



# Understanding the monodominance of *Acacia drepanolobium* in East African savannas: insights from demographic data

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## Abstract

**Key message** The high mortality and low recruitment of the myrmecophytic *Acacia drepanolobium* are not consistent with the demographic rates of monodominant species. The positive conspecific density dependence observed from the spatial analysis is consistent with the defensive benefits conferred by symbiotic ants to trees when they grow close to each other.

**Abstract** Patches of savanna dominated by *Acacia drepanolobium* occur throughout East Africa on nutrient-rich vertisols, also known as black cotton soils. We assessed the survival and recruitment for all freestanding trees with diameter at knee height (dkh)  $\geq 10$  mm in one of such mono-dominated patches (47 ha) at the Mpala Research Centre, Kenya, with the aim of identifying demographic traits that might explain the dominance of this species. Over a mean 6-year interval, mortality and recruitment rates in the habitat were 4.55%/year and 1.42%/year respectively, resulting in a net loss of 17.8% of the initial individuals. Of the 30 species recorded from the first census, 11 decreased in abundance, nine increased, and the remainder 10 did not change in abundance. The monodominant *A. drepanolobium* had a high mortality (4.69%/year), a low recruitment (1.31%/year), and a 19% population decline. There was no evidence of conspecific negative density dependence for this species. Rather, we found a statistically significant positive correlation between the number of conspecific neighbors and individual-level probability of survival, consistent with the “shared defense” benefits that symbiotic ant colonies occupying multiple trees can confer to these latter in a small neighborhood. Thus, mortality of *A. drepanolobium* was higher in areas where it occurred in lower densities, which resulted in an increase in the spatial aggregation of conspecifics. Mortality increased with dkh size classes and was mostly caused by elephants and stem-boring beetles. The demographic rates during the study period in theory are inconsistent with those of monodominant species. The protection against herbivory conferred by mutualistic ants associated with this species remains the most probable explanation of its dominance in this habitat.

**Keywords** *Acacia drepanolobium* · Mpala Research Centre · Monodominance · Mortality · Recruitment

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## Introduction

Tropical biomes are renowned for their high biological diversity, but often include areas dominated by a single species that can make up over 90% of the canopy trees (Hart et al. 1989; Connell and Lowman 1989) or up to 63–85% of the basal area (Henkel 2003; Makana et al. 2011). Such “monodominance” occurs in Neotropical (Nascimento et al. 1997; Marimon et al. 2001; Henkel 2003; Lopez and Kursar 2007; ter Steege et al. 2019) and Paleotropical (Hart et al. 1989; Read et al. 2000; Ibanez and Birnbaum 2014) forests as well as in savanna biomes (Bueno et al. 2014) even in the presence of large species pools that could potentially colonize those habitats. Both ecological and evolutionary mechanisms have been suggested to explain monodominance (Peh

et al. 2011) including mutualistic (e.g. ectomycorrhizal) associations that confer a competitive advantage to monodominant species (McGuire 2007; Corrales et al. 2016) and the adaptation to distinct soils (Kearsley et al. 2017; Nascimento et al. 2017).

In East African arid highlands, on heavy-clay soils, the whistling thorn acacia (*Acacia drepanolobium* Harms ex Y. Sjöstedt) forms monodominant patches, accounting for up to 98% of the individual trees (Young et al. 1997b; Goheen et al. 2004). This species is well known for its symbiotic relationship with four obligate ants (Madden and Young 1992; Young et al. 1997b; Palmer et al. 2010) that inhabit the cavities of modified swollen thorns and protect host trees by swarming, biting, or stinging intruding herbivores (Palmer et al. 2000; Goheen and Palmer 2010). These four mutually exclusive species of ants compete for host trees and vary in their defensive role (Young et al. 1997b; Palmer et al. 2000). Three of the four (*Crematogaster mimosae*, *Crematogaster nigriceps* and *Tetraponera penzigi*) nest exclusively within the swollen-thorn domatia while the competitive dominant *Crematogaster sjostedti* inhabits the stem cavities excavated by the long-horned beetles (Palmer et al. 2008). A single colony of ants may occupy one or multiple adjacent trees (Palmer 2004; Palmer et al. 2010). There is a high energetic cost associated to the maintenance of the ant symbionts that could be achieved only on rich soils (Stanton and Palmer 2011; Pringle et al. 2016). *A. drepanolobium* is one of the frequently eaten food plants for giraffes and black rhino (Young and Isbell 1991; Birkett 2002), both of which are not very sensitive to the symbiotic ants. In contrast, elephants seldom browse on *A. drepanolobium* adult trees when ants are present (Goheen and Palmer 2010), although their destructive effect on seedlings have been well established (Wahungu et al. 2011).

Tree cover in East African savannas is known to be highly dynamic and can undergo rapid fluctuations from dense woodlands to open grasslands and vice versa (Dublin et al. 1990). Although *A. drepanolobium* is a monodominant species with a useful symbiosis and strong habitat preferences, its local distribution is by no means stable. In parts of its distributional range, *A. drepanolobium* is perceived by pastoralists to be aggressively encroaching into rangelands, negatively affecting their structure and function (Terefe et al. 2011), while in others *A. drepanolobium* is displaced by the fire-resistant species *Euclea divinorum* (Wahungu et al. 2013). These two scenarios are possible under different fire/herbivores pressure regimes. The role of vertebrate herbivores and fire as important drivers of vegetation dynamics in the savannas is well documented (Holdo et al. 2009). Although most *A. drepanolobium* are only top-killed and coppice readily after fire, frequent fires can drastically reduce their canopy cover and their density (Okello et al. 2008), and favor the proliferation of more

fire-adapted species (Wahungu et al. 2013). Megaherbivores also exert significant top-down regulation of *A. drepanolobium* cover, and their increase has been associated with substantial decline in population of *A. drepanolobium* (Birkett 2002). Self-replacement of *A. drepanolobium* could occur if the increase in the population of grazers depletes the herbaceous layer, reducing competition between grasses and saplings (Riginos 2009; Porensky and Veblen 2012) or when the population of small-sized herbivores (such as steinbuck and Grant's gazelle) releases the browsing pressure on *A. drepanolobium* saplings (Maclean et al. 2011). Investigating the changes in composition and structure of *A. drepanolobium* monodominant stands is of uttermost importance in understanding how they fluctuate or persist through time.

In northern central Kenya, we established a 120-ha (2400 × 500 m) permanent plot (with the long axis oriented SW–NE) to study the long-term dynamics of a vegetation mosaic (Mutuku and Kenfack 2019). One side of the plot, the focus of this paper, is on black cotton soil and includes a low-density and sparsely distributed *A. drepanolobium* mono-dominated patch. The first complete census of the plot was done between 2011 and 2014. The recent re-census of the plot (2018 to 2020) provided data that could help understand the possible changes that occurred in this plant community and that can shed light into the dominance of *A. drepanolobium*. Here, we address the following questions:

### First

What are the main demographic changes in the black cotton soil habitat? We hypothesize that (1) as for other monodominant species, *A. drepanolobium* will exhibit low mortality and high recruitment rates, and hence will increase in relative abundance; (2) the most palatable species in the system (e.g. *Acacia mellifera*, *A. brevispica*, *Balanites aegyptiaca*, see also (Kartzinel and Pringle 2020)) under herbivore pressure, should decrease in abundance, while less palatable species (e.g. *Croton dichogamus*) should increase in abundance and encroach into the black cotton soil.

### Second

Were there any changes in the spatial pattern of *A. drepanolobium* and were the demographic rates spatially structured? *A. drepanolobium* in the first census was spatially aggregated at small distances (> 0.5 m). We hypothesize that non-random mortality and recruitment can both result in an increase in aggregation of this species (e.g. if they tend to die out of certain preferred and very specific areas) or a decrease in aggregation (if individuals too close to each other compete and die more).

### Third

What were the changes in the size distribution of *A. drepanolobium*? We hypothesize that if the dominance of *A. drepanolobium* represents a transition stage without stable self-replacement, small size diameter trees will experience higher mortality and its population will be shifting towards large size diameter classes.

## Methods

### Study site description

The Mpala plot is located at the Mpala Research Centre, in northern central Kenya, Laikipia County, about 43 km northeast of Nanyuki town. The vegetation of the area is a woody savanna dominated by Fabaceae of the genus *Acacia*. Wildlife is quite diverse, the most abundant of which are elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), plains zebra (*Equus quagga*), oryx (*Oryx Gazella beisa*), elands (*Tragelaphus oryx*), steinbucks (*Raphicerus campestris*). Between 1977 and 2016, wildlife increased noticeably by 7.5% in Laikipia county (Ogutu et al. 2016) and the Kenyan wildlife Service reported an increase of 12% of the elephant population within the Laikipia-Samburu-Marsabit ecosystems between 2012 and 2017 (see <http://www.kws.go.ke/>). In this system, large-scale fires have been increasingly suppressed since the 1960's, therefore, herbivores remain the dominant drivers of vegetation cover (Kimuyu et al. 2014). Rainfall is generally under 650 mm per year but highly variable, and mean temperature ranges between 12 and 24 °C (Augustine and McNaughton 2006; Ojwang et al. 2010). In 2016, Kenya experienced a strong La Niña event with low rainfall and high temperatures that started in June and peaked in November (Uhe et al. 2018). For example, total rainfall in the study area during this six-month period was 58% lower (142 mm) than the 16-years average rainfall (324 mm) over the same months. Details on the plot establishment and methods are provided elsewhere (Mutuku and Kenfack 2019). In summary, the plot traverses two main soil types, that support three clearly defined vegetation types growing side by side. The southwestern part of the plot lies almost entirely on black cotton soils, which transition gradually to the red friable sandy soils at the northern end. The black cotton soil habitat has the lowest diversity in the plot. The adjacent steep slopes on transition soils are the most diverse, dominated by *Croton dichogamus* and *Euclea divinorum*. The northern part of the plot on red sandy loams is dominated by several *Acacia* species. Here, we focus on the southwestern part of the plot on black cotton soil. This soil type has a high clay content and undergoes cycles of shrink-swell and cracking (DeCarlo and Caylor

2019), with low water content during the dry season, and is physically stressful and challenging to most tree species (Young et al. 1997a; Pringle et al. 2016). The black cotton area of the plot was inventoried between late 2011 and late 2013 and included 31,040 permanently marked trees with diameter at knee height (dkh)  $\geq 10$  mm, in 30 species. This area was re-censused between March 2018 and February 2019. It is on almost leveled terrain, with only 10 m of elevation change (Fig. S1) and supports a nearly monospecific vegetation dominated by *A. drepanolobium* but with individuals sparsely and almost uniformly distributed across the landscape (Fig. 1). The species is rare elsewhere in the plot and serves as a good indicator of the black cotton soil. In the absence of soil data, the black cotton soil was delineated using the relative abundance of *A. drepanolobium* in the first census. We considered all quadrats (20 × 20 m) with an *A. drepanolobium* dominance of 2/3 or more as belonging to the black cotton soil. A few quadrats with less than 2/3 of *A. drepanolobium* were also incorporated into our definition of the black cotton habitat if at least three of the adjacent quadrats were within the black cotton soil community. Ultimately, the black cotton soil as defined in the present study covered a continuous patch of 47.04 hectares (Fig. S1).

After completion of the enumeration of the first 50 hectares, we carried out a field survey to identify the main drivers of *A. drepanolobium* mortality in the black cotton soil habitat. The causes of mortality were assessed for a total of 1022 dead individuals of *A. drepanolobium* after a mean 507 days period. Based on visual damages (bark stripping, pollarding, and uprooting) and scars on the stem, each dead tree was assigned to one of four modes of tree death: elephant, elephant/insect, insects and unknown cause of mortality. Other factors of tree mortality such as wind throw or frost are almost absent in the area.



**Fig. 1** A view of the Mpala plot vegetation on black cotton soil, dominated by *Acacia drepanolobium*. The photograph was taken by David Kenfack

## Data analysis

### Calculation of demographic rates

We estimated annual rates of mortality, recruitment and population change using standard methods (Condit et al. 1999). Mortality rate ( $m$ ) was calculated as  $m = (\ln n_0 - \ln S_t)/t$ ; recruitment rate ( $r$ ) as  $r = (\ln n_t - \ln S_t)/t$ ; and the population change ( $\lambda$ ) as  $\lambda = (\ln n_t - \ln n_0)/t$ . Here,  $t$  is the time interval between the two censuses;  $n_0$  the population size during the first census;  $n_t$  the population size during the second census and  $S_t$  the number of survivors at the time of the second census.

### Spatial analysis

The aggregation of *A. drepanolobium* was calculated using the Besag's transformation of Ripley's K function. This technique calculates the average amount of conspecific individuals within a given distance  $r$  of any individual,  $L(r)$ . For a completely random point pattern (uniform Poisson), the expected value of  $L(r)$  is  $r$ . If  $L(r) > r$  the pattern is aggregated at that scale; if  $L(r) < r$  the pattern is regular (overdispersed) at that scale. Using  $L(r)$  we compared:

- aggregation of living individuals in 2011 and in 2018, to check whether there was an increase/decrease in the aggregation of *A. drepanolobium* at any given scale.
- aggregation of dead individuals in 2018 (relative to the living individuals in 2011), to check whether mortality was higher/lower than expected at certain scales.
- aggregation of recruits in 2018 (relative to the living individuals in 2011), to check whether recruitment was more/less intense than expected at certain scales.

In all cases, we used the Lest function in the spatstat R package (Baddeley et al. 2015), using "Ripley" correction and default values for all the other parameters.

### Conspecific density dependence

For each individual in the plot, we counted the number of conspecific individuals in a radius of 2 m. Then, we fitted one survival model for each species with a generalized linear logistic regression:  $\text{logit}(\text{survival}) = \alpha * \text{dkh} + \beta_1 * \log(\text{dkh}) + \beta_2 * [\text{number of conspecifics within 2 m}]$ . If  $\beta_2$  is significantly  $< 0$ , then individual survival is less likely when there are more conspecific neighbors, and thus negative density dependence exists. If  $\beta_2$  is significantly  $> 0$ , then individual survival is more likely when there are more conspecific neighbors. The latter could reflect a range of things, such as positive biotic interactions between conspecific individuals (for example protection by ants from nearby trees in the

case of *A. drepanolobium*), or the existence of strong niche filtering, where most of the individuals of a given species aggregate in certain areas where survival is higher, and tend to die anywhere else.

## Results

### Black cotton soil-wide turnover rates

The second census comprised 25,541 individuals with  $\text{dkh} \geq 10$  mm. During a 6.26-year mean interval, 7697 (24.8%) of the initial 31,051 trees died, at a rate of 4.55%/year. During the same period, 2187 (8.52% of the final tree population) individuals grew into the 10 mm dkh cutoff, at a rate of 1.42%/year, resulting in a net decline of 5524 individuals, at a rate of  $-3.13\%$ /year. There was also a net gain in species richness, with two species (*Hibiscus* sp. and *Psiadia punctulata*) lost, and five species (*Acacia etbaica*, *Canthium pseudosetiflorum*, *Maerua angolensis*, *Pyrostria phyllanthoidea* and *Turraea mombassana*) gained. Eleven species declined in abundance, nine increased in abundance while the remainder 10 species did not change in abundance (supplementary file 3).

Of the 15 most abundant species ( $\geq 20$  individuals in 2018) in the plot, *Acacia nilotica* had the highest mortality (37.1%), followed by *A. drepanolobium* (25.4%) and *Cadaba farinosa* (23.5%). At the other end of the spectrum, the lowest mortality observed was 0.00% for *Euclea divinorum* and 2.44% for *Boscia angustifolia* (Table 1). Among these 15 most abundant species, half of the species had a net population increase with the highest increase recorded for *Rhamnus staddo* (180%) and *Boscia angustifolia* (117%), while the remaining half suffered a net population decline with the greatest loss ( $-28.6\%$ ) observed for *Acacia nilotica*. There was only one strictly non-palatable species, *Croton dichogamus* which had a 25% net increase in abundance between the two censuses. The remaining species, all palatable, had an average 23.8% increase in abundance.

### Population structure and demography of *Acacia drepanolobium*

The diameter distribution of *A. drepanolobium* in both censuses does not show the classic reverse J pattern that is indicative of a population in constant regeneration. The left-skewed bell-shaped diameter distribution (Fig. 2a) indicates a deficit in young individuals.

Survival of *A. drepanolobium* between 2011 and 2018 was 74.6%. In total, 7488 (25.4%) individuals of this species died during this period, at a rate of 4.69% per year. The mortality rate was lower (3.53%/y) for small size diameter trees ( $\text{dkh} < 20$  mm) and increased gradually to over



**Table 1** Demographic rates of the 15 most abundant species in the Mpala black cotton soil habitat

Species	N1	N2	<i>D</i>	<i>R</i>	<i>R</i> rate	<i>D</i> rate	PC rate	<i>S</i> (%)	NC (%)	RAC (%)
All	31,040	25,516	7699	2175	0.014	0.046	−0.031	75.2	−17.8	−
<i>Acacia drepanolobium</i>	29,460	23,850	7488	1878	0.013	0.047	−0.034	74.6	−19.04	−1.44
<i>Acacia mellifera</i>	779	779	103	103	0.022	0.022	0.000	86.8	0	0.54
<i>Balanites aegyptiaca</i>	172	177	17	22	0.021	0.017	0.005	90.1	2.91	0.14
<i>Boscia angustifolia</i>	41	89	1	49	0.126	0.004	0.122	97.6	117.07	0.22
<i>Carissa spinarum</i>	94	89	8	3	0.005	0.014	−0.009	91.5	−5.32	0.05
<i>Rhus natalensis</i>	90	82	10	2	0.004	0.019	−0.015	88.9	−8.89	0.03
<i>Euclea divinorum</i>	42	75	0	33	0.091	0.000	0.091	100.0	78.57	0.15
<i>Scutia myrtina</i>	51	53	4	6	0.019	0.013	0.006	92.2	3.92	0.05
<i>Acacia nilotica</i>	70	50	26	6	0.020	0.073	−0.053	62.9	−28.57	−0.03
<i>Cadaba farinosa</i>	51	47	12	8	0.031	0.044	−0.013	76.5	−7.84	0.02
<i>Acacia gerrardii</i>	46	40	10	4	0.016	0.038	−0.022	78.3	−13.04	0.01
<i>Croton dichogamus</i>	28	35	3	10	0.053	0.018	0.035	89.3	25	0.05
<i>Grewia kakothamnos</i>	31	33	3	5	0.026	0.016	0.010	90.3	6.45	0.03
<i>Acacia brevispica</i>	22	28	4	10	0.070	0.032	0.038	81.8	27.27	0.04
<i>Rhamnus staddo</i>	10	28	1	19	0.177	0.016	0.161	90.0	180	0.08

N1, number of individuals in 2011; N2, number of individuals in 2018; *D*, number of dead individuals between the two censuses; *R*, number of recruits; PC, population change; *S*, Survival; NC, net change; RAC, relative abundance change

11%/y for the largest trees (dkh > 130 mm) (Fig. 2b). Only 7.87% of the 2018 population of *A. drepanolobium* (1878 individuals) were recruits, resulting from a low recruitment rate of 1.31%/year. Hence, there was an important net population decline of −19% (−5610 individuals) at a rate of −3.35%/year. Recruitment rate was lowest (2.59%/y) into the 10–20 mm dkh class and increased gradually to 41.3% for the 140–150 mm dkh class, then decreased to 17%/y for larger trees. The rate of transition was almost constant across dkh classes, with the highest transitions (~10%) recorded for the 90–100 and 120–130 dkh classes. (Fig. 2b).

The relative dominance of *A. drepanolobium* dropped from 94.9 to 93.5% of the total individuals. The population decline affected mostly small size diameter classes (< 50 mm) (Fig. 2a). The larger size classes (> 50 mm) instead increased in abundance (Fig. 2b). Over 5% (2722 individuals) of the individuals from the first census got broken below the initial point of measurement and could not be re-measured during the second census, but coppiced and remained alive. Trees with dkh < 20 mm were the most affected by such breakage, with over 23.5% of the stems broken below the knee height (Fig. 2b).

### Causes of *A. drepanolobium* mortality

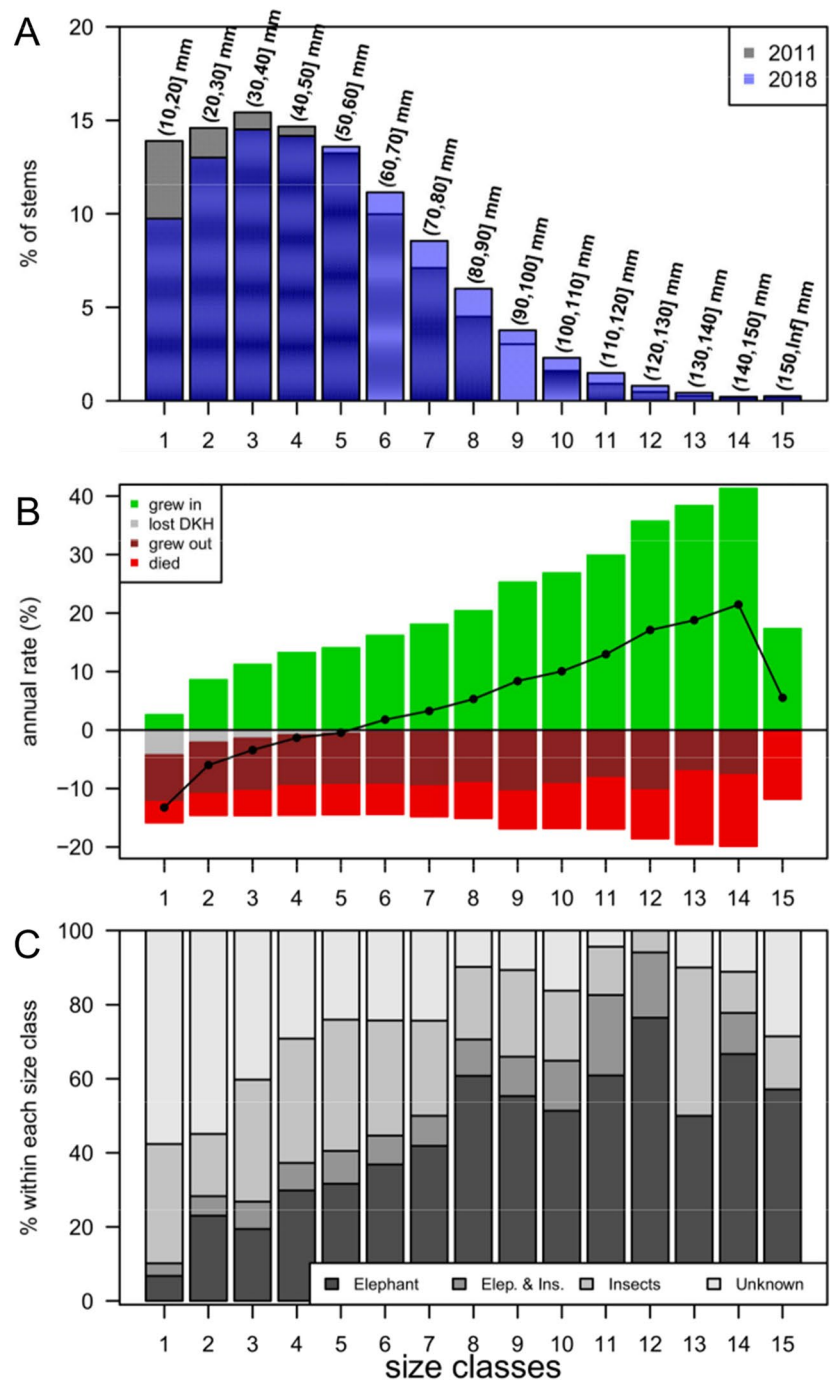
Elephants were identified as the main cause of mortality (34%), followed by damage by stem-boring beetles (Cerambycidae) (28%) and the combined effects of elephants and insects (8.12%). Thirty percent of tree death could not be attributed to any clear cause (Fig. 2c). Mortality

by elephants increased with dkh and was highest in the 120–130 mm dkh class. Mortality by insects was more prevalent in small dkh size classes (< 80 mm dkh). The cause of mortality for most small-sized trees was unknown, with most of them simply missing during the survey (Fig. 2c).

### Spatial patterns of *A. drepanolobium* and density dependence on black cotton soil

*Acacia drepanolobium* was obviously very aggregated at any spatial scale (Fig. 3a), a trend that is already apparent in a visual examination of its distribution map in the studied black cotton soil (Fig. S2). From 2011 to 2018, there was an increase in aggregation at all scales considered, but especially at about 2 m (Fig. 3b), which is consistent with the lack of negative density dependence for this species. In fact, *A. drepanolobium* was the only species for which we found a statistically significant positive correlation between the number of conspecific neighbors and individual-level probability of survival (Fig. 4). Mortality was also spatially aggregated, but only to distances below 35 m, while recruitment was spatially aggregated at all scales, but more so at distances below 15 m (Fig. 3a). The demographic rates of *A. drepanolobium* varied spatially across the black cotton habitat. Areas with high mortality were concentrated towards the transition zone, whereas those of high recruitment occurred roughly in areas where *A. drepanolobium* occurred in lower densities (Fig. 3c, Fig. S2).

**Fig. 2** Size distribution (a), demographic rates per size class (b) and causes of mortality (c) of *Acacia drepanolobium*. Grew in = individuals of the dkh size class that transitioned from the lower dkh size class; grew out = individuals of the dkh size class that transitioned to the higher dkh size class; died = individuals of the dkh class that died; lost dkh = individuals of the dkh size class that were top-killed, but coppiced and remained alive. Elephant = elephant induced mortality; Elep. & Ins = Elephant and insects induced mortality; insects = insects induced mortality; unknown = unknown cause of mortality. The line in b is the net population change for the size classes. The size classes (1–15) are the same in the three panels and aligned across them; the corresponding extents of each size class (in mm) are shown in panel A

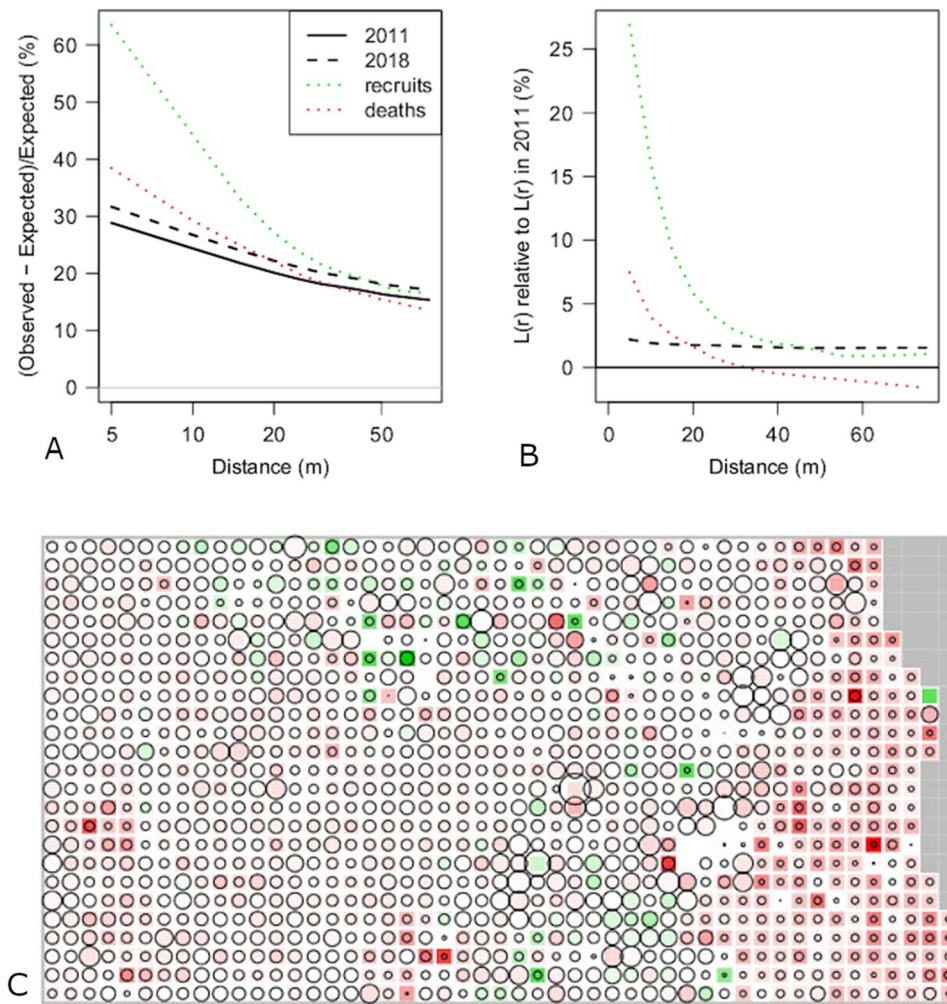


## Discussion & conclusion

### Demography of woody savanna species on black cotton soil

The tree population of the Mpala plot on black cotton soil is quite dynamic. The mortality rate of the entire tree community (4.68%/year) was not only higher than in most forest ecosystems with comparable data (Condit et al. 1999; Makana et al. 2011; Ostertag et al. 2014) but also higher than

in other savanna ecosystems (Vanak et al. 2012; Morrison et al. 2016). Half of the species, including the non-palatable species (*Croton dichogamus*), increased in abundance, particularly towards the transition zone and mostly under *Acacia mellifera* thickets (based on field observations). Indeed, selective browsing by megaherbivores can contribute to the increase in the relative abundance of unpalatable species (Strauss and Packer 2015). The recruitment rate of the entire community of 1.7%/year was comparable to similar savanna ecosystems (Wahungu et al. 2011), as well as other



**Fig. 3** Changes in *Acacia drepanolobium* spatial pattern and spatial distribution of annual rates of population change in the Mpala plot black cotton soil habitat, between the 2011 and 2018 censuses. **a** Aggregation of individuals in both censuses (black lines), aggregation of dead individuals (red line) and aggregation of recruits (green line); these are presented as deviations from the expected, i.e.  $(L(r) - r)/r$ , being  $r$  the distance in m as in the  $x$  axis. **b** Aggregation of living individuals (black lines), aggregation of dead individuals (red line), and aggregation of recruits (green line); these are presented relative to the aggregation of living individuals in the first census, i.e.  $L(r)/$

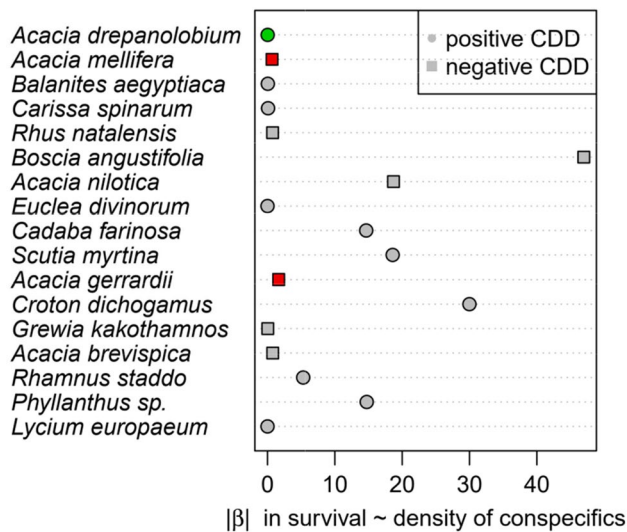
$[L(r)$  of living trees in 2011] (that is why the solid black line corresponding to 2011 is perfectly horizontal). **c** Map of the black cotton soil habitat delineated from the first 50 hectares of the Mpala 120-ha permanent plot. The circles depict the mean diameter of all *Acacia drepanolobium* within the  $20 \times 20$ -m quadrats in the black cotton habitat. The gradient in color intensity from red to green represents the gradient from negative population changes (i.e. high mortality and low recruitment) to positive population changes (i.e. high recruitment and low mortality)

forest ecosystems (Bunyavejchewin 1999; Marques et al. 2009; Shen et al. 2013). Overall, there was a 17% decline in tree density, attributable to herbivory and perhaps equally importantly, to the extended drought that occurred in central and northern Kenya during the study period. Indeed, in 2016, Kenya experienced a strong La Niña event (Uhe et al. 2018). Such a climatic event has been evoked as one of the main drivers of tree mortality in these savannas, which can directly translate into the decrease in tree density (Case et al. 2019). Despite the important decline in tree density, the relative abundance of most species remained relatively unchanged, with the greatest increase recorded for

*Acacia mellifera* (+0.54%) and the greatest decrease for *A. drepanolobium* (−1.44%).

### Underlying causes of the high mortality of *Acacia drepanolobium*

*A. drepanolobium* had high mortality (> 3.5%/year) in all diameter size classes. Elephants and stem-boring beetles were identified as the main causes of this high mortality. Elephant damages were common among individuals with a height of 2 m and above. Prior investigations within the same study area showed that, during a 12-month period in a



**Fig. 4** Results from the survival models linking survival of each common species with stem size and the number of conspecifics within a 2 m radius. The  $\beta$  parameter reflects the strength and direction of the relationship. If the  $\beta$  parameter is positive, the survival of that species increases with a higher density of nearby conspecifics: positive conspecific density dependence (positive CDD), indicated by circles. If the  $\beta$  parameter is negative, the survival of that species decreases with higher densities of nearby conspecifics: negative conspecific density dependence (negative CDD), indicated by squares. Statistically significant results are indicated by red squares (negative CDD) or green circles (positive CDD). Non-significant results are shown in gray

fire-free enclosure, elephants were responsible for the loss of 40% of *A. drepanolobium* trees (Birkett and Stevens-Wood 2005). Stem-boring insects were identified as the second known cause of mortality. It is well known that the stems of *A. drepanolobium* (up to 16% of the host plants) are often damaged by the larvae of the long-horned beetles (Palmer et al. 2008) and other insects that makes them vulnerable to breakage and can lead to increased mortality (Berryman et al. 1985). Finally, the causes of mortality were unknown for a large proportion of dead trees. Among these, there were 270 (26%) standing dead trees that could be assumed to be killed by drought. Indeed, in a nearby enclosure experiment, drought was estimated to be responsible for 27% of *A. drepanolobium* mortality (Birkett and Stevens-Wood 2005). Mortality was spatially aggregated, with areas of high density experiencing lower mortality. These areas may represent the “preferred niche” of *A. drepanolobium* and may overlap with areas with higher soil moisture (Coppock 1994; Tefera and Mlambo 2010), or nutrient-rich areas that affect positively the density, the growth, and the fruiting success of *A. drepanolobium* such as termite mounds (Palmer 2003; Brody et al. 2010) and glades (Donihue et al. 2013). This result is consistent with the observed conspecific positive density dependence in the survival of *A. drepanolobium* (Fig. 4).

In other words, the survival of *A. drepanolobium* is greater in the vicinity of conspecifics which is consistent with the defensive benefits conferred by symbiotic ants to trees when they grow close to each other.

### Underlying possible causes of the low recruitment of *Acacia drepanolobium*

The recruitment of *A. drepanolobium* was low and could not compensate for the high mortality, a result that is consistent with findings of a prior study in a similar ecosystem that reported a low survival of seedlings (Wahungu et al. 2011). In the study area, this species flowers and produces pods and seeds abundantly (Martins 2013). The seeds are not recalcitrant and do not require any pre-treatment or fire to germinate (Okello and Young 2000). Yet, the Mpala stand is not regenerating well and seems to be shifting towards large size diameter individuals. Current factors contributing to the low recruitment of *A. drepanolobium* may include seed predation and seedling herbivory. Prior research has shown that bruchid beetles heavily infest *A. drepanolobium* seeds, with severe negative effects on seed germination (Coe and Coe 1987; Okello and Young 2000; Martins 2013). Once they germinate, most seedlings (up to 40% with height < 0.5 m) of *A. drepanolobium* lack domatia (Young et al. 1997b), and, therefore, are not protected by mutualistic ants against herbivores, which makes them vulnerable to herbivory. Indeed, invertebrate herbivores (grasshoppers, leafhoppers, ants, and beetles) and small-bodied herbivores inflict severe damages to *A. drepanolobium* seedlings and saplings, which in turn can have a pronounced effect on their survival and hamper the recruitment of this species (Shaw et al. 2002; Augustine and McNaughton 2004; Sankaran et al. 2013; Wahungu et al. 2011). However, it has been shown that small *A. drepanolobium* trees (even those lacking domatia), if they have nectaries on leaves, can benefit from the protection of ants patrolling from larger ant colonies on nearby large trees. This could explain the observed positive density dependence in the survival of *A. drepanolobium* (Fig. 4).

### Demographic rates versus dominance *Acacia drepanolobium*

The high mortality and low recruitment rates of *A. drepanolobium* are not consistent with those of monodominant species (Lopez and Kursar 2007; Makana et al. 2011). One of the most plausible explanations for the occurrence of the species-poor *A. drepanolobium* monodominant stand adjacent to the species-rich community is the substrate. Indeed it has been suggested that monodominance (especially in Amazonia) may be primarily associated with edaphic factors (ter Steege et al. 2019). The black cotton soil is physically stressful and challenging to most tree



species (Young et al. 1997a; Pringle et al. 2016). Although *A. drepanolobium* seems to be the only species to thrive in this soil type, its dominance here may not be entirely explained by its competitive superiority, or the non-ability of other plant species to establish in this environment. Large herbivores interact with soil types to promote and maintain the edaphic variation in plant community composition in this study system (Pringle et al. 2016). *A. drepanolobium* can actually germinate and establish in different soil types (Okello and Young 2000) such as nutrient-poor sandy red soils, but their survival and growth in this environment is strongly suppressed by browsers because in these nutrient-poor soils *A. drepanolobium* cannot marshal enough nutrients to pay its only insurance to survival (the symbiotic ants) (Pringle et al. 2016; Palmer et al. 2017). Other plant species such as *Acacia brevispica* can establish in the black cotton soil, but the combination of the stress imposed by the soil and the browsing pressure prevent most individuals of this species from attaining maturity (Pringle et al. 2016). In fact, excluding large mammals in an adjacent black-cotton soil resulted in the increase in the abundance of several non-myrmecophytes, including *A. brevispica* (Goheen and Palmer 2010). Hence herbivory seems to play an important role in regulating the plant species composition in black cotton. The intense browsing pressure in this system confines non-myrmecophytes to low densities (1–16 individuals/ha), while the deterrence by symbiotic ants on megaherbivores limits the browsing pressure on *A. drepanolobium*, which in turn maintains its dominance (Goheen and Palmer 2010). Indeed, it has been suggested that *A. drepanolobium* mono-dominated stands may be an indicator of rangelands that have been subjected to intense grazing and browsing pressure over a long period of time (Coppock 1994; Tefera et al. 2007).

### Underlying causes of the stand structure of *A. drepanolobium*

The diameter distribution of *A. drepanolobium* in Mpala did not show the classic reverse J pattern that is indicative of a population in constant regeneration, but rather, there was a deficiency in saplings. Such a stand structure can be reflective of a demographic imbalance due to the impact of current or past disturbances but, can also be the mark of its specific population growth model (Engone Obiang et al. 2014). This stand structure may be reflective of a population dominated by a single or few cohorts of individuals that recruited more or less at the same time in response to past rare or extreme events (Walker 1993). Such episodic recruitments are not uncommon in the genus *Acacia*, especially in arid zones (Wiegand et al. 2004, 2005; Seymour 2008). Episodic recruitments are often attributed to drastic changes in abiotic factors such as rainfall, drought, and fires.

Although the low recruitment and high mortality of *A. drepanolobium* in Mpala raise concern about its long-term dominance, there was only a 1.44% decline in its relative abundance, which suggest that the decline in tree density affected the entire tree community. These demographic rates may vary significantly through time. The 6-year study interval may not reflect accurately the long-term dynamics of this species. Our study period captured the effect of an unexpected event, the 2016 La Niña, but also the changes in the biotic environment such as the increase in elephant population (Ogutu et al. 2016) and the invasion by the big-headed ants (*Pheidole megacephala*) that extirpates the most aggressive symbiotic ants from their trees (Riginos et al. 2015) all of which lead, to an increase in tree mortality. However, our results and prior research in the system seem to indicate that the low density of *A. drepanolobium* in the black cotton habitat may result from the combined effects of an intense browsing pressure on all its life stages, the damages from elephants and the stem-boring beetles and the stress imposed by the soil. Subsequent censuses will help to better understand the long-term dynamics of this savanna and how *A. drepanolobium* dominance is maintained over time.

**Author contribution statement** DK designed the project, trained field teams, cleaned and analyzed the data and produced the first draft of the manuscript. GA analyzed the data and produced all figures. SK designed the project, collected the mortality data, supervised the field teams in the first census and contributed to the writing of the paper. DK analyzed the data and contributed to the writing of the manuscript. PM designed the project and supervised the field teams.

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**Availability of data and materials** The Mpala plot data are managed by the ForestGEO network and are available under request to plot PIs at (<https://forestgeo.si.edu/explore-data/mpala-termsconditionsrequest-form>).

**Code availability** The codes used are provided as supplemental file 4.

## Declarations

**Conflict of interests** The authors declare no conflict of interests.

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