Savanna Rodents' Selective Removal of an Encroaching Plant's Seeds Increased With Grass Biomass

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In savannas across the planet, encroaching woody plants are altering ecosystem functions and reshaping communities. Seed predation by rodents may serve to slow the encroachment of woody plants in grasslands and savannas. Our goals for this study were to determine if rodents in an African savanna selectively removed seeds of an encroaching plant and if foraging activity was influenced by the local vegetation structure or by the landscape context. From trials with two species of seeds (encroacher = *Dichrostachys cinerea*, non-encroaching overstory tree = *Senegalia nigrescens*) at 64 seed stations, we recorded 1,065 foraging events by seven species of granivorous rodents. We found a strong positive relationship between rodent activity and the number of seeds removed during trials. Foraging events were dominated by rodent seed predators, with <10.6% of events involving a rodent with the potential for secondary dispersal. Rodents selectively removed the seeds of the encroaching species, removing 32.6% more *D. cinerea* seeds compared to *S. nigrescens*. Additionally, rodent activity and the number of seeds removed increased at sites with more grass biomass. Our results suggest a potential mechanistic role for rodents in mitigating the spread of woody plants in grass dominated savannas.

Keywords: ecosystem service, Eswatini, foraging, *Dichrostachys cinerea*, *Senegalia nigrescens*

INTRODUCTION

Globally, savannas are experiencing an increase in woody vegetation, known as woody encroachment (Stevens et al., 2016a,b). Savannas are characterized by a coexistence of trees and grasses, with woody vegetation historically limited by rainfall, fire, herbivory, and competition with grasses (Bond, 2008; Lehmann et al., 2014; Staver and Bond, 2014). However, in the last century, tropical savannas in Africa, South America, and Australia (Stevens et al., 2016b) have seen an increased in abundance of woody plants due to poorly understood and interacting factors, such as atmospheric carbon dioxide, fire regimes, and overgrazing (Sala and Maestre, 2014; Archer et al., 2017). Encroachment, often dominated by a few native plant species, can alter vegetation structure to shade out vegetation in the grassy layer (Scholes, 2003; Charles-Dominique et al., 2018).

This structural and compositional change can alter the ecosystem functions and services that savannas provide, such as altering carbon storage, decreasing water availability, reducing biological diversity, and disrupting socioeconomic conditions through reduced grazing (Huxman et al., 2005; Soto-Shoender et al., 2018). To maintain savannas and their beneficial services, it is important to understand factors that can limit the establishment of woody encroachers, particularly at the seed germination and establishment stage.

One under-studied process that can limit woody plants during the seed germination and establishment stage is post-dispersal seed predation (Ostfeld et al., 1997; Vaz Ferreira et al., 2010). Post-dispersal seed predation can influence the colonization, distribution, and composition of plant communities (Hulme, 1997; Lindquist and Carroll, 2004; Zamora and Matías, 2014). Compositional changes can occur when predators selectively consume seeds of certain species over others (Meiners and Stiles, 1997; Orrock et al., 2006). One group of effective seed predators that can reshape the structure of vegetation are granivorous rodents (Davidson et al., 1984; Brown and Heske, 1990; Hulme, 1993). Rodents can mitigate populations of invasive and exotic plants by predating their seeds (Parker et al., 2006; Pearson et al., 2012) and may have the potential to slow woody encroachment in savannas (Busch et al., 2011; Stanton et al., 2018). However, there is minimal information on how rodents could limit the establishment and spread of encroaching woody plants (Busch et al., 2011; Bergstrom, 2013; Gordon et al., 2016).

Seed consumption by some rodents, other mammals, birds, and insects, can increase the viability of seeds and disperse them to new areas (Schupp, 1993; Miller, 1994b; Crawley, 2000). However, many non-caching granivorous rodents are effective seed predators that destroy the seed upon consumption (Ostfeld et al., 1997; Honek et al., 2009). The extent of rodents' predation and dispersal of seeds is likely a function of environmental conditions. At a local scale, rodents' movements are shaped by vegetation structure, such as grass biomass and shrub cover, which provide cover from predators (Hulme, 1993; Monadjem, 1999a; Loggins et al., 2019b). While less pronounced, rodent activity may also be influenced by different types and configurations of surrounding landscapes (Nupp and Swihart, 2000; Orrock and Damschen, 2005; Ness and Morin, 2008).

Our goals for this study were to determine if rodents in an African savanna selectively removed different woody seeds and varied their activity with changes in local vegetation structure or landscape context. Working in a shrub encroached savanna embedded within a complex landscape matrix, we predicted rodents would selectively remove seeds of a woody encroacher (*Dichrostachys cinerea*). We predicted that the nutritious *D. cinerea* herbivore-dispersed seeds would also be highly palatable for rodents (Irie and Tsuyuzaki, 2011; Xiao and Zhang, 2016) and selected (i.e., removed at a higher rate) over a non-herbivore dispersed tree species (*Senegalia nigrescens*). Additionally, we predicted that fine-scale habitat conditions would have a greater influence on seed removal than the surrounding landscape because of rodents' strong behavioral responses to local vegetation structure (Lima and Dill, 1990; Loggins et al., 2019a).

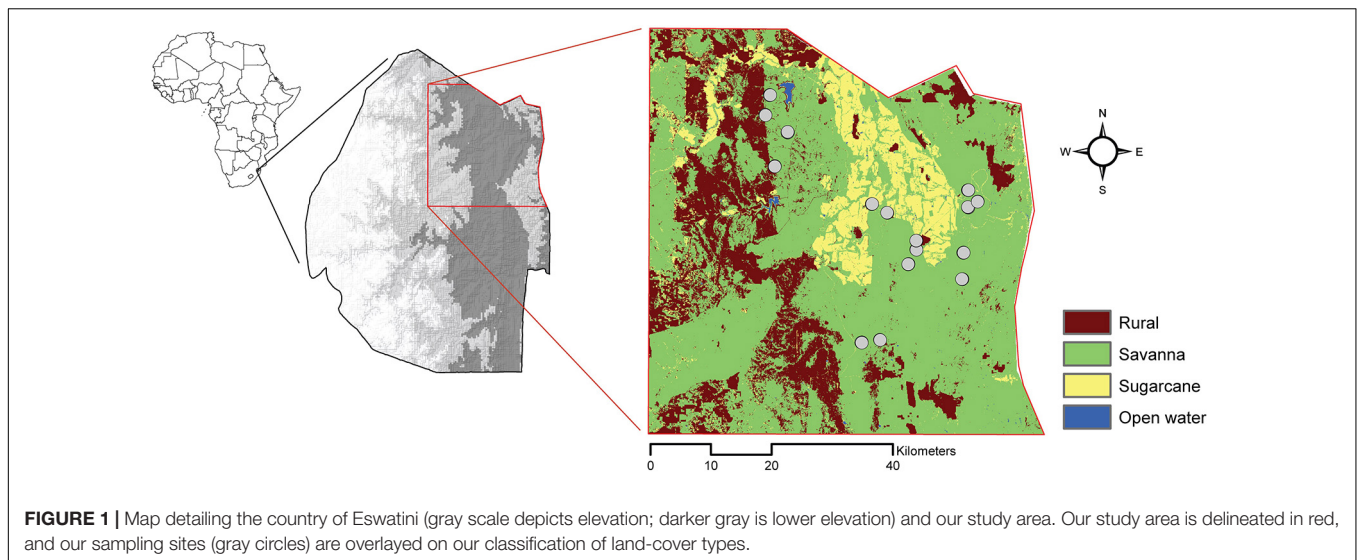## MATERIALS AND METHODS

Study Area

We conducted our study in the subtropical savannas of northeastern Eswatini. This region falls within the Maputaland-Pondoland-Albany biodiversity hotspot, recognized for its high endemism and biodiversity (Smith et al., 2008). A variety of land uses in the region creates a mosaic landscape of irrigated commercial monocultures and rain-fed subsistence agriculture, grazing lands, and protected areas (Bailey et al., 2016; Reynolds et al., 2018).

The native savanna vegetation in this area is characterized by a continuous grass layer dominated by *Themeda triandra* and *Panicum maximum* and interspersed with woody trees and shrubs. The dominant canopy tree is *S. nigrescens* and the shrub layer is dominated by *D. cinerea*. The woody shrub cover in the region has increased steadily over the last 70 years, from 2% to currently >40% (Roques et al., 2001; Sirami and Monadjem, 2011; McCleery et al., 2018; Stanton et al., 2020). The region has mild, dry winters and hot, wet summers. We conducted our study during the winter, June–July 2018, when average temperatures range from 8 to 26°C and the region receives approximately 0–50 mm of its average 600 mm of annual rainfall (Goudie and Price-Williams, 1983).

We conducted our experiments within the Mbuluzi Game Reserve, Mlawula Nature Reserve, Hlane Royal National Park, and the Inyoni Yami Swaziland Irrigation Scheme (IYSIS) cattle ranch. These savannas were embedded within a land-use matrix consisting of protected natural areas, cattle ranches, subsistence agriculture, and intensive sugarcane plantations (Monadjem and Garcelon, 2005; LaScaleia et al., 2018). Our study sites host a variety of rodents with different feeding and habitat preferences. The most common species at our sites (*Mastomys natalensis, Lemniscomys rosalia, Aethomys ineptus,* and *Micaelamys namaquensis*) have variable diets that include seeds (Field, 1975; Kerley and Erasmus, 1991; Monadjem, 1997a, 1998; Chimimba and Linzey, 2008; Hagenah et al., 2009; Mulungu et al., 2011). We have found no evidence suggesting these widespread and well-studied rodents contribute to secondary seed dispersal (Miller, 1994a; Skinner and Chimimba, 2005; Scholtz, 2008; Happold, 2013; White and Midgley, 2021). However, three less common granivorous species (*Saccostomus campestris, Steatomys pratensis,* and *Mus minutoides*) on our sites are known to eat seeds and cache food in their burrows or nests (Hanney, 1965; Ellison, 1993; Hoole et al., 2017) and may facilitate seed dispersal. However, caching by *M. minutoides* has only recently been demonstrated in a laboratory setting and *S. campestris* and *S. pratensis* often reduce their activity during the austral winter (Kern, 1981; Korn, 1987; Monadjem, 1999b), which is when we conducted this study because seeds from the dominant woody plants are most abundant (Donaldson, 1993; Hoffman, 2006).

Site Selection and Landscape Metrics

To understand the influence of the surrounding landscape on the interaction between rodents and seed predation, we created

FIGURE 1 | Map detailing the country of Eswatini (gray scale depicts elevation; darker gray is lower elevation) and our study area. Our study area is delineated in red, and our sampling sites (gray circles) are overlayed on our classification of land-cover types.

a land-cover map from Google Earth Engine which included savanna, agriculture, homestead, and open water (Reynolds et al., 2018; **Figure 1**). We derived a value for each site for compositional (the type and diversity of land cover) and configurational (the shape and arrangement of land cover) landscape heterogeneity (Gustafson, 1998). To derive these measures, we used the *raster* and *SDMTools* packages in R statistical software V 3.5.0 to implement a moving-window analysis and identify gradients in landscape composition and configuration based on variations in land cover (Zhang et al., 2013; Tolessa et al., 2016, R Core Team, 2018). To capture areas of savanna with a variety of surrounding landscapes, we set a window with a 2 km radius and centered sampling landscapes around cells surrounded by at least a 500 × 500 m buffer. Within the 2 km buffer, we calculated two measures of compositional heterogeneity (Shannon diversity index of land cover types and land cover richness) and three measures of configuration heterogeneity (total length of edge between land cover classes, total number of patches, and patch cohesion and landscape division) (Fahrig et al., 2011; **Supplementary Table 1**).

We used principal components analysis (PCA) from the *psych* package to create two orthogonal components of landscape heterogeneity, representing compositional, and configurational heterogeneity (Revelle, 2014). We ranked cells based on their PCA value for compositional and configurational heterogeneity. Using stratified sampling, we then selected 16 sampling landscapes across gradients of compositional and configurational heterogeneity.

We scored sites as low (<33%), medium (34–66%), or high (>67%) compositional and configurational heterogeneity. We stratified the 16 sites based on the following classifications: high compositional and high configurational heterogeneity ($n = 3$), high compositional and medium configurational heterogeneity ($n = 2$), high compositional and low configurational heterogeneity ($n = 2$), medium compositional and medium configurational heterogeneity ($n = 1$), medium compositional and low configurational heterogeneity ($n = 2$), low

compositional and high configurational heterogeneity ($n = 2$), low compositional and medium configurational heterogeneity ($n = 2$), and low compositional and low configurational heterogeneity ($n = 2$).

Vegetation Structure

Our sampling sites were located within relatively open savanna habitats (woody cover 25–40%). To quantify the vegetation structure of the local environment (0.25-ha), we sampled three 50 m transects at each site. We ran two parallel transects at 10 m distance from the center of the site, and a third perpendicular transect through the center point. We measured grass biomass with a disc pasture meter (DPM) every 5 m on each transect (Bransby and Tainton, 1977). We averaged the measures and used a previously calibrated estimate to generate an estimate of biomass in kg/ha (Zambatis et al., 2006). We measured the average canopy cover at each site by taking spherical densiometer readings at every 5 m along each of the three transects and we estimated shrub cover (woody cover <5 m) using the line intercept method on each transect (Canfield, 1941).

Foraging Trials

We conducted foraging trials with seeds from the two dominant woody species in our study area, *S. nigrescens* and *D. cinerea* (family Fabaceae). They are both widespread in southern African savannas (Palgrave and Palgrave, 2015). *D. cinerea* is a common woody encroacher that relies on ingestion by non-rodent herbivores (e.g., ungulates) for both dispersal and dormancy-breaking (Van Staden et al., 1994; Miller, 1995; Dudley, 1999; Tjelele et al., 2012, 2015). The seeds of *D. cinerea* are round and ≈ 4 mm × 5 mm (**Supplementary Figure 1**). The pods are nutritious and are eaten by large herbivores. *S. nigrescens* is a canopy tree with disc-shaped seeds that form in a pod and are dispersed through ballistic dispersal. The seeds of *S. nigrescens* are ≈ 10 mm × 10 mm and flat (**Supplementary Figure 1**). These larger seeds do not require herbivore-assisted dispersal to break dormancy and are damaged if consumed (Miller, 1994b, 1995).

At each sampling site (50×50 m plot, 0.25 ha) we established four seed stations around the center of the site. We placed the seed stations (30 cm diameter tray) halfway under shrubs to increase foraging rates (Loggins et al., 2019b). Prior to trials, we pre-baited trays for 24 h with oats and peanut butter. Then we randomly assigned two seed stations to receive *S. nigrescens* seeds ($n = 40$) and two to receive *D. cinerea* seeds ($n = 60$). We obtained our seeds from Silverhill Seeds and Books[1]. We used 50% more *D. cinerea* seeds than *S. nigrescens* seeds to account for the former's smaller mass and volume. We ran each trial for 24 h and then collected and recorded the number of intact seeds remaining. We classified seeds as remaining seeds if they were scarred or damaged but had an intact cotyledon that could potentially germinate (Bell and van Staden, 1993). The small and hard seeds used in this study often shatter with damage to the cotyledon; thus, to be conservative we considered seeds with >25% damage to the cotyledon as removed (Barnes, 2001). For the next 24-h period, we switched seed species at each station and ran the trial again. Finding no evidence that the common seed predators (*M. natalensis, L. rosalia, A. ineptus,* and *M. namaquensis*) contribute to secondary seed dispersal (Miller, 1994a; Skinner and Chimimba, 2005; Scholtz, 2008; Happold, 2013; White and Midgley, 2021), we assumed the seeds removed by these species were predated. Alternatively, we acknowledged that foraging by the less common *M. minutoides, S. campestris,* and *S. pratensis* may have led to secondary dispersal.

Rodent Activity

To link seed predation to rodent activity, we monitored each seed station with a short-focused camera [Spartan, model SR1-IR(S100), Norcross, GA, United States]. We placed the camera 55 cm above each seed station facing downwards (**Supplementary Figure 2**). Seed trays were marked with a scale bar to aid in identification of rodents using tail and body length (McCleery et al., 2014). We set the motion-sensitive camera to photo, three bursts, with a 5 s trigger interval. To calculate the length of foraging bout we measured the duration of time each individual rodent first and last appeared on camera, with new bouts starting after 20 min of non-detection (Loggins et al., 2019b). When multiple individuals of the same species appeared on camera simultaneously, we noted a foraging bout for the maximum number of individuals seen in the frame. We grouped the ecologically similar *A. ineptus* and *M. namaquensis* as a single species due to the difficulty of distinguishing them on camera; however, the latter species is rarely captured away from rocky outcrops in Eswatini (Monadjem, 1997b) and was therefore not likely to be encountered in this study. All methods were approved by the University of Florida's Institutional Animal Care and Use Committee (#201509045).

Statistical Analyses

Seed Selection

To determine if rodents selected one seed species over the other, we modeled the proportion of seeds removed during each trial as a function of the species of seed. We used proportions to

account for the different number of seeds used for each species. We used a mixed effects model with each seed station as a random effect and fitted to a binomial distribution using the *lme4* package for R (Bates et al., 2015). We considered the proportion of seeds removed to be significantly different if the 95% confidence intervals (CI) of β estimate for seed species did not include zero.

Variation in Seed Removal

To explain variation in seed removal for each species separately, we used the raw count of the number of seeds remaining at each tray. For each species, we considered variation as a function of factors at two different scales, the local scale (vegetation structure at the 0.25 ha scale) and the landscape scale (land use composition and configuration at the 2 km scale). We developed seven *a priori* models to explain differences in the number *D. cinerea* and *S. nigrescens* seeds remaining. We included models with only one fixed variable (canopy cover, shrub cover, grass biomass, compositional heterogeneity, and configurational heterogeneity), as well as global and null models (**Table 1**). We fitted generalized linear mixed models using a generalized Poisson distribution and site as a random effect using the *glmmTMB* package in R (Brooks et al., 2017). We evaluated model fit using Akaike's information

TABLE 1 | Degrees of freedom (DF), Akaike's information criterion corrected for small sample size (AICc), difference in AIC scores (ΔAICc), and AICc weight (AICcwt) of models to explain differences in the numbers of *Dichrostachys cinerea* seeds remaining at seed trays (a), the number of *Senegalia nigrescens* seeds remaining at seed trays (b) and the total time (i.e., number of minutes) rodents foraged at each seed station (c).

Model	DF	AICc	ΔAICc	AICcwt
(a) Number of *D. cinerea* seeds remaining				
Grass biomass	4	386.2	0	0.868
Compositional heterogeneity	4	392.4	6.20	0.039
Null	3	392.8	6.57	0.032
Canopy cover	4	394.1	7.85	0.017
Global	8	394.2	7.97	0.016
Configurational heterogeneity	4	394.2	7.98	0.016
Shrub cover	4	395.0	8.74	0.011
(b) Number of *S. nigrescens* seeds remaining				
Grass biomass	4	435.6	0	0.274
Null	3	435.8	0.20	0.248
Shrub cover	4	436.7	1.10	0.158
Configurational heterogeneity	4	437.4	1.73	0.115
Canopy cover	4	437.6	1.93	0.104
Compositional heterogeneity	4	438.1	2.48	0.079
Global	8	440.7	5.03	0.022
(c) Number of minutes foraging				
Grass biomass	4	721.8	0	0.672
Null	3	725.6	3.85	0.098
Compositional heterogeneity	4	726.1	4.38	0.075
Configurational heterogeneity	4	726.4	4.68	0.065
Shrub cover	4	727.4	5.63	0.040
Canopy cover	4	727.4	5.66	0.040
Global	8	730.1	8.32	0.010

Models for each seed species included individual fixed variables, a global model with all variables, and a null model.

criterion (AICc) corrected for small sample size. We considered models with AICc scores lower than the null model and within four AICc units of the best model to be competing models (Burnham and Anderson, 2002). We considered parameters from competing models to be significant if their 95% CIs did not include zero.

Rodent Activity

To link rodent activity to overall seed removal (i.e., both species), we related the proportion of seeds removed during each trial to the total number of minutes that rodents foraged at each tray. Using both species, we modeled the proportion of seeds removed during each trial as a function of rodent activity with a mixed effects model fitted to a binomial distribution with seed station as random effect. In addition to examining 95% CIs, we evaluated the strength of the relationship by calculating the marginal pseudo-R^2 using the *sjstats* package (Lüdecke, 2021). Next, to determine if activity varied as a function of the species of seed, we modeled the foraging activity during each trial (i.e., total number of minutes of rodent activity). We correlated these count data with the seed species used during the trial using a generalized Poisson distribution and seed station as the random effect. Finally, to determine if rodent activity varied with environmental factors in a manner that reflected variation in measures of seed removal, we fitted generalized linear mixed models to rodent activity using a generalized Poisson distribution and site as a random effect to the same seven models (**Table 1**) and assessed model parsimony and significance as described above.

RESULTS

We recorded 1,065 foraging events by seven species of granivorous rodents during seed experiments that were conducted from June 23–July 26, 2018 (**Supplementary Table 2**). The rodents most frequently detected at the seed stations were the seed predators *M. natalensis* (39.0%, $n = 415$), *A. ineptus/M. namaquensis* (25.4%, $n = 270$), and *L. rosalia* (25.1%, $n = 267$). Rodents with the potential for secondary seed dispersal accounted for only 10.6% of the foraging events. The diminutive *M. minutoides* accounted for 10.1% ($n = 108$) of the activity and we only recorded five foraging events by *S. pratensis* (0.3%, $n = 3$), and *S. campestris* (0.2%, $n = 2$). Of the 64 seed stations used in the experiment, one had no sign of seed removal or rodent activity and two were incorrectly set up; hence, all three were removed from further analysis ($n = 61$).

Comparing the proportion of seeds removed by species, we found that rodents removed a greater proportion of *D. cinerea* than *S. nigrescens* (β = −1.30, 95% CI −2.52 to −0.26, reference = *D. cinerea*). Model predicted estimates suggested that rodents removed 32.6% more *D. cinerea* seeds ($\bar{x} = 0.87$, SE = 0.06) than *S. nigrescens* seeds ($\bar{x} = 0.66$, SE = 0.10).

Examining the influence of the surrounding environment on the number of seeds removed, for both seed species, we found a model with only the fixed effect of grass biomass was the best model with no competing models (**Table 1**). Grass biomass had a significant negative relationship with the number of *D. cinerea*

seeds remaining in trays (β = −0.76, 95% CI −1.26 to −0.26), where the number of *D. cinerea* seeds remaining decreased from 31 to 1 as grass biomass increased from a minimal 1,000 with a maximum of 4,500 kg/ha (**Figure 2**). The relationship between grass biomass and the number of *S. nigrescens* remaining was not significant (β = −0.478, 95% CI −1.07 to 0.12), suggesting a weaker relationship. We found little evidence that seed removal was affected by the broader landscape context (i.e., composition and configuration; **Table 1**).
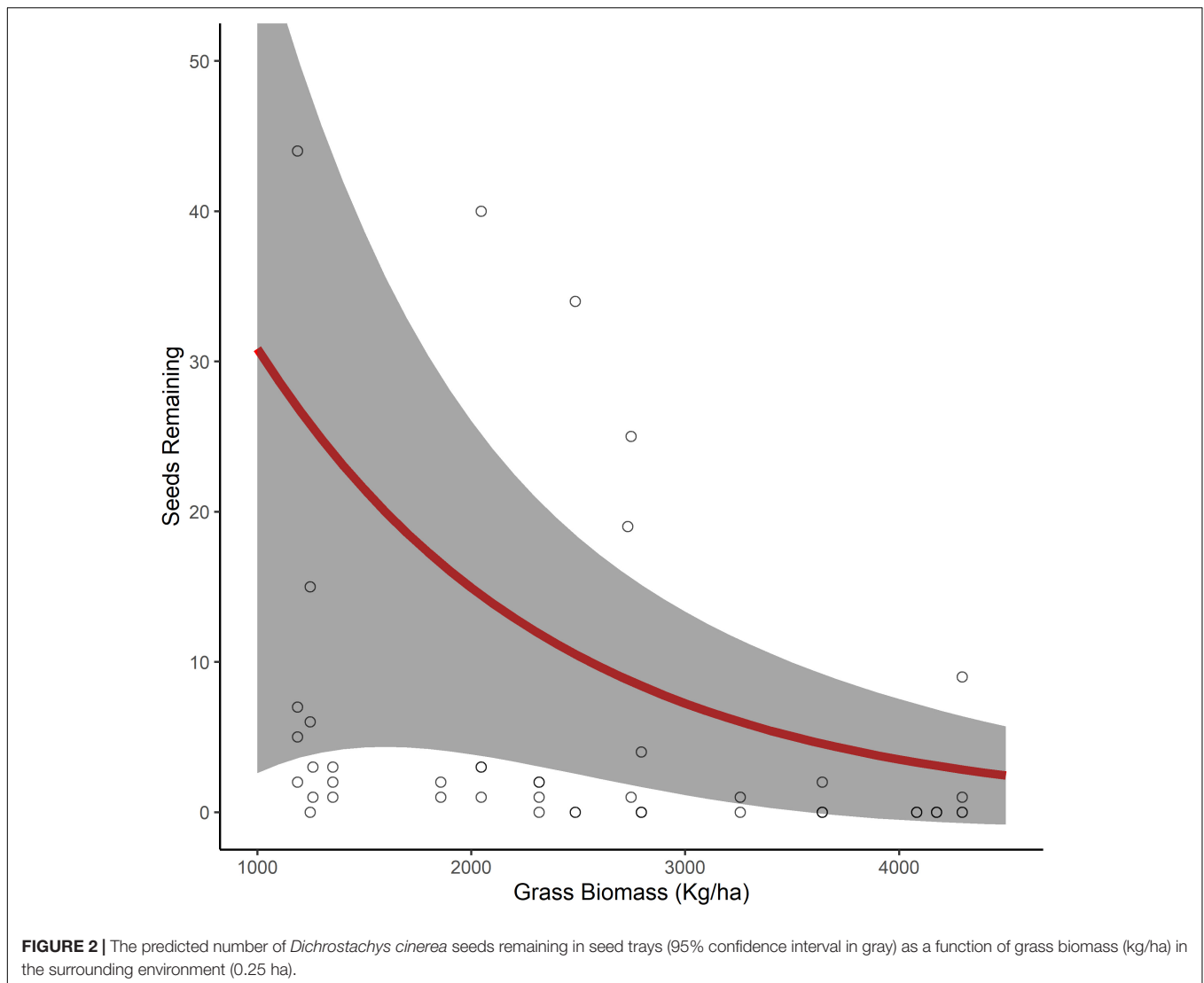
Of the 61 seed stations used to understand seed removal, six had camera failures. Using the seed stations with operational cameras ($n = 55$), we found a strong positive relationship between the proportion of seeds removed and rodent activity (β = 3.19, 95% CI 1.75–4.65, pseudo R^2 = 0.76). However, we found no indication that activity varied with the seed species used during the trial (β = 1.15, 95% CI −0.24 to 0.19, reference = *D. cinerea*). Similar to our investigation of seed removal, we found the best model, with no competing models, to explain variation in rodent activity was a model that included only the fixed effect of grass biomass (**Table 1**). Rodents spent more time foraging in areas with more grass biomass (β = 0.46, 95% CI 0.13–0.80). The total number of minutes increased from approximately 96 to 450 over the range of grass biomass recorded at our sites (**Figure 3**).

DISCUSSION

We found a strong linkage between the removal of seeds and rodent activity, suggesting a potentially important role for rodents in shaping the composition and structure of woody vegetation in savannas. With only a small percentage of rodent activity from rodents with the known ability to cache seeds, we assumed the majority of rodent-seed interactions ended with seed predation. This was particularly true for rodents' interactions with the seeds of the woody encroaching shrub *D. cinerea*. Despite spending similar amounts of time with both seed species, rodents removed 33% more of the seeds from *D. cinerea*.

Rodents' selection of *D. cinerea* may be based on seed properties (e.g., morphology, nutrition, and palatability). The larger *S. nigrescens* seeds may provide rodents with a greater volume of food, but *D. cinerea* likely has a higher nutritional value (Janzen, 1984; Tiffney, 2004). This difference has been documented in the seed pods and may extend to the seeds (Tsopito and Adogla-Bessa, 1998; Aganga and Motshewa, 2007). Additionally, optimal foraging theory predicts that animals select seeds that provide the most nutritional gain for the least amount of energy expended (Charnov, 1976; Brown et al., 1999). The larger *S. nigrescens* seeds may require more energy to handle or increase the rodent's vigilance behavior during foraging (Quenette, 1990). Accordingly, rodents may have selected the smaller seeds of *D. cinerea* to consume food with minimal effort while remaining vigilant.

We also found that the number of seeds removed by rodents and the amount of time rodents spent foraging increased with increases in grass biomass (**Figures 2**, **3**). This supports our prediction that rodents are more strongly influenced by localized vegetation than the surrounding landscape. Thick grass cover is

FIGURE 2 | The predicted number of *Dichrostachys cinerea* seeds remaining in seed trays (95% confidence interval in gray) as a function of grass biomass (kg/ha) in the surrounding environment (0.25 ha).
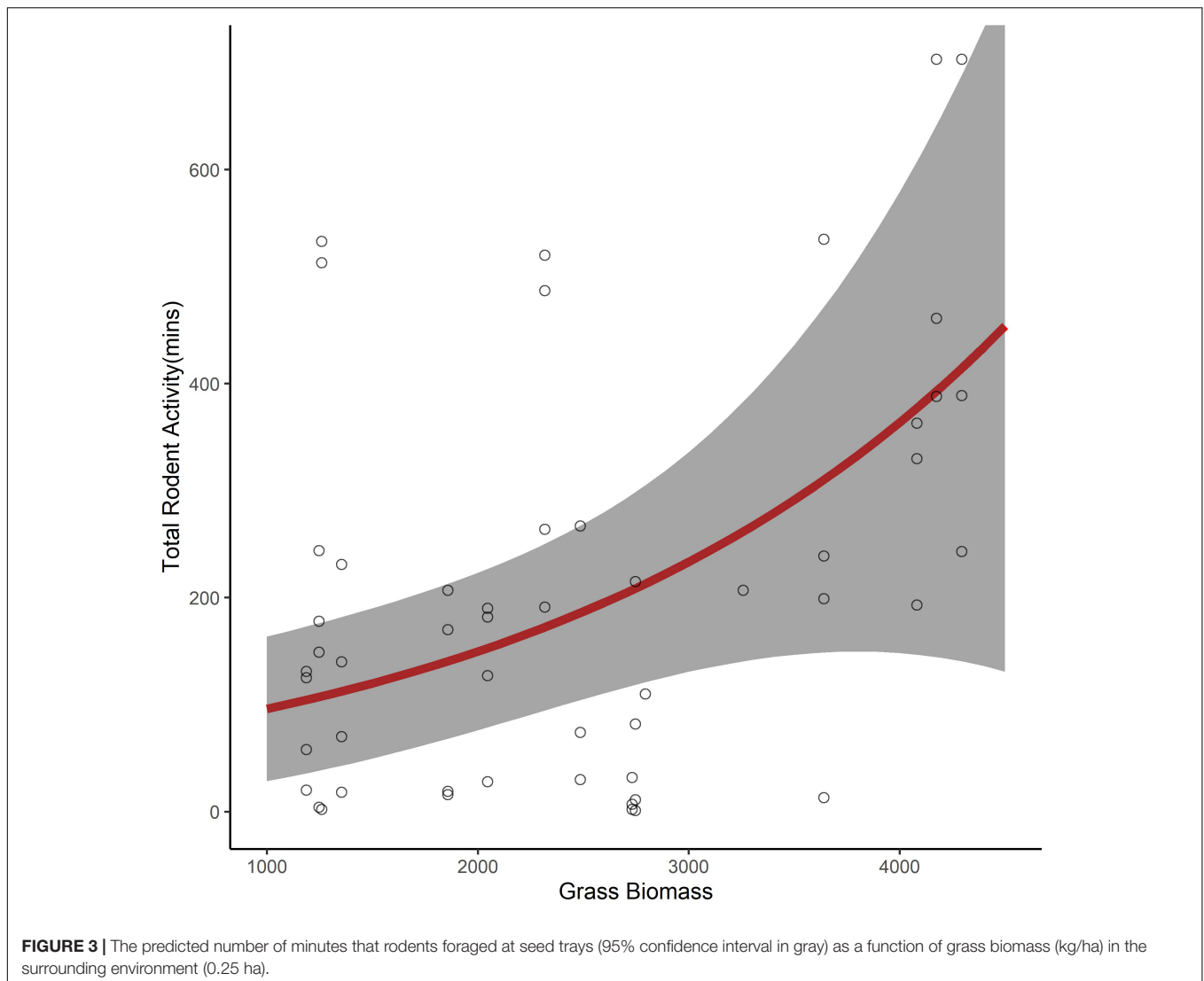
likely to provide rodents with ample food resources and reduce their perception of fear (Banasiak and Shrader, 2016). These findings are consistent with the "landscape of fear" framework (Laundré et al., 2014), where animals alter their movements and behaviors to minimize predation risk while maximizing benefits (e.g., foraging on seeds) (Lima and Dill, 1990; Brown, 1999; Bleicher, 2017).

In savannas, grasses and shrubs compete for resources (e.g., water and light) and areas with a thick grass layer have lower rates of seedling survival, reducing the chances of shrub establishment (Köchy and Wilson, 2000; Rinella et al., 2015; Pierce et al., 2018). Additionally, rodent predation of seeds of encroaching shrubs in areas with thick grass may create a feedback loop, where high grass biomass limits shrub establishment and facilitates rodent seed predation which helps to maintain the dominance of grassy vegetation. This feedback loop may be more pronounced for plants that are herbivore-dispersed such as *D. cinerea*, which rodents appear to select. Nonetheless, the role of rodents may be substantially reduced if the system switches

from an open grassy savanna to an encroached savanna with minimal grassy cover.

Through the removal of seeds, rodents can decrease seedling recruitment (Ostfeld et al., 1997; Nuñez et al., 2008; Yu et al., 2014) and the density of adult plants (Maron and Kauffman, 2006; Larios et al., 2017), altering composition (Louda, 1982; Pearson et al., 2012, 2013) and shaping vegetation (Brown and Heske, 1990; Edwards and Crawley, 1999; Moorhead, 2017). In our savanna system, rodents have the potential to reduce the recruitment of woody encroaching plants; however, we did not consider the role of other herbivores. The nutritious seeds and seed pods of woody encroachers are often consumed and deposited in the dung of non-rodent herbivores, where they can germinate rapidly (Campos-Arceiz and Blake, 2011). This mechanism of dispersal may protect seeds from rodent predation and enhance secondary dispersal (Vander Wall et al., 2005; Enders and Vander Wall, 2011). Additionally, it is plausible that the root suckering version of *D. cinerea* and other encroaching species may be more important than seed

FIGURE 3 | The predicted number of minutes that rodents foraged at seed trays (95% confidence interval in gray) as a function of grass biomass (kg/ha) in the surrounding environment (0.25 ha).

dispersal in the establishment of *D. cinerea* and other encroachers (Wakeling and Bond, 2007).

Shrub encroachment is altering tropical savannas (Stevens et al., 2016a,b) and our results suggest a potential role for rodents in mitigating their spread. However, rodent-shrub interactions will need to be evaluated on more ecologically relevant scales, while accounting for variability in the placement and relative abundance of seeds (Lichti et al., 2014; Yi and Wang, 2015) before we can interpret the role of rodents in limiting the encroachment of woody plants. Future work should explicitly examine rodent and seed interactions (Forget and Wenny, 2005; Wróbel and Zwolak, 2013), instead of assuming seed predation or dispersal based on previous research, laboratory studies, and natural history accounts. If rodents provide this critical service, it highlights the consequences of the loss and decline of seed-eating mammals (Hurst et al., 2014; Mills et al., 2018) and the need to maintain savannas' thick grassy-layer that facilities seed predation, which is threatened by chronic overutilization by domestic and wild ungulates.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the University of Florida's Institutional Animal Care and Use Committee (#201509045).

AUTHOR CONTRIBUTIONS

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021. 676572/full#supplementary-material

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