW, Putz FE (2011) Grass-dominated vegetation, not species-diverse natural savanna, replaces degraded tropical forests on the southern edge of the Amazon Basin. Biological Conservation, 144, 1419-1429.

Veldman, J. W. (2016). Clarifying the confusion: old-growth savannahs and tropical ecosystem degradation. Philosophical Transactions of the Royal Society B: Biological Sciences, 371(1703), 20150306.

752 Veldman, J.W., Overbeck, G.E., Negreiros, D., Mahy, G., Le Stradic, S., Fernandes, G.W.,
753 Durigan, G., Buisson, E., Putz, F.E. and Bond, W.J. (2015b). Where tree planting and forest
754 expansion are bad for biodiversity and ecosystem services. BioScience, 65(10), 1011-1018.

755 Waldram MS, Bond WJ, Stock WD (2007) Ecological Engineering by a Mega-Grazer: White
756 Rhino Impacts on a South African Savanna. Ecosystems, 11, 101-112.

757 Watson, J. E., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., ... & McAlpine, C.
758 (2018). The exceptional value of intact forest ecosystems. Nature ecology & evolution, 2(4),
759 599-610.

760 West, A. G., Bond, W. J., & Midgley, J. J. (2000). Soil carbon isotopes reveal ancient grassland
761 under forest. S. Afr. J. Sci, 96, 253.

762 Whateley A, Porter R (1983) The woody vegetation communities of the Hluhluwe-Corridor-
763 Umfolozi game reserve complex. Bothalia, 14, 745-758.

764 Wickham H (2017) The tidyverse. R package ver. 1.1. 1.

765 Woodward FI, Lomas MR, Kelly CK (2004) Global climate and the distribution of plant
766 biomes. Philos Trans R Soc Lond B Biol Sci, 359, 1465-1476.

767 Wright, J. L., Bomfim, B., Wong, C. I., Marimon-Júnior, B. H., Marimon, B. S., & Silva, L. C.
768 (2021). Sixteen hundred years of increasing tree cover prior to modern deforestation in
769 Southern Amazon and Central Brazilian savannas. Global Change Biology, 27(1), 136-150.

770 Wuyts, B., Champneys, A. R., Verschueren, N., & House, J. I. (2019). Tropical tree cover in a
771 heterogeneous environment: A reaction-diffusion model. PloS one, 14(6), e0218151.

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Author Contributions

HB, WJB, and ACS conceived of the idea. TCD and ACS contributed data. HB collected the data, designed, and performed the analyses with input from TCD and ACS. HB wrote the paper in consultation with WJB, ACS, and TCD.

793 Figure Legends

794 **Figure 1.** Fire Frequency map (left) of Hluhluwe iMfolozi Park from 1955 to 2013 based on
795 Hluhluwe iMfolozi Park records with the Hluhluwe section outlined in red, and (right) the
796 distribution of plots within the Hluhluwe portion of HiP and biomes based on a
797 reclassification of Whateley & Porter (1983) by Charles-Dominique *et al* (2015). Green
798 represents forest, blue represents thickets, and yellow represents savannas. Inset map
799 shows the location of Hluhluwe iMfolozi Park within South Africa.

800

801 Figure 2. Fire Frequency for plots within each vegetation type (indicated by grey text) before
802 and after extreme fires (not including the year of the extreme fire), calculated using the
803 MODIS Active Fires Product from 2000 to 2016. Grey lines link plot points before and after
804 extreme fires. Asterisks indicate significance level (*** <0.05, **** < 0.001, NS = no
805 significant difference).

806

807 Figure 3. Grass biomass in frequently-burnt forests, once-burnt forest, frequently-burnt
808 thicket and savanna, (a) in total, (B) of *Panicum maximum*, and (C) of *Themeda triandra*.
809 Green bars represent forest plots, blue represents thicket, and yellow represents savanna.
810 Error bars indicate standard errors. Points (plot grass biomass) are included to display
811 variation. Shared letters indicate lack of a significant difference within panels based on
812 Wilcoxon signed-rank test, $p < 0.05$.

813

814 Figure 4. Mean cumulative length of all tree species within the four size classes 'before' and
815 'after' the extreme fire in A) savanna, B) frequently-burnt thicket, C) frequently-burnt forest,
816 and D) once-burnt forest. Error bars indicate standard errors. Points represent individual
817 plots.

818 Figure 5. NMDS ordination of the cumulative length of all species in all height classes in
819 plots. Ellipses show the grouping of plots. Species associations used in the composition
820 analyses are based on species found in plots before the extreme fires only. Letters indicate
821 plots, and grey dots indicate species.

822 **Figure 6.** Initial and final composition and structure of savannas in 2007 (A) and 2014 (B),
823 intact thicket (C) and frequently-burnt thicket 7 years after extreme fire (D), intact forest (E)
824 and frequently-burnt forest 7 years after extreme fire (F) and intact forest (G) and once-
825 burnt forest 6 years after fire (H). Panels display the average cumulative length of tree
826 species within each size class for the different time periods 'before' and 'after' the extreme
827 fire. Colours indicate the biome in which these species are predominantly found. Pioneer
828 species are those which were not found in plots sampled before the extreme fire. Data
829 recorded in intact forest and thicket vegetation represent pre-fire space for time
830 substitutions.

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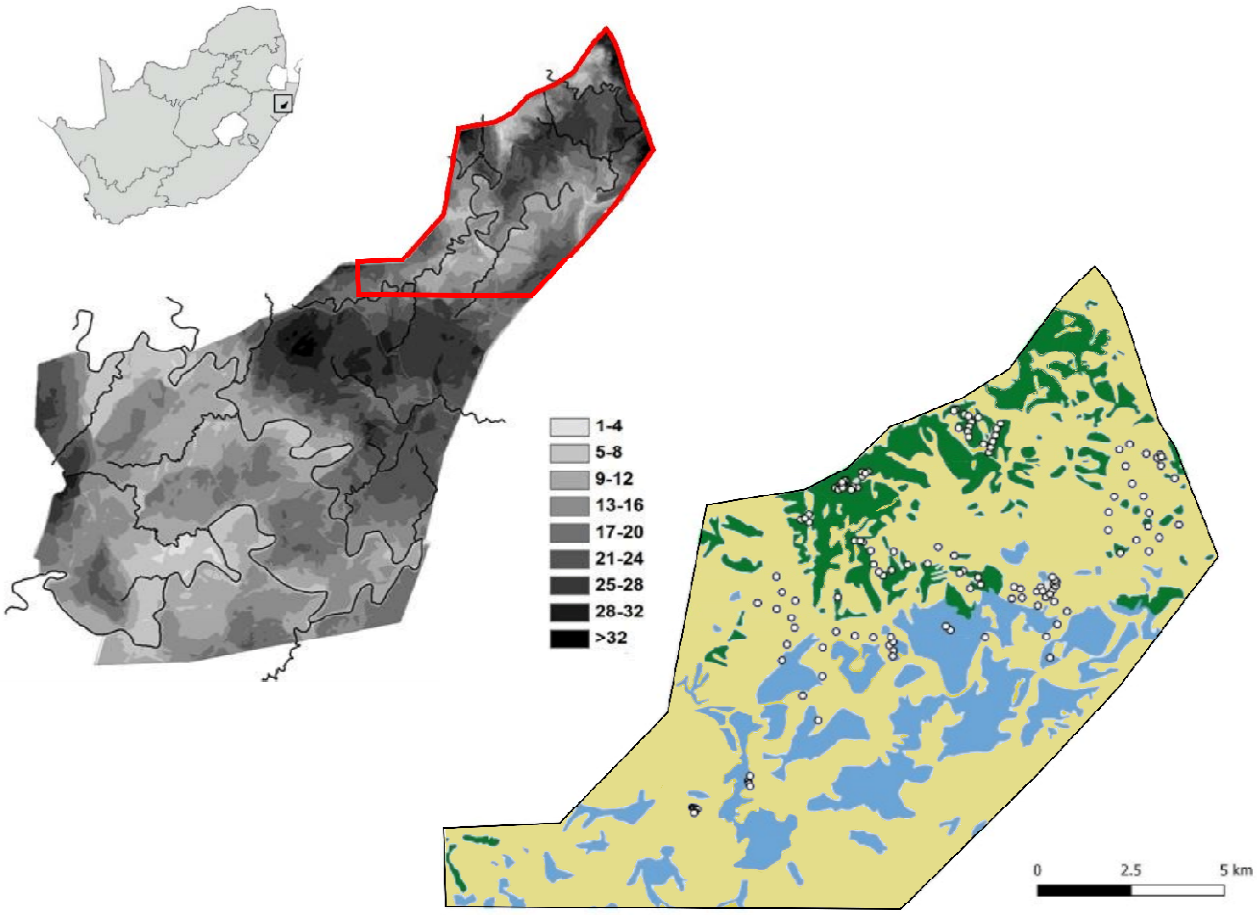

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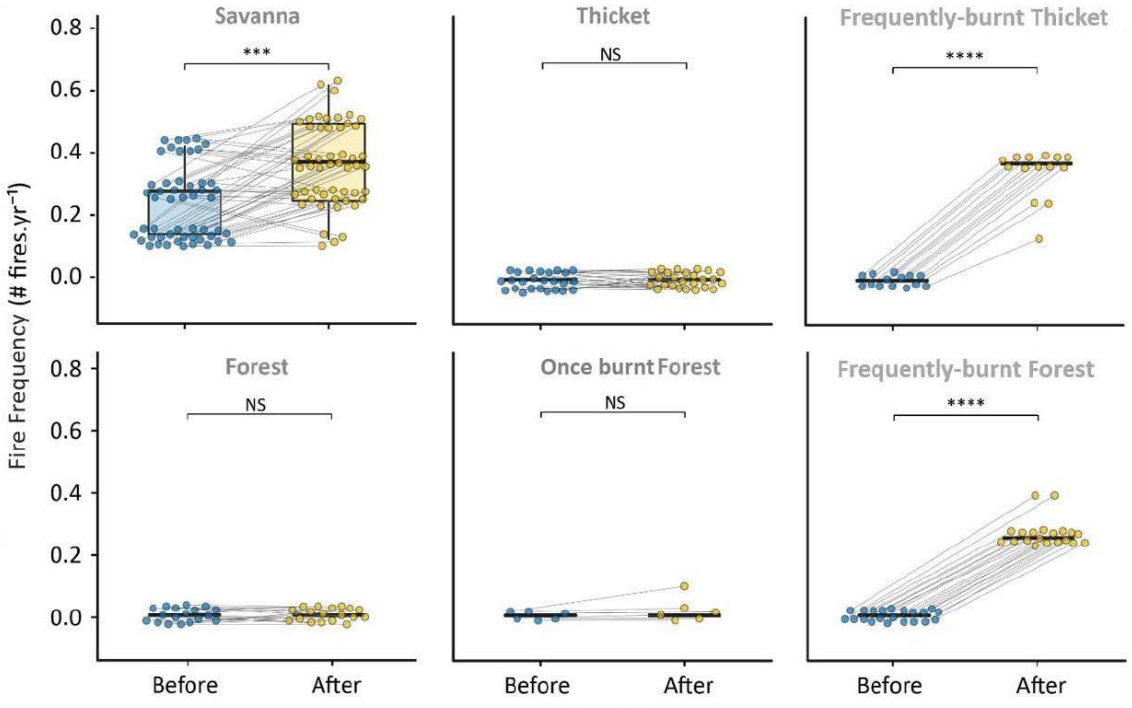

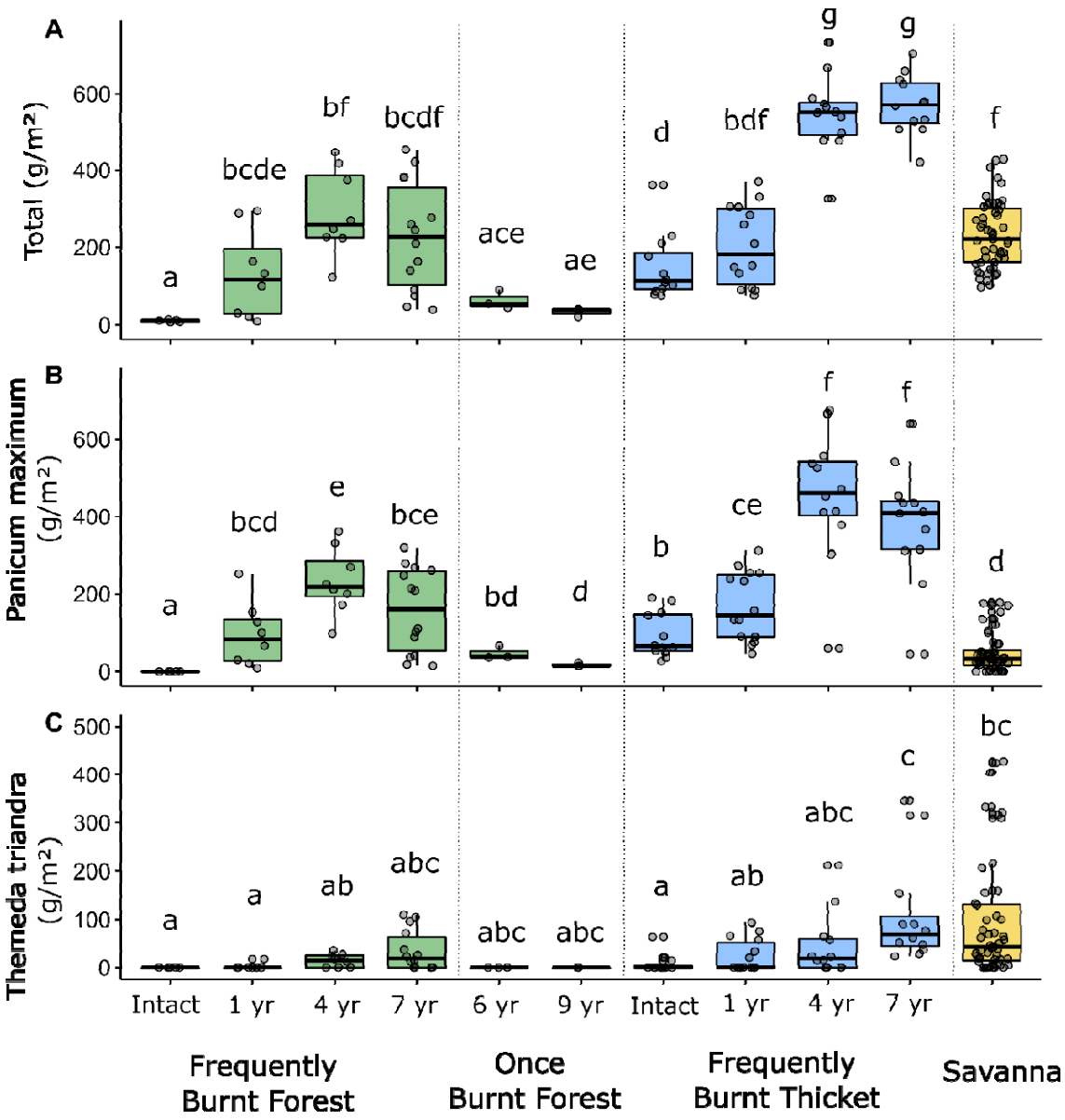

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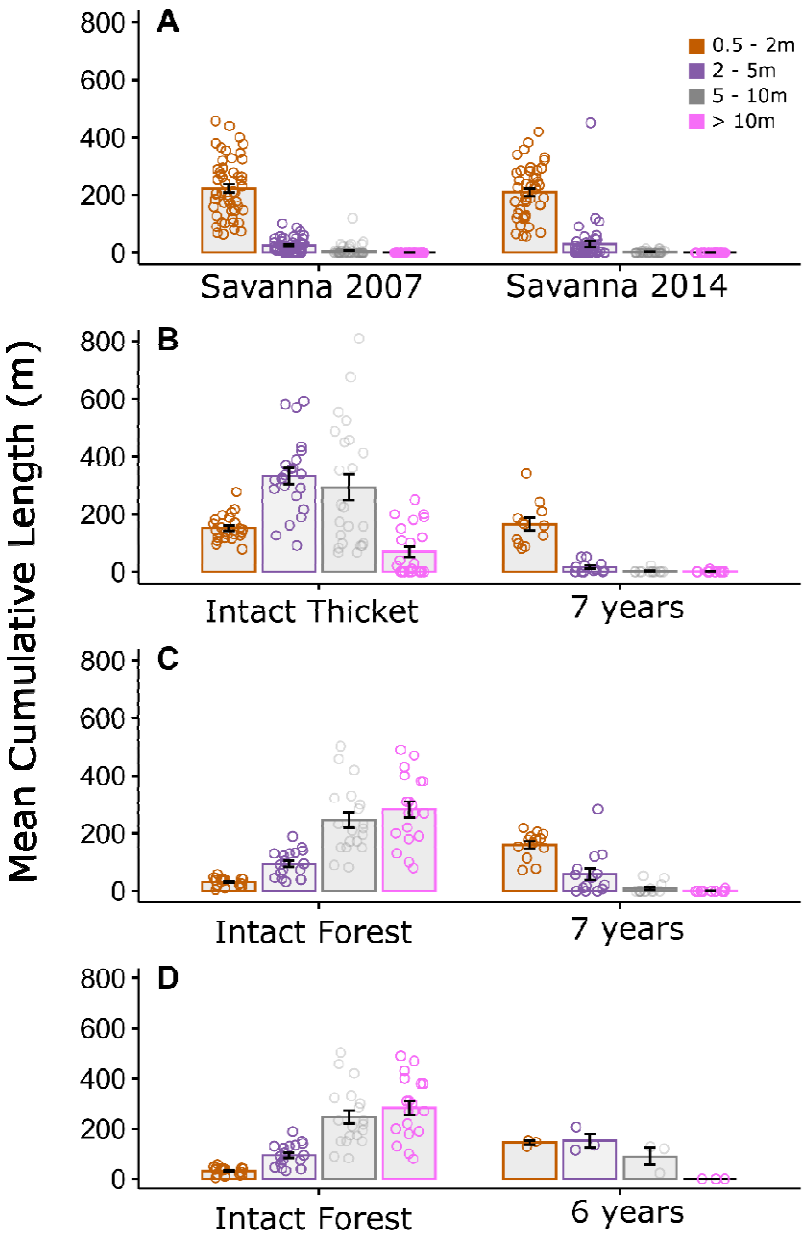

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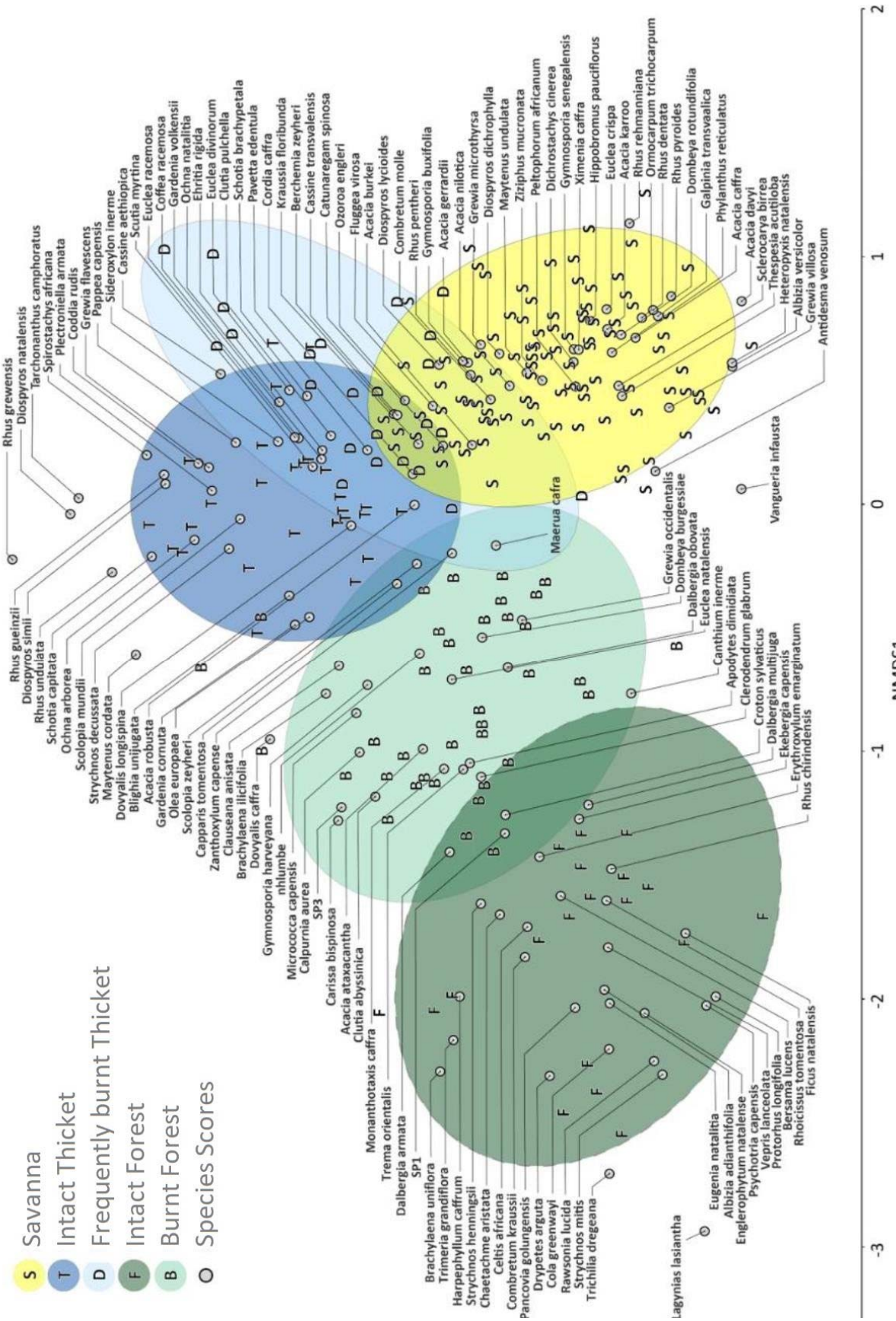

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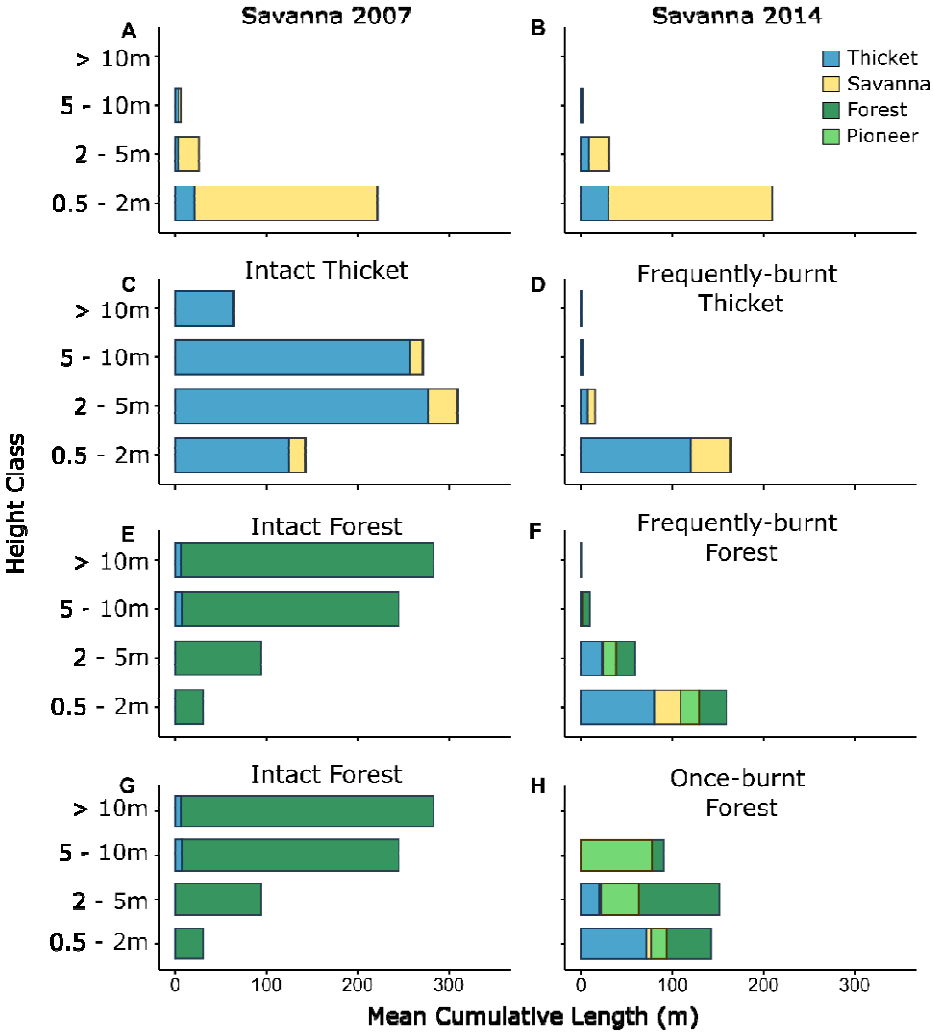

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