1 Pathways of savannization in a mesic African savanna-forest mosaic

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21 Abstract

22 Typically, savannas experience frequent fires, which limit tree cover and promote
 23 flammable grass accumulation, whereas forests and thickets form dense canopies that
 24 exclude fires by reducing C4-grass fuel loads and creating a humid microclimate. However,
 25 extreme fires occasionally burn into these closed canopy systems. Although these are
 26 known to cause tree mortality and can make repeat fires more likely, the long-term
 27 consequences of an extreme fire event for closed canopy vegetation structure and potential
 28 savannization remain largely unknown. Here, we analysed whether an extreme fire event
 29 could, alone, alter species composition, vegetation structure, and fire regimes of closed
 30 canopy ecosystems in a natural savanna-forest-thicket mosaic, or whether successive fires
 31 after an initial extreme fire event were necessary to trigger a biome transition between
 32 these alternative stable states. We found that forests that only burned once recovered,
 33 whereas those that burned again following an initial extreme fire event underwent a
 34 transition from closed-canopy forests to open, grassy systems. Thickets had lower levels of
 35 tree mortality following fires than forests, although repeat fires also led to a transition
 36 towards open grassy systems, structurally resembling savannas. Our results suggest that
 37 while extreme fires set the stage for a biome transition, subsequent fires are necessary for
 38 grass composition to resemble neighbouring savanna grass communities, ultimately
 39 resulting in a savanna fire regime. Savannization, following extreme fire events, is possible
 40 in natural mosaic ecosystems where open and closed canopy vegetation types represent
 41 alternative stable states.

42

43 Introduction

44 Fires are becoming more frequent and severe in forested ecosystems globally (Andela *et al.*,
 45 2019, Jolly *et al.*, 2015). In tropical forests, extreme fires associated with droughts and
 46 agriculture are expanding into forests that historically were not flammable (Chen *et al.*,
 47 2014, Morton *et al.*, 2013). Some authors have hypothesized that these tropical forest
 48 understory fires may result in runaway feedbacks, leading to more frequent fires and to
 49 savannization of forests, resulting in eventual forest collapse (Cochrane, 1999, Barlow &
 50 Peres, 2004, Barlow & Peres, 2008, Silverio *et al.*, 2013, Flores *et al.*, 2016, van Nes *et al.*,
 51 2018). However, although we know that the occurrence of one forest understory fire can
 52 increase the likelihood of subsequent fires, direct evidence for forest savannization by
 53 runaway feedbacks is sparse. Invasive exotic grasses have been shown to invade the forest
 54 understory only locally (Silverio *et al.*, 2013), limited by dispersal (although in
 55 anthropogenically modified environments there is evidence for seed dispersal by trucks (see
 56 Veldman and Putz, 2010)) and possible biogeochemical feedbacks. As a result, the question
 57 of whether fires can actually convert a tropical forest to a savanna, in a natural setting,
 58 remains open.

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

66 forest saplings, but fires stop readily at the savanna-forest boundary, because shade in the
67 forest understory prevents the accumulation of shade-intolerant C4 grasses within meters
68 of the boundary (Charles-Dominique *et al.*, 2018, Hennenberg *et al.*, 2008, Hoffmann *et al.*,
69 2012a). Forest microclimates also reduce wind speeds and increase fuel moisture (Biddulph
70 & Kellman, 1998, Hoffmann *et al.*, 2012b, Little *et al.*, 2012), further hampering fire spread.
71 These feedbacks provide support for the idea that savanna and forest are alternative stable
72 states (Staver *et al.*, 2011a, but see Veenendaal *et al.*, 2015, Hanan *et al.*, 2014). However,
73 the impact of extreme events (especially extreme fires, see Keeley & Pausas, 2019) on the
74 dynamics of these mosaics is largely unknown.

75 One possibility is that mosaics are mostly stable, with distinct distributions and stable edges,
76 not just on short to medium time scales (ten to several hundred years), but also on longer
77 time scales (Killeen *et al.*, 2006, Breman *et al.*, 2012, Rull *et al.*, 2013, Cardoso *et al.*, 2020).
78 This might be the case if savanna-fire feedbacks are very strong (Beckage *et al.*, 2009, Dantas
79 *et al.*, 2016), or if some other process besides fire – e.g., oligotrophy, seasonal flooding – play
80 a strong role in stabilizing savanna-forest distributions within a mosaic (Veenendaal *et al.*,
81 2015, Murphy and Bowman, 2012). In this situation, extreme fires in forests may have fairly
82 negligible medium-term effects on forest structure, acting as a stand-replacing disturbance
83 from which forests recover via succession (Fearnside, 1990, Kennard, 2002, Brando *et al.*,
84 2020) rather than as a trigger of a catastrophic transition.

85 An alternative possibility is that savanna-forest boundaries may be highly dynamic over
86 longer time-scales (Schwartz *et al.*, 1986, West *et al.*, 2000, Staver *et al.*, 2017, Aleman *et al.*
87 2019) and in response to changing climate or climate events (Hirota *et al.*, 2010, Breman *et al.*
88 *et al.*, 2012, Beckett & Bond, 2019, Wright *et al.*, 2021, Sato *et al.*, 2021). Spatially explicit

89 modelling work has argued that fires at the savanna-forest boundary can have major effects
90 on the biogeographic distribution of biomes (Staver *et al*, 2011b, van de Leemput *et al*,
91 2015, Goel *et al*, 2020a, Goel *et al*, 2020b, Wuyts *et al*, 2019) and local observations confirm
92 that boundaries are sometimes dynamic through time (Brook & Bowman, 2006, Silva *et al*,
93 2008, Ibanez *et al*, 2013, Beckett & Bond, 2019). Modern observations also confirm that
94 tropical forests can invade savannas and grasslands especially at the boundary between the
95 two, in Africa (Baccini *et al*, 2017; Aleman *et al*, 2018), South America, and Australia
96 (Marimon *et al*, 2014; Ondeï *et al*, 2017; Stevens *et al*, 2017; Rosan *et al*, 2019).

97 However, modern evaluations of invasions of forests by savannas has predominantly been
98 studied in the Neotropics (Cavelier *et al*, 1998, Veldman and Putz, 2011, Silverio *et al*, 2013,
99 Flores *et al* 2016), typically in the context of invasive exotic grasses, El Niño-fuelled
100 droughts, and deforestation (Nepstad *et al*. 1996, Barlow and Peres, 2004, Barlow and
101 Peres, 2008, Veldman and Putz, 2011, Silverio *et al*, 2013). This work provides invaluable
102 insights into the potential processes of savannization, such as the appearance of grass-
103 dominated systems which differ from old growth savannas (Veldman and Putz, 2011), the
104 susceptibility of forest trees to fire induced mortality (Barlow and Peres, 2008, Staver *et al*,
105 2020), and the invasion of grassy fuels following repeat fires (Veldman and Putz, 2011,
106 Silverio *et al*, 2013). However, these processes typically rely upon the introduction of exotic
107 grass species (which lead to novel fire regimes), and deforestation derived boundaries
108 (Alencar *et al*. 2015) with unclear historical and palaeoecological precedents (but see Flores
109 *et al* 2016).

110 From its conception in the 1940's (Aubreville, 1949, Budowski, 1956), the term
111 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 CO₂ (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

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

Here, we have examined vegetation trajectories after extreme fire events empirically, focusing on a mesic savanna-forest-thicket mosaic in Hluhluwe iMfolozi Park, South Africa, where extreme fires burned into forests and thickets in 2004 and 2008; some of these areas have burned subsequently, while others have not. These changing fire regimes offer an opportunity to examine *in situ* the spectrum of possible outcomes for closed canopy vegetation trajectories. On the one extreme, a forest or thicket experiencing fire might recover its original state (Forest to Forest (FtoF)). In this case, we might expect to see FtoF 1) a reduction in tree cover and biomass that is only temporary, FtoF 2) the inhibition of a regular fire regime (e.g. by suppression of grassy fuels), and FtoF 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 extreme, in a forest switching to savanna (Forest to Savanna (FtoS)), we instead expect: FtoS 1) a reduction in tree cover and biomass that persists through time, FtoS 2) the establishment of a regular fire regime (or at least of sufficient grassy biomass), and FtoS 3) a shift in tree species composition from shade-tolerant species that compete for light to shade-intolerant species 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

the savanna baselines as they burnt in the 2008 fire and were near forest and thicket patches. Intact forest and thicket plots were laid out 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 trajectories after the extreme fires, we made use of a natural experiment, selecting plot locations based on areas that burned in extreme fire events in 2004 and 2008. Some plots were sampled repeatedly, supplemented with once-sampled plots allowing a space-for-time chronosequence to evaluate vegetation change. In 2013, Beckett and Bond (2019) identified regions previously unknown to have burnt in the 2008 fire, we established plots in these areas targeting forest patches that had not burnt since 2008, and others that had burnt repeatedly. Three 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 20m 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 of 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 40m x 10m, within which area we identified every woody plant (including lianas) above 50cm in height and recorded its height as one of four size classes (0.5-2m, 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 = $1.26 + 26.1 \times [\text{DPM}]$, $R^2 = 0.73$, $N = 1745$; 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

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

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

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

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

Once-burnt forests were dominated by pioneer forest species seldom found in the intact forests (especially *Trema orientalis*, *Croton sylvaticus*, and *Dombeya burgessiae*). These trees grew from seed banks, as opposed to the dominance of basally resprouting tree species in frequently-burnt thicket plots. 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), however they were different when considering size class specific species type abundance (Appendix Table S5). Nine years after fire, the once-burnt forests were dominated by forest species in the two smaller size classes, and pioneer species in the second largest size class (Appendix Fig. S2). These plots differed to the frequently-burnt forests in overall and size class specific species type abundance (Appendix Table S4 & S5, Fig. S3.).

Discussion

Extreme fire events 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 by secondary successional pathways, whereas forests and thickets that burned again following the initial extreme fire event underwent a persistent transition from closed-canopy vegetation states to open-canopy grassy systems.

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

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

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

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

The key difference between this study and work published under the savannization umbrella in the Neotropics revolves around the level of anthropogenic influence in these systems. Contemporary savannization in the Amazon is recorded in areas where exotic pasture grasses have invaded degraded forests, increasing fuel loads, and allowing subsequent fires (Silverio *et al.*, 2013). However, paleoecological evidence supports the claim that savannization has occurred in the Neotropics, predating colonial anthropogenic activities, and has been attributed to fire and low CO₂ (Rull *et al.*, 2013, Sato *et al.*, 2021). It is interesting to note the potential impact the disappearance of Neotropical megafauna may have had on the probability of savannization occurring under non-anthropogenic conditions (Owen-Smith, 1987, Johnson, 2009). In HiP, and other African systems, herbivores – particularly African Elephants – may play a role in weakening forest and thicket boundaries by opening the canopy and allowing grass invasion. The role of megafauna in savannization processes has not been sufficiently investigated and offers an interesting avenue for future 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 CO₂ 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.

References

- Aleman JC, Blarquez O, Elenga H et al. (2019) Palaeo-trajectories of forest savannization in the southern Congo. *Biology letters*, 15, 20190284.
- Aleman, J. C., & Staver, A. C. (2018). Spatial patterns in the global distributions of savanna and forest. *Global Ecology and Biogeography*, 27(7), 792-803.
- Aleman, J. C., Fayolle, A., Favier, C., Staver, A. C., Dexter, K. G., Ryan, C. M., ... & Swaine, M. D. (2020). Floristic evidence for alternative biome states in tropical Africa. *Proceedings of the National Academy of Sciences*, 117(45), 28183-28190.
- Alencar, A. A., Brando, P. M., Asner, G. P., & Putz, F. E. (2015). Landscape fragmentation, severe drought, and the new Amazon forest fire regime. *Ecological applications*, 25(6), 1493-1505.
- Andela N, Morton DC, Giglio L et al. (2019) The Global Fire Atlas of individual fire size, duration, speed and direction. *Earth System Science Data*, 11, 529-552.
- Archibald S, Beckett H, Bond WJ, Coetsee C, Druce DJ, Staver AC (2017) Interactions between Fire and Ecosystem Processes. In: *Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story*. (eds Cromsigt JP, Archibald S, Owen-Smith N) pp Page.
- Archibald, S., Bond, W. J., Hoffmann, W., Lehmann, C., Staver, C., & Stevens, N. (2019). Distribution and determinants of savannas. *Savanna woody plants and large herbivores*, 1-24.
- Aubréville, A. (1949). *Climats, forêts et désertification de l'Afrique tropicale*.

501 Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D., & Houghton, R. A.
502 (2017). Tropical forests are a net carbon source based on aboveground measurements of
503 gain and loss. *Science*, 358(6360), 230-234.

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

506 Balfour DA, Howison OE (2002) Spatial and temporal variation in a mesic savanna fire
507 regime: responses to variation in annual rainfall. *African Journal of Range & Forage Science*,
508 19, 45-53.

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

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

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

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

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

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

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

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

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

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

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

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

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

539 Brando, P. M., Balch, J. K., Nepstad, D. C., Morton, D. C., Putz, F. E., Coe, M. T., et al. (2014).
540 Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *PNAS*,
541 111(17), 6347–6352.

542 Brando, P. M., Nepstad, D. C., Balch, J. K., Bolker, B., Christman, M. C., Coe, M., & Putz, F. E.
543 (2011). Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size,
544 wood density and fire behavior. *Global Change Biology*, 18(2), 630–641.

545 Brando, P. M., Soares-Filho, B., Rodrigues, L., Assunção, A., Morton, D., Tuchsneider, D., ...
546 & Coe, M. T. (2020). The gathering firestorm in southern Amazonia. *Science advances*, 6(2),
547 eaay1632.

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

551 Breman, E., Gillson, L., & Willis, K. (2012). How fire and climate shaped grass-dominated
552 vegetation and forest mosaics in northern South Africa during past millennia. *The Holocene*,
553 22(12), 1427-1439.

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

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

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

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

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

566 Cavelier, J., Aide, T., Santos, C., Eusse, A., & Dupuy, J. (1998). The savannization of moist
567 forests in the Sierra Nevada de Santa Marta, Colombia. *Journal of Biogeography*, 25(5), 901-
568 912.

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

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

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

575 Chen Y, Morton D, Jin Y et al. (2014) Erratum: Long-term trends and interannual variability
576 of forest, savanna and agricultural fires in South America (*Carbon Management* (2013) 4: 6
577 (617-638)).

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

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

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

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

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

590 Durigan, G (2020) Zero-fire: not possible nor desirable in the Cerrado of Brazil. *Flora*,
591 151612.

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

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

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

599 Flannigan M, Cantin AS, De Groot WJ, Wotton M, Newbery A, Gowman LM (2013) Global
600 wildland fire season severity in the 21st century. *Forest Ecology and Management*, 294, 54-
601 61.

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

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

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

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

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

613 Hanan, N. P., Tredennick, A. T., Prihodko, L., Bucini, G., & Dohn, J. (2014). Analysis of stable
614 states in global savannas: is the CART pulling the horse?. *Global Ecology and*
615 *Biogeography*, 23(3), 259-263.

616 Hennenberg KJ, Goetze D, Szarzynski J, Orthmann B, Reineking B, Steinke I, Porembski S
617 (2008) Detection of seasonal variability in microclimatic borders and ecotones between
618 forest and savanna. *Basic and Applied Ecology*, 9, 275-285.

619 Higgins, SI, & Scheiter, S (2012). Atmospheric CO₂ forces abrupt vegetation shifts locally,
620 but not globally. *Nature*, 488(7410), 209-212.

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

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

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

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

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

635 Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DM
636 (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. Nat
637 Commun, 6, 7537.

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

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

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

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

647 Killeen, T. J., Chavez, E., Peña-Claros, M., Toledo, M., Arroyo, L., Caballero, J., ... & Steininger,
648 M. (2006). The Chiquitano dry forest, the transition between humid and dry forest in

649 eastern lowland Bolivia. In *Neotropical savannas and seasonally dry forests* (pp. 214-233).
650 CRC Press.

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

654 Legendre P, Legendre LF (2012) *Numerical ecology*, Elsevier.

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

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

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

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

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

667 Nepstad, D. C., Verssimo, A., Alencar, A., Nobre, C., Lima, E., Lefebvre, P., ... & Brooks, V.
668 (1999). Large-scale impoverishment of Amazonian forests by logging and
669 fire. *Nature*, 398(6727), 505-508.

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

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

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

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

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

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

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

685 Rosan, T. M., Aragão, L. E., Oliveras, I., Phillips, O. L., Malhi, Y., Gloor, E., & Wagner, F. H.
686 (2019). Extensive 21st-century woody encroachment in South America's
687 savanna. Geophysical Research Letters, 46(12), 6594-6603.

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

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

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

697 Scheiter S, Higgins SI, Osborne CP, Bradshaw C, Lunt D, Ripley BS, Taylor LL, and Beerling DJ
698 (2012) Fire and fire-adapted vegetation promoted C₄ expansion in the late Miocene. *New*
699 *Phytologist* 195, no. 3: 653-666.Schwartz D, Mariotti A, Lanfranchi R, Guillet B (1986)
700 13C/12C ratios of soil organic matter as indicators of vegetation changes in the Congo.
701 *Geoderma*, 39, 97-103.

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

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

706 Silva, LCR, Sternberg L, Haridasan M, Hoffmann WA, Miralles-Wilhelm F, and Franco
707 AC.(2008) Expansion of gallery forests into central Brazilian savannas. *Global Change Biology*
708 14, no. 9: 2108-2118.

709 Silverio DV, Brando PM, Balch JK, Putz FE, Nepstad DC, Oliveira-Santos C, Bustamante MM
710 (2013) Testing the Amazon savannization hypothesis: fire effects on invasion of a
711 neotropical forest by native cerrado and exotic pasture grasses. *Philos Trans R Soc Lond B*
712 *Biol Sci*, 368, 20120427.

713 Simpson KJ, Ripley BS, Christin PA, Belcher CM, Lehmann CE, Thomas GH, and Osborne CP.
714 (2016) Determinants of flammability in savanna grass species. *Journal of Ecology*, 104(1),
715 138-148.

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

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

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

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

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

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

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

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

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

738 Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M. S., Rödiger, E., ... & Huth, A.
739 (2018). Global patterns of tropical forest fragmentation. *Nature*, 554(7693), 519-522.

740 Touboul, J. D., Staver, A. C., & Levin, S. A. (2018). On the complex dynamics of savanna
741 landscapes. *Proceedings of the National Academy of Sciences*, 115(7), E1336-E1345.

742 Uhl, C., Clark, H., Clark, K., & Maquirino, P. (1982). Successional patterns associated with
743 slash-and-burn agriculture in the upper Rio Negro region of the Amazon basin. *Biotropica*,
744 249-254.

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

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

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

754 Veldman JW, Buisson E, Durigan G et al. (2015a) Toward an old-growth concept for
755 grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment*, 13, 154-
756 162.

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

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

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

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

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

770 Watson, J. E., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., ... & McAlpine, C.
771 (2018). The exceptional value of intact forest ecosystems. *Nature ecology & evolution*, 2(4),
772 599-610.

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

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

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

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

780 Wright, J. L., Bomfim, B., Wong, C. I., Marimon-Júnior, B. H., Marimon, B. S., & Silva, L. C.
781 (2021). Sixteen hundred years of increasing tree cover prior to modern deforestation in
782 Southern Amazon and Central Brazilian savannas. Global Change Biology, 27(1), 136-150.

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

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

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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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861 **Figure 1.** Fire Frequency map (left) of Hluhluwe iMfolozi Park from 1955 to 2013
 862 based on Hluhluwe iMfolozi Park records with the Hluhluwe Game Reserve section
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Figure 5. NMDS ordination of the cumulative length of all species in all height classes in transects. Ellipses show the grouping of transects. Species associations used in the composition analyses are based on species found in transects before the extreme fire events only. Letters indicate the position of transects, grey dots indicate the species scores.

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