UC Riverside

UC Riverside Previously Published Works

Title

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

Permalink

https://escholarship.org/uc/item/1kp338jn

Journal

Journal of Animal Ecology, 88(9)

ISSN

0021-8790

Authors

Cecil, Eric M
Spasojevic, Marko J
Cushman, J Hall

Publication Date

2019-09-01

DOI

10.1111/1365-2656.13033

Peer reviewed

eScholarship.org Powered by the California Digital Library
University of California

Accepted Article

Journal of Animal Ecology

J. HALL CUSHMAN (Orcid ID : 0000-0003-3210-4261)

Article type : Research Article

handling editor: M. Noelia Barrios-Garcia

Running head: Cascading effect of large herbivores on arthropods

Cascading Effects of Mammalian Herbivores on Ground-Dwelling Arthropods: Variable Responses across Arthropod Groups, Habitats and Years

Eric M. Cecil[1], Marko J. Spasojevic[2] and J. Hall Cushman[3]*

[1] Department of Biology, Sonoma State University, Rohnert Park, California 94928, USA

[2] Department of Evolution, Ecology, and Organismal Biology, University of California – Riverside, Riverside, California 92521, USA

[3] Department of Natural Resources & Environmental Science, University of Nevada, Reno, Nevada 89557, USA

*Corresponding author: jhcushman@unr.edu

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1365-2656.13033
This article is protected by copyright. All rights reserved.

Accepted Article

Abstract

1. Large mammalian herbivores are well known to shape the structure and function of ecosystems worldwide and these effects can in turn cascade through systems to indirectly influence other animal species. A wealth of studies have 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 exclosure 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, aboveground 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.

This article is protected by copyright. All rights reserved.

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

Introduction

Abundant and widely distributed across nearly all terrestrial habitats worldwide, 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 (Hobbs 1996; Olff & Ritchie 1998; Bardgett & Wardle 2003; Johnson & Cushman 2007; Martin *et al.* 2010; Borer *et al.* 2014; 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 (Suominen & Danell 2006; Foster, Barton & Lindenmayer 2014; Keesing & Young 2014; van Klink *et al.* 2015). 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

This article is protected by copyright. All rights reserved.

Accepted Article

numerous studies have shown that herbivores can have positive effects on arthropod communities (Joern 2005; Melis *et al.* 2007; Farrell *et al.* 2015). Still other studies have not detected an effect of large herbivores on arthropod communities (Rambo & Faeth 1999; Bestelmeyer & Wiens 2001; 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 worldwide, and facilitate an array of essential ecosystem services (e.g., pest control, herbivory, pollination, decomposition)(Seastedt & Crossley 1984; Coupe & Cahill 2003; Prather *et al.* 2013).

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.

This article is protected by copyright. All rights reserved.

Accepted Article

Accepted Article

Our research focuses on addressing two central research questions: 1) 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? 2) Are changes in percent 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.

Methods

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 1030-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 and 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 and Cushman 2007). *Lupinus*-dominated grasslands are located on a mix of soil formations, either completely in Sirdrak sand (derived

This article is protected by copyright. All rights reserved.

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 and 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 leveling off. Since 1998, the herd has typically fluctuated between 400-600 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 and 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, these detritivores live in the soil and litter in great numbers, however this low

This article is protected by copyright. All rights reserved.

Accepted Article

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.

Herbivore-exclosure experiment

This study centered around a large-scale elk-exclosure experiment established by the National Park Service and U.S. Geological Survey in 1998. The on-going experiment occurs within a 300-ha area and consists of 24 36 × 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 (Johnson and Cushman 2007; Ender et al. 2017; Richter, Spasojevic and Cushman, *unpublished data;* Lee, Spasojevic and Cushman, *unpublished data*), small mammals (Ellis & Cushman 2018), plant functional traits (Lee, Spasojevic and Cushman, *unpublished data*) and soil characteristics (Dodge, Eviner and Cushman, *unpublished data*).

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 x 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

This article is protected by copyright. All rights reserved.

Accepted Article

year that coincided with peak herbaceous plant biomass – between April 29th and May 21st in 2015 and between May 18th and May 27th 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 (Beattle & Oliver 1994).

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 x 50 cm quadrats centered over each pitfall trap, with thatch heights recorded at the four corners of each quadrat. We also evaluated the effect of elk on

This article is protected by copyright. All rights reserved.

Accepted Article

aboveground biomass by clipping all standing herbaceous plant material and accumulated plant litter to ground level after each year's arthropod trapping in five 25 x 25 cm quadrats stratified within the center of each plot and in the center 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 percent cover of shrubs using point-intercept sampling in 1 m^2 quadrats with 36 points placed directly over each of 9 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 x 50 cm quadrats that were stratified systematically throughout each of the 24 plots in our exclosure experiment. At each of 36 points per quadrat, we recorded total number of plant species encountered. We restricted vegetation sampling to the central 30 x 30 m area of each plot so as to reduce possible edge effects caused by fencing. We then calculated the Shannon diversity index (H'; Shannon & Weaver 1949) for each plot because it is weighted for abundance and is less correlated with species richness than Simpson's diversity index.

Soil Bulk Density

We quantified bulk density of the soil in each of the plots in our elk exclosure 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 x 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 lab, where they were weighed, oven dried at 60^o C for 72 hr and weighed again. We calculated bulk density (ρ) of each subsample as ρ

This article is protected by copyright. All rights reserved.

Accepted Article

$= M_D / V_S$, 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.

Statistical Analysis

Arthropod community composition. To account for variation in sampling effort due to 1) loss of pitfall traps disturbed by animals and 2) 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; 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).

This article is protected by copyright. All rights reserved.

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 9999 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, Gorley & Clarke 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, percent 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 percent 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

This article is protected by copyright. All rights reserved.

Accepted Article

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 modeling (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 included percent shrub cover, aboveground 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 percent 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 Akai
ke information criterion (AICc) procedure and sequential tests (9999 permutations).

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

This article is protected by copyright. All rights reserved.

Accepted Article

using forward stepwise selection and Akaike information criterion (AICc) procedure to select among environmental predictor variables (percent 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.

Results

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

This article is protected by copyright. All rights reserved.

Accepted Article

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).

Elk significantly increased the richness of ant genera and beetle morpo-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.

Vegetation and Environmental Factors

This article is protected by copyright. All rights reserved.

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 aboveground 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 were 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

This article is protected by copyright. All rights reserved.

Accepted Article

decreased with increasing plant diversity (H') and shrub cover and there was a trend for bristletail abundance to increase with rising levels of herbaceous biomass (Table 3).

Discussion

In our 18-year exclosure 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, aboveground 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 environments,

This article is protected by copyright. All rights reserved.

Accepted Article

by reducing herbaceous biomass and shrub cover, which in turn creates environments that favor mobile ground-dwelling arthropods adapted for open environments and disfavoring 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), suggest 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 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 was much greater in

This article is protected by copyright. All rights reserved.

Accepted Article

than 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, has been implicated in displacing native detritivores (Singer, Bello & Snyder 2012) and is associated with argentine ants (Human & Gordon 1997). Despite finding vast numbers of woodlice, we did not identify

This article is protected by copyright. All rights reserved.

Accepted Article

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 (Wolkovich, Bolger & Holway 2009; Farrell *et al.* 2015). 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.

This article is protected by copyright. All rights reserved.

Accepted Article

Accepted Article

Acknowledgements

We are indebted to the following individuals for assistance in the field as well as sorting specimens in the lab – Vanessa Dodge, Cody Ender, Caprice Lee, Elias Lopez, Megan Gaitan, Andrew Benson, Andrea Leith, Manuel Hernandez, Lizzie Defrancesca, Elizabeth Grewal, Ryan Galloway, Magdalena Reese, Marisol Luna, Rachel Bever, Kayla Charness, Dino Sbardellati, Ashley Pereira, Amanda Young, Ali Olea, Erin Whittingham, David Dippe, Ian Barnes, and Launa Naretto. Thanks to Tim Bernot at Point Reyes National Seashore for his help maintaining the exclosure experiment. Fran Keller provided invaluable support with arthropod identifications throughout the entire project. Special thanks go to Dan Crocker for his guidance with our statistical analyses. The paper has been improved by comments from Caroline Christian and Dan Crocker. This project has been generously supported by grants from the Sonoma County Fish and Wildlife Commission and Sonoma State University.

Data Accessibility

Data are available from the Dryad Digital Repository: DOI: doi:10.5061/dryad.7rn6dd8 (Cecil et al. 2019).

Author Contributions:

E.M.C. designed the study, performed the sampling, analyzed 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.

This article is protected by copyright. All rights reserved.

Accepted Article

Literature Cited

Anderson, M., Gorley, R.N. & Clarke, R.K. (2008) *Permanova+ for Primer: Guide to Software and Statisticl Methods*. Primer-E Limited.

Bardgett, R.D. & Wardle, D.A. (2003) Herbivore-mediated linkages between aboveground and belowground communities. *Ecology,* **84,** 2258-2268.

Beals, E.W. (1984) Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research,* **14,** 1-55.

Beattle, A.J. & Oliver, I. (1994) Taxonomic minimalism. *Trends in Ecology & Evolution,* **9,** 488-490.

Bestelmeyer, B.T. & Wiens, J.A. (2001) Ant biodiversity in semiarid landscape mosaics: the consequences of grazing vs. natural heterogeneity. *Ecological Applications,* **11,** 1123-1140.

Borer, E.T., Seabloom, E.W., Gruner, D.S., Harpole, W.S., Hillebrand, H., Lind, E.M., Adler, P.B., Alberti, J., Anderson, T.M., Bakker, J.D., Biederman, L., Blumenthal, D., Brown, C.S., Brudvig, L.A., Buckley, Y.M., Cadotte, M., Chu, C., Cleland, E.E., Crawley, M.J., Daleo, P., Damschen, E.I., Davies, K.F., DeCrappeo, N.M., Du, G., Firn, J., Hautier, Y., Heckman, R.W., Hector, A., HilleRisLambers, J., Iribarne, O., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Leakey, A.D.B., Li, W., MacDougall, A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Mortensen, B., O'Halloran, L.R., Orrock, J.L., Pascual, J., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M., Smith, M.D., Stevens, C.J., Sullivan, L.L., Williams, R.J., Wragg, P.D., Wright, J.P. & Yang, L.H. (2014) Herbivores and nutrients control grassland plant diversity via light limitation. *Nature,* **508,** 517-520.

This article is protected by copyright. All rights reserved.

Bultman, T.L. & DeWitt, D.J. (2008) Effect of an invasive ground cover plant on the abundance and diversity of a forest floor spider assemblage. *Biological Invasions,* **10,** 749.

Clarke, K.R. (1993) Nonparametric Multivariate Analyses of Changes in Community Structure. *Australian Journal of Ecology*, **18,** 117-143.

Coupe, M.D. & Cahill, J.F. (2003) Effects of insects on primary production in temperate herbaceous communities: a meta‐analysis. *Ecological Entomology*, **28,** 511-521.

Dias, N., Hassall, M. & Waite, T. (2012) The influence of microclimate on foraging and sheltering behaviours of terrestrial isopods: implications for soil carbon dynamics under climate change. *Pedobiologia,* **55,** 137-144.

Ellis, T.D. & Cushman, J.H. (2018) Indirect effects of a large mammalian herbivore on small mammal populations: Context‐dependent variation across habitat types, mammal species, and seasons. *Ecology and Evolution*.

Farrell, K.A., Harpole, W.S., Stein, C., Suding, K.N. & Borer, E.T. (2015) Grassland arthropods are controlled by direct and indirect interactions with cattle but are largely unaffected by plant provenance. *Plos One,* **10,** e0129823.

Foster, C.N., Barton, P.S. & Lindenmayer, D.B. (2014) Effects of large native herbivores on other animals. *Journal of Applied Ecology,* **51,** 929-938.

Hobbs, N.T. (1996) Modification of ecosystems by ungulates. *The Journal of Wildlife Management***,** 695-713.

Hölldobler, B. & Wilson, E.O. (1990) *The ants*. Harvard University Press.

Human, K.G. & Gordon, D.M. (1997) Effects of Argentine ants on invertebrate biodiversity in northern California. *Conservation Biology*, **11,** 1242-1248.

Joern, A. (2005) Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. *Ecology*, **86,** 861-873.

This article is protected by copyright. All rights reserved.

Accepted Article

Johnson, B.E. & Cushman, J. (2007) Influence of a large herbivore reintroduction on plant invasions and community composition in a California grassland. *Conservation Biology*, **21,** 515-526.

Kashiwagi, J.H. (1985) Soil survey of marin county, California.

Keesing, F. & Young, T.P. (2014) Cascading Consequences of the Loss of Large Mammals in an African Savanna. *Bioscience*, **64,** 487-495.

Kruskal, J.B. & Wish, M. (1978) Multidimensional Scaling Sage University Papers Series. Quantitative Applications in the Social.

Martin, J.-L., Stockton, S.A., Allombert, S. & Gaston, A.J. (2010) Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: lessons from a deer introduction. *Biological Invasions*, **12,** 353-371.

Melis, C., Sundby, M., Andersen, R., Moksnes, A., Pedersen, B. & Røskaft, E. (2007) The role of moose Alces alces L. in boreal forest–the effect on ground beetles (Coleoptera, Carabidae) abundance and diversity. *Biodiversity and Conservation*, **16,** 1321-1335.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) Package 'vegan'. *Community ecology package, version*, **2**.

Olff, H. & Ritchie, M.E. (1998) Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution*, **13,** 261-265.

Prather, C.M., Pelini, S.L., Laws, A., Rivest, E., Woltz, M., Bloch, C.P., Del Toro, I., Ho, C.-K., Kominoski, J., Newbold, T.A.S., Parsons, S. & Joern, A. (2013) Invertebrates, ecosystem services and climate change. *Biological Reviews*, **88,** 327-348.

Rambo, J.L. & Faeth, S.H. (1999) Effect of vertebrate grazing on plant and insect community structure. *Conservation Biology*, **13,** 1047-1054.

This article is protected by copyright. All rights reserved.

Accepted Article

Seastedt, T. & Crossley, D. (1984) The influence of arthropods on ecosystems. *Bioscience,* **34,** 157-161.

Singer, C., Bello, N.M. & Snyder, B.A. (2012) Characterizing prevalence and ecological impact of non-native terrestrial isopods (Isopoda, Oniscidea) in tallgrass prairie. *Crustaceana,* **85,** 1499-1511.

Smith, E. (1970) Biology and structure of some California bristletails and silverfish (Apterygota: Microcoryphia, Thysanura). *Pan-Pacific Entomologist,* **46,** 212-225.

Staver, A.C. & Bond, W.J. (2014) Is there a 'browse trap'? Dynamics of herbivore impacts on trees and grasses in an African savanna. *Journal of Ecology,* **102,** 595-602.

Suominen, O. & Danell, K. (2006) Effects of large herbivores on other fauna. *Ecosystem Dynamics and Conservation* (eds K. Danell, R. Bergstrom, P. Duncan & J. Pastor), pp. 383-412. Cambridge University Press, Cambridge.

Team, R.C. (2016) A language and environment for statistical computing. R Foundation for statistical computing, 2015; Vienna, Austria.

Underwood, E.C. & Christian, C.E. (2009) Consequences of prescribed fire and grazing on grassland ant communities. *Environmental Entomology,* **38,** 325-332.

van Klink, R., van der Plas, F., van Noordwijk, C., WallisDeVries, M.F. & Olff, H. (2015) Effects of large herbivores on grassland arthropod diversity. *Biological Reviews,* **90,** 347-366.

Wolkovich, E.M., Bolger, D.T. & Holway, D.A. (2009) Complex responses to invasive grass litter by ground arthropods in a Mediterranean scrub ecosystem. *Oecologia,* **161,** 697-708.

This article is protected by copyright. All rights reserved.

Accepted Article

Accepted Article

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 x G		E x Y		G x Y		E x G x 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

This article is protected by copyright. All rights reserved.

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 (percent shrub cover, herbaceous biomass, thatch height, plant diversity (H') and soil bulk density).

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

This article is protected by copyright. All rights reserved.

Accepted Article

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, (percent 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	+			

This article is protected by copyright. All rights reserved.

Accepted Article

FIGURE LEGENDS

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 (± S.E.) 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 (± S.E.) for plots classified within a group. Symbols closer to each other are more similar than those further apart.

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 (± S.E.) for plots classified within a group. Symbols closer to each other are more similar than those further apart.

Figure 4. Mean (±1SE) abundance of ants (a), beetles (b), spiders (c), mites (d), woodlice (e) and bristletails as a function of elk (present or excluded), grassland (*Bacchariss*-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.

This article is protected by copyright. All rights reserved.

Figure 5. Mean (±1SE) 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).

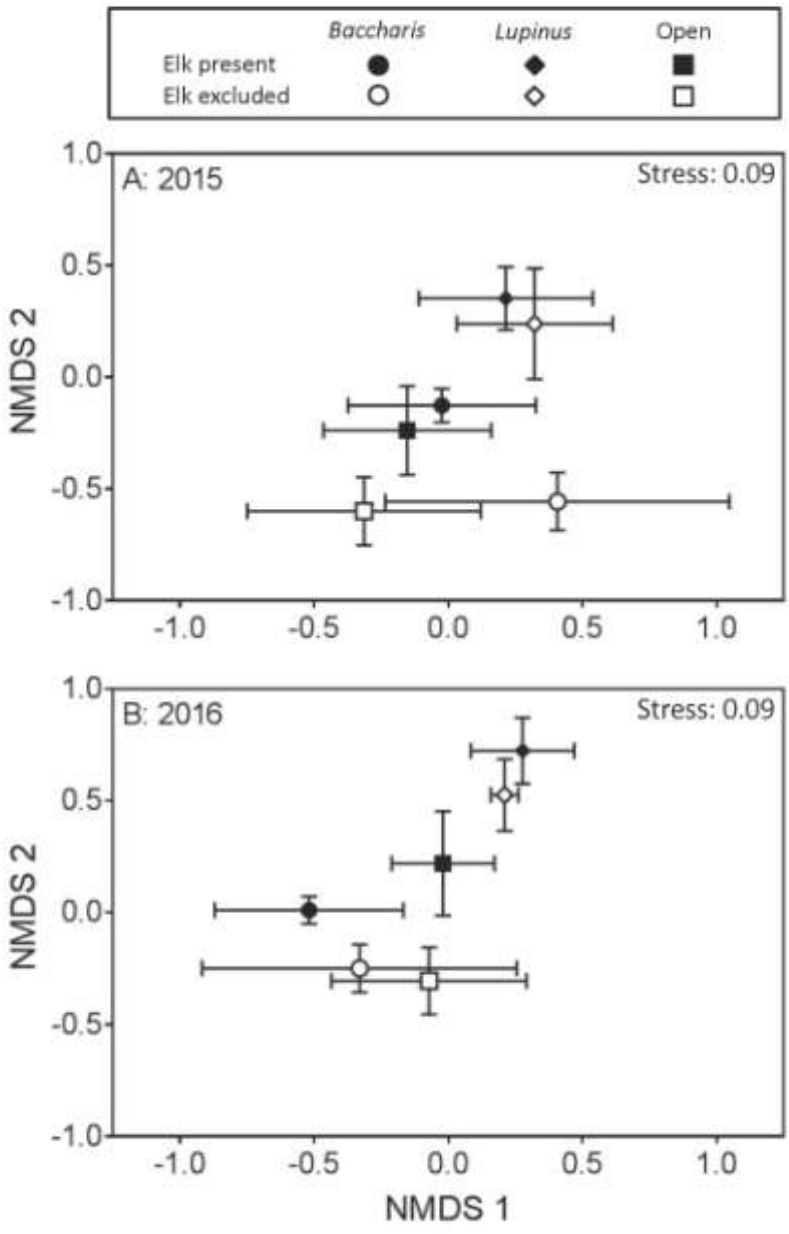
Figure 6. Mean (±1SE) shrub cover, herbaceous biomass and thatch height in 2015 and 2016 as a function of elk (present or excluded) and grassland type (*Baccharis*-dominated, *Lupinus*-dominated, or shrub-free grassland). Letters over the bars correspond to the results from Tukey multiple comparison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

Accepted Article

This article is protected by copyright. All rights reserved.

Accepted Article

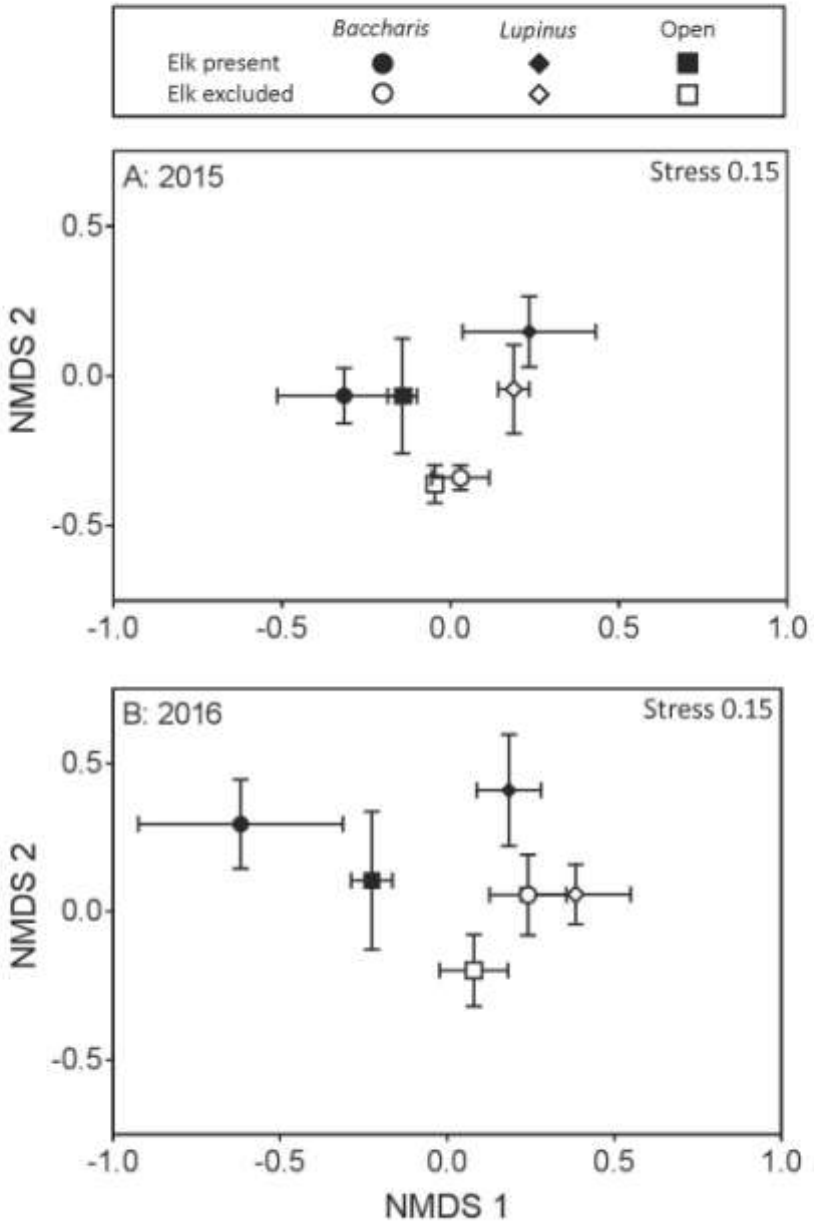
Figure 1



This article is protected by copyright. All rights reserved.

Accepted Article

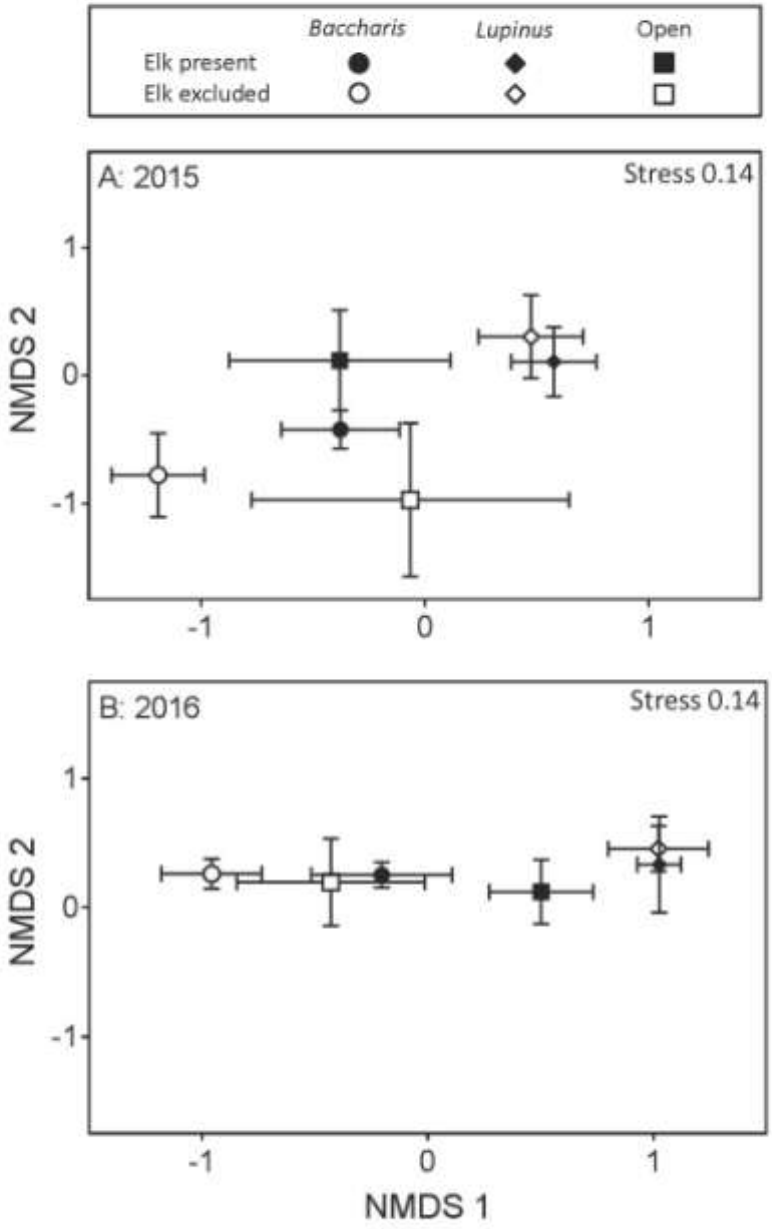
Figure 2



This article is protected by copyright. All rights reserved.

Accepted Article

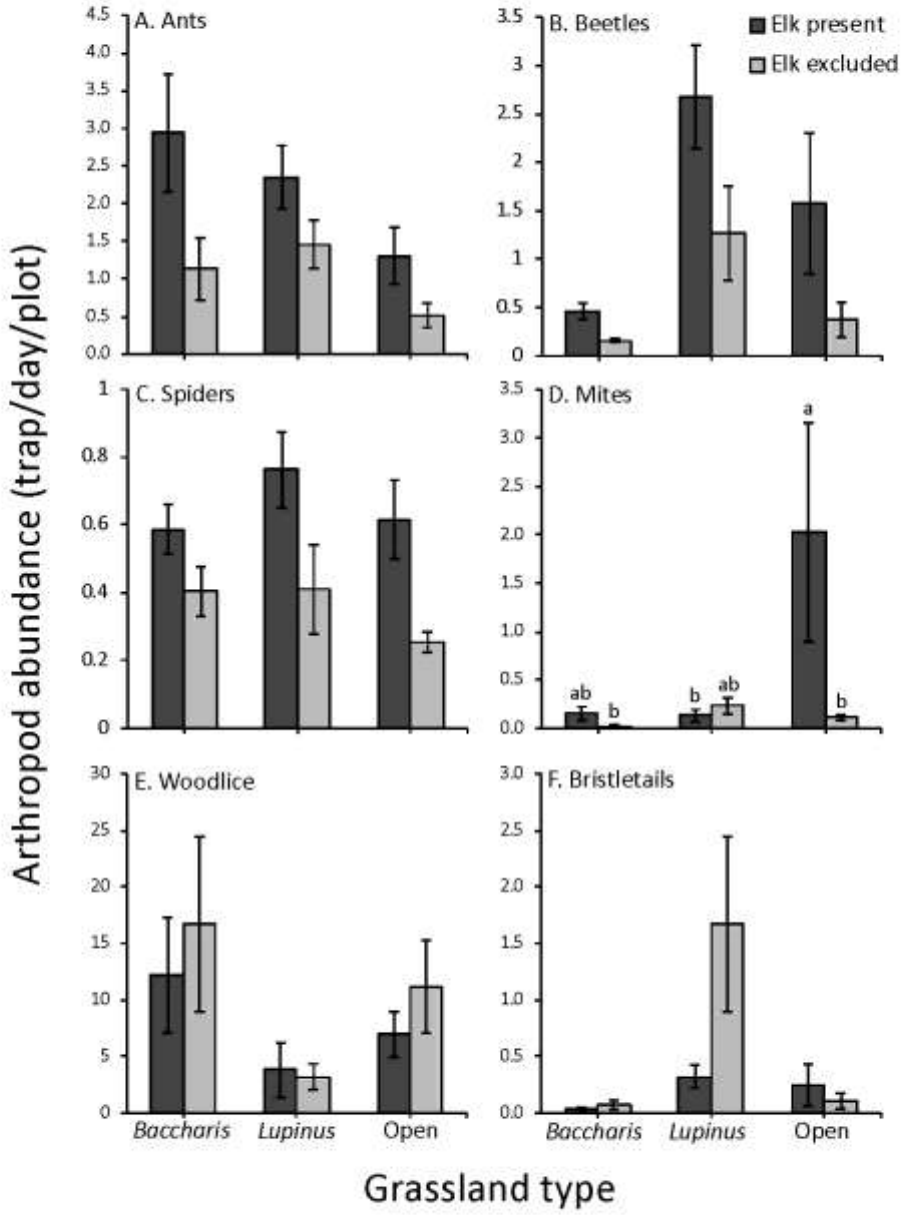
Figure 3



This article is protected by copyright. All rights reserved.

Accepted Article

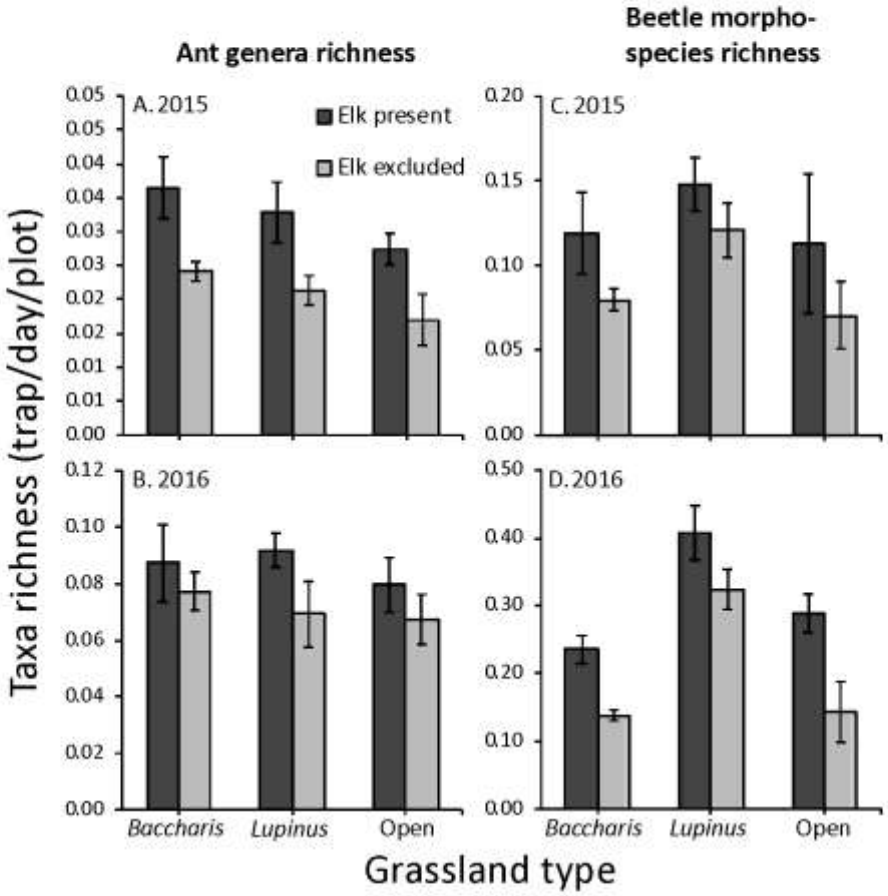
Figure 4



This article is protected by copyright. All rights reserved.

Accepted Article

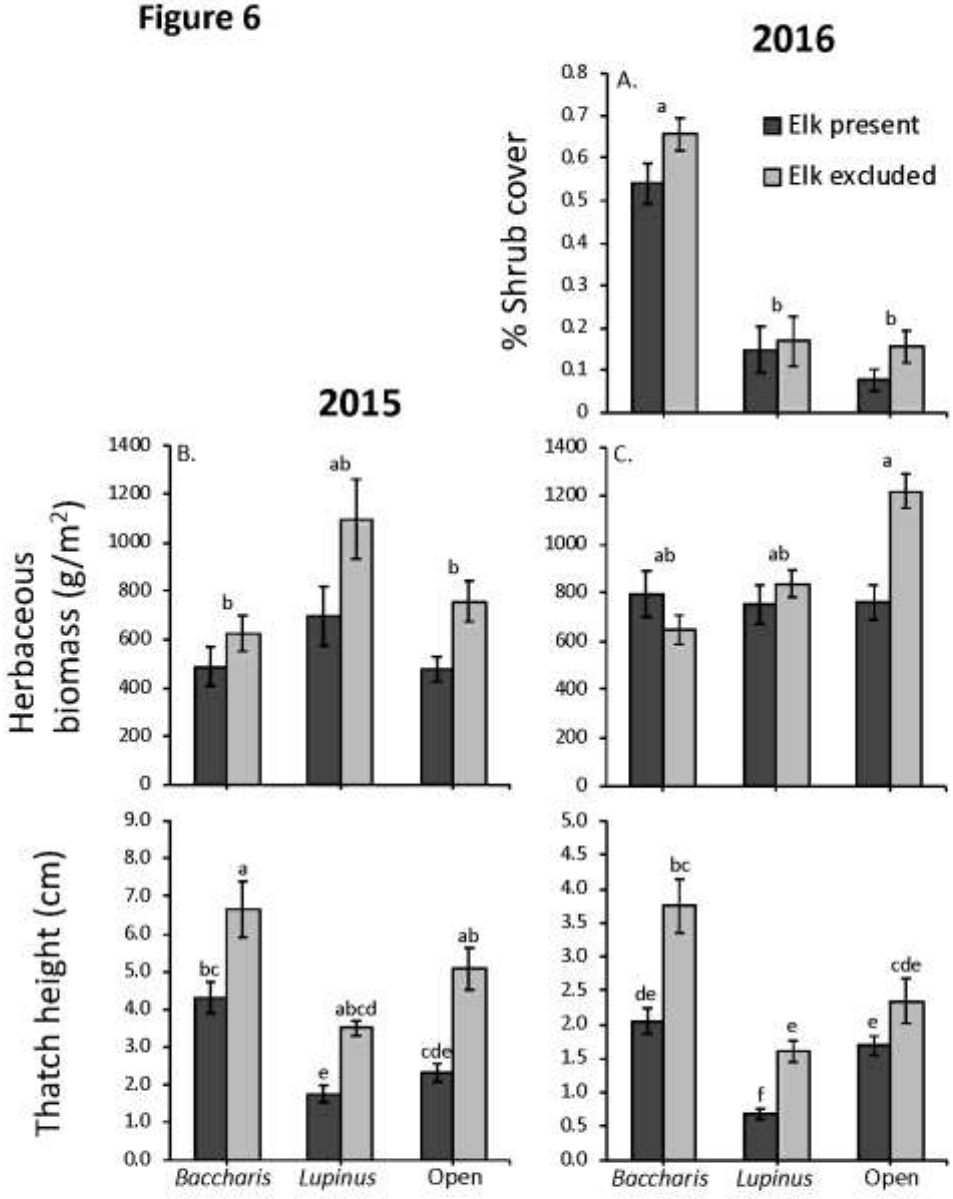
Figure 5



This article is protected by copyright. All rights reserved.

Accepted Article

Figure 6



This article is protected by copyright. All rights reserved.