

Ecosystem-wide responses to fire and large mammal herbivores in an African savanna

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Abstract

Fire and large mammal herbivores (LMH) are the principal top-down forces maintaining savanna structure. Nonetheless, experiments designed to investigate interactions between fire and LMH are rare in savannas, and relationships between environmental variation and biodiversity in the context of fire and LMH are poorly understood. This study addresses these gaps by manipulating the presence of LMH and early and late dry season fires in a tropical African savanna. In addition, this work simultaneously explores environmental variables including soil and foliar quality, vegetation cover, and nearby water sources to more holistically describe factors affecting savanna functioning and biodiversity.

After one year of experimental treatments, changes in vegetation were already apparent. Shrub abundance and richness and grass richness were higher in the absence of LMH, while grass biomass increased three-fold in burned plots as compared to unburned plots. Foliar nutrients tended to increase in open plots, while phenolics decreased. Amphibian abundance decreased with early burns and was higher with LMH. In contrast, small mammal abundance and richness increased without LMH and with time since fire. Richness and foraging of LMH were highest after late burns.

These results demonstrate ecosystem-wide effects of LMH, illustrating the importance of considering multiple taxa when designing fire management programs. For example, burning negatively affected amphibians and small mammals and changed vegetation at the same time it increased LMH foraging. In the long-term, this experiment will shed light on interacting effects of fire and LMH on savanna biodiversity and function.

Keywords: amphibians, biodiversity, herbivory, insects, mammals, nutrients, phenolics, reptiles

1. INTRODUCTION

Ecosystems are structured by consumers from the top-down and by resources from the bottom-up. Some drivers of ecosystem dynamics, however, produce both top-down and bottom-up effects. For example, fire and herbivores act as top-down consumers while also influencing bottom-up dynamics via altered nutrient cycling and changes in the composition of savanna vegetation. Studies of top-down and bottom-up effects of fire and herbivores have quantified plant diversity, plant adaptations to fire and herbivory (Bond and Midgley, 2001; Bond and Keely, 2005; Charles-Dominique et al., 2015), nutrient cycling (Coetsee et al., 2008; Coetsee, 2011; Holdo and Mack, 2014; Hempson et al., 2015a; Pellegrini et al., 2015), and changes in plant defenses (Scogings et al., 2017; Chinder et al., 2020). However, less attention has been paid to the influence of fire and herbivory on biodiversity broadly, and there are few fully factorial studies that evaluate the interactions between fire and large mammal herbivores (LMH; Levick et al. 2009; Burkepile et al. 2016; LaMalfa et al. 2019; Ngugi et al., 2022). We therefore have a limited understanding of the interacting effects of fire and LMH on savanna biodiversity and functioning.

Both fire and herbivory consume vegetation, playing distinct but interacting top-down roles. In savannas, fire acts from the top-down as a generalist consumer (Bond and Keely, 2005). LMH are more selective as top-down forces, foraging on preferred plants (Kartzinel et al., 2015; Hutchinson et al., 2022; Pansu et al., 2022). Importantly, fire and LMH also interact, as herbivory affects fire regimes. Browsers, which feed on woody vegetation, indirectly promote fire by limiting the encroachment of less combustible woody plants into grasslands, while grazers reduce fire by consuming flammable grasses (Archibald and Hempson, 2016).

From the bottom-up, fire affects vegetation by changing nutrient availability, although effects are context dependent (Van de Vijver et al., 1999; Coetsee et al., 2008; Pellegrini et al., 2015; Butler et al. 2018). For example, 50 years of fire treatments on largely granitic soils in Kruger National Park in South Africa show that ammonium concentrations were highest in soils without fire while nitrate concentrations were highest with annual burns, and these results vary seasonally (Coetsee et al., 2008). Further north in Kruger, on richer, primarily basalt soils, over 50 years of fire treatments resulted in higher soil C and N in unburned plots, while P was unaffected by fire (Pellegrini et al., 2015). In Tanzania, fire similarly reduces N in areas with sandy loam soils (Van de Vijver et al., 1999).

The literature is also unclear regarding the extent to which LMH affect nutrient cycling. For example, soil N increases with grazing in the Serengeti National Park in Tanzania (McNaughton, 1997), but soil N is not affected by grazing in Hluhluwe-iMfolozi in South Africa, although foliar nutrients are higher in grass growing in grazed sites (Stock, 2010; Coetsee, 2011). On nutrient poor soils in Kruger, grazed sites have higher soil N (on an area, not mass basis), but the effect of grazing is not present in more nutrient rich sites (Holdo and Mack, 2014).

The extent to which fire affects herbivory depends, in part, on the timing of a burn. Nutrient rich vegetation regenerating in recently burned areas often serves as a magnet for LMH (Archibald and Bond, 2004; Sensenig et al., 2010; Parrini and Owen-Smith, 2010; Allred et al., 2011; Archibald et al., 2013; Donaldson et al., 2018). However, hot burns late in the dry season can be twice as intense as early dry season (cold) burns (Mbow et al., 2000; Mulqueeney and Goodman, 2011), resulting in top-kill (the destruction of aboveground tissue, while roots are able to resprout) and the loss of vegetation (Trollope and Tainton, 1986; Sackey and Hale, 2008). On

the other hand, later season hot burns may be closely followed by rains that promote vegetation regrowth (Mbow et al., 2000).

Plants may also respond to fire and herbivory with changes in their defensive chemistry.

As fire and herbivores affect soil nutrients or light availability, the carbon:nitrogen (C:N) balance in plants changes, resulting in differential investments in C-based phenolic defenses as predicted by the carbon:nutrient balance hypothesis (CNBH; Bryant et al., 1983) and the growth-differentiation balance hypothesis (GDBH; Herms and Mattson, 1992; Hattas et al., 2017). For example, concentrations of condensed tannins increase in miombo seedlings post-fire, potentially due to increased light levels and therefore greater C assimilation (Chinder et al., 2020).

Browsing also affects concentrations of C-based phenolic defenses in savannas by altering C availability and C-demands for growth, although responses vary between species (Scogings et al., 2011, 2014, 2017).

The strong influence fire, LHM, and their interactions have on plant communities likely produces cascading effects on savanna biodiversity broadly. To understand ecosystem-wide responses, a range of taxa must be evaluated, but comprehensive data on a diversity of savanna species are lacking. For example, a meta-analysis included just four studies on the response of vertebrate communities to fire in Africa (Pastro et al., 2014). Fire heterogeneity has sometimes been used as a proxy for measuring biodiversity (Bond and Archibald, 2003). This is an oversimplification, however, as the timing as well as the extent of fire have consequences for species dependent on resources such as green forage, grass seed, and tall grass habitats. In addition, declines of LMH across Africa affect other animals through changes in plant communities, competition, facilitation, and predation (Jeffries and Lawton, 1984; McNaughton et al., 1988; Gebeyehu and Samways, 2002; Tscharntke, 1995; Leriche et al., 2003; Ben-Ari and

Inbar, 2013; Klink et al., 2015). For example, large mammal exclosure studies show insect abundance increases with declines in mammalian grazing (Samways and Kreuzinger, 2001; Goheen et al., 2004; Jonsson et al., 2010). In addition, insects are sensitive to fire due to their limited dispersal abilities, particularly in their immature stages (Siemann et al., 1997; Swengel, 2001).

Effects of fire and LHM on fauna are taxa specific and may change over time. Insect populations can recover quickly from fire, especially when a burn is followed by rains that support vegetation regrowth (Radford and Andersen, 2012). Reptiles and amphibians seem to be slower to recover from fire (Abom and Schwarzkopf, 2016), and recovery of small mammal populations can occur within a year of fire (Monadjem and Perrin, 2003; Shaw et al., 2021). Small mammal species also differ in their site fidelity, affecting their vulnerability to fire and resulting habitat change (Monadjem and Perrin, 1997; Morris et al., 2011). Interacting effects of fire and LMH on insects, herpetofauna, and small mammals are largely unknown and require comprehensive studies.

To better understand the effects of fire and LMH on savanna biodiversity broadly and savanna functioning in terms of vegetation dynamics, we established a factorial experiment in Gorongosa National Park, Mozambique. We present the results of the first year of what will be a long-term study and quantify responses of soils, plants, insects, herpetofauna, and small and large mammals to fire and LMH as well to environmental factors. The fire regime and presence of LHM were hypothesized to have unique effects on vegetation and fauna (Tables 1, S1). In addition, we hypothesized that vegetation cover and biomass and the proximity of water resources may be positively correlated with biodiversity (Tables 1, S1).

2. METHODS

1. Study site

The Gorongosa Savanna Ecology Experiment is in a Rift Valley Lowland Woodland landscape (Lötter et al., 2021) in Gorongosa National Park (GNP), Mozambique (-18°58', 34°20', ~25 m a.s.l.). The experimental area covers ~197-ha. Woody plant communities include a mixed broadleaf savanna dominated by *Combretum adenogonium* (Combretaceae) which transitions to a more open savanna co-dominated by *Acacia (Vachellia) robusta* and *Acacia (Senegalia) nigrescens* (Fabaceae). The most common shrub is *Capparis erythrocarpos* var. *rosea* (Capparaceae), and common grasses include *Megathyrsus maximus*, *Panicum infestum*, *P. coloratum*, *Urochloa mosambicensis*, and *Digitaria eriantha*. Soils are silty clay loams. The average annual temperature is 24.1° C, and average annual precipitation is 1053 mm. The area is a mesic savanna with a dry season extending from April to November; 86% of rain falls between November and March. Between 2001 and the start of the experiment in 2020, the study area burned every 2-3 years, and the last fire recorded before the experiment was in 2016 (Table S2). The biomass of large mammal herbivores derived from full aerial counts of 129,393 hectares of savanna habitat in Gorongosa in 2020 and 2022 averaged 5,938 kg/km². This biomass figure is moderate to high in comparison to areas with similar mean annual precipitation (East 1984, Hempson et al. 2015b).

2. Study design

In December 2020, three 30 x 30 m enclosure (fenced) plots were established in ten replicate blocks; fences were 2 m tall, and the top wires were electrified to prevent elephant damage. Each block consisted of three enclosure plots and three open plots and averaged 1.15 ha in size. Blocks were randomly located within the study area, maintaining a minimum distance of 100 m between them. Plots within the blocks were a minimum of 20 m apart. They were located to avoid large termite mounds and to contain at least one tree. Treatment levels were randomly assigned to the plots. One pair of open and closed plots was subject to a cold burn (beginning of the dry season) on 18-20 May 2021, and another pair of plots was subject to a hot burn (middle of the dry season) on 15-16 September 2021. The first rain after the cold burn was 19 mm on 22-23 May 2021. After the hot burn, the first rain was 5.3 mm on 19 September 2021. Two control burn plots, one fenced and one open, burned due to escaped embers during the hot burn, so they were treated as hot burn plots in analyses. Abbreviated sampling and data analysis methods follow; full methods are in the online Supplementary Information.

3. Soil and vegetation measurements

Soil samples were taken before the experiment and one year after the first cold burns for C and N analyses. Diameter at breast height (DBH) of all trees was measured just before the enclosures were installed and after one year. At the same time as the DBH measurements, the area of all *C. erythrocarpos* var. *rosea* shrubs was estimated by measuring their length and width. Shrub richness and abundance were measured just after the enclosures were installed and again after one year in four 25-m² subplots in each plot (Figure S1).

Grass biomass was measured at 56 points across seven transects in each plot, and percent cover of grasses and herbaceous plants were measured in 16 1-m² subplots in the plots at the beginning of the experiment and before and after the controlled burns (Figure S1). Grass

richness was measured once during the rainy season at the beginning of the experiment and after one year. One to two weeks after each fire, the area burned was measured in the same subplots as grass cover. The height of burn scars on all trees was simultaneously measured to indicate the intensity of the fires.

Leaf samples of focal species representing the most abundant grasses and woody species were collected for elemental analysis (C, N, Ca, K, Mg, P, Si, and Na) and for analysis of total phenolics after one year. The focal species were *M. maximus*, *U. mosambicensis* (grasses), *C. erythrocarpos* var. *rosea* (a shrub), *A. nigrescens*, and *A. robusta* (trees).

4. Insect sampling

Crickets (Gryllidae: Orthoptera) were the focal insect group because they are reliable indicators of habitat quality (Andersen et al., 2001), omnivorous (Capinera, 2020), and are relatively easy to sample (Clayton, 2002); all species in the study area are ground-dwelling. Gryllidae is species rich and widely distributed across Africa (Robillard et al., 2014; Jaiswara et al., 2018), with 1083 species described from the continent (Cigliano et al., 2023). Crickets were collected monthly in nine pitfall traps per plot separated from each other by 5 m along two diagonal lines across the plots.

5. Herpetofauna sampling

Amphibians and reptiles were assessed with visual searches and pitfall traps monthly. The pitfall traps were the same as those in the cricket collections. Habitat characteristics that may influence the presence of amphibians and reptiles were also measured. In the grass and forb cover subplots, leaf-litter cover and litter depth were measured. Downed tree trunks in the plots were counted, and their diameters were measured 1.3 m from the base. Pans (potential

amphibian breeding sites) within 200 m of the center of each plot were counted using QGIS v. 3.20.

6. Small mammal sampling

Small mammals were sampled using Sherman traps (23 x 9 x 8 cm). Six traps were spaced 9 m apart along two 28 m transects separated by 9 m in each plot (three traps per transect). The traps were left open for three consecutive nights during each sampling period. During the first sampling period, traps were set in all the plots. One week after the cold burn, traps were set in the burned and control burn (no fire) plots. One week after the hot burn, only the plots subject to the late season fire and the control burn plots were sampled.

7. Large mammal sampling

LMH were surveyed using camera traps in the open plots. Foraging intensity was calculated for the four most common species (waterbuck, impala, warthog, and nyala) based on the number of individuals photographed in a foraging posture during the sampling period.

8. Data analyses

Vegetation data were analyzed with linear mixed models using block as a random factor with the lme4 package (Bates et al., 2015). Heterogeneity of variance was verified before proceeding with analyses, and variables were log-transformed as necessary. Predictor variables included the fire and exclosure treatments as well as their interaction and descriptions of the intensity of the fires (quantified as (a) the average area burned in the sub-subplots and (b) the average height of fire scars on trees at the plot level). For analyses of grasses and forbs, measurements of biomass, richness, and cover measured in the same period at the beginning of the experiment were included as covariates.

Soil C and N were analyzed with ANOVA to determine if there was variation between blocks before the fire treatment was implemented. Samples after the first cold and hot burn were also analyzed with ANOVA to test the effects of the fire regime and large mammal exclosures. Foliar elements were analyzed with MANOVA, and total phenolics were analyzed with ANOVA for each focal species.

Cricket, amphibian, reptile, small mammal abundance and richness were examined with generalized linear mixed models with plot identity as the random factor using the lme4 package (Bates et al., 2015). Variables included allowed for testing of direct and indirect effects of fire and the presence of large mammals as well as effects of season and habitat characteristics. Models were simplified using backward selection by comparing AIC scores with the AICcmodavg package (Mazerolle, 2023). The simplest, best fit models are presented, and the predictors included in the full models are summarized in Table S1. All analyses were run using R v. 4.0.3 (R Core Team, 2020).

3. RESULTS

1. Soils and vegetation

The average plot area burned after the hot fires was 81.9% versus 64.8% after the cold fires. Soil C and N did not vary due to the fire or large mammal exclosure treatments. Grass biomass after one year was about three times higher inside versus outside exclosures, and it was about 25 g / m² higher in burned plots as compared to unburned plots. Biomass was slightly higher in plots that experienced a hot burn and in plots where fires were more intense, based on the height of burn scars (Table S4; Figure 1). Grass cover after one year was on average 84.6% in closed plots

and 61.6% in open plots. Forb cover after one year, in contrast, was 2.3% in closed plots and 5.8% in open plots. Grass cover also increased with the application of fire, particularly hot burns (Table S4; Figure 1). Forb cover in April 2022 decreased with area burned and was positively correlated with cover measured the year prior (Table S4; Figure 1). Grass richness after one year was ~2.94 species in plots closed to LMH and ~2.61 in open plots. Grass richness was also positively correlated with richness the previous year (Table S4; Figure 1).

Shrub abundance and richness increased in plots closed to large mammals, and both variables decreased in response to the area that actually burned within plots (results demonstrating change in abundance and richness over time in Table S4; Figure 1). After one year, the abundance of shrubs in open plots was 0.93 ± 2.49 ; the abundance in exclosure plots was 2.27 ± 1.89 . After one year, shrub richness in open plots was 0.4 ± 1.02 ; richness in closed plots was 1.33 ± 0.94 . *Capparis erythrocarpos* var. *rosea* growth and abundance were not affected by the treatments after one year. The relative growth rate of tree diameter and tree basal area were not affected by fire or the presence of large mammals after one year.

2. Foliar elements and phenolics

Foliar elements responded to the fire regime and presence of large mammals differently for each focal species; significant results are described here (full model and significant sub-model MANOVA results are in Table S5). The sum of bases in *A. nigrescens* leaves increased in open plots (means for all contrasts described are reported in Table S6). Foliar P increased in *A. robusta* in plots exposed to hot burns relative to plots with cold burns and unburned plots. Sulfur in *U. mosambicensis* was similar in plots with cold and hot burns and lower in unburned plots.

In the complete MANOVA for *U. mosambicensis*, foliar elements were overall higher in plots open to LMH. Specifically, P, S, and Si were higher in open plots. Percent N, however, was higher in *U. mosambicensis* protected from LMH. In the complete MANOVA, foliar elements in *M. maximus* were higher in open plots. Specifically, the sum of bases in *M. maximus* was higher in open plots. Percent C in *C. erythrocarpos* var. *rosea* leaves was higher in exclosures. In contrast, foliar P and Si were higher in *C. erythrocarpos* var. *rosea* in open plots.

Overall, total phenolics were higher in the two acacia species relative to *C. erythrocarpos* var. *rosea* and the two grass species (Figure 2). The average concentration for *A. nigrescens* was 95.1 ± 9.4 mg/g; for *A. robusta* it was 41.2 ± 2.1 mg/g. *Capparis erythrocarpos* var. *rosea* and *M. maximus* produced similar concentrations of phenolics (27.1 ± 1.8 and 27.3 ± 0.9 mg/g, respectively). *Urochloa mosambicensis* had the lowest concentrations of phenolics (18.6 ± 0.5 mg/g). The concentration of total phenolics in *C. erythrocarpos* var. *rosea* was lower in open plots, and it was marginally lower in *M. maximus* in open plots as well (Table S7; Figure 2).

3. Insect responses

The abundance and richness of crickets was very seasonal and was two times higher in the rainy vs. the dry season. Cricket abundance and richness were lower in plots with greater *C. erythrocarpos* var. *rosea* cover (the most abundance shrub). Crickets were also more abundant in plots closer to more sources of water (Table S8). Crickets were not affected by the fire or LMH treatments (Figures 3a,b).

4. Amphibian responses

Amphibian abundance and richness were higher in plots open to LMH. Amphibian abundance was lowest in plots that experienced cold burns (Figures 3c,d). Seasonality was also important for amphibian abundance and richness; both were highest in the rainy season. Amphibian abundance decreased as grass biomass and shrub cover increased. Amphibian richness similarly decreased with shrub abundance and increased in plots surrounded by more pans (Table S9).

5. Reptile responses

Reptile abundance and richness were not affected by the experimental treatments (Figures 3e,f), but both abundance and richness were higher in the dry season. Abundance and richness were also higher in plots closer to more sources of water and in plots with more shrubs (Table S10).

6. Small mammal responses

Small mammal abundance and richness were higher in plots closed to LMH (Figures 3g,h). The abundance of small mammals increased with time since fire. Both abundance and richness were lower in plots with more grass biomass. Small mammal richness decreased in plots with more shrubs and was lowest in September, before the hot burn (Table S11).

7. Large mammal responses

Large mammal richness was highest in plots with hot burns and lowest in unburned plots. Richness also increased with tree basal area and decreased slightly with grass biomass (Table S12; Figure 4). Impala, waterbuck, and warthogs had the highest foraging intensity in plots with hot burns followed by plots with cold burns. Nyala foraging was similar in control and hot burn plots and lowest least in cold burn plots. Impala and waterbuck had higher foraging intensity in plots with more grass biomass, while warthogs foraged more in plots with lower biomass. All species foraged more often in plots with more grass cover. Impala, waterbuck, and warthogs foraged more in plots with more pans nearby, and nyala foraged more in plots with greater tree basal area (Table S12; Figure 5).

4. DISCUSSION

Analyses of interactions between fire, LMH, and environmental variation allow for a mechanistic evaluation of savanna functioning and biodiversity. Our data describe the initial results of what will be a long-term study, and interesting patterns are already emerging, although these may change as treatment effects become more established and environmental conditions vary over time. Many of our hypotheses were supported, while others were not. For example, after one year of controlled burns and mammalian exclosures, there were clear changes in vegetation, but insects were more responsive to season than fires or the presence of large mammals. Vegetation parameters affected by fire and LMH in turn were correlated with herpetofauna and small mammal richness, and direct effects of fire and mammal exclosures were detectable for

amphibians and small mammals. LMH responded positively to hot burns, and their foraging also generally increased with vegetation cover. We examine these interactions in detail below.

After one year of experimental conditions, herbaceous vegetation responded more than woody plants to the fire and herbivore treatments. Grass biomass and percent cover increased with burning only in the absence of mammals, possibly because mammals feed on regenerating vegetation post-burn (Archibald and Bond, 2004; also demonstrated by our foraging data). More intense fires, as measured by burn scar height, also led to more grass biomass. The richness of grass species was higher in the absence of large mammals, and forbs responded in the opposite manner, potentially due to a release from competition with grasses where grazers limit grass growth. This same result has been found on the floodplain of GNP (Guyton, 2018).

Although herbaceous vegetation is quicker to respond to treatments than woody plants, there are already signs woody cover is changing as the abundance and richness of shrubs increased in the absence of large mammals and decreased in areas where fires were more extensive; much of the change was due to losses of shrubs in plots open to large mammals. In GNP in particular, relationships between woody cover and large mammals are very apparent. The loss of over >95% of large mammals during Mozambique's war for independence and civil war led to increased tree cover (Daskin et al., 2016). Together, these results support data from other sites demonstrating the importance of fire and LMH in maintaining open savannas (Staver et al., 2009; Midgley et al., 2010; Pringle et al., 2015).

Foliar nutrients tended to increase in the presence of LMH, supporting the importance of large herbivores in nutrient cycling (Archibald, 2008; Coetsee et al., 2011). This is not a ubiquitous pattern, however, as three decades of herbivore exclusion did not affect soil C, N, or P in Kruger National Park (KNP; Holdo and Mack, 2014). Conclusions regarding the responses of

foliar nutrients are limited after only one year of experimental burns, but burning is already related to increased P in *A. robusta*. A long-term study, also from KNP, indicates fire reduces soil P (Malongweni and van Tol, 2022), so it will be interesting to follow these results over time.

Plant defenses were affected by the presence of LMH, although not consistently across species, as is also the case in other studies (Scogings et al., 2013; Wigley et al., 2022). We cannot be sure that individuals sampled for chemical analyses necessarily suffered herbivory themselves. Nonetheless, species whose concentrations of phenolics were lower in plots open to herbivores, *C. erythrocarpos* var. *rosea* and *M. maximus*, likely experienced herbivory as they are favored by herbivores in GNP (Potter et al., 2022). In contrast, the acacias sampled were large trees that may have experienced less browsing. Although *U. mosambicensis* is also favored by grazers, it produces low levels of phenolics and therefore does not seem to rely on phenolics as a defense mechanism. *Capparis erythrocarpos* var. *rosea* and *M. maximus* may have become C limited in plots open to herbivores and have reduced their investments in C-based phenolic defenses (Scogings et al., 2011). Similarly, *A. robusta* and five other *Acacia* species do not respond to simulated herbivory in South Africa (Hean and Ward, 2012), although total phenolics are higher in individuals of *Acacia tortilis* protected from herbivores (Wigley et al., 2022). Soil C and N did not change with our treatments, so our data were not appropriate for tests of the CNBH (Bryant et al., 1983).

Our hypotheses regarding the response of insects were not supported, possibly because insect populations recover quickly from fire (Radford and Andersen, 2012). Nonetheless, long-term studies suggest insect populations may change with fire (Kerstyn and Stiling, 1999; Swengel, 2001; Meyer et al., 2002; Knight and Holt, 2005; Joubert et al., 2016). As fire and mammals begin to have more pronounced long-term effects on vegetation in our experiment,

insect populations are likely to change (Joubert et al., 2016). For example, crickets were less abundant where *C. erythrocarpos* cover was higher. As shrubs increased in the absence of fire and large mammals, it is likely ground-dwelling crickets' preferred habitat may be compromised in the future. Although Orthoptera are good indicators of habitat change (Andersen et al., 2001), further work with other insect taxa will illustrate effects of fire and LMH more broadly, and research on Coleoptera is currently underway in the experiment.

Herpetofauna are also relatively understudied in terms of their response to fire and large mammals in savannas. Responses of reptiles to fire are species specific (Trainor and Woinarski, 1994). Limited data on amphibians in tropical savannas indicate fire reduces their abundance (Gomes dos Anjos et al., 2021), but fire may increase the abundance of species preferring densely wooded areas (Barbault, 1976). In our experiment, amphibians declined with cold burns. Amphibians and reptiles were both very seasonal, and their presence was associated with fine scale changes in habitat. Amphibians, for example, were more abundant in areas with less grass biomass and fewer shrubs, and unsurprisingly, their richness increased in plots near pans and with greater tree coverage. The higher abundance of amphibians in plots with less grass might be the result of increased visibility and thus a higher likeliness of recording amphibians in plots with less plant biomass. However, reptiles increased in abundance and richness in areas with more shrubs and responded positively to the proximity of pans. Thus, visibility is not the most likely explanation for the changes observed. Our results are similar to those found for several species of skinks whose abundance is positively related to moisture and grass cover (Trainor and Woinarski, 1994).

Small mammals were more abundant and species rich in plots closed to herbivores, as hypothesized, although small mammals also responded negatively to grass biomass and shrub

abundance, which were higher in closed plots. Similarly, in Eswatini, vegetation cover is negatively correlated with small mammal abundance, while vegetation greenness, triggered by fire, is positively related to small mammal density (Monadjem and Perrin, 2003). Small mammal abundance increased with time since fire in our experiment, and work from Eswatini also shows small mammals avoid recently burned areas (Monadjem and Perrin, 1997).

As predicted, the richness of LMH in the open plots was highest after hot burns as was foraging by impala, waterbuck, and warthog. This result is likely due to nutrient rich, regenerating vegetation in recently burned areas, which often serves as a magnet for LMH (Archibald and Bond, 2004; Parrini and Owen-Smith, 2010; Allred et al., 2011; Donaldson et al., 2018). Large mammal richness and incidences of browsing by nyala were also higher in plots with greater tree basal area. Tree cover increases browser and mixed feeder abundance in drier savannas as well (Smit and Prins, 2015).

The diversity of taxa and plant traits analyzed in this work contribute to a broader understanding of savanna functioning. After one year, our data indicate that relatively short-lived species that reproduce quickly may be more resistant and resilient to disturbance, as found in other ecosystems (Radford and Andersen, 2012). In addition, fire management is a pressing concern with climate change, and our results indicate management should be informed by comprehensive studies, as we documented taxa-specific responses to fire regimes. Our data also demonstrate the importance of large mammal conservation. Even short-term losses of large mammals altered vegetation, changing habitat quality for smaller animals. Nonetheless, these results may change over time, and the long-term value of the Gorongosa Savanna Ecology Experiment should become evident in the years to come. Future potential outputs of the experiment include testing of the alternative biome states hypothesis (Pausas and Bond, 2020)

and developing a mechanistic understanding of savanna biodiversity. In sum, documenting the effects of fire and LMH as well as their interactions will improve our understanding and conservation of disturbance-prone ecosystems, and this experiment will continue to offer insights on ecosystem resistance and resilience into the future.

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Author contribution statement

TJM designed the experiment, helped collect data, analyzed the data, and wrote the manuscript. OJA, HA, AC, and BSCT collected data and edited the manuscript. AA and DFM collected data. KG helped analyze the camera trap data and edit the manuscript. MES helped design the experiment and edit the manuscript. LJC helped with mammal data collection and identification. MOR helped with herpetofauna data collection, identification, and edited the manuscript. PN helped with insect data collection and identification.

Data availability statement

The data supporting the findings of this study are available at Dryad:
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763 **Table 1.** Hypotheses tested in the Gorongosa Savanna Ecology Experiment. A version of this
 764 table with relevant references for each hypothesis can be found in the Supplementary
 765 Information (Table S1)

Savanna response	Hypothesis
Soil C and N	Soil C and N may be higher after cold burns where LMH are present, followed by areas experiencing hot burns where LMH are present, as fire and herbivores may increase the breakdown of organic material and nutrient cycling. Hot burns may cause greater volatilization and losses of C and N.
Woody plant growth	Woody plant growth may increase in the absence of LMH and fire. Hot burns may have a stronger negative effect on woody plants than cold burns.
Grass biomass, cover and richness	Grass biomass and cover may increase in the absence of LMH, particularly where hot burns are applied. Grass richness may be higher in the presence of mammals and in plots with cold burns, as LMH and cold burns may promote heterogeneity through intermediate disturbance and herbivory.
Leaf C and nutrients	Similar to changes in soils, foliar C, N, and other elements may be higher after cold burns where LMH are present, followed by areas experiencing hot burns where LMH are present.
Total phenolics	Total phenolics may be higher in plants from unburned plots where available N is potentially lowest, as predicted by the CNBH. Total

	phenolics may be lower in plots closed to LMH where plants may suffer less herbivory due to the induction of defenses with herbivore pressure.
Insects	Insect abundance and richness may be highest where fire and LMH are excluded and may also vary seasonally, being highest in the wet season.
Herpetofauna	Indirect effects of fire and LMH may affect amphibian and reptile abundance and richness through changes in vegetation. Amphibians and reptiles may be more abundant and species rich in areas undisturbed by fire and large mammals.
Small mammals	Small mammals may be more abundant and species rich where fire and large mammals are absent.
Insects, herpetofauna, and small mammals	Insects, herpetofauna, and small mammals may be more abundant and species rich in areas subject to cold rather than hot burns. The intensity of fire may negatively affect abundance and richness, while the time since the last fire may be positively related to abundance and richness. Vegetation cover and the number of pans may be positively correlated with abundance and richness.
Large mammal herbivores	LMH may be more species rich and forage more in plots subject to hot rather than cold burns as forage regenerates. LMH richness may be higher in plots near more sources of water and where vegetation biomass and cover are higher.

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Figure 1. Box plots of changes in (A) the abundance and (B) richness of shrubs after one year of experimental conditions, and (C) grass biomass, (D) grass cover, (E) forb cover, and (F) grass richness in plots open and closed to large mammals experiencing different burn regimes. Shrub abundance and richness were higher in plots closed to LMH. Grass biomass was also higher inside exclosures, especially where fire was applied. Grass cover was higher in the exclosures and was highest in plots with hot burns. In contrast, forb cover was highest in plots exposed to LMH. Grass richness was highest in plots protected from LMH

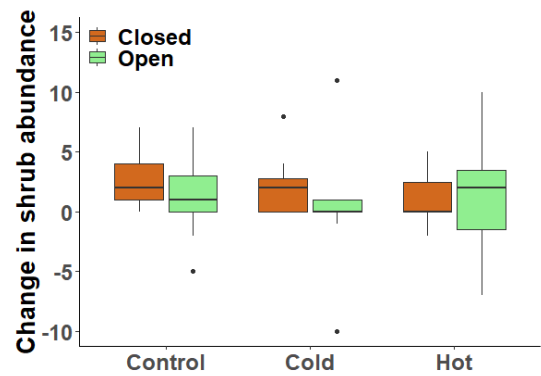
Figure 2. Concentrations of total phenolics of the five most common woody and grass species in the experiment (A. *Capparis erythrocarpos* var. *rosea*, B. *Acacia nigrescens*, C. *Acacia robusta*, D. *Megathyrsus maximus*, and E. *Urochloa mosambicensis*). Phenolics were significantly higher in *C. erythrocarpos* var. *rosea* plants growing inside exclosures. Phenolics were also marginally higher in *M. maximus* protected from large mammals

Figure 3. Abundance and richness of crickets (divided by the number of sampling days in each collection period as they differed between months; A, B), amphibians (C, D), reptiles (E, F), and small mammals (G, H) in relation to the fire and LMH exclosure treatments. Amphibian abundance and richness were higher in plots open to LMH, while small mammal abundance and richness were higher in exclosures. Amphibian abundance was lowest in plots experiencing cold burns

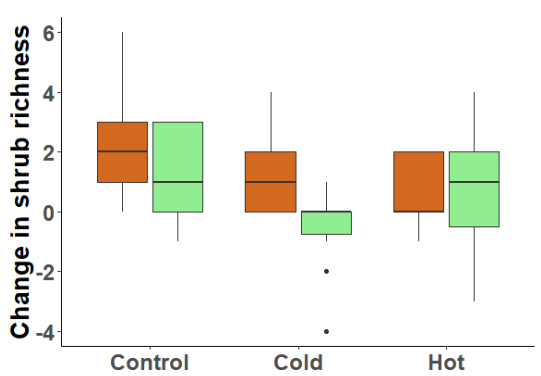
Figure 4. Large mammal herbivore richness in different burn regimes. Richness was greatest after hot burns

Figure 5. Number of individuals of the four most abundant LMH observed foraging in the plots. Impala, waterbuck, and warthog all foraged more in plots with hot burns followed by plots with

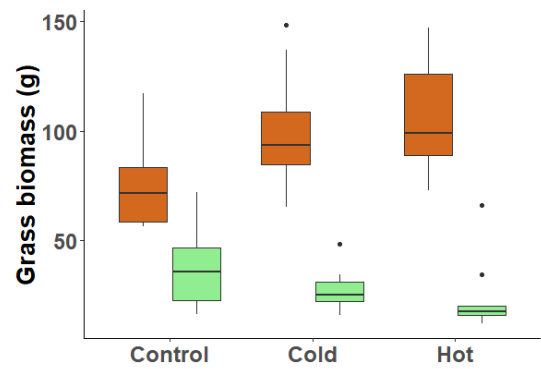
790 cold burns. Nyala were observed foraging in control and hot burn plots with roughly equal
791 frequency and foraged the least in cold burn plots



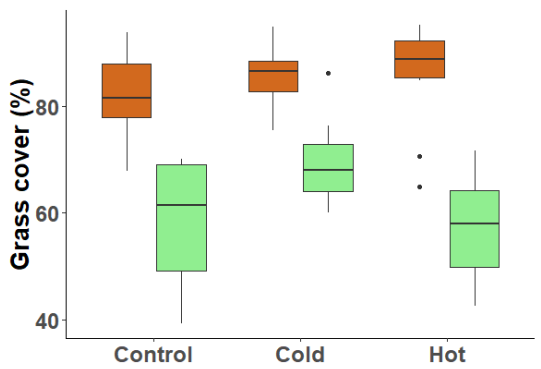
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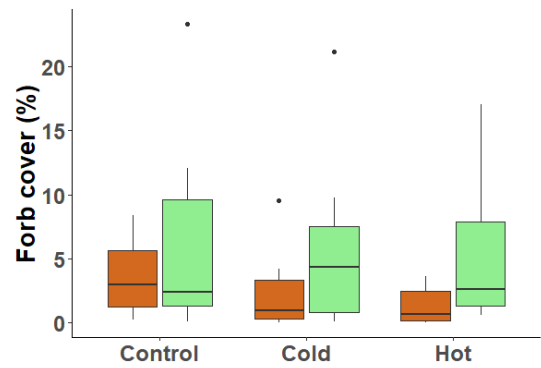
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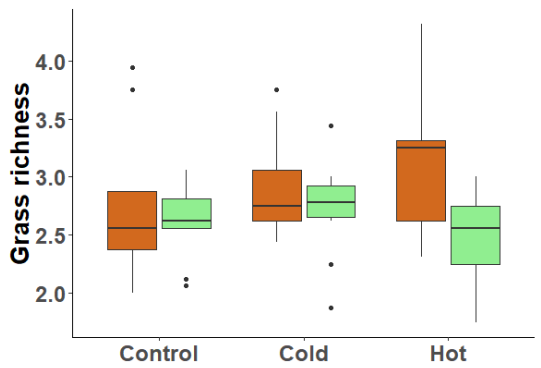
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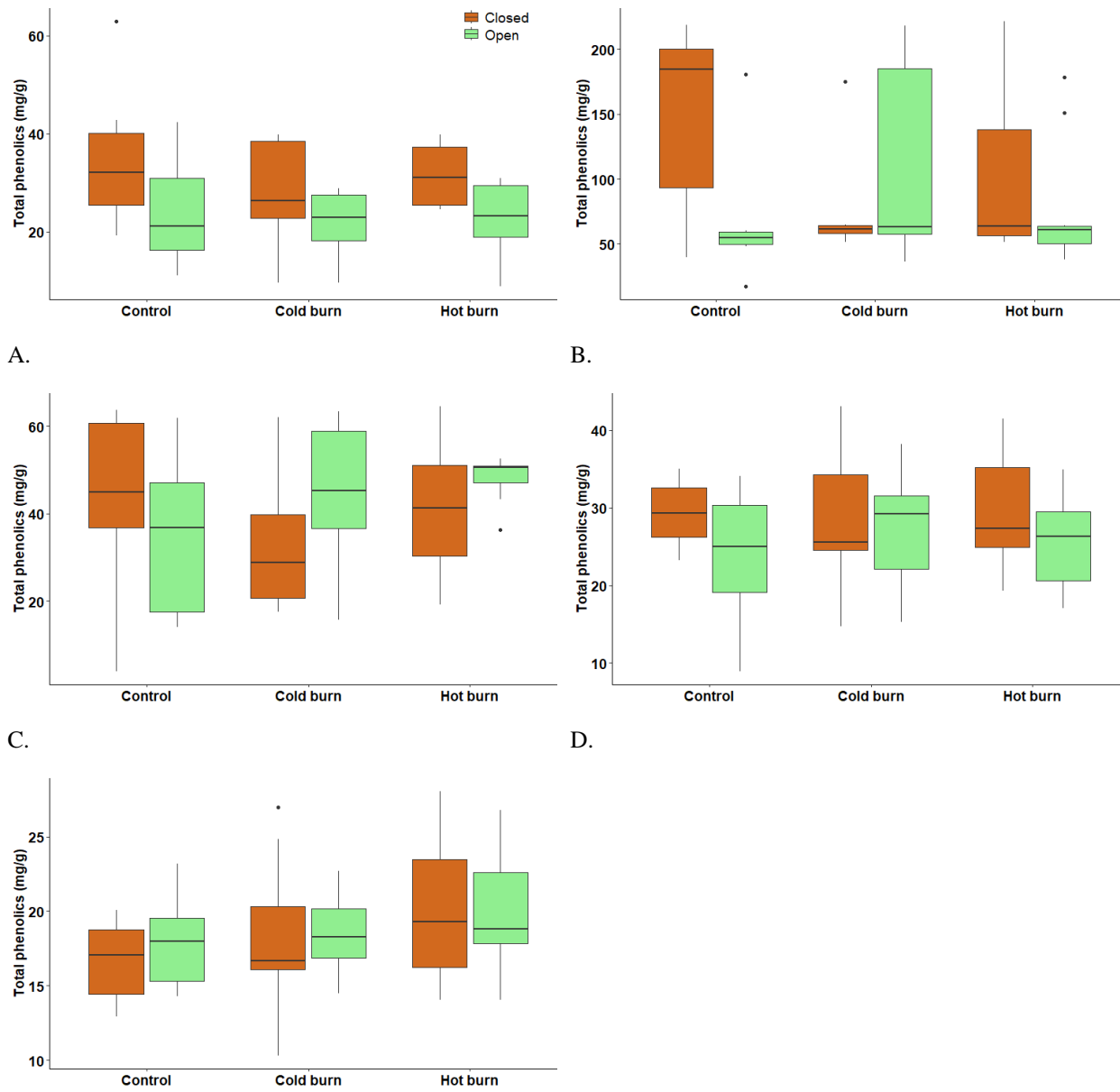


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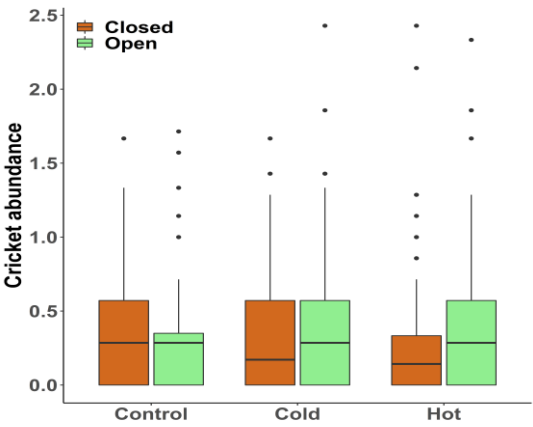


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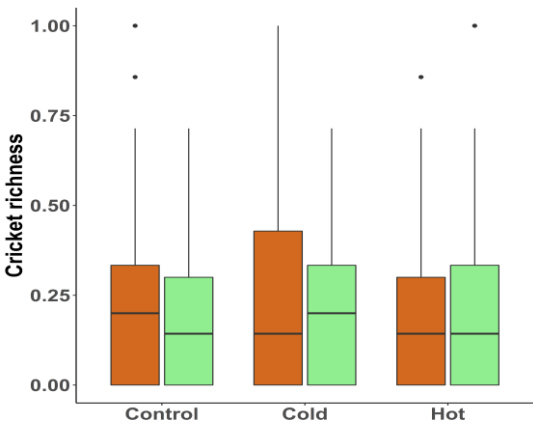
792 **Figure 1.**



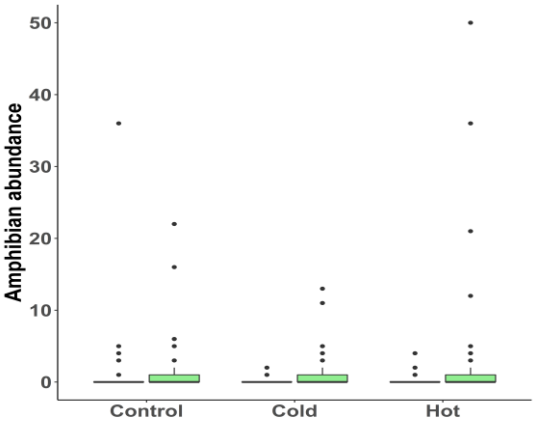
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Figure 2.



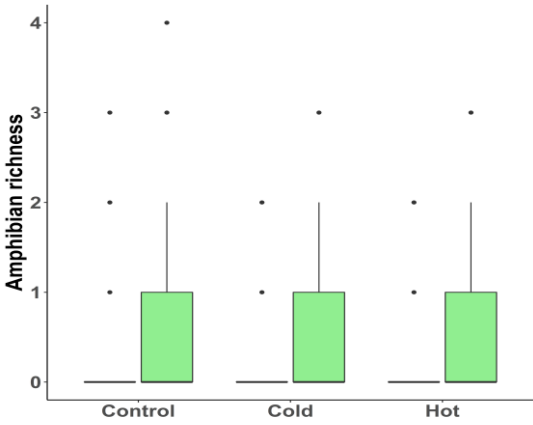
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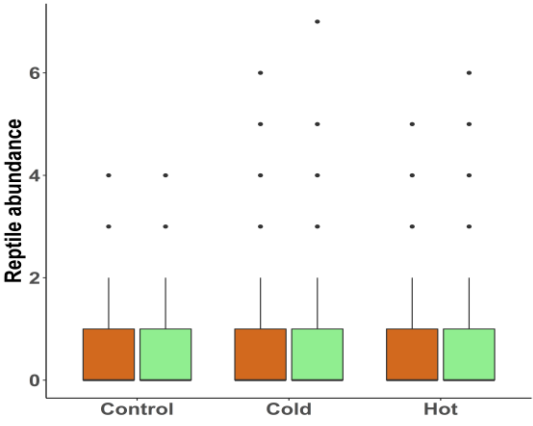
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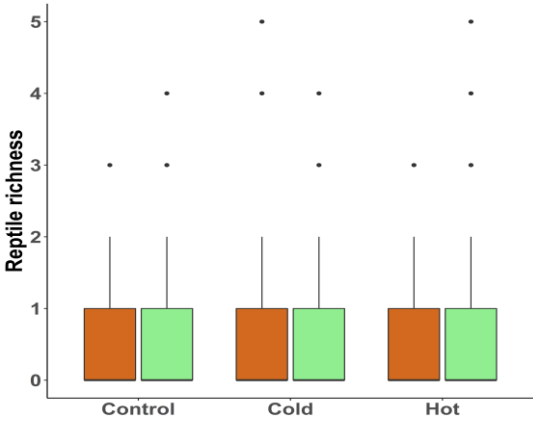
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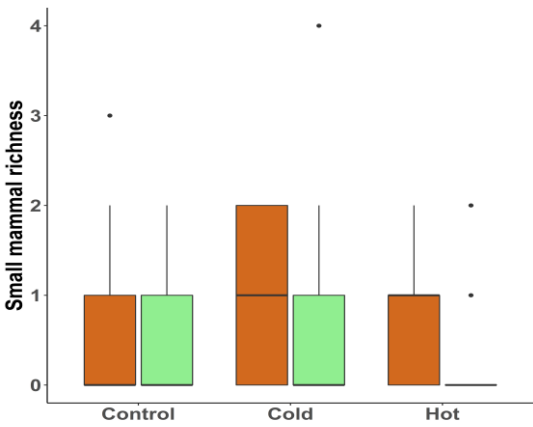
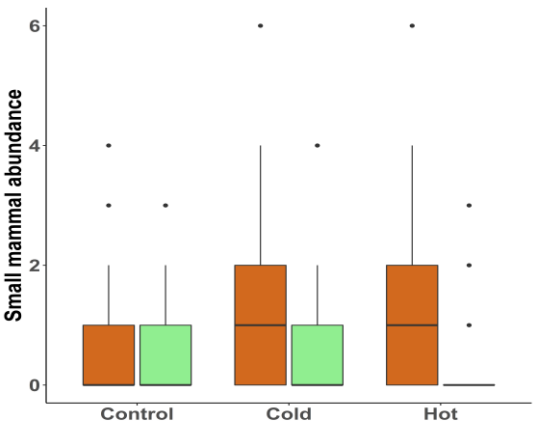
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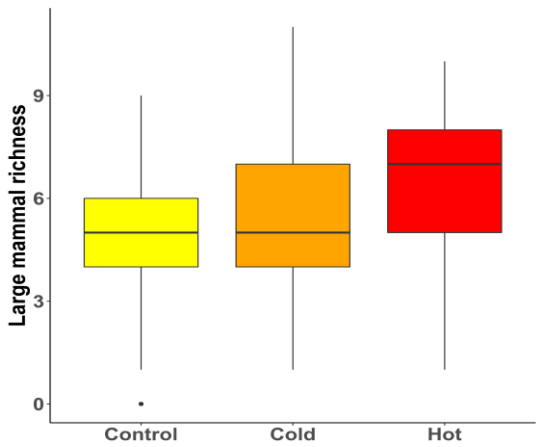
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Figure 3.

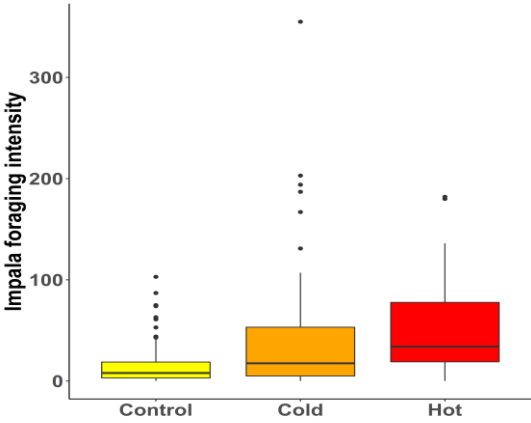
H.

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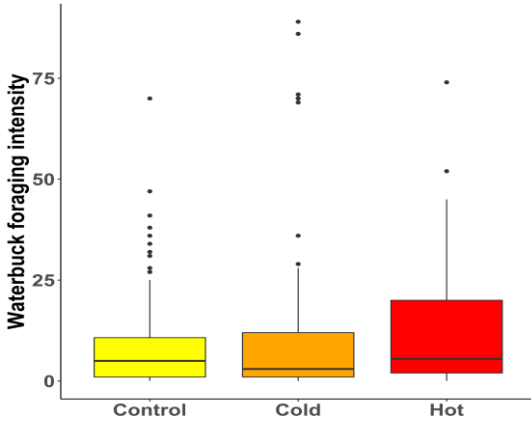


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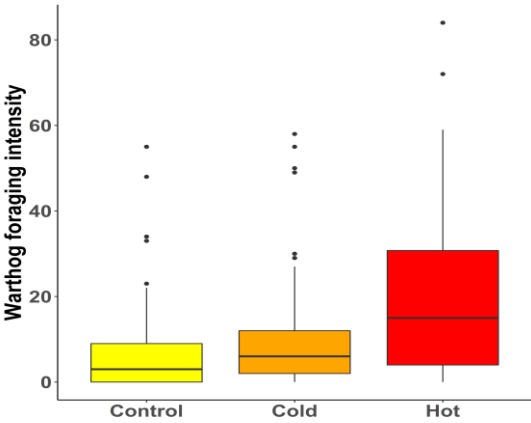
799 **Figure 4.**



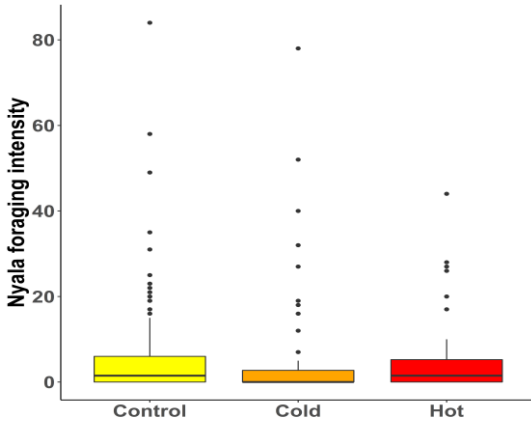
A.



B.



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Figure 5.