




# Drought and fire determine juvenile and adult woody diversity and dominance in a semi-arid African savanna

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## Abstract

The aim of this study was to understand how communities of adult and juvenile (seedlings and saplings) woody plants were impacted by fire and the 2014–2016 El Niño drought in Kruger National Park, South Africa. We used a landscape-scale fire experiment spanning 2013–2019 in a semi-arid savanna in the central west of Kruger National Park (mean annual precipitation, 543 mm). Adult and juvenile woody species composition were recorded during and after the drought in 40 plots that experienced a mix of no fire, moderate fire, and frequent fire treatments. Using multivariate modeling, we related community composition in juvenile and adult woody plants to year of sampling and the experimental fire treatments. Post-drought, there was significant adult woody plant top-kill, especially in dominant species *Dichrostachys cinerea* (81% reduction in abundance), *Acacia nigrescens* (30%), and *Combretum apiculatum* (19%), but there was no significant change in adult species richness. Two years post-drought, abundance of all juveniles decreased by 35%, and species richness increased in juveniles in both the frequent fire (7%) and no fire treatments (32%). Counter-intuitively, the El Niño drought increased species richness of the woody plant community due to the recruitment of new species as juveniles, a potential lasting impact on diversity, and where different fire regimes were associated with differences in community composition. Drought events in semi-arid savannas could drive temporal dynamics in species richness and composition in previously unrecognized ways.

## KEYWORDS

adults, diversity, drought, fire, juveniles, Kruger national park, semi-arid savanna, woody community

## 1 | INTRODUCTION

Central to understanding the persistence and dynamics of savanna ecosystems are processes of recruitment and mortality (Bond, 2008). Savanna ecosystems are characterized by demographic bottlenecks where juvenile trees and shrubs are "trapped" in small size classes by

fire and browsing (Bond et al., 2017). In African savanna ecosystems, the prevalence of fire and herbivory shapes both demography and community composition as species unable to tolerate these disturbances are either unable to establish seedlings from seeds, further recruit as saplings from seedlings or are filtered from the ecosystem via mortality (Hoffmann et al., 2012). In absence of fire and herbivory,

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competition for resources from grasses may also prevent successful seedling establishment (Morrison et al., 2019, Ward, 2005). In semi-arid savannas, seedling establishment and sapling recruitment to adult size classes can be infrequent and episodic (Domec et al., 2006, Gignoux et al., 2009). It has been previously suggested that woody plant establishment and recruitment might be linked to extreme rainfall events and changes in herbivory and fire pressures that can be caused by drought reducing grass productivity and competition (Wilson and Witkowski, 1998, Kraaij and Ward, 2006). From 2014 to 2016, an El Niño drought event occurred across southern Africa (Baudouin et al., 2017). Here, we examine how drought and fire independently and interactively relate to juvenile and adult woody plant community composition in a semi-arid savanna.

At first order, savanna plant communities are controlled by rainfall and rainfall seasonality, where annual dry seasons of 4–9 months typify savannas the world over (Solbrig et al., 1996). As such, savanna plants have adapted to seasonal water shortages. Drought is characterized as prolonged and extreme below average water availability relative to local mean annual precipitation that extends into one or more wet seasons (Sankaran, 2019) and multi-annual droughts have been shown to occur periodically in savanna ecosystems—especially semi-arid ones (Mason and Tyson, 2000, Tyson et al., 2002). Drought has been observed to cause mortality and dieback within juvenile and adult tree communities (Case et al., 2019, Fensham et al., 2009, Sankaran, 2019) and reductions in plant species richness (van Aardt et al., 2020, Sankaran, 2019). Tree mortality was reported in the 2014–2016 drought in the Nkulu area, near Skukuza, in the Kruger National Park in South Africa (Case et al., 2019), and also recorded in savannas of north-eastern Australia post the “millennium” drought (Fensham et al., 2009). On the contrary, Abbas et al. (2019) recorded little mortality in a different conservation area near Kruger over the same 2014–2016 drought.

Fire impacts savanna distribution (Lehmann et al., 2011, Ratnam et al., 2011, Staver et al., 2011), and some of the traits that enable tolerance of fire and seasonal water shortages may also be important in drought resilience. Many woody species in African savannas have thick insulating bark that protects under regimes of frequent fire (Charles-Dominique et al., 2017). Furthermore, storage of carbohydrates in thickened, bud-bearing, and underground storage organs enable resprouting even on nutrient-poor and well-drained soils prevalent in savannas (February et al., 2019, Osborne et al., 2018, Charles-Dominique et al., 2017). In relation to drought tolerance, deep-rooting species such as *Sclerocarya birrea* have been found more resilient to drought than shallow-rooting species such as *Combretum* species or *Dichrostachys cinerea* (Zhou et al., 2020, Tomlinson et al., 2012). Some species such as *Ximenia caffra* and *Brachystegia* species are able to reproduce by establishing shoots from roots, which makes them well adapted to avoid frequent fires by spreading over wider areas (Chidumayo, 2004) and also possibly resilient to long-term drought impacts. *Dichrostachys cinerea*, an encroaching species recorded as experiencing high mortality in the 2014–2016 drought (Case et al., 2019), is fire resistant by reproducing both sexually and vegetatively via rhizomes (Walters

et al., 2004). Some species produce large numbers of juvenile only from seed banks (e.g., *Acacia tortilis*) (Witkowski and Garner, 2000), of which only few individuals need to survive drought and fire to develop into adult trees (Chesson, 1983). In sum, species that proliferate in seasonally dry and frequently burned savannas may have traits related to efficient water or nutrient uptake and storage, and resilience to defoliation and top-kill that in turn may increase species resistance to drought.

The response of woody plant communities to drought, fire, and their additive and interactive effects remains unclear and is a long-term knowledge gap in savanna ecology (Walker et al., 1987, Case et al., 2019). Here, we aimed to identify and understand changes in the abundance, richness, and community composition of woody adult and juvenile (seedlings and saplings) plants after an El Niño driven drought from 2014 to 2016 in a semi-arid savanna (Figure S1) across three different fire treatments. In our study, juvenile woody plants are defined as a plant with height <1 m and include both plants germinating from a seed or resprouting after top-kill. Data were collected from an experiment, established in 2013, that manipulates fire and grazing in the Satara land system of the Kruger National Park, and where monitoring woody vegetation commenced in 2016 (Donaldson et al., 2018). Over the ~18-month drought (Figure S1), rainfall decreased by over 50% which desiccated grasses and reduced grass biomass and grazing intensity (Figure S1, Figure S2). Grazing intensity is defined by the occurrence and density of grass-eating herbivores such as zebra, wildebeest, or buffalo (Donaldson et al., 2018). Recording of woody plants was undertaken during (2016) and after the drought (2018 and 2019) to gauge impacts on woody vegetation under different fire and grazing conditions. We hypothesized that (a) juvenile woody plant richness and abundances would increase post-drought on no burn treatments because drought reduced grazing and grass competition during drought, and that an absence of fire allowed new species to establish after drought; and (b) mortality in the adult plant community would be linked to prolonged water stress during drought but that the level of mortality would be mediated by fire treatment with less mortality on no burn treatments.

## 2 | METHODS

### 2.1 | Study site

The study was conducted in the Satara Land System of the Kruger National Park (KNP), South Africa (S 24°23'35", E 31°46'41"). The study site has a seasonally dry, semi-arid, and frost-free climate where most rain (78%) falls in the wet season from November to April (Donaldson et al., 2019). In Satara, mean annual rainfall averages 543 mm (Swemmer, 2020). Rainfall dropped to 332 and 140 mm respectively over the 2014/15 and 2015/16 rainy seasons (Figure S1). In the absence of drought, fire return periods of ~3 years are the norm in this landscape (van Wilgen et al., 2004, Donaldson et al., 2018, Govender et al., 2006). Soils are dominantly clayey basalt

soils (Venter et al., 2003), which have higher water retention probabilities than sandy soils and can support high woody aboveground biomass in absence of fire and herbivory (Colgan et al., 2012). Across Satara, savannas are dominated by *Sclerocarya birrea* and *Acacia nigrescens* alongside *Dichrostachys cinerea* and various *Combretum* species (mainly *C. molle*, *C. apiculatum*, *C. imberbe*, and *C. mossambicense*). The  $C_4$ -grasses *Bothriochloa radicans*, *Digitaria eriantha*, *Panicum coloratum*, *Urochloa mosambicensis*, and *Themeda triandra* dominate (Donaldson et al., 2018, Oudtshoorn, 1999, Knapp et al., 2012).

## 2.2 | Experimental design and data collection

Rainfall data from the Satara weather station (S 24°22'30", E 31°37'30", elevation 380m), operated by South Africa National Parks (SANParks), for the period April 2014 to April 2019 (the date of the final survey of woody plants) were analyzed. As soil properties are fairly consistent across the study site, no soil variables were used to define drought. We only used below-average mean annual rainfall to define drought (Donaldson et al., 2018). Rainfall totals during and post-drought (April – April) were: 1) 2014–2016 = 472.4 mm (~236 mm per year); 2) 2016–2018 = 986.2 mm (~493 mm per year); and 3) 2017–2019 = 862.4 mm (~430 mm per year). In analyses presented here, year of sampling was used as a categorical variable (equivalent to cumulative rainfall) to predict changes in woody species abundance and diversity in response to drought.

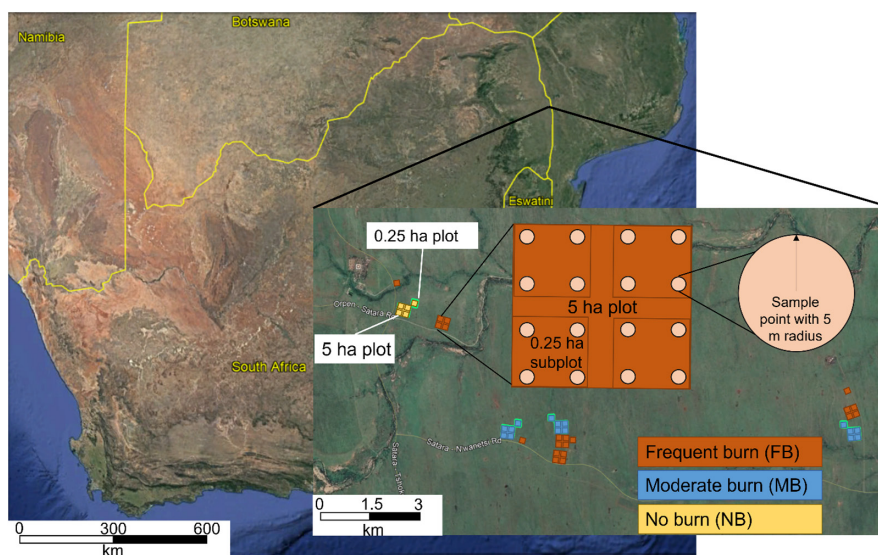
Woody plant communities were sampled in 2016 during the drought, post-drought in 2018 and 2019 and, logistics prevented sampling in 2017. Individual woody plants were not marked to track individual-level growth and mortality; rather, community-level

responses were prioritized. Three fire treatments, set up within a fire-grazing manipulation initiated in 2013 by Donaldson et al. (2018) (Figure 1), were sampled: (i) no fire from 2013 to 2019, (ii) moderate fire, 2x from 2013–2019 (wildfires which occurred in 2016 and 2017), and (iii) frequent fire, app. 5x from 2013–2019 (experimental fires in 2013, 2014, and 2015, wildfires in 2016 and 2017). Fire treatments were implemented across a series of 5-ha plots (with 4x0.25-ha subplots in each) and 0.25-ha plots. Each of the 0.25-ha plots/subplots contained nested circular points, each with a 5 m radius (=78.54 m<sup>2</sup>). This resulted in a total of 160x78.54 m<sup>2</sup> circular points that were sampled. The season of burn varied from April to November. Fire treatment was used categorically in our analyses.

For our study, woody plants were monitored over a total area of 1.26-ha consisting of

- (i) 20 circular points on the no burn treatment (20 \* 78.54 m<sup>2</sup> = 1570.8 m<sup>2</sup>),
- (ii) 60 circular points on the moderately burned treatment (60 \* 78.54 m<sup>2</sup> = 4712.4 m<sup>2</sup>),
- (iii) 80 circular points on the frequently burned treatment (80 \* 78.54 m<sup>2</sup> = 6283.2 m<sup>2</sup>)

Because the fires were small, they tended to concentrate herbivores (Archibald et al., 2005), so both the grazing and browsing intensities were higher on the burned plots, but there was no difference in intensity between the single 0.25-ha plots and the 0.25-ha subplots that were within the 5-ha plots (Donaldson et al., 2019, Voysey et al., 2021). Based on data from Donaldson et al. (2018) and measurements in 2019, grass height decreased from 2013 to 2019 and was lowest in 2019 on the frequently burned treatments



**FIGURE 1** Profile of the experimental design within the Satara land system in the Kruger National Park, South Africa. Sampling was conducted on 8x 5-ha plots (each with 4x 0.25-ha subplots) and 8x 0.25 plots. Each 0.25-ha plot contained 4x circular points with a 5 m radius, in which juvenile and adult woody species were counted and measured. Juveniles were classified as any individuals less than 1 m height, germinating from seeds, or resprouts, root shoots, or coppices. Diameter was measured at 20cm height of the largest stem. Individuals with multiple stems were counted as one individual. The aerial images were used from Google earth on January 27, 2021. The depiction of the plots/subplots/sampled points are not to scale

( $5.1 \pm 1.7$  cm) post-drought, while grass biomass decreased on all fire treatments from 2013 to 2017, but then increased again in 2019, while being highest on the no burn treatments ( $511.8 \pm 171.9$  g/m<sup>2</sup>) (Figure S2).

In each year of sampling in April, woody plant species and height of the tallest stem (m) were recorded to understand community composition. At this time, year plants are still in leaf and able to be identified. Juveniles were defined as individuals <1 m height, and this size class incorporated plants that had either germinated from seed or were resprouting from rootstock. Individuals >1 m height were classed as adults, and the survey incorporated both shrubs and trees. A 1-m height threshold was chosen based on a previous study in the Kruger National Park examining drought impacts (Case et al., 2019), and where woody plants >1 m height have been shown to recover from drought via established root systems (Case et al., 2020b, Wilson and Witkowski, 1998). Each juvenile or adult with multiple stems was counted as one individual, and only the tallest stem of a multi-stemmed individual was measured. For all adults, stem diameter (cm) was measured at 20 cm height aboveground on the tallest stem. Individuals which had no leaves and were clearly desiccated with no live buds were recorded as dead.

During the drought, competitive tussock grasses all but disappeared on the burned and grazed plots, and even the unburned plots had substantial reductions in basal cover (Figure S2). Donaldson et al. (2018) showed via dung counts that herbivores slowly moved off these heavily utilized patches during the drought, as there was no forage, and they did not return immediately once the drought broke. Herbivory post-drought was therefore lower than before, especially on the burned plots. The first fire applications occurred again in 2018, so woody plants were also released from fire for ~2 years post-drought. The data presented here therefore need to be interpreted in the context of prolonged and intense water stress, followed by favorable conditions for woody establishment and recruitment.

### 2.3 | Data analyses

Rank-abundance curves were calculated for each fire treatment-year combination from the field data to show absolute dominance of woody species within a community and visualize change in abundances over time. We used the BiodiversityR package in R, version 4.0.2 (RStudio-Team, 2016). Change in adult and juvenile community composition from 2016 to 2019 between each fire treatment was compared with identify trends and differences in community composition. By calculating species richness and species evenness for points nested within subplots and plots respectively, we were able to account for different sample sizes between fire treatments given the unbalanced design. Significant changes in species richness and evenness between years of measurement per fire treatment were determined with a one-way analysis of variance (ANOVA) test (Miller Jr, 1997). Dissimilarities between species richness and abundance in each fire treatment per year of sampling were calculated with the

Bray dissimilarity index, which quantifies dissimilarities pairwise on a scale from 0 (equal species richness and abundance) to 1 (complete turnover). More details on rank-abundance curves can be found in the supplementary material of this study.

Adult and juvenile community composition were modeled separately to test how these two demographic groups respond to drought and fire. Multivariate abundance models using the R package "gllvm" (Niku et al., 2019, Wang et al., 2012) were constructed. These models fit a generalized linear model (GLM) to the abundance of each species and calculate species-specific intercepts and regression coefficients (effect sizes) in relation to predictors. Models then interpret relationships between the whole community and predictors to identify both variation in species composition and indicator species responses. Thereby, the model expresses the change in abundance of individual species relative to the entire community between years of sampling and fire treatment. Spatial autocorrelation was unlikely to have occurred due to the close vicinity of all plots in a relatively homogenous environment as part of the original experimental design. All analyses were carried out in R, version 4.0.2 (RStudio-Team, 2016).

With GLLVMs, the global model was constructed as:

$$GLM_{(i,j,n)} = gllvm(y_{(i,j,n)} \sim x_1 * x_2 + LV + \text{offset}(\log(n)) + (1|plot|subplot|point)),$$

where  $i$  = size class (adults, juveniles),  $j$  = species,  $n$  = number of points sampled in each fire treatment,  $y$  = woody species abundance data,  $x_1$  = fire treatment (FB, MB, NB),  $x_2$  = year of sampling (2016, 2018, 2019), and LV = latent variable. The response variables were counts of individuals among woody plant species (= abundance), with year of sampling and fire treatment as categorical predictor variables. One latent variable (LV) was incorporated into model calculations to test for intra-species correlations. A full subsets analysis was undertaken for each demographic group to determine the relative importance of each term, where all terms were included on an a priori basis, and to test for additive versus interactive effects of fire and drought. The offset term accounted for the difference in sampled species and their abundances due to the variation in sampling intensity among treatments by adding a log-normal function to the number of sampled points ( $n$ ) per fire treatment and thereby assuming a normal data distribution (Kotze et al., 2012, Tian and Wu, 2007). The random effect (1|plot|subplot|point) accounted for the nested design and repeated sampling in 2016, 2018, and 2019. Models were specified with a negative binomial distribution and the spread of residuals versus fitted values indicated a good fit to the data and the appropriate use of a negative binomial distribution.

Seven GLLVMs (seven in each full subsets analysis of adults and juveniles) were compared and ranked using Akaike information criterion (AIC) to identify the best model fit for the data (Sober, 1981). The most supported model was assessed by the lowest AIC value, and delta AIC ( $\Delta$ AIC) was used to estimate the difference between the best model fit and the next best model fit. All models with a  $\Delta$ AIC <2 were considered a good fit to the data (Symonds and Moussalli, 2011).

To understand how species abundance responded to drought and fire, effect sizes from the model were plotted to allow



comparison between the responses of adults and juveniles. Effect sizes for each species expressed an increase (positive effect size), decrease (negative effect size), or no change in predicted abundance with reference to drought (Year 2016) and fire treatment (moderate fire).

A shortcoming of using an offset term to account for differences in samples sizes is that rare species may be missed because of the weighting imbalance of sampling between fire treatments. We therefore, as a supplementary analysis, used bootstrapping of 20 random resamples per treatment with replacement and 10,000 replications of the data to run using the GLLVMs where treatments have equal sample size. This approach used the minimum number of sampled points of a fire treatment (i.e., 20 sampled points on the no burn treatments) to eliminate the uneven sampling across fire treatments. We then applied the same GLLVMs as described, except without the offset term. Further details of the bootstrapping approach and results are presented in the supplementary material.

To better understand species co-existence in specific communities between fire treatments and year as well as how much variance in species abundance data can be explained by fire treatments and year, a redundancy analysis (RDA) on abundance data, stored in a species by site data matrix, was used. The redundancy analysis function `rda` from the package “vegan” (Oksanen et al., 2013) was used to run the RDA, and the `ggord` function within `ggplot` (Wickham et al., 2016) was used to plot the RDA. The RDA enabled plotting of species communities relative to the predictors. An RDA of adult and juvenile abundances per 0.25-ha plot/subplot for Year 2016 illustrated differences in species community composition between fire treatments, and changes in each species' abundances along fire treatments after drought. Results were plotted via partial ordination with a latent variable using gaussian approximations of the maximum log-likelihood function. The relationship of response variable and predictors was then projected into an ordination space, using the RDA.

### 3 | RESULTS

#### 3.1 | Changes in adult and juvenile abundance and diversity

Overall, total number of adult plants declined by 41% from 580 individuals in 2016 to 341 individuals in 2019 over the study area (1.26-ha) (Table 1, Figure 2). The largest absolute declines in adult stems from 2016 to 2019 were observed in *Dichrostachys cinerea* (from  $322 \pm 4.8$  individuals (55.5% of all adults in 2016) to  $61 \pm 1.9$  (17.9% of all adults in 2019)), *Acacia nigrescens* ( $83 \pm 0.6$  (14.3%) to  $60 \pm 0.3$  (17.6%)) and *Combretum apiculatum* ( $74 \pm 0.8$  (12.8%), to  $60 \pm 0.6$  (17.6%)) (Table 1, Table S1, Figure 2). While this can be interpreted as significant post-drought mortality, it is also possible a proportion of individuals were top-killed and reverted to the juvenile size class. Small errors with plot relocation are also possible but unlikely to result in these dramatic and consistent changes.

In juveniles, the absolute number of individuals decreased by 35% from 3378 individuals in 2016 to 2185 individuals in 2019

(Table 2, Figure 2). *Dichrostachys cinerea* also saw the highest decline, from 1439 ( $\pm 6.4$ ) individuals (42.6%) in 2016 to 998 ( $\pm 4.8$ ) (45.7%) in 2019 (Table 2, Table S1, Figure 2).

Total number of species recorded as adults across the sampled area increased by 20% from 16 in 2016 to 20 species in 2019. Although, in 2019, *Sclerocarya birrea* (Anacardiaceae) and *Commiphora glandulosa* (Burseraceae) were lost, and six new species appeared in the adult size class, *Lannea schweinfurthii*, *Ozoroa engleri* (both Anacardiaceae), *Combretum mossambicense* (Combretaceae), *Ormocarpum trichocarpum* (Fabaceae), *Grewia bicolor* (Malvaceae), and *Flueggea virosa* (Phyllanthaceae). Total number of species recorded as juveniles increased by 29% from 17 species in 2016 to 24 species in 2019 across the whole study area, of which two species *Rhus gueinzii* (Anacardiaceae) and *Euclea divinorum* (Eberaceae) disappeared, but nine species appeared: *Ozoroa engleri* (Anacardiaceae), *Ehretia amoena* (Boraginaceae), *Gymnosporia senegalensis* (Celastraceae), *Combretum mossambicense* (Combretaceae), *Dalbergia melanoxylon*, *Ormocarpum trichocarpum* (both Fabaceae), *Grewia bicolor* (Malvaceae), *Ximenia caffra* (Olacaceae), and *Flueggea virosa* (Phyllanthaceae) (Table S1). *Combretum molle* appeared in 2018 on frequently burned plots, but disappeared again in 2019. In adults, species richness at a sample point level did not change between years and was higher on the unburned treatments (Figure 3a). Despite the recording of new species in adults, species evenness at sample point level remained similar on all fire treatments from 2016 to 2019 and was highest on the no burn treatments across all years of sampling (Figure 3b). In juveniles, mean species richness at sample point level increased significantly ( $p < .001$ ) on the frequently burned treatments from 2.4 ( $\pm 1.3$ ) in 2016 to 2.6 ( $\pm 1.3$ ) in 2018 and further to 2.7 ( $\pm 1.3$ ) in 2019 (7% increase from 2016 to 2019) (Figure 3a). While on the moderately burned treatments, mean species richness decreased significantly ( $p < .001$ ) from 3.1 ( $\pm 2$ ) in 2016 to 2.8 ( $\pm 1.4$ ) in 2018, and then decreased slightly to 2.7 ( $\pm 1.5$ ) in 2019 (13% decrease from 2016 to 2019) (Figure 3a). On the unburned treatments, mean species richness increased significantly ( $p < .001$ ) from 2.2 ( $\pm 1.3$ ) in 2016 to 2.4 ( $\pm 1.3$ ) in 2018 and further increased to 2.7 ( $\pm 1.4$ ) in 2019 (32% increase) (Figure 3a). Additionally, 7 of 12 of the new juvenile species recorded in 2018 or 2019 were not of the same family, showing a turnover in both species and family composition (Table 2, Table S1). Juvenile species evenness at the sample point level increased ( $p < .05$ ) on the unburned treatments from 0.51 ( $\pm 0.13$ ) in 2016 to 0.61 ( $\pm 0.13$ ) in 2019, while a decrease from 0.52 ( $\pm 0.12$ ) in 2016 to 0.36 ( $\pm 0.1$ ) was observed on moderately burned plots in 2019 (Figure 3b). Similar to adults, juvenile species evenness was highest on the no burn treatments across all years of sampling, but decreased significantly on moderately and frequently burned treatments (Figure 3b). Species richness and abundances in adults were most dissimilar between moderately burned plots, where communities were most similar in 2018 and 2019 but dissimilar compared with 2016. In fact, moderately burned plots in 2016 were most dissimilar compared to all other fire treatments and years of sampling (Figure 3c). Across juveniles, frequently burned and moderately burned plots in 2016 were more similar in species richness and abundance compared with 2018 and 2019 (Figure 3d).

**TABLE 1** Overview of all adults woody plant species recorded on the 160 sampled points (each with a 5 m radius = 78.54-m<sup>2</sup>) in the Satara land system and their abundance (number of individuals) with the standard error (se), and each species proportion (in %) of the entire species abundance in each year of sample year, ordered by family.

Family	Species	Adults								
		2016			2018			2019		
		Abund	se	Prop (%)	Abund	se	Prop (%)	Abund	se	Prop (%)
Anacardiaceae	<i>Lannea schweinfurthii</i>	NA	NA	NA	2	0	0.6	2	0.1	0.6
	<i>Ozoroa engleri</i>	NA	NA	NA	1	0	0.3	1	0	0.3
	<i>Rhus gueinzii</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA
	<i>Sclerocarya birrea</i>	1	0	0.2	NA	NA	NA	NA	NA	NA
Boraginaceae	<i>Ehretia amoena</i>	NA	NA	NA	NA	NA	NA	4	0.1	1.2
Burseraceae	<i>Commiphora africana</i>	7	0.1	1.4	3	0	0.9	5	0.1	1.5
	<i>Commiphora glandulosa</i>	1	0.3	0.2	2	0	0.6	NA	NA	NA
Celastraceae	<i>Gymnosporia senegalensis</i>	NA	NA	NA	21	0.3	6.5	12	0.2	3.5
Combretaceae	<i>Combretum apiculatum</i>	74	0.8	12.8	61	0.6	18.8	60	0.6	17.6
	<i>Combretum hereroense</i>	11	0.1	1.9	14	0.1	4.3	11	0.1	3.2
	<i>Combretum imberbe</i>	13	0.1	2.2	24	0.1	7.4	23	0.3	6.7
	<i>Combretum molle</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA
	<i>Combretum mossambicense</i>	NA	NA	NA	21	0.2	6.5	23	0.2	6.7
	<i>Terminalia prunioides</i>	6	0.1	1	4	0.1	1.2	4	0.1	1.2
Ebenaceae	<i>Euclea divinorum</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA
	<i>Euclea natalensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA
Fabaceae	<i>Acacia exuvialis</i>	12	0.1	2.1	2	0	0.6	8	0.2	2.3
	<i>Acacia nigrescens</i>	83	0.5	14.3	60	0.3	18.5	58	1.4	17
	<i>Acacia tortilis</i>	8	0.1	1.4	11	0.1	3.4	8	0.1	2.3
	<i>Cassia abbreviata</i>	4	0.1	0.7	8	0.1	2.5	9	0.1	2.6
	<i>Dalbergia melanoxylon</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA
	<i>Dichrostachys cinerea</i>	322	3	55.5	57	1.9	17.6	61	1.5	17.9
	<i>Ormocarpum trichocarpum</i>	NA	NA	NA	2	0.1	0.6	4	0.1	1.2
	<i>Peltophorum africanum</i>	23	0.3	4	5	0.1	1.5	6	0.1	1.8
	<i>Philenoptera violacea</i>	3	0.1	0.5	18	0.2	5.6	19	0.2	5.6
Malvaceae	<i>Grewia bicolor</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA
Olacaceae	<i>Ximenia caffra</i>	1	0	0.2	NA	NA	NA	1	0	0.3
Phyllanthaceae	<i>Flueggea virosa</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA
Rhamnaceae	<i>Ziziphus mucronata</i>	11	0.1	1.9	8	0.1	2.5	11	0.2	3.2
	All species	580	5.8	100.3	324	4.3	99.9	330	5.7	96.7

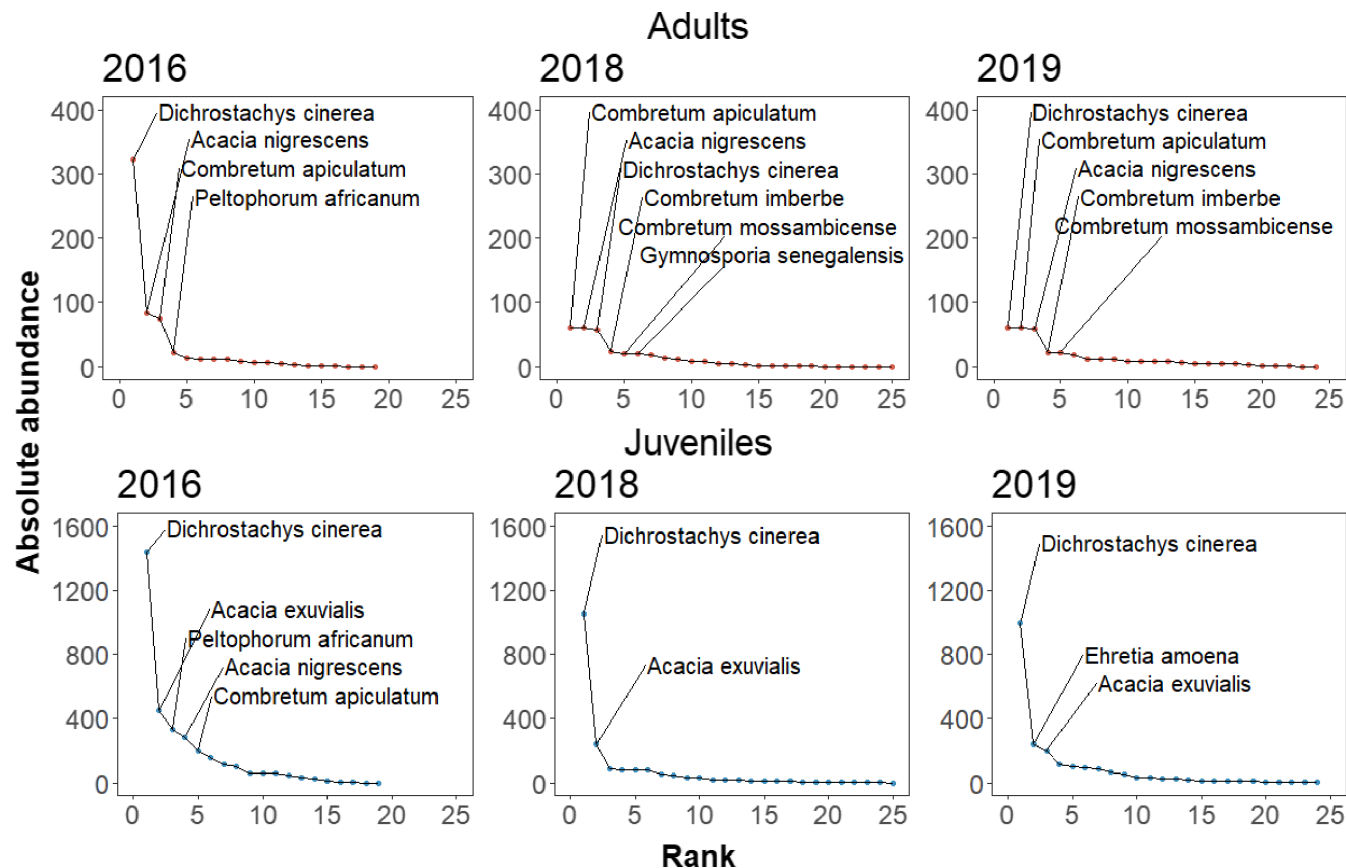
Note: Absence of species per year is marked with NA, thereby indicating when a species appeared or disappeared.

Across both adults and juveniles, unburnt plots were most similar from 2016 to 2019 (Figure 3c, d).

### 3.2 | Patterns of tree demography between adults and juveniles

In models examining adult and juvenile woody plant abundance (response variables), the most supported model contained fire

treatments and sampling year as additive predictors for both adults (AIC = 5514.82, Figure 4c) and juveniles (AIC = 11331.83, Figure 4d). All other models had  $\Delta$ AIC >2 and were therefore less supported (Figure 4c, Figure 4d). Similar results were obtained for models based on bootstrapped data, where the most supported models for both adults (AIC = 11092.13, Figure S4c) and juveniles (AIC = 20942.28, Figure S4d) contained fire treatment and sampling year as additive predictors rather than interactive. For the models run with original data and an offset term, both sampling year and fire



**FIGURE 2** Rank-abundance plots showing the dominance of adult and juvenile woody plant species across all fire treatments in the Satara land system categorized by year of sampling. The year 2016 represents a drought year with 472.4 mm rainfall over 2 years prior to sampling, and 2018 and 2019 represent post-drought years with 986.2 mm and 862.4 mm rainfall over 2 years prior to sampling, respectively. Labeled names represent species with a total number of individuals of greater than 5% abundance

treatments significantly impacted adult and juvenile abundances, where the model explained 47% variance for adults and 28% variance for juveniles. We therefore concluded that the effect of year of sampling on woody plant species abundances was consistent across fire treatments (Wang et al., 2012).

### 3.3 | Patterns of demography between years of measurement

The following results present the relative change in each species abundance proportional to the abundances of the entire woody community between years and fire treatments from the gllvm modeling. Out of all species, adult abundances of *Gymnosporia senegalensis* and *Combretum mossambicense* increased the most from 2016 to 2018 (Table S1, Table S2, Figure 4a), even though these species have a relatively low abundance across points of measurement (Figure 2). Abundance of these two species continued to increase in 2019, and increased abundances of *Flueggea virosa* and *Ormocarpum trichocarpum* were also observed (Table S1, Table S2, Figure 4a). The highest increase in juvenile abundance was also observed in *Gymnosporia senegalensis*, *Combretum mossambicense*, and *Ormocarpum trichocarpum* in 2018 and 2019 (Table S1, Table S3, Figure 4b) suggesting that

both establishment of seedlings and recruitment of juveniles to adult size classes were promoted in these species over this time period.

*Sclerocarya birrea* and *Ximenia caffra* adult abundance decreased the most from 2016 to 2018 (Table S1, Table S2, Figure 4a). In 2019, decrease in abundance was highest in *Commiphora glandulosa* and again *Sclerocarya birrea* (Table S1, Table S2, Figure 4a). At individual species level, abundance of *Dichrostachys cinerea* decreased highest out of all species from in 2018 and 2019 (Figure 2), but relative decrease proportional to the community was higher in *Sclerocarya birrea*, *Ximenia caffra*, or *Commiphora glandulosa* (Figure 4a). In juveniles, abundances of *Sclerocarya birrea* did not respond in 2018 and 2019, while *Commiphora glandulosa* responded positively in 2018, but negatively in 2019 (Table S2, Table S3, Figure 4b).

### 3.4 | Patterns of demography on fire treatments

The most significant ( $p < .05$ ) and the highest increase in adult abundances was on the unburned treatments, relative to the moderate treatments observed in *Ximenia caffra*, *Cassia abbreviata*, and *Commiphora glandulosa* (Table S1, Table S2, Figure 4a). Of these species, abundances of *Ximenia caffra* decreased on unburned treatments in juveniles, while the others did not change (Table S1,

**TABLE 2** Overview of all juvenile woody plant species recorded on the 160 sampled points (each with a 5 m radius = 78.54-m<sup>2</sup>) in the Satara land system and their abundance (number of individuals) with the standard error (se), and each species proportion (in %) of the entire species abundance in each year of sample year, ordered by family.

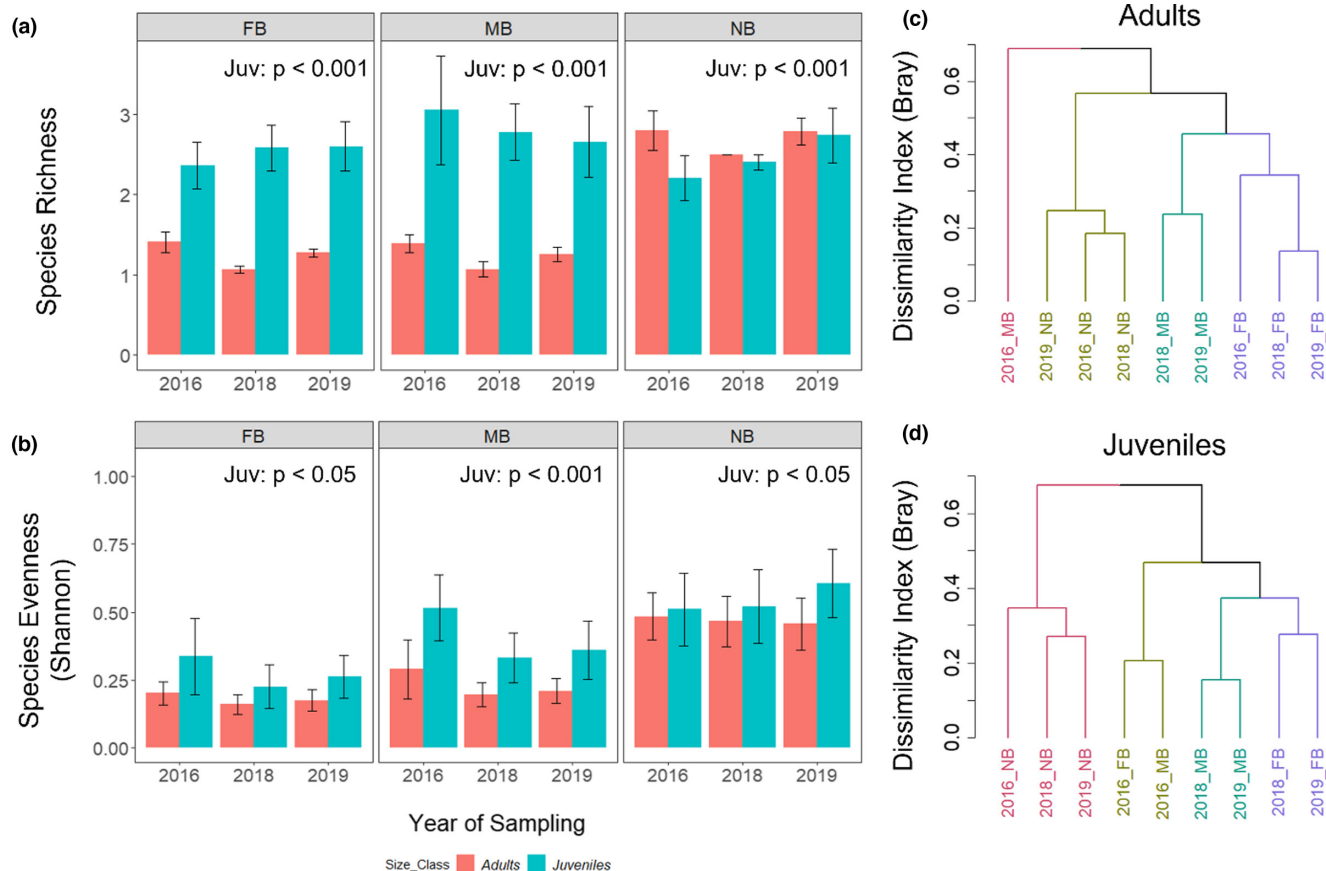
Family	Species	Juveniles								
		2016			2018			2019		
		abund	se	prop (%)	abund	se	prop (%)	abund	se	prop (%)
Anacardiaceae	<i>Lannea schweinfurthii</i>	59	1.6	3.3	12	0.2	0.6	12	0.2	0.5
	<i>Ozoroa engleri</i>	NA	NA	NA	6	0.1	0.3	4	0.1	0.2
	<i>Rhus gueinzii</i>	12	0.2	0.4	1	0	0.1	NA	NA	NA
	<i>Sclerocarya birrea</i>	99	0.6	2.9	19	0.1	1.8	29	0.3	1.3
Boraginaceae	<i>Ehretia amoena</i>	NA	NA	NA	NA	NA	NA	245	2.2	11.2
Burseraceae	<i>Commiphora africana</i>	33	0.7	1	79	1	4.1	90	1.1	4.1
	<i>Commiphora glandulosa</i>	NA	NA	NA	4	0.1	0.2	NA	NA	NA
Celastraceae	<i>Gymnosporia senegalensis</i>	NA	NA	NA	84	0.8	4.4	51	0.6	2.3
Combretaceae	<i>Combretum apiculatum</i>	203	2	6	49	0.3	2.6	69	0.4	3.2
	<i>Combretum hereroense</i>	159	1.7	4.7	9	0.1	0.5	8	0.1	0.4
	<i>Combretum imberbe</i>	116	1.1	3.4	15	0.2	0.8	5	0.1	0.2
	<i>Combretum molle</i>	NA	NA	NA	16	0.2	0.8	NA	NA	NA
	<i>Combretum mossambicense</i>	NA	NA	NA	54	0.6	2.8	119	1.4	5.4
	<i>Terminalia prunioides</i>	23	0.2	0.7	NA	NA	NA	11	0.3	0.5
Ebenaceae	<i>Euclea divinorum</i>	2	0.1	0.1	1	0	0.1	NA	NA	NA
	<i>Euclea natalensis</i>	NA	NA	NA	1	0	0.1	NA	NA	NA
Fabaceae	<i>Acacia exuvialis</i>	449	2.1	13.3	240	1.5	12.6	201	1.3	9.2
	<i>Acacia nigrescens</i>	286	1.1	8.5	91	0.4	4.8	102	0.5	4.7
	<i>Acacia tortilis</i>	46	0.4	1.4	10	0.1	0.5	3	0.1	0.1
	<i>Cassia abbreviata</i>	59	1	1.7	6	0.1	0.3	7	0.1	0.3
	<i>Dalbergia melanoxylon</i>	NA	NA	NA	2	0.1	0.1	21	0.4	1
	<i>Dichrostachys cinerea</i>	1439	6.9	42.6	1051	3.9	55.1	998	4.1	45.7
	<i>Ormocarpum trichocarpum</i>	NA	NA	NA	82	0.7	4.3	97	0.8	4.4
	<i>Peltophorum africanum</i>	332	2.1	9.8	34	1	1.8	28	0.4	1.3
	<i>Philenoptera violacea</i>	4	0.1	0.2	33	0.4	1.7	31	0.4	1.4
Malvaceae	<i>Grewia bicolor</i>	NA	NA	NA	NA	NA	NA	14	0.2	0.6
Olacaceae	<i>Ximenia caffra</i>	NA	NA	NA	NA	NA	NA	23	0.3	1.1
Phyllanthaceae	<i>Flueggea virosa</i>	NA	NA	NA	NA	NA	NA	13	0.1	0.6
Rhamnaceae	<i>Ziziphus mucronata</i>	57	0.8	1.7	10	0.1	0.5	4	0.1	0.2
	All species	3378	22.7	101.7	1909	12	100.9	2185	15.6	99.9

Note: Absence of species per year is marked with NA, thereby indicating when a species appeared or disappeared.

Table S3, Figure 4b). In contrast, the highest decrease in adults on unburned treatments was observed in *Combretum mossambicense*, followed by *Peltophorum africanum* (Table S1, Table S2, Figure 4a), of which only *C. mossambicense* decreased in juveniles (Table S1, Table S3, Figure 4b). Further decreases in juvenile abundances on unburned treatments were observed in *Terminalia prunioides*, *Combretum mossambicense*, *Combretum hereroense*, *Rhus gueinzii*, *Dalbergia melanoxylon*, and *Ximenia caffra* (Table S1, Table S3, Figure 4b).

On frequently burned plots relative to moderately burned plots, adult abundances increased highest in *Cassia abbreviata*, followed by *Commiphora glandulosa* and *Grewia bicolor* (Table S1, Table S2, Figure 4a). Because *C. glandulosa* decreased in 2019, but increased on frequently and unburned treatments, abundances must have overall decreased on moderately burned plots. In juveniles, neither of these species' abundances changed significant on frequently burned plots (Table S1, Table S3, Figure 4a). The most significant decrease in adult abundances on frequently burned plots





**FIGURE 3** Change in mean species richness (a) and species evenness (b) of woody plant species between fire treatments (frequently burned/grazed plots (FB), moderately burned/grazed plots (MB), and unburnt/ungrazed 0.25-ha plots/subplots (NB)) and years (2016, 2018, and 2019) in the Satara land system. Red bars and blue bars represent the mean relative species richness (a) and mean relative species evenness (b) per year of adults (red) and juveniles (blue) of woody plant species, respectively. Significant changes in species richness and evenness are indicated by the p-values which were determined in an ANOVA test. The species evenness is based on the Shannon index. Panels c and d show dissimilarities in species communities for adults (c) and juveniles (d) between fire treatments each year of sampling. Dissimilarities are defined by species richness and species' abundance and are expressed by the Bray dissimilarity index (0 = equal species richness and abundance, 1 = complete turnover)

was observed in *Lanea schweinfurthii* and *Ozoroa engleri* (Table S1, Table S2, Figure 4a), where neither of these species responded in juveniles (Table S1, Table S2, Figure 4a).

The only species that exhibited significant increases as juveniles on the frequently burned treatments were *Combretum molle* and *Euclea natalensis* (Table S1, Table S3, Figure 4a). On the frequently burned treatments, in juveniles, the most significant decrease was observed in *Commiphora glandulosa* (Table S1, Table S3, Figure 4b). None of these species were among the dominant species in the adult size class.

### 3.5 | Redundancy analysis

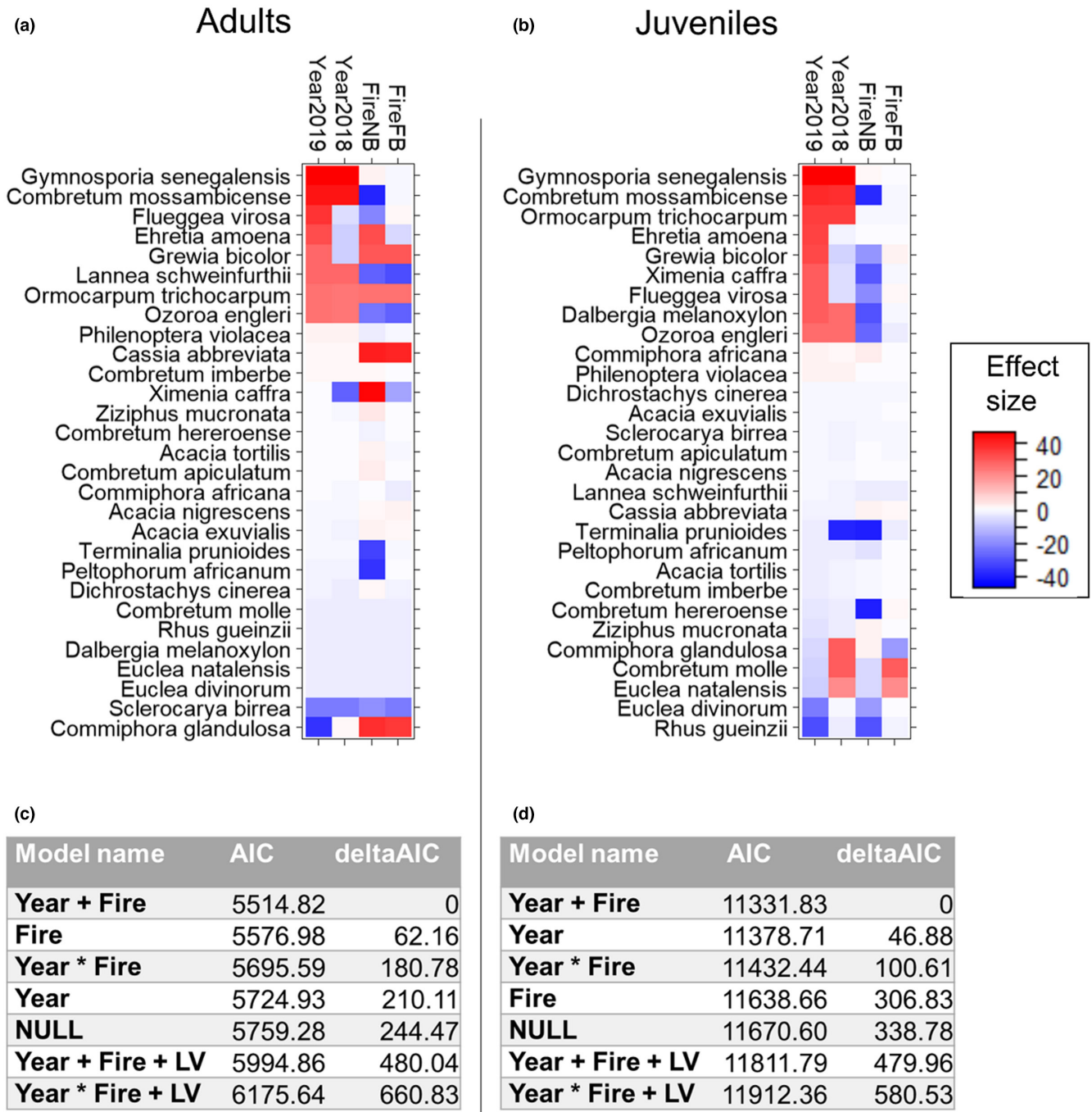
Using a RDA, the axes represented the variance of adult and juvenile species communities within each year of sampling, and between fire treatments. For both adults and juveniles, year of sampling and fire treatments were highly significant in predicting variation in species abundances ( $p < .01$ ) and could explain about ¼ of data variance.

For adults, RDA1 explained 53.7% of data variance, and RDA2 explained 20.6% of data variance. Variation was highest in abundances of *Dichrostachys cinerea* across years, especially on unburned treatments, followed by *Combretum apiculatum* with highest variation on moderately and unburned treatments. All other species varied little in abundance as they are located in the center of the RDA plot (Figure 5).

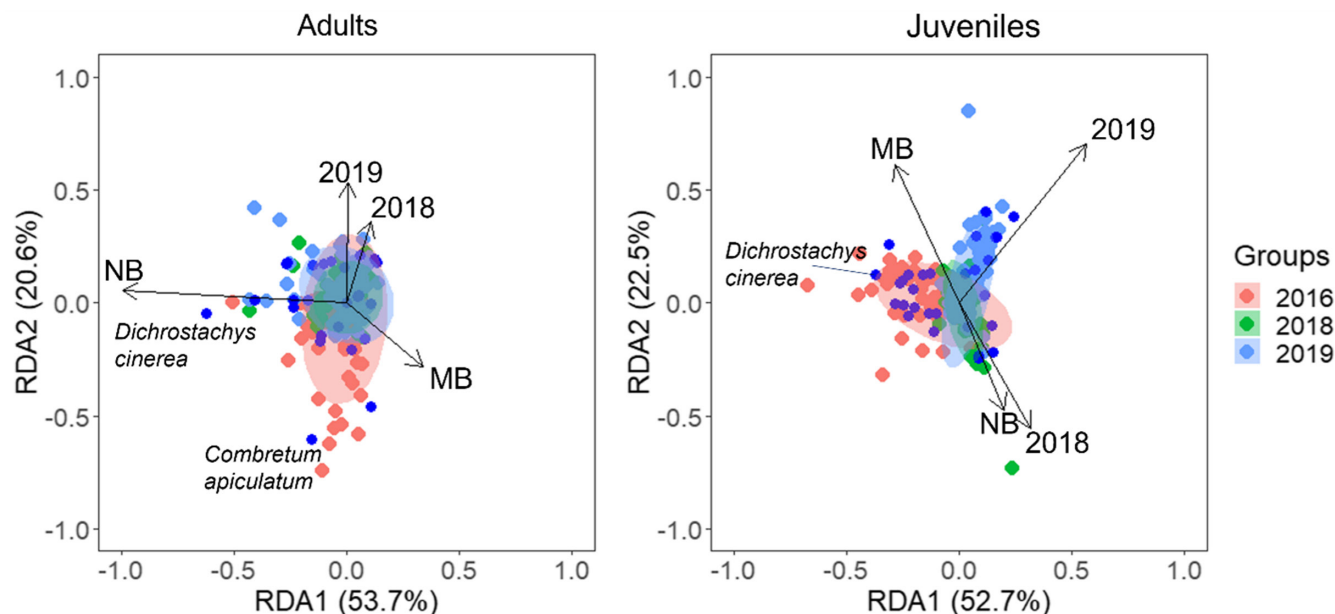
For juveniles, the RDA supported that abundances varied more strongly between years than between fire treatments, confirming an increase in abundances of multiple species in 2018 and 2019 relative to 2016 (Figure 5). The RDA1 explained 52.7% of data variation, and the RDA2 explained 22.5% of data variation. Similar to adults, most species co-exist, as they are centered on the RDA plot (Figure 5).

## 4 | DISCUSSION

Adult and juvenile community composition and abundance were impacted by drought and fire although additively rather than



**FIGURE 4** Effect sizes (ES) representing the change in abundance per woody species proportional to entire community and in relation to 2016 and moderately burned treatments (a, b), estimated with multivariate generalized linear latent variable models (GLLVM) models that used year and fire as predictor variables and were evaluated with Akaike information criterion (AIC) tests (c, d). Thus, increasing ESs show increasing abundances when compared to 2016, and FB respectively. Red fields show increases, blue fields depict decreases in abundance. Plots are ordered from increasing (high ESs) to decreasing abundances (low ESs) in reference to the year 2019. Tables (c, d) show an overview of GLLVM test results from the AIC for optimal model selection for adults (c) and juveniles (d). The best model fit is indicated by the lowest AIC value, or delta AIC = 0, respectively. The response variables used in the GLMs were adult and juvenile abundances (number of individuals per species in each sampling point) respectively. Predictor variables were year of sampling (equal to cumulative rainfall values of two years prior to year of sampling); fire treatments applied to sampling point (frequently burned (FB), moderate burn (MB), and no burn (NB)), and one latent variable (LV) = latent variable accounting for factor of herbivory. Random effects of nested samples were assumed across sampled years and included in the models



**FIGURE 5** Redundancy analysis (RDA) conducted on species abundances per site in relation to the significant predictor variable (fire, year) for adults and juveniles. The plots represent how species communities are composed within the Satara land system along environmental predictors, and how much data variance in species abundances can be explained by the year and fire treatments. The first redundant component explained 53.7% of the data variation in adults and 52.7% in juveniles respectively. Colored points represent sampled sites per year for adults (red = 2016; green = 2018; light blue = 2019). Ellipses comprise the average extent of adult and juvenile abundances measured on all sites per year and per fire treatments within data variance. Black arrows depict the direction of each predictor variable in reference to frequently burned treatments and the year 2016 respectively. The further two species are apart on the plot, the less likely they are to co-exist in the same area

via an interaction, likely because of the sequence of drought and fire. Post-drought, there was substantial loss of adult stems of *Dichrostachys cinerea*, *Acacia nigrescens*, and *Combretum apiculatum*—approximately 43% of total adult plants from 2016 to 2019. However, our sampling methodology could not distinguish mortality and top-kill because woody plants were tracked per plot rather than at an individual level. Hence, we could not differentiate adults that returned to the juvenile size classes. For example, several juvenile *D. cinerea* were resprouting at stem bases (Figure S4). *Acacia nigrescens* and *Dichrostachys cinerea* showed reductions in both adult and juvenile abundances, suggesting drought death. However, changes in abundance did not significantly alter overall adult community composition (Figure 2, Figure 4a), or species evenness on the no burn treatment across the fire treatments (Figure 3b). The reduction in point spread across RDA space (Figure 5) may have been driven by the decrease in the dominant encroaching and root-suckering *Dichrostachys cinerea* (Figure 2) and suggested that community composition post-drought decreased in homogeneity. In comparison, the juvenile community was more dynamic. Juvenile diversity, species richness, and evenness increased post-drought in the no burn treatments, while species evenness decreased on moderately and frequently burned treatments (Figure 3). The recording of six new species in 2019 suggests establishment and recruitment of new species were facilitated by the drought via changes in available niche space due to reduced competition from grass (February et al., 2013, Morrison

et al., 2019). Post-drought, both *Gymnosporia senegalensis* and *Combretum mossambicense* had the largest positive increase in effect size in both adult and juvenile abundances, suggesting both species benefited from the altered environmental conditions. Similar results in effect sizes were observed when bootstrapping data was used in the modeling approach instead of an offset term to account for uneven sample sizes. However, the model run with bootstrapped data did not include *Ximenaia caffra* (Figure S3), showing that rare species may actually be missed instead of accounted for when using bootstrapping when rare species are present in a population. While some of our observed compositional changes may be due to exact relocation of circular points, all points were marked with metal rods as there was known animal activity at these sites. However, in this case, we would expect random variation in numbers, rather than the clearly directional patterns observed in the dataset. Furthermore, sampling in 2017, the year immediately after the drought, may have revealed further insight on when changes in woody communities took place.

The variable demographic patterns and species-specific responses likely reflect a diversity of life-history strategies coexisting within savanna ecosystems. For example, there was relatively rapid recovery by *Combretum apiculatum* to adult size classes in contrast with the persistent reduction in adult numbers of *Acacia nigrescens*. These differences in recovery could be attributed to the palatability of *C. apiculatum*, which is preferred less by browsers than *A. nigrescens* because of its relatively dense and tough leaves (Lenfers

et al., 2017). Differences in species-specific growth rates that have been shown to be higher in *C. apiculatum*, and are controlled by root biomass accumulation and growth into deeper soil layers to access water, may also be responsible for differences in recovery between *C. apiculatum* and *A. nigrescens*, while *D. cinerea* being a species with relatively shallow rooting (Tomlinson et al., 2019, Tomlinson et al., 2012, Zhou et al., 2020). In fact, species with access to deep water via tap roots as adults are likely to have higher survival and more likely to recover from drought. However, adult abundances of *Sclerocarya birrea* decreased from 2016 to 2019, even though this species is known for its deep-rooting systems (Mariod and Abdelwahab, 2012) and therefore being relatively drought tolerant (Dzikiti et al., 2022). Drought resistance of *S. birrea* is largely driven by deep roots and available soil water rather than leaf-level resistance strategies (Dzikiti et al., 2022), it may be that soil water tables strongly varied locally, and *S. birrea* individuals succumbed to insufficient water availability. Another reason may be that random shifts in sampling points due to point relocation from animals have led to the observed decrease in *S. birrea* abundance. Furthermore, clayey basalt soils around Satara with low rooting permeability may also complicate deep-water access and thereby make woody plants more vulnerable to droughts via affecting physiological water potential (Case et al., 2020a, Fensham et al., 2015). In juveniles, abundances of three *Combretum* species were lower in the no burn treatments compared with the frequently burned treatments, suggesting these species are highly tolerant of fire, patterns that were found to be similar in the Niassa Reserve in Mozambique (Ribeiro et al., 2008). Especially, *C. mossambicense*, which appeared in 2018 growing in long singular stems with stalkless leaves out of soil cracks (Figure S4), increased on all moderately and frequently burned treatments in both the adult and juvenile size class. The appearance and increase in *C. mossambicense* suggest high stem-growth rates post-drought where individuals grew into the adult size class within just two years if fires maintained low grass density and the soil cracks provided adequate conditions for seed germination. In contrast, *Commiphora* species (*C. glandulosa* and *C. africana*) were found primarily in the no burn treatments, and as juveniles, suggesting positive recruitment benefits of long fire return intervals for these species (Charles-Dominique et al., 2015, Dantas and Pausas, 2013).

Post-drought, species richness increased by 29% in the juvenile woody community with the increase greatest on the no burn treatments (32%), and where species evenness increased by 10% (Figure 3b). However, on all frequently and moderately burned plots, there was a progression to higher species richness but less individuals per species, as abundances of all species found in 2016 decreased in 2018, and further decreased in 2019. Especially, the most abundant species *D. cinerea*, *Peltophorum africanum*, *Acacia nigrescens*, and *Acacia exuvialis* species decreased on all frequently and moderately burned plots from 2016 to 2019, which suggests that fire removed drought-weakened individuals which reduced tree density post-drought, while abundances remained stable on no burn plots. However, rare species were gained in 2018 and 2019 on frequently and moderately burned plots (i.e., *Combretum mossambicense*, *Ehretia*

*amoena*, and *Ximenia caffra*). This suggests that drought may create refuges for rare species in conjunction with fire by removing competitive individuals from other species and suppressing dense grass growth, which added higher functional diversity to a woody savanna population. The reduction in herbivore pressure that occurred at the overall landscape for several years after the drought (Donaldson et al., 2019) may have benefited the juvenile recruitment as several species that increased in abundance are considered highly preferred browse (e.g., *Ormocarpum trichocarpum* and *Ehretia amoena*) (Boon and Pooley, 2010, Burrows et al., 2018). As shown in the redundancy analysis (Figure 5), drought and fire explained about ¼ of variance in species abundances of adults and juveniles, which suggests that community composition is also structured by other environmental variables (e.g., herbivory) and species-specific traits.

Out of the new juvenile species recorded, seven appeared in 2018, of which one disappeared a year later, leaving six new species in 2019 that were from plant families not previously recorded at the study site (Table 2). These newly recruited species were *Ehretia amoena* (Boraginaceae), *Commiphora glandulosa* (Burseraceae), *Gymnosporia senegalensis* (Celastraceae), *Euclea natalensis* (Ebenaceae), *Grewia bicolor* (Malvaceae), *Ximenia caffra* (Olacaceae), and *Flueggea virosa* (Phyllanthaceae)—a high diversity of families. While an increase in species post-drought may lead to changes in succession and species composition, such gain of species can be ephemeral if resources are too scarce, competition with grasses is too high, or fires and herbivory remove juvenile plants (Archibald et al., 2021, Kraaij and Ward, 2006). While some individuals may have been suppressed by intense grazing and browsing before the drought and were therefore not visible (e.g., *Ormocarpum trichocarpum*), others are likely to be recruits which have either seedbanks that respond to drought by germination with post-drought rainfall (Figure S4c, Figure S4d) (Joubert et al., 2013, Tessema et al., 2017), or colonize post-drought via a diverse range of dispersal, fire-resistance, physiological, and anatomical functional traits. For example, *Flueggea virosa* is dispersed via insects and birds, while *Ximenia caffra*, *Gymnosporia senegalensis*, and *Grewia bicolor* regenerate by coppice or root suckers that can increase survival due to increased rooting area (Fern et al., 2014). From the newly recorded species in 2019, *X. caffra*, *E. amoena*, *G. senegalensis*, *E. natalensis*, *G. bicolor*, and *F. virosa* can grow in a wide range of habitats, that is, lowland savannas across sandy flats, river banks to higher rainfall areas close to forests (Fern, 2020, Fern et al., 2014), supposedly making them very adaptable to changing environmental conditions. Additionally, the dispersal of *F. virosa* via birds and insects, as well as the occurrence of species associated with termite mounds (e.g., *C. glandulosa*, *X. caffra*, and *G. bicolor*) (Van der Plas et al., 2013) suggests a link with animal-mediated dispersal. Of these woody species, different leaf phenologies have been recorded, as some are deciduous (e.g., *Ehretia amoena* and *Grewia bicolor*), while others are evergreen (e.g., *Gymnosporia senegalensis*) (Schmidt et al., 2002, Verdcourt, 1991), suggesting the new species likely encompass a diversity of life-history strategies to overcome drought.



When comparing our results with findings from other studies, we suggest that despite the short-term mortality and top-kill, many species are well adapted to drought in semi-arid savannas via diversity of species-specific traits found in both juvenile and adult life stages (February et al., 2013). Drought regulates the abundance of less resistant species such as *D. cinerea* where abundances declined by 30.7% in adults and 81.1% in juveniles in line with the ~45% found elsewhere in KNP (Case et al., 2020b, Case et al., 2019). Another study from the KNP in Pretoriuskop (mean annual rainfall of 737mm) found that recruitment into adult size classes was more likely during drought years (February et al., 2013). With predicted increases in droughts in tropical savannas and associated shifts in rainfall (Dai, 2013, Trenberth et al., 2014), diversity and abundance post-drought may increase in some areas, while others experience high levels of woody plant mortality (Case et al., 2019). A similar pattern of new species recruiting post-drought was previously observed in the Serengeti, Tanzania (mean annual rainfall ~600 to >1000mm) (Anderson et al., 2015), where recruitment was associated with soil factors such as soil bulk density. Overall, it becomes clear that local rainfall and soils combined with distinct herbivory and fire regimes have highly variable impacts on plant communities.

## 5 | CONCLUSION

Drought can reduce abundance of entire woody plant communities in adult and juvenile size classes. However, drought can have a positive impact on diversity, although such impact can vary relative to fire regime before drought, suggesting a diversity of species-specific life-history strategies to tolerate and proliferate with stress and disturbance. Post-drought rainfall may trigger seed production, dispersal, germination of seeds in long-term seedbanks, and the resprouting of the rootstocks of drought-adapted species, while deep-rooting species seem to recover best from drought. Moreover, post-drought reduction in browse pressure and fire frequency can enable palatable or fire-sensitive species to establish and recruit in landscapes where they are usually filtered out of the community by competition from grasses and disturbance. Drought and fire may thus both induce demographic bottlenecks and facilitate changes in community composition where the effects of either drought or fire on woody species are differentiated.

### AUTHOR CONTRIBUTIONS

SA, CL, and FT conceived the work. FT, EHM, and JED collected the data. FT analyzed the data. FT wrote the paper with inputs from CL, SA, JED, and CP.

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### CONFLICTS OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no conflicts of interest and no involvements that might raise the question of bias in the work reported or in the conclusions stated.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3ffb79m7> (Trotter et al. 2022).

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