Pathways of savannization in a mesic African savanna-forest mosaic

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Abstract

Typically, savannas experience frequent fires, which limit tree cover and promote flammable grass accumulation, whereas forests and thickets form dense canopies that exclude fires by reducing C4-grass fuel loads and creating a humid microclimate. However, extreme fires occasionally burn into these closed canopy systems. Although these are known to cause tree mortality and can make repeat fires more likely, the long-term consequences of an extreme fire event for closed canopy vegetation structure and potential savannization remain largely unknown. Here, we analysed whether an extreme fire event could, alone, alter species composition, vegetation structure, and fire regimes of closed canopy ecosystems in a natural savanna-forest-thicket mosaic, or whether successive fires after an initial extreme fire event were necessary to trigger a biome transition between these alternative stable states. We found that forests that only burned once recovered, whereas those that burned again following an initial extreme fire event underwent a transition from closed-canopy forests to open, grassy systems. Thickets had lower levels of tree mortality following fires than forests, although repeat fires also led to a transition towards open grassy systems, structurally resembling savannas. Our results suggest that while extreme fires set the stage for a biome transition, subsequent fires are necessary for grass composition to resemble neighbouring savanna grass communities, ultimately resulting in a savanna fire regime. Savannization, following extreme fire events, is possible in natural mosaic ecosystems where open and closed canopy vegetation types 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 were not flammable (Chen *et al.*, 2014, Morton *et al.*, 2013). 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 for 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 in anthropogenically modified environments there is evidence for seed dispersal by trucks (see Veldman and Putz, 2010)) and possible biogeochemical feedbacks. As a result, the question of whether fires can actually convert a tropical forest to a savanna, in a natural setting, remains open.

Historically and today, fires burn frequently in 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 the establishment of fire-sensitive

forest saplings, but fires stop readily at the savanna-forest boundary, because shade in the forest understory prevents the accumulation of shade-intolerant C4 grasses 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 alternative stable states (Staver *et al.*, 2011a, but see Veenendaal et al, 2015, Hanan et al, 2014). 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). In this situation, extreme fires in forests may have fairly negligible 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 has argued that fires at the savanna-forest boundary can have major effects on 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) and local observations confirm that boundaries are sometimes dynamic through time (Brook & Bowman, 2006, Silva *et* al, 2008, Ibanez *et al,* 2013, Beckett & Bond, 2019). Modern observations also confirm that tropical forests can invade savannas and grasslands especially at the boundary between the two, in Africa (Baccini et al., 2017; Aleman et al., 2018), South America, and Australia (Marimon et al., 2014; Ondei et al., 2017; Stevens et al., 2017; Rosan et al., 2019).

However, modern evaluations of invasions of forests by savannas has predominantly been studied in 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, such as the appearance of grass-dominated systems which differ from old growth savannas (Veldman and Putz, 2011), the susceptibility of forest trees to fire induced mortality (Barlow and Peres, 2008, Staver *et al,* 2020), and the invasion of grassy fuels following repeat fires (Veldman and Putz, 2011, Silverio *et al,* 2013). However, these processes typically rely upon the introduction of exotic grass species (which lead to novel fire regimes), and deforestation derived boundaries (Alencar *et al*. 2015) with unclear historical and palaeoecological precedents (but see Flores et al 2016).

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 forest subject to

anthropogenic pressures such as farming and deforestation (Nyerges, 1990, Uhl *et al*, 1982, Cochrane, 1999, Nepstad *et al*, 1999). The term rose to prominence following predictions of large-scale Amazonian Forest die off under elevated CO_2 (Cox *et al,* 2004) and is widely used in the contemporary literature to refer to a reduction of tree biomass and species associated with forest ecosystems. In doing so, the savanna biome is – unintentionally - associated with degraded, species-poor forests and identified as an early successional stage of forest vegetation (Veldman, 2016, Bond, 2016, Schmidt *et al*, 2019). The term savannization should be used to refer to the conversion of one vegetation state (typically forests) into a savanna and the establishment of the processes regulating savannas, which is possible in regions of the world where savannas and forests represent alternative stable states (Staver & Levin, 2012, Archibald *et al*, 2019, Aleman *et al*, 2020).

Perpetuating the usage of the term to refer to anthropogenic degradation undermines the value and antiquity of the savanna biome and reinforces a widely held – yet critically incorrect – belief that savannas are an anthropogenically derived vegetation type (Veldman *et al*, 2015a, Veldman, 2016). As such, we believe the question of whether extreme fires can cause a biome switch between forests and savannas in a natural setting has not yet been settled but is increasingly relevant in an age of climate extremes. Vegetation mosaics of alternative stable states offer a rare opportunity for testing the concept in a natural setting.

This question has both theoretical and practical importance. From the perspective of understanding ecological processes, we have no clear understanding of the possible role of extreme fires in biogeographic transitions between savanna and forest (*e.g.*, Aleman et al 2019) and in shaping transitions in response to changing climate (Beckett & Bond 2019). From a practical perspective, recent decades have seen significant increases in deforestation

135 and fragmentation of intact tropical forests (Watson et al, 2018; Taubert et al, 2018). The
136 most commonly proposed solution to this is to plant trees in order to restore fragmented
137 landscapes (e.g., the Bonn Challenge, REDD+; Veldman et al, 2015b), but this can be harmful
138 to the natural, biodiverse, open systems found in these mosaics (Bond and Parr, 2010,
139 Veldman et al, 2015b, Ratnam et al, 2011). Understanding the stability and dynamics of
140 savanna-forest mosaics would help to justify and inform the management of these systems
141 as mosaics, with a focus on the preservation of savannas as well as forests (Bond & Parr,
142 2010).

143 Here, we have examined vegetation trajectories after extreme fire events empirically,
144 focusing on a mesic savanna-forest-thicket mosaic in Hluhluwe iMfolozi Park, South Africa,
145 where extreme fires burned into forests and thickets in 2004 and 2008; some of these areas
146 have burned subsequently, while others have not. These changing fire regimes offer an
147 opportunity to examine *in situ* the spectrum of possible outcomes for closed canopy
148 vegetation trajectories. On the one extreme, a forest or thicket experiencing fire might
149 recover its original state (Forest to Forest (FtoF)). In this case, we might expect to see FtoF
150 1) a reduction in tree cover and biomass that is only temporary, FtoF 2) the inhibition of a
151 regular fire regime (e.g. by suppression of grassy fuels), and FtoF 3) a transient shift to early-
152 successional forest trees species (light-loving but not as fire tolerant as savanna species)
153 that eventually transitions back to the original forest state. On the other extreme, in a forest
154 switching to savanna (Forest to Savanna (FtoS)), we instead expect: FtoS 1) a reduction in
155 tree cover and biomass that persists through time, FtoS 2) the establishment of a regular
156 fire regime (or at least of sufficient grassy biomass), and FtoS 3) a shift in tree species
157 composition from shade-tolerant species that compete for light to shade-intolerant species
158 that require open environments and 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 states 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. Occasionally, one finds patches of C3 grasses and herbaceous plants among the litter layer (Charles-Dominique *et al,* 2015). Thickets are 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 shade-tolerant grasses (Charles-Dominique *et al,* 2015) and savannas are classified as having discontinuous tree cover with a continuous layer of C4 grasses. Forest and thicket patches naturally abut savannas with 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), and 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 a relatively frequent fire regime with a mean and median fire return interval of 2.9 and 1.3 years, respectively (Balfour and Midgley, 2008).

On the 14th and 15th of September 2008, an extreme fire event occurred in the Hluhluwe section of HiP and, unlike typical savanna fires, it burned through large tracts of thicket and forest. Aerial photography of the region from 1937 to 2013 shows a gradual increase in closed canopy patch sizes from 1937 to 1992, and major loss events from 1992 to 2013 (Beckett & Bond, 2019), associated with this fire event. These extreme fires resulted from a combination of air temperatures above 30°C, relative humidity below 30%, and wind speeds averaging more than 25km/hr with gusts to 30km/h or more (Bradstock et al 2009; Browne & Bond, 2011). In this region, these conditions are exceedingly rare, over the period of 2001 to 2008, less than three days of these extreme fire weather conditions occurred, with the longest consecutive record of 11 hours occurring on the day of the extreme fire event in 2008 (Browne & Bond, 2011). 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 these were chosen as

205 the savanna baselines as they burnt in the 2008 fire and were near forest and thicket
206 patches. Intact forest and thicket plots were laid out in mature unburnt vegetation patches
207 (Fig. 1), as mapped by Whateley and Porter (1983) and by aerial-photograph-derived
208 vegetation maps (Beckett & Bond, *2019*). These represent our pre-fire baselines for forest
209 and thicket communities and, along with the 2007 savanna plots, are referred to from here
210 on as our 'before' dataset, while burnt plots represent the 'after' dataset.

211 To determine vegetation trajectories after the extreme fires, we made use of a natural
212 experiment, selecting plot locations based on areas that burned in extreme fire events in
213 2004 and 2008. Some plots were sampled repeatedly, supplemented with once-sampled
214 plots allowing a space-for-time chronosequence to evaluate vegetation change. In 2013,
215 Beckett and Bond (2019) identified regions previously unknown to have burnt in the 2008
216 fire, we established plots in these areas targeting forest patches that had not burnt since
217 2008, and others that had burnt repeatedly. Three plots were laid out in a forest that
218 burned in a separate fire in 2004 and sampled nine and 11 years after the fire. These three
219 plots (with 20m buffers on all sides) covered approximately 80% of the burnt forest area.
220 One of these plots was burnt again in 2012 and was excluded from the 11 year resampling
221 as it had no analogues. The data from nine years after the fire are included in the analyses,
222 while the repeat sample of 11 years are only included in figures in the Supplementary
223 Materials for interest. Plot sampling dates, repeat sample dates and vegetation history are
224 summarized in Appendix S1.

225 Each plot measured 40m x 10m, within which area we identified every woody plant
226 (including lianas) above 50cm in height and recorded its height as one of four size classes
227 (0.5-2m, 2-5m, 5-10m, and >10m). In 103 of the 134 sites, the grass layer was evaluated at

20 points along the plot; grass biomass was measured via disk pasture meter (DPM) and the dominant grass species recorded beneath the disk. 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, which can be calibrated locally (Bransby and Tainton, 1977, grass biomass = 1.26 + 26.1*[DPM], R2 = 0.73, N = 1745; Waldram et al, 2007).

Fire occurrence

Fire frequency of each plot from 2001 to 2016 was derived from a combination of the Ezemvelo KwaZulu Natal Wildlife fire records for HiP and personal observations. The EKZNW fire records are hand drawn maps from rangers responsible for sections of the park. These indicate the general location of the fire, but do not include information on fine-scale fire refugia and unburnt vegetation patches within the burned area (see Fig. 1). Instances where the EKZNW fire records indicated fires burning into large forest patches were compared with MODIS Active Fire Detections (MCD14DL, Collection 6). MODIS Active Fires maps thermal anomalies within 1km pixels using the MODIS MOD14/MYD14 Fire and Thermal Anomalies algorithm (Giglio *et al.*, 2003). MODIS Active Fires increases the probability that fires within forests are detected since alternative approaches based on burn scar mapping are sensitive to obstruction from the forest canopy.

Data analysis and statistics

Aerial photography and vegetation maps were analysed using Quantum GIS 3.0.0 (Quantum GIS Development Team, 2018). Statistical analyses were performed in R (version 3.4.0, R. Core Team, 2017), using the packages *vegan* (Oksanen *et al.*, 2013) and *tidyverse* (Wickham, 2017). Fire frequency before and after extreme fire events was compared using a Wilcoxon

signed-rank test for non-parametric paired data. Grass biomass was estimated using the relationship published by Waldram *et al* (2007) and comparisons between vegetation types and time periods were investigated using a Wilcoxon signed-rank test for non-parametric paired data. We used a multivariate analysis of variance (MANOVA) to test for differences in the total mean cumulative length of the vegetation types at different time periods and followed this with a series of ANOVA models to test for significant differences between vegetation types within the size classes. Cumulative length is a composite measure of species importance, similar to basal area, which combines stem density (values reported in Appendix S2) and tree height into a single value (Fei *et al.*, 2005). This is done by combining the height of all individuals of a species and allows for a weighted index where large trees contribute more to the overall score than small trees. We performed an NMDS Ordination on a Bray-Curtis species dissimilarity matrix of the cumulative length of each tree species for the 'before' plots, representing vegetation communities which that had not experienced the extreme fire event, namely, the intact forest, intact thicket, and 2007 savanna plots. Data were transformed using a Hellinger transformation to account for large abundances (Legendre & Legendre, 2012). Species were assigned to a biome (forest, thicket, or savanna) based on their association with sites in the NMDS ordination; species not found before the extreme fire event were classified as pioneer species. We then performed a Principal Coordinates Analysis (PCoA) and a pairwise permutational MANOVA on a Bray-Curtis dissimilarity matrix of the total cumulative length in each plot, as well as within the size classes to identify changes in the composition of these species types.

Results

Establishment of a savanna fire regime

Forests and thickets rarely burned, with intact forest and thicket sites experiencing no fires between 2000 and 2016 (Fig. 2). Savanna sites, in contrast, burned several times in a decade. In fact, fire frequency (FF) increased from approximately one fire every four years (FF = 0.24.yr^{-1} (SD = 0.11)) before the 2008 extreme fire event to one fire every three years (FF = 0.36.yr^{-1} (SD = 0.13); t = -11.8, df = 43, $p < 0.05$) after 2008. Thicket patches that burned in the 2008 extreme fire event quickly established a savanna fire regime with sites burning on average once every three years (FF = 0.34.yr^{-1} (SD = 0.07)) , compared to no fires from 2000 to 2007.

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

Colonisation by savanna grasses

Intact thicket and forest plots differed from savanna plots in having closed canopies and little or no grass in the understory (Fig. 3). Savanna plots had on average 233g.m^{-2} (SD = 87)of grass biomass whereas intact thicket and forest patches had 148g.m^{-2} (SD = 84) and 10g.m^{-2} (SD = 2.8) respectively (Fig. 3). Frequently-burnt thicket and frequently-burnt forest plots showed an increase in grass biomass following successive fires, with grass biomass four and 22 times higher than intact thicket and forest plots respectively (Fig. 3). Once-burnt forest plots had relatively high, but variable, grass biomass (130g.m^{-2} (SD = 114)) in the first year after the extreme fire events, grass biomass by the end of the study, 9 years later, was

less variable (33g.m^{-2} (SD = 11)), approaching the levels of intact forest grass biomass. In terms of grass species, *Panicum maximum* colonised forests and thickets immediately after fire, whereas *Themeda triandra* increased in abundance where fires occurred repeatedly (Fig. 3).

Trajectories in woody structure

Forest, thicket, and savanna plots displayed distinct woody structural profiles (See Appendix S3), with most savanna trees in the smallest size class, most forest trees in the largest size class, and an even spread between the two intermediate size classes in thicket (Fig. 4, Appendix S3). Savanna plots showed little change in structure between 2007 and 2014 despite an increase in fire frequency (Pillai's Trace = 0.039, approx $F(3,91) = 1.238$, $p = 0.301$, Appendix S3).

Thicket plots that burned frequently were different to Intact thicket plots (Pillai's Trace = 0.76, approx $F(4,30) = 23.406$, $p < 0.001$, Appendix S3) and had a comparable structure to savanna plots seven years after the extreme fire (Pillai's Trace = 0.15, approx $F(4,51) = 2.2415$, $p = 0.077$, Appendix S3), with most trees in the smallest size class. Similarly, forests that burned multiple times were different to intact forests (Pillai's Trace = 0.89, approx $F(4,28) = 58.734$, $p < 0.001$) and converged to a savanna-like vegetation structure (Pillai's Trace = 0.20, approx $F(4,53) = 3.3665$, $p = 0.016$) 7 years after the extreme fire event, with comparable numbers of trees in the smaller two size classes and differences in the larger two size classes (Appendix S3).

Six years after the fire, once-burnt forests were different to intact forests (Pillai's Trace = 0.902, approx $F(4,17) = 38.902$, $p < 0.001$) and savannas (Pillai's Trace = 0.77, approx $F(3,43) = 46.72$, $p < 0.001$). The six year once-burnt and the frequently-burnt forests were also

320 different (Pillai's Trace = 0.61, approx F(4,12) = 4.72, p = 0.016), with the second largest size
321 class contributing to the majority of the difference between the two (F(1,15) = 21.96, p <
322 0.001). Nine years after the fire, the relationships between once-burnt forests and intact
323 forests (Pillai's Trace = 0.761, approx F(4,17) = 13.499, p < 0.0001), savannas (Pillai's Trace =
324 0.767, approx F(3,43) = 47.296, p < 0.0001) and frequently-burnt forests (Pillai's Trace =
325 0.716, approx F(4,12) = 7.5689, p = 0.003) were similar to those of the six year once-burnt
326 forests (Appendix S3, Appendix Fig. S1), however the cumulative length in the second
327 largest size class of once-burnt forests was approaching that of the intact forests (F(1,20) =
328 3.641, p = 0.071).

329 Trajectories in woody species composition

330 Forest, thicket, and savanna plots were characterized by distinct woody species assemblages
331 (Fig. 5, Appendix Table S4 & Table S5The overall (Appendix Table S4) and size class specific
332 (Appendix Table S5) abundance of species types within savannas did not differ between
333 2007 and 2014 (Fig. 6).

334 Compositionally, frequently-burnt thickets differed from savannas 7 years after the extreme
335 fire event (Fig. 6, Appendix Table S4 & S5), this is most evident in the smallest size class
336 where frequently-burnt thickets were dominated by a mixture of basally resprouting thicket
337 species, *e.g.*, *Euclea racemosa, Euclea divinorum* and *Berchemia zeyheri*, and a proportion of
338 savanna species, including *Acacia karroo (=Vachellia karoo), Acacia nilotica (=V. nilotica),*
339 *Dichrostachys cinerea, Cordia caffra, Combretum molle* and *Rhus (= Searsia) pentheri* (Fig. 5),
340 compared to savannas which very rarely had thicket species recruiting.

341 By contrast, seven years after the extreme fire event, the composition of frequently-burnt
342 forests had completely switched to dominance by a number of thicket species, including

343 *Euclea natalensis* and *Euclea racemosa,* and savanna species (see Fig. 5 & 6). These plots
344 also differed from savannas (Appendix Table S4 & S5) in the composition of species in the
345 smallest size class and more closely resembled the frequently-burnt thickets.

346 Once-burnt forests were dominated by pioneer forest species seldom found in the intact
347 forests (especially *Trema orientalis, Croton sylvaticus,* and *Dombeya burgessiae*). These
348 trees grew from seed banks, as opposed to the dominance of basally resprouting tree
349 species in frequently-burnt thicket plots. After 6 years, these once-burnt forests recovered
350 some species characteristic of mature forest, including *Englerophytum natalense* and
351 *Chaetacme aristata*, in smaller size classes, although the larger size classes remained
352 dominated by the unique pioneer forest assemblage (Fig. 6). The once-burnt forests (after
353 six years) were not different to the frequently-burnt forests in overall abundance of species
354 types (Appendix Table S4), however they were different when considering size class specific
355 species type abundance (Appendix Table S5). Nine years after fire, the once-burnt forests
356 were dominated by forest species in the two smaller size classes, and pioneer species in the
357 second largest size class (Appendix Fig. S2). These plots differed to the frequently-burnt
358 forests in overall and size class specific species type abundance (Appendix Table S4 & S5, Fig.
359 S3.).

360 Discussion

361 Extreme fire events differ from typical savanna fires in penetrating beyond the biome
362 boundaries, often opening up the canopy of closed forest or thicket. Here, we found that
363 forests that burned only once recovered by secondary successional pathways, whereas
364 forests and thickets that burned again following the initial extreme fire event underwent a
365 persistent transition from closed-canopy vegetation states to open-canopy grassy systems.

366 The grass layer was first dominated by *Panicum maximum* but gradually replaced by the
367 more flammable *Themeda triandra* (Simpson et al, 2016). Woody species composition was
368 the slowest to respond to woody structural change, and we observed only minimal
369 colonization of woody savanna species into the new grass layer over a decade of post-burn
370 observations.

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

380 In the transition from closed canopy vegetation states to savanna, initial grass colonization
381 was dominated by *Panicum maximum*, which accumulated biomass rapidly. However, with
382 seven years of repeated fires, *Themeda triandra* gained in dominance in open-canopy
383 systems. These replacement patterns are consistent with our understanding of these two
384 species; *Panicum maximum* (Paniceae) is often observed in relatively shaded savanna
385 environments and is known to retain moisture longer into the dry season (Simpson et al,
386 2016), whereas *Themeda triandra* (Andropogoneae) prefers open, full-sun environments
387 (Downing & Marshall, 1980, Kinyamario *et al.*, 1995) and is highly flammable but slower to
388 colonise new environments (O'Connor & Everson, 1998).

On the time scale of a decade, however, novel savannas differed from old-growth natural savannas in their woody-layer composition (see also Veldman, 2016), and colonization of open habitats by savanna trees was slower than grass colonization. While forest canopies opened up readily, allowing grasses to colonise, the woody community remained depauperate of savanna trees (see also Veldman & Putz, 2011 and theoretical predictions described by Staver and Levin, 2012, Touboul et al, 2018). Thickets differed from forests in that, even when burned repeatedly, they retained a tree community dominated by thicket species (probably resprouts). Meanwhile, forests that only burned once were colonised mostly by a unique pioneer assemblage. However, in novel savannas, a frequent fire regime eventually depleted thicket and forest remnants, and we hypothesize that savanna species will eventually colonise (see also Charles-Dominique et al, 2015b); we suggest further observation of previously closed-canopy areas that continue to experience frequent fires.

Notably, we also found that forests could recover readily from a singular extreme fire event, as long as a fire-free interval of a decade allowed the canopy to close, shading out grass fuels and setting the system on a trajectory to its previous state. Forests likely recovered primarily from a seed bank, with an early-successional forest composed of rapidly growing pioneers (*i.e.*, *Trema orientalis, Croton sylvaticus, Celtis africana*) and the clonally spreading liana *Dalbergia armata*. These species excluded light-demanding grasses, likely by shading and microclimate effects that also make the environment suitable for the establishment of climax forest species (see also Pammenter et al. 1985).

Thickets also recovered from a single fire readily but differed somewhat from forest in their post-fire recovery. While forest recovery occurred through pioneer species germination and was accompanied by a complete species turnover, structural recovery in thickets instead

occurred through basal resprouting. Notably, fire-driven tree mortality in thickets was low, as in savannas, contrasting with much higher tree mortality in 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 (Staal et al, 2020, Staver *et al*, 2020).

Our study is a rare documentation of invasion of grass-fuelled fires into closed forest and thickets communities in a natural and ancient African savanna-forest-thicket mosaic. Our results offer a few key insights. Firstly, we provide evidence for extreme fires as a mechanism by which savannas might have invaded forests before the introduction of invasive exotic species. Fires are implicated in the rise of the savanna biome from the late Miocene (Bond *et al.*, 2003, Keeley & Rundel, 2005, Scheiter *et al*, 2012, Behrensmeyer & Freeman, 2018), by opening up forests and allowing shade-intolerant savanna grasses to spread, perhaps by gradual invasion 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, then grass invasion, and finally by the arrival of savanna trees. However, on-the-ground observations of how this savannization process proceeds in a natural ecosystem are very few.

Secondly, we also provide rare direct support for the longstanding hypothesis that runaway fire feedbacks, following an initial extreme fire, might plausibly result in the savannization of tropical forests (Cochrane, 1999) without the need for human interference. As in the Amazon, these extreme fire events present a rare but real problem. At our site, the combination of conditions associated with extreme fire development – air temperatures

435 above 30°C, relative humidity below 30% and wind speeds gusting to 30+km/h (Bradstock *et*
436 *al.*, 2009) – occurred on only 3 full days over the period between 2001 and 2008, with the
437 longest consecutive record of 11 hours occurring on the day of the extreme fire event in
438 2008, on the 15th September. Their rarity makes conditions like these difficult to predict
439 with any accuracy; however, we can be confident that days like these are likely to increase
440 in frequency as temperatures rise and aridity increases in the future, making extreme fires
441 an accelerating concern in savanna-forest mosaics, just as they are elsewhere (Jolly *et al.*,
442 2015, Flannigan et al, 2013). Transitions from forest to savanna are indeed possible, and
443 likely to increase in potential extent in future.

444 The key difference between this study and work published under the savannization
445 umbrella in the Neotropics revolves around the level of anthropogenic influence in these
446 systems. Contemporary savannization in the Amazon is recorded in areas where exotic
447 pasture grasses have invaded degraded forests, increasing fuel loads, and allowing
448 subsequent fires (Silverio *et al*, 2013). However, paleoecological evidence supports the claim
449 that savannization has occurred in the Neotropics, predating colonial anthropogenic
450 activities, and has been attributed to fire and low CO_2 (Rull *et al*, 2013, Sato *et al*, 2021). It is
451 interesting to note the potential impact the disappearance of Neotropical megafauna may
452 have had on the probability of savannization occurring under non-anthropogenic conditions
453 (Owen-Smith, 1987, Johnson, 2009). In HiP, and other African systems, herbivores -
454 particularly African Elephants – may play a role in weakening forest and thicket boundaries
455 by opening the canopy and allowing grass invasion. The role of megafauna in savannization
456 processes has not been sufficiently investigated and offers an interesting avenue for future
457 research.

Preventing or suppressing extreme fires is challenging in savannas where fires are used as a management tool under less extreme conditions. In savannas, woody encroachment has long been a conservation concern, with widespread observations of increases in the woody component of savannas (Stevens *et al.*, 2017), particularly in savannas where fire is suppressed instead of actively managed (Silva et al, 2008, Durigan, 2020). This trend is predicted to intensify as increasing CO_2 favours C3 trees over C4 grasses (Higgins & Scheiter, 2012; Bond & Midgley, 2000, Moncrieff et al, 2014) – suggesting that, while forests are at increased risk of savannization, savannas are also at increased risk of forest expansion and woody encroachment. We suggest that widespread fire suppression is clearly not the solution to preventing extreme fires. We should aim instead for a rationalized fire management policy, allowing and encouraging fires in fire-dependent savannas but minimizing fires under extreme conditions, especially in fire-sensitive forests. Most crucially, we suggest that, barring subsequent fires, which are not inevitable, forests can recover readily from the effects of extreme fires.

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Author Contributions

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

Figure Legends

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

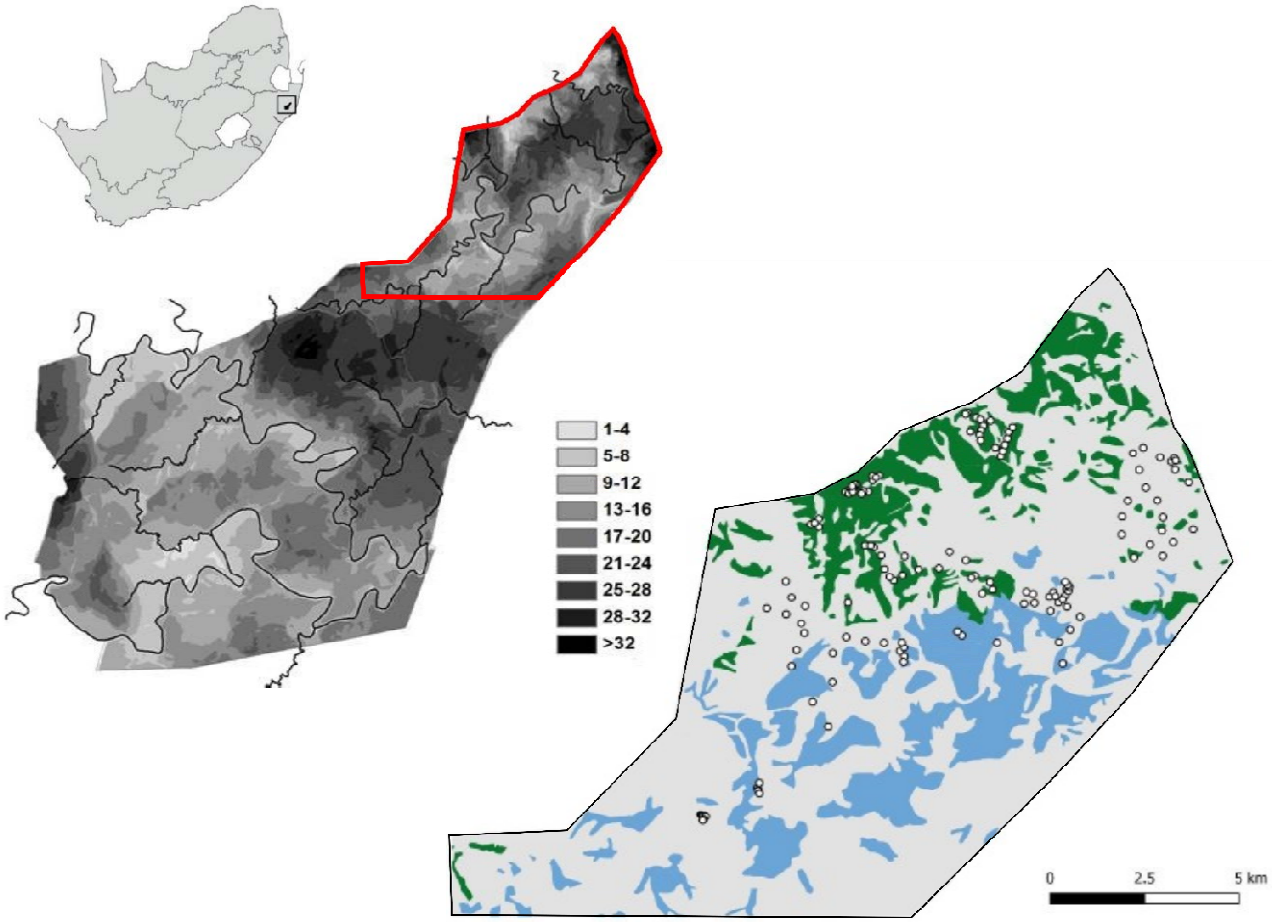
Figure 2. Fire Frequency for plots within each vegetation type (indicated by grey text) before and after extreme fire events (not including the year of the extreme fire event), calculated using the MODIS Active Fires Product from 2000 to 2016. Grey lines link plot points before and after extreme fire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

Figure 3. Changes in the (A) total biomass of grass found in all plots for frequently-burnt forests, once-burnt forest, frequently-burnt thicket and savanna, and two dominant grass species, (B) Panicum maximum and (C) Themeda triandra. Green bars represent forest plots, blue represents thicket, and yellow represents savanna. Error bars indicate standard error. Points (plot grass biomass) are included to display variation. Shared letters indicate lack of a significant difference within panels based on Wilcoxon signed-rank test, $p < 0.05$.

Figure 4. Mean cumulative length of all tree species within the four size classes 'before' and 'after' the extreme fire event in A) Savanna, B) Frequently-burnt Thicket, C) Frequently-burnt Forest, and D) Once-burnt Forest. Error bars indicate standard error. Points represent individual plots.

Figure 5. NMDS ordination of the cumulative length of all species in all height classes in plots. Ellipses show the grouping of plots. Species associations used in the composition analyses are based on species found in plots before the extreme fire events only. Letters indicate the position of plots, grey dots indicate the species scores.

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



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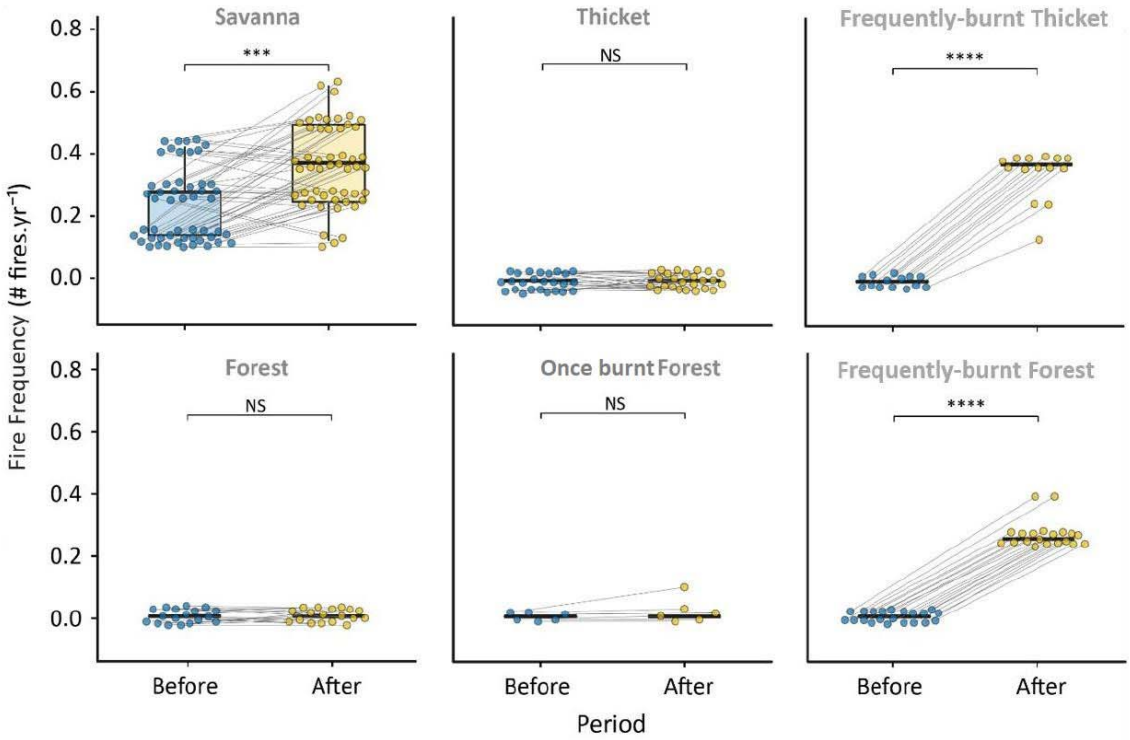

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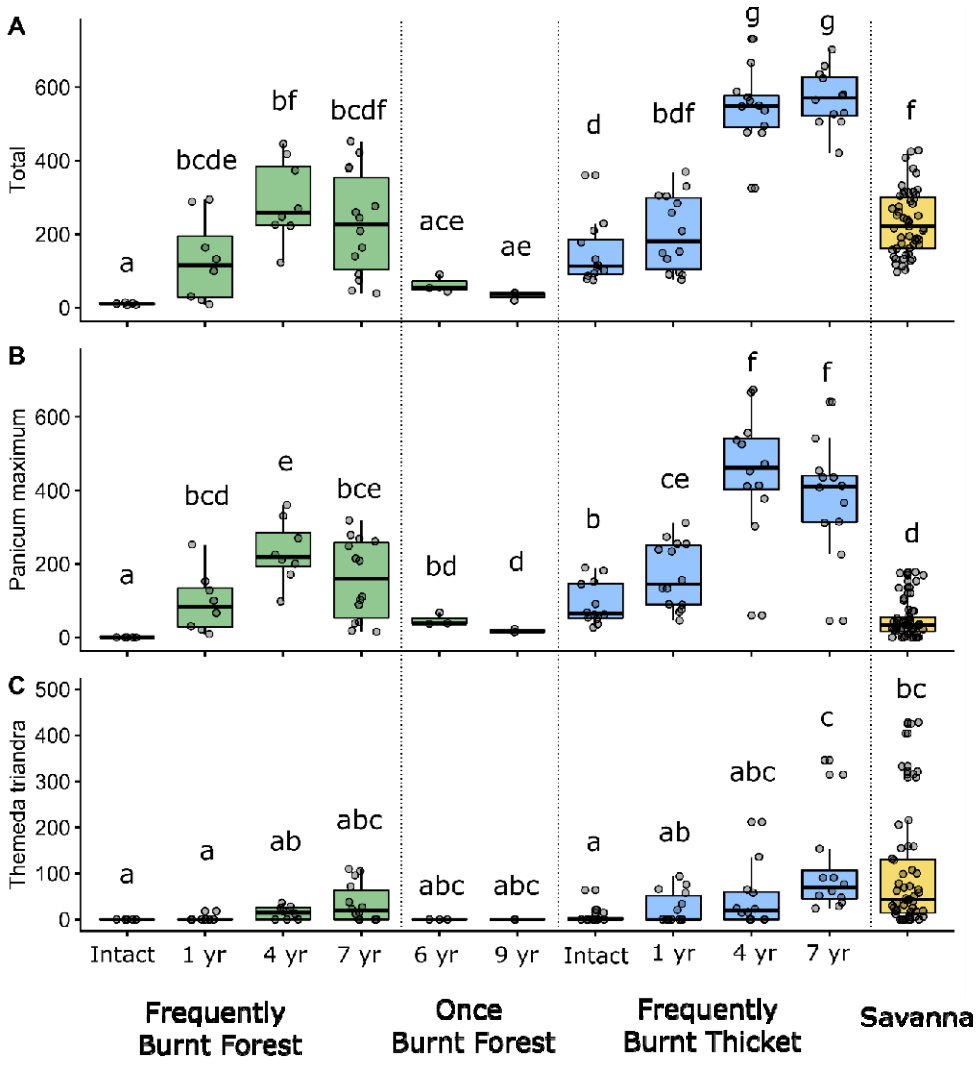

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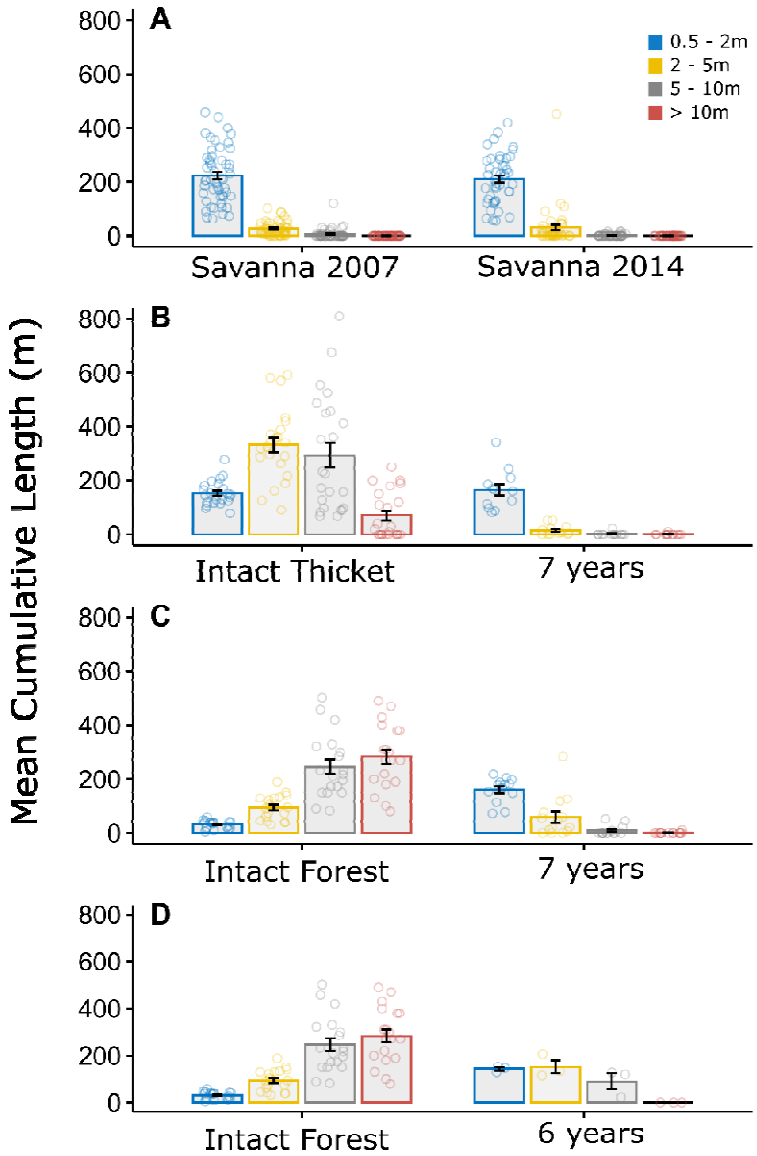

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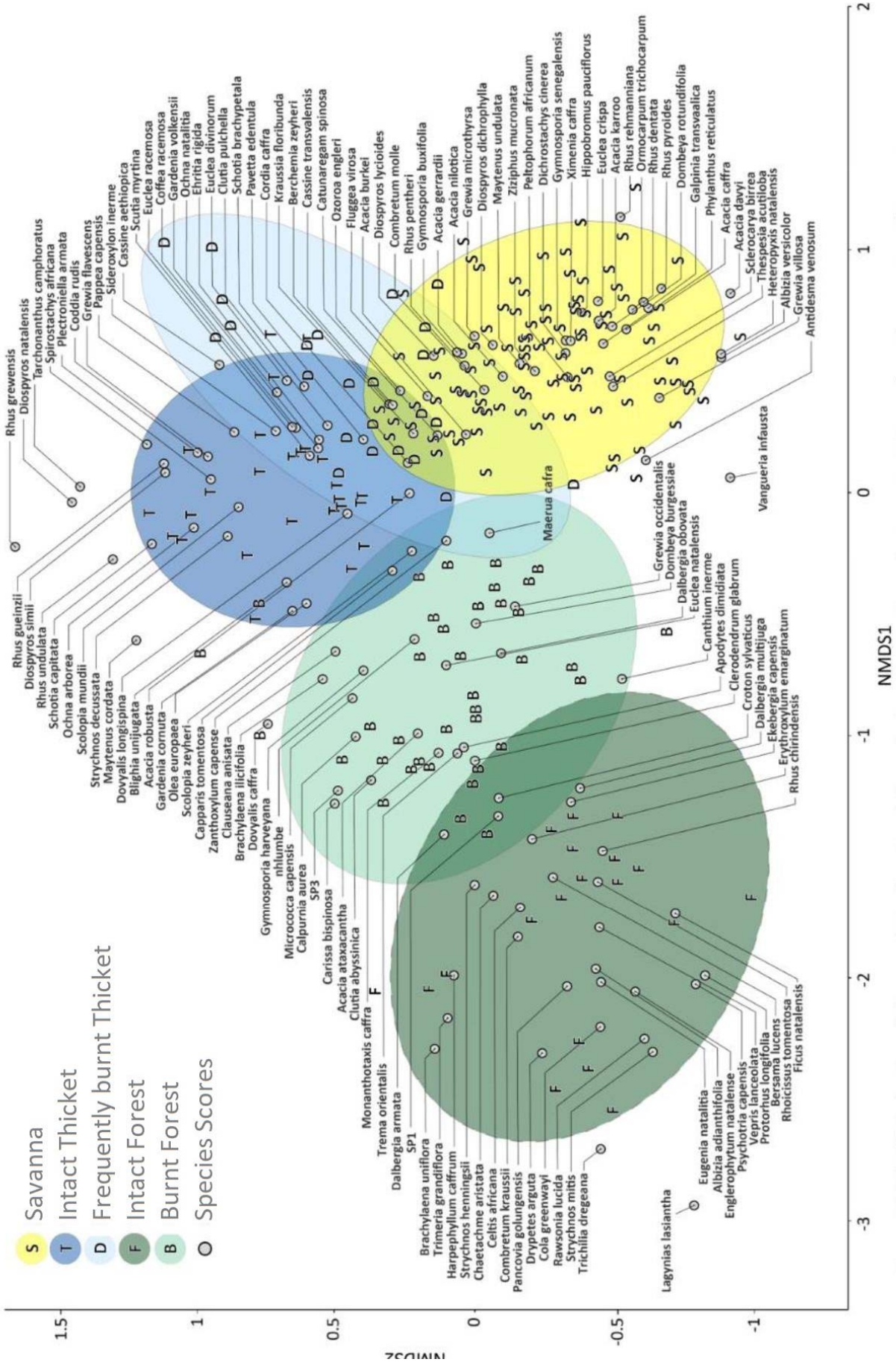

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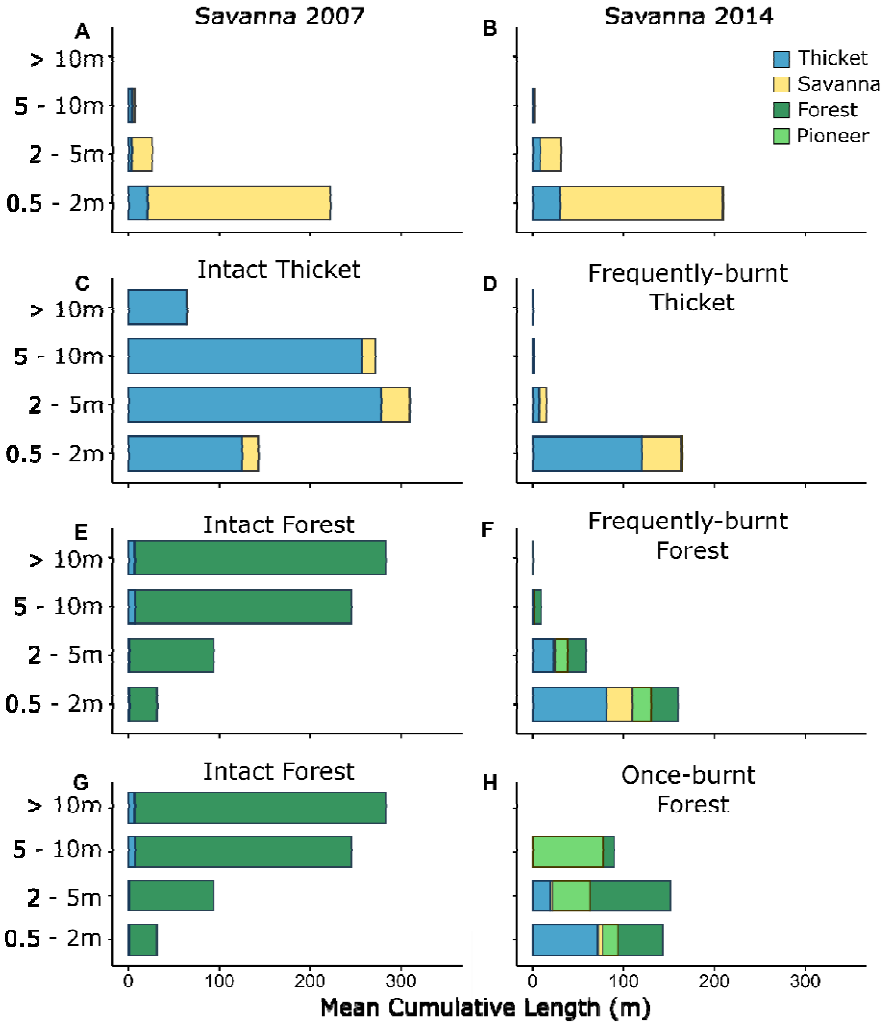

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