Fire frequency drives habitat selection by a diverse herbivore guild impacting top-down control of plant communities in an African savanna

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Abstract:

In areas with diverse herbivore communities such as African savannas, the frequency of disturbance by fire may alter the top–down role of different herbivore species on plant community dynamics. In a seven year experiment in the Kruger National Park, South Africa, we examined the habitat use of nine common herbivore species across annually burned, triennially burned and unburned areas. We also used two types of exclosures (plus open access controls) to examine the impacts of different herbivores on plant community dynamics across fire disturbance regimes. Full exclosures excluded all herbivores > 0.5 kg (e.g. elephant, zebra, impala) while partial exclosures allowed access only to animals with shoulder heights ≤ 0.85 m (e.g. impala, steenbok). Annual burns attracted a diverse suite of herbivores, and exclusion of larger herbivores (e.g. elephant, zebra, wildebeest) increased plant abundance. When smaller species, mainly impala, were also excluded there were declines in plant diversity, likely mediated by a decline in open space available for colonization of uncommon plant species. Unburned areas attracted the least diverse suite of herbivores, dominated by impala. Here, herbivore exclusion, especially of impala, led to strong declines in plant richness and diversity. With no fire disturbance, herbivore exclusion led to competitive exclusion via increases in plant dominance and light limitation. In contrast, on triennial burns, herbivore exclusion had no effect on plant richness or diversity, potentially due to relatively little open space for colonization across exclosure treatments but also little competitive exclusion due to the intermediate fire disturbance. Further, the diverse suite of grazers and browsers on triennial burns may have had a compensating effect of on the diversity of grasses and forbs. Ultimately, our work shows that

differential disturbance regimes can result in differential consumer pressure across a landscape and result in heterogeneous patterns in top–down control of community dynamics.

Keywords: plant diversity | herbivores | community dynamics | plant communities | fire

Article:

Abiotic and biotic forces often interact to drive community dynamics and ecosystem function (Chase et al. 2000). For grasslands and savannas worldwide, herbivory and fire are dominant forces that shape plant abundance, diversity and vegetation heterogeneity (Collins et al. 1998, Koerner and Collins 2013, Koerner et al. 2014). Humans however, have simultaneously altered both disturbance regimes by reducing the diversity of native herbivores, eliminating them completely, or replacing them with livestock (du Toit and Cumming 1999, Fuhlendorf et al. 2009) and by grossly modifying natural fire regimes (van Langevelde et al. 2003). Such alterations to these biotic and abiotic disturbances impact ecosystem function and the ecosystem services provisioned by human-impacted grasslands and savannas worldwide (Knapp et al. 2004, Fuhlendorf et al. 2009).

Extensive work in African savannas has documented how ungulate herbivory affects plant community composition and ecosystem processes (McNaughton 1985, Young et al. 2013, Koerner et al. 2014). However, much less attention has been given to the role of herbivore diversity and the effects of different herbivores on plant communities. The impact of herbivory may depend, in part, on the body size, feeding mode, foraging behavior, and nutritional requirements of different herbivore species (Owen-Smith 1988, du Toit and Cumming 1999). For example, selective removal experiments have shown strong effects of larger herbivores (e.g. rhinoceros, hippopotamus) on herbaceous plant biomass and diversity, but inconsistent effects of smaller ungulates (Verweij et al. 2006, Waldram et al. 2008). Although studies have begun to address the role of different herbivores in community dynamics, especially different size guilds of herbivores, little is known about how the impact of different herbivores changes under different abiotic regimes (but see Goheen et al. 2013).

Fire affects plant communities directly by removing herbaceous biomass, increasing primary productivity, altering community composition, and decreasing woody plant density (Higgins et al. 2007, Smith et al. 2013). Indirectly, fire may alter top–down control by attracting herbivores to the nutritious regrowth facilitated by a recent burn (Archibald and Bond 2004, Sensenig et al. 2010, Eby et al. 2014b). In addition, decreasing fire frequency increases herbaceous vegetation and tree density, providing more cover for predators (Hopcraft et al. 2005). This potential increase in risk may lead to avoidance by many herbivore species (Riginos and Grace 2008, Burkepile et al. 2013, Ford et al. 2014). Yet, the abundant trees in infrequently burned savannas can facilitate high soil nitrogen and palatable, nutrient-rich grass species that may also attract herbivores (Treydte et al. 2008). How herbivores manage potential tradeoffs between food and risk may depend on diet, body size, susceptibility to predators and escape tactics (Grange and Duncan 2006, Hopcraft et al. 2010, Burkepile et al. 2013). For example, smaller herbivores may select for more frequently burned areas due to their need for higher quality forage and lower predation risk. In contrast, larger herbivores may utilize less frequently burned areas since they can typically subsist on poorer quality diets and are often less vulnerable

to predators (Owen-Smith 1988, Van Soest 1996, Sensenig et al. 2010, Eby et al. 2014b). These differences may result in different suites of herbivores selecting for different fire-impacted habitats within the landscape, with potentially cascading effects on plant communities.

For seven years, we examined the impact of ungulate herbivores on herbaceous plant abundance and diversity across different fire regimes in the Kruger National Park (KNP), South Africa. KNP houses the historical suite of herbivorous mammals typical of southern African savannas, ranging in size from the ~5700 kg African savanna elephant *Loxodonta africana* to the 10 kg steenbok *Raphicerus campestris* and including the three most abundant species viz. impala *Aepyceros melampus*, Burchell's zebra *Equus quagga* and blue wildebeest *Connochaetes taurinus*. We separated the effects of larger versus smaller herbivores using two different types of exclosures paired with adjacent open access areas. Full exclosures excluded all mammalian herbivores > 0.5 kg (e.g. elephant, zebra, impala, steenbok) while partial exclosures allowed access only to animals with shoulder heights equal to or less than 0.85 m (e.g. impala, steenbok). These exclosures and open access areas were replicated across annually burned, triennially burned and unburned areas of savanna in central KNP. We expected differential habitat selection by different herbivore species to result in heterogeneous top–down impacts of herbivores across fire regimes. Our main predictions were that: 1) smaller herbivores (e.g. impala) would be attracted to annual burns likely due to higher quality forage. This would result in strong impacts of smaller herbivores on plant communities, with increases in plant cover and decreases in plant diversity only when all herbivores were excluded (i.e. effect of full exclosures > effect of partial exclosures with potentially no effect of the partial exclosures); 2) a diverse suite of herbivores would be attracted to triennial burns likely due to periodic increases in forage quality and a diversity of vegetation (i.e. grasses, forbs, and woody browse). This would result in strong impacts of both larger (e.g. zebra, wildebeest) and smaller (e.g. impala) herbivores on the plant community. We expected increases in plant cover and decreases in diversity in both exclosure treatments but with the strongest effects occurring in full exclosures (i.e., large effects of both exclosure types with effect of full exclosures > effect of partial exclosures due to compounding effects of excluding all herbivores); 3) only the largest herbivores (e.g. elephant) would frequent unburned areas due to higher predation risk associated with dense woody vegetation and their tolerance of relatively poorer quality forage. This would result in marginal effects of herbivore removal on plant communities with little impacts of herbivore exclusion on overall plant cover or diversity (i.e. small effects of both exclosure types).

Material and methods

Study location and experimental design

The Kruger National Park, South Africa (22° 5'to 25°32'S, 30°50' to 32°2'E) encompasses nearly 2 million hectares of African savanna protected since 1898. In 1954, a series of Experimental Burn Plots (EBPs) was established to investigate the effects of fire frequency on the park's flora and fauna. Experimental burns at varying intervals and unburned fire exclusion areas are replicated in separate ~7 ha plots (Biggs et al. 2003). We focused on the annually burned, triennially burned, and unburned treatments at each of two EBP replicates (referred to as the N'Wanetsi and Satara EBP strings) in central KNP near the Satara rest camp (24°23'52"S,

31°46'40"E). From 2007–2013, the annual plots were burned every year prior to the growing season with the triennial plots burned in 2007, 2010 and 2013.

During our study, precipitation averaged 518 mm (range 397–684 mm) (Supplementary material Appendix 1 Fig. A1), with the majority falling during the wet season (Sept–Mar). Vegetation in the region comprises a mixture of C_4 grasses (e.g. *Bothriochloa radicans, Digitaria eriantha, Urochloa mosambiscensis*), annual and perennial forbs, and woody plants (e.g. *Senegalia* [previously *Acacia*] *nigrescens, Dichrostachys cinerea*). Central KNP supports a diverse assemblage of mammalian herbivores (> 10 kg; Supplementary material Appendix 1 Table A1) with impala, zebra, wildebeest, African buffalo *Syncerus caffer*, and elephant being abundant. Herbivore abundance and grazing intensity in this area is considered moderate for regional savannas (du Toit 2003), averaging 104 kg of herbivore/hectare (Burkepile et al. 2013). Hyena *Crocuta crocuta* (13.9 ind./100 km^2) and lion *Panthera leo* (12.7 ind./100 km^2) are the most common predators in the region while leopard *Panthera pardus* (3.5 ind./100 km^2) and cheetah *Acinonyx jubatus* (2.2 ind./100 km^2) are less common (Mills and Funston 2003). All of these species of predators use a wide variety of habitats (Mills and Funston 2003), but denser vegetation often increases the chance for successful kills (Funston et al. 2001, Burkepile et al. 2013).

In November 2006, prior to the 2007 growing season, we established an experiment to test for the effects of different sized herbivores on herbaceous vegetation composition. We controlled access to plant communities using exclosures that selectively excluded herbivores of different sizes. The experimental design consisted of three treatments: 1) full exclosures, 2) exclosures starting at a height of 0.85 m (hereafter 'partial exclosures'), and 3) open access areas. Full exclosures excluded all herbivores > 0.5 kg. Partial exclosures excluded all animals with a shoulder height 0.85 m or greater (e.g. zebra, wildebeest, buffalo; Supplementary material Appendix 1 Table A1) but allowed access to smaller herbivores (e.g. impala, steenbok). Open access areas allowed all herbivores. Full exclosures measured 7 m in diameter (enclosing 38.5 m^2 of savanna) and consisted of diamond mesh to a height of 1.2 m, with a bailing-wire barrier at 2 m (Koerner et al. 2014). Partial exclosures, also 7 m in diameter, consisted of bailing-wire barriers at 0.85, 1.0, 1.2, 1.5, and 2 m above the ground. Open access areas were permanently marked to facilitate repeated sampling. Exclosures larger (Goheen et al. 2013, Young et al. 2013) and smaller (McNaughton 1985, Anderson et al. 2007) than these have shown significant effects of herbivores on plant communities. Our exclosures were replicated widely across and within burn regimes to capture much of the heterogeneity in vegetation composition.

We replicated herbivore exclosures across annually burned, triennially burned, and unburned plots in the Satara and N'Wanetsi EBP's (n = 2 plots per burn type). The Satara and N'Wanetsi EBP's were separated by ~10 km. Burn plots within each EBP (e.g. within the Satara EBP) used in our study were separated by ~1–3.5 km depending on the spatial layout of the EBP. Each burn plot contained n = 5 replicates per exclosure type (n = 10 replicates of each exclosure per fire treatment). Exclosures and open access areas were located to avoid trees and large shrubs. Replicates of the exclosures were arranged in a blocked design with one replicate of each treatment grouped so that each treatment had similar initial plant abundance and community composition based on visual assessment.

The different burn treatments generated different vegetation structure. Growing season grass height averaged 56.2 cm on annual burns, 72.1 cm on triennial burns, and 87.6 cm on unburned areas (Burkepile et al. 2013). Woody vegetation density also differed across burn types with individuals > 1 m in height averaging 3.3 ind./400 m^2 in annual burns, 15.7 ind./400 m^2 in triennial burns, and 23.6 ind./400 m^2 in unburned areas (Burkepile et al. 2013).

Herbivore abundance

From 2008–2013, we used dung counts to survey relative herbivore use of the burn regimes. Dung surveys reliably estimate relative use of different areas across a landscape (Barnes 2001). Although we did conduct both diurnal and nocturnal driving surveys of herbivore abundance during this period, we focus here on the dung count data as it captures the abundance of larger, rarer species better than do driving surveys (Burkepile et al. 2013). Further, dung counts integrate both diurnal and nocturnal use of habitat and likely more directly reflect the impact of different herbivores across the burn regimes (Burkepile et al. 2013). We surveyed 50 × 4 m transects, established parallel to the short axis of each burn plot (n = 7 per plot), every other month during the growing season and identified dung piles (Stuart and Stuart 2000). After counting, we removed dung to avoid recounting during subsequent surveys.

Efficacy of herbivore exclosures

We used two methods to determine the efficacy of the partial exclusion of larger herbivores ≥ 0.85 m at the shoulder. First, every ~4 weeks during the growing seasons of 2007 and 2008 we identified and counted herbivore tracks (Stuart and Stuart 2000) inside 4-m^2 sample plots in each open access area and paired partial exclosure in the annually burned plots. We did this only in the annually burned plots as these had a significant amount of bare soil subsequent to fires where we could easily identify tracks. Second, we identified dung piles inside the partial exclosures and in 7-m diameter open access areas across all burn regimes. Although we did not quantitatively assess the efficacy of the full exclosures, we never saw herbivore dung inside them during the duration of our experiment.

Plant community responses

In 2007–2013, we surveyed herbaceous plant community composition twice during the growing season: in January and again in March to capture peak abundance of early and late-season species, respectively. We surveyed one permanent 4-m^2 sample plot (divided into four 1-m^2 subplots) in each exclosure and paired open access area. Within each subplot, we estimated the percent cover (to the nearest 1%) for each plant species (Koerner et al. 2014). We also estimated the amount of exposed bare ground (i.e. % area not covered by vegetation), dung, and dead leaf litter. We used the maximum cover value of each species over the growing season estimated from either early- or late-season surveys and averaged these across the four 1-m^2 subplots per plot to calculate plant cover (total, grass and forb), species richness (total (S), grass (S_G), and forb (S_F)), Shannon–Wiener diversity (H), and Berger–Parker index D (dominance index), which is simply the relative abundance of the most abundant species in each sample plot.

Statistical analyses

We calculated Ivlev's electivity index (Ivlev 1961) as a measure of relative habitat selection by herbivore species among the three burn types using the dung count data (Ivlev 1961). Selectivity for or against the non-treatment habitat matrix surrounding the EBP's was not assessed. We used the equation $Ei = (ri - ni)/(ri + ni)$ where ri is the proportion of all individuals of a given herbivore species that were found on the ith type of burn plot and ni is the proportion of the ith type of burn plot available to herbivores out of the total area represented by all the burn types (i.e. proportion of the total experimental burn area made up of the ith type of burn type; for example annual burns represented 31.5% of the total experimental burn area in the study). Confidence intervals (95%) for Ivlev's index were calculated following Strauss (1979). Selection for or against a burn type was considered significant when the 95% CI were either above or below zero, respectively. For simplicity, we summed dung count data across all years to estimate overall selectivity of herbivores for the different burn regimes across the study duration. We recognize that there is likely yearly variability for how different herbivores use the different burn regimes due to many factors such as timing of the burns, rainfall, and vegetation cover. Yet, we were primarily interested in how cumulative herbivore abundance and selectivity would have translated into long-term impacts on plant community dynamics. Thus, we focused on the overall patterns of herbivore abundance.

For plant community metrics, we used a nested mixed-effects model to determine whether the response variable differed among herbivore treatments, among years, and whether there was a herbivore by year interaction. Replicates of exclosures were nested within blocks nested within EBP string (N'Wanetsi or Satara). EBP string and block nested within EBP string were included as random factors. For each response variable, each burn frequency was analyzed separately because: 1) the effects of fire on plant communities are well established after 50 + years of fire manipulation and 2) we were interested in the effects of herbivores on plant communities in the specific burn regimes. Residuals from the model were checked for homoscedasticity using residual plots against fitted values and against herbivore treatments and years. If significant heteroscedasticity was observed, we weighted observations by year or herbivore treatment, where necessary (Zurr et al. 2009). Data were log- or square-root transformed when weighting did not sufficiently homogenize the variances. In the presence of a significant effect of herbivores, but no interaction with year, we used Tukey's HSD post hoc test for all pairwise comparisons among herbivore treatments. If there was a significant interaction between herbivore treatment and year, we used Tukey's HSD to make all pairwise comparisons of herbivore treatment within each year. We did not make cross-year comparisons in order to reduce the number of post hoc tests and limit the severity of the correction to significance levels.

All statistics were conducted in R ver. 3.0.0 (< www.r-project.org >). Mixed effects models were run using the 'nlme' package (Pinheiro et al. 2013) and post hoc comparisons conducted using the 'multcomp' package (Hothorn et al. 2008).

Data deposition

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.f34p5 > (Burkepile et al. 2016).

Results

Herbivore abundance and selectivity across burn regimes

Nine species of herbivores showed up on our dung surveys. Impala, zebra, and wildebeest were the most abundant herbivores (Fig. 1), while elephant, kudu and buffalo were also frequent visitors of the different burns. Different burn regimes attracted different suites of herbivores. Elephant, zebra, wildebeest and steenbok selected for annual burns while buffalo, impala, and warthog used them in proportion to their abundance (Fig. 2A). No herbivore species showed positive selection for triennial burns but giraffe, buffalo, zebra, kudu, impala, warthog and steenbok all used them in proportion to their abundance (Fig. 2B). Impala selected for unburned areas while elephant, giraffe, buffalo and kudu used these burns in proportion to their abundance (Fig. 2C).

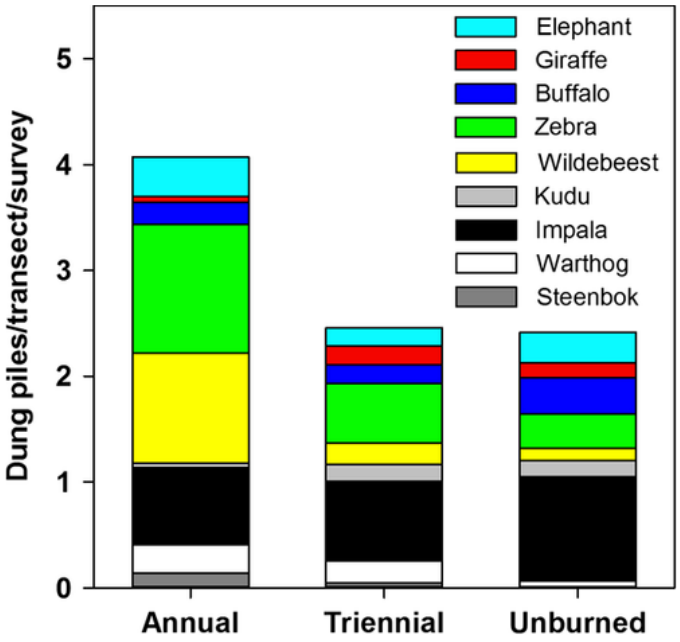

Figure 1. Herbivore abundance across the burn types expressed as density of herbivore dung averaged across all years of the study. Bars are mean values for each herbivore species. Error bars have been eliminated for clarity. Herbivore species are presented in decreasing order of body size.

Efficacy of herbivore exclosures

Track and dung surveys showed that adults of common large herbivores such as zebra and wildebeest, which were abundant in the adjacent open access areas, were successfully excluded by the partial exclosures (Supplementary material Appendix 1 Fig. A2). We recorded tracks of immature zebra or wildebeest inside the partial exclosures only very rarely (< 1% of the time). In contrast, tracks and dung of impala were abundant in both the partial exclosures and adjacent open access areas (Supplementary material Appendix 1 Fig. A2). Both track and dung surveys

suggested that impala used open access areas and partial exclosures similarly as there were no differences in either metric between treatments ($p > 0.5$ in all cases; one-factor ANOVA).

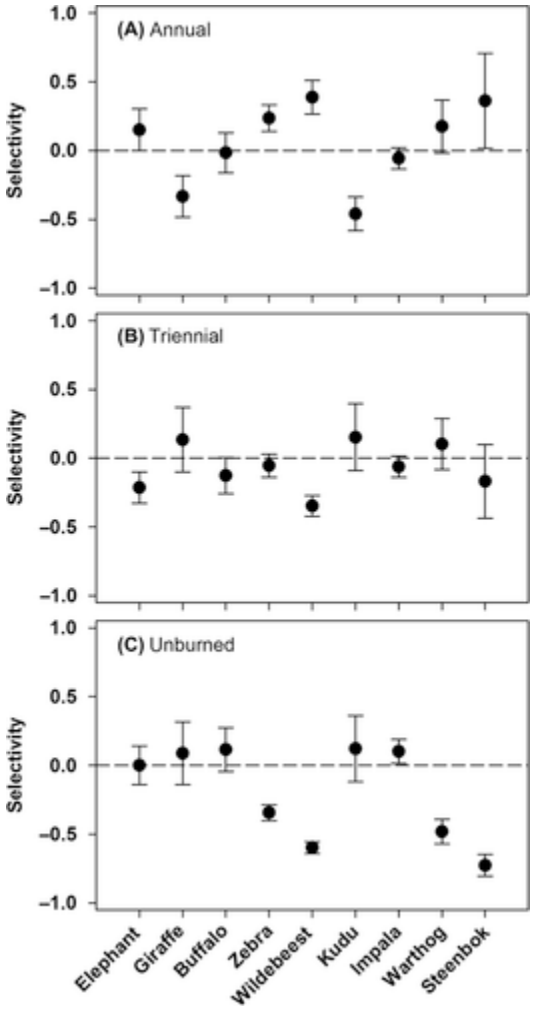

Figure 2. Selectivity (Ivlev's electivity index) by different herbivore species across annual burns (A), triennial burns (B), and unburned areas (C) summed across all years of the study. Data are means and 95% confidence intervals. Positive numbers denote selection for a burn treatment while negative numbers denote selection against burn treatment. Selectivity 95% confidence intervals that cross the zero line were not considered significant. Herbivore species are presented in decreasing order of body size.

Plant abundance responses

In annual burns, both full and partial exclosures had higher overall plant cover than open access areas (Fig. 3A, Supplementary material Appendix 1 Table A2) as well as less bare ground (Supplementary material Appendix 1 Fig. A3, Table A3). Most of this increase was due to increased grass cover (Fig. 3D) when removing the larger herbivores (e.g. zebra, wildebeest, etc). In annual burns, forb cover showed no effect of herbivore exclusion (Fig. 3G) but a strong year effect.

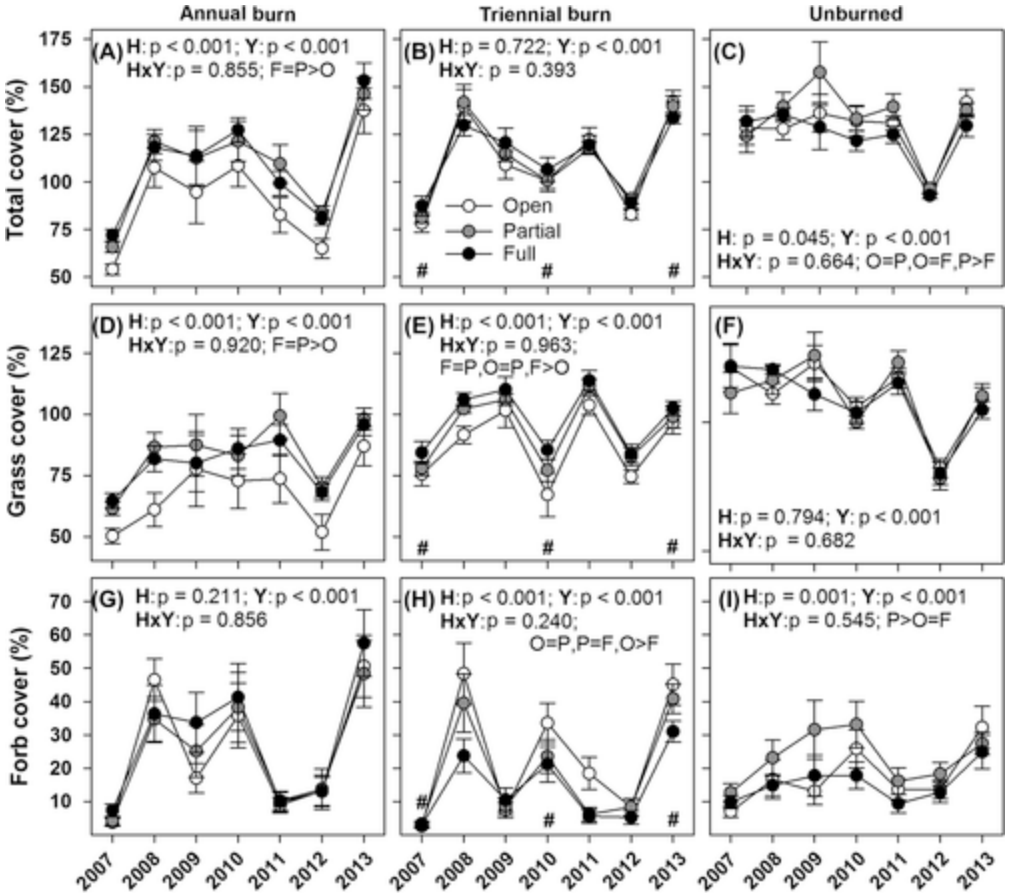

Figure 3. Cover of all plants (A–C), grasses (D–F), or forbs (G–I) across herbivore exclosures and burn treatments for each year of the study. Cover is often over 100% due to high three-dimensional complexity. Data are means with standard errors. Statistics are from mixed-effects models testing for effects of herbivore treatment (H), year (Y), and their interaction (H × Y). When effects of herbivore treatment are significant, post hoc tests are represented below mixed-effect model results. For example, 'O > P = F' would represent post hoc tests where the open access treatment would be greater than both the partial and full exclosure but the partial and full exclosure would not be different than one another. Burns in triennial regime noted with #.

In triennial burns, exclusion of herbivores had no net effect on overall plant cover (Fig. 3B, Supplementary material Appendix 1 Table A2). However, herbivore exclusion increased grass cover (Fig. 3E) and decreased forb cover (Fig. 3H) and bare ground (Supplementary material Appendix 1 Fig. A3, Table A3). Grass cover was highest when the smaller herbivores were also excluded, but the partial exclosures showed no significant effect. Similarly, forb cover decreased with increasing herbivore exclusion.

In unburned areas, patterns were more complex. Overall plant cover was highest in partial exclosures and lowest in full herbivore exclosures (Fig. 3C, Supplementary material Appendix 1 Table A2). Responses of forbs likely caused partial exclosures to have the highest cover, as they were most abundant in partial exclosures in most years (Fig. 3I). There was no herbivore effect on grass cover in unburned areas (Fig. 3F). Both full and partial exclusion yielded more litter and

less bare ground than in open access areas (Supplementary material Appendix 1 Fig. A3, Table A3).

Plant richness and diversity responses

On annual burns, herbivore exclusion did not impact either plant species richness (Fig. 4A) or dominance (Fig. 4G). However, diversity was highest in open access areas and lowest in full exclosures. The intermediate effect of partial exclusion was not significantly different from the open access areas but was trending ($p = 0.102$) towards being higher than in the full exclosures (Fig. 4D, Supplementary material Appendix 1 Table A5). This pattern suggests that exclusion of only larger herbivores had a marginal effect on diversity but that the largest effects on diversity occurred when smaller herbivores were also excluded.

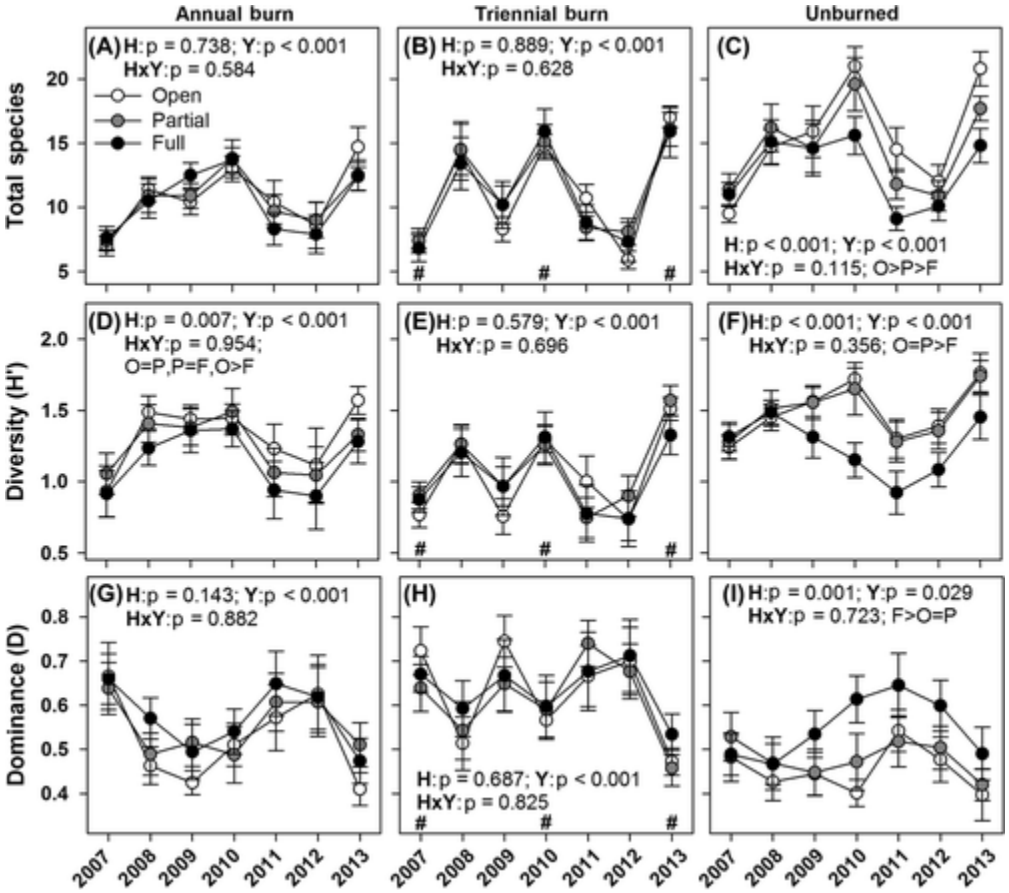

Figure 4. Total plant species (A–C), species diversity (D–F), or dominance (G–I) across herbivore exclosures and burn treatments for each year of the study. Data are means with standard errors. Statistics as in Fig. 3. Burns in triennial regime noted with #.

On triennial burns, herbivore exclusion did not affect any measures of richness, dominance, or diversity (Fig. 4B, 4E, 4H). Yet, in unburned areas, herbivore exclusion reduced total species richness as well as grass and forb richness (Fig. 4, Supplementary material Appendix 1 Fig. A4, Table A4). Excluding only the larger herbivores reduced species richness relative to open access areas. Also excluding smaller herbivores resulted in even further declines in species richness.

Dominance increased significantly in the full exclosures but was low in partial exclosures and open access areas. Together these changes in richness and dominance resulted in full exclosures having lower species diversity than either partial exclosures or open access areas (Fig. 4F, Supplementary material Appendix 1 Table A5).

Discussion

Across seven years of experimental herbivore exclusion, we found that the frequency of fire disturbance mediated the impact of different ungulate herbivores on plant community composition in an African savanna. Surprisingly, many of our initial hypotheses about where different groups of herbivores would impact plant community dynamics were incorrect. We expected herbivore selectivity for burned areas to result in strong top–down impacts of smaller herbivores on annual burns and both larger and smaller herbivores on triennial burns. Instead, on annual burns, exclusion of larger herbivores, mostly zebra and wildebeest, increased plant abundance but had little effect on plant diversity. Exclusion of smaller herbivores, particularly impala, on annual burns resulted in modest declines in plant diversity but no changes in species richness. Triennial burns attracted a diverse suite of herbivores. Yet, in contrast to our predictions, there were no effects of herbivore exclusion on plant richness or diversity despite increased grass cover and decreased forb cover with exclusion of smaller herbivores. In unburned areas, we expected minimal impact of herbivore exclusion due to low herbivore abundance. Yet, we saw some of the most pronounced changes in plant communities here. Herbivore exclusion, particularly of the abundant impala, resulted in strong declines in species richness and diversity and increases in dominance. Ultimately, our work shows that differential disturbance regimes can result in differential consumer pressure across a landscape and result in heterogeneous patterns in top–down control of community dynamics.

Differential disturbance regimes and heterogeneous top–down control

The intensity or frequency of disturbance can impact community processes and regulate species diversity (Connell 1978, Huston 1979). In some cases, differential disturbance determines top–down pressure from consumers by impacting consumer abundance or consumer identity (Sousa 1979, Archibald et al. 2005, Reed et al. 2011). Here, fire frequency determined selection of different herbivore species for different areas of the landscape, which translated into differential impacts of herbivory across fire regimes. An absence of disturbance with complete fire suppression in the unburned areas resulted in the strongest impacts of herbivore removal on plant communities. This was contrary to our expectations as we expected unburned areas to have only a few, larger herbivores due to dense vegetation that likely increases predation risk (Riginos and Grace 2008, Burkepile et al. 2013, Ford et al. 2014).

Yet, partial exclosures led to increases in overall plant cover, especially of forbs, likely due to the exclusion of elephant and kudu which both browse forbs. Notably, exclusion of impala led to the most dramatic impacts on plant communities resulting in lowered species richness, increased plant dominance, increased plant litter, and overall lower diversity (Fig. 4, 5). The increase in dominance, typically of the most abundant C_4 grasses, is often correlated with a decline in species richness and diversity (Koerner et al. 2014). Increases in both dominant plants and litter cover likely increased competition for light, which is a common mechanism resulting in declines

in overall species richness and diversity (Borer et al. 2014). The strong impact of impala in unburned areas was particularly surprising as we expected impala to target annual and triennial burns to take advantage of potentially higher quality forage (Sensenig et al. 2010, Eby et al. 2014b) and avoid unburned areas due to increased predation risk. Yet, impala were the most abundant herbivore on unburned areas. They may have been attracted to unburned areas due to abundant palatable grass species (e.g. *Digitaria eriantha* and *Panicum maximum*). Further, our previous data show that impala may be at no greater risk in areas of tall grasses and dense woody vegetation (Burkepile et al. 2013).

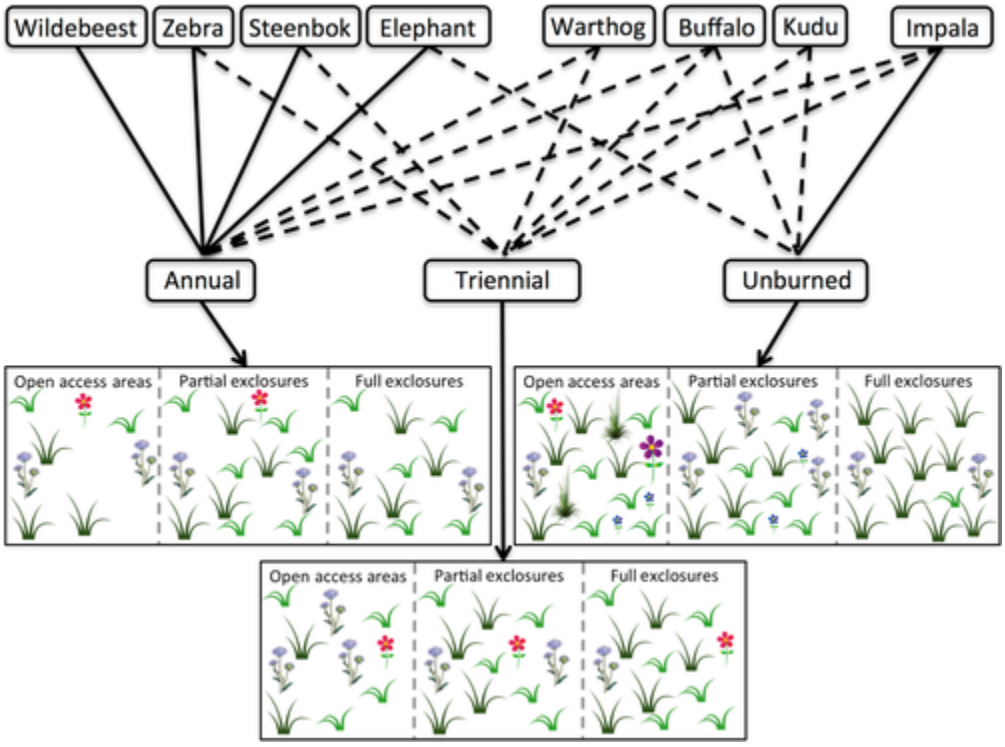

Figure 5. Summary figure outlining herbivore selectivity patterns for the different burn regimes and the impact of those herbivores on plant community composition and diversity. Solid lines connecting herbivore species to burn regimes denote selection for that burn type, while dashed lines denote usage of the burn in proportion to abundance. No connecting lines between herbivore species and certain burn regimes denotes selection against that burn type. For example, elephant selected for annual burns, selected against triennial burns, and used unburned areas in proportion to their abundance. Giraffe are omitted for clarity as they would not have fed on the herbaceous plant communities. Plant communities in each burn regime are represented by grasses (green tufts), forbs (flowers), and bare ground (white space). Different sizes, shapes, and colors of grasses and forbs represent relative abundance of different species. For example, in unburned areas, plant species richness was highest in open access areas, intermediate in partial exclosures, and lowest in full exclosures. Similarly, for annual burns, bare ground was highest in open access areas and similarly low in partial and full exclosures.

At the other end of the disturbance spectrum, frequent fires attracted a diverse suite of herbivore species but resulted in minimal impact on plant diversity despite strong increases in plant cover. Grazers such as wildebeest and zebra selected for annual burns, as did steenbok and elephant

(Fig. 1, 2, 5). We expected this pattern as previous studies showed many herbivores are attracted to increased forage quality or lowered predation risk that comes with frequent burning (Archibald and Bond 2004, Sensenig et al. 2010, Burkepile et al. 2013, Eby et al. 2014b). Exclusion of larger herbivores (e.g. zebra and wildebeest) led to increases in plant cover, particularly grasses, on annual burns. Yet, there were only slight declines in plant diversity with herbivore exclusion and no changes in either species richness or dominance (Fig. 5). Further, these declines occurred only when smaller herbivores (e.g. impala) were also excluded.

The impacts of herbivores on plant diversity in annual burns may have been linked to frequent fire facilitating open space. The abundant bare ground (often over 30% cover) in areas open to herbivores likely facilitated colonization by forbs and annual grasses that increased species diversity, essentially a lottery model of species coexistence (Wilson and Tilman 2002). Bare ground decreased with herbivore exclusion, likely leading to the moderate decreases in plant diversity (Fig. 5). Yet, even in herbivore exclosures, bare ground was often over 20% cover. This persistent, fire-generated open ground likely resulted in minimal competition for space and light, opposite to what we saw in unburned areas, and minimized the impact of abundant herbivores on plant community composition.

Intermediate levels of disturbance often result in the highest species diversity due to the coexistence of both pioneering species and competitively dominant species (Connell 1978). Triennial burns, our intermediate level of disturbance, attracted a diverse suite of grazers and browsers, potentially due to periodically high forage quality and a diversity of food resources (e.g. grasses, forbs, woody browse). Yet, exclusion of these abundant herbivores did not affect plant richness dominance or diversity (Fig. 4) despite significant changes in grass and forb cover (Fig. 3). It could be that neither of the mechanisms resulting in diversity declines in the annual burns and unburned areas were at work in triennial burns. In annual burns, the decrease in bare ground with herbivore exclusion likely lowered available space for colonization by forbs and annual grasses, thereby slightly suppressing diversity. In unburned areas, increasing plant dominance, litter cover, and competition for light with herbivore exclusion likely led to the large declines in richness and diversity. Yet, in triennial burns, there was often < 10% bare ground even in open areas suggesting low potential for colonization of subordinate species. But, the intermediate burns also kept down litter cover and minimized competition for light thereby minimizing competitive exclusion by dominant species. Thus, the relative frequency of disturbance by fire appears to mediate two main mechanisms whereby herbivores impact plant diversity, the generation of open space and the prevention of competitive exclusion via plant dominance and light limitation.

Why do abundant herbivores yield minimal impacts on plant diversity?

Other exclusion studies involving diverse herbivore communities in African savannas have shown mixed results of herbivore removal on plant diversity, with some studies showing significant declines in plant diversity (McNaughton 1979, Belsky 1992, Anderson et al. 2007, Porensky et al. 2013, Young et al. 2013) while others show little effect (Jacobs and Naiman 2008, Goheen et al. 2013, Koerner et al. 2014). A surprise from our study was the lack of consistent, strong effects of herbivore removal on plant diversity and richness across all fire regimes despite significant effects on both grass and forb abundance. Only in unburned areas did

herbivore removal strongly affect both plant richness and diversity. There were only moderate declines in plant diversity, but not richness, on annual burns and no consistent effects of herbivore removal on species richness or diversity in triennial burns. We hypothesize two, non-mutually exclusive, potential reasons for these inconsistent effects.

First, moderate levels of productivity in our region of KNP may preclude strong impacts of herbivore exclusion on overall plant diversity despite strongly impacting plant abundance. Part of the heterogeneity in the responses seen across African savannas may be due to differences in rainfall or productivity as many of the studies that show significant effects of herbivore removal on plant diversity are in areas of comparatively higher rainfall. In areas of high productivity, herbivore removal often results in declines in diversity as rapid growth of dominant species in these areas of high resources results in competitive exclusion of subordinate species (Olff and Ritchie 1998, Proulx and Mazumder 1998, Bakker et al. 2006). In contrast, in areas of low productivity herbivore exclusion often results in increases in species richness and diversity. When herbivores are present, they often eat plants to local extinction as impacted individuals have few resources available to replace lost tissue. Yet, protection from herbivory facilitates recovery and/or recolonization of palatable species resulting in an increase in diversity (Olff and Ritchie 1998).

Our experiment in central KNP may show modest impacts of herbivore removal on species diversity because our site is moderately productive. The moderate resources may allow plant species to recover fast enough from herbivory to avoid local extinction. As a result, respite from herbivory does not result in the reestablishment of palatable species previously lost. Further, herbivore removal results in minimal competitive exclusion as compared to higher productivity areas. Thus, there may be increases or decreases in the abundance of existing species but little species turnover once herbivores are removed. The one exception appeared to be in unburned areas, where plant litter accumulated in herbivore exclosures over the course of the study. This litter accumulation likely increased light limitation, similar to what happens more quickly when herbivores are excluded from high productivity habitats, resulting in exclusion of smaller, subordinate species.

A second possible reason for these muted responses in species diversity and richness could be the net impact of a diverse suite of herbivores on plant communities. Many studies that show strong impacts of herbivores on plant diversity typically focus on one or a very limited subset of grazing species (e.g. bison, cattle, African buffalo) that remove competitively dominant grasses and facilitate subordinate forb species (Collins et al. 1998, Bakker et al. 2006, Eby et al. 2014a). Thus, when these grazers are removed, the competitively superior grasses dominate and outcompete forb and subordinate grass species that are lost from the system, lowering plant diversity.

However, in areas with diverse herbivore guilds, there may be little net impact of herbivore exclusion on diversity due to compensatory effects of different herbivore species (Ritchie and Olff 1999, Duffy 2002). For example, in sagebrush steppe, grazing by cattle offset the impacts of forb browsing by elk, mule deer and jackrabbits, resulting in little changes in plant diversity when all herbivores were excluded (Ritchie and Wolfe 1994). Here in KNP, when all herbivores are present, grazers could consume grasses and reduce their competitive impacts, while browsers

will also consume forbs, potentially suppressing species diversity. When all herbivores are removed, grasses would likely become competitive dominants with the removal of grazers and outcompete forbs that begin to colonize with the removal of browsers. These combined effects could result in little change in plant richness and diversity following the removal of herbivores.

For example, in triennial burns where browsers and grazer abundance appeared similar, we saw significant increases in grass cover and decreases in forb cover with herbivore removal. Yet, we saw no changes in species richness or diversity, just as one would predict if the combined effects of grazers and browsers offset each other in their impacts. In fact, the strongest impact of herbivore exclusion on plant diversity was in the unburned areas, which had the least diverse suite of herbivores (Fig. 1, 2, 5). Impala, the dominant herbivore in unburned areas, are mixed feeders but primarily graze grasses in the wet season (Estes 1991). Thus, the exclusion of impala likely facilitated grass dominance at the expense of diversity of forbs and subordinate grasses, similar to excluding dominant grazers in other systems. Further, the studies in African savannas that show strong impacts of herbivore removal on species diversity are often from places that are dominated by large herds of grazing ungulates (Serengeti, McNaughton 1979, Belsky 1992, Anderson et al. 2007).

Conclusions

In African savannas, studies often address either the distribution of herbivores (Archibald and Bond 2004, Riginos and Grace 2008, Sensenig et al. 2010) or the impacts of herbivores on plant communities (McNaughton 1985, Verweij et al. 2006, Waldram et al. 2008) but rarely both (but see Ford et al. 2014). Our work shows that disturbance, in this case fire frequency, determines how different herbivore species use the landscape and, in turn, how these herbivores impact plant community dynamics. Much of the previous work on the impact of different herbivores on African savanna plant communities has been done only under one abiotic regime (Verweij et al. 2006, Waldram et al. 2008) or across relatively straightforward productivity gradients spanning large spatial scales (Belsky 1992, Goheen et al. 2013, Young et al. 2013). These relatively consistent habitats may have resulted in similar suites of herbivores and similar impact on plant communities across the landscape. In contrast, our study focused on a gradient of fire disturbance that likely impacted multiple aspects of habitat selection (e.g. forage quality, forage quantity, predation risk) over relatively small spatial scales. Other studies of individual herbivore species show that habitat selection can be an important determinant of how herbivores impact plant communities (Fortin et al. 2005, Kauffman et al. 2010, Ford et al. 2014). Further, our work emphasizes how differences in habitat preferences across different herbivore species can shape the spatially heterogeneous impacts of diverse herbivore guilds on vegetation dynamics.

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Supplementary material (available online as Appendix oik-02987 at < www.oikosjournal.org/appendix/oik-02987 >). Appendix 1.

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