Original Research Article

Fire and herbivory shape soil arthropod communities through habitat heterogeneity and nutrient cycling in savannas

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ABSTRACT

Soil arthropods are important components of savannas, contributing to nutrient cycling and thus primary productivity. To investigate how fire and mammalian herbivores influence arthropod food webs, we used two long term herbivore exclosures (ca. 20 y) and burning trials (ca. 5-y return) located along rivers in Kruger National Park, South Africa. Herbivory and fire will usually have negative effects on soil arthropods although this can be variable, and dependent on multiple aspects of habitat structure and nutrient cycling. We hypothesised that in our sites, the more chronic herbivory disturbance would have stronger and more effects than fire, and that both fire and herbivory would decrease arthropod abundance, biomass and diversity via changes to habitat structure and nutrient cycling.

We used a structural equation model to investigate these mechanisms, and to compare these drivers. This model supported our hypothesis that herbivory had more and stronger effects than fire, largely through indirect flow-on effects. We also found evidence to support a 'tolerance/avoidance' hypothesis, in that herbivory increased soil arthropod diversity by decreasing soil nutrients. Herbivores also decreased arthropod biomass and abundance in total and in all trophic groups excluding omnivores.

Fire and herbivory are closely linked, careful consideration should be made when making decisions in the management of either. In some areas either driver may be more dominant, as was the case in our research. Further studies should incorporate a range of fire frequencies and intensities, as well as herbivore types, densities and abundances.

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1. Introduction

Soil arthropods are important biotic components of many ecosystems, playing a role in the above- and below-ground food webs that support nutrient cycling and primary productivity (Mulder et al., 2008; Malmström 2010; Coleman et al. 2017). The arthropod meso- and macro-fauna in soil promote decomposition and microbial activity by creating biopores, fragmenting plant debris and redistributing organic matter and microorganisms (Hendrix et al. 1990; Coleman et al., 2017; Frouz 2018). In savanna ecosystems soil arthropods are rarely studied but play an important, if not conspicuous, role (Franklin et al. 2005). While disturbance generally has negative effects on soil arthropods (Bardgett 2002), the influence of fire and herbivory is multifaceted and may have positive, negative or neutral effects (Kral et al. 2017; Wang et al. 2018). This variability depends on arthropod taxa, vagility, life stage and trophic group (Pryke and Samways 2012; Schon et al. 2012; Kral et al., 2017; Yekwayo et al. 2018). Impacts of disturbance are greater with longer, hotter burns (Malmström 2010; Kral et al., 2017) and, larger, denser populations of vertebrate herbivores (Vandegehuchte et al. 2017). Certain herbivore assemblages also create more disturbance than others (Wang et al., 2018). These two drivers also interact; pyric-herbivory or the temporal and spatial variation of burnt and grazed areas in contiguous patches is known to create heterogeneity and diverse habitats for e.g. insects, birds and mammals (Fuhlendorf and Engle 2004) and likely more representative of evolutionary disturbance regimes (Fuhlendorf et al., 2009).

Soil arthropods can be resilient to the direct effects of fire (Pressler et al. 2019). This is likely due to the depth at which they live, their ability to bury themselves and the availability of refugia like logs and rock piles (Pressler et al., 2019). Depth is especially important, with arthropods that live more than ca. 2−5 cm belowground able to avoid direct mortality (Thom et al. 2015). Soil arthropods may be less resilient, however, to the direct effects of abundant large herbivores, chiefly trampling, which compacts soils, reduces habitat space and may kill larger taxa (Swengel 2001).

The indirect, long-term effects of fire and herbivory may be relatively more influential on soil arthropods compared to short-term effects such as trampling and fire intensity. Increases in plant diversity due to fire and herbivory (Savadogo et al. 2008) may increase soil arthropod diversity through niche diversification. Vegetation cover is decreased by both fire and herbivory (Nemec, 2014), leading to more bare ground, higher soil temperatures and reduced soil moisture. This may cause arthropod desiccation and mortality (Vasconcelos et al., 2009; Katagiri and Hijii 2017), but may also promote earlier hatching and emergence of below-ground larvae/nymphs (Kral et al., 2017). Furthermore, certain taxa are more abundant in warm, dry areas (Petersen et al. 2004). Such dry disturbed soils may also inhibit fungal growth (Bergner et al., 2004; Cairney and Bastias, 2007; Pressler et al., 2019), especially of sensitive mycorrhizal fungi (Gehring and Whitham 2002), indirectly reducing the biomass or abundance of fungivores. Fire and herbivory can reduce resources (soil organic matter, detritus, leaf litter, vegetation) via combustion (Seastedt et al. 1986; Gonzalez-perez, Gonzales-villa, Almendros and Knicker 2004), compaction (Cumming and Cumming 2003) and the subsequent erosion these may cause (Cotrufo et al., 2016; Pressler et al., 2019). Such resource loss has been linked to reductions in arthropod diversity, abundance, and biomass (Seastedt, 1984; Vasconcelos et al., 2009). Conversely, fire and herbivory can also alter ecosystem productivity, creating nutrient-rich forage (Larsen and Work, 2003), compensatory growth, and increased root exudates (Bardgett and Wardle 2003; Vandegehuchte et al., 2015), which may increase herbivorous arthropod diversity, abundance and biomass. Any effects at one trophic level may also initiate trophic cascades, affecting predators and omnivores through bottom-up effects (Gongalsky and Persson, 2013) or vice versa. Rivers and the associated riparian zones also influence how fire and herbivory interact (Smit and Archibald 2019). Productive riparian zones with tall shady trees attract water-dependent herbivores (e.g. elephant; Smit and Ferreira 2010; Smit and Archibald 2019) that remove understory vegetation, reducing fuel loads and suppressing fires (Smit and Archibald 2019). Relatively high soil moisture in riparian zones may also be a major driver increasing arthropod diversity, abundance, and biomass, independent of fire or herbivory (Tanaka and Tanaka 1982). Finally, herbivores create game paths, feeding patches and wallows in riparian areas, the subsequent discontinuity in vegetation may disrupt burns, with the combined effect increasing habitat heterogeneity (Jacobs and Naiman 2008), which may increase arthropod diversity.

Ecosystem productivity is an important contributor to the variability in the effects of herbivory on soil arthropods (Bardgett and Wardle 2003; Bakker et al. 2006). The "tolerance/avoidance" hypothesis states that in productive ecosystems the beneficial effects of herbivory may compensate for the negative effects, thus increasing arthropod diversity, abundance or biomass, but in less productive ecosystems there may be fewer benefits to offset disturbance, thus reducing arthropod diversity, abundance or biomass (Vandegehuchte et al., 2017). Alternately, the "foraging intensity" hypothesis suggests that high ecosystem productivity may attract so many herbivores that the only manifested effects are those of disturbance, while in less productive areas the lower density of herbivores may mean the benefits outweigh the costs (Daskin and Pringle, 2016). These authors tested these contrasting theories in a meta-analysis and found that the strength of the negative effects of herbivores on consumers was lower in more productive ecosystems, consistent with the "tolerance/avoidance" hypothesis. They found no consistent impacts on arthropods, however, possibly due to insufficient taxonomic resolution. We developed mechanistic hypotheses that encompass the tolerance/avoidance and foraging intensity ideas while including other potential mechanisms for fire/herbivory effects on arthropods and their drivers.

We first hypothesised that the acute or intermittent disturbance of fire, with an approximate 5-year return in these savannas (van Coller et al. 2018), would result in weaker or fewer apparent effects on arthropods compared to the more chronic or frequent disturbance of herbivory. Although there may be complex interactions and trade-offs between fire and herbivory, we then hypothesised that, with all effects taken into account, both disturbances will decrease soil arthropod abundance, biomass and/or diversity via alterations in habitat heterogeneity (Mechanism 1) and/or nutrient cycling (Mechanism 2).

These two mechanisms may result in numerous different effects of either driver, we expected four different effects: Mechanism 1 Hypothesis 1 (M1H1), M1H2, M2H1 and M2H2.

In Mechanism 1 (habitat heterogeneity), hypothesis 1 (hereafter referred to as M1H1) fire and herbivory decrease herbaceous and woody vegetation cover, which is exacerbated in the riparian zone, increasing incident light and heat thus decreasing soil moisture (Figs. 1 and 2). This may result in either a direct effect decreasing arthropod diversity and/or total abundance, and biomass, or any trophic levels biomass/abundance. In contrast to the negative effect of M1H1, in hypothesis 2 (M1H2), fire and herbivory are expected to increase herbaceous species richness through niche diversification, subsequently increasing arthropod diversity, abundance and biomass, and/or the abundance and biomass of lower trophic level arthropods. In Mechanism 2 (nutrient cycling), hypothesis 1 (M2H1) fire directly increases plant-available nutrients, herbivory may also increase nutrients, but only in the more productive riparian zone. Nutrient enrichment subsequently increases arthropod diversity, abundance or biomass and/or lower trophic levels abundance and biomass (Figs. 1 and 2). Alternately, hypothesis 2 (M2H2), states that nutrients may decrease via reductions of mineralisation brought about by a loss in soil moisture as hypothesised in M1H1 with subsequent reductions in arthropod diversity, abundance or biomass and/or lower trophic levels (Figs. 1 and 2). This loss of nutrients may also decrease herbaceous species richness, resulting in reductions in the same arthropod variables as M1H2. Finally, through any of these effects, bottom-up trophic cascades may be apparent resulting in indirect losses or increases in omnivore or predator abundance or biomass.

2. Methods

2.1. Study sites

The research was carried out using two long-term ecological research sites (LTERs), specifically herbivore exclosures with burning treatments established in 2001 on granitic soils within the savanna biome in the Kruger National Park (KNP), South Africa (Fig. 3). Nkuhlu (24°59′16″S 31°46′26″E, 70 ha) is in the southern extent of the KNP located on the Sabie River, has a relatively higher rainfall and occurs on Eutric Regosols while Letaba (23°45′28″S 31°26′18″E, 42 ha) is in the centre of the park located on the Letaba River at relatively lower rainfall on Ferric Luvisols. The exclosures comprise four treatments with herbivore exclusion and/or differential burning: no herbivory, no fire; no herbivory plus fire; herbivory no fire; herbivory plus fire. The exclosures exclude all herbivores larger than hares (ca. > 5 kg) and are divided into burn- and no-burn blocks. The adjacent unfenced areas (Nkuhlu: 25 ha, Letaba: 36 ha) are open to herbivory but protected from fire on one side by a 400 m wide buffer area and open to herbivory and fire on the other. Fire treatments at Nkuhlu were established in 2002 (Govender, 2016) with fires occurring in June to October approximately once every five years (van Coller et al., 2018). The more arid Letaba exclosure had slightly longer periodicity, with burns once every five to six years based on the available biomass to burn (T. Swemmer pers. comm. Dec-2017). The Nkuhlu exclosures are characterized by Granite Lowveld (SVl 3) and Letaba exclosures by Lowveld Rugged Mopaneveld (SVmp 6) vegetation types (Mucina and Rutherford 2006). For more detail on the ecology of each area see Supplementary material A.
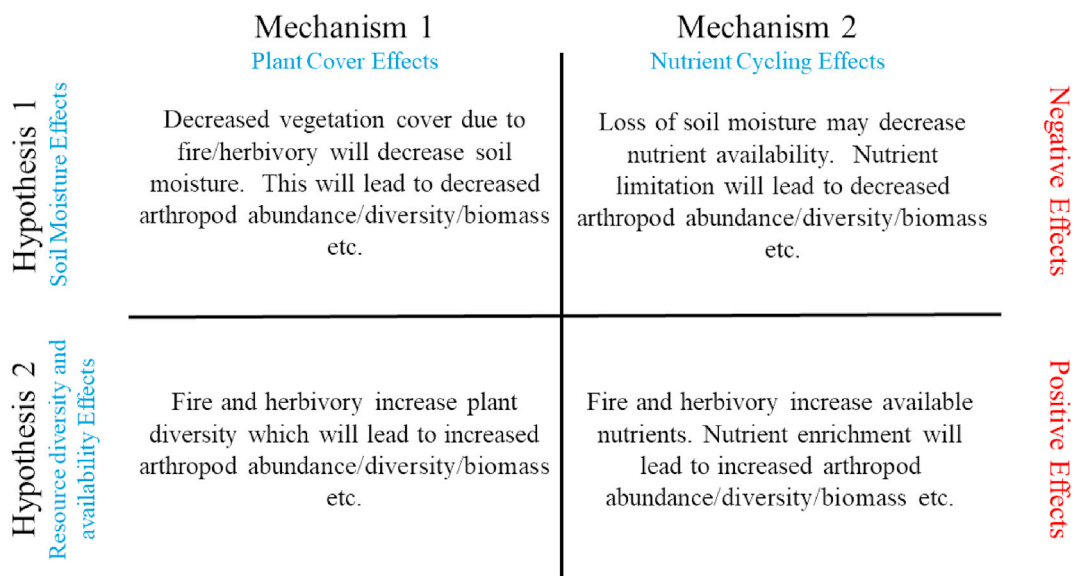

	Mechanism 1 Plant Cover Effects	Mechanism 2 Nutrient Cycling Effects	
Hypothesis 1 Soil Moisture Effects	Decreased vegetation cover due to fire/herbivory will decrease soil moisture. This will lead to decreased arthropod abundance/diversity/biomass etc.	Loss of soil moisture may decrease nutrient availability. Nutrient limitation will lead to decreased arthropod abundance/diversity/biomass etc.	**Negative Effects**
Hypothesis 2 Resource diversity and availability Effects	Fire and herbivory increase plant diversity which will lead to increased arthropod abundance/diversity/biomass etc.	Fire and herbivory increase available nutrients. Nutrient enrichment will lead to increased arthropod abundance/diversity/biomass etc.	**Positive Effects**

Fig. 1. The four different effects we expected, organised by mechanism and hypothesis, and whether the effect results in a negative or positive effect on arthropod abundance, diversity or biomass etc.
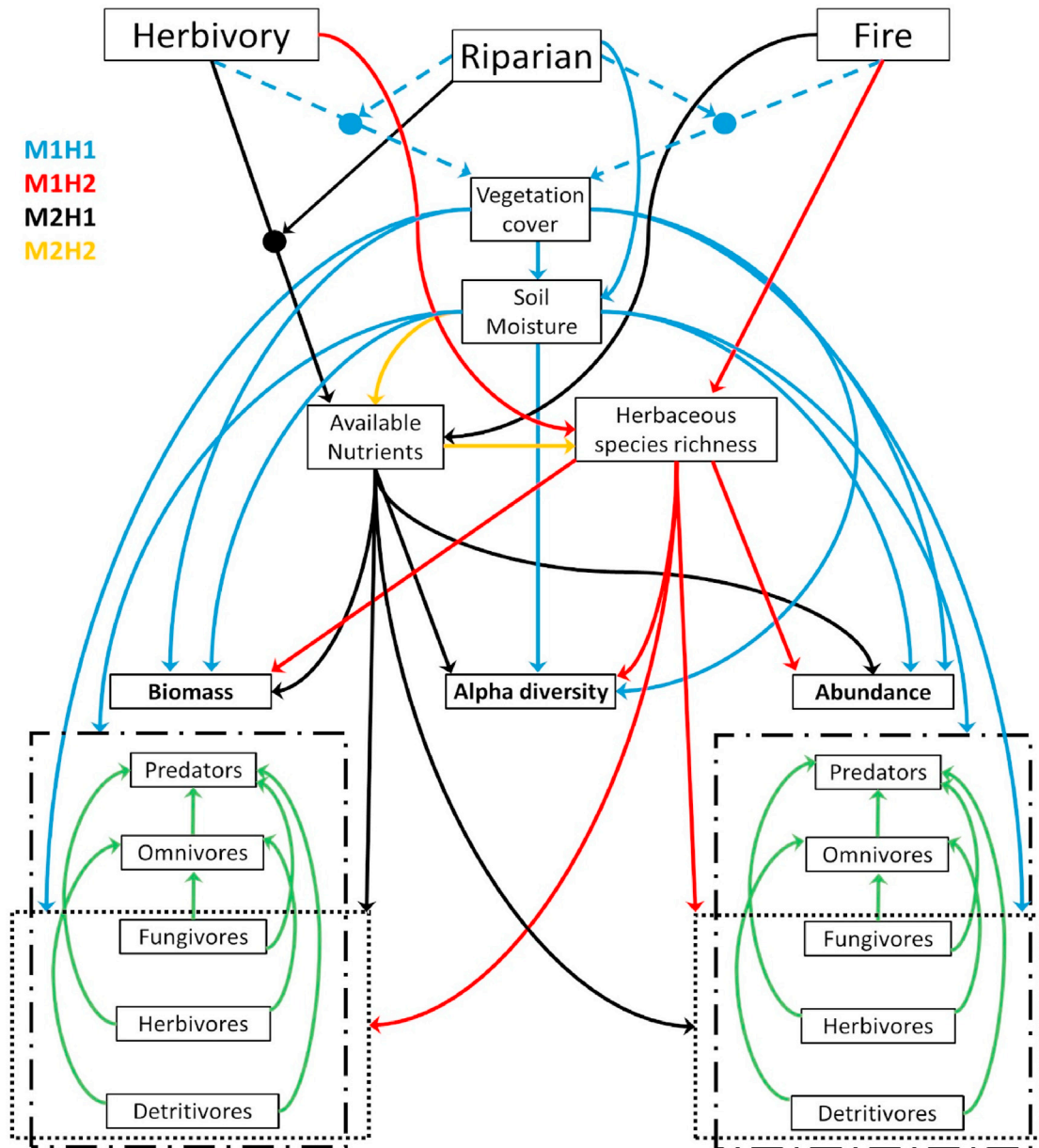
Fig. 2. Conceptual diagram of the four sub-hypotheses and the two types of mechanisms by which fire and herbivory have multiple direct and indirect effects on total and trophic soil arthropod abundance, biomass and family diversity. Cascading effects are independent of previous effects (as in any SEM), so a positive effect of vegetation cover (which is decreased by herbivory) on arthropod biomass constitutes a negative effect of herbivory on biomass. Solid arrows show positive effects and dashed arrows negative effects, arrow heads show hypothesised flow of causation, the colour of the arrows denotes the hypothesis as in the key, except for green arrows which show potential bottom-up effects between trophic levels. Note that M2H2 (yellow) arrows indicate only main drivers for brevity. Where two arrows intersect on a spot this shows one variable is hypothesised to influence the other, either making the effect more positive or more negative. Dash-dot boxes indicate any trophic level while dot-boxes indicate lower trophic levels only. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Mean annual precipitation (MAP) is a primary driver of fire in savannas (Smit and Archibald 2019). Areas above 600 mm MAP support the grass biomass for continuous burns and are primarily influenced by fire, while areas below 400 mm MAP are more influenced by herbivory as grasses are too sparse to burn (Venter et al., 2018; Smit and Archibald 2019). The intermediate range 400−600 mm MAP is where fire and herbivory commonly interact (Smit and Archibald 2019). The mean annual rainfall for Nkuhlu is ca. 560 mm as measured at Skukuza, while the mean daily temperature is 21.9 °C (Siebert and Eckhardt 2008), putting Nkuhlu near the top of the range where herbivory and fire have interactive effects (Smit and
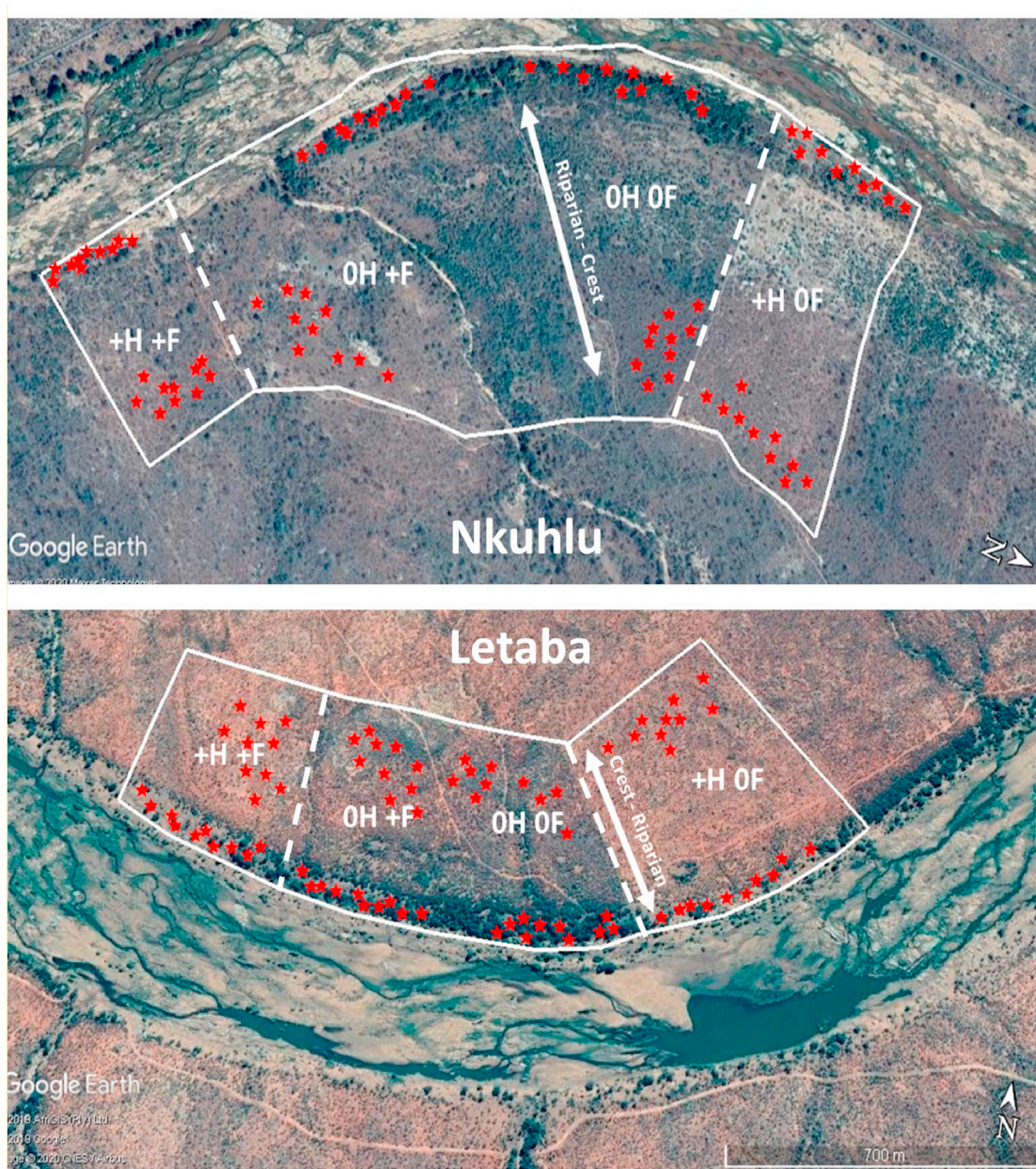
Fig. 3. Map of study sites, showing catenal stratification, treatments, and sample sites where 0H 0F denotes no herbivory or fire and +H + F denotes herbivory or fire. Sampling avoided the sodic area between crest and riparian zones. Dashed lines denote the fence line of the exclosure between treatments.

Archibald 2019). Letaba is drier and hotter than Nkuhlu with a mean annual rainfall of ca. 400 mm and a mean daily temperature of 23.3 °C (Siebert et al. 2010) close to the lower end of the range (Smit and Archibald 2019).

2.2. Field methods

Within the sites, slopes running down to the rivers are associated with catenas which introduce topo-edaphic heterogeneity. Together with soil types (soil maps; Kruger National Park (KNP), 2018), the catenas provided an ecologically meaningful basis upon which to stratify sampling. We constrained our sampling to crest and riparian areas of the catena on a single soil type within the fire and herbivory treatments. Within this catenal stratification, we randomised sampling by creating 15 random GPS sampling points constrained to polygons around the appropriate soil forms using QGIS (reference. 3.08, GNU General Public License). We chose 10 of these 15 random points in the field as replicates per treatment based on

greatest distance from other replicates, the similarity of topography, avoidance of small ephemeral streams and disturbances by animals. At each of the replicate sites within each treatment, we randomly selected five sampling points, within a ca. 5 m radius of the central GPS waypoint. At each of these points, we sampled bulk soil with a soil auger ($\varnothing$10 cm, 0−20 cm depth) after removing all surface organic debris as well as bulk density from 8 to 13 cm depth using a 100 cm^3 stainless steel sample ring (Eijelkamp Soil & Water, Netherlands). The five bulk soil cores were pooled and homogenised in a bucket and split into two sub-samples. The first subsample was mixed with ca. 500 mL of litter, bagged in plastic and immediately stored on ice until transfer to refrigeration at ca. 4 °C and processed within 7−8 days for arthropod extraction. The second subsample was used for soil physico-chemical analysis. Approximately 20 g of this second sub-sample sample was immediately sieved to 2 mm and frozen for later gravimetric calculation of soil field moisture after weighing, drying at 105 °C to constant weight (ca. 2 days) and re-weighing. Bulk soil samples for elemental analysis were air-dried (ca. 7 days) before further processing. We also clipped leaves and stems of grasses, forbs, and small trees/saplings and collected plant litter at each sampling point within the ca. 5 m radius of the central GPS point. These clippings/litter samples were mixed, and sub-samples taken, dried at 60 °C to constant weight (ca. 3 days).

2.3. Elemental and chemical analyses

Air-dried bulk soil samples for physico-chemical analysis were sieved to 2 mm and sent for routine chemical analyses (Elsenburg Laboratory, Research and Technology Development, Department of Agriculture, Elsenburg, South Africa). Analyses included pH (1 M KCl extracts), exchangeable acidity (K$_2$SO$_4$), as well as plant-available ions (P, K, Ca, Mg and Na), extracted in 1% (w/v) citric acid and measured on inductively coupled plasma spectrometry. Loss on ignition measurements were performed on 5 g subsamples of the 2 mm air-dried soil, and the weight losses at 105°, 550° and 1000 °C were recorded to estimate soil residual humidity, organic matter, and carbonates and residual water, respectively (Heiri et al. 2001). Sub-samples of soil, litter, and vegetation were ground into a fine powder using a ball mill and analysed for δ^{15}N, δ^{13}C, total C and N using mass spectrometry. Approximately 10 μg of soil powder and 2.5 mg of litter and foliar powder were weighed into tin capsules (5 × 9 mm; Säntis Analytical, Teufen, Switzerland). The samples were then combusted in a Flash 2000 organic elemental analyser and the gases passed into a Delta V Plus isotope ratio mass spectrometer (IRMS) via a Conflo IV gas control unit (all from Thermo Scientific, Bremen, Germany). In-house standards and one International Atomic Energy Agency (IAEA) standard (USGS25) were used to calibrate the results. Nitrogen and carbon stable isotopes were expressed relative to atmospheric nitrogen and Pee Dee Belemnite, respectively (Peterson and Fry 1987; Evans 2001).

2.4. Plant species composition and cover

Percent species composition of herbs, graminoids, and small woody plants was measured by estimating cover occurring within five replicate 1 m^2 quadrats at each subsample point. Plant basal and foliar cover was estimated as a percentage of the area of the quadrat. Plant cover and plant species composition (richness) were calculated by pooling counts from the five quadrats per subsample. Measures of normalised difference vegetation index (NDVI, as a proxy for vegetation vigour) and fractional woody plant cover were extracted from satellite imagery in 10 m^2 plots around each GPS sample point (approximating our sampling area), using the Google Earth Engine cloud computing platform for earth observation data analysis (Gorelick et al., 2017). All metrics were extracted using imagery between 2016 and 2018 and thus represent an integrated measure of median NDVI and woody cover for this period. NDVI assesses whether the target being observed contains live green vegetation or not and, has been widely used as an indicator of vegetation productivity in savannas (Svoray et al. 2013; Ali et al., 2013). Woody cover was measured using satellite imagery as described by Venter et al. (2018). For a detailed summary of remote sensing methods see Supplementary Material B.

2.5. Arthropod sampling and processing

Soil arthropods were collected into 100 mL propylene glycol from soil and leaf litter placed in Tullgren funnels for 7 days. The funnel apparatus used 30 W lamps 100 mm above the surface of the samples to provide both heating and drying. Arthropods were counted, measured and identified to family using a dissection microscope then assigned to trophic groups based on the literature. We constrained our analysis to five soil arthropod trophic groups: predators (including parasitoids and hematophages), omnivores, herbivores, fungivores, and detritivores. We based our analyses on trophic levels rather than family groups to lump data and avoid zero-inflation. Where families were both herbivorous and fungivorous these were included in both trophic groups. If larval stages had different feeding strategies to adults, they were grouped into separate trophic levels.

Biomass was calculated for all arthropods following the regression equations of Wardhaugh (2013) where arthropods are grouped into size categories based on the ratio of body length to width. For each size category, we used the equation: *ln weight = ln a + ln b (ln length × ln width)*, where *a* and *b* are the slope and intercept from the equations set out in Wardhaugh (2013). Biomass per family was calculated by multiplying biomass by the number of individuals in each family group while total biomass per replicate was calculated as the sum of biomass for all families and trophic level biomass the sum of all families within each of the five trophic groups. Total arthropod abundance was calculated as the sum of arthropods per replicate and

trophic abundance as the sum per trophic level. All biomass and abundance values were expressed per kilogram of dry soil. Arthropod alpha diversity was calculated at the family level using the Simpson's diversity index.

2.6. Replication in large-scale natural field experiments

While replication is essential for strictly inductive studies, sacrificing spatial and temporal scales to obtain replication is not helpful in understanding large-scale ecosystems (Hargrove and Pickering, 1992; Carpenter 1996; Korpimäki and Norrdahl, 1998; Persson et al., 1999; Klemola et al., 2000). Thus, regions or landscapes need not, and indeed cannot, be 'replicated' (Hargrave and Pickering, 1992). Sampling within large-scale, unreplicated natural field experiments is within a legitimate hypothetico-deductive framework. It is appropriate to statistically test the connection between the treatment and the outcome, as argued by Oksanen (2001), who stated that "inferential statistics are not only instructional in these cases but only polite to the reader". We chose two sites that had similar experimental design (riparian and crest areas along a river) as a reasonable approach to testing hypotheses about the dynamics of savanna systems involving large organisms (ungulates and their predators) and events (fire) where inferential statistics were based on multiple replicates within treatment areas. In our study design we have not considered our sites as replicates, because they are clearly distinct systems from different vegetation types and subject to different management regimes. Within our sites the exclosures were not replicated, which is an immutable part of the studies set up decades ago. These are, however, spatially large areas within which we took replicated samples. While this design has been stigmatised as "pseudoreplication" following Hulbert (1984), Oksanen (2001) has argued that it is a legitimate approach given the common constraints on ecological work. Consequently, we have produced a model that combines all our data so that statistical power is maximized. We controlled for the nestedness of the design by using mixed effect models where the nestedness was fixed as a random effect. The nestedness of our study design was defined as follows: two study sites Letaba and Nkuhlu (savanna), within which are riparian and crest areas (zone), across which are exclosures split into herbivory and no-herbivory blocks (herbivory), throughout which are burn and no-burn blocks (fire).

2.7. Statistical analyses

All statistical analysis was performed in R version 3.5.1 (R Development Core Team, 2017). We assessed data homogeneity, normality, and covariance using histograms, covariance matrices, Shapiro-tests, normality distribution plots, and boxplots. To produce our generalised linear structural equation model, we used 'PiecewiseSEM' (Lefcheck 2016) where each component model was specified using generalised linear mixed-effects models (GLMMs) using a restricted maximum likelihood method (REML) (function 'lme', package 'nlme', Pinheiro et al., 2018). For each component model we specified the nested structure of the study design as random with the hierarchy set as savanna (Letaba or Nkuhlu) − zone (riparian or crest) − exclosure (herbivory or no herbivory) − fire (or no fire), using 'lme' and the following code: "*random = ~1|Savanna/Riparian/Herbivory/Fire*". We also incorporated the factor variables of fire treatment, herbivore exclosure, and catenal zone into each component model as fixed interacting factors (*Fire * Herbivory * Riparian*). For the forb and grass species richness component models we fit GLMMs using Penalized Quasi-Likelihood (function 'glmmPQL', package 'MASS', Venables and Ripley, 2002) in order to specify the family as Poisson distributed. We checked the heterogeneity of our component models using plots of the residuals vs. the fitted values. For the two component models involving arthropod abundance and diversity we needed to specify a variance structure weighted by soil moisture to account for the heterogeneity of residuals. All other component models (i.e. excluding forb and grass richness, and arthropod abundance and diversity) used log transformed data.

As the variables soil N, C, K, Ca, Mg, and Na (but importantly not P) covaried strongly, we used a principal component analysis (PCA) to coerce these data into a single variable (PC1, hereafter referred to as 'soil nutrients') that captured their variability (80% variability explained by PC1). We then rescaled this variable from negative values to values ranging between 0 and 1 (checking this did not alter the variance), to maintain a similar scale to the previous data. The structural equation model used both this composite variable and soil P as the two components of soil nutrients.

The validity of the causal structural equation model was determined using a directional separation (d-sep) test (Shipley 2009). This test consists of finding the 'basis set' B_u of independence claims implied by a directed acyclic causal graph (i.e. a box and arrow diagram involving no feedback loops) that, together, expresses the full set of dependence and independence claims, and subsequently obtaining the probability p_i associated with each of the k independence claims in B_u, using the appropriate tests (we used GLMMs). The respective p_i were combined using the equation $C = -2 \sum_1^k \ln(p_i)$, and the C statistic was compared to a chi-square (χ^2) distribution with $2k$ degrees of freedom (Shipley 2009; Laliberté and Tylianakis 2012). A causal model can be rejected if the *P*-value associated with its C statistic is < 0.05, as a significant *P*-value implies that the data depart from what would be expected under a causal model (Shipley 2009). We calculated the indirect effects of herbivory and fire on each arthropod variable by multiplying the path coefficients for each independent path, then taking the sum of these paths for each arthropod variable. The detail of the SEM components used are presented in supplementary material.

3. Results

Our SEM was necessarily more complicated than our conceptual model as there were multiple components to several variables such as plant cover and richness and soil nutrients. Thus, we have removed some insignificant result arrows to avoid an overcomplicated diagram that is difficult to interpret. For a description of all component models see Supplementary

Material Section C. A simpler presentation of the continuous data (Fig. 4) that does not control for flow on effects, factors (i.e. herbivory, fire or riparian zone) or the nested nature of the study design can be used to help inform the results of the model.

Herbivory and fire had very few direct effects independent of the flow on effects seen in the model (Table 1). Herbivory directly increased grass richness (Table 1 and Fig. 5) and decreased NDVI in an interaction with the riparian zone (Fig. 5). Fire decreased forb richness when interacting with the riparian zone (Fig. 5) but increased forb richness when no other flow on effects were controlled for (Table 1). Neither herbivory or fire directly influenced any arthropod variables, however, herbivory and fire combined increased arthropod diversity and biomass when not controlling for any flow-on effects (Table 1). This interaction was not apparent in the model, however, where herbivory alone increased arthropod diversity through multiple flow-on effects. The key difference between fire and herbivory was that herbivory decreasing NDVI had cascading effects to all environmental variables and 8 of the 13 arthropod variables (Fig. 5). Fire decreasing forb richness was independent of any other environmental variable, and only then influenced detritivore and predator abundance (Fig. 5).

Herbivory decreased total vegetation cover in the form of NDVI, which was exacerbated in the riparian zone, as shown by the significant negative interaction between the factors Riparian and Herbivory (Fig. 5). This interaction then set off cascades where NDVI increased soil moisture and nutrients, moisture increased soil nutrients and P, and P decreased grass and forb species richness (Fig. 5). The initial negative effect of herbivory on NDVI means herbivory (exacerbated by the riparian zone) indirectly decreased moisture (M1H1), P and nutrients, but indirectly increased grass and forb species richness (M2H2). Herbivory also independently increased grass species richness (M1H2), while fire interacted with the riparian zone to decreased forb species richness, opposing our M1H2 hypothesis (Fig. 5). Arthropod biomass and abundance were both increased by NDVI and soil moisture, as such were negative indirect effects of herbivory, as hypothesised in M1H1. Arthropod alpha diversity (at family level) was increased by soil moisture (M1H1) and grass richness (M1H2), but decreased by nutrients (M2H1), two positive and one negative effect of herbivory (i.e. nutrients, grass richness and moisture respectively). Fungivore biomass was decreased by both NDVI and soil moisture (M1H1), although, there were no significant bottom up cascades to predator or omnivore biomass (Fig. 5). The only significant bottom up cascades in biomass were between herbivores/detritivores and predators, however, neither detritivore or herbivore biomass were significantly influenced by any environmental variable (arrows removed for clarity). Arthropod abundance showed two significant bottom up cascades, where
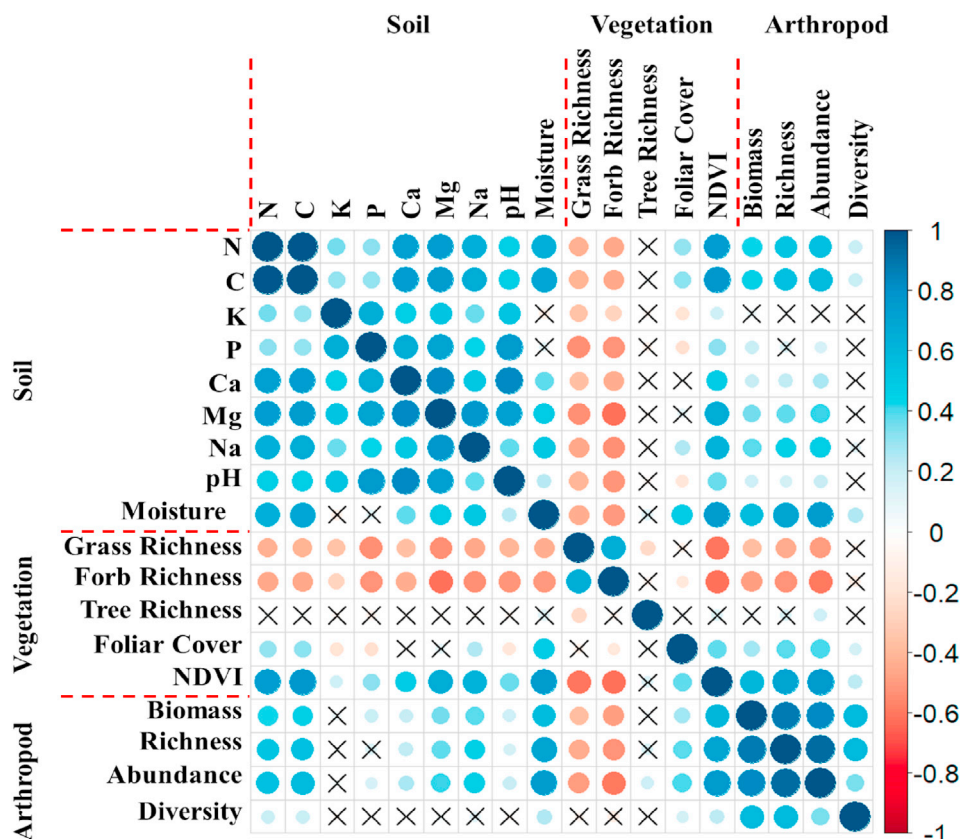
Fig. 4. Spearman's Rank correlation matrix of fourteen of the predictor variables used or considered in the model, together with the main arthropod response variables. Where a positive relationship is blue and a negative relationship red, and the size and shade of the circle shows effect size. Relationships marked by a black X are insignificant, all other relationships are significant at p < 0.05. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

The effects of herbivory and fire independent of any continuous predictors and flow-on effects. Each model uses linear mixed-effects models to control for the opposing effect (Herbivory or Fire) and the effect of riparian zone, savanna is fixed as random, along with nestedness as savanna/riparian/herbivory/fire. Values are effect sizes ±standard error and significance: ***p < 0.0001, **p < 0.001, *p < 0.05, NS = not significant.

|	Herbivory	Fire	Herb x Fire
Soil characteristics			
Total N %	−0.01 ± 0.02 NS	−0.01 ± 0.02 NS	0.01 ± 0.02 NS
Total C %	−0.01 ± 0.06 NS	−0.01 ± 0.04 NS	0.04 ± 0.06 NS
K (mg kg^{-1})	−0.07 ± 0.08 NS	−0.11 ± 0.08 NS	0.22 ± 0.11 NS
P (mg kg^{-1})	−0.23 ± 0.13 NS	−0.08 ± 0.13 NS	0.42 ± 0.19 NS
Ca (cmol + kg^{-1})	−0.05 ± 0.11 NS	−0.06 ± 0.11 NS	0.12 ± 0.16 NS
Mg (cmol + kg^{-1})	−0.03 ± 0.07 NS	−0.01 ± 0.05 NS	0.08 ± 0.07 NS
Na (mg kg^{-1})	−0.04 ± 0.12 NS	0.02 ± 0.05 NS	0.18 ± 0.07 NS
pH	−0.01 ± 0.01 NS	0.01 ± 0.01 NS	0.01 ± 0.02 NS
Moisture %	−0.03 ± 0.07 NS	0.01 ± 0.02 NS	0.02 ± 0.03 NS
Vegetation characteristics			
Grass sp. rich	**0.81 ± 0.18***	0.17 ± 0.19 NS	−0.34 ± 0.26 NS
Forb sp. rich	0.41 ± 0.27 NS	**0.29 ± 0.09***	**−0.36 ± 0.13***
Tree sp. rich	0.02 ± 0.17 NS	0.06 ± 0.17 NS	−0.08 ± 0.25 NS
Foliar cover %	−11.8 ± 12.8 NS	−6.75 ± 6.01 NS	14.3 ± 8.5 NS
NDVI	−0.01 ± 0.02 NS	−0.01 ± 0.02 NS	0.01 ± 0.02 NS
Arthropod characteristics			
Diversity	−0.16 ± 0.10 NS	−0.24 ± 0.09 NS	**0.40 ± 0.13***
Abundance	−0.40 ± 0.59 NS	−0.35 ± 0.26 NS	0.81 ± 0.37 NS
Biomass	−0.69 ± 0.94 NS	−0.80 ± 0.55 NS	**2.05 ± 0.78***

detritivores and herbivores increased predator abundance (Fig. 5). Detritivore abundance was decreased by forb richness (M1H2) and herbivore abundance was increased by NDVI (M1H1). The effect of forb richness on detritivore abundance is the only significant indirect effect of fire on any arthropod variable, where fire increased detritivore (and predator) abundance through decreasing forb richness (Fig. 5). Herbivory also indirectly decreased fungivore, herbivore and detritivore abundance through the effects of NDVI (M1H1) and forb richness (M2H2), and decreased predator abundance through the bottom up cascades between herbivores/detritivores and predators (Fig. 5).

Herbivory had 16 total pathways in which it influenced the arthropods, while fire had only two (Table 2). In addition, although herbivory, fire and the riparian factors were incorporated into every model they had no direct effects on any arthropod variables. Herbivory increased arthropod diversity when all paths were considered (5 total paths, with 4 positive paths and one negative: Table 2). For example, herbivory decreased diversity via soil moisture (path: −0.50 * 0.27 * 0.06 = −0.0081), but increased diversity via nutrients from moisture (path = 0.05), nutrients from NDVI (path = 0.12), grass richness from herbivory directly (path = 0.037) and grass richness from soil P (path = 0.00001), where the sum of all paths = 0.21 (Table 2), a net positive effect of herbivory on arthropod diversity. All other indirect effects of herbivory were negative, where herbivory decreased arthropod abundance and biomass, and predator, fungivore, herbivore and detritivore abundance, and fungivore biomass (Table 2). Fire only had two paths, both from fire decreasing forb species richness resulting in increased detritivore abundance and predator abundance in an apparent bottom-up effect (Table 2). Where fire and herbivory interacted to both affect predator and detritivore abundance this resulted in a sum negative effect on predators and a sum positive effect on detritivores (Table 2).

4. Discussion

Herbivory and fire had multiple indirect effects on soil arthropods in the two studied savannas. Herbivory set off multiple trophic cascades through decreasing vegetation cover (NDVI) and fire set off one cascade via reducing forb richness. Through NDVI, herbivory had consistently more and stronger effects on all the environmental and arthropod variables compared to fire, supporting our first hypothesis. However, we expected more effects from fire than were apparent. We also expected herbivory and fire to interact in multiple ways, but the one apparent interaction was through forb richness. Fires in savannas generally have stronger effects at more frequent intervals between burns (Sheuyange et al. 2005; Smit et al., 2010), and a 5-year return may be too infrequent to have a strong influence, especially in relation to the constant pressure of herbivory. The inclusion of some fire effects demonstrates these areas are not simply a 'brown world' (i.e. herbivore controlled), but somewhere near brown along a spectrum between brown and 'black worlds' (i.e. fire controlled) (Bond 2005).

Herbivory was hypothesised to interact with the riparian zone to increase soil nutrients (M2H1). This would align with the ideas of Daskin and Pringle (2016), where in productive ecosystems like riparian zones, the beneficial effects of herbivory, one of which is nutrient enrichment (Bardgett and Wardle 2003; Vandegehuchte et al., 2015), would outweigh any negative effects and increase arthropod diversity, abundance or biomass (i.e. the "tolerance/avoidance" hypothesis). While herbivory did increase arthropod diversity, it did not do so via a direct positive interaction between nutrients and the riparian zone. An interaction was apparent; however, it was more subtle and more in line with M2H2 than M2H1 (Figs. 1 and 2). The exclusion of large mammalian herbivores in our study caused a subsequent gain in vegetation cover, soil moisture and soil nutrients (as
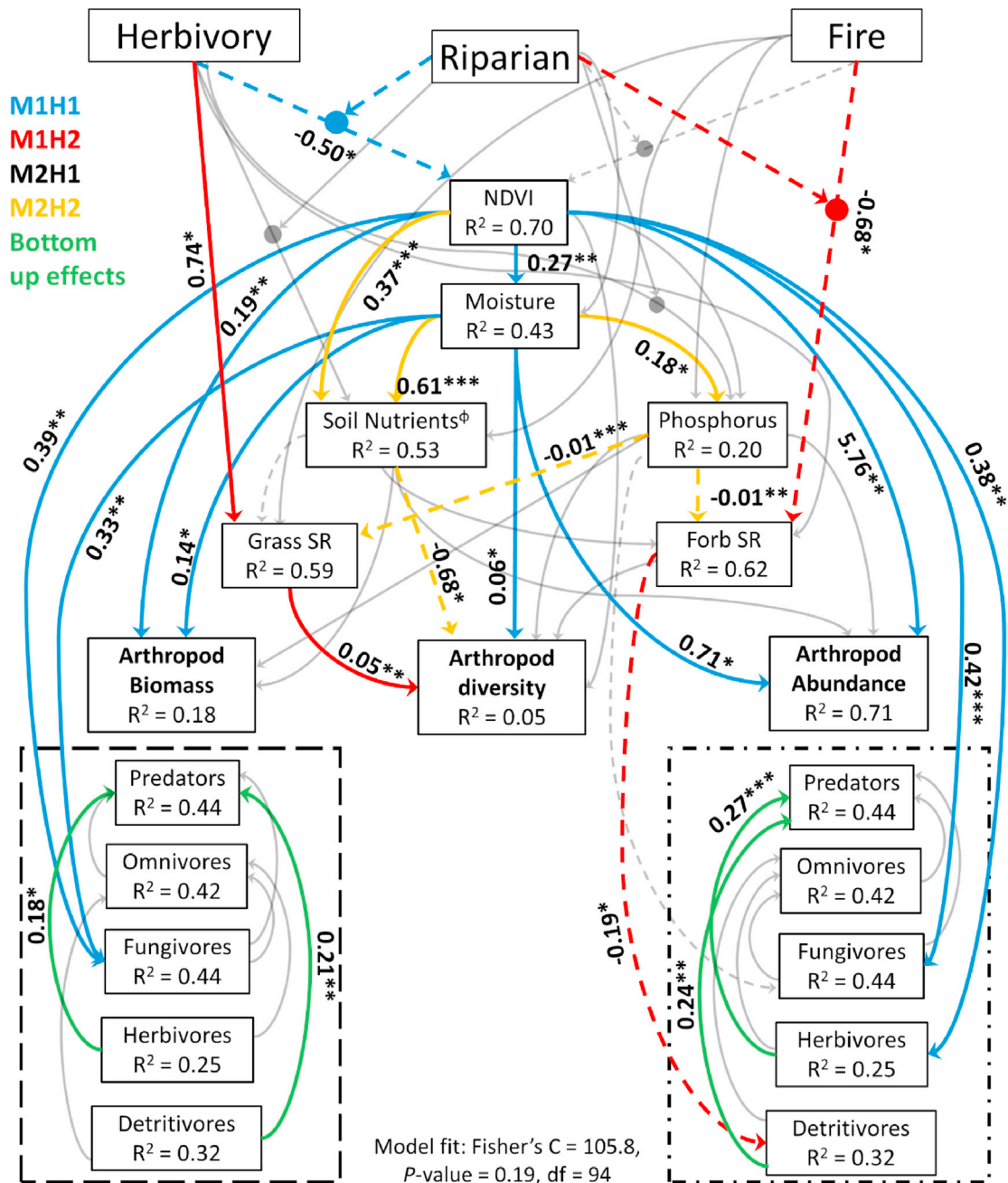
Fig. 5. Structural equation model (SEM) where dashed arrows are negative effects and solid arrows positive effects and arrow heads shows the hypothesised direction of effect. Smaller transparent grey arrows are insignificant hypotheses. Values alongside arrows are standardised path coefficients. The significance of the path coefficients is denoted by asterisks where * $P < 0.05$, **$P < 0.01$, ***$P < 0.001$. An interaction term is denoted where lines intersect on a spot, the path coefficient is presented for this interaction term and not for either effect independently. A dashed line pointing to this circle denotes a negative interaction, where one effect makes the other more negative. Marginal R^2 values are presented which only consider the fixed effects, not the random effects. The dashed line box contains all trophic groups by biomass and the dash-dot box the trophic groups by abundance. For clarity of viewing, the insignificant relationships between the three factor variables (i.e. herbivory, fire and riparian) and any arthropod variable are removed from the diagram. Φ = where 'Nutrients' is the PC1 composite variable containing soil N, C, K, Ca, Mg, and Na. Model fits well based on a d-sep test where Fisher's C = 105.803 with P-value = 0.191, on 94 degrees of freedom. Abbreviation: SR = species richness, NDVI = normalised difference vegetation index.

hypothesised in M2H2). Such a gain of soil nutrients likely arose from increased leaf litter breakdown and mineralisation rates as a result of higher soil moisture (Pellegrini et al., 2015), and potentially an increase in woody cover, which may redistribute nutrients from deeper to shallower areas in the soil profile (Weltzin and Coughenour 1990; Skarpe 1992). Such effects are likely compounded by the riparian zone, where vegetation cover, soil moisture and nutrients are naturally high. Thus overall,

Table 2
The total number of significant paths and the sum of the indirect effects of fire and herbivory on arthropod diversity, abundance and biomass, and all trophic levels' abundance or biomass.

	Herbivory		Fire		Interactive effect
	Total Paths	Sum effect	Total Paths	Sum effect	
Diversity	5	0.21	0	0	NA
Abundance	2	−2.97	0	0	NA
Predators	2	−0.05	1	0.03	−0.02
Omnivores	0	0	0	0	NA
Fungivores	1	−0.21	0	0	NA
Herbivores	1	−0.19	0	0	NA
Detritivores	1	$-4e^{-5}$	1	0.12	0.11
Biomass	2	−0.10	0	0	NA
Predators	0	0	0	0	NA
Omnivores	0	0	0	0	NA
Fungivores	2	−0.23	0	0	NA
Herbivores	0	0	0	0	NA
Detritivores	0	0	0	0	NA
Total	16	−3.54	2	0.15	−3.39

herbivory decreased vegetation cover and soil moisture with a cascading decrease in soil nutrients in riparian zones. A loss of large herbivores likely resulted in long-term 'nutrient loading'. We expected such nutrient enrichment to correspond with increased arthropod diversity (Kirchner 1977; Sedlacek et al., 1988; Siemann et al., 1998) but this was not the case. In contrast, soil nutrients directly decreased arthropod diversity, while soil P decreased diversity by decreasing grass species richness. High soil nutrients have been shown to decrease herbaceous species diversity (Gross et al., 2000; Rajaniemi 2001, 2002), possibly from increased competition between species for the available nutrients (Abrams 1995; Rajaniemi 2001). Additionally, high plant richness is generally linked to higher arthropod diversity and richness (Szentkiralyi and Kozar 1991; Siemann et al., 1998; Knops et al., 1999; Haddad et al. 2000), likely via increased variety of leaf and root litter, root exudates and microbial biomass (Eisenhauer et al., 2010; Sabais et al., 2011) leading to niche diversification. Why soil nutrients directly decreased arthropod diversity is less clear, however, as most research demonstrates intermediary effects (Nijssen, WallisDeVries, and Siepel, 2017). High soil nutrients, especially nitrogen, may directly decrease arthropod diversity simply through chemical stress, a mechanism common in aquatic ecosystems, which may also occur in moist soils (Nijssen, WallisDeVries, and Siepel, 2017) such as those found within our riparian zones in the absence of herbivory. While nutrient enrichment can increase arthropod diversity in the short term (Kirchner 1977; Sedlacek et al., 1988; Siemann et al., 1998), long-term nutrient loading, which is likely happening here, will decrease diversity of both arthropods and vegetation (Haddad et al. 2000). As such, we found evidence to support the 'tolerance/avoidance' hypothesis of Daskin and Pringle (2016), in that herbivory increased soil arthropod diversity by decreasing nutrients in an interaction with the productive riparian zone. It was not simply via positive effects, however, but through the combined negative (nutrient loss) and positive effects (grass richness gain) of herbivory, and how these interacted.

In contrast to diversity, total arthropod abundance and biomass, along with multiple trophic levels were decreased by large herbivores. These losses were mediated through the reduction of NDVI and soil moisture (as hypothesised in M1H1) and the cascading effect to forb richness. While reduced soil moisture may benefit certain arthropod taxa (Petersen et al. 2004; Kral et al., 2017), the loss of moisture resulted in lower arthropod abundance and biomass (and diversity), suggesting the negative effects of moisture loss, i.e. arthropod desiccation and mortality (Vasconcelos et al., 2009; Katagiri and Hijii 2017), outweighed any positive effects. Such dry disturbed soils may also inhibit fungal growth (Bergner et al., 2004; Cairney and Bastias, 2007; Pressler et al., 2019), potentially explaining how moisture decreased fungivore biomass. NDVI may have reduced arthropod abundance and biomass, and the herbivore (abundance) and fungivore (biomass and abundance) trophic levels through reducing food availability, where low vegetation cover reduces leaf and root litter, root exudates, and microbial biomass (Hansen 2000; Armbrecht et al. 2004; Wardle et al., 2006; Sabais et al., 2011). Forb richness may have reduced detritivore abundance due to the relatively low quality of their roots (and subsequent exudates and litter), especially when compared to grasses (Bessler et al., 2009). The detritivore trophic group largely consisted of multiple Collembola families, which feed in and around roots and can be negatively affected by forb richness (Sabais et al., 2011). So, while large mammalian herbivores increased arthropod diversity, they decreased all other components of the food web. Diversity is generally touted as the more important ecosystem component, enhancing resilience and functionality (Elmqvist et al., 2003). If there are too few individuals of a diverse range of species, however, then that diversity is likely to have little effect.

Contrary to our hypothesis, fire and herbivory did not have only negative effects on soil arthropod food webs. While fire had few effects, those it did have were positive, and herbivory simultaneously increased diversity but decreased abundance and biomass. It is known that the impact of large mammalian herbivores on soil arthropods varies based on herbivore abundance and diversity (Vandegehuchte et al., 2017). Thus, the impact of herbivory on soil arthropod food webs and soil food webs in general will likely be further clarified by studies that define the type, density and abundance of herbivores. It is likely that the natural variability of mammalian herbivore diversity and abundance across a savanna will result in different degrees to which herbivory increases soil arthropod diversity or decreases their abundance and biomass. Our research sites did not

test the effect of the shifting mosaic of burnt and grazed areas of different age since disturbance (pyric-herbivory; Fuhlendorf et al. 2004). However, the entire area in this study could be considered as such a mosaic so that future studies might compare the biotic diversity and structure of conventionally managed areas with the long term ecological research site. Further understanding of soil food web drivers will be assisted by studies incorporating a range of known fire frequencies and intensities, as well as herbivory types, densities and abundances.

Data availability statement

Data used to support this study is available on Open Data UCT (https://zivahub.uct.ac.za/) as well as the Kruger National Park data repository.

CRediT authorship contribution statement

Joshua Thoresen: Methodology, conceived the ideas and designed methodology, Data curation, collected the data, processed samples, Formal analysis, analysed the data, led the writing of the manuscript. **Marie-Liesse Vermeire:** Methodology, conceived the ideas and designed methodology, Data curation, collected the data, processed samples. **Zander Venter:** Data curation, collected the data, All authors contributed critically to the drafts and gave final approval for publication. **Graeme Wolfaard:** Data curation, collected the data. **Jennifer Adams Krumins:** Methodology, conceived the ideas and designed methodology. **Michael Cramer:** Methodology, conceived the ideas and designed methodology. **Heidi-Jayne Hawkins:** Methodology, conceived the ideas and designed methodology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01413.

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