


The effects of herbivore aggregations at water sources on savanna plants differ across soil and climate gradients

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Abstract. Water sources in arid and semiarid ecosystems support humans, wildlife, and domestic animals, forming nodes of activity that sculpt surrounding plant communities and impact critical grazing and soil systems. However, global aridification and changing surface water supply threaten to disrupt these water resources, with strong implications for conservation and management of these ecosystems. To understand how effects of herbivore aggregation at water impact plant communities across contexts, we measured herbivore activity, plant height, cover (trees, grasses, forbs, and bare ground), diversity, and composition at 17 paired water sources and matrix sites across a range of abiotic factors in a semiarid savanna in Kenya. The effects of proximity to surface water and herbivore aggregation on plant communities varied substantially depending on soil and rainfall. In arid areas with nutrient-poor sandy soils, forb and tree cover were 50% lower at water sources compared to neighboring matrix sites, bare ground was 20% higher, species richness was 15% lower, and a single globally important grazing grass (*Cynodon dactylon*) dominated 60% of transects. However, in mesic areas with nutrient-rich finely textured soils, species richness was 25% higher, despite a 40% increase in bare ground, concurrent with the decline of a dominant tall grass (*Themeda triandra*) and increase in *C. dactylon* and other grass species near water sources. Recent rainfall was important for grasses; cover was higher relative to matrix sites only during wet periods, a potential indication of compensatory grazing. These findings suggest that effects of herbivore aggregation on vegetation diversity and composition will vary in magnitude, and in some cases direction, depending on other factors at the site. Where moisture and nutrient resources are high and promote the dominance of few plant species, herbivore aggregations may maintain diversity by promoting grazing lawns and increasing nondominant species cover. However, in arid conditions and sites with low nutrient availability, diversity can be substantially reduced by these aggregations. Our results highlight the importance of considering abiotic conditions when managing for effects of herbivore aggregations near water. This will be particularly important for future managers in light of growing global aridification and surface water changes.

Key words: abiotic effects; edaphic conditions; grazing; grazing gradient; grazing lawn; plant–herbivore interaction; species richness; vegetation cover; water sources.

INTRODUCTION

Climate change and human development are rapidly altering the landscape of terrestrial water sources and their associated ecological communities (de Wit and Stankiewicz 2006, Vörösmarty et al. 2010), especially in dryland systems that cover 41% of the globe (Millennium Ecosystem Assessment 2005). However, in these arid systems, scarce surface waters can also aggregate domestic animals and wildlife, causing profound changes to

surrounding plant communities (Landsberg et al. 2003, Hoshino et al. 2009) because of herbivore effects on plant biomass, morphology, and community composition (Olff and Ritchie 1998, Jia et al. 2018).

In some cases, heavy herbivore aggregation near water can cause negative effects on plant and soil communities, including denuding vegetation, reducing plant diversity, reducing abundance of palatable plants, and driving soil erosion. These effects have been observed in dry areas across the globe, from Chaco forests in Argentina (Macchi and Grau 2012), Iranian rangelands (Shahriary et al. 2012), and the West African Sahel (Turner 1998), to the Mojave Desert in the United States (Brooks et al. 2006). However, in other contexts, herbivores can increase

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vegetation growth, cover, or diversity, as observed in grazing lawns (Hempson et al. 2015), grazing manipulations (Porensky et al. 2013, Charles et al. 2017), and vernal pools (Marty 2015). It thus seems likely that the net effects of herbivore aggregation at surface water sources—defined here as above-ground areas where freshwater collects—on plant communities will vary based on additional ecological stressors that constrain plant growth, notably including rainfall quantity, rainfall variability, and soil nutrient limitations. Together these factors impact the magnitude of animal aggregation (e.g., low rainfall may cause stronger aggregations near water (Valeix 2011)), and plant resilience to herbivory and trampling (e.g., Louthan et al. [2013]). Despite these clear conceptual links, and imminent changes in rainfall (Intergovernmental Panel on Climate Change 2014) and surface water supply (de Wit and Stankiewicz 2006), we have limited understanding of how abiotic factors modulate the often severe effects of increased herbivore aggregation at water sources on plant communities. This is a significant knowledge gap given that these water sources provide critical resources to humans, their domestic animals, and wildlife, and will be increasingly important in the face of aridification; an accelerating process that will likely result in drylands covering more than half of Earth's surface within this century (Huang et al. 2016).

Animal aggregations at water sources often create conspicuous radial vegetation patterning around water (sometimes termed piospheres [Lange 1969]), in which many plant species decline due to grazing (Wesuls et al. 2012, Moreno García et al. 2014) and trampling (Andrew 1988, Thrash and Derry 1999). These water sources greatly contribute to the landscape heterogeneity that characterizes savanna mosaics (Belsky 1995). However, despite several studies that portray water sources as having largely negative effects on surrounding vegetation, others have also found evidence for increased nutrient inputs near water (Tolsma et al. 1987, Perkins and Thomas 1993, Thrash and Derry 1999, Stumpp et al. 2005, McCauley et al. 2017), especially for nitrogen and phosphorus that can be limiting in savanna systems (Pellegri 2016).

Perhaps not surprisingly, given the multiple and sometimes contradictory effects that water sources can have on plants, a variety of plant community responses to provisional water sources and their management have been observed. Although plant height and cover generally decline (Thrash and Derry 1999), nutrient-dense, fast-growing (Moreno García et al. 2014), and annual plants (Hoshino et al. 2009, Wesuls et al. 2012) tend to increase under heavy grazing near water. However, plant responses as a function of proximity to water sources vary based on environmental variables such as habitat, year (Wesuls et al. 2012), distance to alternative water supply, soil, and prior rainfall (Thrash and Derry 1999). Plant diversity patterns are more variable, with some studies reporting a steep decline in species richness (Landsberg et al. 2003) and diversity (Jawuoro et al.

2017) near water, and others finding mixed or no significant effects (Stumpp et al. 2005, Cheng et al. 2011). Underlying site differences, such as mean annual precipitation, soil type, and grazing history could explain why some plant responses are observed in one location, but not another (Stumpp et al. 2005, Wesuls et al. 2012). However, there remains no unifying explanation of these divergent results, and no examination of this question in a semiarid context that characterizes much of the world's grazing lands, where mean annual precipitation exceeds the extremely low levels (<200 mm/yr) found in the studies cited above.

Exclosure experiment studies that have explored grazing effects on plant communities across environmental contexts may provide explanations for why plant responses to herbivore aggregations at water have been variable. A recent global meta-analysis showed herbivores to have strong negative effects on plant reproduction, biomass, abundance, and survival across ecosystems, and that changes in plant species richness and evenness are context dependent (Jia et al. 2018). Exclosure studies in grasslands have found that although herbivores can increase plant diversity, this varies by soil, rainfall, and herbivore type (Olf and Ritchie 1998, Augustine and McNaughton 2006, Bakker et al. 2006, Young et al. 2013, Charles et al. 2017, Riginos et al. 2018). In general, when grazing is moderate and rainfall is high, herbivores are thought to increase species richness by reducing dominant species cover (Koerner et al. 2018), allowing rarer species to persist (Milchunas et al. 1988, Osem et al. 2002). In savannas, grazing can increase light and convert tall grass areas into more productive grazing lawns (McNaughton 1984, Hempson et al. 2019), and their ability to do so is more pronounced in the absence of fire (Archibald and Hempson 2016). Thus, herbivores may increase plant diversity by promoting grazing lawns around water sources where they otherwise may not occur. However, it is unknown whether context-dependent patterns found from exclosure experiments and grazing-lawn studies may explain contrasting results in the piosphere literature, thus informing management decisions in a variety of contexts.

Exclosure studies have also found that soil type, aridity, and seasonality can modulate herbivore effects on plants. Plant species richness tends to increase in the presence of herbivores on more nutrient-rich soils and decrease on nutrient-poor soils (Olf and Ritchie 1998, Young et al. 2013). Aridity can modulate the effects of herbivory: in arid areas, grazing often reduces plant diversity, but has a unimodal effect in mesic areas, in which diversity increases with moderate grazing intensity (Milchunas et al. 1988, Bakker et al. 2006). Finally, seasonality affects the degree to which certain plants compete for resources or facilitate growth, resulting in dominance shifts during wet and dry seasons (Veblen 2008). The role of these abiotic factors in modulating herbivore impacts could be magnified at water sources,

given that aggregations can vary based on seasonality and aridity (Valeix 2011).

We explored three outstanding questions about the net effects of water sources and herbivore aggregation on plants. We asked (Q1) How do water sources and their associated herbivore aggregations affect total plant cover and abundance of different plant groups, and how does this relationship vary across the landscape based on water limitation (soil type and season)? We expected that understory height and plant abundance (for trees, forbs, grasses) would decline near water, and that these effects would be starkest where higher water stress reduces grazing resilience. However, given that increased water and nutrients could potentially mitigate herbivore impacts on plants, we expected smaller effects in wetter areas with higher nutrients. We extended this question to ask: (Q2) How do water sources and their associated herbivore aggregations affect plant diversity (as measured by species richness, Shannon diversity, Faith's phylogenetic diversity, and mean pairwise distance), and does this vary by context? Considering that herbivores often reduce total plant cover, we expected plant diversity to also decline near water, where grazing and trampling would create environmental filters allowing few species to survive. We expected diversity declines to be greatest in dry periods and arid areas, where abiotic conditions are a compounding filter. However, we also expected that diversity may increase where herbivores reduce cover of dominant plants in wetter areas with higher nutrients. Finally, we investigated species-specific patterns to answer: (Q3) Which plants respond positively and negatively to water sources across contexts? Given previous results in very arid regions, we expected that grazing resistors that are limited by more competitive species would increase near water, but that others would decline. We expected this compositional change to be more pronounced where abiotic conditions are stressful to many plants (arid, nutrient-poor, sandy soil). Together, we expected these findings to reveal context dependence in plant compositional changes at water sources, providing insight into management strategies for maintaining plant diversity or grazing species abundance in different conditions.

METHODS

Site

Fieldwork was conducted at Mpala Research Centre in Laikipia County, Kenya (0.301150–0.488934° N, 36.810568–36.901265° E, 1,600-m elevation). Mpala is a mixed wildlife conservancy and cattle ranch featuring, in addition to cows (*Bos taurus*), which account for approximately 30% of mammalian herbivore biomass (Augustine 2010), a diverse array of wild herbivores including elephants (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), zebra (*Equus quagga* and *Equus grevyi*), buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*),

and dik-dik (*Madoqua kirkii*) (see Augustine [2010] for relative densities of all herbivores), which are supported by man-made water sources created using small earth dams along seasonally dry drainages (Fig. 1B). Fieldwork was conducted at 17 man-made water sources (average 400 m in perimeter) and paired matrix sites across a rainfall gradient (450–700 mm rainfall per year [Franz et al. 2010]), a range corresponding to transition from subdesert scrub to grass–tree savanna (Shorrocks 2007; Fig. 1). Eight of the 17 water sources featured nutrient-rich, silt/clay soil with marked shrink–swell dynamics, and nine featured nutrient-poor high-drainage sandy soil (Fig. 1; Appendix S1: Fig. S1). Matrix sites were selected by drawing a 1-km line from each water source in a random direction within a predetermined range of degrees that controlled for elevation (± 25 m) and soil type. To capture seasonal dryness for all sites (Fig. 1E) we used a prior 30-d aggregate from daily rainfall data from Mpala (Caylor et al. 2017).

Vegetation surveys

Six 150-m transects were surveyed at each water source and its paired matrix site for each of four sampling seasons (November 2015, February 2016, August 2016, and September 2017) selected to span a range of seasonal conditions. Transects (consistent across seasons) extended radially from the water's edge and were spaced at 60-degree intervals (Fig. 1B). At matrix sites, we began each transect 10 m from the center to mimic the spatial sampling of watering sources (Fig. 1C). At each 5-m interval, we dropped a single 1-m pin and recorded the maximum height of each plant species touching the pin at any height. For taller plants, we recorded any individual that would have intersected with the pin above 500 mm as >500 mm for November 2015 and February 2016; and individuals above 1,000 mm were recorded as >1 m for August 2016 and September 2017. To ensure these sampling differences did not affect results, we truncated all measurements to 500 mm and reran analyses. Results were almost identical (Appendix S2: Table S1), and we thus presented full data-set results.

Soil

During August 2016, we collected and aggregated five topsoil (0–2 cm, approximately 10-cm-diameter) samples from three locations: the water's edge, 50 m away from water, and at the matrix site (1 km away) for each of the 17 study pairs. Aggregate samples were dried, sieved through 2-mm mesh, and analyzed for total exchange capacity, estimated nitrogen release, pH, percentage of organic matter, S, P (Bray II), Ca, Mg, K, Na, B, Fe, Mn, Cu, Zn, and Al at Brookside Laboratories (New Bremen, Ohio, USA). Soils were classified as silt/clay or sand according to location and models published by Franz et al. (2010) (Appendix S1: Fig. S1A). The

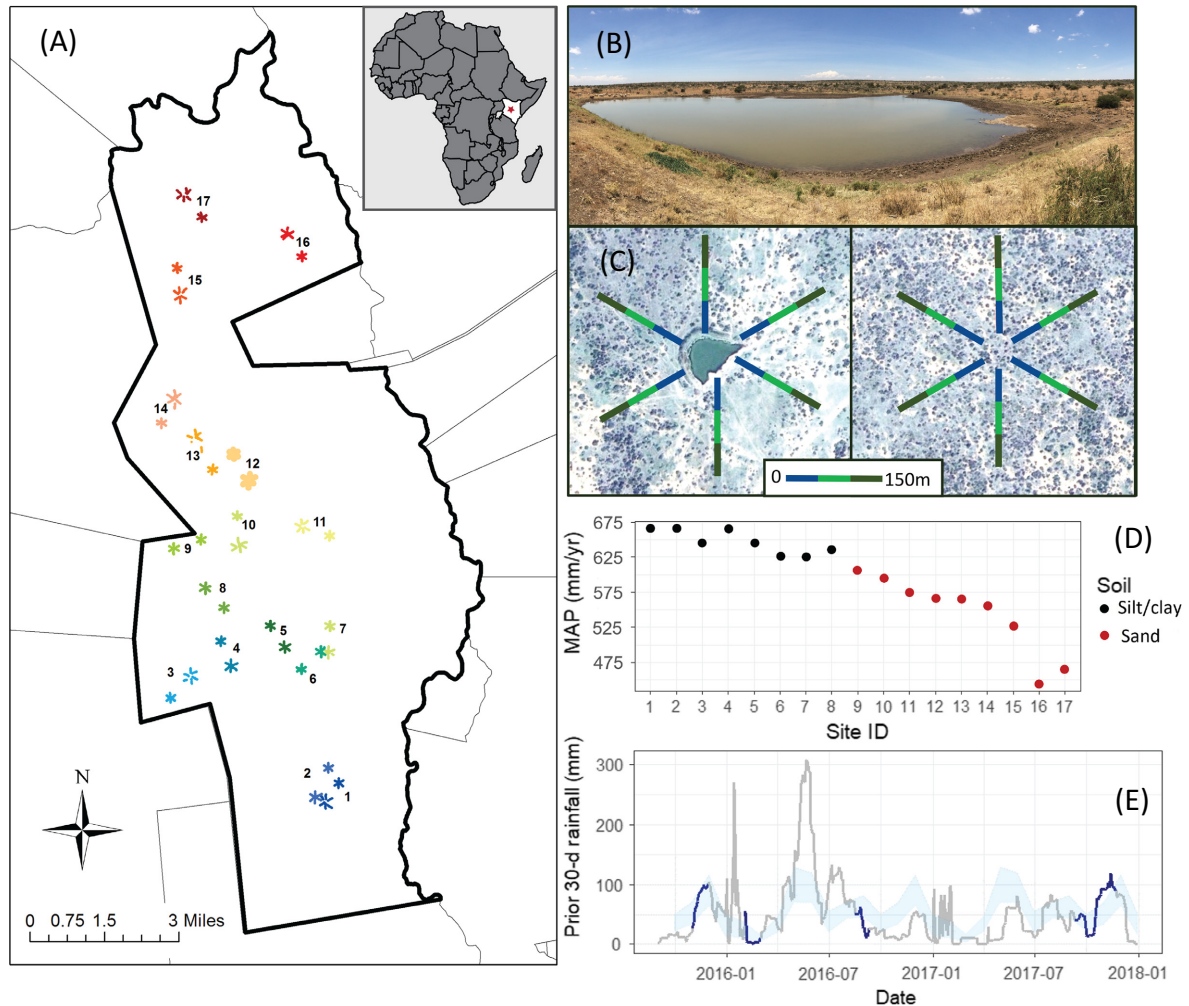


FIG. 1. (A) The 17 research locations across MRC spanned an aridity gradient ranging from 455 mm rainfall/yr (deep red) to 675 mm rainfall/yr (deep blue). Water sources (B) were paired with matrix sites randomly located 1 km from any water supply. (C) Transects extended 150 m radially from each site and were binned into three 50-m intervals. (D) Sites were spread across a rainfall gradient across two soil types. (E) Sampling spanned four periods (dark blue segments) that varied in prior rainfall totals (historical mean \pm 95% confidence interval [CI] for each month shaded in light blue).

silt/clay soils (known as black cotton) are pellic vertisols characterized by shrink–swell dynamics, high productivity, and relatively low drainage, covering half of Laikipia and common across semiarid Africa (Riginos 2009, International Union of Soil Sciences Working Group World Reference Base 2015). Sandy soils (commonly referred to as “red” soils) are ferric and chromic luvisols with lower productivity and better drainage than silt/clay soils, and also widespread throughout southern Africa (Augustine and McNaughton 2006, Pringle et al. 2007, Young et al. 2013). We performed linear discriminant analysis in JMP Pro 15 (SAS) to validate this grouping and to examine nutrient differences (Appendix S1: Table S1, Fig. S1C). We found that Mn, % silt, Fe, and Cu sufficiently discriminated between soil types with 97% accuracy. We also used linear mixed-effect models (LMMs) with post hoc tests to compare

both soil types near water and at matrix sites (Appendix S1: Table S2).

Herbivore dung surveys and camera trapping

Dung surveys were conducted concurrently to all vegetation surveys to measure animal aggregation near water. We counted fresh herbivore dung piles within a 1-m² quadrat every 10 m along each transect at all water sources and matrix sites. Dung was considered fresh if perceived to be less than 4 d old (internal and external moisture, arthropod presence, and odor) and was classified as grazer (zebra, cow, buffalo), mixed (elephant, impala), or browser (dik-dik, giraffe). For each herbivore type and 50-m interval along transects, we calculated total dung pile count at water sources and matrix sites across all sampling periods ($n = 102$; 3 distance

intervals \times 17 locations \times 2 site types per herbivore group). We analyzed herbivore dung counts at water sources and matrix sites by herbivore guild using a generalized linear mixed effects model with a Poisson distribution (Appendix S3: Tables S2–S5). Herbivore dung density patterns were similar across guilds, and, considering previous work in this system in which total herbivory was the main driver of plant responses (Veblen et al. 2016), we used the sum of all counts as a measure of herbivore pressure.

Although dung counts have been shown to be a reliable metric of herbivore density on a broad scale (Barnes 2001), they do not necessarily indicate that herbivores spend more time trampling or foraging in locations where dung counts are higher (e.g., midden use and foraging avoidance by dik-dik [Ezenwa 2004]). Therefore, we used camera-trapping data to determine if broad-scale dung patterns matched finer-scale behavioral patterns (see Appendix S3: Section S2 for full details). Finally, to assess the degree to which our dung and camera-trap data agreed with each other, we ran a Spearman's rank correlation test on dung and camera counts matched by herbivore, site (water vs. matrix), and location ($n = 72$).

Q1: Height and cover analyses

To explore relationships between understory height and herbivore aggregation at water sources, we calculated mean maximum grass or forb height across all six transects at each 5-m interval for each water source or matrix site. For cover measurements, we aggregated pin hits within three sampling rings: 0–45 m, 50–95 m, or 100–145 m from water or matrix center, calculating the percentage of pins touching “grass,” “forb,” “tree/shrub,” or “bare ground” (out of a maximum 60 pin hits per distance band). Thus, for trees, percent cover refers to any cover above 1 m. We modeled understory height and percent cover of each plant group using LMMs: fixed effects included sampling ring distance, soil type (silt/clay vs. sand), mean annual precipitation (MAP), prior rainfall (30-d aggregate), and herbivore dung density, and their interactions with site type (water source or matrix). We modeled location ($n = 17$) and sampling period ($n = 4$) as crossed random effects. We applied square-root transformations when necessary (forb, bare ground, and height models) to achieve residual normality and checked for variance inflation (*car* package [Fox and Weisberg 2011]). We performed regressions and model selection using the *lme4* and *lmerTest* packages (Bates et al. 2015, Kuznetsova et al. 2017) in R studio 4.0.1 (R Development Core Team 2016).

Q2: Diversity analyses

We calculated species richness (SR) by summing the number of species found across the six transects within

each concentric 50-m ring at water sources and matrix sites for each location and season. Because SR depends on abundance (i.e., locations with more plants are likely more speciose), we also calculated rarified SR using the *vegan* package (Oksanen et al. 2016) and used LMMs to explore variation over the same parameters as in models of plant cover, using the same model selection methods described above. We repeated this procedure for Shannon diversity, which was calculated for each 50-m ring using each species' proportion of total pin hits. To ensure SR calculations were unaffected by greater spatial area in outer rings or larger water sources, we verified that SR did not change among concentric rings at matrix sites or as a function of water-source perimeter (Appendix S6: Tables S1, S2).

To explore other diversity metrics that account for evolutionary history, we created a phylogenetic tree using the Phylomatic tool, version 3⁴ (Webb and Donoghue 2005) and based on the APG III (2009) phylogeny, using genus-level classification if species were not available. We used Phylocom 4.2 to add branch lengths based on (Gastauer and Meira-Neto 2013). We chose three metrics to investigate phylogenetic changes at water sources, calculating Faith's pairwise difference (PD), mean pairwise distance (MPD), and abundance weighted MPD on the site (each concentric ring) by species matrix (Tucker et al. 2017; Appendix S7). We compared PD to a null model that randomized species abundances within sites while maintaining sample richness (richness argument to *ses.PD* function in *picante*). We modeled standardized effect sizes (PD_{SES}) using sampling ring distance, soil type, prior rainfall, MAP, herbivore dung density, and their interactions with site type (water or matrix) as fixed effects, and location and season as random effects. We selected the best model using backwards stepwise selection using the step function in the *lmerTest* package, and we repeated this analysis for mean pairwise distance (MPD_{SES} and $MPD_{SES.AB}$), controlling for richness using null models (Webb et al. 2008).

To focus analyses on changes in height, cover, and diversity metrics, we also conducted LMMs on paired differences at matrix sites vs. water sources. Results were similar to full LMMs and are provided in Appendix S8: Table S1.

For all LMM analyses, given that soil and MAP were highly correlated (i.e., silt/clay soil occurred only in high MAP areas), we compared models including either MAP or soil as a predictor. In all models except understory height and abundance-weighted MPD, soil type explained more variation than MAP, but we noted that rainfall effects were likely to be important, although they were not significant because of the strong correlation with soil type. Thus, we referred to silt/clay soils as “mesic” and sandy soils as “arid” in our results.

⁴ <http://phylodiversity.net/phyloomatic/>

Q3: Species-specific analyses

We used two approaches to investigate species-specific differences at water sources. First, we assessed dominant plant diversity at each site, following van der Westhuizen et al. (2005). Specifically, for each transect and 50-m sampling ring, we identified the single species with the greatest percent cover, including bare ground as an option (out of 60 pin hits). We compared the relative frequency of these dominant species at water sources vs. matrix sites on both soil types across locations ($n = 17$) and seasons ($n = 4$). Second, we conducted a constrained redundancy analysis (RDA) on all plant species and sites (defined as each 50-m ring), using Hellinger distances to avoid overweighting rare species (Legendre and Gallagher 2001). Our explanatory factors were MAP, 30-d rainfall, herbivore dung counts, and the interaction between soil type and distance from water. To improve interpretability, we created a single variable to account for distance from water by assigning matrix sites to 1,000 m and each distance bin near water to the midpoint (i.e., 25, 75, and 125 m). We evaluated model parameters and significance of RDA axes using permutational ANOVAs ($n = 999$ permutations) using the *anova.cca* function in the *vegan* package (Oksanen et al. 2016).

RESULTS

Differences in soil properties

Nutrient-rich silt/clay soils had significantly higher estimated nitrogen release, total exchange capacity, Ca, Mg, K, Mn, Al, % silt, and % organic matter than sandy soils. Although silt/clay soils generally had higher nutrient values than sandy soils, sandy soils were higher in % sand, Fe, and P, an important plant nutrient. Soils near water were also higher in S, Na, B, pH, P, and Fe; but they were lower in Al. There were no differences in % clay, Zn, or Cu (Appendix S1: Table S2).

Effect of water sources on herbivore aggregation

Dung counts and camera-trap data showed that grazers and mixed feeders were 1.5–2 times more abundant at water sources than matrix sites (Fig. 2). Meanwhile, browser dung and camera-trap counts were only slightly elevated near water. Soil was significant in the model of dung counts for mixed feeders: counts were lower on mesic silt/clay than arid sand at both water and matrix sites. However, there was no significant interaction between soil and site (water vs. matrix) for any group. Dung counts and camera trap sightings were significantly and moderately correlated (Spearman's $\rho = 0.52$, $P < 0.001$, $n = 72$). This agreement suggests consistent broad patterns in herbivore aggregations around water. Finally, distance to water (i.e., the interaction between transect distance and site type) explained 50% of total

dung count variation (62% including soil type and its interaction with water), indicating that water proximity describes most of the variation in herbivore aggregation, with some differences by soil type. Specifically, total dung counts were ~1.3 times higher on sand compared to silt/clay. However, on both soils, dung counts at water sources vs. matrix sites were 1.6 times higher (all distances) and 2.25 times higher in the 0–50-m zone. Detailed results are provided in Appendix S3: Section S1.

Q1: Effect of water sources and herbivore aggregation on understory height and tree, grass, forb, and bare ground cover

Grass cover was 13% lower at water sources compared to matrix sites on mesic silt/clay soils (means \pm SE: $73.3\% \pm 1.4$ vs. $84.0\% \pm 1.1$), and it was further reduced in areas with high herbivore dung density (Table 1, Fig. 3A). However, the opposite effect was true for trees: tree cover was 50% greater near water ($16.1\% \pm 1.0$ vs. $10.4\% \pm 0.7$) and increased with increasing herbivore dung density (Fig. 3B). Remarkably, the relationships between herbivore density and grass and tree cover were entirely reversed on arid sandy soils ($F_{1,392} = 5.717$, $P = 0.02$ for the interaction between herbivores and soil for grass cover and $F_{1,398} = 20.864$, $P < 0.001$ for tree cover), where increasing herbivore density was associated with increased grass cover and reduced tree cover at both water and matrix sites (Fig. 3A, B). There was a 17% reduction in tree cover at water sources relative to matrix sites on these arid sandy soils ($19.5\% \pm 1.2$ vs. $23.5\% \pm 1.3$), where herbivore dung density was also substantially elevated.

Patterns in water and herbivore effects on forb cover were similar on both soil types: forb cover was elevated at intermediate levels of herbivore dung density, but declined by more than half where herbivores were most abundant at water sources and where they were least abundant at matrix sites (Fig. 3C). Bare ground cover increased with increasing herbivore dung density on mesic silt/clay soils such that it was 2.5 times higher near water (0–45 m) compared to matrix sites ($22.3 \pm 2.5\%$ vs. $8.9 \pm 1.8\%$). Interestingly, this effect was much smaller on arid sand ($25.2\% \pm 2.2$ vs. $20.2\% \pm 2.7$; Fig. 3D).

The effect of prior rainfall was significantly different at water sources and matrix sites in all models except tree cover. Understory height (any species < 1 m), grass, and forb cover had more positive associations with increased rainfall at water sources, and the opposite was true for bare ground cover. Mean annual precipitation was not an important factor in any model of cover because it closely correlated with soil type, which explained more variation in plant cover across the rainfall gradient. However, MAP did explain more variation than soil type in the understory height model. Vegetation height had a negative relationship with dung density

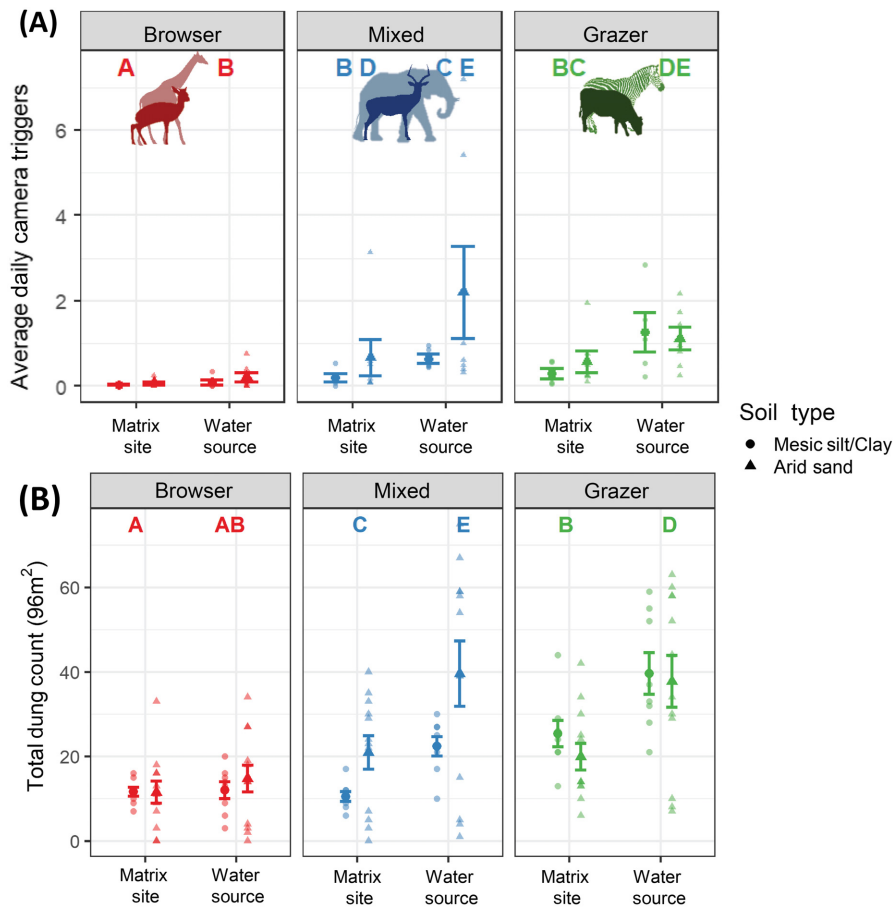


FIG. 2. Measurements of herbivore activity at water sources and matrix sites (means \pm SEs) using (A) camera trapping and (B) dung counts show that mixed feeders and grazers were more strongly associated with water, with smaller effects for browsers. There were no major differences depending on soil type, except that dung counts for mixed feeders were higher on arid sand than mesic silt/clay. Dung density is averaged across all concentric rings; Appendix S3; Fig. S1 illustrates high dung aggregation in rings closest to water. Letters denote significantly different groups across soils (with Tukey's adjustment).

at mesic water sources, and a positive relationship with dung density at arid water sources ($F_{1, 4142} = 14.68$, $P < 0.001$ for the three-way interaction between herbivores, site type, and MAP; Table 1; Appendix S4; Table S1).

Location was a significant random effect in all models, but period was only important in models of understory height.

Q2: Effect of water sources and herbivore aggregation on plant diversity

Rarefied species richness (SR), Shannon diversity (SD), and Faith's PD (PD) were highly dependent on soil context: on mesic soils, these diversity metrics were higher near water than matrix sites (14–22%, 8–15%, and 7–30% increases, respectively, in the 100 m closest to water; Table 2). However, on arid soils, diversity (SR, SD, and PD) at water sources was lower than at matrix sites, and this effect was strongest in the innermost

sampling rings (14%, 19%, and 12% decrease, respectively in the 50 m closest to water; $P = 0.007$, <0.001 , and 0.002 ; Table 2; Appendix S4; Table S1 and Fig. S2). These results are likely explained by the interaction between herbivore dung density and soil type, in which increased dung on mesic silt/clay soils (but not arid sand) was associated with higher diversity (Fig. 4). Meanwhile, prior rainfall corresponded with increased diversity at all sites for all metrics except abundance weighted MPD, with further increases at water sources for SD and PD ($P = 0.01$ for both interactions).

After controlling for SR, the relationship between herbivore dung density and PD (PD_{SES}) differed between matrix sites and water sources. At matrix sites, where dung density was lower, there was a positive relationship between herbivore dung density and PD_{SES} and abundance weighted MPD ($MPD_{SES,AB}$), but near water, where herbivore dung density was higher, there was a negative relationship. Furthermore, PD_{SES} , MPD_{SES} , and $MPD_{SES,AB}$ were lower on silt/clay than arid sand.

TABLE 1. Linear mixed-effect model estimates ± SEs, *T* values, and *P* values are shown in each table cell for grass, forb, tree, and bare-ground cover and understory height.

Predictor	Grass	Forb (sqrt)	Tree	Bare (sq. rt.)	Height (sq. rt.)
Intercept	0.67 ± 0.05 13.98 (<0.001)	0.26 ± 0.04 6.27 (<0.001)	0.28 ± 0.04 6.84 (<0.001)	0.43 ± 0.05 8.34 (<0.001)	14.21 ± 1.43 9.95 (<0.001)
Water	-0.02 ± 0.03 -0.77 (0.44)	-0.08 ± 0.05 -1.51 (0.13)	0.00 ± 0.01 0.22 (0.83)	0.14 ± 0.03 4.99 (<0.001)	-2.69 ± 0.36 -7.56 (<0.001)
Rainfall	-0.00 ± 0.00 -0.34 (0.73)	0.02 ± 0.00 6.52 (<0.001)		-0.00 ± 0.00 -1.54 (0.12)	0.01 ± 0.02 0.46 (0.65)
Water × rainfall	0.01 ± 0.00 2.63 (0.009)	0.01 ± 0.00 3.13 (0.002)		-0.01 ± 0.00 -2.97 (0.003)	0.13 ± 0.03 4.58 (<0.001)
Transect distance [mid]		-0.00 ± 0.02 -0.17 (0.86)	0.03 ± 0.01 2.67 (0.008)	-0.00 ± 0.02 -0.12 (0.90)	(Continuous distance)
Transect distance [outer]		-0.04 ± 0.02 -2.00 (0.046)	0.02 ± 0.01 1.52 (0.13)	0.04 ± 0.02 1.89 (0.06)	-0.00 ± 0.00 -0.62 (0.54)
Water × [mid]		0.10 ± 0.03 3.50 (<0.001)		-0.07 ± 0.03 -2.74 (0.006)	0.01 ± 0.00 3.76 (<0.001)
Water × [outer]		0.16 ± 0.03 5.59 (<0.001)		-0.12 ± 0.03 -4.67 (<0.001)	
Soil [silt/clay]	0.22 ± 0.04 5.12 (<0.001)		-0.22 ± 0.03 -8.71 (<0.001)	-0.16 ± 0.03 -4.56 (<0.001)	
Water × [silt/clay]	-0.11 ± 0.02 -4.51 (<0.001)		0.04 ± 0.02 2.12 (0.034)	0.11 ± 0.02 5.22 (<0.001)	
Map					0.24 ± 0.46 0.51 (0.61)
Water × MAP					-0.15 ± 0.22 -0.69 (0.49)
Herbivores	0.08 ± 0.11 0.75 (0.45)	0.78 ± 0.21 3.78 (<0.001)	-0.40 ± 0.09 -4.51 (<0.001)		-0.25 ± 0.91 -0.27 (0.78)
Water × herbivores		-0.80 ± 0.23 -3.49 (<0.001)			-2.32 ± 1.16 -2.00 (0.045)
Soil [silt/clay] × herbivores	-0.44 ± 0.19 -2.39 (0.017)		0.65 ± 0.14 4.57 (<0.001)		
Water × [silt/clay] × herbivores					2.16 ± 0.88 2.46 (0.014)
Map × herbivores					-3.97 ± 1.06 -3.76 (<0.001)
Water × map × herbivores					
σ ²	0.01	0.01	0.01	0.01	10.17
τ ₀₀ Location	0.00	0.00	0.00	0.00	3.18
τ ₀₀ Season	0.01	0.00	0.01	0.01	7.20
Marginal R ² /conditional R ²	0.170/0.571	0.344/0.557	0.197/0.598	0.228/0.600	0.057/0.533

Notes: Parameters positively and negatively associated with vegetation near water have solid and dotted borders, respectively. Intercepts correspond to inner rings, matrix sites, and sandy soils. Rainfall and mean annual precipitation are scaled to centimeters per 30 d and centimeters per year, respectively. Bold terms indicate statistical significance at *P* < 0.05.

MAP did not explain more variation than soil type in any diversity metric except MPD_{SES,AB}. Increased herbivore dung density was associated with increased MPD_{SES,AB} at matrix sites, but not at water sources (Table 2; Appendix S4; Fig. S2).

Q3: Effect of water sources and herbivore aggregation on plant species responses

Dominant species composition (i.e., the relative frequencies of the most common plants on each transect) near water also varied by soil type. On mesic silt/clay soil, there were fewer dominant species at matrix sites than water sources, while the reverse was true on arid

sandy soils (Fig. 5). Furthermore, bare ground became increasingly prevalent with water proximity on mesic silt/clay, but it remained consistent on arid sandy soils. Notably, on silt/clay soils, the grass *Themeda triandra* was the most common species on 40% of matrix site transects, but only 7% of transects near water. Meanwhile, on sandy soils, the grass *Cynodon dactylon* was the most abundant plant for 18% of matrix site transects, but this shifted to 60% of transects near water. For the redundancy analysis, constrained variance accounted for 21% of total variance (overall model test: *F*_{6,389} = 17.65, *P* = 0.001), with 78% of constrained variance explained by the first two axes: Axis 1 (64.23% variance, *F*_{1,389} = 68.01, *P* = 0.001) was strongly associated with

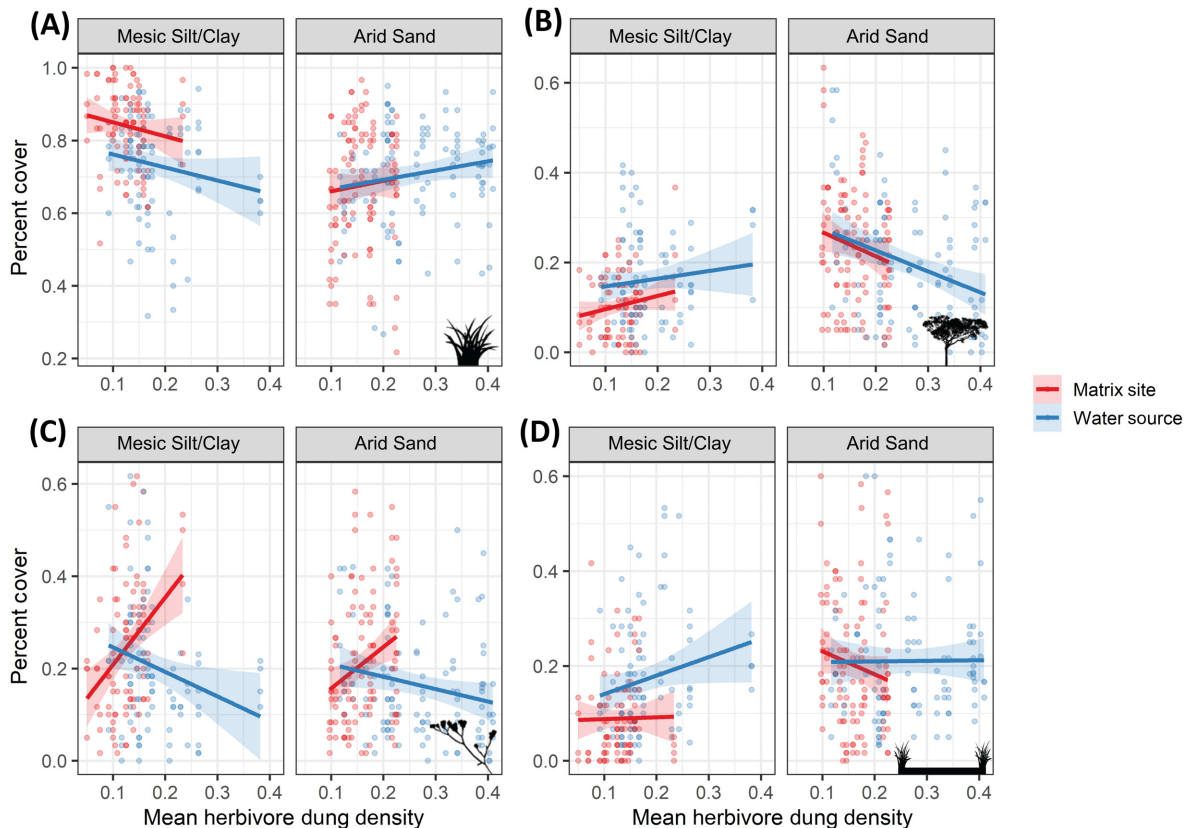


FIG. 3. Percent cover for (A) grasses, (B) trees, (C) forbs, and (D) bare ground are visualized along a continuum of herbivore dung density (counts per sampling ring) across soil types (facets), and at both water sources (blue) and matrix sites (red).

MAP, soil, and herbivore dung variables, and Axis 2 (13.75% variance, $F_{1,389} = 14.56$, $P = 0.001$) was strongly associated with prior rainfall and outward distance from water (Fig. 6). All model parameters were significant in stepwise selection. *Cynodon dactylon* was associated with increasing herbivore dung counts, and *Themeda triandra* was associated with higher MAP areas (mesic silt/clay soils; Fig. 6).

DISCUSSION

Our results indicate that water-source proximity, which was closely related to increased herbivore dung and activity, strongly characterized plant communities, and that abiotic factors influence the degree and direction of these effects. On mesic silt/clay soil, total grass cover declined, but the rise in grazing-lawn species and trees resulted in a ~25% increase in species richness, Shannon diversity, and phylogenetic diversity where herbivores gathered within a 50-m radius surrounding water. Meanwhile, on arid sandy soil, trees and forbs declined, resulting in a ~15% decrease in diversity. Remarkably, a dominance change for two key grasses, *Themeda triandra* and *Cynodon dactylon*, provided a clear signal of differing plant communities near water on

each soil type. Our observations contrast with piosphere studies that document strongly negative herbivore impacts around water. We suggest that idiosyncratic previous results may have arisen partly because of site differences in plant stressors. For example, this may explain why (Landsberg et al. 2003) found that richness was highest in wetter, more nutrient-rich piospheres, and lowest on drier piospheres with more nutrient-poor sandy soils, despite similar grazing histories, another important co-factor that can modulate plant responses to herbivory.

Q1: How does water source proximity and herbivore aggregation describe variation in total plant cover across different plant groups?

Our finding that mean understory height decreased at water sources corresponded with our expectations and is supported by other studies (Andrew 1988, Landsberg et al. 2003, Egeru et al. 2015). This is likely because of increased grazing and trampling due to herbivore aggregation (Egeru et al. 2015; Fig. 2; Appendix S3: Fig. S1). In addition to increasing bare patches and reducing grass height (Graetz and Ludwig 1976), increased grazing pressure can shift plant species composition to

TABLE 2. Linear mixed-effect model estimates \pm SEs, T values, and P values are shown in each table cell for plant diversity metrics.

Predictors	SD	Richness	PD	PD _{SES}	MPD _{SES}	MPD _{absSES}
(Intercept)	2.30 \pm 0.09 26.81 (<0.001)	11.00 \pm 0.52 21.17 (<0.001)	1,028.92 \pm 87.45 11.77 (<0.001)	-2.89 \pm 0.39 -7.50 (<0.001)	-2.88 \pm 0.92 -3.12 (0.002)	-9.33 \pm 4.75 -1.96 (0.049)
Water	-0.48 \pm 0.10 -4.99 (<0.001)	-1.36 \pm 0.50 -2.72 (0.007)	-228.34 \pm 73.73 -3.10 (0.002)	1.35 \pm 0.29 4.63 (<0.001)	0.10 \pm 0.04 2.87 (0.004)	10.38 \pm 3.15 3.29 (0.001)
Rainfall	0.04 \pm 0.01 5.65 (<0.001)	0.27 \pm 0.03 9.07 (<0.001)	28.00 \pm 4.83 5.80 (<0.001)	0.06 \pm 0.01 3.75 (<0.001)		
Water \times rainfall	0.02 \pm 0.01 2.59 (0.010)		16.12 \pm 6.25 2.58 (0.010)			
Transect distance [mid]	0.05 \pm 0.05 1.14 (0.26)	0.24 \pm 0.30 0.79 (0.43)	-4.90 \pm 36.09 -0.14 (0.89)			-0.70 \pm 0.24 -2.95 (0.003)
Transect distance [outer]	0.07 \pm 0.05 1.41 (0.16)	0.34 \pm 0.30 1.15 (0.25)	-3.99 \pm 35.94 -0.11 (0.91)			-0.94 \pm 0.23 -4.06 (<0.001)
Water \times [mid]	0.28 \pm 0.08 3.56 (<0.001)	1.25 \pm 0.49 2.55 (0.011)	188.14 \pm 59.58 3.16 (0.002)			
Water \times [outer]	0.29 \pm 0.08 3.79 (<0.001)	1.23 \pm 0.47 2.61 (0.009)	171.12 \pm 57.02 3.00 (0.003)			
Soil [silt/clay]	-0.47 \pm 0.09 -5.12 (<0.001)	-2.64 \pm 0.61 -4.33 (<0.001)	-271.61 \pm 77.19 -3.52 (<0.001)	-0.58 \pm 0.18 -3.24 (0.001)	-1.45 \pm 0.34 -4.32 (<0.001)	
Water \times soil [silt/clay]	0.32 \pm 0.07 4.71 (<0.001)	1.95 \pm 0.43 4.55 (<0.001)	152.62 \pm 51.93 2.94 (0.003)			
MAP						0.07 \pm 0.08 0.81 (0.42)
Water \times MAP						-0.13 \pm 0.05 -2.58 (0.01)
Herbivores	-0.40 \pm 0.35 -1.15 (0.25)	-3.77 \pm 2.19 -1.72 (0.09)	-199.96 \pm 271.31 -0.74 (0.46)	4.56 \pm 1.62 2.81 (0.005)		62.68 \pm 19.86 3.16 (0.002)
Water \times herbivores				-6.68 \pm 1.73 -3.86 (<0.001)		-18.63 \pm 4.40 -4.23 (<0.001)
Soil [silt/clay] \times herbivores	2.46 \pm 0.52 4.71 (<0.001)	12.47 \pm 3.27 3.81 (<0.001)	994.10 \pm 397.22 2.50 (0.012)			
Water \times [silt/clay] \times herbivores						
MAP \times herbivores						
Water \times MAP \times herbivores	0.08 0.01 0.00	2.96 0.46 0.06	43,210.54 8,907.18 14,105.07	0.70 0.10 0.26	4.30 0.29 3.04	-0.94 \pm 0.36 -2.65 (0.008)
σ^2						
τ_{00} Location						
τ_{00} Season						
Marginal R^2 /conditional R^2	0.394/0.477	0.344/0.442	0.262/0.519	0.139/0.430	0.078/0.480	0.130/0.615

Notes: Parameters positively and negatively associated with diversity near water have solid and dotted borders respectively. Intercepts for models correspond to matrix sites, inner rings, and sandy soils. Rainfall and mean annual precipitation (MAP) are scaled to centimeters per 30 d and centimeters per year, respectively. Bold terms indicate statistical significance at $P < 0.05$. PD, pairwise difference; MPD, mean pairwise distance; MPD_{ab}, abundance-weighted MPD; SES, standardized effect sizes.

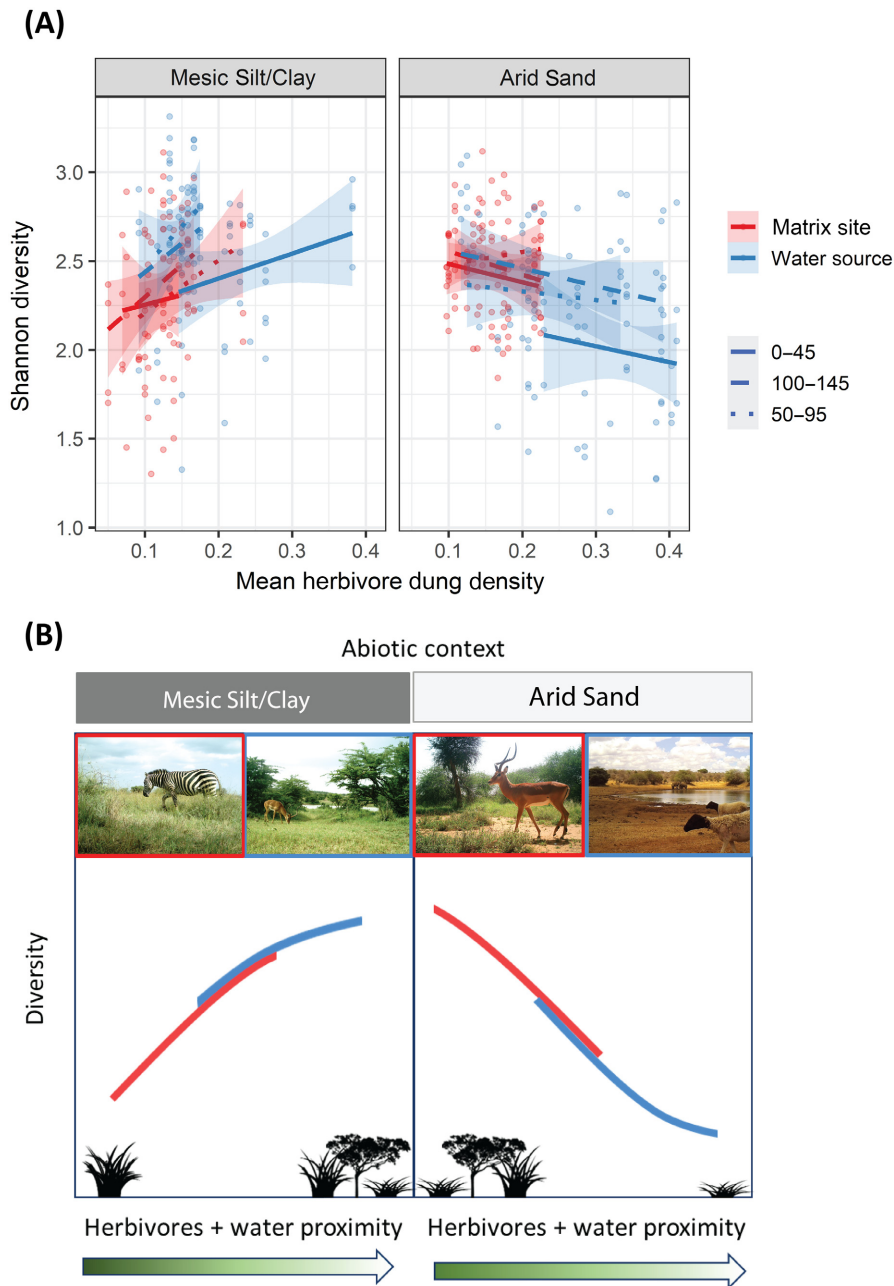


FIG. 4. (A) Diversity tended to increase with herbivore dung density (counts per sampling ring) on mesic silt/clay soil but decreased on arid sandy soil. Because dung counts were elevated at water sources, diversity was higher at silt/clay water sources compared to matrix sites, and diversity was lower at sandy soil water sources compared to matrix sites. (B) A schematic of our results illustrates increased diversity and a transition from grass to grass/trees with increased herbivore activity at silt/clay sites, and decreased diversity and a transition from grass/trees to grass on sandy soil. Camera-trap sightings at matrix sites (bordered in red) and water (bordered in blue) on different soils are also shown.

shorter species that spread laterally (Wesuls et al. 2012, Hempson et al. 2015), as is typical of grazing laws (McNaughton 1984, Hempson et al. 2015).

Tree, forb, and grass cover analyses indicated complex responses dependent on soil, herbivore aggregation, and prior rainfall. For grasses, cover increased at water

sources relative to matrix sites during wet periods in both soil contexts. This may indicate compensatory growth, when grazers stimulate higher nitrogen uptake following rainfall that also releases herbivore-derived nutrient inputs, resulting in positive vegetation responses (McNaughton 1979). Indeed, elevated recent rainfall

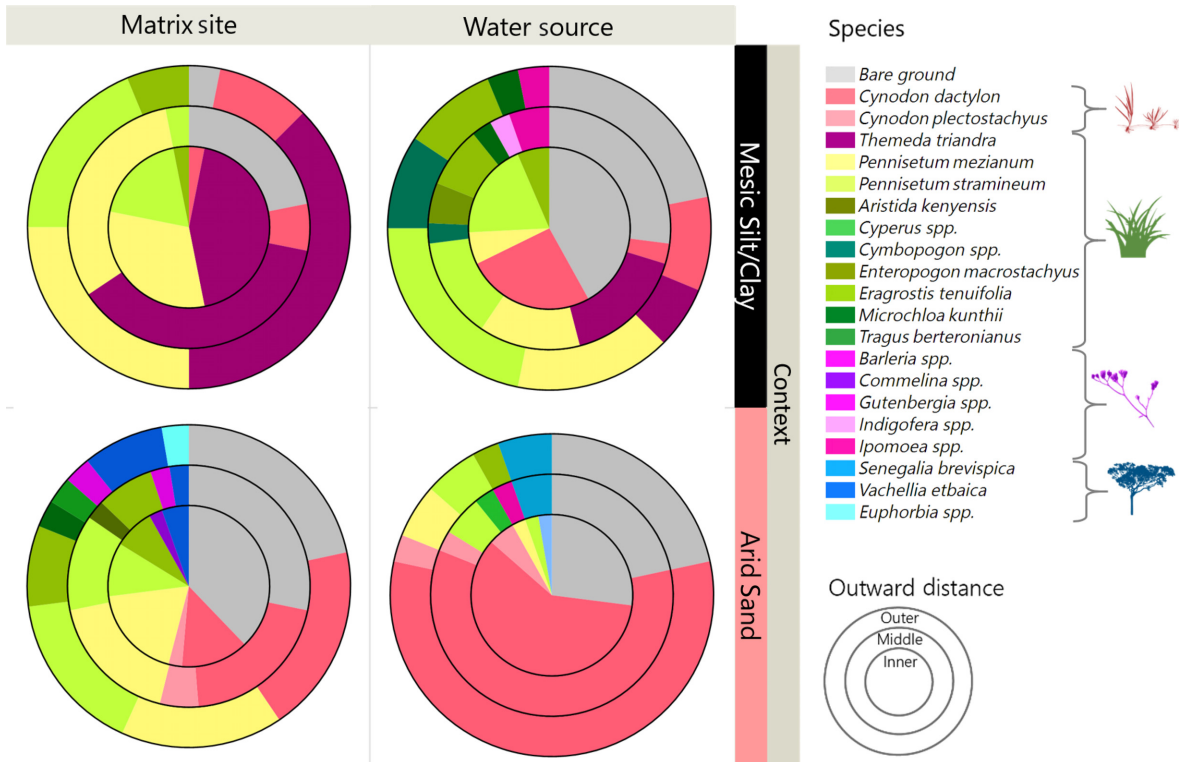


FIG. 5. Pie charts show the relative frequency of the single most common species on each transect (i.e., had the greatest percent cover) for the four different soil and water contexts. Differences across pie charts show that few species dominated on mesic silt/clay matrix sites (*Themeda triandra* and *Pennisetum* spp.), and only one species, *Cynodon dactylon*, typically dominated at arid sand water sources. Sampling ring distance from center (0–45, 50–95, and 100–145 m), which was closely associated with increased herbivore dung counts, is overlaid for each pie chart, demonstrating increasing effects with decreasing proximity to water (and thus, increasing herbivore aggregation).

flattened the inverse relationship between herbivore dung counts and grass cover near water on silt/clay soils and resulted in increasing grass cover with increasing herbivore dung counts on sandy soils (Fig. 3B, D, F; Appendix S4: Fig. S1). A similar effect was found in an experimental manipulation of cattle grazing in this system, in which several productivity measures increased in the presence of cattle (Charles et al. 2017).

Plant groups responded to water sources and herbivore aggregations differently on mesic silt/clay soils compared to arid sandy soils. On mesic silt/clay, trees increased while grass cover decreased near water, suggesting that grazing and abiotic factors can suppress tall grasses that are common on these soils and which exclude other species. Previous studies have shown that herbivores can increase tree establishment by reducing competitively dominant grasses (Milchunas et al. 1988, Osem et al. 2002). Our dung count results suggested that mixed feeders such as elephants were less common on silt/clay soil, possibly reducing tree herbivory relative to grazer pressure on grass. Other studies of tree–grass relationships in this system have found a negative relationship between tree density and

grass biomass, and that this may be modulated by soil texture for some dominant species (Riginos and Grace 2008, Riginos et al. 2009). Indeed, one study on black-cotton soils found that grass competition could be just as important in limiting tree growth as herbivory and fire (Riginos 2009). Higher soil moisture near water sources can also facilitate tree growth on silt/clay soil. Because water is readily retained in fine soil particles compared to sand, deeper-rooted trees may benefit from water proximity in a mesic silt/clay context. Other studies have also noted denser tree cover near drainages on fine-textured soils (Scholes and Archer 1997). Finally, although the mesic silt/clay soils in our study were higher in most nutrients examined (most notably in estimated nitrogen release and K), they were lower in phosphorus than arid sandy soils. Thus, increased soil phosphorus, a possible limiting nutrient to savanna trees (Pellegrini 2016), near water (Appendix S1: Table S2), lower mixed feeder herbivory (Appendix S3: Table S3), higher MAP and soil moisture, and tall grass reduction may explain why trees increased at water sources on silt/clay soils while other plant groups declined.

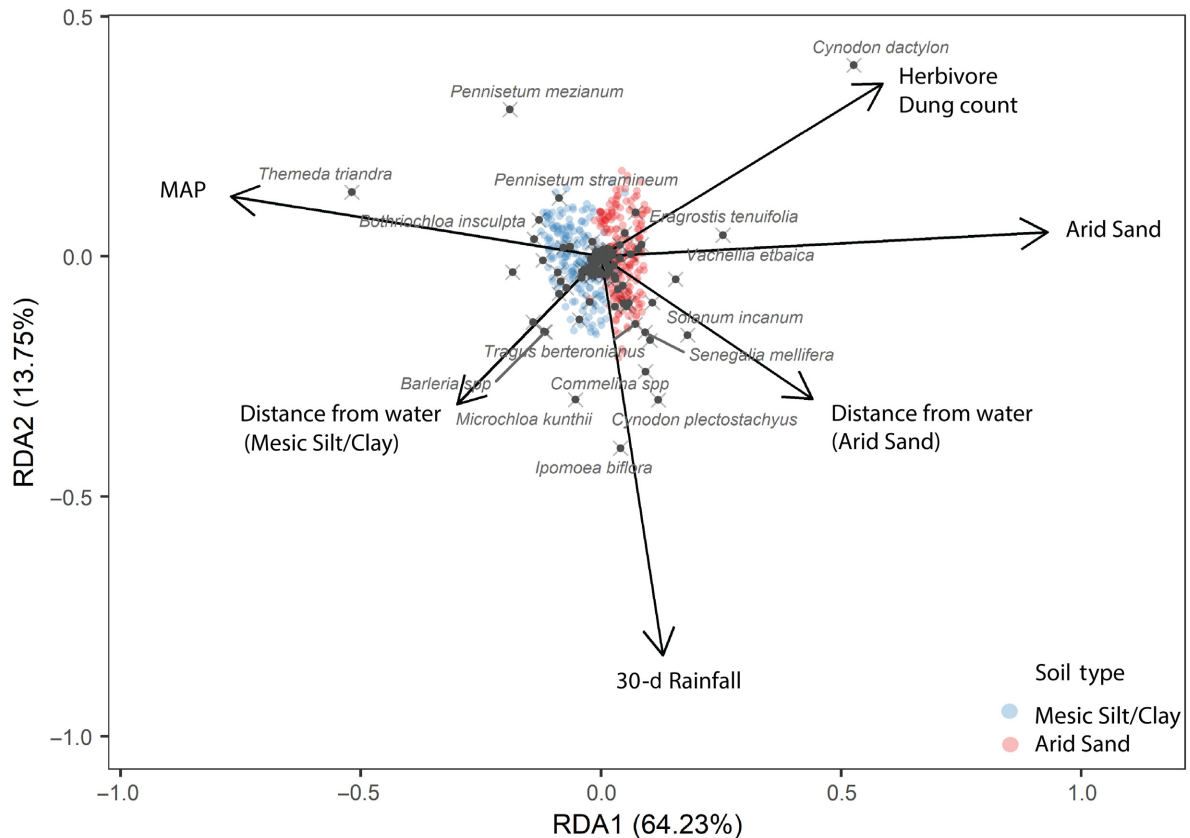


FIG. 6. Redundancy analysis triplot of sites (colored circles corresponding to 50-m sampling rings), plant species (labeled when weights on the first two axes exceeded 0.05), and environmental predictors (vectors). Mean annual precipitation and soil predictors were strongly associated with the first (horizontal) axis, which explained most of the constrained variance, and rainfall was strongly associated with the second (vertical) axis.

Q2: Do water sources and herbivore aggregations describe variation in plant diversity? Do abiotic factors mediate this relationship?

Given lower plant abundance near arid sandy water sources, it is unsurprising that species richness, Shannon diversity, and phylogenetic diversity were lower in these areas (Fig. 4A; Appendix S4: Fig. S2). On arid sandy soil, diversity in the inner ring around water was very low, echoing previous findings in which the region closest to water had almost no vegetation (Perkins and Thomas 1993, Thrash and Derry 1999). However, we also found that richness and diversity increased up to 25% near water on silt/clay soil compared to matrix sites. This is likely because of removal of dominant tall grass by trampling and grazing, facilitating growth of otherwise outcompeted species (Scholes and Archer 1997, Osem et al. 2002). The positive relationship between Shannon diversity and prior rainfall near water (Table 2) also shows that seasonal rainfall promotes plant abundance and evenness near water, a finding supported by a nearby enclosure study, in which the positive effect of rainfall on evenness was greater in treatments with megaherbivores or cattle as a result of nondominant

species colonizing bare patches (Porensky et al. 2013). This suggests that increased moisture and/or reduced herbivore activity during the wet season can promote growth of other species, and that water limitation and increased herbivory can act as environmental filters (Fig. 4B).

We also found that PD mirrored SR patterns at water sources. This was expected, given that these two metrics can be highly correlated (Cadotte et al. 2009, Tucker et al. 2017). When we used null models to control for species richness, we found fewer differences between water sources and matrix sites for PD and MPD, contrary to expectations. This is likely because PD and SR were highly correlated for our phylogenetic tree (Pearson's $r = 0.92$) because of tree shape, size, and spatial aspects (Tucker and Cadotte 2013). After controlling for richness, the effect of herbivores showed a similar unimodal pattern, in which diversity was maximized at intermediate levels of herbivore aggregation (Appendix S4: Fig. S2).

One possible reason for divergent diversity patterns on different soil types is that effects could depend on limitations in below-ground resources (nutrients and water) and disturbance (herbivory and trampling), or above-

ground competition. This balance may be viewed as a transition from environmental filtering, in which compounding stressors such as aridity, lower soil nutrients, and herbivore pressure can constrain many species (Poorter and Garnier 2007), a scenario observed on arid sandy soils; to niche partitioning, in which herbivory coupled with increased soil moisture and nutrients can allow additional species, including highly productive and palatable grazing lawn grasses, to grow by dominant species removal (Osem et al. 2002), a scenario on mesic silt/clay soils. The balance of these above- and below-ground variables can inevitably have strong effects on plant diversity and community composition (Maire et al. 2012), and thus will be central considerations for the management of grazing herbivores around water.

Q3. Which plants have positive and negative responses to water proximity and herbivore aggregation across contexts?

On mesic nutrient-rich silt/clay soils, the reduction of *Themeda triandra*, one of the most important species in tropical grasslands worldwide (Snyman et al. 2013), at water sources resulted in a more diverse array of species comprising cover (Fig. 5). Although *T. triandra* can decrease diversity by excluding other plant species (Fynn et al. 2004), it also declines under heavy herbivory and drought, likely because its above-ground seed reproduction is vulnerable to trampling and grazing (O'Connor 1994, Snyman et al. 2013). Meanwhile, we found the opposite pattern on arid sandy soils; *Cynodon dactylon*, a globally important grazing species, was the most common species on 60% of water source transects. *C. dactylon* is able to propagate in heavily grazed areas (van der Westhuizen et al. 2005, Jawuoro et al. 2017), likely because of its ability to produce both stolons and rhizomes (Dong and de Kroon 1994). We postulate that these opposite responses can be attributed to variation in dominant plant reproductive and growth traits whose trade-offs become apparent across a gradient ranging from high competition (high abiotic resources and low herbivory) to elevated stress (low abiotic resources and high herbivory).

This dominance change for only two species in opposing contexts is consistent with the framework outlined in Hempton et al. (2019) for grassland systems: With increasing herbivore pressure near water, plant communities were comprised of an economically important grazer resistor (*C. dactylon*), and in areas of lower herbivore pressure and no fire, plant communities were dominated by a widespread generalist tolerator (*T. triandra*). Our results also aligned with a global pattern that large herbivores can have opposite effects on plant diversity depending on environmental context. Indeed, a meta-analysis of North American and European grasslands (Bakker et al. 2006) found that large herbivores increased plant diversity in high-productivity areas, but decreased diversity in low-productivity sites, although

(Koerner et al. 2018) found that herbivore-induced change in dominance was most important across rainfall contexts.

Confounding factors

Although natural experiments like this study allow for large-scale analyses, they are limited by lack of environmental gradient replication, introducing potential confounding factors. In this system, MAP and soil type are collinear: nutrient-rich silt/clay soils occur in high MAP areas and sandy soils occur in drier areas; thus, results attributed to soil may have also been driven by rainfall (Fig. 1D). Although a rainfall gradient exists within each soil type, we did not detect a significant signal of MAP in most models. Studies incorporating a broad rainfall gradient across soil types may reveal a stronger signal of MAP, an important gradient in this system (Goheen et al. 2013) and across grasslands globally (Rodríguez-Castañeda 2013). Additionally, our measurement of seasonality as the accumulated 30-d rainfall total likely varies in relevance to different plants, as growth and uptake vary among species and functional groups (Breshears and Barnes 1999, Ogle and Reynolds 2004). Further, in many grassland ecosystems, fire and herbivory interact to shape plant communities (Archibald and Hempson 2016, Donaldson et al. 2018, Hempson et al. 2019). Fire has not been a major consumer in the study area for over 60 yr (Okello et al. 2008), because of fragmentation by roads and suppression by humans (Pringle et al. 2015), an increasingly common pattern (Andela et al. 2017). Thus, our results are likely largely driven by herbivore, soil, and rainfall interactions.

Although our study suggests that the net effects of herbivores and soil moisture at water sources on plant communities are mediated by soil type and rainfall, it is also likely that the degree to which herbivores impact vegetation at water varies seasonally and across a rainfall gradient, as aridity may promote animals to more strongly congregate near water. Additional experimental studies could assess the impacts of adding, removing, or partially fencing water sources on herbivore behavior, plant responses, diversity, and ecosystem functioning.

Our results are broadly applicable to naturally occurring or anthropogenic water sources, but it is likely that plant cover around boreholes or water troughs (the focus of most previous work; e.g. Thrash and Derry [1999]) is heavily reduced by herbivores, as these water sources provide little additional moisture to compensate for trampling and grazing in very concentrated areas (Stumpp et al. 2005). Finally, although we did not quantify drainage depth or water source hydrology, they likely describe variation in plant responses that we were unable to capture. For example, water transports several nutrients through drainage systems, which may explain underlying soil nutrient differences at water sources compared to matrix sites. Given the global importance

of natural and anthropogenic water sources like those in our study (e.g., O'Connor, [2001], Lasage et al. [2008]), our results provide valuable insight into vegetation responses at these key savanna resources.

Management implications

Humans and their domestic animals increasingly rely on water sources to mitigate the effects of increased rainfall stochasticity and drought susceptibility (Lasage et al. 2008), and the same is likely to be true for wildlife. However, amid rapid climatic changes and development, humans are dramatically modifying surface water supply and distribution (de Wit and Stankiewicz 2006, Gosling and Arnell 2016), requiring a clearer understanding of the impacts of water sources to inform decisions about how to manage wildlife, water, and plants in a compatible manner. Water manipulation is a powerful tool that has been used by managers to control herbivore effects across a landscape (Smit et al. 2007); however, our results suggest that recommendations based on water-source density (e.g., Thrash and Derry [1999]) should be placed in context with specific herbivore and abiotic variables, which can vary greatly even on small spatial and temporal scales. Coupling our findings with prior work suggests three key management conclusions:

- 1) When nutrients and moisture are plentiful such that few competitively dominant plants thrive, increasing herbivore pressure near water likely promotes plant diversity and grazing lawns, but may also increase bare patches relative to the surrounding area. Therefore, managers in such systems may increase diversity and grazing opportunities by establishing water points and maintaining moderate herbivore grazing pressure while monitoring for bare ground increases.
- 2) In drier, low nutrient conditions, increasing herbivore pressure near water can reduce plant diversity such that resilient grazing-lawn grasses are the few remaining species. In these scenarios, managers should note that increased grazing will lead to diversity declines, but that increases in grazing-lawn species may buffer against substantial increases in bare ground.
- 3) As found in previous work, in highly arid contexts and under heavy grazing conditions (exceeding those in this study), almost all plants will likely decline. In this context, managers could provide additional provisional water sources to dilute impacts on vegetation, provided that herbivore pressure does not also increase. Notably, as climates shift and drylands expand, managers will need to adjust grazing practices around water points to avoid the proliferation of bare ground and to maintain plant diversity.

Our findings provide practical insights for managing water sources, wild and domestic herbivores, and vegetation in savanna systems, and they highlight that abiotic

factors can explain the direction and extent of long-term effects of water sources and herbivore aggregations on plant composition and diversity. This will likely become an increasingly important topic amid continually changing water supplies across arid landscapes.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2422/full>

OPEN RESEARCH

Plant height, community data sets, and code for analyses (Titcomb 2021) are available from the Environmental Data Initiative in the EDI Data Portal: <https://doi.org/10.6073/pasta/8478b5dc9acb50c9c62bdbdc852cd825>