Pathways of forest 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 form dense canopies that exclude fires by reducing C4-grass fuel loads and creating a humid microclimate. However, extreme fires occasionally burn into forests. Although these are known to kill forest trees and can make repeat fires more likely, the long-term consequences of an extreme fire event for forest structure and potential forest savannization remain largely unknown. Here, we analysed whether an extreme fire event could, alone, alter forest species composition, vegetation structure, and fire regimes, or whether successive fires after an initial extreme fire event were necessary to trigger a biome transition. 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. Our results suggest that, while extreme fires set the stage for a biome transition, subsequent fires are necessary for flammable grasses to colonise and establish, ultimately resulting in a savanna fire regime.

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. Grasses invade the forest understory only locally (Silverio *et al.*, 2013), limited by dispersal and possible biogeochemical feedbacks. As a result, the question of whether fires can actually convert a tropical forest to a savanna remains open.

Historically and today, fires burn frequently in savannas, at a rate of several per decade, but rarely penetrate beyond intact forest margins (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 (Breman et al, 2012, 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., soil – plays 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, 2020). 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 by savanna of forests (i.e., forest savannization) has been studied predominantly in the Neotropics (Cavelier et al, 1998, Veldman and Putz, 2011, Silverio *et al*., 2013, Flores et al 2016), and even then typically in the context of invasive 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 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 grass fuels following repeat fires (Veldman and Putz, 2011, Silverio *et al*, 2013). However, these processes typically involve novel fire regimes and boundaries (Alencar *et al*. 2015) with unclear historical and palaeoecological precedents (but see Flores et al 2016). The question of whether fires can cause a biome switch between savannas and forests has not yet been settled, but is increasingly relevant in an age of extreme fires. Natural mosaics offer a rare opportunity for testing these ideas.

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, 2015a), 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 mosaic in Hluhluwe iMfolozi Park, South Africa, where extreme fires burned into forests in 2004 and 2008; some of these areas have burned subsequently, while others have not. These changing fire regimes offering an opportunity to examine *in situ* the spectrum of possible outcomes for forest vegetation trajectories. On the one extreme, a forest experiencing fire might recover its original forest state. 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, 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.

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). Forests in Hluhluwe are differentiated into scarp forests (which we refer to as forests here onwards) and thicket (a form of dry forest characteristic of HiP, *sensu* Charles-Dominique et al 2015a). In HiP, forest patches naturally abut savannas with a full complement of savanna ungulate herbivores. 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 forest patch sizes from 1937 to 1992, and major forest 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

In order to determine vegetation trajectories after the extreme fires, we used a set of transects in which structure and species composition of woody plants were recorded. Given the rarity of these extreme events, generating replicates at will is challenging. We made use of a natural experiment, selecting transect locations based on areas that burned in the extreme fire event in 2008 and subsequent fires. Some transects were sampled repeatedly, supplemented with once-sampled transects allowing a space-for-time chronosequence to evaluate vegetation change. Three of the transects were laid out in forest that burned in a separate fire in 2004 and sampled nine and 11 years after the fire and are included in the Supplementary Materials. Transect sampling dates and repeat sample dates are summarized in Appendix S1. Intact forest and thicket transects 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*). See Appendix S1 for the vegetation history. Forest, thicket, and savannas 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).

A total of 131 transects 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. Each transect measured 40m x 10m, within which area we identified every woody plant 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 transect; grass biomass was measured via disk pasture meter (DPM, grass biomass = 1.26 + 26.1*[DPM], R2 = 0.73, N = 1745; Waldram et al,2007) and the dominant grass species recorded beneath the disk.

Fire occurrence

Fire frequency of each transect from 2001 to 2016 was derived from a combination of the MODIS Active Fire Detections (MCD14DL, Collection 6) and Ezemvelo KwaZulu Natal Wildlife fire records for HiP. 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. 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. The MODIS Active Fires data were used to verify the fire maps where they indicated fires burning in the forests.

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 calibrated 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 height into a single value (Fei *et al.*, 2005). We performed an NMDS Ordination on a Bray-Curtis species dissimilarity matrix of the cumulative length of each tree species for transects that had not experienced the extreme fire event. 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 transect, 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

246 decade. In fact, fire frequency (FF) increased from approximately one fire every four years
247 (FF = 0.24 ± 0.11) before the 2008 extreme fire event to one fire every three years (FF = 0.36
248 ± 0.13; t = -11.8, df = 43, $p < 0.05$) after 2008. Thicket patches that burned in the 2008
249 extreme fire event quickly established a savanna fire regime with sites burning on average
250 once every three years (FF = 0.34±0.07), compared to no fires from 2000 to 2007.

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

257 Colonisation by savanna grasses

258 Intact thicket and forest transects differed from savanna transects in having closed canopies
259 and little or no grass in the understory (Fig. 3). Savanna transects had on average 233±87
260 $g.m^{-2}$ of grass biomass whereas intact thicket and forest patches had 148±84 $g.m^{-2}$ and
261 10±2.8 $g.m^{-2}$ respectively (Fig. 3). Frequently burnt thicket and frequently burnt forest
262 transects showed an increase in grass biomass following successive fires, with grass biomass
263 four and 22 times higher than intact thicket and forest transects respectively (Fig. 3). Once
264 burnt forest transects had relatively high, but variable, grass biomass (130±114 $g.m^{-2}$) in the
265 first year after the extreme fire events, grass biomass decreased over time to 33±11 $g.m^{-2}$ by
266 the end of the study 9 years later, approaching the levels of intact forest grass biomass. In
267 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 transects 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 transects 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 transects that burned frequently were significantly different to Intact thicket transects (Pillai's Trace = 0.76, approx $F(4,30) = 23.406$, $p < 0.001$, Appendix S3) and had a comparable structure to savanna transects 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 significantly 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 significantly 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 significantly 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, $p > 0.05$).

Trajectories in woody species composition

Forest, thicket, and savanna transects were characterized by distinct woody species assemblages (Fig. 5, Appendix Table S4 & Table S5). Forest and thicket differed compositionally from each other, with thickets showing no evidence of succession towards forest. The overall (Appendix Table S4) and size class specific (Appendix Table S5) abundance of species types within savannas did not differ significantly 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 karoo), 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 transects 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 transects. 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 significantly different to the frequently burnt forests in overall abundance of species types (Appendix Table S4), however they were significantly 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), and differed significantly 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 forest edge, 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 that burned again following the initial extreme fire event underwent a persistent transition from closed-canopy forest 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 forests to open, fire-dependent vegetation, structurally resembling savannas. This transition occurred on the time scale of a decade, which suggests that savanna-forest mosaics are likely dynamic even in short-to-medium term. The occurrence of a subsequent frequent fire regime 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 to savanna occurred.

In the transition from forest 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 forested areas that 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 subsequent 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 comparable to 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 the first we know of to document grass-fuelled fires invading intact closed forest and thicket communities in a natural and ancient African savanna-forest-thicket mosaic. Our results offer a few key insights. Firstly, we provide evidence for fire as a mechanism by which savannas might have invaded forests in the past. 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) – probably by increasing forest canopy openness, then grass invasion, and finally by the arrival of savanna trees. However, until now, on-the-ground observations of how this savannization proceeds in a natural ecosystem have been lacking.

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). As in the Amazon, these extreme fire events present a rare but real problem. At our site, the combination of conditions necessary for an extreme fire event to develop – 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.

However, one of the challenges of preventing extreme fires is the necessity of using fire 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.

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.

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.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Silverio DV, Brando PM, Balch JK, Putz FE, Nepstad DC, Oliveira-Santos C, Bustamante MM (2013) Testing the Amazon savannization hypothesis: fire effects on invasion of a

neotropical forest by native cerrado and exotic pasture grasses. Philos Trans R Soc Lond B Biol Sci, 368, 20120427.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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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 and (right) the distribution of transects and biomes based on the eighteen vegetation communities of Whateley & Porter (1983), which have been re-classified into three distinct biomes (Charles-Dominique *et al,* 2015a). Green represents forest, blue represents thickets, and grey represents savannas. Inset map shows the location of Hluhluwe iMfolozi Park within South Africa.

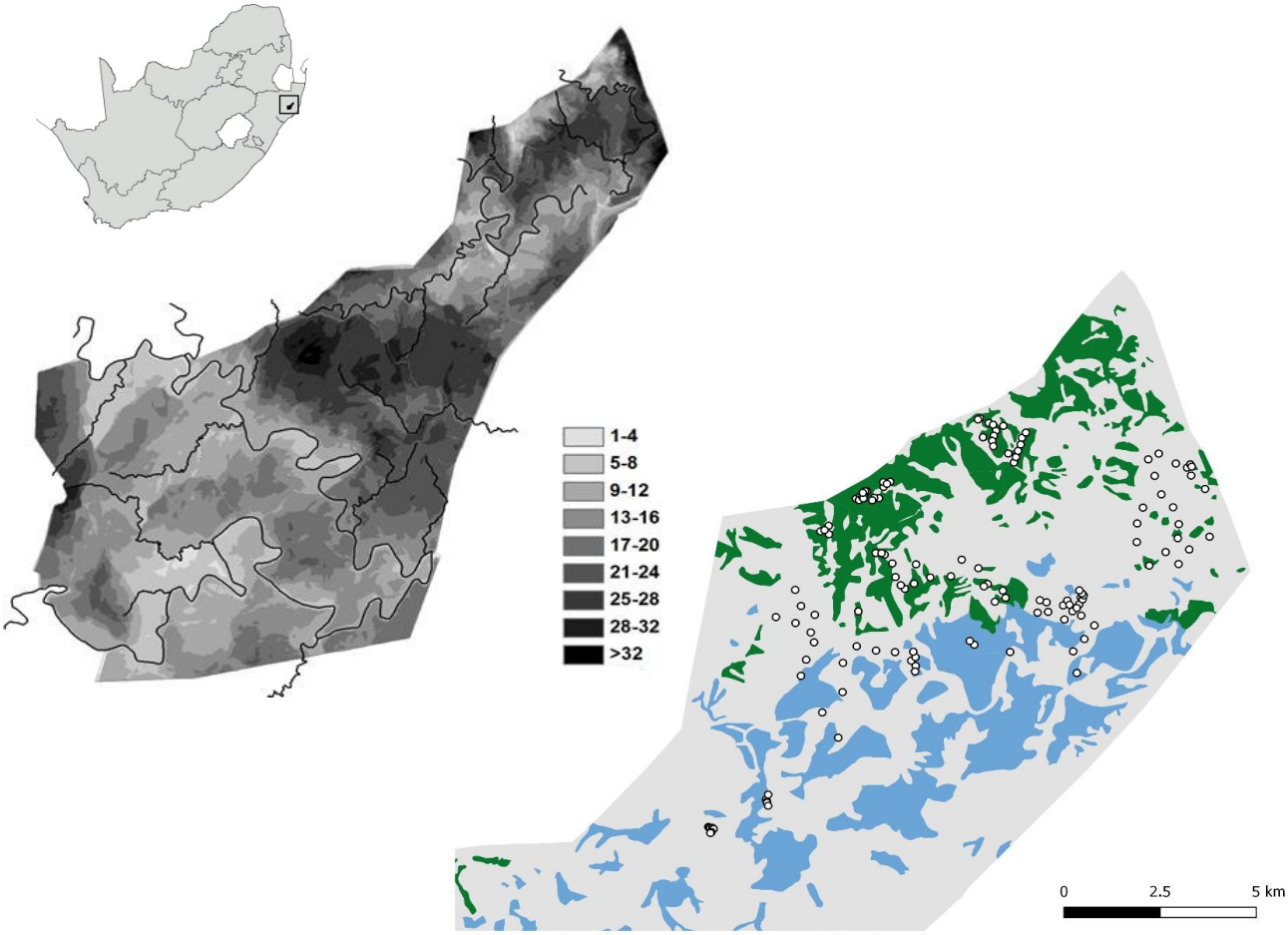
Figure 2. Fire Frequency for transects within each vegetation type (indicated by grey text) before and after extreme fire events (not including the year of the extreme fire event), calculated using the MODIS Active Fires Product. Grey lines link transect points before and after extreme fire events. Asterisks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

Figure 3. Changes in the (A) total biomass of grass found in all transects 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 transects, blue represents thicket, and yellow represents savanna. Error bars indicate standard error. Points (transect grass biomass) are included to display variation. Letters indicate significant differences 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 transects.

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.

Figure 6. Initial and final composition and structure of savannas in 2007 (A) and 2014 (B), intact (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 (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 transects sampled before the extreme fire event.



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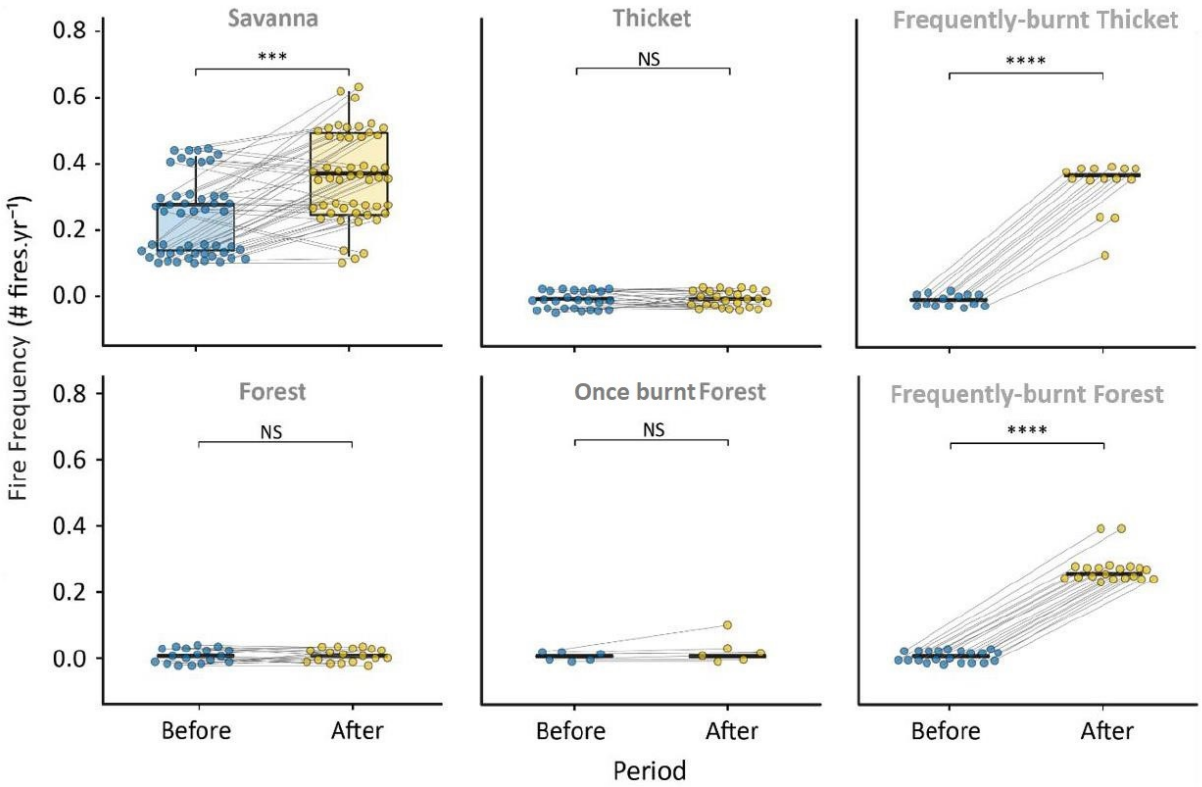

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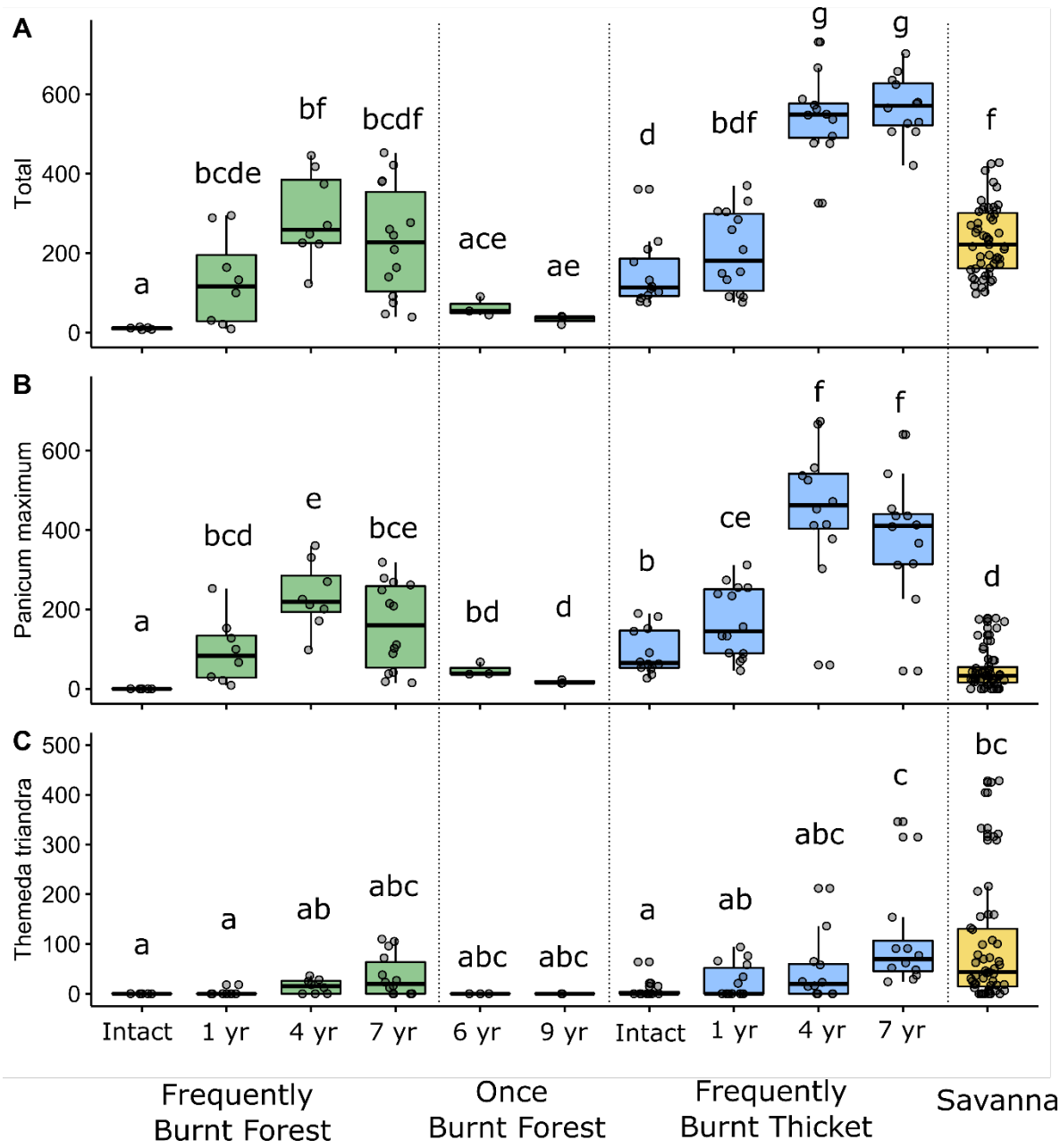

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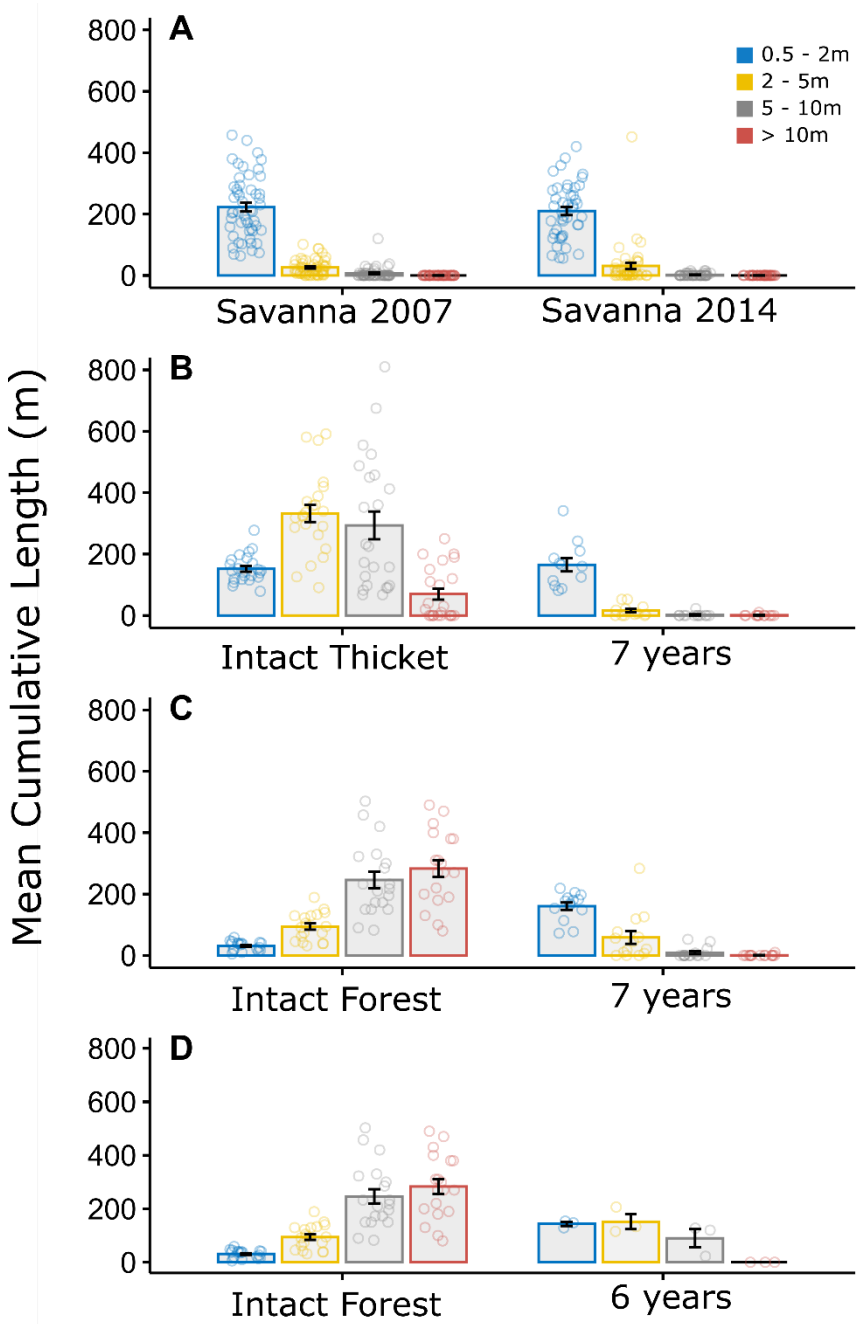

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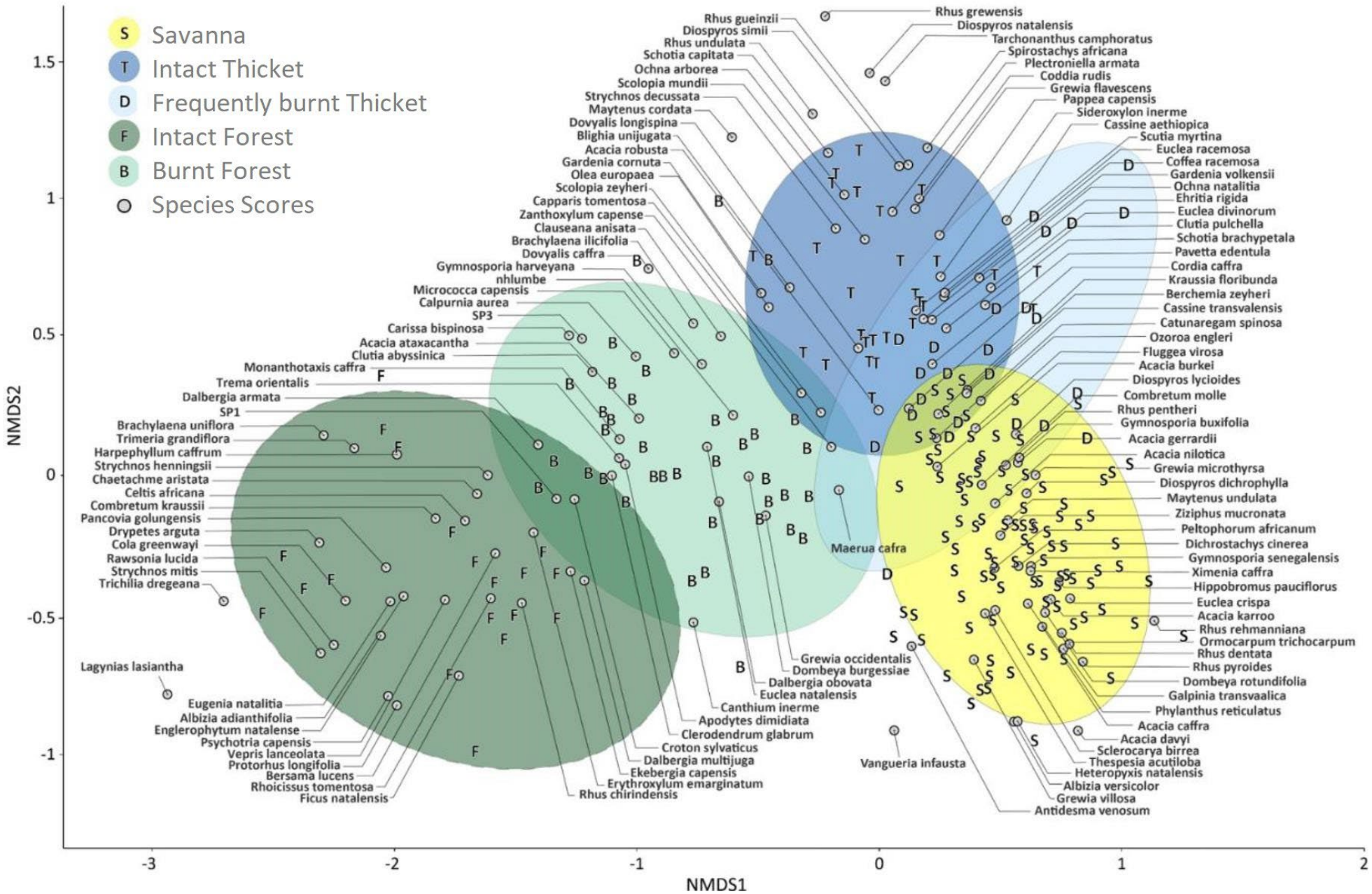

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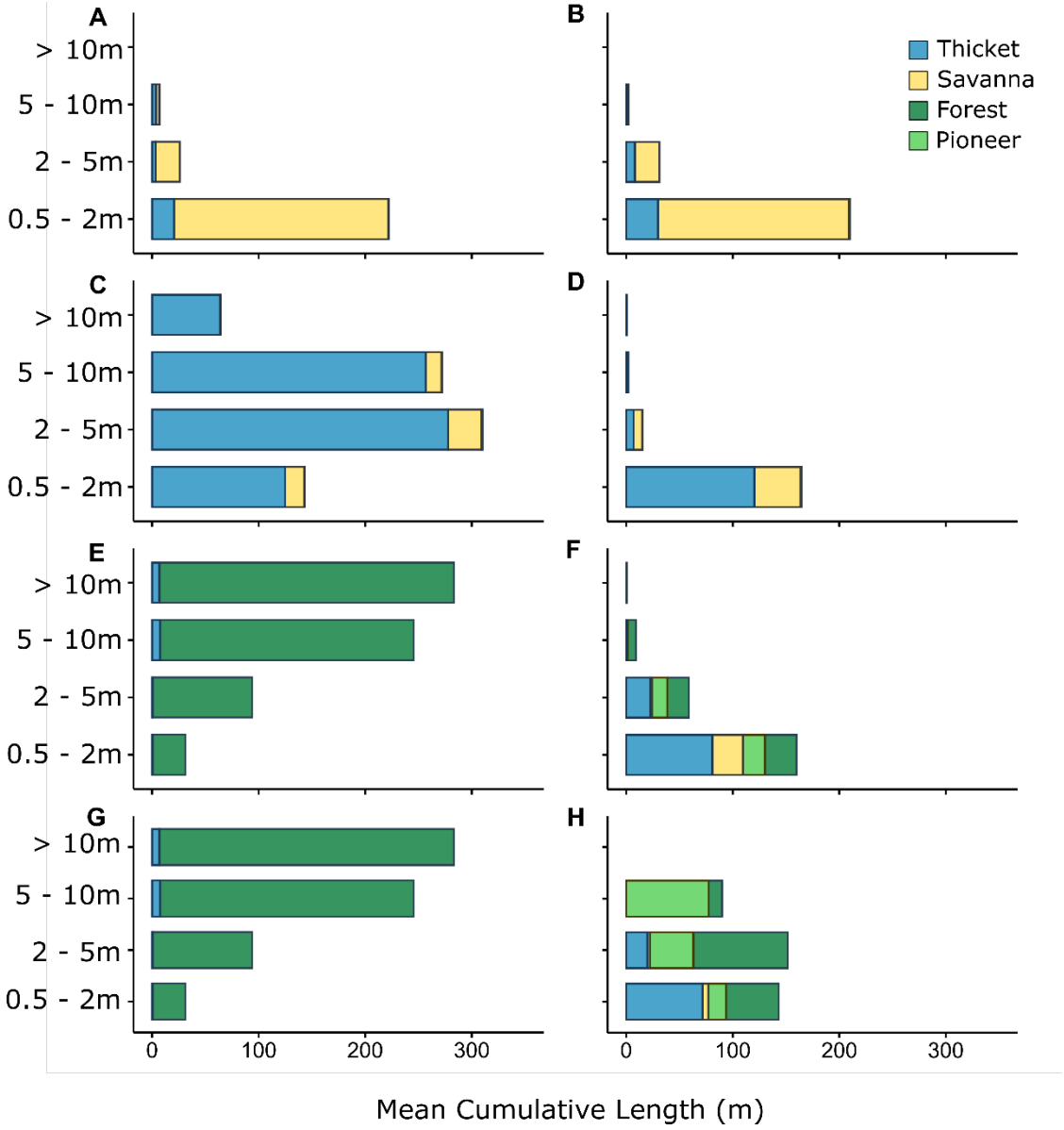

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