

# **Pyric herbivory: Understanding fire-herbivore interactions in Gorongosa National Park**

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## Preface

In order to better understand the controlled burns, or quemadas frias, in Gorongosa, I went out to the field this past summer with the team in charge of lighting the fires. It really is quite a simple process, and the team had already begun before I had even made it out of the cab of the truck. Two men with drip-torches burned a strip along the road and another deeper into the savanna, leaving a trail of fire in their wake. Taking the wind into account, they used the road as a natural firebreak to prevent the fires from spreading out of the area of interest. A dozen or so men stood at the ready with big rubber beaters and a couple more with water backpacks to further maintain control of the flames.

The flames moved fairly quickly through the grass, though the speed and strength of the fires were largely determined by the wind. The ground left behind by the fires was not completely denuded by the flames; small patches of only partially charred grass escape. The flames in areas with particularly dry grass were able to grow large enough to reach the lower branches of trees, wilting and burning their leaves up to two meters high. Where the grass was still partially green, however, the ground smoldered rather than erupting into full-fledged flames. Because of sunlight and humidity levels, the team was only able to work between about 10:30 in the morning and 3:00.

On the drive out, I had asked Alfredo Matavele from the Department of Conservation and Law Enforcement about how they decide when and where to light the fires. He told me that their main goal is to burn areas that are very dry to accomplish two things: prevent late-season fires that can easily grow out of control and remove old vegetation to promote nutritious regrowth. Every year they burn a big circle around Gorongosa to create a firebreak of sorts that prevents fires from communities in the buffer zone from spreading into the park. Like Gorongosa's controlled burns, these communities burn their surroundings to renew the land for better crops and to protect their settlements from larger late-season fires. They may also light fires to help with hunting, using the flames as a way to flush animals from

the bush.

I asked how the recent cyclone Idai might have affected this year's burning. According to Matavele, the combined effects of the dry wet season before the cyclone and the serious flooding that followed increased the proportion of dry and dead grass by July, leading to a greater risk of large late-season fires in the park and prompting the burn team to light more controlled burns. All of the rangers, or *fiscais*, stationed around the park were instructed to keep an eye on the grass in their area and let Matavele know if it seems to be getting too dry. Because Gorongosa employs so many *fiscais*, they are able to monitor large portions of the landscape and thus instate an effective, if informal, burning regimen.

It is clear that these fires have an immediate and dramatic impact on the animals in the area, from insects all the way up to large mammalian herbivores. The sky above the flames was littered not only with ash but also with huge flutters of butterflies and clouds of grasshoppers escaping the blaze. Every now and then a stray oribi or kudu darted out from the grassland to cross the road to safety. The men walking with the drip-torches did their best to save any animals they came across that would not otherwise be able to make it out, such as tortoises. Not all the animals are so lucky, however. When I visited the park in 2017, we found a huge python very close to one of the main roads that had been singed almost to death in a fire. It looked as though it had tried to escape to a termite mound but had not quite made it all the way to the top and died about a week later from its wounds. Witnessing the immediate impacts of these fires made me curious about the way plants and animals respond to their long-term effects, leading to the development of this project.

## Abstract

Fire plays a major role in determining the structure and dynamics of tropical savannas. By removing old biomass and promoting nutritious regrowth, it facilitates the coexistence of grass and trees characteristic of these ecosystems. Though extensive research has been conducted on the immediate and lasting effects of these disturbances on the density and nutritional quality of vegetation, the interactive effects of fire and herbivory on the nutritional landscape are more poorly understood. The frequency with which an area burns may dictate the overall palatability and biomass density of savanna grasses, generating heterogeneity in the vegetation available to grazers and promoting herbivore diversity through niche partitioning.

This study examines the interaction of fire, vegetation and herbivores in Gorongosa National Park in Mozambique, in which controlled burns are used as a tool of active management. I found that though the amount of vegetation available to grazers did not vary significantly with fire frequency or herbivory pressure, forage material had significantly higher protein and calcium content in areas with higher grazing intensity and burn frequency. I also found that ungulates tend to avoid recently burned areas, but that small ungulates in general and nonruminants in particular return to burned patches more quickly than large ungulates and ruminants. Accordingly, fires create a heterogeneous landscape of burned and unburned patches that ungulates selectively graze upon based on their body size and digestive strategy.

## 1 Introduction

For decades, ecologists have been trying to determine the factors contributing to the characteristically high diversity of mammalian herbivores in the African savanna. Many mechanisms have been invoked to explain their coexistence: perhaps the presence of some herbivore species facilitates the existence of others by stimulating grass regrowth during the growing season, or perhaps uneven predation pressure on certain species limits competition for resources. Different herbivore species might each occupy their own location in dietary

niche-space, selecting different plants or plant parts while foraging to decrease competition with other species [1–6]. This coexistence still remains an open question in many savanna ecosystems and continues to be an intriguing topic of research today.

At the broadest scale, resource partitioning be the result of the different foraging strategies utilized by mammalian herbivores. Grazers eat predominantly  $C_4$  grasses; browsers subsist mostly on  $C_3$ , non-grass plant material such as trees, shrubs, and forbs [5]. Allometric scaling, or size-dependent organismal characteristics, might also affect the ways in which herbivores interact with their environment, altering their perception of resource availability [7] and influencing their utilization of certain forage characteristics [8]. Jarman and Bell first investigated the effect of herbivore body size on grazing site selection in the early 1970s [9, 10], which has led to more recent research detailing resource partitioning along the quality/quantity axis [11, 12]. This hypothesis is particularly applicable to savanna environments, because their characteristic variation in rainfall and fire create a heterogeneous landscape that might foster herbivore diversity based on allometric selection for forage quality [13, 14]. However, as compelling as this hypothesis may be, ecologists have struggled to find strong empirical support for size-dependent resource selection. This study combines insight from allometric scaling and fire ecology to understand how the characteristic heterogeneity of African savannas is created and maintained by fires and how it affects the grazing behavior of animals of varying body size.

## 1.1 Herbivore Grazing Patterns

In the early 1970s, Richard Bell set out to document the forces driving the migration patterns of large grazing herbivores in Tanzania’s Serengeti National Park. He proposed that not all species of grazing herbivores eat the same part of the grass, which he thought to be the result of differences in their digestive systems and metabolic rates. In the Serengeti, Bell noted, zebras tend to move through an area first after a rainfall, and by grazing relatively indiscriminately on all plant parts they prime the landscape for wildebeest, which



selectively eat only certain grass tissues and leave the rest behind for the species that come later. Through this pattern of succession, many species of herbivores are able to temporally partition their resource utilization [10].

Bell went on to explain that there are two main drivers of the pattern of succession: digestive strategy and body mass of herbivore species. Most even-toed ungulates (a taxonomic group including antelope and giraffes) are ruminants, relying on pregastric fermentation to digest their food. These animals are effective at extracting protein from their food but require significant amounts of time and energy to do so. For this reason, they need to be relatively selective of the material they graze upon, choosing plant tissues and species with high protein content and low lignin content. Conversely, nonruminants such as zebras and warthogs carry out the fermentation process in their small intestine. Food passes much more quickly through the digestive system of such animals, but they are not able to extract as much protein from plant matter as ruminants. Unlike ruminants, which are thought to select for highly nutritious plant matter, nonruminants are less limited by the rate of passage of material through the gut and therefore are generally thought to be less choosy about the quality of their forage material, instead focusing on consuming large quantities of food [10, 15]. Body mass also plays a role in determining herbivores' selectivity for grazing sites. Smaller animals have higher metabolic rates and therefore higher relative maintenance requirements. To meet these requirements, they are thought to be more selective in their foraging, eating mostly the most nutritious plants and plant tissues. Small ungulates are also better suited physically to this feeding style because of their small stature and more delicate mouth parts. [9, 10].

Though these theories of herbivore grazing selectivity are useful generalizations, recent work suggests that the factors influencing foraging behavior might be more complex than originally proposed by Jarman and Bell. Few studies have convincingly empirically supported the Jarman-Bell principle, and researchers are currently re-evaluating the grazing-succession model for the Serengeti [16]. New technology, such as DNA metabarcoding, has allowed

researchers to have a more finely-tuned understanding of the extent to which the diets of various ungulate species overlap and how much the above theoretical frameworks hold true under scrutiny. By analyzing the species composition and richness of the diets of large mammalian herbivores, researchers have found that though dietary overlap is greatest between species with similar guild assignments (ie those that ate proportionally similar amounts of grass and browse) and with similar body sizes, each herbivore species has a unique diet [6]. This suggests that though resource partitioning may be important in promoting diversity among mammalian herbivores, factors other than body size and foraging strategy might determine the degree to which species' diets overlap. However, not all mammalian herbivore communities have similarly low degrees of interspecific dietary overlap. For example, a study of the mammalian herbivore community in Mozambique's Gorongosa National Park (PNG) in 2016 found high levels of dietary overlap between species, particularly in grazers [17]. PNG is by no means a typical ecosystem, as it is still recovering from a decades-long armed conflict and its large mammalian herbivore community is still in flux. However, the relatively high degree of interspecific dietary niche overlap suggests that there is still more to learn about the extent to which the Jarman-Bell Principle governs herbivore foraging behavior, especially in PNG.

## 1.2 Landscape Heterogeneity in the Savanna Ecosystem

The dynamics of savanna ecosystems are defined by a suite of large-scale processes such as fire and herbivory, the interaction of which creates spatially and temporally heterogeneous landscapes characterized by extensive grasslands interspersed with trees and shrubs [18–20]. Uneven grazing pressure, combined with the effects of rainfall and soil fertility, influence the frequency and intensity of savanna fires, creating patches of unburned, slightly burned, and severely burned areas that then become dominated by different vegetation types [21, 22]. Fire is generally understood to be a key factor in preventing the dominance of trees over the grassland, as areas that burn more frequently have been shown to have a lower quantity

and diversity of woody vegetation [22–24]. Frequent burning events also affect understory vegetation, reducing total grass biomass while promoting the regrowth of high-quality forage material with low fiber content and high protein content [20, 25, 26]. Extensive research has also focused on changes in savanna vegetation immediately following a fire, showing that the young plant regrowth is much more nutritious and palatable to herbivores than the old, fibrous vegetation consumed by the fire [21, 27–33].

Burn intensity is largely influenced by seasonality, with late dry season fires burning hotter and spreading farther than those occurring earlier in the season [23, 34]. In many savanna ecosystems, wildlife managers and local community members light controlled fires, or “cold burns”, in the early dry season to reduce the fuel load of inevitable late-season fire and promote a seasonal mosaic composed of recently burned, previously burned, and unburned land [35, 36]. Such is the case in PNG: every year, park officials light a series of cold burns throughout the road network and around the periphery of the park to prevent more dangerous late-season fires. However, very little empirical data is currently available on the effects of such fires on the surrounding plant and herbivore communities in PNG. To date, most research on fire ecology in savannas has focused either on wild fires [27, 33, 35, 37] or manipulated fire exclosures [20, 22, 23, 25] but very few have examined the effects of prescribed burns. Recent research suggests that the unique dynamics of managed fires, like those in PNG, might impact the landscape in ways distinct from completely natural or completely controlled fires [38], highlighting the need for further research on the effects of the cold burns of PNG on the surrounding plant and herbivore communities.

### **1.3 Pyric Herbivory**

Perhaps more ecologically important than the independent effects of grazing or fire on the savanna ecosystem is the interaction between the two processes, termed pyric herbivory [33]. Previous studies have found that grazers tend to be drawn towards recently burned areas and away from those that burned in the more distant past, and by selectively grazing

upon these patches decrease the fuel load and therefore affect the probability of future fires [25, 26, 33]. Fires remove desiccated vegetation and promote highly nutritious regrowth with higher concentrations of Ca, P, N, Mg, and K [27–32] and herbivores feeding on this post-fire regrowth have been shown to exhibit greater mass gains [39, 40]. Moreover, fires have been shown to influence the movement and foraging patterns of herbivores, even more so than other factors such as actual evapotranspiration and soil fertility [37]. As a result, savanna and grassland ecosystems that burn more frequently have been shown to have greater abundance and diversity of herbivores on regional scales [20, 25, 37, 41–44].

## 1.4 Thesis Aims

The goal of this study is the interactions between herbivory and fire in PNG at the landscape scale. I interrogate the following questions: Where do fires happen in PNG? How do these fires affect the quality and quantity of vegetation? And how does this in turn affect herbivore landscape use patterns?

I use multiple lines of evidence to address these questions. First, I will examine how a location’s fire return interval, or average time between fire events, is influenced by major landscape factors such as its distance from rivers, Lake Urema, and the road network. Secondly, I will investigate the response of vegetation to the combined effects of herbivory and fire, modeling how physical characteristics such as percent grass cover and woody biomass density and chemical characteristics such as protein, Ca, and P content vary with these factors. Finally, I will investigate how herbivores respond to the presence of fire by examining ungulate diversity and abundance in burned and unburned sites over the course of a year and analyzing how selection for burned or unburned areas changes with increasing time since fire. Combined with the vegetation data, this will allow me to understand how ungulates in PNG alter their grazing behavior in response to fire-induced changes in the quality and availability of forage material.

I expect fires to be significantly more frequent in areas close to the road network and

to Chitengo, as park officials often focus on these areas when setting their controlled burns in the early dry season. Conversely, I expect fires to be less frequent in areas close to Lake Urema and near rivers due to patchier fuel loads and greater moisture content of understory vegetation [45]. I also expect fires to be less frequent in locations close to pans, because these areas retain water longer into the dry season and their nutrient-rich vegetation attracts large herbivores which keeps fuel load low [46, 47]. Based on the results of previous research in other savanna and grassland ecosystems [20, 22, 23, 25, 26], I predict that areas that burn more frequently will have lower densities of woody and understory biomass but more nutritious understory vegetation (as measured by protein content) than areas that burn less frequently. I also expect these areas to attract a greater diversity and abundance of ungulates, as was found to be the case in other ecosystems [20, 25, 33, 41–43]. I expect small ungulate species in general and ruminants in particular to be more likely to occupy burned areas than larger ungulates and nonruminants, but for this trend to become weaker with increasing time since fire.

Fires are major drivers of ecosystem change, but there is very little recent empirical data on the effects of the controlled burns in PNG. A broader goal of this study is to lay the groundwork for further research into the impacts of these large-scale disturbances, the results of which could potentially help inform management decisions in the future.

## 2 Methods

### 2.1 Study Species

In this study, I examined the landscape occupancy and utilization of 16 species of large mammalian herbivores (Table 1). Of these species, 14 were ruminants and two were hindgut fermenters. Species were also classified by *a priori* guild assignments, which broadly describe their foraging behavior as browsing, grazing, or mixed-feeding. As mentioned above, grazers eat predominantly grasses and sedges whereas browsers feed almost exclusively on forbs and

woody plants. Some species, such as impala, are classified as “mixed feeders”, switching back and forth between guilds as forage availability allows [16, 48].

Common Name	Latin Name	Digestive System	<i>A priori</i> Guild	Average Body Mass (kg)	Estimated Density (individuals km <sup>-2</sup> )
Buffalo	<i>Syncerus caffer</i>	Ruminant	Grazer	450	0.318
Bushbuck	<i>Tragelaphus scriptus</i>	Ruminant	Browser	30	0.957
Duiker, Common	<i>Sylvicapra grimmia</i>	Ruminant	Browser	16.7	0.013
Duiker, Red	<i>Cephalophus natalensis</i>	Ruminant	Browser	12	0.011
Eland	<i>Taurotragus oryx</i>	Ruminant	Mixed-feeder	340	0.046
Elephant	<i>Loxodonta africana</i>	Hindgut fermenter	Browser	1725	0.318
Hartebeest	<i>Alcelaphus lichtensteini</i>	Ruminant	Grazer	125	0.311
Impala	<i>Aepyceros melampus</i>	Ruminant	Mixed-feeder	40	3.501
Kudu	<i>Tragelaphus strepsiceros</i>	Ruminant	Browser	136	1.111
Nyala	<i>Tragelaphys angasii</i>	Ruminant	Mixed-feeder	73	1.072
Oribi	<i>Ourebia ourebi</i>	Ruminant	Grazer	20	2.304
Reedbuck	<i>Redunca arundinum</i>	Ruminant	Grazer	40	5.957
Sable Antelope	<i>Hippotragus niger</i>	Ruminant	Grazer	185	0.450
Warthog	<i>Phacochoerus africanus</i>	Hindgut fermenter	Grazer	45	6.225
Waterbuck	<i>Kobys ellipsiprymnus</i>	Ruminant	Grazer	160	32.227
Wildebeest	<i>Connochaetes taurinus</i>	Ruminant	Grazer	123	0.326

Table 1: Characteristics of species considered in this study [48–52].

## 2.2 Study Site

This study was conducted in Gorongosa National Park (PNG), a protected area encompassing 3,688 km<sup>2</sup> of land in the Sofala province of Mozambique, located at the southern end of the Great Rift Valley System (−18°58′N, 34°21′S). The vegetation of PNG is highly varied, ranging from montane forest and grassland to miombo/mixed woodlands and alluvial plains. PNG receives an annual rainfall of approximately 700–900mm, most of which occurs in the wet season between December and May. During this time, almost 40% of the park floods, leaving behind a highly productive floodplain in the dry season that can support many species of herbivores [53, 54].

This study was concentrated around the road network of the park, which is located entirely within the Rift Valley Region (Figure 1). The vegetation in these areas consists of mixed *Acacia-Combretum* savannas and open grasslands. All data collection for this study was conducted between mid-June and mid-August 2019 with the exception of the long-term

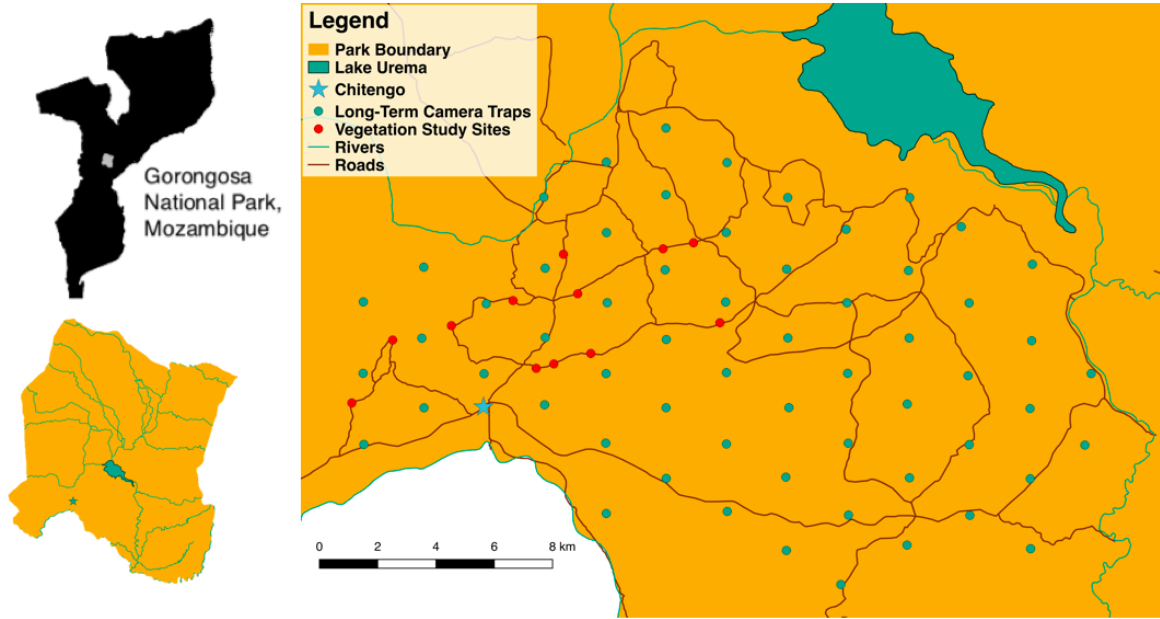


Figure 1: Map of long-term camera trap locations and vegetation study sites, showing locations of Lake Urema, Chitengo, rivers, and roads. Insets show the location of Gorongosa National Park within Mozambique and the location of Lake Urema, rivers, and Chitengo within PNG.

camera trap data which was collected between July 2017 and July 2018.

PNG is a unique system to study because of its recent history of biological collapse and recovery. First established as a hunting reserve under Portuguese rule in the early 1920s, Gorongosa was renowned for its wide diversity of large mammals and became a national park in 1960. By 1974, Mozambique had declared its independence from Portugal and within three years was mired in an intense civil war centered in the Gorongosa region of the Sofala province. The war lasted 15 years (1977 - 1992) during which time Gorongosa's wildlife was hunted intensively for food and sale, leading to more than a 90% decline in large-herbivore biomass [52, 55].

Since the early 2000s, the Gorongosa Restoration Project has been working to implement active management strategies to help restore PNG's ecosystem to a healthy and stable state by complimenting natural recovery processes of remnant populations with translocations and reintroductions from other places in southern Africa. As mentioned above, part of the active management strategy utilized by the Gorongosa Restoration Project has involved

lighting cold burns in the early dry season to remove dry vegetation and prevent larger, more dangerous fires later in the dry season. However, this fire management program is not particularly formalized or cohesive throughout the park: rather than have a strictly organized fire program as has been done in other savanna ecosystems [21], rangers simply focus their burning efforts on areas that seem particularly dry.

There is clear evidence that the past two decades has seen substantial overall increases in wildlife biomass in PNG. However, the current composition of herbivore species differs significantly from pre-war herbivore communities. Before the war, large herbivores such as elephant, buffalo, and hippo comprised almost 90% of biomass in PNG, whereas in 2018 they totaled a mere 23%, overshadowed by waterbuck populations which now account for almost 75% of large herbivore biomass (see Table 1 for the most recent density estimates of the species considered in this study, based on wildlife counts from 2018). Because carnivore populations have also been slow to rebound after the war, it is possible that weak competition and predation pressures have contributed to the asymmetric recovery of the large mammalian herbivore community [52].

## **2.3 Research Methods**

### **2.3.1 Fire Return Interval**

**PLOT SETUP** - To evaluate the effects of fire on vegetation characteristics, I established 12 plots in places with different fire histories using a 500m resolution fire regime map based on the Burned Area product from NASA’s MODIS satellites (MCD64A1) [56]. Fire return interval (fire frequency, FRI) was calculated for the period from 2000-2018. I selected six approximate locations of interest in open woodland habitats with  $FRI < 2$  years and six in similar habitats but with  $FRI > 2$  years. A random number generator was used at each approximate location to determine which side of the road to go to, as well as the angle and distance from the road. This point became the first corner of the plot, and the other three



were placed using cardinal directions to make an 18m x 18m plot. See Figure 1 for map of PNG and study sites.

VEGETATION SURVEYS - After setting up the 18m x 18m plot, four 1m x 1m quadrats were placed in each of the corners and surveyed on a fine scale (Figure 2). The height of the tallest grass was recorded, as well as the percent cover of grasses, forbs, and sedges. All the biomass in a 0.5m x 0.5m subsection of these quadrats was then destructively sampled and taken back to the lab to measure the fresh weight. These samples were dried at 55°C for at least 48 hours, until they had been dried to a constant weight, providing an estimate for dry matter production per square meter and dry matter content of the foliage. The dried foliage from the four quadrats within each of the 12 study sites was pooled and sent to the University of Wisconsin-Madison Soil and Forage Analysis Lab for standard near infrared reflectance spectroscopy (NIRS) and supplemental wet chemistry analyses. All the understory biomass in the 0.5m x 0.5m area was analyzed, providing an estimate of the quality of the vegetation of each site. The NIRS and wet chemistry forage analyses provided estimates of crude protein (CP), neutral detergent fiber (NDF), lignin, ash, and several minerals for each sample. These surveys were conducted between June 19th and June 30th, 2019.

UNDERSTORY BIOMASS SURVEYS - In each of the 12 vegetation study sites, 36 measurements were taken with a disk pasture meter (DPM) to estimate the overall biomass of the 18m x 18m plot. 47 paired observations from across the 12 sites were used to determine the relationship between aboveground dry matter production and DPM measurements (recorded as the settling height of the metal disk), following the basic methodology outlined in [57] and [58]. The data were first analyzed using a simple linear regression analysis of dry matter production as a function of disk settling height, and were analyzed again with the disk settling height subjected to logarithmic, square, square root, and reciprocal transformations to ensure the best linear fit of the regression. The results of these regression analyses are

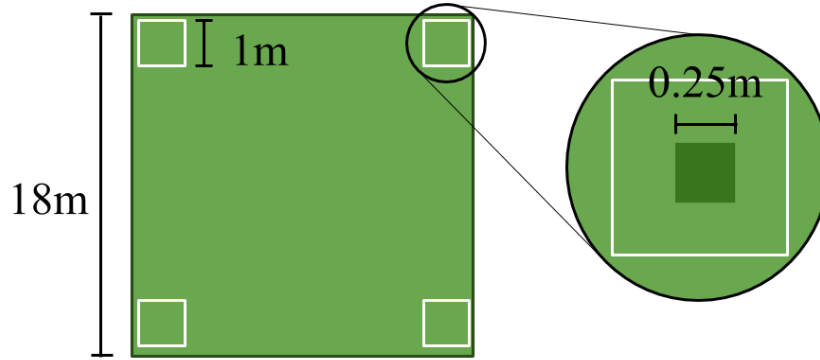


Figure 2: Schematic of plot layout for vegetation surveys. The large green square on the left represents one whole 18m x 18m plot and each of the four white squares are the 1m x 1m quadrats that were used for species composition surveys. A small 0.25m x 0.25m square within each quadrat was clipped to the ground, dried, and sent to a lab for nutrient analysis.

presented in Table 2, and based on the  $R^2$  values I found that taking the square root of the disk height provided the best fit. There was one outlier in the data, indicated in Figure 3 with a red outline, that was excluded from these analyses. For all further analyses of biomass quantity, the data used are estimates of dry matter production converted from DPM measurements based on this relationship.

Transformation	$R^2$	Intercept	Slope
$X$	0.3275	130.27	22.06
$\log(X)$	0.3644	16.30	152.71
$X^2$	0.2378	207.2771	1.0633
$\sqrt{(X)}$	0.384	-11.89	118.04
$\frac{1}{X}$	0.3521	414.99	-663.96

Table 2: Results of regression analyses of aboveground dry matter production as a function of disk height based on 47 paired observations. Disk height was subjected to logarithmic, square, square root, and reciprocal transformations. 48 paired observations were recorded, but one was an outlier and was thus excluded from these analyses.

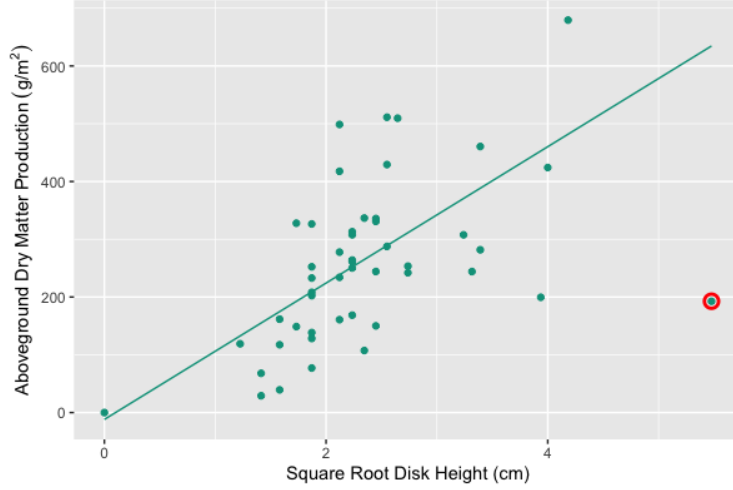


Figure 3: Linear regression showing the relationship between understory dry matter production and the square root of disk settling-height based on 47 paired observations. The point highlighted in red is an outlier and was excluded from analysis. The calibration equation is  $y = -11.89 + 118.04x$  ( $R^2 = 0.384$ ),

WOODY BIOMASS SURVEYS - I estimated the volume of the trunks of all the trees in each study site by measuring their height and circumference at breast height (approximately 1.3m from the ground). To estimate the height of a tree, a researcher of a known height was used as a unit of measure and stood at the base of the tree while another researcher counted how many of these units tall the tree was. These height measurements were later converted into standard units of measure. From these values, the volume of the trunk of each tree was estimated by approximating the shape to be that of a cone and using the equation:  $V = \pi r^2 \frac{h}{3}$  [59]. Woody biomass was calculated using the average wood density for eight major tree species found in [60] and [61].

CAMERA TRAPS - Bushnell Trophy Cam Trail Cameras were used to further monitor herbivore behavior in each of the study plots. The cameras were strapped to trees near the plots at a height of approximately 1m and programmed to record minute-long videos when stimulated by motion. Cameras automatically switched from color mode during the day to infrared mode (black and white) at night, allowing for 24-hour behavioral classifications. Six cameras were rotated through the twelve plots over the course of five weeks between June

26th and August 9th, 2019 to obtain two to three weeks of video footage for each study site except for plots 4 and 10, the number of days of footage was limited to one week due to camera malfunctions. Videos with no animals in which the cameras were triggered by wind or other objects were removed prior to further analysis. A total of 685 videos recorded individuals of the 16 study species in Table 1 across all 12 study sites. See Table S1 for the total number of days of video and number of videos containing species of interest recorded in each study site.

Each video was analyzed using Behavioral Observation Research Interactive Software (BORIS). Behavior was categorized into the following broad classes: (1) Grazing: the individual is foraging with their head down, eating grass or forbs; (2) Browsing: the individual was foraging with their head up, feeding on woody plant species; (3) Other: the individual was standing still, walking, or running. (Though eating C<sub>4</sub> forbs is technically browsing, it was often difficult to distinguish what plants herbivores were eating and thus all head-down foraging was considered to be grazing.) The number and species of each animal in the video was recorded along with the time of day (day or night) and the amount of time the animals spent in each behavior class. In videos with more than one individual of a given species, the activity of only one randomly selected focal individual of that species was recorded. These data were used to measure herbivore site selection by calculating the combined grazing pressure of all species at each site using the following equation:

$$grazing\ pressure = \sum_{species} \frac{total\ time\ grazing}{total\ hours\ of\ video}$$

### 2.3.2 Herbivore Succession

Data were collected using Bushnell TrophyCam camera traps spaced across the woodland south of Lake Urema over the course of one dry season (July - September) and one wet season (December - March) from 2017-2018. The grid of 60 cameras encompassed 300km<sup>2</sup> in the savanna woodland (Figure 1), which is relatively accessible through PNG's road network

and has a high density of large mammals [62,63] (see also <https://www.biointeractive.org/classroom-resources/wildcam-gorongosa>).

Each camera was mounted on a tree at a height of 1 meter and was placed facing an open area or small game trail to maximize animal detections and minimize false triggers. Cameras were programmed to take two photographs per trigger event with a delay of 30 seconds between triggers. This study considered all observations of a given species within 15 minutes of each other to be part of the same detection. The animals in each photograph were identified by trained undergraduate volunteers at the University of California, Berkeley under the supervision of Kaitlyn Gaynor, postdoctoral researcher at the National Center for Ecological Analysis and Synthesis. The *camtrapR* package in R was used to generate a record of detections from the photographs [63,64].

The study used all the camera trap data from July 1st, 2017 to July 1st, 2018 with a 15-minute buffer between each sighting to prevent repeated observations of the same individual at one point in time. Due to environmental factors and mechanical issues, the camera traps used in this study were often not functional for the entire duration of the time they were set up in the field. Based on the data from the photos taken by these cameras, a camera operation matrix was created to describe the dates each camera was functional during the time span of this study, which was then used to calculate the number of days of operation during a given time period.

The following analyses were conducted on a weekly basis over the course of the year. For each of the 60 cameras, a ‘weeks since fire’ variable was created by subtracting the date of the most recent fire at the camera from the date of each time period of analysis. To examine the transient effects of fires, locations were considered to be ‘burned’ during the 52 weeks (one year) following a fire, after which point they returned to the ‘unburned’ class. Dates of fires were determined from camera trap images of the fires. 48 of the 60 cameras did not witness any fires within a year of July 1st, 2017; 10 cameras recorded only one fire in this time period; and two cameras recorded two fires. See Table S2 for a list of fires with coordinates

and dates. Of the 12 total cameras witnessing fire events in this time period, 10 were located in areas with  $\text{FRI} < 2$  years. The frequency and locations of camera observations of the 16 focal ungulate species shown in Table 1 were used in the analyses described below.

## **2.4 Statistical Analyses**

### **2.4.1 Occurrence of Fire in PNG**

To understand what factors influence the frequency with which fires occur across PNG, I built a linear model of an area's FRI as a function of its distance from rivers, distance from Lake Urema, distance from pans, distance from the road network, and distance from Chitengo, including all these factors in one model. I included distance from roads and distance from Chitengo in this model because most of the fires that occur in PNG are controlled burns set by park officials as a way to lower the risk of more dangerous late-season fires causing damage to areas frequented by people in the park.

### **2.4.2 Vegetation Response to Fire**

I examined changes in vegetation in response to the frequency with which it was subjected to fire using a series of linear models. First I constructed a linear regression model of percent cover of graminoids as a function of FRI and grazing pressure, including both factors as fixed effects and site as a random effect to control for the pseudoreplication of the four sampling locations within each study site. I then built a similar model of percent cover of forbs, and another of understory biomass. Finally, I constructed another model of woody biomass with FRI and grazing pressure as fixed effects, but not including site as a random effect as there was only one data point per site.

In addition to these models of basic vegetation composition, I also examined the impact of fire and herbivory on the nutrient content of understory vegetation. I constructed a linear model of crude protein content with FRI and grazing pressure as fixed effects, again not

including site as a random effect because there was only one data point per site. I rebuilt this model once to analyze phosphorous content as a function of FRI and grazing pressure, and again to analyze calcium content as a function of FRI and grazing pressure.

### 2.4.3 Herbivore Response to Fire

COMMUNITY-LEVEL ANALYSES - The effects of the fires on herbivore populations were first examined at the community level. Herbivore diversity at each camera was calculated on a weekly basis over the course of the year using the Shannon diversity index calculated using the *vegan* package (version 2.5-6) in R [65,66].

Two linear models were constructed to examine the effect of fires on herbivore diversity. First, a linear model of diversity as a function of burn status (burned vs not burned in the past year) was constructed to understand herbivores' relative utilization of burned vs unburned areas. To examine how this site selection changed over the course of the year, a second model was constructed of diversity at burned sites as a function of date and time since fire.

SPECIES-LEVEL ANALYSES - To evaluate how herbivores of different sizes and gut types utilize burned and unburned areas differently, analyses of herbivore succession were also performed at the species level using a relative abundance index (RAI) to monitor herbivore abundance at each camera. RAI is defined as the number of captures per camera-day, which takes into account the unequal operating times of the cameras [67]. RAI was calculated for each species at each camera on a weekly basis following a fire event, as was done with the community-level analyses.

There were many weeks in which some species had an RAI of zero, which skewed the distribution of RAI values far away from normal. To overcome this issue, I used a hurdle model approach, first building logistic regression models to understand the processes driving the presence or absence of each species during each week and then linear regression models

to examine the factors underlying the RAI of the species that were present.

I used this hurdle model approach first to understand how the presence and abundance of herbivore species were affected by burn status (burned vs not burned in the past year), constructing a logistic regression model of species presence as a function of burn status and a linear regression model of species abundance as a function of burn status. I then used logistic and linear regression models to examine changes in species presence and abundance in burned areas as a function of time since fire and seasonality.

In an effort to understand which characteristics of an herbivore species might determine their sensitivity to a fire event, the above models were reconstructed including body mass and gut type as fixed effects. In all analyses, body mass values were log-transformed to meet assumptions of normality.

## **3 Results**

### **3.1 Occurrence of Fire in PNG**

Based on the results of a linear model, I found that a location's FRI changed significantly with distance from rivers, Chitengo, and roads (see Table 3). FRI tends to decrease with increasing distance from rivers but increase with increasing distance from Lake Urema, Chitengo, or from roads. This suggests that fires are more frequent along the road network and close to Lake Urema or Chitengo, but are more rare in locations close to rivers. FRI tended to be slightly higher in locations farther away from Lake Urema and closer to pans, but these results were not statistically significant.

### **3.2 Vegetation Response to Fire**

To understand how the vegetation available to herbivores as forage varies due to fire and grazing pressure, I built a series of linear models of certain vegetation characteristics across



	Estimate	Std. Error	t value	Pr(> t )	
(Intercept)	-3.9104	2.3710	-1.65	0.1066	
<b>Distance from Lake Urema</b>	0.2035	0.1018	2.00	0.0520	*
<b>Distance from Rivers</b>	-1.2764	0.2658	-4.80	< 0.0001	*
<b>Distance from Chitengo</b>	0.0013	0.0002	8.22	< 0.0001	*
Distance from Pans	-0.0012	0.0011	-1.13	0.2647	
<b>Distance from Roads</b>	1.3487	0.3269	4.13	0.00028	*

Table 3: Results of a linear model of FRI as a function of distance to Lake Urema, distance to rivers, distance to Chitengo, distance to pans, and distance to roads ( $F(5, 42) = 17.19$ ,  $p < 0.0001$ ). Asterisks and bold text are included to denote statistical significance.

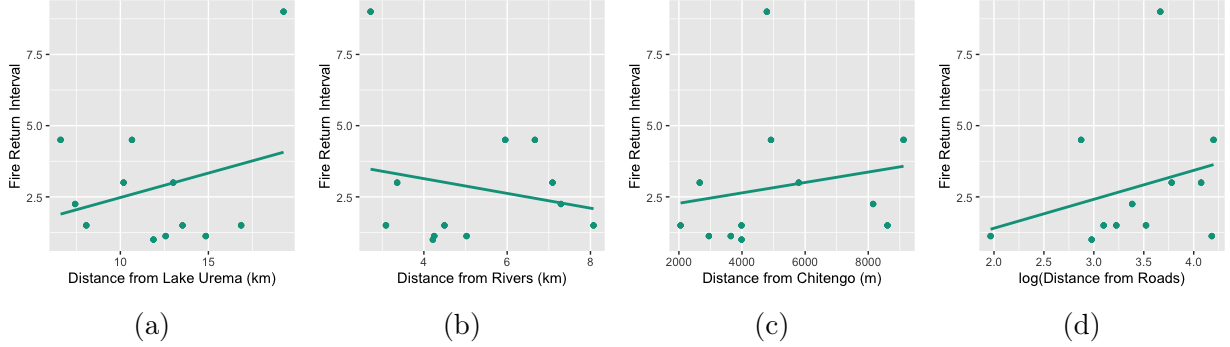


Figure 4: Change in FRI as a function of (a) distance from Lake Urema, (b) distance from Rivers, (c) distance from Chitengo, and (d)  $\log(\text{distance from roads})$ . Distance from roads was originally measured in meters and log-transformed to meet assumptions of normality. Points represent measured values; lines represent results of separate linear regressions for each predictor variable.

different fire regimes, using data collected from the twelve vegetation survey sites. Based on the results of these linear models, neither fire regime nor herbivory pressure significantly altered the percent cover of graminoids or forbs (See Figure 5a and b). Understory biomass was also not significantly affected by FRI or herbivory (See Figure 5c). Likewise, neither FRI nor herbivory significantly affected the density of aboveground woody biomass ( $F_{33,44} = 1.891$ ,  $p = 0.1451$ ), nor did they significantly influence the average mass per tree ( $F_{3,47} = 1.428$ ,  $p = 0.2464$ ). However, the total number of trees in each  $18\text{m} \times 18\text{m}$  plot did decrease significantly with increasing FRI (Figure 5d).

I also modeled several chemical characteristics of the understory vegetation as a function of FRI and herbivory pressure and found that crude protein content was significantly higher in areas with more intense grazing pressure, a trend that became stronger with increasing FRI (Figure 6). This suggests that in areas that burn more frequently, the relationship between grazing pressure and the crude protein content of understory vegetation is weaker than in

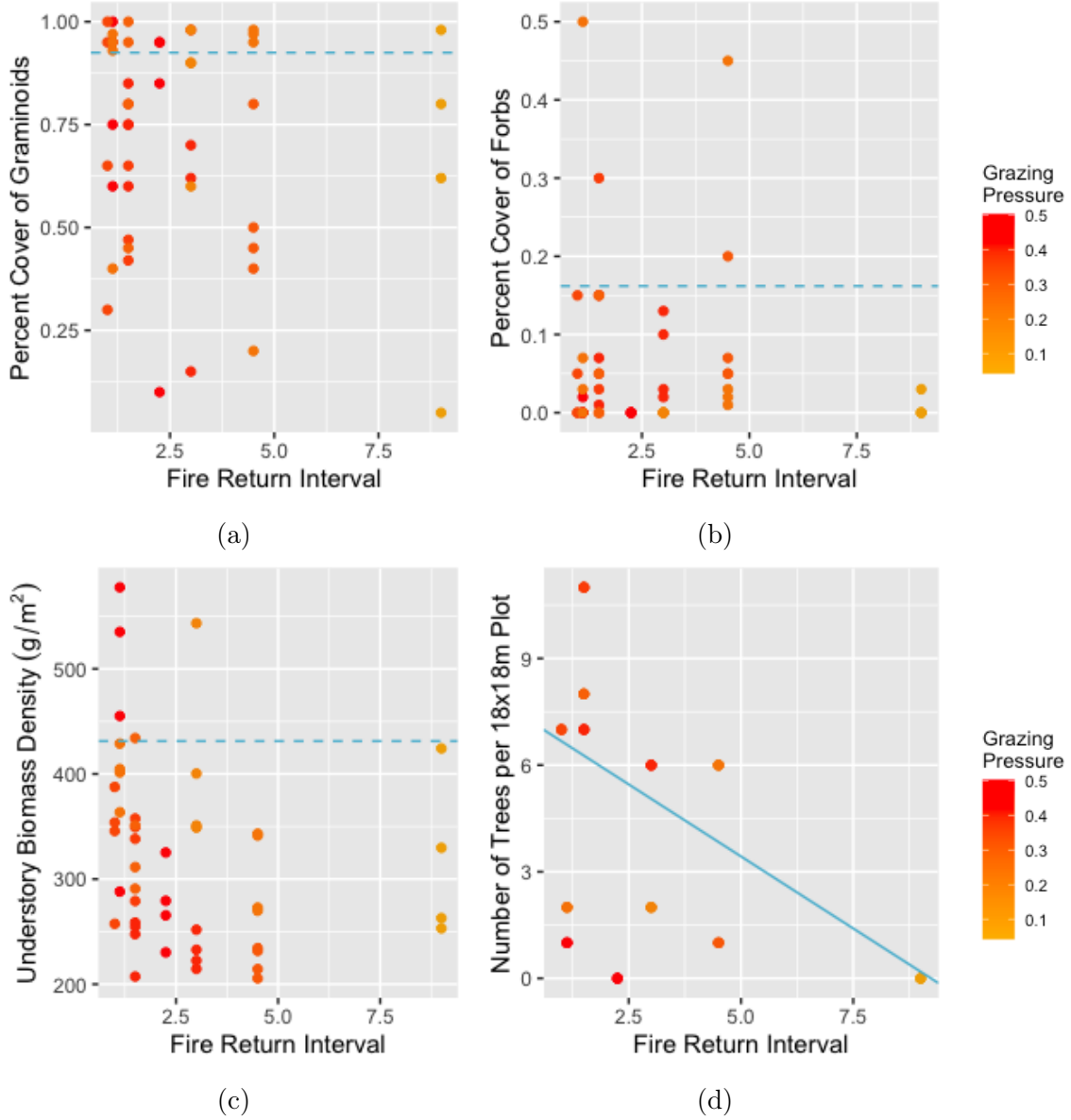


Figure 5: Vegetation characteristics as functions of FRI and grazing pressure. Points represent measured values, lines represent results of separate linear regression models for each predictor variable. Dashed lines indicate non-significant relationships.

(a) Percent cover of graminoids (grasses and sedges) as a function of FRI and grazing pressure (FRI:  $t_{44} = -0.909$ ,  $p = 0.368$ ; herbivory:  $t_{44} = -0.452$ ,  $p = 0.554$ ; FRI  $\times$  herbivory:  $t_{44} = -0.597$ ,  $p = 0.554$ ).

(b) Percent cover of forbs as a function of FRI and grazing pressure (FRI:  $t_{44} = -1.608$ ,  $p = 0.115$ ; herbivory:  $t_{44} = -1.521$ ,  $p = 0.1354$ ; FRI  $\times$  herbivory:  $t_{44} = 1.277$ ,  $p = 0.2084$ ).

(c) Understory biomass density as a function of FRI and grazing pressure (FRI:  $t_8 = -0.388$ ,  $p = 0.708$ ; herbivory:  $t_8 = -0.031$ ,  $p = 0.976$ ; FRI  $\times$  herbivory:  $t_8 = -2.127$ ,  $p = 0.066$ ).

(d) Tree density as function of FRI and grazing pressure (FRI:  $t_{44} = -2.217$ ,  $p = 0.0319$ ; herbivory:  $t_{44} = -0.506$ ,  $p = 0.6153$ ; FRI  $\times$  herbivory:  $t_{44} = 0.047$ ,  $p = 0.963$ ).

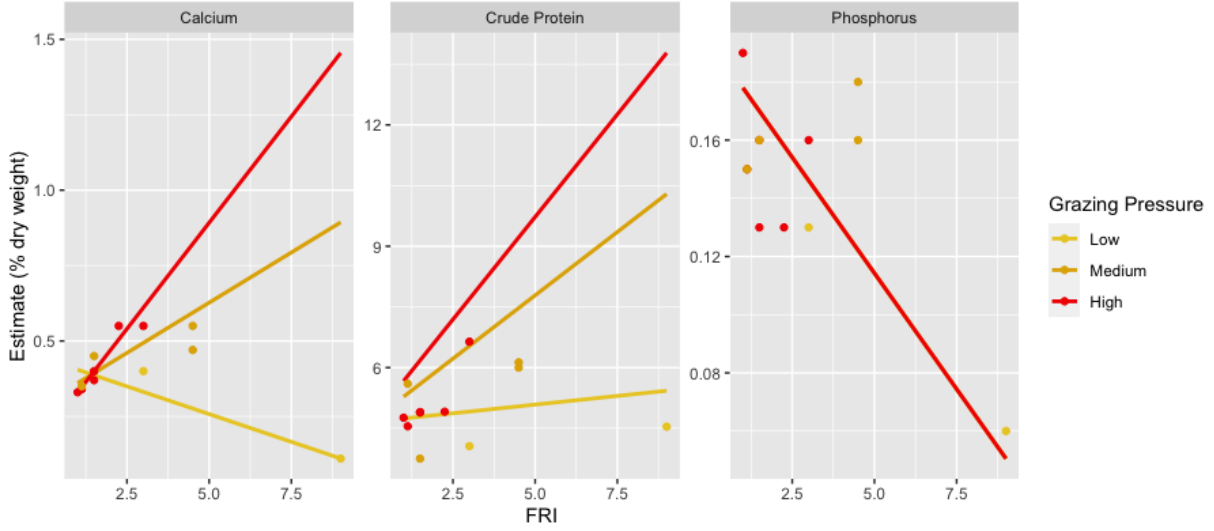


Figure 6: Crude protein, calcium, and phosphorus content of understory vegetation based on FRI and grazing pressure. Points represent measured values of nutrient content from each plot ( $n = 12$ ); lines represent results of linear regression models of crude protein (FRI:  $t_8 = -0.605$ ,  $p = 0.5619$ ; herbivory:  $t_8 = -0.832$ ,  $p = 0.42932$ ; FRI  $\times$  herbivory:  $t_8 = 2.560$ ,  $p = 0.0337$ ), calcium (FRI:  $t_8 = -6.949$ ,  $p = 0.0001$ ; herbivory:  $t_8 = -4.146$ ,  $p = 0.0032$ ; FRI  $\times$  herbivory:  $t_8 = 9.988$ ,  $p < 0.0001$ ), and phosphorus: (FRI:  $t_8 = -3.107$ ,  $p = 0.0166$ ; herbivory:  $t_8 = -1.357$ ,  $p = 0.2118$ ; FRI  $\times$  herbivory:  $t_8 = 2.010$ ,  $p = 0.793$ ).

areas that burn less frequently. Phosphorus content followed a similar trend, increasing with grazing pressure, especially in areas with high FRI. Phosphorus, however, did not differ significantly with grazing pressure, simply decreasing with increasing FRI.

### 3.3 Herbivore Response to Fire

COMMUNITY-LEVEL ANALYSES - Shannon diversity index did not differ significantly between locations that had experienced fire in the past year and those that were unburned ( $F_{1,1463} = 1.449$ ,  $p = 0.2288$  - see Figure 7a). Similarly, at the cameras that did burn, Shannon diversity did not change significantly with seasonality or time since fire, as shown in Figure 7b.

SPECIES-LEVEL ANALYSES - The results of a logistic regression model of the presence of species as a function of burn status showed that red duiker, impala, oribi, warthog, and waterbuck were significantly more likely to be found in unburned areas than in burned areas and hartebeest were significantly less likely to be found in unburned areas than in burned areas (see Figure S1a for mean presence of each species at burned and control cameras and

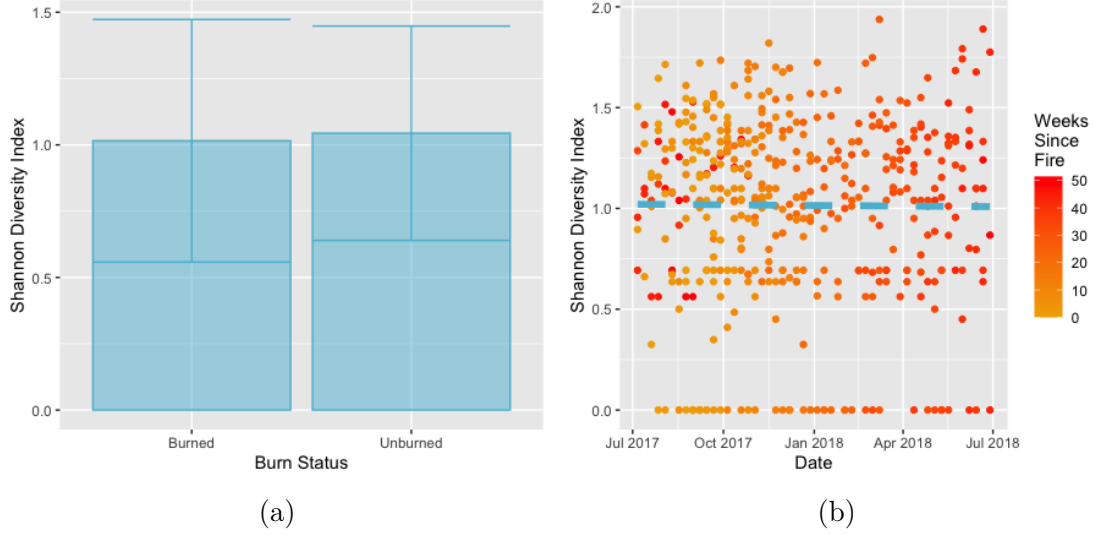


Figure 7: **(a)** Shannon diversity index of ungulates as a function of burn status. Bar height represents mean weekly diversity of locations burned in the previous year and of those that did not burn; errorbars represent standard error of the mean. **(b)** Shannon diversity index of ungulates in burned areas over time. Points represent weekly diversity of burned locations over the course of a calendar year, colored by time since fire; line represents result of linear model ( $F_{3,454} = 0.7313$ ,  $p = 0.5337$ ).

Table S3 for results of model). Bushbuck, impala, kudu, nyala, reedbuck, sable, and warthog were all significantly less likely to occupy a burned patch later in the year and with increasing time since fire; common duiker were significantly less likely to occupy a burned patch later in the year (see Figure S1b and c for mean presence of each species over the course of a calendar year and as a function of time since fire and Table S4 for results of logistic regression model).

A linear model of non-zero RAI as a function of burn status showed that only warthog and waterbuck were significantly more abundant in areas without a recent history of fire, as shown in Figure S2a and Table S5. No species was significantly more or less abundant in burned areas later in the year or with increasing time since fire (see Figure S2b and c for mean RAI of each species over the course of a calendar year and as a function of time since fire and Table S6 for results of linear regression model).

The above models were repeated with the addition of body mass and gut type as fixed effects. Based on the result of a model of site occupancy as a function of burn status, body mass, and gut type, I found that likelihood of occupancy of unburned sites decreased significantly with increasing body mass ( $\chi^2_1 = 15.22$ ,  $p < 0.0001$ ) and was generally lower

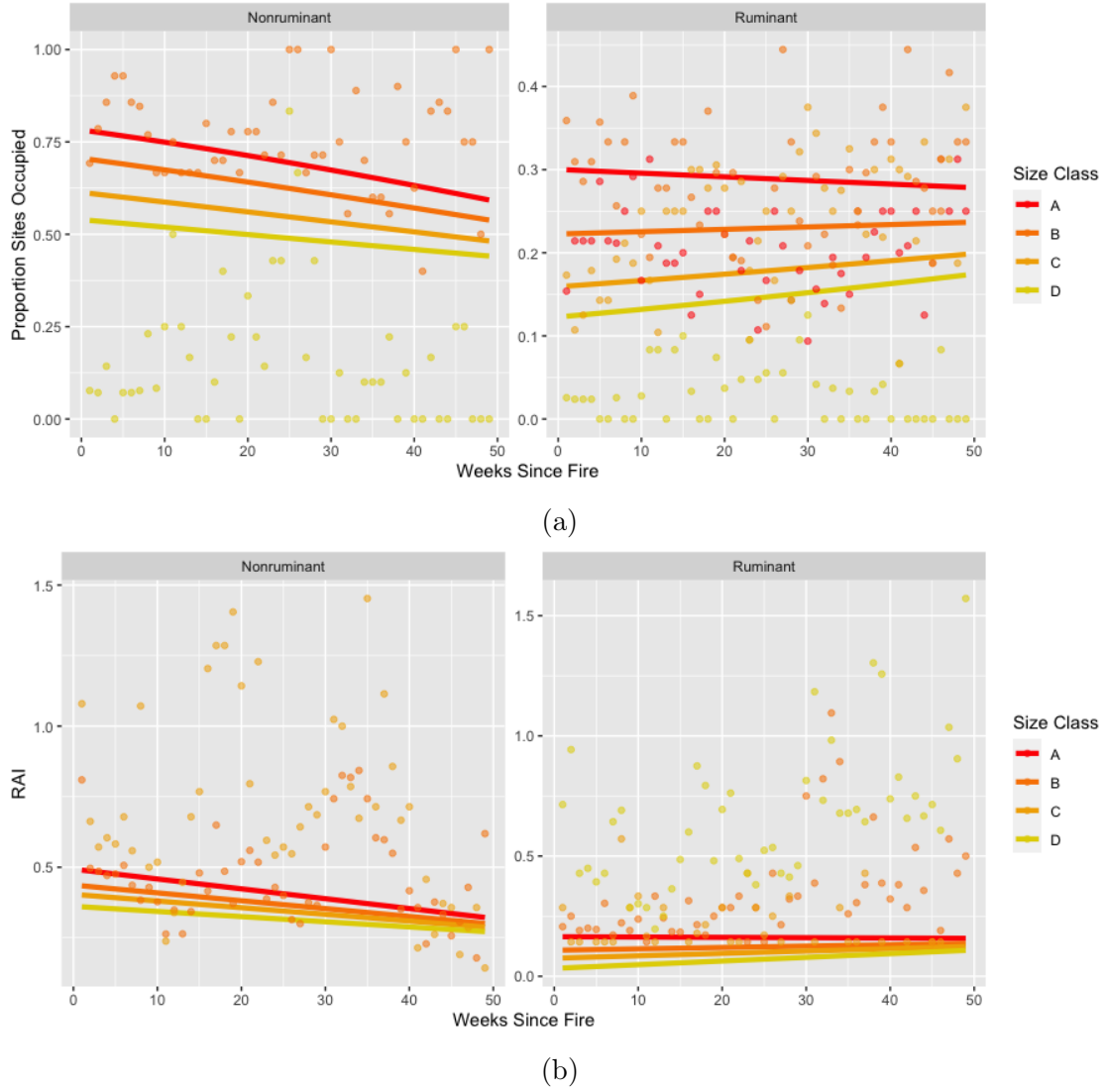


Figure 8: **(a)** Presence and **(b)** RAI of ungulates at burned locations as a function of time since fire, body mass, and gut type. In each figure, points represent mean weekly values for each gut type and size class. Size classes were determined as follows: A:  $2.77 \leq \log(\text{mass}) \leq 3.69$ ; B:  $3.69 < \log(\text{mass}) \leq 4.22$ ; C:  $4.22 < \log(\text{mass}) \leq 4.91$ ; D:  $4.91 < \log(\text{mass}) \leq 7.45$ . These values were determined by calculating the minimum, 1st quartile estimate, mean, 3rd quartile estimate, and maximum values of  $\log(\text{mass})$ .

Lines represent **(a)** result of logistic regression model of presence with size, gut type, weeks since fire, and seasonality as fixed effects and **(b)** result of linear regression model of RAI with size, gut type, weeks since fire, and seasonality as fixed effects. Seasonality is not included in either **(a)** or **(b)** because it had no significant effect on the values. For ease of viewing, the regression lines were drawn using only four distinct body sizes: A ( $\log(\text{mass}) = 2.77$ ), B ( $\log(\text{mass}) = 3.69$ ), C ( $\log(\text{mass}) = 4.22$ ), and D ( $\log(\text{mass}) = 4.91$ ).

in ruminants ( $\chi^2_1 = 12.92$ ,  $p < 0.0001$ ). Similarly, a model of RAI as a function of burn status, body mass, and gut type found that ungulates were significantly more abundant in unburned areas than burned areas, and though this trend did not appear to diminish with body size it was weaker in ruminants than in nonruminants ( $\chi^2_1 = 4.4228$ ,  $p = 0.0355$ ).

Though ruminant presence at burned sites generally increased with increasing time since fire, nonruminants followed the opposite trend ( $\chi^2_1 = 7.40$ ,  $p = 0.0066$ ), as can be seen by the general trends shown in Figure 8. In both ruminants and nonruminants, the presence of larger-bodied species tended to increase with increasing time since fire relative to smaller-bodied species ( $\chi^2_1 = 6.72$ ,  $p = 0.0095$ ). In the panel of Figure 8a pertaining to nonruminants, the largest size class of herbivores ('D') decreases less dramatically than the other size classes; in the panel pertaining to ruminants the largest class increases more dramatically than the other size classes. As a result, the predicted values for each size class become more similar with increasing time since fire. Seasonality was not shown in this figure because it did not significantly affect the presence of herbivores, regardless of body size or gut type ( $\chi^2_1 = 0.76$ ,  $p = 0.3838$ ).

Similarly, the abundance of ruminants tended to increase with increasing time since fire while the presence of nonruminants tended to decrease over the same time period, as can be seen by the general trends shown in Figure 8b ( $\chi^2_1 = 1.78$ ,  $p = 0.0474$ ). Regardless of gut type, abundance of larger-bodied species tended to increase with increasing time since fire relative to smaller-bodied species ( $\chi^2_1 = 4.03$ ,  $p = 0.0029$ ). In the panel of Figure 8b pertaining to nonruminants, the largest size class of herbivores ('D') decreases less dramatically than the other size classes; in the panel pertaining to ruminants the largest class increases more dramatically than the other size classes. As a result, the predicted values for each size class become more similar with increasing time since fire. As above, seasonality had no significant affect on RAI ( $\chi^2_1 = 0.0621$ ,  $p = 0.8033$ ).

## 4 Discussion

The interacting effects of fire and grazing have been shown to be major drivers of the complex dynamics of savanna and grassland ecosystems worldwide, but before this study, very little empirical information existed on the effects of fire in Gorongosa National Park. The goal of this study was to examine the interactions of fire, vegetation, and herbivory in PNG and lay the groundwork for future research on pyric herbivory in the park.

### 4.1 Occurrence of Fire in PNG

As expected, fire frequency was significantly higher in areas close to the road network and to Chitengo, likely a result of the early dry-season controlled burns lit by park officials to reduce the risk of larger, more dangerous late dry-season fires. Fire frequency was also significantly lower in areas closer to rivers, as was expected, likely because of greater understory vegetation moisture content and patchier fuel loads, as was found to be the case in riparian zones of the western US [68] and in Kruger National Park (KNP) in South Africa [45, 69]. Surprisingly, fires were more frequent in areas closer to Lake Urema. None of the sites considered in this analysis were close enough to Lake Urema to experience flooding in a typical year, but perhaps other environmental features, such as soil characteristics, differ in relation to distance from the lake and in turn affect the likelihood of fire. Distance from pans did not significantly affect the frequency with which sites burn, suggesting that any characteristics that might reduce the likelihood of fire (such as higher water content and lower grass biomass [46, 47]) are localized to the immediate vicinity of the pan and do not extend into the surrounding savanna.

### 4.2 Vegetation Response to Fire

Previous research on the effects of fire-grazer interactions on grass communities suggest that in the absence of fire, herbivory should have a relatively stronger impact on understory

biomass than in areas with frequent fires [27,42,43,70,71]. Based on these studies, I expected the frequency of fires and the intensity of grazing pressure to significantly affect the density and composition of understory vegetation in PNG. However, I did not find this to be the case: percent cover of graminoids and of forbs did not change significantly with herbivory pressure regardless of FRI; nor did understory biomass density (Figure 5). It is possible I was unable to fully capture variation in the composition of understory vegetation by examining plant functional type, and that the combined effects of FRI and herbivory act more strongly upon the species composition of a site’s vegetation. There might also be other factors responsible for the density and composition of understory biomass, such as time since last burn. Future studies might examine the more transient effects of fire on understory vegetation, modeling these factors as a function of time since fire and herbivory pressure rather than FRI and herbivory pressure.

Despite not finding significant changes in the physical properties of understory vegetation, I did find that fire frequency and grazing pressure significantly alter the chemical composition of understory vegetation. Though phosphorus content did not change significantly with grazing pressure, crude protein and calcium content were significantly higher in areas with more intense grazing, and even more so in areas with infrequent fires (Figure 6). Based on these results, it is unclear whether intense grazing pressure at these sites stimulates the growth of nutritious vegetation, as has been shown to lead to the formation of grazing lawns in other savanna ecosystems [42,71,72], or whether herbivores are selectively grazing in areas with the most nutritious vegetation. However, these results do suggest that this relationship between nutrient content and herbivory is stronger in areas that burn less frequently, suggesting that fire significantly changes plant-herbivore interactions.

Unlike other studies that found woody biomass density and individual tree size to generally be lower in areas with frequent fires [20–22,25,26,73–76], I did not find this to be the case in PNG. Surprisingly, the number of trees per 18m  $\times$  18m plot also did not decrease in response to increases in fire frequency as was the case in other savanna ecosystems [77],



instead increasing in areas with lower FRI (Figure 5d). It is possible that the fires in PNG are not intense enough or large enough to significantly stunt the growth of already-established trees but instead are able to facilitate the recruitment of new trees. Future studies might track the size and intensity of these fires to understand more fully the extent to which they are able to alter tree communities.

The 18-year fire history used in this study might not be representative of the longer-term fire history of the locations considered here. Much of the previous research on the effects of fire on woody vegetation has occurred in experimental burn plots in South Africa’s Kruger National Park (KNP) that have been subjected to prescribed fires in different seasons and at different frequencies for over 50 years [22, 23, 34, 76]. As a result, these experimental burn plots have had regular and consistent fire return intervals for decades. Such is not the case with the sites examined in this study. Very little information exists on the fire history of PNG, and the FRI of each of the sites examined here was calculated based on MODIS satellite data of the number of times burned in the last 18 years without consideration of the regularity of these fires. Future studies of the effects of fire on woody vegetation in PNG might take into account time since last burn in addition to FRI to be mindful of irregularities in the occurrence of fires.

It is also possible that the  $18\text{m} \times 18\text{m}$  plots surveyed in this study were not large enough to capture the response of woody vegetation to fire. The experimental burn plots of KNP are significantly larger, each covering 7 ha [22, 23, 34, 76]. It may be necessary for future studies in PNG to examine woody vegetation on similarly large spatial scales to fully capture fire-related dynamics.

### **4.3 Herbivore Response to Fire**

Though I expected ungulate diversity to be higher in recently burned areas than in unburned areas in PNG, I did not find this to be the case: ungulate diversity was not significantly different between burned and unburned areas (Figure 7a). Moreover, diversity in burned

areas did not change significantly with time since fire. Unlike the findings of previous studies that found higher levels of ungulate diversity in regions with frequent instances of fire [37], this study focused on highly localized diversity levels. The data presented here suggest that in PNG, the diversity of ungulates utilizing burned patches in the year following a fire does not differ significantly from the diversity of ungulates in unburned areas of the park.

Several species were more likely to be found in unburned patches than burned patches but very few were significantly more abundant in such areas. The higher sensitivity of presence than abundance to fire suggests that these species have some minimum standard for forage material below which a site can sustain no individuals but above which herbivore density at the site is limited by factors other than the vegetation, such as overall population density. In areas where fire prevents a sufficiently high quantity and quality of forage material, all nearby individuals would avoid grazing upon the patch; conversely, in locations that meet the foraging standards of a species, any number of individuals in the surrounding areas could feed upon the patch. The results of this study suggest that fires in PNG affect the number of patches that satisfy these requirements for several ungulate species and by doing so influence the herbivores' utilization of burned areas. To test this theory, future studies might examine species RAI values in burned and unburned areas in relation to the estimated overall densities of each species shown in Table 1.

The model of species presence over time found several significant three-way interaction terms between weeks since fire, date, and several species (Table S4). Though it is difficult to interpret just exactly what these three-way interaction terms mean, they suggest that these species are all significantly less likely to occupy burned patches later in the year and with increasing time since fire, but when these factors acted in parallel (ie before the next years' fires), the effect was somewhat diminished. These three-way interaction terms contribute very little to the predicted proportion of burned patches occupied relative to the two-way interactions of date and species or weeks since fire and species, suggesting that this may not be a particularly ecologically significant phenomenon.

When interpreting these species-specific results, it is important to consider that due to small sample sizes, it is possible that these trends are governed by stochasticity more so than meaningful ecological trends. As such, the analyses of body mass and gut type might shed more light on the ecological processes driving the interactions between fire, vegetation, and herbivory. As predicted, ungulate selection for unburned patches differed significantly with body size and gut type, suggesting that allometric scaling and digestive strategy do play a role in ungulate site selection, just as was proposed by Jarman and Bell [4, 9, 10], and that the effect of fire on the landscape is large enough to influence these trends. The data suggest that small-bodied ungulates in general and nonruminants in particular select for burned patches significantly sooner after fire events than larger-bodied ungulates and ruminants, regardless of seasonality. Sensenig *et al.* (2010) found a negative relationship between body mass and burn preference; here I found a positive relationship between body mass and burn avoidance. However, where they found that ruminants utilized burned patches more frequently than nonruminants, here I found the opposite to be true in PNG [20].

A notable aspect of Figure 8 is that nonruminants are presented to be generally more abundant than ruminants, which is not the case for the overall herbivore assemblages of PNG [53]. Presence and RAI were calculated on a per-species basis and then assigned values for gut type and body mass. Because only two nonruminant species (elephant and warthog) were considered in these analyses, each of their observed presence and RAI contributed much more significantly to the overall models of gut type and body mass than the fourteen species of ruminants. The average proportion of sites occupied and RAI of warthogs was much higher than most ruminants, skewing the estimates of these values for nonruminants to be much higher. It is therefore difficult to generalize these results to understand how utilization of burned patches is affected by gut type. Instead, these results primarily reflect how warthogs in particular utilize burned patches differently than all the ruminants. Perhaps if I had examined a more even distribution of ruminant and nonruminant species as was done in Sensenig *et al.* (2010), I would have also found a different relationship between gut type and

burn preference [20].

The results of the size- and gut-based models of patch occupancy and RAI over time suggest that time since fire, rather than date, determines the selectivity of ungulates for burned areas. This is surprising, given the extreme seasonality of PNG. During the wet season, Lake Urema swells to cover up to 40% of the park, forcing many animals off the floodplain and deeper in to the woodland [63]. Because the flooding causes such an extreme loss of terrestrial habitat space, I expected preference for unburned areas to change with the season, but such was not the case. The areas examined in this study were concentrated along the road network and do not experience the worst of the flooding, so the insignificant effect of seasonality on burn preference suggests that in places such as these that do not flood, ungulate site selection is governed more significantly by the occurrence of fire than changes in seasonality.

It is likely that ungulate selectivity of burned patches in PNG is driven by fire-induced changes in vegetation, as was found to be the case in several previous studies [20, 25, 26, 31, 33, 37, 39–44]. Though future research is needed to quantify post-burn changes in vegetation quality and quantity on a fine temporal scale, the results of this study suggest that frequently burned areas do have more highly nutritious understory forage material, suggesting that more recently burned areas would also have higher-quality forage material. Moreover, of the 12 burned locations considered in this study to examine herbivore response to fire, 10 were located in areas with  $FRI < 2$  years, suggesting that some of the conclusions drawn from the vegetation surveys can be used to understand the factors influencing herbivore grazing selection for burned patches. To understand the transient effects of fire on vegetation in PNG, future work might involve vegetation surveys similar to those conducted for this study carried out on a weekly or monthly basis following a fire to quantify how the quality and quantity of vegetation changes over time. Ideally, to reduce the effects of stochasticity due to small sample sizes, future work would examine more than 12 study sites over the same time period.

It is also possible that the allometric patterns of selectivity for burned sites presented in this study are the result of factors other than vegetation quality and quantity, such as predator avoidance, feeding style, and interspecific competition [2,78,79]. Ungulate species in PNG have been shown to respond strongly to other environmental features such as tree cover and termite mounds [63], and it would be interesting in the future to explore the contribution of these factors relative to fire in determining the landscape use patterns of ungulates in the park.

Regardless of other factors that might contribute to ungulate site selection, the results of this study suggest that fire is an important disturbance to the landscape in PNG and has lasting impacts on plant and herbivore communities, altering the nutrient content of vegetation and influencing species-level ungulate landscape use patterns. More broadly, this suggests that the controlled burns of PNG have a greater impact on the surrounding landscape than simply lowering the risk of late-season fires and as such could be used more strategically as a management tool. Megaherbivores have been especially slow to recover from the war-induced collapse of PNG [52], but intelligent use of prescribed burns could aid in their recovery. Large herbivores are attracted to burned areas, but only after sufficient time has passed to allow the vegetation to regrow. Perhaps intentionally burning large swaths of land, such as the grasslands west of the Rio Musicadzi, would encourage the return of bulk more grazers like buffalo to PNG. Fires play an integral role in the development and maintenance of savanna landscapes across the globe, and in a recovering ecosystem such as Gorongosa National Park, it is essential that the impacts of these disturbances on the landscape are fully understood so that they can be used intelligently to facilitate the restoration of a stable ecosystem.

**This paper represents my own work in accordance with University regulations.**

**Maria Stahl**

**May 4th, 2020**

## 5 Appendix

### 5.1 Research Methods

Plot	1	2	3	4	5	6	7	8	9	10	11	12
Days of Video	18	12	14	10	17	17	20	19	20	7	14	19
Number of Videos	61	133	54	38	16	40	78	97	47	14	5	102

Table S1: Days of recorded video and number of videos containing species of interest from camera traps in each of 12 study sites.

Camera	Latitude	Longitude	Burn 1	Burn 2
A10	-18.99254	34.3117	11/6/16	
B07	-18.95957	34.33033	8/21/17	
B09	-18.98108	34.33122	7/21/17	
E08	-18.97007	34.39047	9/5/16	
E10	-18.99155	34.39053	9/3/16	6/21/17
E12	-19.01331	34.39089	9/5/16	
F01	-18.89402	34.40934	7/17/17	
F07	-18.95938	34.41	8/21/17	
F11	-19.00232	34.41034	8/23/17	
G08	-18.96947	34.42969	9/10/16	8/20/18
I08	-18.96937	34.46918	6/29/17	
I10	-18.99097	34.46956	8/20/17	
I12	-19.01319	34.46984	8/23/17	
J09	-18.97872	34.4887	7/2/17	
K08	-18.9698	34.50842	7/20/17	
K12	-19.01297	34.50941	9/9/17	
L11	-19.00148	34.52897	9/11/17	
M10	-18.99093	34.54668	9/13/17	

Table S2: Coordinates and dates of fires witnessed by cameras within a year of July 1st, 2017.

## 5.2 Results: Herbivore Response to Fire

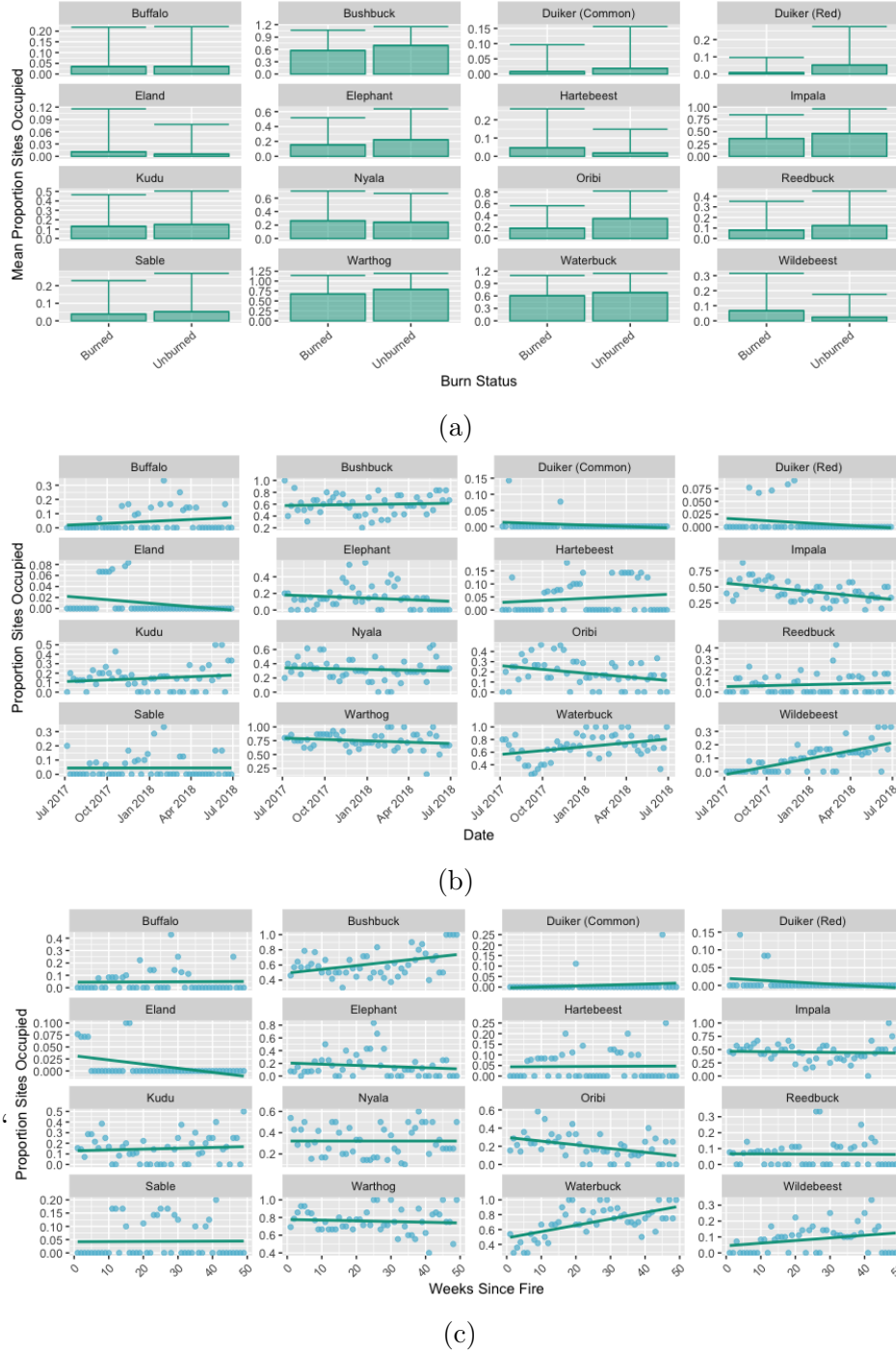


Figure S1: (a) Presence of ungulate species as a function of burn status. Bar height represents mean weekly proportion of burned and unburned sites at which each herbivore species was present; errorbars represent standard error of the mean. (b) Presence of ungulates at burned locations over the course of a calendar year. Points represent the weekly proportion of burned sites at which each species was present, lines represent result of logistic regression model. (c) Presence of ungulates at burned locations as a function of time since fire. Points represent the weekly proportion of burned sites at which each species was present, lines represent results of logistic regression model.

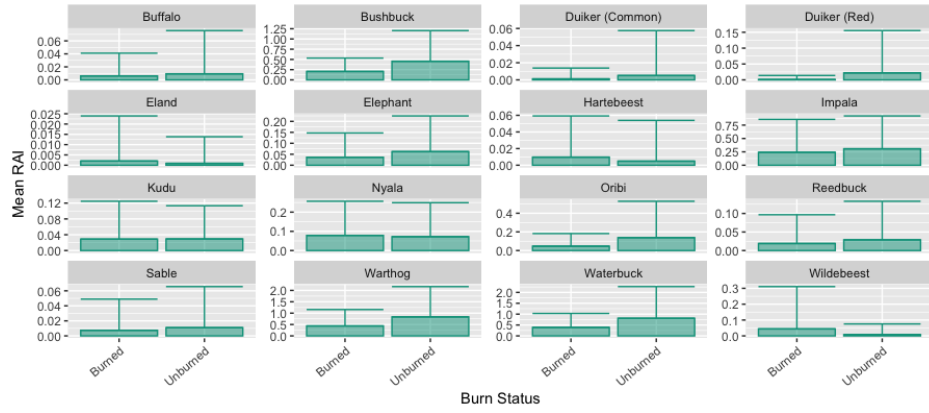
	Estimate	Std. Error	z value	Pr(> z )	
<b>(Intercept)</b>	-3.3241	0.2170	-15.32	< 0.0001	*
Unburned	0.0248	0.2381	0.10	0.9171	
<b>Bushbuck</b>	3.6136	0.2314	15.62	< 0.0001	*
<b>Duiker (Common)</b>	-1.5090	0.4987	-3.03	0.0025	*
<b>Duiker (Red)</b>	-1.5090	0.4987	-3.03	0.0025	*
<b>Eland</b>	-1.1694	0.4377	-2.67	0.0075	*
<b>Elephant</b>	1.6268	0.2432	6.69	< 0.0001	*
SpeciesHartebeest	0.3233	0.2865	1.13	0.2591	
<b>Impala</b>	2.7495	0.2323	11.84	< 0.0001	*
<b>Kudu</b>	1.4190	0.2472	5.74	< 0.0001	*
<b>Nyala</b>	2.2979	0.2350	9.78	< 0.0001	*
<b>Oribi</b>	1.8083	0.2404	7.52	< 0.0001	*
<b>Reedbuck</b>	0.8894	0.2616	3.40	0.0007	*
Sable	0.0903	0.3007	0.30	0.7639	
<b>Warthog</b>	4.0530	0.2330	17.39	< 0.0001	*
<b>Waterbuck</b>	3.7506	0.2317	16.18	< 0.0001	*
<b>Wildebeest</b>	0.6799	0.2694	2.52	0.0116	
<b>Unburned × Bushbuck</b>	0.5036	0.2544	1.98	0.0477	*
Unburned × Duiker (Common)	0.8704	0.5252	1.66	0.0975	
<b>Unburned × Duiker (Red)</b>	1.9134	0.5147	3.72	0.0002	*
Unburned × Eland	-0.7711	0.5137	-1.50	0.1333	
Unburned × Elephant	0.4174	0.2658	1.57	0.1164	
<b>Unburned × Hartebeest</b>	-1.0538	0.3330	-3.16	0.0016	*
Unburned × Impala	0.3992	0.2547	1.57	0.1171	
Unburned × Kudu	0.1350	0.2708	0.50	0.6181	
Unburned × Nyala	-0.1426	0.2581	-0.55	0.5808	
<b>Unburned × Oribi</b>	0.8400	0.2624	3.20	0.0014	*
Unburned × Reedbuck	0.4388	0.2848	1.54	0.1233	
Unburned × Sable	0.2872	0.3268	0.88	0.3795	
<b>Unburned × Warthog</b>	0.5537	0.2566	2.16	0.0310	*
Unburned × Waterbuck	0.3022	0.2546	1.19	0.2352	
<b>Unburned × Wildebeest</b>	-1.0976	0.3105	-3.53	0.0004	*

Table S3: Results of logistic regression model of site occupancy of 16 focal ungulate species as a function of burn status. Asterisks and bold text are included to denote statistical significance.

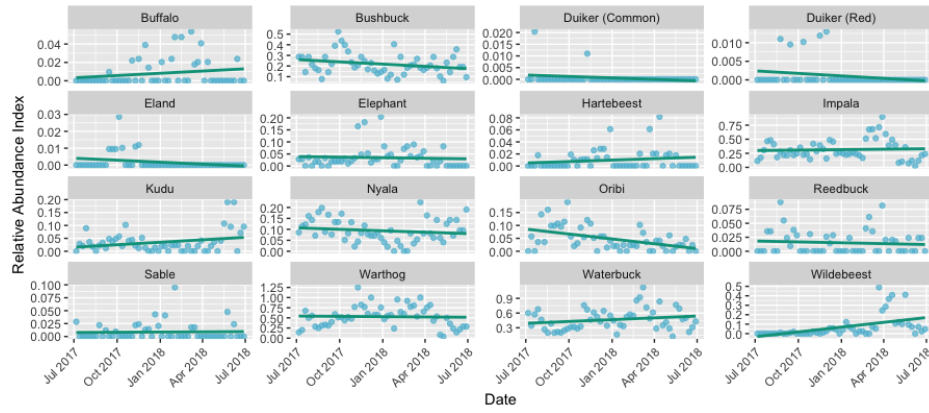


	Estimate	Std. Error	z value	Pr(> z )	
<b>(Intercept)</b>	-568.9844	201.6608	-2.82	0.0048	*
<b>Bushbuck</b>	665.2561	210.0704	3.17	0.0015	*
Duiker (Common)	-3.8374	961.2304	-0.00	0.9968	
Duiker (Red)	-220.0528	560.0342	-0.39	0.6944	
Eland	-288.5793	501.0549	-0.58	0.5647	
Elephant	100.5206	228.2890	0.44	0.6597	
Hartebeest	154.3562	266.8866	0.58	0.5630	
<b>Impala</b>	830.8367	210.4489	3.95	0.0001	*
<b>Kudu</b>	666.6250	215.9675	3.09	0.0020	*
<b>Nyala</b>	667.9370	210.4232	3.17	0.0015	*
<b>Oribi</b>	613.4531	213.3229	2.88	0.0040	*
<b>Reedbuck</b>	697.5821	229.1773	3.04	0.0023	*
Sable	415.3927	255.4095	1.63	0.1039	
Warthog	651.7857	213.0405	3.06	0.0022	*
Waterbuck	411.3583	211.1844	1.95	0.0514	
Wildebeest	149.1143	257.1219	0.58	0.5620	
<b>Date</b>	0.0324	0.0115	2.81	0.0050	*
<b>Weeks Since Fire</b>	12.2052	5.3001	2.30	0.0213	*
<b>Date × Bushbuck</b>	-0.0379	0.0120	-3.15	0.0016	*
Date × Duiker (Common)	0.0001	0.0551	0.00	0.9990	
Date × Duiker (Red)	0.0127	0.0321	0.40	0.6919	
Date × Eland	0.0167	0.0288	0.58	0.5611	
Date × Elephant	-0.0056	0.0131	-0.43	0.6656	
Date × Hartebeest	-0.0088	0.0153	-0.58	0.5631	
<b>Date × Impala</b>	-0.0474	0.0120	-3.94	0.0001	*
<b>Date × Kudu</b>	-0.0381	0.0124	-3.08	0.0021	*
<b>Date × Nyala</b>	-0.0381	0.0120	-3.16	0.0016	*
<b>Date × Oribi</b>	-0.0350	0.0122	-2.87	0.0042	*
<b>Date × Reedbuck</b>	-0.0399	0.0131	-3.04	0.0024	*
Date × Sable	-0.0238	0.0146	-1.63	0.1038	
<b>Date × Warthog</b>	-0.0371	0.0122	-3.04	0.0024	*
Date × Waterbuck	-0.0234	0.0121	-1.93	0.0532	
Date × Wildebeest	-0.0085	0.0147	-0.58	0.5645	
<b>Weeks Since Fire × Bushbuck</b>	-14.2588	5.5297	-2.58	0.0099	*
Weeks Since Fire × Duiker (Common)	13.6428	31.6027	0.43	0.6660	
Weeks Since Fire × Duiker (Red)	13.3427	37.3612	0.36	0.7210	
Weeks Since Fire × Eland	5.4622	30.0430	0.18	0.8557	
Weeks Since Fire × Elephant	2.1763	6.1708	0.35	0.7243	
Weeks Since Fire × Hartebeest	-2.1552	7.1065	-0.30	0.7617	
<b>Weeks Since Fire × Impala</b>	-17.4287	5.5337	-3.15	0.0016	*
<b>Weeks Since Fire × Kudu</b>	-15.8045	5.6662	-2.79	0.0053	*
<b>Weeks Since Fire × Nyala</b>	-14.1100	5.5367	-2.55	0.0108	*
<b>Weeks Since Fire × Oribi</b>	-12.8798	5.6335	-2.29	0.0222	*
<b>Weeks Since Fire × Reedbuck</b>	-17.2519	5.9633	-2.89	0.0038	*
Weeks Since Fire × Sable	-8.0681	6.7839	-1.19	0.2343	
<b>Weeks Since Fire × Warthog</b>	-14.0739	5.6042	-2.51	0.0120	*
Weeks Since Fire × Waterbuck	-7.6295	5.5539	-1.37	0.1695	
Weeks Since Fire × Wildebeest	-9.7230	6.1993	-1.57	0.1168	
<b>Date × Weeks Since Fire</b>	-0.0007	0.0003	-2.31	0.0209	*
<b>Date × Weeks Since Fire × Bushbuck</b>	0.0008	0.0003	2.59	0.0096	*
Date × Weeks Since Fire × Duiker (Common)	-0.0008	0.0018	-0.43	0.6673	
Date × Weeks Since Fire × Duiker (Red)	-0.0008	0.0021	-0.36	0.7154	
Date × Weeks Since Fire × Eland	-0.0003	0.0017	-0.19	0.8463	
Date × Weeks Since Fire × Elephant	-0.0001	0.0004	-0.35	0.7252	
Date × Weeks Since Fire × Hartebeest	0.0001	0.0004	0.31	0.7595	
<b>Date × Weeks Since Fire × Impala</b>	0.0010	0.0003	3.16	0.0016	*
<b>Date × Weeks Since Fire × Kudu</b>	0.0009	0.0003	2.79	0.0052	*
<b>Date × Weeks Since Fire × Nyala</b>	0.0008	0.0003	2.56	0.0106	*
<b>Date × Weeks Since Fire × Oribi</b>	0.0007	0.0003	2.29	0.0221	*
<b>Date × Weeks Since Fire × Reedbuck</b>	0.0010	0.0003	2.90	0.0038	*
Date × Weeks Since Fire × Sable	0.0005	0.0004	1.19	0.2324	
<b>Date × Weeks Since Fire × Warthog</b>	0.0008	0.0003	2.52	0.0118	*
Date × Weeks Since Fire × Waterbuck	0.0004	0.0003	1.39	0.1657	
Date × Weeks Since Fire × Wildebeest	0.0006	0.0004	1.56	0.1180	

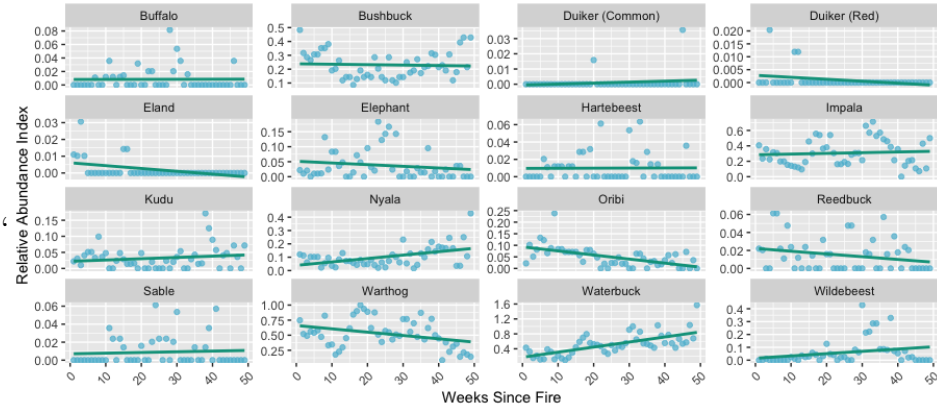
Table S4: Results of logistic regression model of presence of 16 focal ungulate species in burned areas as a function of weeks since fire. Asterisks and bold text are included to denote statistical significance.



(a)



(b)



(c)

Figure S2: (a) RAI of ungulate species as a function of burn status. Bar height represents mean weekly RAI of each species in burned and unburned sites at which each herbivore species was present; errorbars represent standard error of the mean. (b) RAI of ungulates at burned locations over the course of a calendar year. Points represent the weekly RAI of each species at burned sites at which each species was present, lines represent results of linear regression model. (c) RAI of ungulates at burned locations as a function of time since fire. Points represent the weekly RAI of each species at burned sites at which each species was present, lines represent results of linear regression model.

	Estimate	Std. Error	t value	Pr(> t )	
(Intercept)	0.2279	0.1531	1.49	0.1367	
Unburned	0.0286	0.1861	0.15	0.8778	
Bushbuck	0.2190	0.1573	1.39	0.1637	
Duiker (Common)	-0.0565	0.2696	-0.21	0.8341	
Duiker (Red)	-0.0850	0.3491	-0.24	0.8076	
Eland	-0.0493	0.3828	-0.13	0.8975	
Elephant	0.0014	0.1669	0.01	0.9931	
Hartebeest	0.0234	0.2041	0.11	0.9086	
<b>Impala</b>	0.3815	0.1612	2.37	0.0180	*
Kudu	-0.0155	0.1691	-0.09	0.9271	
Nyala	0.0460	0.1627	0.28	0.7776	
Oribi	0.0735	0.1638	0.45	0.6535	
Reedbuck	-0.0089	0.1750	-0.05	0.9594	
Sable	-0.0197	0.1937	-0.10	0.9189	
<b>Warthog</b>	0.4547	0.1569	2.90	0.0038	*
<b>Waterbuck</b>	0.4447	0.1575	2.82	0.0048	*
Wildebeest	0.3070	0.1868	1.64	0.1003	
Unburned $\times$ Bushbuck	0.2107	0.1910	1.10	0.2701	
Unburned $\times$ Duiker (Common)	0.0923	0.3267	0.28	0.7775	
Unburned $\times$ Duiker (Red)	0.2562	0.3735	0.69	0.4928	
Unburned $\times$ Eland	-0.0357	0.4726	-0.08	0.9397	
Unburned $\times$ Elephant	0.0332	0.2021	0.16	0.8693	
Unburned $\times$ Hartebeest	-0.0287	0.2946	-0.10	0.9224	
Unburned $\times$ Impala	0.0442	0.1948	0.23	0.8207	
Unburned $\times$ Kudu	-0.0459	0.2066	-0.22	0.8240	
Unburned $\times$ Nyala	0.0101	0.1984	0.05	0.9594	
Unburned $\times$ Oribi	0.0883	0.1979	0.45	0.6555	
Unburned $\times$ Reedbuck	-0.0030	0.2128	-0.01	0.9889	
Unburned $\times$ Sable	-0.0231	0.2403	-0.10	0.9233	
<b>Unburned <math>\times</math> Warthog</b>	0.4233	0.1905	2.22	0.0263	*
<b>Unburned <math>\times</math> Waterbuck</b>	0.5835	0.1912	3.05	0.0023	*
Unburned $\times$ Wildebeest	-0.3543	0.2850	-1.24	0.2139	

Table S5: Results of linear regression model of RAI of 16 focal ungulate species as a function of burn status ( $F_{31,13863} = 57.75$ ,  $p < 0.0001$ ). Asterisks and bold text are included to denote statistical significance.

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-19.2870	141.0613	-0.14	0.8913
Bushbuck	26.3058	142.3094	0.18	0.8534
Duiker (Common)	19.4299	676.2383	0.03	0.9771
Duiker (Red)	19.4299	599.3504	0.03	0.9741
Eland	-79.8557	1222.2161	-0.07	0.9479
Elephant	9.5629	146.4159	0.07	0.9479
Hartebeest	-34.2254	247.1322	-0.14	0.8899
Impala	-25.1955	143.0049	-0.18	0.8602
Kudu	29.0446	146.1725	0.20	0.8425
Nyala	37.1288	143.1880	0.26	0.7954
Oribi	32.6459	145.4574	0.22	0.8224
Reedbuck	75.4464	172.2602	0.44	0.6615
Sable	31.7616	155.2191	0.20	0.8379
Warthog	-22.3160	142.0173	-0.16	0.8752
Waterbuck	58.4900	142.0772	0.41	0.6806
Wildebeest	-122.8686	220.4169	-0.56	0.5773
Date	0.0011	0.0081	0.14	0.8902
Weeks Since Fire	0.0827	3.3798	0.02	0.9805
Date× Bushbuck	-0.0015	0.0082	-0.18	0.8555
Date× Duiker (Common)	-0.0011	0.0389	-0.03	0.9771
Date× Duiker (Red)	-0.0011	0.0344	-0.03	0.9741
Date× Eland	0.0046	0.0701	0.07	0.9479
Date× Elephant	-0.0005	0.0084	-0.06	0.9482
Date× Hartebeest	0.0020	0.0142	0.14	0.8901
Date× Impala	0.0015	0.0082	0.18	0.8583
Date× Kudu	-0.0017	0.0084	-0.20	0.8426
Date× Nyala	-0.0021	0.0082	-0.26	0.7954
Date× Oribi	-0.0019	0.0083	-0.22	0.8230
Date× Reedbuck	-0.0043	0.0099	-0.44	0.6615
Date× Sable	-0.0018	0.0089	-0.20	0.8378
Date× Warthog	0.0013	0.0082	0.16	0.8723
Date× Waterbuck	-0.0033	0.0082	-0.41	0.6822
Date× Wildebeest	0.0071	0.0127	0.56	0.5774
Weeks Since Fire × Bushbuck	-0.1999	3.4151	-0.06	0.9533
Weeks Since Fire × Duiker (Common)	-0.0827	31.6537	-0.00	0.9979
Weeks Since Fire × Duiker (Red)	-0.0827	69.7398	-0.00	0.9991
Weeks Since Fire × Eland	-0.3710	75.6209	-0.00	0.9961
Weeks Since Fire × Elephant	0.0079	3.6309	0.00	0.9983
Weeks Since Fire × Hartebeest	1.1916	6.2624	0.19	0.8491
Weeks Since Fire × Impala	0.2451	3.4366	0.07	0.9431
Weeks Since Fire × Kudu	-0.5181	3.5043	-0.15	0.8825
Weeks Since Fire × Nyala	-0.1474	3.4476	-0.04	0.9659
Weeks Since Fire × Oribi	-0.1588	3.4891	-0.05	0.9637
Weeks Since Fire × Reedbuck	-0.1782	3.6382	-0.05	0.9609
Weeks Since Fire × Sable	-0.2724	3.7542	-0.07	0.9422
Weeks Since Fire × Warthog	0.7333	3.4075	0.22	0.8296
Weeks Since Fire × Waterbuck	-0.6677	3.4098	-0.20	0.8448
Weeks Since Fire × Wildebeest	1.5012	3.6214	0.41	0.6785
Date × Weeks Since Fire	-0.0000	0.0002	-0.03	0.9787
Date × Weeks Since Fire × Bushbuck	0.0000	0.0002	0.06	0.9529
Date × Weeks Since Fire × Duiker (Common)	0.0000	0.0018	0.00	0.9978
Date × Weeks Since Fire × Duiker (Red)	0.0000	0.0040	0.00	0.9990
Date × Weeks Since Fire × Eland	0.0000	0.0043	0.00	0.9962
Date × Weeks Since Fire × Elephant	-0.0000	0.0002	-0.00	0.9992
Date × Weeks Since Fire × Hartebeest	-0.0001	0.0004	-0.19	0.8494
Date × Weeks Since Fire × Impala	-0.0000	0.0002	-0.07	0.9438
Date × Weeks Since Fire × Kudu	0.0000	0.0002	0.15	0.8798
Date × Weeks Since Fire × Nyala	0.0000	0.0002	0.05	0.9621
Date × Weeks Since Fire × Oribi	0.0000	0.0002	0.05	0.9617
Date × Weeks Since Fire × Reedbuck	0.0000	0.0002	0.06	0.9553
Date × Weeks Since Fire × Sable	0.0000	0.0002	0.08	0.9396
Date × Weeks Since Fire × Warthog	-0.0000	0.0002	-0.22	0.8281
Date × Weeks Since Fire × Waterbuck	0.0000	0.0002	0.20	0.8384
Date × Weeks Since Fire × Wildebeest	-0.0001	0.0002	-0.42	0.6734

Table S6: Results of linear regression model of RAI of 16 focal ungulate species in burned areas as a function of weeks since fire ( $F_{63,1847} = 4.07$ ,  $p < 0.0001$ ).

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