

Cascading effects of mammalian herbivores on ground-dwelling arthropods: Variable responses across arthropod groups, habitats and years

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Abstract

1. Large mammalian herbivores are well known to shape the structure and function of ecosystems world-wide, and these effects can in turn cascade through systems to indirectly influence other animal species. A wealth of studies has explored the effects of large mammals on arthropods, but to date they have reported such widely varying results that generalizations have been elusive. Three factors are likely drivers of this variability: the widely varying life-history characteristics of different arthropod groups, the highly variable landscapes that mammalian herbivores commonly inhabit and temporal variation in environmental conditions.

2. Here, we use an 18-year-old enclosure experiment stratified across three distinct coastal prairie habitats in northern California to address the effects of a reintroduced mammalian herbivore, tule elk (*Cervus canadensis nannodes*) on the composition, richness and abundance of ground-dwelling arthropods over two years with very different precipitation regimes.

3. We found that elk shifted the composition of arthropod communities, increasing the abundance of ants, beetles, spiders and mites, decreasing the abundance of woodlice and bristletails in some but not all habitats types, and having no effect on the abundance of bugs, crickets and springtails. Elk also increased richness and changed the composition of ant genera and beetle morpho-species. Interestingly, the effects of elk on arthropod composition, richness and abundance varied little between years, despite very different precipitation levels, biomass accumulation and thatch height.

4. Elk reduced shrub cover, above-ground herbaceous biomass and thatch height and increased soil compaction, and these changes predicted the abundance and richness of arthropods, although taxonomic groups varied in their responses, presumably due to differences in environmental requirements.

5. *Synthesis.* Our research highlights the importance of using long-term experiments to assess the cascading effects of large herbivores on the composition of ground-dwelling arthropod communities and to identify the mechanisms that indirectly shape arthropod responses to herbivores among variable habitats and years in order to develop a greater understanding of the variable responses of arthropods to large mammalian herbivores.

KEYWORDS

environmental heterogeneity, exclosure experiments, ground-dwelling arthropods, indirect effects, large mammalian herbivores

1 | INTRODUCTION

Abundant and widely distributed across nearly all terrestrial habitats world-wide, large mammalian herbivores are well known to shape the structure and function of ecosystems by altering plant structure, community composition and diversity, litter deposition, soil characteristics and nutrient cycling (Bardgett & Wardle, 2003; Borer et al., 2014; Forbes et al., 2019; Hobbs, 1996; Johnson & Cushman, 2007; Martin, Stockton, Allombert, & Gaston, 2010; Olf & Ritchie, 1998; Staver & Bond, 2014). These effects can in turn directly and indirectly influence a wide range of animal assemblages, including other mammals, reptiles, birds and arthropods (Foster, Barton, & Lindenmayer, 2014; Keesing & Young, 2014; van Klink, Plas, Noordwijk, WallisDeVries, & Olf, 2015; Suominen & Danell, 2006). Although there is a rich history of research investigating the impact of mammalian herbivores on arthropod communities, studies have reported highly variable results and generalizations have been elusive. Recent meta-analyses by Foster et al. (2014) looking at native herbivores and van Klink et al. (2015) who included both native and domestic herbivores have found that many studies document negative effects of large herbivores on arthropod abundance, species richness and diversity. Lind et al. (2017) also found that native mammalian herbivores reduce arthropod biomass. However, these results are far from universal and numerous studies have shown that herbivores can have positive effects on arthropod communities (Farrell, Harpole, Stein, Suding, & Borer, 2015; Joern, 2005; Melis et al., 2007). Still, other studies have not detected an effect of large herbivores on arthropod communities (Bestelmeyer & Wiens, 2001; Rambo & Faeth, 1999; Underwood & Christian, 2009). Understanding the effects of large mammals on arthropods is of particular importance because these invertebrates play central roles in terrestrial food webs, represent the bulk of biodiversity world-wide and facilitate an array of essential ecosystem services (e.g. pest control, herbivory, pollination, decomposition; Coupe & Cahill, 2003; Prather et al., 2013; Seastedt & Crossley, 1984).

In order to develop a predictive framework for how mammalian herbivores affect arthropod communities, it is important to explicitly address and understand the drivers of these variable outcomes. Foster et al. (2014) suggested that generalizations will emerge by considering three key factors. First, arthropod groups have widely varying life-history characteristics and these differences can lead to variability in how they respond to the changes caused by herbivores. Second, mammalian herbivore species commonly inhabit vast landscapes that exhibit extensive variation in topography, soil characteristics and productivity – and while rarely studied, such spatial heterogeneity will likely cause substantial variability in the effects of herbivores on arthropod assemblages. Third, these landscapes experience substantial seasonal and annual variation in both

precipitation and temperature, and such temporal variation will undoubtedly influence the response of arthropods to mammalian herbivores. Addressing each of these potential sources of variation is essential for developing a comprehensive and predictive framework for understanding the drivers of context-dependent outcomes in mammal-arthropod interactions.

Here, we use an 18-year-old exclosure experiment stratified across three distinct habitats to evaluate the influence of a native mammalian herbivore – tule elk (*Cervus canadensis nannodes*) – on ground-dwelling arthropod communities in northern California. Our research focuses on addressing two central research questions: (a) Do mammalian herbivores alter the composition, richness and abundance of ground-dwelling arthropods and do these effects vary across grassland types, arthropod groups or years? (b) Are changes in per cent shrub cover, herbaceous biomass, thatch height, plant diversity (H') and soil bulk density mechanisms by which large herbivores alter arthropod communities? Given that large herbivores are known to create more open environments, by reducing woody shrub cover and accumulated plant biomass (Suominen & Danell, 2006), we hypothesize that these environmental changes are likely to benefit mobile ground-dwelling arthropod groups and negatively affect sessile arthropods associated with litter and living in soil.

2 | MATERIALS AND METHODS**2.1 | Study system**

Our research was conducted on Tomales Point in Point Reyes National Seashore, approximately 65 km northwest of San Francisco. Bordered by the Pacific Ocean to the west and Tomales Bay to the east, Tomales Point is a 1,030-ha peninsula that experiences a Mediterranean-type climate, with moderate rainy winters and cool, foggy summers with very little precipitation. The coastal grasslands on Tomales Point are inhabited by native and exotic herbaceous plant species interspersed with native shrubs. Three distinct habitat types occur within our 300-ha study area: *Baccharis*-dominated grasslands, *Lupinus*-dominated grasslands and open grasslands. Open grasslands occur on the Kehoe soil formation (derived from Cretaceous granitic parent rock; Kashiwagi, 1985) and are dominated by herbaceous species and largely devoid of shrubs (Johnson & Cushman, 2007). *Baccharis*-dominated grasslands occur on a subvariant of the Kehoe formation (Kashiwagi, 1985) and are characterized by herbaceous patches mixed with dense stands of *Baccharis pilularis* (Asteraceae), a long-lived native shrub (Johnson & Cushman, 2007). *Lupinus*-dominated grasslands are located on a mix of soil formations, either completely in Sirdrak sand (derived from a Quaternary dune sandstone parent rock) or a mixture of Sirdrak

sand and Kehoe variant (Kashiwagi, 1985). The latter soils are extremely well-drained, resulting in much drier conditions than in *Baccharis*-dominated or open grasslands (V. Dodge & J. H. Cushman, unpublished data). *Lupinus*-dominated grasslands are predominantly open areas interspersed with a short-lived, native, nitrogen-fixing shrub, *Lupinus arboreus* (Fabaceae).

Tule elk (*Cervus canadensis nannodes*), a native ungulate that previously dominated much of coastal and central California, once numbered 500,000 individuals, but hunting and land conversion during the Gold Rush brought them to the brink of extinction by the mid-1800s (McCullough, 1969). The dramatic decline prompted efforts to protect elk, bolster their numbers and reintroduce them to over 20 different sites in California. In 1978, tule elk were reintroduced to a designated wilderness area on Tomales Point, which had historically been used for cattle ranching for over 100 years. Upon reintroduction, elk populations grew rapidly for two decades, reaching approximately 450 individuals before levelling off. Since 1998, the herd has typically fluctuated between 400 and 600 individuals, although censuses between 2014 and 2016 indicated that the population has declined to fewer than 300 animals, possibly due to prolonged drought (D. Press, unpublished data). The diet of tule elk at Tomales Point consists primarily of herbaceous forbs and grasses, but they also consume shrub foliage during the winter months when there is less herbaceous material available (Gogan & Barrett, 1995).

The ground-dwelling arthropod community of Point Reyes is comprised of an array of taxa. Ants, beetles and spiders are abundant and widespread in this landscape; these taxa represent the bulk of arthropod diversity found at Point Reyes. Woodlice are especially abundant, and these detritivores live in the soil and litter in great numbers; however, this low richness group is composed of only two exotic species *Porcellio scaber* and *Armadillidium vulgare*. Similarly, bristletails, springtails and mites can be found throughout the system in high numbers.

2.2 | Herbivore-exclosure experiment

This study centred around a large-scale elk exclosure experiment established by the National Park Service and U.S. Geological Survey in 1998. The ongoing experiment occurs within a 300-ha area and consists of 24 36 m × 36 m plots distributed equally among three above habitat types. Within each of the three habitat types, there are four pairs of plots, with one plot within each pair randomly assigned fencing to exclude elk and another plot spaced 3 m away left unfenced to serve as a control. The fencing that surrounds each exclosure plot is 2.5 m tall and effectively excludes elk, but not other small- or mid-sized herbivores such as deer or hares (J. H. Cushman, *personal observation*). Other studies using this exclosure experiment have shown that elk exert major influences on the plant community (Ender, Christian, & Cushman, 2017; Johnson & Cushman, 2007; C. M. Lee, M. J. Spasojevic, & J. H. Cushman, unpublished data; C. Richter, M. J. Spasojevic, & J. H. Cushman, unpublished data), small mammals (Ellis & Cushman, 2018), plant functional traits (C. M. Lee, M. J. Spasojevic, & J. H. Cushman, unpublished data) and soil

characteristics (V. Dodge, V. Eviner, & J.H.Cushman, unpublished data).

2.3 | Arthropod sampling

To assess the effects of elk on the abundances and community composition of ground-dwelling arthropods in 2015 and 2016, we placed 9 pitfall traps within each of the 24 plots in the exclosure experiment, positioning traps in a 3 × 3 grid with 9 m separating each trap. Pitfall traps were buried flush to the ground and consisted of 250-ml specimen cups with lids, each measuring 95 mm deep and 58 mm in diameter. We selected trapping periods for each year that coincided with peak herbaceous plant biomass – between 29 April and 21 May in 2015 and between 18 May and 27 May in 2016. Due to the extensive time required to open and collect traps for all 24 plots in the experiment, we divided plots into north and south groups and staggered the sampling periods between these groups by two days. In 2015, we left traps open for 20 days. Because capture rates were so high this first year, we opened traps for only 7 days in 2016.

To collect arthropods in each trap, we removed trap lids and filled traps with 100 ml of 50% propylene glycol, 50% DI water and a drop of unscented dish soap to break the surface tension of the liquid. We then fitted the opening of each trap with a wire mesh screen to reduce the incidental capture of shrews. The largest opening of these screens measured 14 mm, which effectively allowed for the capture of most arthropod species present in the system. We rinsed the captured contents of pitfall traps in deionized water and preserved specimens in 70% EtOH. We excluded flying insects and arthropods smaller than 2 mm and then sorted and identified arthropods into the smallest practical taxonomic designations. Woodlice, spiders, bristletails, mites, bugs, crickets, springtails, harvestmen, earwigs, centipedes and millipedes were sorted and counted to the taxonomic level of order. Ants were sorted and identified to genera. Beetles were identified to family and then to morpho-species (Beattie & Oliver, 1994).

2.4 | Vegetation sampling

To assess the effect of elk on thatch accumulation, we determined the depth of thatch surrounding each pitfall trap after each year's arthropod-trapping period. We quantified thatch height using 50 cm × 50 cm quadrats centred over each pitfall trap, with thatch heights recorded at the four corners of each quadrat. We also evaluated the effect of elk on above-ground biomass by clipping all standing herbaceous plant material and accumulated plant litter to ground level after each year's arthropod trapping in five 25 cm × 25 cm quadrats stratified within the centre of each plot and in the centre of each plot quarter. We dried biomass in a 60°C oven for at least 48 hr prior to weighing. To assess the effect of elk on woody vegetation, we quantified per cent cover of shrubs using point-intercept sampling in 1 m² quadrats with 36 points placed directly over each of nine pitfall traps within each plot. We recorded the presence or absence of shrubs within 1 cm of each point.

To determine the effect of elk on plant species diversity, we assessed species composition in May and June of 2016 using point-intercept sampling. We quantified species-specific plant cover within 12 50 cm × 50 cm quadrats that were stratified systematically throughout each of the 24 plots in our enclosure experiment. At each of 36 points per quadrat, we recorded total number of plant species encountered. We restricted vegetation sampling to the central 30 m × 30 m area of each plot so as to reduce possible edge effects caused by fencing. We then calculated the Shannon diversity index (H') for each plot because it is weighted for abundance and is less correlated with species richness than Simpson's diversity index.

2.5 | Soil bulk density

We quantified bulk density of the soil in each of the plots in our elk enclosure experiment in March of 2015. We collected soil cores from nine equally spaced locations within each plot, avoiding the outer 3 m edge. Each of these subsamples was collected using a slide hammer soil core with a 5.1 cm diameter × 5.1 cm depth liner (A.M.S. American Falls, Idaho). We placed all subsamples in plastic Ziploc bags, stored them in a cooler while in the field and then transported them back to the laboratory, where they were weighed, oven-dried at 60°C for 72 hr and weighed again. We calculated bulk density (ρ) of each subsample as $\rho = M_D/V_S$, where M_D = weight of oven-dried soil and V_S = volume of soil core. As soils were not rocky or gravelly, stones were not removed from samples prior to determining bulk density. The bulk densities of all nine subsamples were averaged prior to statistical analysis.

2.6 | Statistical analysis

2.6.1 | Arthropod community composition

To account for variation in sampling effort due to (a) loss of pitfall traps disturbed by animals and (b) differences in the duration of sampling between years, we converted the data on arthropod abundances to rates of capture (total pitfall captures per plot/trap/day) prior to analysis. We then used non-metric multidimensional scaling (NMDS) of Bray–Curtis dissimilarity (Beals, 1984) based on arthropod relative abundance in the Vegan package in R (Oksanen et al., 2013; R Core Team, 2016) to visualize changes in arthropod community composition as a function of elk (present or excluded), grassland type (*Baccharis*-dominated, *Lupinus*-dominated and shrub-free grasslands) and year (2015 and 2016). In these analyses, we examined the arthropod community at three taxonomic scales – orders/families, ant genera and beetle morpho-species. Prior to analysis, we relativized arthropod abundance and created Bray–Curtis dissimilarity matrices. We evaluated our NMDS figures as good representations of arthropod community composition based on “stress”, which is a measure of departure from monotonicity in the relationship between the dissimilarity in the original n -dimensional space and distance in 2-dimensional

ordination space (Kruskal & Wish, 1978). In general, stress values <0.1 correspond to a good indication of the similarities between samples, whereas stress values >0.2 indicate a poor relationship. Stress values represent only how well the dissimilarity among sites is represented in a two-dimensional figure, but do not affect the statistical analysis quantifying differences between groups (Clarke, 1993).

To test for differences in the composition of orders/families, ant genera and beetle morpho-species, we used multivariate analysis of variance (PERMANOVA) in PRIMER 6 + PERMANOVA (Anderson, Gorley, & Clarke, 2008) with mixed models containing elk (present, excluded), grassland type (*Baccharis*-dominated, *Lupinus*-dominated and shrub-free grasslands) and year (2015 and 2016) as fixed effects and plot pair (1–12) nested within grassland type as a random effect. All PERMANOVA tests were based on 9,999 permutations in a restricted model using type III sum of squares. To determine which taxa contributed most to the elk effect on community composition at the order/family level, we used the similarity percentages (SIMPER) routine in PRIMER (Anderson et al., 2008), which calculates the average contribution of individual taxa to the average dissimilarity between groups that are known to differ based upon PERMANOVA results.

We evaluated the response of arthropod abundance, order and family groups, ant genera richness, beetle morpho-species richness, per cent shrub cover, herbaceous biomass and thatch height using linear mixed models in JMP 13 Pro (SAS Institute, Cary, NC), with elk (present, excluded), grassland type (*Baccharis*-dominated, *Lupinus*-dominated and shrub-free grasslands), year (2015 and 2016) and their interactions as fixed effects and plot pair (1–12) nested within grassland type as a random effect. For vegetation variables, we nested quadrat within plot pair and designated it as a random effect. For per cent shrub cover, which was sampled once, we removed year from the model as a fixed effect. Four arthropod groups (harvestmen, earwigs, centipedes and millipedes) were excluded from analyses due to insufficient number of captures (Table 1). To ensure that assumptions for linear mixed models were met, we visually assessed all model residuals for approximate normality and checked for homoscedasticity of residual plots. When necessary, we Box–Cox transformed arthropod abundance values to meet model requirements. If grassland type or any interaction terms were significant in our models, we followed up with Tukey multiple comparison tests to evaluate differences among means.

To test the hypothesis that elk modify the composition of arthropod community by indirectly modifying the environment, we used distance-based linear modelling (DistLM), a multivariate linear regression analysis. This procedure selects the best-fitting combination of environmental variables predicting arthropod community composition and calculates the proportion of arthropod community variation that can be attributed to each variable. Similar to redundancy analysis or canonical correspondence analysis, DistLM generates pseudo- F and p values through a permutation routine comparing environmental predictor variables against community matrices (dissimilarity or resemblance). As environmental predictor variables, we

TABLE 1 Results from linear mixed models evaluating abundance of ants, beetles, spiders, mites, woodlice, bristletails, bugs, crickets and springtails as a function of elk (present or excluded), grassland (*Baccharis*-dominated, *Lupinus*-dominated or open grassland) and year (2015 and 2016)

Taxa	Elk (E)		Grassland (G)		Year (Y)		E × G		E × Y		G × Y		E × G × Y		Model R ²
	F _{1,27}	p	F _{2,9}	p	F _{1,27}	p	F _{2,27}	p	F _{1,27}	p	F _{2,27}	p	F _{2,27}	p	
Ants	20.80	<0.001	2.73	0.118	21.42	<0.001	0.72	0.494	0.63	0.434	1.10	0.347	0.05	0.952	77.2
Beetles	44.89	<0.001	2.85	0.110	0.11	0.738	0.07	0.932	0.17	0.683	2.04	0.149	1.90	0.169	91.9
Spiders	50.22	<0.001	0.65	0.543	26.55	<0.001	1.85	0.177	1.18	0.287	4.77	0.017	9.18	0.001	82.9
Mites	7.07	0.013	2.83	0.111	9.67	0.004	6.88	0.004	0.97	0.332	2.77	0.081	0.22	0.806	69.7
Woodlice	0.09	0.767	1.10	0.373	1.16	0.291	2.79	0.079	1.25	0.274	5.14	0.013	0.33	0.721	86.7
Bristletails	2.01	0.168	2.70	0.121	9.11	0.006	3.03	0.065	0.05	0.831	1.37	0.270	0.27	0.767	84.8
Bugs	0.37	0.549	3.31	0.084	12.25	0.002	1.77	0.189	0.08	0.783	5.62	0.009	1.17	0.327	60.3
Crickets	0.09	0.767	0.56	0.592	6.41	0.018	1.68	0.205	0.01	0.917	0.53	0.594	1.25	0.304	55.3
Springtails	0.06	0.816	1.39	0.297	3.74	0.064	0.58	0.568	0.18	0.674	3.51	0.044	0.02	0.982	58.1

included per cent shrub cover, above-ground dry herbaceous biomass, depth of accumulated dead plant biomass on the soil surface (hereafter referred to as thatch), plant species diversity (H') and soil bulk density. Prior to analysis, we examined the predictor variables for normality and collinearity. To meet normality requirements of predictor variables, we log (x + 1)-transformed thatch depth, soil bulk density and plant diversity (H') and arc-sine-transformed per cent shrub cover. Shrub cover, soil bulk density and plant diversity (H') were each sampled once and because these variables are unlikely to change quickly, we used them predictor variables for both years. For data on arthropod orders/families, ant genera and beetle morpho-species, we fitted DistLM with forward stepwise selection using Akaike information criterion (AICc) procedure and sequential tests (9,999 permutations).

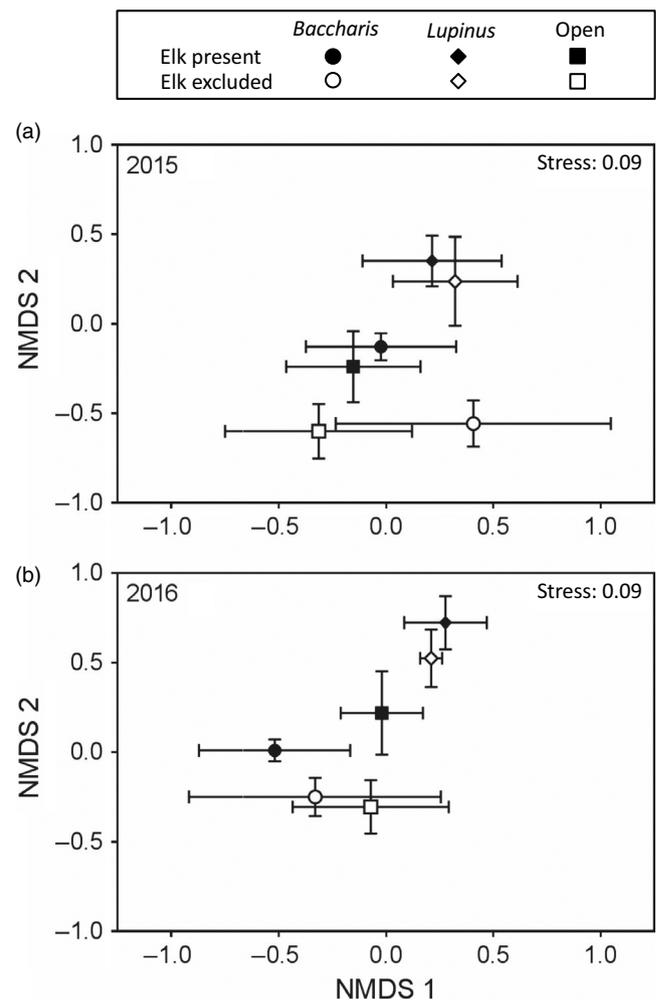


FIGURE 1 Non-metric multidimensional scaling ordination plots visualizing composition differences of arthropod orders/families in 2015 (a) and 2016 (b) as a function of elk (present or excluded), grassland type (*Baccharis*-dominated, *Lupinus*-dominated or shrub-free grassland) and year (2015 and 2016). Each symbol represents the mean NMDS scores (±SE) for plots classified within a group. Symbols closer to each other are more similar than those further apart

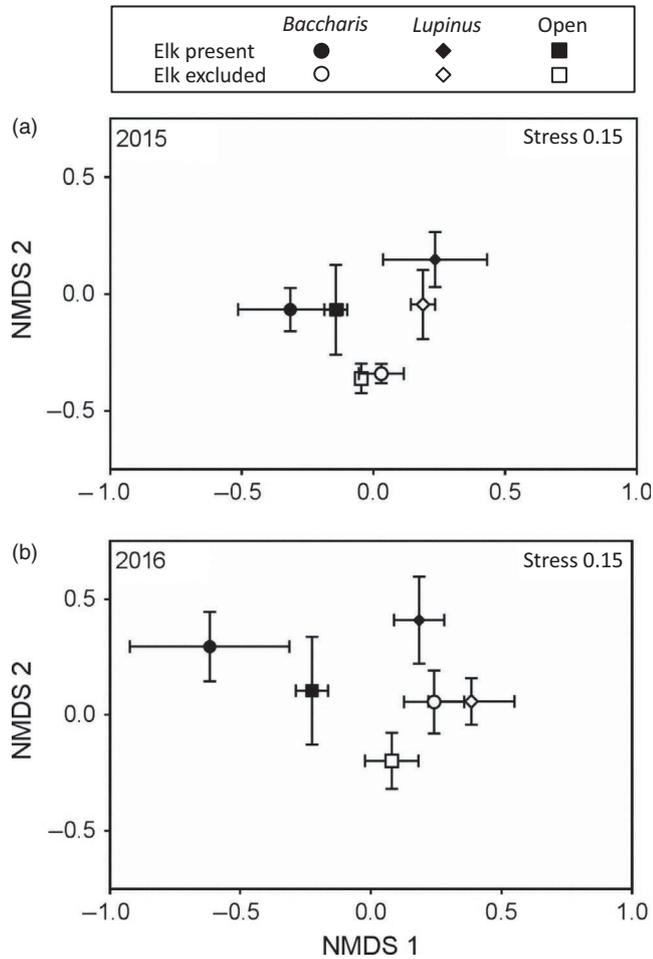


FIGURE 2 Non-metric multidimensional scaling ordination plots visualizing composition differences of ant genera in 2015 (a) and 2016 (b) as a function of elk (present or excluded), grassland type (*Baccharis*-dominated, *Lupinus*-dominated or shrub-free grassland) and year (2015 and 2016). Each symbol represents the mean NMDS scores (\pm SE) for plots classified within a group. Symbols closer to each other are more similar than those further apart

2.6.2 | Vegetation and environmental factors

To test our hypothesis that the abundance of arthropod taxa was affected indirectly through elk modification of environmental variables, we used multiple linear regressions (JMP 13 Pro) to relate environmental variables with the abundance of the six most numerous order level arthropod taxa. Model selection was fitted using forward stepwise selection and Akaike information criterion (AICc) procedure to select among environmental predictor variables (per cent shrub cover, herbaceous biomass, thatch height, plant diversity (H') and soil bulk density). To meet model assumptions, we evaluated predictor variables for multicollinearity by examining VIF values and examined model residuals for approximate normality. For analyses with highly skewed model residuals, we $\log(x + 1)$ -transformed both the response and predictor variables in order.

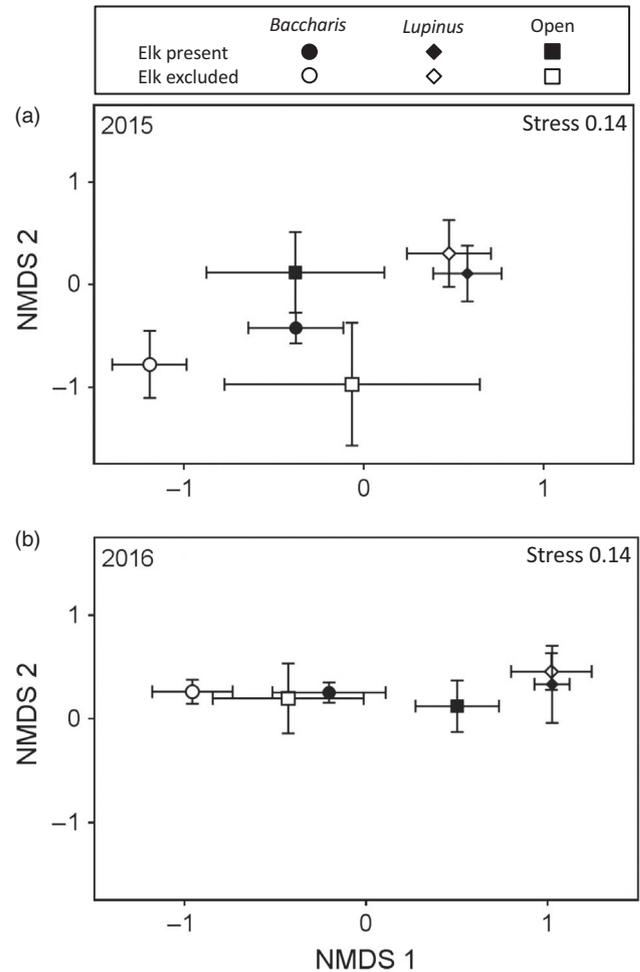


FIGURE 3 Non-metric multidimensional scaling ordination plots visualizing composition differences of beetle morpho-species in 2015 (a) and 2016 (b) as a function of elk (present or excluded), grassland type (*Baccharis*-dominated, *Lupinus*-dominated or shrub-free grassland) and year (2015 and 2016). Each symbol represents the mean NMDS scores (\pm SE) for plots classified within a group. Symbols closer to each other are more similar than those further apart

3 | RESULTS

3.1 | Arthropod community composition

In this study, we captured 72,145 ground-dwelling arthropods over 5,046 pitfall trap days during two sampling periods (May 2015 and 2016). The most abundant taxa in these samples were woodlice (46,000), beetles (10,594), ants (6,842), spiders (2,073), bristletails (1,926) and mites (1,558; Appendix S1). These six groups accounted for 97% of the total number of arthropods collected. We found that elk altered the composition of arthropod orders/families ($F_{1,9} = 5.63$, $p = 0.007$; Figure 1), ant genera ($F_{1,9} = 5.88$, $p = 0.005$; Figure 2) and beetle morpho-species ($F_{1,9} = 2.53$, $p = 0.038$; Figure 3), with no evidence that the effects of elk on these groups varied among grassland types ($F_{2,9} = 1.70$, $p = 0.119$; $F_{2,9} = 0.87$, $p = 0.52$; $F_{2,9} = 1.26$, $p = 0.26$, respectively). Although the

composition of the three arthropod groups differed significantly between the two sample years ($F_{1,9} = 6.92, p = 0.002$; $F_{1,9} = 3.11, p = 0.042$; $F_{1,9} = 7.57, p = 0.002$, respectively), the effects of elk on them did not vary between years ($F_{1,9} = 0.18, p = 0.85$; $F_{1,9} = 0.97, p = 0.43$; $F_{1,9} = 1.43, p = 0.24$, respectively). Six arthropod taxa – woodlice, beetles, ants, bristletails, spiders and mites – were identified as accounting for 91% of the elk-mediated differences in community composition (Appendix S2). Elk increased the contribution of beetles, ants, spiders and mites to the community, accounting for 46.5% of the total difference in community composition. Conversely, elk decreased the contribution of woodlice and bristletails to the community, accounting for 44.9% of the total difference in composition.

Elk significantly increased the abundance of beetles, ants, spiders and mites, but had no direct influence on woodlice, bristletails,

bugs, crickets, nor springtails (Table 1, Figure 4). The effect of elk on abundance varied with grassland type for three of the nine arthropod groups – mite abundance was positively influenced by elk in shrub-free grasslands and unaffected in the other two grassland types; there was a trend for woodlice abundance to be negatively affected by elk in *Baccharis*-dominated and open grasslands and unaffected in *Lupinus*-dominated grasslands; and bristletail abundance was negatively affected by elk in *Lupinus*-dominated grasslands and unaffected elsewhere (Table 1). Although the abundances of many groups varied significantly between years, the effect of elk on them did not vary between years (Table 1). We detected a significant three-way interaction for spiders, with their abundances being positively affected only in *Baccharis*-dominated and shrub-free grasslands in 2015 and *Lupinus*-dominated and shrub-free grasslands in 2016 (Table 1, Figure 4).

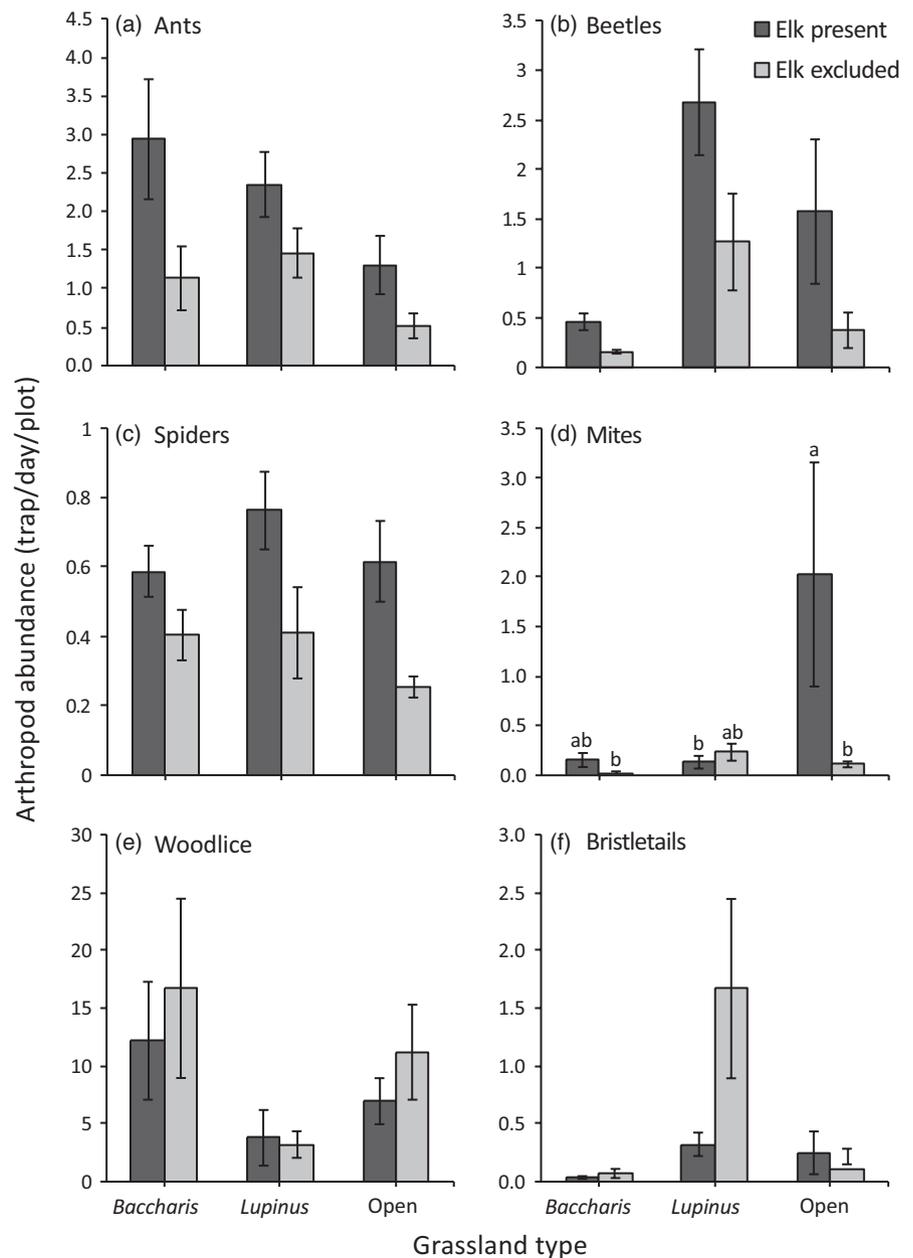


FIGURE 4 Mean (± 1 SE) abundance of ants (a), beetles (b), spiders (c), mites (d), woodlice (e) and bristletails as a function of elk (present or excluded), grassland (*Baccharis*-dominated, *Lupinus*-dominated or shrub-free grassland) and year (2015 and 2016). Letters over the bars correspond to the results from Tukey multiple comparison tests

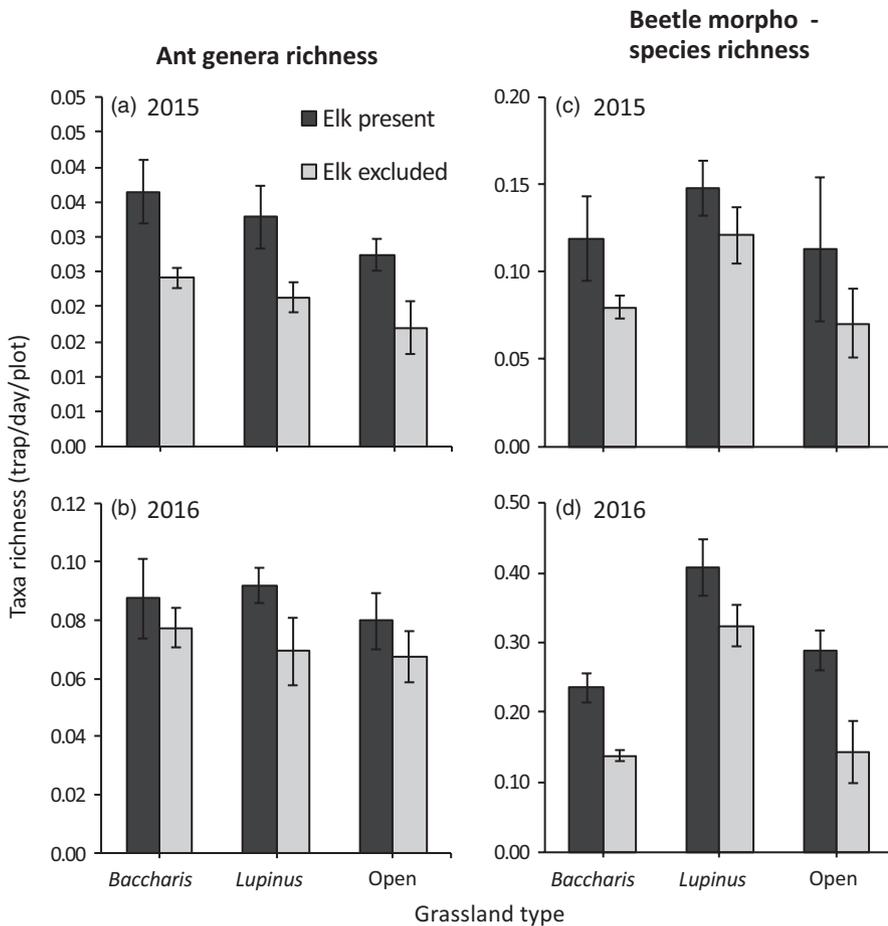


FIGURE 5 Mean (± 1 SE) taxa richness of ant genera and beetle morpho-species in 2015 and 2016 as a function of elk (present or excluded) and grassland type (*Baccharis*-dominated, *Lupinus*-dominated or shrub-free grassland)

Elk significantly increased the richness of ant genera and beetle morpho-species (Figure 5; $F_{1,27} = 24.17$, $p < 0.001$; $F_{1,27} = 35.50$, $p < 0.001$, respectively), with these effects not varying among grassland type ($F_{2,27} = 0.13$, $p = 0.734$; $F_{2,27} = 1.35$, $p = 0.277$, respectively). The effects of elk on beetle richness varied significantly between years ($F_{1,27} = 6.51$, $p = 0.017$), with elk increasing richness in 2016 but not 2015. Similarly, there was a trend for the effects of elk to vary between years for ant genera richness ($F_{1,27} = 3.22$, $p = 0.084$), with elk having a greater positive effect on genera richness in 2015 than 2016.

3.2 | Vegetation and environmental factors

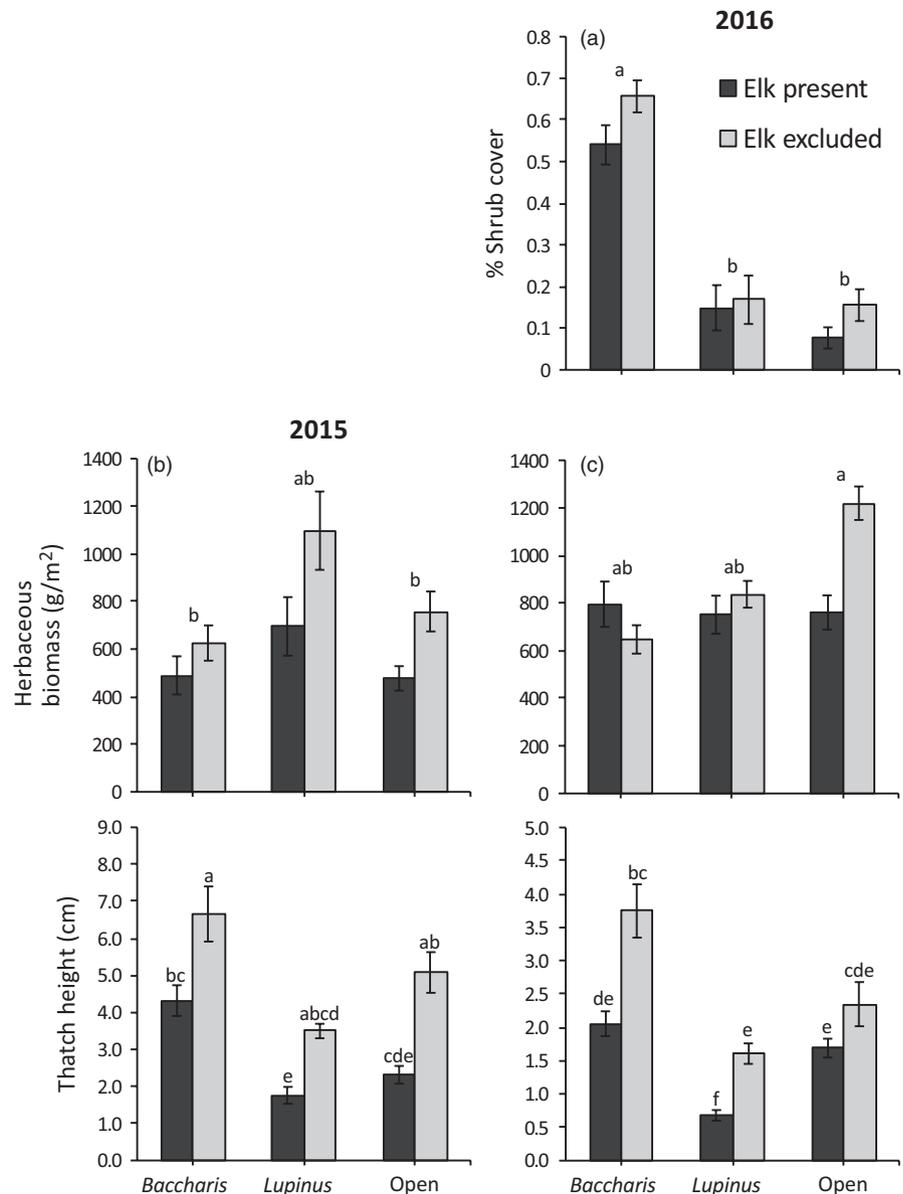
Elk significantly reduced shrub cover ($F_{1,106} = 4.07$, $p = 0.046$), and this effect did not vary among grassland types ($F_{2,108} = 0.37$, $p = 0.689$; Figure 6). Elk also reduced above-ground herbaceous biomass ($F_{1,218} = 25.18$, $p < 0.0001$), and this effect varied among grassland types ($F_{2,218} = 5.55$, $p = 0.004$), with reductions occurring in *Lupinus*-dominated and open grasslands but not *Baccharis*-dominated ones. We also detected a trend for the effects of elk on biomass to differ between years ($F_{1,218} = 3.47$, $p = 0.064$), with influences being more consistent in 2015. Elk significantly reduced the height of thatch ($F_{1,317} = 132.64$, $p < 0.0001$) and this effect varied with grassland type and year ($F_{2,315} = 4.19$, $p = 0.016$). Elk reduced thatch height in all grassland types in

2015 but only in *Baccharis*-dominated and *Lupinus*-dominated grasslands in 2016.

We found that the composition of arthropod orders/families was influenced by thatch depth, plant diversity (H') and shrub cover (Table 2), with the entire model accounting for 24.5% of the variation. We also found that the composition of ant genera and beetle morpho-species was both influenced by plant diversity (H'), thatch depth, shrub cover and soil bulk density (Table 2). Collectively, these analyses accounted for 30.8% of the compositional variation in ant genera and 28.8% of beetle morpho-species groups.

We found that five environmental variables altered by elk were also predictors of the abundance of arthropod taxa. Ant abundance decreased with increasing thatch and increased with increasing shrub cover (Table 3). The abundance of beetles decreased with increasing levels of thatch (Table 3). We detected a trend for spider abundance to decrease with increasing herbaceous biomass and increasing thatch height, although the overall amount of variation explained by this relationship was low (Table 3). Mite abundance increased with increasing plant diversity and showed a decreasing trend with increasing thatch height, although again the overall amount of variation explained by this relationship was low (Table 3). The number of woodlice declined with increasing soil density and increasing thatch, but was positively associated with increasing shrub cover (Table 3). Bristletail taxa abundance decreased with increasing plant diversity (H') and shrub cover, and there was a trend

FIGURE 6 Mean (± 1 SE) shrub cover, herbaceous biomass and thatch height in 2015 and 2016 as a function of elk (present or excluded) and grassland type (*Baccharis*-dominated, *Lupinus*-dominated or shrub-free grassland). Letters over the bars correspond to the results from Tukey multiple comparison tests



for bristletail abundance to increase with rising levels of herbaceous biomass (Table 3).

4 | DISCUSSION

In our 18-year enclosure experiment, we found that elk shifted the composition of arthropod communities, increasing the abundance of ants, beetles, spiders and mites, decreasing the abundance of woodlice and bristletails in some but not all habitat types, and having no effect on the abundance of bugs, crickets and springtails. Elk also increased the richness of ant genera and beetle morpho-species as well as changed their composition. In addition, elk reduced the cover of native shrubs, above-ground herbaceous biomass and thatch height and increased soil compaction. These alterations of environmental conditions were likely key factors driving the observed shifts in arthropod composition, richness and abundance, although taxonomic

groups varied in their responses to these variables, presumably due to differences in environmental requirements. Collectively, our results documented that a large mammalian herbivore had cascading, indirect effects on ground-dwelling arthropod communities across an exceptionally heterogeneous environment during two years that varied greatly in precipitation and biomass accumulation.

Our results contrast markedly with the primary findings of two recent meta-analyses, which each independently concluded that large herbivores generally have negative effects on arthropod abundance and richness, primarily through resource limitation and disturbance (Foster et al., 2014; van Klink et al., 2015). Lind et al. (2017) also found that mid-to-large-sized mammalian herbivores reduced total arthropod biomass in experiments replicated across 13 temperate grasslands. Suominen and Danell (2006) suggested that the effects of large herbivores on ground-dwelling arthropods should vary depending on the latter's life-history characteristics. They reasoned that large herbivores create more open

Arthropod group	Variable	Pseudo-F	p	% Variation	% Cumulative
Order/family	Thatch height	7.76	0.001	14.4	
	Plant diversity (H')	3.31	0.037	5.9	
	% Shrub cover	2.42	0.079	4.2	24.5
Ant genera	Plant diversity (H')	6.31	0.0001	12.1	
	Thatch height	5.49	0.001	9.6	
	% Shrub cover	2.81	0.040	4.7	
	Soil bulk density	2.53	0.058	4.1	30.4
Beetle morpho-species	Plant diversity (H')	5.52	0.0001	10.7	
	Thatch height	5.47	0.0001	9.7	
	% Shrub cover	2.69	0.010	4.6	
	Soil bulk density	2.32	0.027	3.8	28.8

TABLE 2 Results of multivariate regression analysis (DistLM) demonstrating the indirect effects of elk on the composition of order/family, ant genera and beetle morpho-species as a function of environmental variables (per cent shrub cover, herbaceous biomass, thatch height, plant diversity (H') and soil bulk density)

environments, by reducing herbaceous biomass and shrub cover, which in turn creates environments that favour mobile ground-dwelling arthropods adapted for open environments and disfavoured sessile litter- and vegetation-dwelling species. Our results in general support this view, where elk increase the abundance of mobile taxa such as ants, beetles and spiders while reducing the number of comparatively less-mobile, litter-dwelling bristletails and soil-dwelling woodlice (in some habitat types). Our work, and that of Suominen and Danell (2006), suggests that arthropod groups with widely divergent life-history characteristics will vary greatly in how they respond to the environmental changes caused by herbivores, and that considering arthropods as a single group will often mask these differences.

While the effects of large herbivores on arthropods are notoriously variable within and among studies and through time, we found that the effects of elk in our system were remarkably robust, generally persisting across three very different habitats and two very different years. Of the nine arthropod groups we focused on, only three showed any evidence for the effect of elk to vary among habitat types. Elk had a significant positive effect on mite abundance only in open grasslands, whereas there were no such effects in the two shrub-dominated grasslands. For both bristletails and woodlice, we detected trends for the effects of elk to vary among grassland types: bristletails were negatively affected by elk in *Lupinus*-dominated grasslands and nowhere else, whereas elk had a weak negative effect on woodlice abundance in two of the grassland types and not

TABLE 3 Results of linear multiple regression demonstrating indirect effects of elk on the abundance of ants, beetles, spiders, mites, woodlice and bristletails as a function of environmental variables (per cent shrub cover, herbaceous biomass, thatch height, plant diversity (H') and soil bulk density)

Taxa	Environmental variables	Variable F-value	Variable p-value	Sign of effect	Model F-value	Model p-value	R ²
Ants	Thatch height	22.87	<0.0001	-	11.96	<0.0001	0.35
	% Shrub cover	10.46	0.001	+			
Beetles	Thatch height	14.66	0.0004	-	14.66	0.0002	0.24
Spiders	Herb. biomass	3.35	0.074	-	2.73	0.076	0.11
	Thatch height	2.55	0.117	-			
Mites	Plant diversity (H')	6.08	0.018	+	3.92	0.027	0.15
	Thatch height	2.32	0.135	-			
Woodlice	Soil bulk density	10.23	0.003	-	4.98	0.005	0.25
	% Shrub cover	4.88	0.033	+			
	Thatch height	3.73	0.060	-			
Bristletails	Plant diversity (H')	12.84	0.001	-	7.53	0.0004	0.34
	% Shrub cover	4.10	0.049	-			
	Herb. biomass	3.31	0.076	+			

in *Lupinus*-dominated grasslands. Moreover, given the tremendous differences in precipitation between our two focal years, we were surprised that, other than the abundance of spiders, we did not detect more differences in the influence of elk between years on the composition or abundance of arthropod groups. The first year of our study, 2015, was the tail end of a historic drought, whereas the second year, 2016, was a much wetter year with over double the amount of precipitation. Associated with these annual differences, the amounts of herbaceous biomass in 2016 were much greater than in 2015. The consistency of our findings between years, despite these and other temporal differences, suggests that the cumulative effect of elk on the recipient environment has had a greater influence on arthropod community than variation in herbaceous biomass, thatch height or climate differences among habitats or between years.

Vegetation characteristics helped explain many of the responses of different arthropod groups in our system. Ants were more abundant in areas with higher shrub cover and lower levels of thatch, likely due to the influence of the dominant ant genera in our system, *Formica*, which is a long-legged, mobile taxa preferring shaded areas (Hölldobler & Wilson, 1990). Ground-dwelling beetles are a heterogeneous group with varied life-history traits and were only positively associated with lower levels of thatch. We found higher numbers of ground-dwelling spiders in areas with decreasing levels of thatch and biomass, likely because these mobile predators prefer open areas (Bultman & DeWitt, 2008). Mites exhibited strong habitat preferences, being found almost exclusively in open grasslands that had high plant diversity and low levels of thatch. Woodlice are terrestrial crustaceans susceptible to desiccation that shelter in soil and moist shaded areas (Dias, Hassall, & Waite, 2012). Consistent with these life-history traits, woodlice abundance increased with shrub cover and less compact soil but also decreased with rising levels of thatch. Bristletails, a primitive insect associated with plant litter and loose soils (Smith, 1970), were found in high abundance only in the *Lupinus*-dominated grassland in areas with low shrub cover, low plant diversity and high values of biomass.

Although not explicitly addressed by this study, it is important to acknowledge that invasive arthropods and plant species can have considerable influence on arthropod communities. Woodlice, the dominant exotic arthropod in our system, have been implicated in displacing native detritivores (Singer, Bello, & Snyder, 2012) and are associated with Argentine ants (Human & Gordon, 1997). Despite finding vast numbers of woodlice, we did not identify any Argentine ants or recognize any other exotic arthropod species. Interestingly, while we did not find that elk significantly impacted the abundance of woodlice, variation in this group was still the largest driver of variation between arthropod communities in the presence or absence of elk (Appendix S2). While this pattern may be driven by the sensitivity of SIMPER analyses to dominant species, it may also reflect indirect effects of the elk on the environment; unfortunately, we are unable to tease apart such indirect effects with our experimental design. Additionally, exotic annual grasses are abundant across our study area and are known to decrease richness and shift the composition of arthropod assemblages (Farrell et al., 2015; Wolkovich, Bolger, & Holway, 2009). It is notable that thatch, largely consisting of senesced exotic grasses, had a negative association with

arthropod abundances. This outcome may be due to limiting arthropod mobility but has also been associated with changing resource quality. By removing this accumulated exotic biomass, tule elk, a reintroduced endemic herbivore, are mitigating the effects of an exotic plant invasion and creating an environment that is more like its native state.

In conclusion, our results suggest that elk had a strong influence on arthropod community structure across a heterogeneous environment and that these effects were due largely to reduced thatch accumulation and shrub cover as well as increased plant diversity and soil compaction. Our research highlights the importance of using long-term experiments to assess the cascading effects of large herbivores on the composition of ground-dwelling arthropod communities at different taxonomic scales and across heterogeneous environments. Thus, it is critically important to study and identify the mechanisms that indirectly shape arthropod responses to herbivores among variable habitats and over multiple years, which will allow for greater understanding about the dynamics of variable responses of arthropods to large mammalian herbivores.

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AUTHORS' CONTRIBUTIONS

E.M.C. designed the study, performed the sampling, analysed the data and wrote the manuscript. J.H.C. conceived and designed the study, assisted with data analysis and co-wrote the paper. M.J.S. assisted with data analysis and co-wrote the paper.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.7rn6dd8> (Cecil, Spasojevic, & Cushman, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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