

# Journal of Ecology

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Article type : Research Article

Handling Editor: Matthew Heard

## **Browsing is a strong filter for savanna tree seedlings in their first growing season**

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/1365-2745.13745](https://doi.org/10.1111/1365-2745.13745)

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## Abstract:

1: Newly germinated seedlings are vulnerable to biomass removal but usually have at least six months to grow before they are exposed to dry-season fires, a major disturbance in savannas. In contrast, plants are exposed to browsers from the time they germinate, making browsing potentially a very powerful bottleneck for establishing seedlings.

2: Here we assess the resilience of seedlings of 10 savanna tree species to top-kill during the first 6 months of growth. Newly-germinated seeds from four dominant African genera from across the rainfall gradient were planted in a common garden experiment at the Wits Rural Facility and clipped at 1 cm when they were ~2, 3, 4, and 5 months old. Survival, growth, and key plant traits were monitored for the following 2.5 years.

3: Seedlings from environments with high herbivory pressure survived top-kill at a younger age than those from low-herbivore environments, and more palatable genera had higher herbivore-tolerance. Most individuals that survived were able to recover lost biomass within 12 months, but the clipping treatment affected root mass fraction and branching patterns.

4: *Synthesis*: The impact of early browsing as a demographic bottleneck can be predicted by integrating information on the probability of being browsed and the probability of surviving a browse event. Establishment limitation through early-browsing is an under-recognised constraint on savanna tree species distributions.

Keywords: browse-trap, demographic bottlenecks, distribution limits, herbivory, resprouting, seedling establishment, survival, tolerance

## Introduction:

Trees in savanna landscapes have spread from other biomes by evolving traits that allow them to survive the strong selective forces of fire, herbivory, grass competition and drought (Simon *et al.*, 2009; Charles-Dominique *et al.*, 2016; Bond, 2019). These selective forces, together with temperature, are important controls on the current structure and function of savannas (Lehmann *et al.*, 2014). It therefore follows that disturbances such as fire and herbivory are fundamental determinants of the distribution ranges of savanna

plant species (Staver *et al.*, 2012a; Charles-Dominique *et al.*, 2017b; Stevens *et al.*, 2018), leaving classical climate envelope models insufficient for predicting the consequences of global change for our diverse and economically important savanna tree communities (Pausas & Bond, 2019).

Savanna trees are often considered to be constrained at the recruitment stage – with top down controls such as fire and herbivory preventing existing saplings from recruiting to adult size classes (Higgins *et al.*, 2000; Augustine & McNaughton, 2004). However, an important, and less well researched limitation occurs at the establishment stage: seedling survival is a necessary first hurdle for any tree to persist in a savanna environment. Recruitment bottlenecks slow rates of recruitment to adult size classes, but establishment bottlenecks can filter individuals and species from plant communities and are therefore important to study when assessing range limits of particular species. We define establishment as survival through the early vulnerable growth stage (~ 1 growing season) after which a tree can tolerate disturbance.

Seedling survival (establishment) is strongly constrained by water availability (Joubert *et al.*, 2008).

Germinating savanna seedlings need to grow a root system within one growing season sufficient to provide their water requirements during a 4-6 month dry season. These seedlings are also exposed to fire and herbivory at this early stage. Gignoux *et al.* (2009) demonstrated that fire controlled the species composition of the savanna tree layer in a savanna ecosystem in Lamto, Ivory Coast: seedlings that had sufficient stored reserves to resprout after the first fire event were able to survive and establish. The other species were excluded from the system.

Most seedlings are at least 6-8 months old before they experience their first fire event in the dry season. Herbivory, however, can occur at any time, and early herbivory of savanna seedlings might be a fundamental constraint on species composition and tree density in some savanna ecosystems. The ability to resprout in the first weeks/months after germination – at a time when resources are required for rapid shoot and root extension – probably comes at a cost. We expect that not all savanna tree species will be able to survive early herbivory events, and that the ability of very young seedlings to resprout after herbivory should depend on the probability of being exposed to herbivory.

Mammalian herbivory pressure varies at both local (Burkepile *et al.*, 2013) and regional (Hempson *et al.*, 2015) scales. Intermediate-rainfall environments have higher densities of browsers and mixed feeders:

average values can reach over 800kg km<sup>-2</sup> (or ~14 mesobrowsers km<sup>-2</sup>) (Hempson *et al.*, 2015; Augustine *et al.*, 2020). These are the environments where there might be selection for early resprouting. In wetter environments, where browse pressure is lower but competition is higher, investment in early resprouting might trade-off with the need for above-ground height gain. In contrast, in very arid environments rapid root extension to access soil water reserves might be more important than storing resources for resprouting at an early age (Boonman *et al.*, 2020).

Moreover, early resprouting is unlikely to have evolved in plants that are not intrinsically palatable. Palatability to mammalian browsers is related to leaf traits such as SLA, nitrogen and phosphorus content, tannins and other secondary metabolites (Hattas *et al.*, 2011). There are strong phylogenetic controls on tree palatability: of the three major plant clades in African savannas (Osborne *et al.*, 2018) members of the Mimusoideae are generally more selected by browsers than members of the Combretaceae, with Detarioideae containing some of the least preferred species (Owen-Smith & Cooper, 1987). Therefore we expect that the degree to which mammalian herbivory acts as a selective force on young seedling survival depends both on the functional traits of a species, and the environmental conditions in its range. In fact, certain species ranges might even be controlled by their ability to survive these early herbivory events.

Early herbivory events differ from later herbivory events in being much more destructive. Even a very selective browser like an impala will browse the entire shoot of a young seedling, including the apical buds (Wilson & Kerley, 2003). Therefore, when plants survive and resprout after early herbivory, their architectures and allocation strategies might be impacted for several years, possibly setting the growth trajectory for the rest of their adult lives. As plants grow, their stem diameters increase and browsers start to nibble leaves, rather than biting off shoots. The stem diameter at which a seedling's main stem is no longer damaged by a browse event we called the "seedling bite escape diameter" and is a key seedling demographic parameter - equivalent to "escape height" for saplings in the "fire trap" (Bond *et al.*, 2012)).

Here we investigate the onset and impact of the ability to resprout after defoliation across a range of savanna tree species in a phylogenetically controlled common garden experiment at the Wits Rural Facility (WRF) in South Africa. We selected representative species from four major plant clades across three rainfall classes.

We tested several hypotheses:

- 1: Species from intermediate rainfall (400-600mm MAR) savannas have the strongest resprouting response at a very early age.

2: Plants from palatable clades (*Senegalia* and *Vachellia* in the Mimosoideae) are more resilient than plants from less palatable clades (Detarioideae and Combretaceae).

3: Plants that survive early herbivory events will have increased below-ground allocation and more branched architectures.

We also developed a simple 3- parameter model to predict the herbivore density at which species with different resprouting abilities are likely to be excluded from a savanna community. We expected that:

1: Species with early resprouting abilities and rapid stem growth rates will persist at herbivore densities where other species are filtered out through early seedling mortality.

2: Unpalatable species will persist in high browsing environments independent of their resprouting abilities.

Methods:

Field site:

The study was carried out at the Wits Rural Facility (WRF), a 350 ha research station of the University of the Witwatersrand, in the central savanna Lowveld area of Limpopo Province, South Africa (~31° 06E, 24°30 S).

The semi-arid region has a mean annual rainfall of ~650 mm, occurring mainly in summer (October–April) (Shackleton, 1997). The underlying geology is dominated by granite and gneiss, giving rise to a catenal sequence of sandy, infertile soils on hillcrests and sodic clays in the footslopes (Mucina & Rutherford, 2006).

The savanna vegetation is dominated by trees in the Combretaceae and Mimosoideae clades (Mucina & Rutherford, 2006).

The experiment was located within the research station property on a sandy upland. Prior to planting, the site was cleared of all vegetation and the soil was loosened using hoes and picks to ensure a uniform substrate for the experiment. The site was fenced off to prevent herbivore browsing, and grass competition was kept to a minimum. Seedlings were watered regularly to prevent water stress.

Study design:

We chose three species representative of particular rainfall environments from each of four common savanna tree clades: *Combretum*, *Vachellia*, *Senegalia*, and Detarioideae (Osborne et al., 2018, Fig. 1). We linked

location data from GBIF <https://doi.org/10.15468/dl.hp6m69> accessed 16 April 2016 to information on rainfall (<https://www.worldclim.org/data/index.html#>), and identified common species from each clade found in low (< 600mm MAR), medium (600-800 MAR), and high (>800MAR) rainfall classes in southern Africa (Fig. 1, Table S1). We also quantified the mean browser density in each species' distribution range from spatial data in (Hempson *et al.*, 2015).

[[Figure 1 here]]

At the beginning of the growing season (September 2016) we germinated several hundred seeds from each species at a nursery at Wits Rural Facility. Seed pretreatments varied between clade: seeds from the genus *Vachellia* were scarified through immersion in boiling water; *Combretum* and *Brachystegia* seeds were soaked in water and *Colophospermum mopane* and *Senegalia* seeds required no pre-germination treatments. Two species from the Detarioideae (*Burkea africana* and *Brachystegia spiciformis*) failed to survive after germinating so we only had *Colophospermum mopane* in the experiment from this clade. The time taken to germinate varied between species (see SI), however, the date that the first green leaf material emerged was noted so that we had an exact age for each individual. When the plants were approximately 2 weeks old we transplanted them into the field and assigned them to one of five treatments: clipped at 2 months, 3 months, 4 months, 5 months, and not clipped (control). For each treatment 12 replicates of each species were spread across three different blocks in a randomized block design (Fig. 2) – making a total of 720 plants in the experiment. At first there were insufficient germinations for *Senegalia caffra* and *Senegalia mellifera* so these species were re-planted two months later and did not receive the 4 or 5 month clip treatments (Table S1).

Germination started on the 1<sup>st</sup> September, and most species had signs of green leaf material by the 12<sup>th</sup> September (range from 6<sup>th</sup> to the 17<sup>th</sup> except for *S. caffra* and *S. mellifera* that were re-germinated on the 22<sup>nd</sup> October and leaves emerged on the 29<sup>th</sup> October). Seedlings were planted into treatment blocks in the ground on the 14<sup>th</sup> October 2016.

[[Figure 2 here]]

#### Herbivory experiment

Each month between November 2016 and February 2017 one of the herbivory treatments was applied. Due to travel constraints we had to harvest all individuals at once, so actual ages ranged from 66 to 77 at the date

of first clip (Table S1). This clip was termed the “two-month treatment” for convenience, but all analyses were run on the actual age of the individual seedlings. The herbivory treatment imposed was to remove all the above ground biomass >1cm above the cotyledon with clippers. Before clipping we recorded the seedling’s stem diameter, height above ground, the length of the longest stem, and the total stem length (total length of all woody stems). Height above ground gives an indication of competitive ability and light environment, however, due to variations in architectures between species and treatments, total stem length is the best indicator of above-ground biomass (Fig. S5). Spine length was recorded for spinescent species, and the clipped biomass was weighed. Degree of branching was quantified as the ratio of the total branch length to the length of the longest branch (sensu Archibald & Bond, 2003).

Measurements were taken immediately before clipping and one month after clipping until the end of the experiment. At the end of the first growing season in March 2017 all plants were re-measured including the control plants. Plants were then left to grow for another year, after which the saplings were re-measured, excavated to a depth of 30cm and harvested to determine the root mass fraction (ratio of below-ground to above-ground biomass - Boonman et al., 2020).

#### Encounter rate:

To assess the probability seedlings of each species are browsed (herbivore preference) we ran an encounter rate experiment. We laid out 10 seedlings each of a range of savanna species in an open woodland site at Wits Rural Facility. Individuals were randomly placed in a grid where each plant was placed 2m away from neighboring plants. Seedlings were left in the field for 24 hours after which they were assessed for signs of browsing. Not all species in the clipping experiment were represented in this experiment, so to make our results more robust we added data from the literature collected in a similar manner and summarized by genus (Table S6). The dominant browsers at the site were impala (*Aepyceros melampus*) and duiker (*Sylvicapra grimmia*), with some kudu (*Tragelaphus strepsiceros*) Stocking density at WRF is ~34 mesobrowsers km<sup>-2</sup> which is high even for intermediate-rainfall savannas.

#### Analysis:

A generalized linear mixed effect model with a binomial error distribution was used to assess survival to the end of the first growing season (March 2017). Rainfall class (high, medium, low), clipping date and genus were

included as fixed effects, and plot number was a random effect. A full set of candidate models were assessed including independent, additive and interaction terms (Table S2). The Akaike Information Criterion was used to identify the model with the best explanatory power.

We then predicted survival probability per species using a generalized linear model with an interaction between treatment date and species, and quantified the time to reach 20% survival for each species.

Recovery was assessed using a multiple regression with clipping date, genus, and rainfall class as predictor variables, and regrowth one month after clipping as the response. The same three predictor variables were used to assess their impact on aboveground, belowground, total biomass, root mass fraction and stem diameter at the end of the experiment (~18 months after clipping). We ran individual t-tests between control and clipped plants for each species, treatment and sample date. The time taken to fully recover above-ground biomass (time to recovery) was defined as the first date after clipping when the difference between the treatment and control was not significant. For each species and treatment and time period we also calculated the percentage recovery as  $\text{mean\_stem\_length}_{\text{treatment}} / \text{mean\_stem\_length}_{\text{control}} * 100$  and plotted this over time.

Differences in the root mass fraction and branching pattern were compared before and after clipping to see whether the herbivory treatment had any effect on biomass allocation or architecture. In this model clip age and species were predictor variables. Species-specific stem growth rates were calculated from a linear model with  $\log(\text{stem diameter})$  as a response and plant age and species as predictors (Fig. S4). We summarized the encounter rate data to determine the daily probability of tree species from each genus being encountered by a browser. Tests for normality and homogeneity of variances were run for all analyses. Where necessary (for biomass and stem diameter) the data were logged to enable parametric analyses. R statistical software (R Core Team 2014) and the package lme4 (Bates et al. 2014) were used to fit the mixed effects models.

Model:

Survival of and recovery from an individual browse event is not necessarily indicative of a species' ability to tolerate early herbivory in the field as some species can avoid herbivory through being unpalatable or growing very fast. To understand this we integrated information on survival with data on growth rates and the probability of being eaten. Stem growth rates ( $GR_{\text{stem}}$ ) and survival probabilities ( $P_{\text{surv}}$ ) over time for each species were available from our clipping experiment. The encounter rate data provided a genus-level



estimate of the daily probability of being eaten ( $Eat_{prob}$ ). To accommodate varying herbivore densities we assumed a linear relationship between the daily probability of being eaten and herbivore density: i.e. we fit a line through zero to the encounter rate at 34 mesoherbivores/km<sup>2</sup> to extrapolate this across all herbivore densities (see Chevrier *et al.*, (2012) and Speed *et al.*, (2013) for field data justifying the use of this linear relationship and Ben-Shahar (1998) and Gadd (2002) for discussion of this assumption for elephants). This daily encounter rate, accumulated over time, provided the cumulative probability of being eaten as a function of plant age and herbivore density.

At some point seedling stems become large enough that a browser will no longer top-kill the plant but will nibble the leaf material around the stem (Wilson & Kerley, 2003). We termed this the “bite escape diameter” and it represents a key demographic bottleneck which acts at the seedling stage. A similar concept; “escape height” has been used to describe a demographic bottleneck at the sapling stage (Moncrieff *et al.*, 2011; Walters, 2012; Churski *et al.*, 2017). “Escape height” represents the height at which woody saplings are above the reach of different browser species – i.e. their height gain is no longer restricted by browsing. “Bite escape diameter”, in contrast, represents the stem diameter when seedlings become immune to total top-kill by browsers because their stems are too thick to be bitten off. As some seedlings invest in stem elongation, and others in lateral stem growth, there is large variation in the age at which different seedlings reach bite escape diameter. In the fire literature there are analogous concepts related to the stem diameter at which trees can resist top-kill by fire (Hoffmann & Solbrig, 2003), and the height at which their canopies escape the flames (Bond *et al.*, 2012).

We used information from Wilson and Kerley (2003 Table 2) to identify bite escape diameters for unarmed vs spinescent tree species. We used the values for small browsers but see supplementary material for an assessment of how the bite escape diameter for larger browsers like kudu affects seedling survival. Our modelled species-specific stem growth rates were then used to calculate the time to reach escape diameter ( $T_{escape}$ ). See Table S7 for a full set of model parameters and their derivation.

We then contrasted the degree to which early herbivory events act as environmental filters on the 10 savanna tree species studied here by quantifying survival probability over time for the range of herbivore densities observed in savanna ecosystems in Africa. We assessed the approximate herbivore density at which different savanna tree species would be excluded from a system ( $SurvProb < 10\%$ ) due to browser bottlenecks in the first year of growth.

## Results:

### 1: Survival of browse event

Seedlings quickly became tolerant to the simulated herbivory as they matured. Within four months the majority of individuals were able to resprout after being completely defoliated. Species from drier systems were tolerant of herbivory at younger ages: 10% survived herbivory at 2 months and over 40% at 3 months (Fig. S1). In comparison no high-rainfall individuals survived the 2 month clip, and less than 30% survived the 3 month clip.

The generalised linear mixed effect model with the best explanatory power for seedling survival included treatment date, genus and rainfall class (Table 1, Table S2). Probability of survival after clipping increased with seedling age (clipdate) and genera from low and medium rainfall environments had higher post-clip survival rates than those from high rainfall. There was also a significant interaction between genus and treatment date: Combretum species were slower to accumulate tolerance to clipping than species from the two mimosoid genera (*Senegalia* and *Vachellia*), although certain species (*Combretum collinum*) had very high initial tolerance. Fitted responses for each species (Fig. 3, Table S3) were used predict the time it takes to reach 20% survival. Species from drier systems reach 20% survival faster than species from wetter systems.

Table 1: Parameter estimates for the best logistic model fitted to survival data at different ages for species from four genera and three rainfall classes. Plot was included as a random intercept and ClipAge was scaled by the standard deviation to improve convergence. Coefficients for the interaction term with ClipAge are in comparison with ClipAge:Combretum

Parameter	Estimate	Std.Error	z-value	P-val
<i>Fixed effects</i>				
<b>Intercept</b>	<b>-1.04</b>	0.32	-3.19	<0.01
<b>ClipAge</b>	<b>0.72</b>	0.24	2.96	<0.01
Colophospermum > Combretum	-0.53	0.45	-1.16	n.s
Senegalia > Combretum	0.09	0.36	0.24	n.s
Vachellia > Combretum	0.41	0.26	1.56	n.s

<b>Low &gt; High</b>	<b>1.01</b>	0.32	3.19	<0.01
<b>Med &gt; High</b>	<b>0.52</b>	0.28	1.83	<0.1
ClipAge:Colophospermum	0.55	0.44	1.26	n.s
<b>ClipAge:Senegalia</b>	<b>1.57</b>	0.52	3.00	<0.01
<b>ClipAge:Vachellia</b>	<b>0.77</b>	0.28	2.81	<0.01
<i>Random effects</i>	Variance			
Plot_no	0.26			

[[Figure 3 here]]

## 2: Regrowth and recovery

Regrowth a month after clipping varied by clip month, genus, and rainfall class (Fig. 4). The best model included all these factors and explained 40% of the variance in height gain one month after clipping (Table S4). Generally, *Vachellia* and *Colophospermum* regrew faster ( $t = 3.36$  and  $3.38$  respectively,  $p < 0.001$ ) than *Senegalia* and *Combretum* ( $t = 0.099$ ,  $p > 0.05$ ). Plants from higher rainfall environments regrew more quickly than plants from low rainfall environments ( $t = 2.7$  and  $4.4$  respectively,  $p < 0.01$ , Table S4). The greatest height gain was observed in individuals that were cut at approximately 4 months of age, which could grow up to 100mm in the month following the clip (Fig. 4).

[[Figure 4 here]]

We assessed the time taken for each species to recover above-ground biomass (total branch length = to that of control plants) for each treatment (Fig. 5/Table S5). On average the individuals clipped at 4 months recovered lost biomass to control levels within 1 to 2 months of clipping – faster than those clipped at 5 months. Species from dry environments took longer to regrow lost biomass (Table S5). At harvest, ~18

months after germination, all treatments had fully recovered and there was no significant difference in above-ground biomass between treatments ( $p=0.064$ , Fig. S2). Although there were no treatment effects, the low rainfall species had significantly lower biomass than the medium and high-rainfall species (Tukey HSD,  $p < 0.001$ ), and the *Combretum* species were all significantly smaller than species from the other three genera (Tukey HSD,  $p < 0.001$ ).

[[Figure 5 here]]

### 3: Traits before and after clipping

By the end of the experiment clipped plants were more likely to be branched than unclipped ones ( $z = 3.042$ ,  $p = 0.002$ : coefficient = 1.0063). There were strong species differences (Fig. 6) but no evidence that responses to clipping varied by genus or rainclass ( $\Delta AIC < 1$  from best model). Plants clipped at 2 months were more likely to be branched than other treatments ( $z = 3.202$ ,  $p = 0.001$ , coefficient 3.29), but as only seven individuals survived the 2 month treatment this might be confounded by low sample size.

[[Figure 6 here]]

Root mass fraction generally decreased with time since clip (Fig. S3) and at harvest, approximately 18 months after initial clipping there were no treatment effects on root mass fraction ( $p > 0.05$ , Table 2). However, the below-ground biomass of the 3 month (estimate = -0.36,  $P < 0.05$ ) and 5 month (estimate = -0.53,  $P < 0.001$ ) treatments, and the stem diameter of the 3 month treatments (estimate = -0.39,  $P < 0.01$ ) were still lower than control plants (Table 2). Species from wetter environments had higher above and below-ground biomass and stem diameters when grown in a water unlimited experimental situation (med>low  $P < 0.05$ , high>low  $P < 0.001$ ). However, they invested less belowground (RMF med<low  $P < 0.05$ , high<low  $P < 0.1$ ) than species from drier environments. *Senegalia* and *Combretum* species were always smaller than *Vachellia* and *Colophospermum*

*Table 2: Testing whether early clipping affects biomass allocation and stem diameter of recovered trees one year later.*

*Table shows the AIC values for the two best models (which always included an interaction between genus and rainfall class). By 18 months there was no observable effect of clipping treatment on above-ground biomass or root mass fraction (RMS), but the below-ground biomass of the 3 month (estimate = -0.36,  $P < 0.05$ ) and 5 month (estimate = -0.53,  $P <$*

0.001) treatments and the stem diameters of the 3 month treatment (estimate = -0.42,  $P < 0.001$ ) were still lower than control plants. See Fig. S2 for plots of these responses.

Models	d.f.	AIC	$\Delta$ AIC	Weight
AGmass ~ clipmonth + genus * rainclass	15	925.3	0.00	0.61
<b>AGmass ~ genus * rainclass</b>	11	926.3	-0.99	0.37
<b>BGmass ~ clipmonth + genus * rainclass</b>	15	735.0	0	0.98
BGmass ~ genus * rainclass	11	744.7	-9.63	0.01
<b>RMF ~ genus + rainclass</b>	11	279.6	0	0.81
RMF ~ clipmonth + genus + rainclass	15	276.3	-3.33	0.16
<b>StemDiameter ~ clipmonth + genus + rainclass</b>	15	346.6	0	0.95
StemDiameter ~ genus + rainclass	11	353.3	-6.73	0.03

#### 4: Modelling consequences for seedling survival in the first year of life:

Because species grow at different rates (Fig. S4) and resist browsing at different diameters (Wilson & Kerley, 2003), the age at which they reached seedling bite escape diameter ranged from 76 (69-83) days (*Senegalia nigrescens*) to 189 (175-210) days (*Combretum molle*) (Table 3). This, combined with variation in their ability to survive a browse event when it occurs, and different herbivore preferences (Table 3), resulted in a range of modelled probabilities of survival (Fig. 7). Plants that are less preferred (eg Combretaceae), or can increase stem diameters quickly to escape herbivores (*Senegalia nigrescens*), had the highest overall survival rates. The differences in survival probability between species of different genera were larger than the differences between species of the same genus across a rainfall gradient (Fig. 7). As herbivore density increases the differences in survival probability between species become more pronounced. The browsing intensity at which a species cannot establish (defined here as <10 percent survival) ranges from 24 to 49 impala km<sup>-2</sup> (Table 3). This is a maximum value as it assume no other environmental filters are operating (we watered our seedlings throughout and removed the grass competition), and therefore represents only the herbivory filter.

Table 3: Key parameters affecting the ability to survive early browse events for each species in the experiment. Estimated mesobrowser density at which survival probability is <10% is also shown (this value represents unlimited water and no grass competition and is likely to be lower in field conditions).

Species	Rainfall class	Age where >20% of plants resprout (days)	Age at escape diameter (Days)	Herbivore preference score*	Probability of surviving to six months (12 impala km <sup>-2</sup> )	Threshold browse intensity where less than 10% of individuals survive (impala km <sup>-2</sup> )
<i>Vachellia erioloba</i>	low	81 (90-73)	97 (90-103)	0.32	0.44 (0.39-0.48)	33
<i>Vachellia exuvialis</i>	med	81 (91-71)	121 (118-124)	0.32	0.37 (0.33-0.42)	28
<i>Vachellia sieberiana</i>	high	95 (107-86)	93 (89-96)	0.32	0.41 (0.39-0.45)	31
<i>Senegalia mellifera</i>	low	101 (111-86)	148 (145-151)	0.29	0.32 (0.28-0.36)	24
<i>Senegalia nigrescens</i>	med	95 (103-86)	76 (69-83)	0.29	0.56 (0.52-0.61)	47
<i>Senegalia caffra</i>	high	115 (117-101)	149 (143-156)	0.29	0.33 (0.27-0.40)	24
<i>Combretum collinum</i>	low	41 (70-30)	NA	0.16	0.57 (0.51-0.63)	49
<i>Combretum hereroense</i>	med	67 (91-31)	162 (157-168)	0.16	0.54 (0.48-0.59)	44
<i>Combretum molle</i>	high	101 (117-81)	189 (175-210)	0.16	0.47 (0.43-0.53)	36
<i>Colophospermum mopane</i>	low	90 (103-76)	135 (129-141)	0.17	0.54 (0.49-0.59)	44

\*herbivore preference is defined as the proportion eaten vs available scaled to WRF encounter rates. See Table S6

[[Figure 7 here]]

Discussion:

Experimental results:

In our experiment species from lower-rainfall environments, which often have higher browser densities, were able to resprout at a younger age than species from higher-rainfall environments. Although aridity itself selects for early resprouting ability (Schwilk & Ackerly, 2005; Zeppel *et al.*, 2015), palatable genera still showed higher survival at young ages than unpalatable suggesting that browsing is a selective force on this trait. If fire were selecting for early resprouting we would expect species from wetter, more fire-prone savannas to show higher survival. High-rainfall savanna species had very low survival at early ages, but this increased rapidly and once they were ~100 days old they were effectively resilient to above-ground biomass removal. i.e. they would survive a fire that occurred after the first growing season, but not an early browse event. The data support the hypothesis that browsing acts as a demographic bottleneck for tree seedlings, and that this bottleneck is more severe for palatable species from lower rainfall environments.

Recovery was surprisingly fast for all genera and clip ages - some recovered lost biomass within one month, and most species and treatments had fully recovered within 6-12 months (Fig. 5, Table S5). These data align with other evidence that recovery from defoliation, while requiring some initial inputs from stored reserves (Yi & Liu, 2014), quickly comes to depend on current photosynthate (Paula & Ojeda, 2009). The rate of recovery after defoliation depended on the timing of the event: plants that were clipped in the middle of the growing season regrew much more quickly than those that were clipped at a very young age or at the end of the growing season (Fig. 4). The slow rate of recovery of very young plants can be explained by lack of stored reserves, but slow growth of the older plants must be related to phenological patterns of growth or resource allocation (Schutz *et al.*, 2009) because water availability and air temperature did not change significantly throughout the experiment (Fig. S7).

Linking the responses observed here to the particular traits which enable rapid resprouting is the next step. Botha *et al* (2020) found that age, stem diameter and number of basal leaf buds all significantly predicted survival after topkill in a range of species from savanna and forest environments. Boonman *et al* (2020) found

that seedlings from drier areas invested in root elongation and those from wetter areas invested in resprouting and stored reserves. This contradicts our results, and needs further investigation for seedlings of different ages.

Clipped plants, independent of rainfall class or genus, were significantly more likely to be branched than unclipped ones (Fig. 6). Branching is effective for resisting browsing and protecting leaves and structures (Charles-Dominique et al, 2017), but it also slows height gain (Moncrieff et al, 2011), and the rate at which individual stems can reach “seedling bite escape diameter” (each stem is smaller when there are more stems). Induction of branching by herbivory, which is ubiquitous across many plant groups (Lewis et al, 1987; Häslér, Senn, & Edwards, 2008; Wigley et al., 2019) could therefore represent an adaptive response of the plant to these trade-offs (Karban et al, 1999). Alternatively, branching could just be a physiological accident caused by a temporary loss of apical dominance after a browse event (Wise & Abrahamson, 2008).

Belowground biomass at the end of the experiment was found to be significantly lower for the 3 month and 5 month clips but this did not impact root mass fraction, so there was no evidence of either over- or under-compensation.

#### Modelling results:

Our experiment demonstrates that herbivory has the potential to act as an absolute filter killing very small (<2 month) tree seedlings, but our modelling results show that the strength of the herbivore filter also depends on seedling palatability and time to reach herbivore-proof sizes. Species in the *Combretum* genus grow slowly, and take a long time to reach herbivore proof sizes but due to low palatability are more likely to persist under very high densities of herbivores. Preferred seedlings (especially *Vachellia* but also *Senegalia*) will be more exposed to early herbivory events, but this is compensated by strong early resprouting response and the ability to reach herbivore escape diameters in a shorter time frame.

Overall our model shows that tolerance and resistance traits (Archibald *et al.*, 2019) such as resprouting and rapid stem growth are less effective than avoidance traits (being unpalatable or highly defended) for seedling survival. The less-preferred species had the highest survival despite having poorer resprouting abilities and slower stem growth rates (Table 3). These results are partially corroborated by field experiments demonstrating that unpalatable “increaser” species recruit better and dominate at the expense of more



palatable “decreaser” species under heavy browsing (Moe *et al.*, 2009), but contradicted by others, which found that browsers uniformly prevented seedling establishment across all tree functional types (Sankaran *et al* 2013).

In our model the browser densities where browsing can effectively prevent establishment are quite high (over 20 individuals per km<sup>2</sup> for most species). Average impala density in the Kruger National Park is 8 impala km<sup>-2</sup>, and the mean for the distribution range of the species with the highest browse exposure (*V. exuvialis*) is only 12 per km<sup>2</sup>. These area-averaged values however, do not represent the herbivore densities experienced by individual seedlings (Augustine 2020). Locally, browser densities can exceed 50 per km<sup>2</sup> on grazing lawns and herbivore hotspots (Burkpile *et al.*, 2013) and the WRF itself had a density over 30 per km<sup>2</sup>.

Moe *et al* ( 2009) found that 10% seedling survival is reached at ~20 impala per km<sup>2</sup> in field conditions in the Chobe Valley in Botswana. The values in our model are higher than this, probably because it predicts survival in the absence of any other factor limiting seedling survival, and does not include repeat browse events. Morrison *et al* (2019) found grass competition decreased survival by 3-4 times, and Cardoso (2016) recorded up to 80% mortality due to water stress in a West-African savanna. When combined with other causes of early seedling death field survival rates could therefore be <25% of what we present here. Therefore our results are consistent with field observations and suggest that browsing can be a filter of tree seedlings, and that this varies strongly between species with different functional traits. Better data on encounter rates under different environmental conditions and herbivore densities would be required to produce predictive models of seedling survival.

#### Species-specific responses:

The statistical analyses indicated that responses could be generalized across phylogenetic groups and rainfall classes, but as we only had one species for each rainfall/genus combination this conclusion did depend on the species chosen being representative. In a similar study on Australian myrtaceae Chong *et al* (2007) found large differences in resprouting capacity between species that could not be generalized across functional groups. Some exceptional species in our study include *Combretum collinum* (low rainfall), which has a unique early growth strategy using its large cotyledons as its main photosynthetic mechanism for several months, and separating its main shoot from its cotyledon by several centimeters, making it very resilient to browsing. This species-specific strategy probably means our analyses over-estimated the resilience of other low-rainfall Combretaceae to browsing.

Moreover, *V. exuvialis* which is exposed to the highest herbivory pressure in its geographic range (Fig. 1) showed the lowest modelled survival probability (Table 3). This is probably because our model only considered survival after one browse event, and *V. exuvialis* has characteristics that make it very resilient to repeated herbivory (for example it has a high density of leaf buds below 1cm (Botha et al., 2020) and does not lose its photosynthetic capacity when top-killed). By expanding these experiments to encompass repeat browse events it should be possible to develop full predictive models of browser impacts on seedling establishment for key savanna tree species.

#### Conclusions and implications:

Fires and herbivory are most frequently considered to shape savanna through top-kill, rather than death, of individual plants (Higgins et al., 2000; Staver et al., 2012), by preventing recruitment of saplings into adult trees. In this study we show that mortality induced by herbivory in the early seedling stage is another important demographic bottleneck and can shape vegetation composition by filtering species from communities. These drivers select for earlier resprouting abilities than would be expected were fire (Gignoux et al., 2009) the only cause of topkill.

These results have implications for understanding the impact of past land use change and current management regimes. Replacement of an indigenous browse:grazer mix with cattle-dominated ecosystems may remove an important establishment bottleneck resulting in the establishment and dominance of fast-growing woody species that are no longer being filtered by browsers (Augustine & McNaughton, 2004). This might help to explain the pattern of certain species, mostly palatable legumes, driving woody encroachment (O'Connor et al, 2014; Stevens et al, 2016), and the difficulties of using fire alone to control it.

Alternatively, natural game numbers tend to fluctuate spatially and temporally but domestic game and livestock management favors sedentary grazing and browsing resulting in heavier and more persistent browse pressure across landscapes. In these instances we should be able to predict which syndromes of species are likely to be filtered out and which will persist in the environment. Data presented here suggest that palatable species like legumes will fall out of the population and the landscape will slowly become dominated by slow growing, unpalatable species (Moe et al., 2009).

The literature on herbivore impacts on tree demographics often focus on rare and herbivore-sensitive species (Lombard et al, 2001; O'Connor et al, 2007). However, here we highlight that changes in browsing regime have the potential to act on common widespread species across extensive spatial scales. The modelling approach developed in this paper could be expanded to provide useful predictions of the significant changes in tree establishment rates that are likely to be experienced in rangelands and conservation areas as herbivore regimes change. These results are important due to mosaic of land-uses that are occurring across rangelands of Africa and helps us predict which species/genera will likely thrive or experience significant declines with changes in land management.

### Acknowledgements

We thank Frank Nyathi for assistance with field work and Elizabeth Telford for her enthusiastic help in excavating and weighing the below-ground biomass. We thank Stephen Young, Zemijo Kimmie, Benko Kimmie, and Zaid Kimmie for donating their holiday time to measuring seedlings and watching impala. Thank you to the staff of the WRF – especially Minah Nkuna and Cameron Watts – for enabling this research. Support was provided from National Research Foundation grants ACYS (114695), SASSCAL (11858 ) and (N00665/116333). Thank you to two anonymous reviewers for your helpful suggestions and guidance.

### Author contributions:

SA and NS conceived the ideas, SA, NS, and WT together designed the methodology; SA CM and NS collected the data; SA and NS analysed the data; SA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

### Data Archiving:

The datasets and code used to produce these results are available from 10.5281/zenodo.4972083.

### Figure captions:

Figure 1. Three species from each of four different clades were chosen according to the mean annual rainfall in their distribution range (b): Low (<600 MAR), intermediate (600-800mm), and high (>800mm) respectively. Species from intermediate rainfall bands are exposed to higher browsing pressure (c), although the mean

values reported here are not accurate representations of local browse intensity (see Table S1 for information on the browse intensity experienced by the particular seeds used in the experiment). Within the Mimosoideae we included three species from each of *Vachellia* and *Senegalia*: although both genera are palatable, *Senegalia* species are generally better defended against herbivores (Kruger *et al.*, 2017). Unfortunately, both *B. africana* and *B. spiciformis* seedlings did not successfully germinate, so only the low rainfall Detarioideae *C. mopane* could be used in the experiment.

Figure 2. The experimental plot layout consisting of five herbivory treatments (clipped at 2, 3, 4, and 5 months and an unclipped control). For each treatment 12 replicates of each species were spread across three different blocks in a randomized block design – 4 individuals of each species per block – making a total of 720 plants in the experiment. a) photograph taken at month 4 of the experiment with a clipped plot in the foreground and a control in the background. b) *Vachellia karroo* at two months (unclipped), c) clipped seedling resprouting, and d) one month regrowth after being clipped at 3 months.

Figure 3: Fitted responses to simulated herbivory for 10 species from four different genera. Species were classified as high, medium, or low rainfall species based on the Mean Annual Rainfall of their distribution range (See Table S1). Tolerance (survival through resprouting) is delayed in high rainfall species relative to low-rainfall species, and species from intermediate rainfalls had the highest survival when clipped at a very young age. Combretaceae were slower to develop tolerance than fine-leaved acacia species, although they could have high initial tolerance.

Figure 4: Regrowth measured exactly one month after the simulated browse event. Genus and rainfall class affected regrowth potential, as did the age at which the plant was clipped. Interestingly the 4 month clip showed the fastest regrowth: i.e. the plants that were oldest when clipped did not regrow the fastest. See Table S4 for statistical model results. There are few data for the 2 month clip as very few individuals survived.

Figure 5: Number of months to recover biomass from a once-off clip for each species and treatment.

Recovery was quantified as  $(\text{mean clipped} - \text{mean unclipped}) * 100$ . Anovas were also run for each species, clip month, and time period to assess when the treated plants were not significantly different from unclipped plants (Table S5). All plants were sampled 1, 6, 12, and 18 months post clipping. Some treatments were sampled more frequently at the beginning.

Figure 6: All species showed increased branching after being clipped (except *S. mellifera* in which all the control plants were also branched). Darker shades indicate higher rainfall environments. A mixed effect model found no evidence for genus or rainfall explaining branching response.

Figure 7: A simple model illustrating how resprouting response interacts with palatability (probability of being eaten), herbivore density, as well as time to seedling bite escape diameter, to determine the chances that a seedling will survive the browser bottleneck for the first six months of its life. Although species from low-rainfall environments are more likely to survive a particular browsing regime, the differences in palatability and stem growth rates interact with resprouting abilities to determine overall survival rates. This model did not include regrowth response after browsing, or repeated browse events so is for illustrative, rather than predictive purposes.

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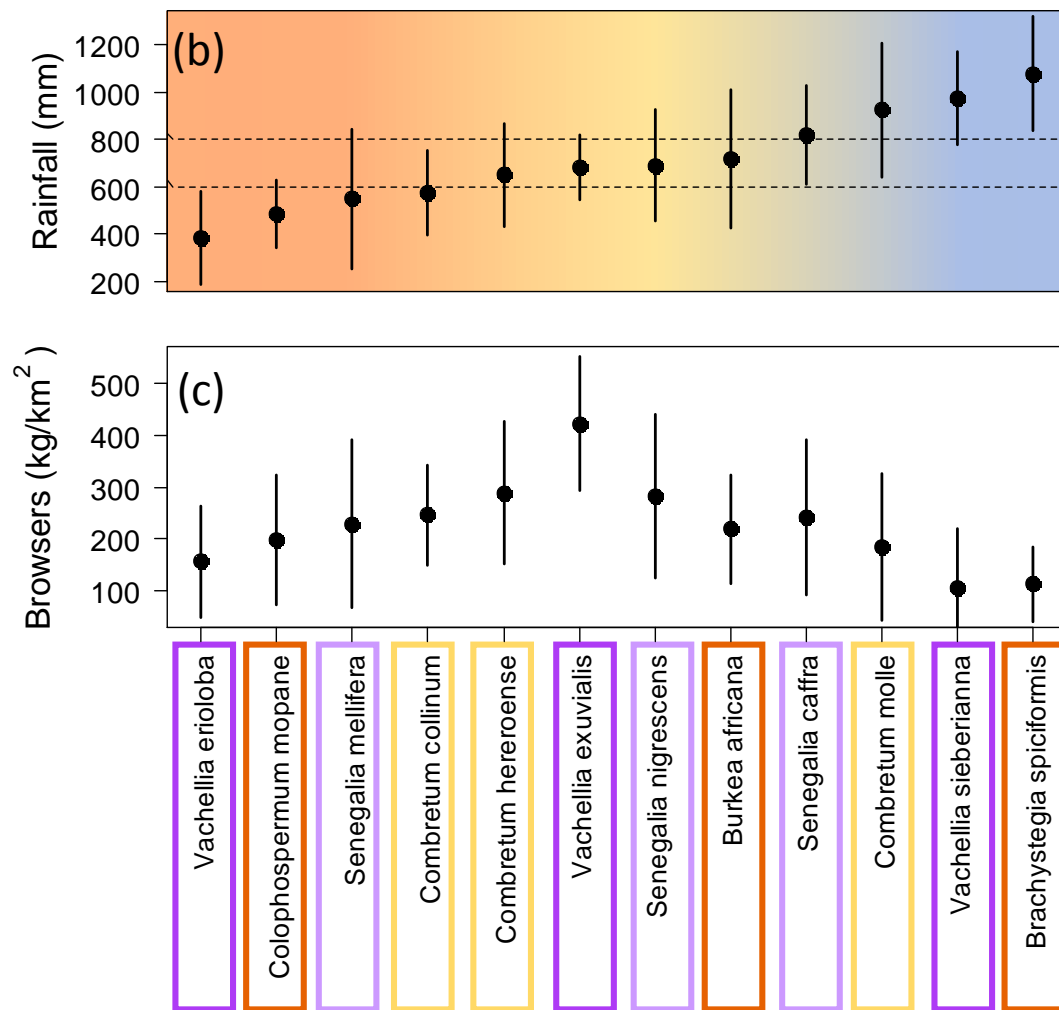
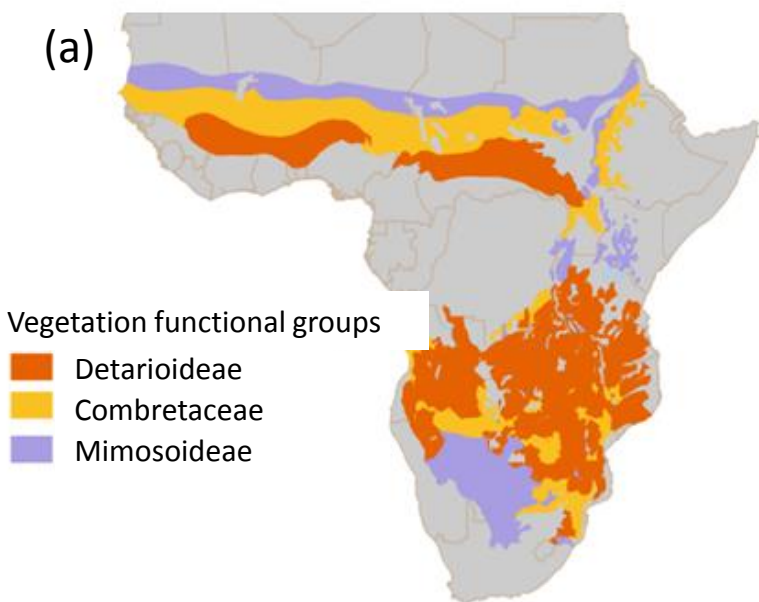
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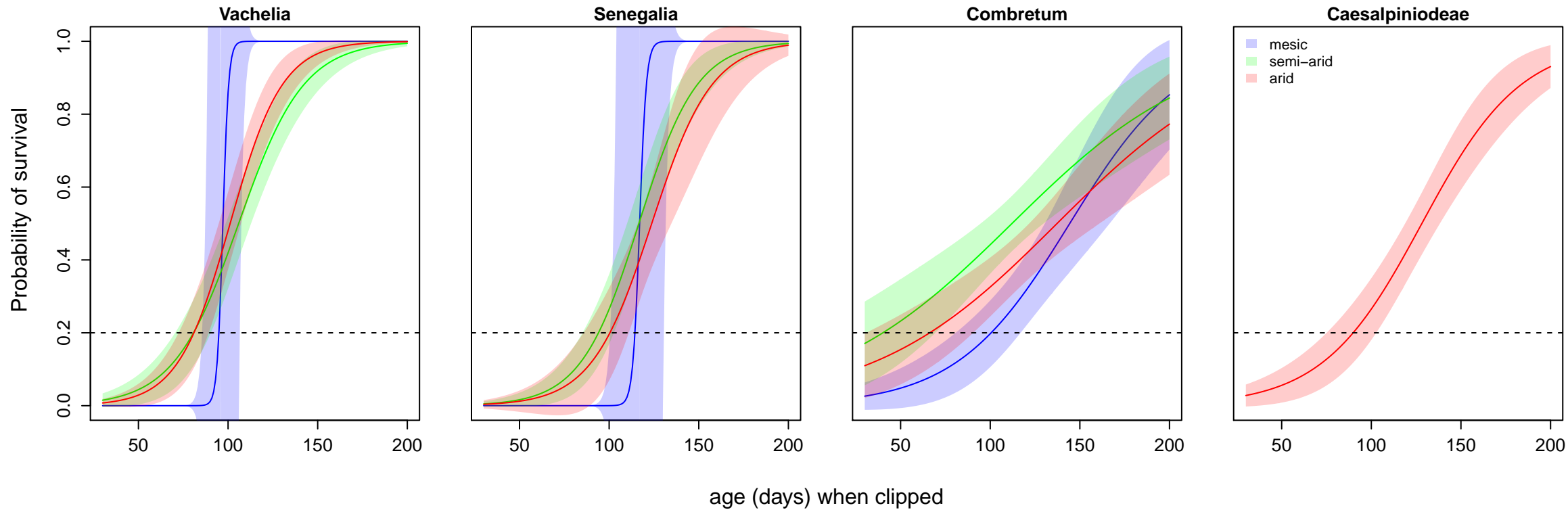
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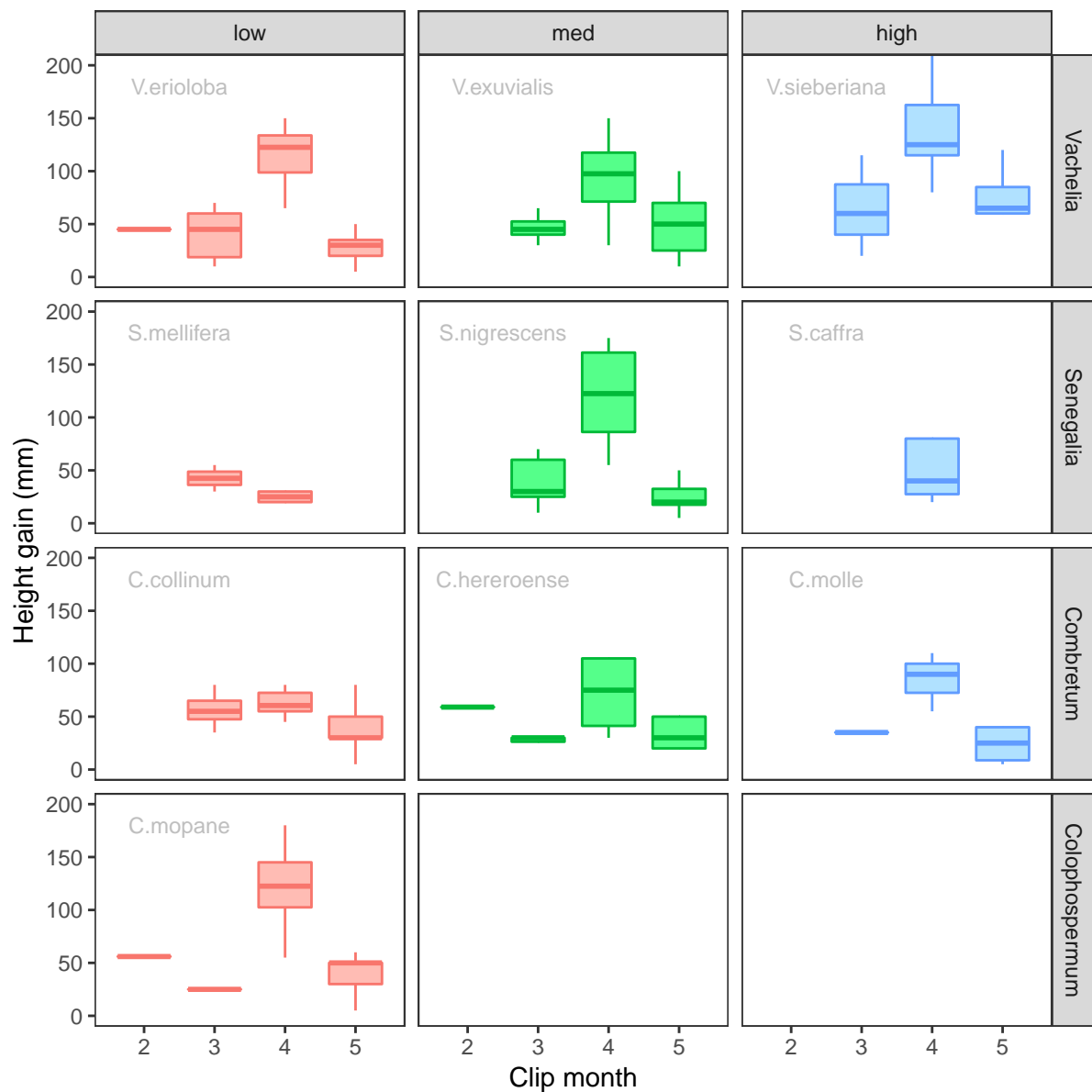


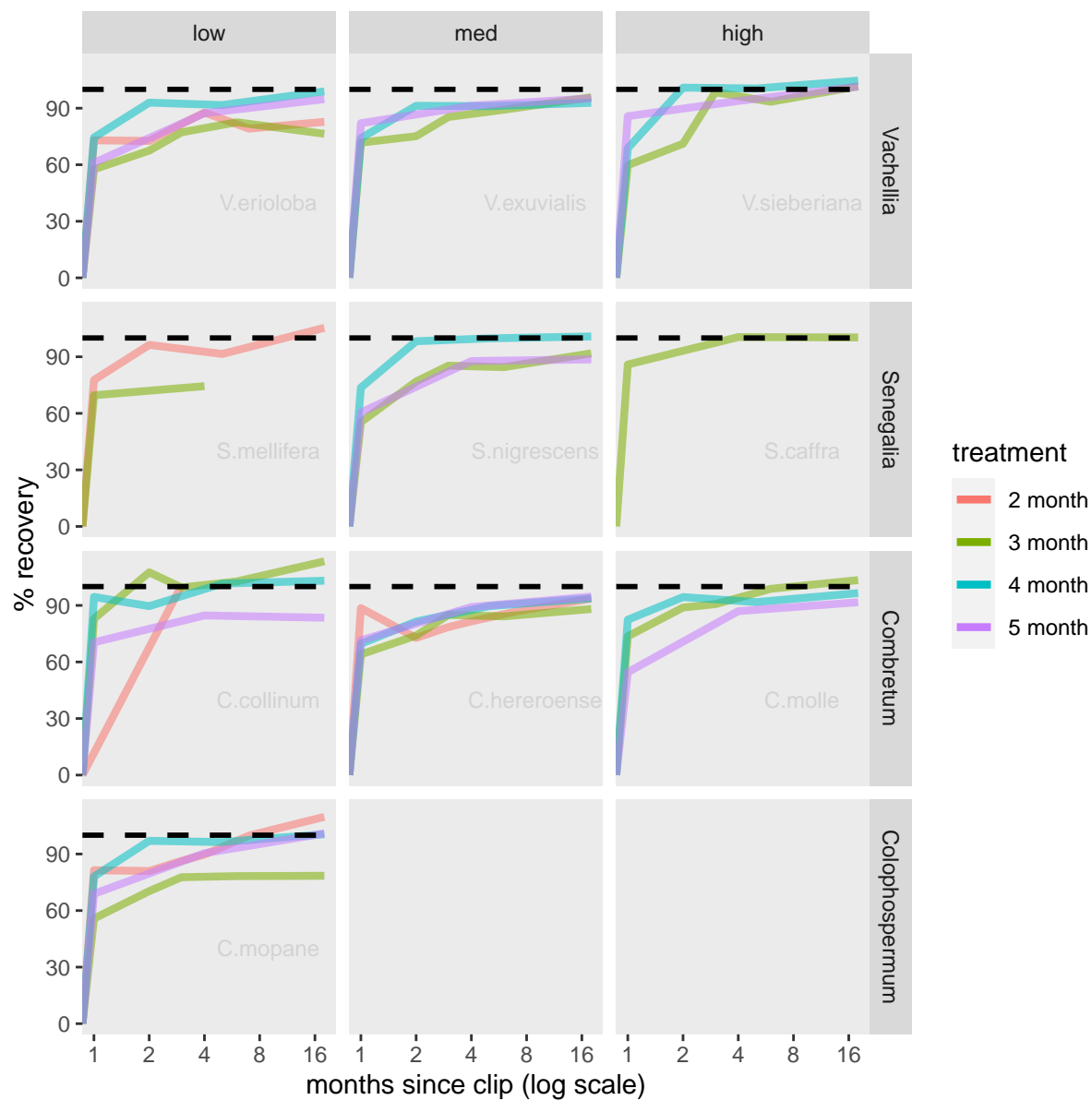
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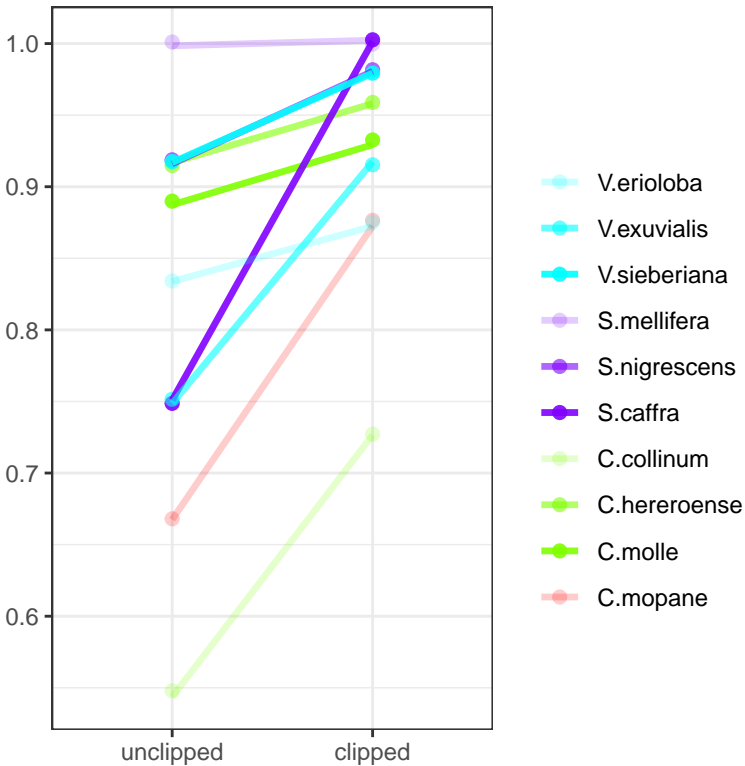






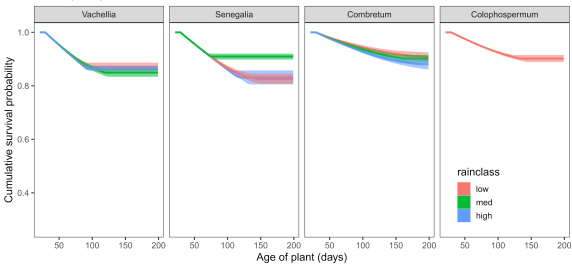


Probability of branching





~ 2 Impala per km<sup>2</sup>



~ 12 Impala per km<sup>2</sup>

