

AN ABSTRACT OF THE THESIS OF

Kelly Anne Farrell for the degree of Master of Science in Zoology presented on June 28, 2011.

Title: Vertebrates, Arthropods, and Invasive Plants: An Investigation of the Top-Down and Bottom-Up Interactions of Multiple Herbivore Guilds in a Grassland System

Abstract approved:

Elizabeth T. Borer

David R. Maddison

Humans are increasing the scale and frequency of many natural disturbances, as well as adding novel disturbances to ecosystems. This thesis uses the arthropod community as a metric to examine the multi-trophic responses to disturbances in California grasslands. Chapter 2 explores how the long-term exclusion of native vertebrate herbivores has impacted arthropod community and trophic structure at Hastings Natural History Reserve. Chapter 3 investigates the impacts of grazing and invasive plants on the arthropod community in a manipulative plant provenance x grazing experiment that had been in place for two years at the Sierra Foothills Research and Extension Center.

Few long-term studies have explored the interactions between vertebrate herbivore guilds and the arthropod community. We studied the long-term impact on arthropod community structure and composition of removing vertebrate herbivores from a California oak savannah. We used paired plots to sample arthropods and plant communities inside and outside 11 long-term vertebrate exclosures. We found that arthropods respond to vertebrate access mainly via plant compositional shifts, but that different groups of vertebrates cause changes via different pathways. Large herbivores, including deer, caused a shift from native perennial to exotic annual plants which increased plant nutritional content and supported more herbivore and detritivore

arthropods. Burrowing vertebrates such as gophers reduced the predatory arthropod community by reducing vegetation structure, releasing other arthropod groups and resulting in an overall increase in arthropod abundance. These results highlight that alterations to different parts of the vertebrate community can have qualitatively different effects on arthropod community structure.

The invasion and spread of non-native plants and the prevalence of livestock grazing are two human-induced disturbances that can have widespread ecosystem impacts. We used a manipulative study to examine how the replacement of native perennial grasses by exotic annual grasses and the introduction of heavy cattle grazing impact arthropod community structure. Arthropod richness, diversity, and abundance did not vary predictably between native perennial and exotic annual grass communities, though arthropods responded to plant community characteristics. In the presence of grazing, arthropod biovolume increased in annual grass treatments, which could trigger a positive-feedback cycle with vector-transmitted plant pathogens to further increase the prevalence of non-native annual grasses. Arthropod community was strongly impacted by cattle grazing, which decreased the biovolume of predatory arthropods, causing a top-down increase in herbivorous arthropod biovolume. Grazing thus impacts plant composition both through the direct removal of biomass and increased plant species evenness, and through arthropod-mediated impacts.

Together, these studies show that human alterations of different vertebrate guilds can impact the trophic structure of the arthropod community. Because arthropods mediate a number of ecosystem services, disturbances that alter arthropod assemblages can have far-reaching ecosystem impacts. By exploring the mechanisms by which manipulations of the vertebrate guild alter arthropod community, this thesis demonstrates the importance of horizontal and vertical diversity in multi-trophic interactions.

© Copyright by Kelly Anne Farrell
June 28, 2011
All Rights Reserved

Vertebrates, Arthropods, and Invasive Plants: An Investigation of the Top-Down and
Bottom-Up Interactions of Multiple Herbivore Guilds in a Grassland System

by
Kelly Anne Farrell

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented June 28, 2011
Commencement June 2012

Master of Science thesis of Kelly Anne Farrell presented on June 28, 2011.

APPROVED:

Co-Major Professor, representing Zoology

Co-Major Professor, representing Zoology

Chair of the Department of Zoology

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Kelly Anne Farrell, Author

ACKNOWLEDGEMENTS

There are many people to thank for their contributions to my progress through this study, whether their help came in the form of academic support, logistical support, or camaraderie. First, I would like to thank those who guided my academic growth. My adviser Dr. Elizabeth Borer saw my potential when I visited OSU to interview with a different professor in a different department, and worked with me from the beginning to develop a project that both satisfied my interests and opened my mind to larger ecological theory and implications. She has been patient with my academic growth, my personal indecisions, and the successes and failures of my project iterations, and her guidance has been invaluable. Dr. David Maddison, my co-adviser, has been an enormous source of support since he took over as my “in house” adviser with Dr. Borer’s departure. Even though my research topics are outside the realm of his own, he has been instrumental in teaching me about arthropod handling, writing, and data management. I am grateful to Dr. Tom Kaye for serving on my committee to keep my ideas grounded towards broader management applications, and I thank Dr. Barbara Bond for acting as my graduate representative.

Dr. Bruce McCune helped me enormously in understanding how to appropriately apply multivariate statistics to my work, and Dr. Eric Seabloom, as well as fellow zoology graduate students, have helped me tune my knowledge and use of univariate statistics. I thank my peers in the B-S lab (Angela Brandt, Phoebe Zarnetske, Wendy Phillips, Sean Moore, Lydia O’Halloran) and the Maddison lab (Kojun Kanda) for sharing advice, expertise, and friendship.

Much of my field and laboratory work depended on the help and generosity of others. I am grateful to Dr. Katherine Suding and Dr. Stanley Harpole for being so open to sharing their experimental plots for me to sample arthropods in, along with Claudia Stein who oriented me to the fields. Shawn Gerrity, with his expertise in everything, made my sample collection a reality. It would have been impossible for me to

complete my arthropod sorting without the help of numerous student workers and volunteers who overcame the tedium of sorting miniscule specimens out of grass seeds: Sierah Edwards, Caitlyn O'Mealy, Tiffany Mitchell, Ron Lyons, Chelsea Wolf, Rachel Steele, Kimberly Barrella, Jacky Schultz, Rogelio Ayala, and Jonathan Truong. I was especially grateful for the good attitude and spunk of Jacky Schultz and my other volunteers who kept the lab lively. Financially, the National Science Foundation (DEB 0235624, EF 0525666, DEB 0444217 to Dr. Borer and Dr. Seabloom), the Integrated Hardwood Range Management Program, and USDA Managed Ecosystems Grant #2006-01350 to Dr. Suding and Dr. Harpole funded the experimental setup, data collection, and arthropod sorting.

The logistical support of both the Botany & Plant Pathology and Zoology departments has been invaluable during my time here. I am indebted to Dr. John Fowler and the BPP department for helping me acquire the Diversity Pipeline Fellowship which funded my first year at Oregon State University and for making so easy the transition to the Zoology department. The Zoology department has provided important financial and logistical support, and T., T., and T. have always been helpful, cheerful, lifesavers in the office. I truly appreciate the opportunity I have been given to be a teaching assistant while at Oregon State, and to be able to exercise my pedagogical and organizational creativity by revising labs with Amy Harwell, who has shown endless support for my teaching endeavors.

The OSU Cycling Club has given me a needed outlet to find camaraderie while exploring the beautiful Pacific Northwest and the 2011 road racing team especially has given me undying support to do things I never thought possible. The contradancers here in Corvallis have welcomed me with open arms into the community outside the university, giving me a surrogate family while mine is so far away. My parents, John and Maggie Farrell, have been positive and motivating throughout my journey here and I thank them for their continual support. My housemates and friends have kept

me motivated and sane – thank you Erin, Mariya, Mark, Robyn, Casey, and all my zoology and botany companions.

CONTRIBUTION OF AUTHORS

Dr. Elizabeth T. Borer is a coauthor on Chapters 2 and 3. She collected and identified the arthropod specimens used in Chapter 2, and provided plant data collected concurrently from that system to pair with the arthropod data in analysis. She provided extensive suggestions and feedback on both chapters during the writing process.

TABLE OF CONTENTS

	<u>Page</u>
Chapter 1: Introduction	2
Chapter 2: Vertebrate herbivores control grassland arthropod community via plant compositional and structural shifts.....	6
2.0 Abstract.....	6
2.1 Introduction	7
2.2 Methods	9
2.3 Results	14
2.4 Discussion	16
2.5 Works Cited.....	19
Chapter 3: Grassland arthropods are controlled by indirect interactions with vertebrate grazers and by nutritional quality of invasive plants	30
3.0 Abstract.....	30
3.1 Introduction	31
3.2 Methods	33
3.3 Results	38
3.4 Discussion	40
3.5 Works Cited.....	44
Chapter 4: General conclusions	62
Bibliography.....	65
Appendices	74
Appendix A	75
Appendix B.....	79

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
Figure 2.1. Ordination of plots in arthropod space based on the similarities in arthropod familial representations in each plot.....	29
Figure 3.1. Examples of arthropod specimens from each trophic group	57
Figure 3.2. Plot experimental treatments	58
Figure 3.3. Response of total plot arthropod biovolume to grass provenance and grazing treatments.	59
Figure 3.4. NMS ordination of plots in species space.....	60
Figure 3.5. Number of squared changed steps as a result of reshuffling morphospecies correlations with grazing 10,000 times.	61

LIST OF TABLES

<u>Table</u>	<u>Page</u>
Table 2.1 Number of arthropod families classified to each trophic group.....	24
Table 2.2. Correlations of arthropod trophic groups and environmental components with NMS axes.....	25
Table 2.3. Correlations of arthropod community and arthropod guilds to measures of vertebrate access and plant community characteristics.....	26
Table 2.4: The response of arthropod community abundance and richness to each set of vertebrates after accounting for plant richness and cover using mixed effects models.	27
Table 2.5. Results of perMANOVAs evaluating differences in proportional arthropod family abundances across vertebrate-exclusion fences.....	28
Table 3.1. Responses of the plant community to experimental treatments.....	54
Table 3.2. Results of linear model testing for significant impact of environmental parameters on arthropod diversity measures and biovolume of arthropod trophic guilds.....	55
Table 3.3. Results of perMANOVAs evaluating differences in proportional morphospecies abundances between experimental treatments.	56

LIST OF APPENDIX TABLES

<u>Table</u>	<u>Page</u>
Table A.1: Table of arthropod taxa in Hastings native vertebrate exclosure experiment	76
Table B.1: Table of arthropod morphospecies from Sierra Foothills grass provenance x grazing experiment, with grazing correlations.....	79

Vertebrates, Arthropods, and Plants: An Investigation of the Top-Down Effects and
Bottom-Up Responses of Multiple Herbivore Guilds in a Grassland System

Chapter 1: Introduction

Natural disturbances such as fire, landslides, and windfalls can displace dominant plant species and are essential for maintaining Earth's high level of biodiversity (Connell 1978). They can facilitate the maintenance of disturbance-adapted species, such as long-leaf pine in a fire-dominated ecosystem or perennial forbs in a prairie habitat, which would otherwise be out-competed by other species. Natural disturbances differ in the spatial scale at which they affect an ecosystem and the temporal scale at which they occur, but intermediate disturbance frequency is hypothesized to promote the highest species diversity (Connell 1978).

Humans are increasing the scale and frequency of many natural disturbances, as well as adding novel disturbances to ecosystems. Direct disturbances, including land use conversion, are widespread; approximately 12% of the Earth's ice-free surface has been converted to agriculture and 22% to pasture alone (Ramankutty et al. 2008). Fire suppression in recent decades has allowed woody species to encroach into prairies, displacing native flora and fauna, and has allowed thick underbrush to grow in forest systems, increasing the severity of forest fires when they do occur. Indirect disturbances are also prevalent; for instance, nutrient runoff from agriculture can increase the frequency of algal blooms.

Manipulation of mammalian densities through hunting, livestock, and habitat modification has caused multi-trophic disturbance in many systems. Mammalian herbivores can alter plant species richness and composition directly through their feeding preferences, but also indirectly by altering nutrient cycling (Bakker et al. 2004) or through soil disturbance (e.g., Davidson and Lightfoot 2008). Introducing domestic livestock drastically increases herbivore densities while adding a novel megaherbivore to a system. Grazing alters plant richness and evenness (Bakker et al. 2006, Schultz et al. 2011, Milchunas and Lauenroth 1993) and also contributes to soil

disturbance and compaction. Similarly, the extirpation of predators for the perceived threat they pose to livestock allows native mammalian herbivores to increase in abundance, leading to decreased plant recruitment (Ripple and Beschta 2004) and increased stream bank erosion (Beschta and Ripple 2009).

The introduction of non-native species represents another of the greatest modifications humans have made to natural systems. Cumulatively, the annual cost associated with invasive species in the United States alone is over \$136,000 million (Pimentel et al. 2000), though economic costs do not describe the total ecological damage caused by exotic species (Parker et al. 1999). A plant's abundance in its native habitat is a good predictor of its abundance in non-native habitat (Firn et al. 2011), but as globalization increases the introductions of new exotic species (Hulme 2009, Levine and D'Antonio 2003), and as introduced species expand their ranges (Seabloom et al. 2006), the prevalence of invasive plants in a habitat will increase. Because exotic plants alter ecosystem processes including hydrological and geomorphological cycles, nutrient cycling, disturbance regimes, stand structure, and the recruitment of native plant species (Gordon 1998), their potential impact to the native plant community and ecosystem services can be unproportionally high given their abundances.

Changes in the plant community alter the performance of ecosystem services such as nutrient cycling, pollination, carbon sequestration, runoff and erosion control, and native biodiversity, and can also cause both bottom-up and top-down changes in animal populations. Herbivorous arthropods increase in richness with plant richness, mainly as an effect of the increasing resource diversity of a diverse plant assemblage, and drive a corresponding increase in predator abundance (Haddad et al. 2009). Concurrently, changes in plant structural composition alter predatory arthropod richness and abundance (Dennis et al. 2001), which could affect herbivorous arthropod diversity.

Understanding the ways in which disturbances affect multiple levels within ecosystems can help us manage those ecosystems for recovery. A severely degraded system may be in an alternate state that requires multiple restorative measures to overcome constraints of degraded abiotic and biotic factors (Suding et al. 2004). Altering the factors that have the strongest constraints against restoration can help transition that ecosystem back to its desired state. For example, the reintroduction of wolves in parts of their former range has restored an important top-down control on ungulate herbivores, with plant populations recovering after decades of over-browsing (Beschta and Ripple 2009). Understanding that top-down controls often travel through more trophic levels than bottom-up processes (Borer et al. 2006), and determining the ecological factors that regulate top-down controls, can lead us in the right direction.

In my thesis, I use the arthropod community as a metric to examine the multi-trophic responses to disturbances in California grasslands. Arthropods represent a full suite of trophic guilds, have relatively short life spans that let them reflect current ecological conditions, vary at small spatial scales, and are a species-rich group, with different species responding to different types of biotic and abiotic conditions. Furthermore, arthropods are important mediators of ecosystem services, including pollination, decomposition, and nutrient cycling, and are prey at the base of many vertebrate food webs. They vector both plant and animal disease, are important consumers of biomass (Coupe and Cahill Jr 2003), and can alter vegetation structure through their trophic interactions (Schmitz 2009).

In Chapter 2, I explore how the long-term exclusion of native vertebrate herbivores has impacted arthropod community and trophic structure at Hastings Natural History Reserve in California. In it, I use arthropod data collected by Dr. Elizabeth Borer in

2006 to test how vertebrate access, vertebrate-induced changes in the plant community, and landscape-scale plant community patterns affect arthropods.

In Chapter 3 I investigate the impacts of grazing and invasive plants on the arthropod community. I describe arthropod samples I collected in the spring of 2009 from a manipulative grazing x plant community factorial experiment initiated by Dr. Katherine Suding and Dr. W. Stanley Harpole in the Sierra Foothills grasslands of California. I consider both the experimental effects and plant community effects on the structure of the arthropod community.

Finally, in Chapter 4 I present general conclusions about the relative importance of plant community, disturbances, and trophic interactions in shaping the arthropod community. Chapters 2 and 3 are both in preparation for submission for publication as multi-author papers, with my adviser Dr. Elizabeth Borer as co-author on both, and Dr. Katherine Suding, Dr. W. Stanley Harpole, and Claudia Stein as co-authors on the Sierra Foothills experiment. In both cases, Dr. Borer provided guidance on analysis and comments on the text. In addition, Dr. Borer was responsible for sample collection in the Hastings Reserve. Dr. Suding and Dr. Harpole initiated the experimental design and setup of the Sierra Foothills experiment and with Claudia Stein were responsible for the collection of plant data from that experiment.

Chapter 2: Vertebrate herbivores control grassland arthropod community via plant compositional and structural shifts

Kelly Anne Farrell and Elizabeth T. Borer

2.0 ABSTRACT

Indirect interactions between vertebrate and invertebrate herbivores may have important ecosystem-level ramifications via plant compositional shifts. By altering plant community richness and biomass, herbivores can affect ecosystem services such as pollination and nutrient cycling. In spite of this, few long-term studies have explored the interactions between vertebrate herbivore guilds and the arthropod community. Here we studied the long-term impact on arthropod community structure and composition of removing vertebrate herbivores from a California oak savannah. We used paired plots to sample arthropods and plant communities inside and outside 11 vertebrate exclosures that had been in place for 14-41 years. We found that arthropods respond to vertebrate access mainly via plant compositional shifts, but that different groups of vertebrates cause changes via different pathways. Large herbivores, including deer, caused a shift from native perennial to exotic annual plants which increased plant nutritional content and supported more herbivore and detritivore arthropods. Burrowing vertebrates such as gophers reduced the predatory arthropod community by simplifying vegetation structure, releasing other arthropod groups and resulting in an overall increase in arthropod abundance. These results highlight that alterations to different parts of the vertebrate community can have qualitatively different effects on arthropod community structure, potentially changing the performance of ecosystem services.

2.1 INTRODUCTION

Much effort has been expended on examining the total and relative effects of vertebrate and invertebrate herbivores on terrestrial plant communities (e.g., Crawley 1989, Bigger and Marvier 1998), but the competitive relationship between these consumer groups has received substantially less attention (but see e.g., Huntzinger et al. 2008, Gómez and González-Megías 2002). Indirect effects between vertebrate and arthropod herbivores have been documented for a variety of mammalian herbivores: for example, with livestock (Dennis et al. 2008, Lindsay and Cunningham 2009, Dennis et al. 2001); native ungulates (Rambo and Faeth 1999, Gómez and González-Megías 2002); elephants (Pringle et al. 2007, Jonsson et al. 2010); and burrowing mammals (Bangert and Slobodchikoff 2006, Davidson and Lightfoot 2007, Davidson et al. 2010, Huntzinger et al. 2008). Few of these studies have examined the mechanisms by which arthropods respond to vertebrate access, and fewer have tested the differing impacts of multiple drastically different vertebrate guilds on arthropod community structure.

As the diversity of the herbivore guild increases, potential interactions among its members are more varied. Indirect interactions between large and small vertebrate herbivores can range from competition to facilitation, mediated through their impacts on the plant community (Davidson et al. 2010, Bakker et al. 2009, Arsenault and Owen-Smith 2002). Similar plant-mediated compensatory effects exist between closely and distantly related species of insect herbivores, and also between vertebrate and insect herbivores (Ohgushi 2005).

The ways in which each group of vertebrate herbivores impacts plant richness, biomass, nutritional content, and cover could have qualitatively different impacts on the arthropod community. Ungulates and other large grazing herbivores generally reduce plant biomass and cover while increasing the nutrient concentration of regenerating plants (Arsenault and Owen-Smith 2002). These changes reflect

modification in the amount of primary productivity and nutritional quality available to consumers, which limits the number or types of invertebrates that can be supported (Wimp et al. 2010). Through preferential grazing, both native and exotic ungulates can change plant species richness and composition (Seabloom et al. 2009, Parker 2006), which alters the number of niches and resource types available to invertebrates and is closely linked to arthropod assemblage (Haddad et al. 2001, Haddad et al. 2009, Siemann et al. 1998, Knops et al. 1999, Siemann 1998, Murdoch et al. 1972, Novotny et al. 2006, Schaffers et al. 2008). Mound-constructing vertebrates increase plant richness at the landscape scale but decrease plant cover and height on their mound structures (Davidson & Lightfoot 2006) and introduce soil disturbance to the landscape. These plant characteristics reflect the amount of habitat structural heterogeneity available for arthropods, which alters arthropod community structure and trophic group composition (Murdoch et al. 1972, Dennis et al. 2001, Gardner et al. 1995).

Humans are altering the types and numbers of vertebrate herbivores in many habitats across the globe through release from predators, livestock grazing, hunting, invasive species introduction, and habitat modification. Co-occurring groups of unrelated vertebrate herbivores have synergistic effects on both the plant and arthropod community (Davidson et al. 2010) that can change the performance of ecosystem services mediated by arthropods. To understand how human activities alter biodiversity and ecosystem functioning, we must examine diversity both within and between trophic levels.

Here we examine the interplay between multiple groups of vertebrate herbivores, the plant community, and the arthropod community in a California grassland system. We use a set of long-term exclosures that prevented access by combinations of large, burrowing, and climbing vertebrate herbivores to ask whether the arthropod community varies in response to herbivore-induced vegetation changes. Because

multitrophic interactions may be quantitatively or qualitatively different than expected from the single-trophic interactions they are composed of (Duffy et al. 2007), we examine the response of each arthropod trophic guild as well as the response of arthropod community structure as a whole.

2.2 METHODS

Study Site

Our study was conducted in May and June 2006 at Hastings Natural History Reserve, a 2,500-acre University of California Natural Reserve located near Carmel Valley in Monterey County, California, USA (36°23'17" N, 121°32'60" W). It is dominated by grasslands and oak savannah, with annual mean precipitation of 530 mm/year and elevation ranging from 467-953 m. Agricultural grazing has been absent from the reserve since its inception in 1937, and the vertebrate population is dominated by a relatively intact suite of native herbivores and carnivores.

Vertebrate Exclosures

Our research utilized 11 long-term fenced experimental exclosures, ranging in age from 14-41 years (mean age 29 years), to quantify the effects of vertebrate herbivory on the aboveground invertebrate community. These exclosures had been constructed by multiple researchers examining different aspects of vertebrate presence and ranged both in size (from 16m² to 5000m²) and in the types of vertebrates they excluded.

Large vertebrate exclosures (N = 6) used barbed wire and wire mesh to prevent access by large consumers including mule deer (*Odocoileus hemionus*).

Burrowing vertebrate exclosures (N = 3) used fine mesh extending above and below ground to prohibit access by small animals including rabbits (*Sylvilagus audubonii*), gophers (*Thomomys bottae*), and voles (*Microtus californicus*).

These exclosures also prohibited large vertebrate access as described above.

Climbing (rodent) and Burrowing vertebrate exclosures (N = 3) used the large and fine mesh described above coupled with metal flashing to prohibit access by all non-flying vertebrates.

Unfenced plots (N = 11) provided access to all vertebrates and were paired with each fenced plot.

One of the large vertebrate exclosures contained a smaller burrowing vertebrate exclosure within it. The two portions of the plot were used separately for analyses comparing different vertebrate treatments (large vertebrate exclosure versus burrowing vertebrate exclosure), though they were never included as separate replicates in the same analysis. One unfenced plot was paired to this two-part exclosure.

Arthropod collection and identification

Arthropods were collected via pitfall traps paired inside and outside of exclosures. They were opened for two periods of 3 days: May 1-3, 2006, and June 10-13, 2006. All arthropods were identified to family, with several exceptions: some groups of the class Arachnida were identified to subclass (Acarina) or order (Opiliones and Araneae, which was divided into three size classes). Because arthropod abundances vary temporally, each plot's two collection date samples were combined to give a single, more representative sample.

Trophic categories were assigned to each arthropod group to examine how different guilds respond to vertebrate access using taxonomic guides and family accounts (Appendix Table A.1). Family-level feeding modes were assigned only for families with clear trophic identities and a single, main, family-level food source. All families containing geographically-relevant members with different food sources were excluded from these groupings (Appendix Table A.1). Only trophic groups that contained more than two arthropod groups were retained in trophic analyses (Table 2.1).

Plant community characteristics

A concurrent study measured plant community characteristics inside and outside the vertebrate enclosure plots during peak vegetation biomass in May and June 2005 (Seabloom et al. 2009). Percent cover was estimated separately for each plant species in 20 x 50 cm quadrats, with the number of quadrats scaled to the enclosure size such that there was one quadrat for every 1 meter of linear dimension. The amount of woody cover was estimated as the proportion of quadrats that had canopy cover greater than 0. Plant community summary variables (percent cover of native and exotic species, richness of native and exotic species, percent woody cover, biomass) were used to model arthropod measures, since plant and arthropod community characteristics are highly correlated.

Statistical analysis

All arthropods collected were used in univariate analyses, while multivariate analyses excluded unidentifiable specimens that could influence family-compositional analyses. Univariate tests were conducted in R (version 2.8.1, The R Foundation for Statistical Computing), using the MASS (Venables and Ripley 2002), lattice (Sarkar 2008), and vegan (Oksanen et al. 2010) packages. We examined the response of each trophic group to vertebrate access and plant community with mixed-effects regression models, using experimental block (paired fenced and unfenced plots) as a random effect. Vertebrate access, plant biomass, total plant cover, and native and exotic plant richness were fixed effects. Plant variables were included both to test whether trophic groups responded predictably to plant community measures and to examine vertebrate impacts on arthropod abundance, richness, evenness, and diversity after accounting for arthropod associations with plants.

We examined whether the arthropod community responded to plant characteristics using generalized linear models (glm) to test arthropod abundance and richness and a

linear model for arthropod evenness. We did not use mixed effects modeling for this component of the analyses, because we wanted to test for arthropod responses at the landscape scale, examining their overall responses to plant community changes regardless of how it varied across the reserve; however, results were qualitatively similar when we analyzed these relationships with mixed-effects models. All models initially included the same parameters as for the trophic groupings, and backwards selection with AIC was used to find the best-fitting model.

Arthropod responses to different groupings of vertebrates were examined separately using mixed effects models with experimental block as a random effect. To maintain degrees of freedom given the low number of replicates of some fence types, models used only vertebrate access, plant richness, and plant cover as fixed effects.

Multivariate analyses were conducted in PC-ORD (McCune and Medford 2010, version 6.243 beta). Beginning with a matrix of 22 plots and 82 arthropod taxa, data were first transformed by excluding arthropod taxa that occurred in fewer than 2 plots, resulting in a matrix of 22 plots and 46 taxa. The removal of rare species decreases noise in the data while increasing the detection of patterns in community relationships (McCune and Grace 2002). The data were then relativized by maximum for each arthropod taxon, scaling the abundance of each taxon between 1 (its highest presence in any plot) and 0 (not occurring in a plot). This transformation is appropriate for data sets in which the abundance of one group may be drastically different than the abundance of another group; it prevents super-abundant taxa from masking patterns of less abundant taxa (McCune and Grace 2002, McCune personal communication). In this data set, for example, it prevents the collembolan families, which numbered in the hundreds or thousands of individuals per plot, from masking the signals of coleopteran and hemipteran families, which occurred in very small numbers per plot.

Permutational-based multivariate analyses of variance (PerMANOVAs) were carried out to compare arthropod family composition between plots with and without vertebrate access using Sørensen distance measure after the methods of Anderson (2001). Sørensen distance considers the similarity of the proportional representations of taxa between samples, regardless of the absolute numbers of individuals, and for this reason can detect qualitative changes in species assemblages regardless of quantitative changes. Paired fenced and unfenced plots were blocked for analysis. As well as testing for the influence of all vertebrates on arthropod family composition (11 pairs), two additional perMANOVAS tested the effects of select vertebrate groups: one used only plots that excluded burrowing animals and their paired unfenced plots (6 pairs); the other used only plots that excluded large animals without excluding burrowers and their paired unfenced plots (6 pairs). There were not enough plots that excluded climbing animals to separately test for their effects on arthropod community composition.

The plant and vertebrate plot-level characteristics influencing arthropod family composition were examined with a nonmetric multi-dimensional scaling (NMS) ordination with Sørensen distance measure. The ordination plotted each plot's location in 46-dimensional arthropod-space, with each axis representing the proportional abundance of a single arthropod taxon within a plot. Using a random starting configuration, 50 runs with real data, and 50 runs with randomized data, dimensions were collapsed into the smallest number of axes that adequately explained the data. Solution dimensionality was selected following the recommendation of PC-ORD combined with examination of a scree plot. Outlier analysis did not reveal any plot to have an average distance from other plots more than 2 standard deviations greater than the total mean of distances between plots. Environmental characteristics of each plot were overlaid onto the final ordination to find the correlations between environmental variables and ordination axes. To correlate the prevalence of trophic

guilds with the ordination of plots in family space, we overlaid a matrix (AS') of the proportional representation of trophic guilds in each plot onto the ordination.

2.3 RESULTS

A total 20,026 individual arthropods were collected, representing 85 arthropod families or groups. Of these, 48 groups occurred in more than one plot, and 6 groups were found in at least 20 of the 22 plots (see Appendix Table B.1).

Arthropod responses to plant community

At the landscape level, arthropods showed some correlations with the plant community. The amount of plant cover in a plot was slightly but significantly positively correlated with arthropod abundance; specifically, the number of detritivores increased with plant cover (Table 2.3). Native plant richness and exotic plant richness had different relationships with the arthropod community. Surprisingly, native plant richness was negatively correlated with arthropod abundance, even though it was positively correlated with detritivore abundance and not strongly correlated with the abundances of other trophic groups. Both predators and detritivores were negatively correlated with exotic plant richness, which was also negatively correlated with arthropod evenness, though not significantly. The amount of available primary productivity in the system, measured as plant biomass, was suggestively negatively correlated with arthropod evenness, and was negatively associated with detritivore abundance. Arthropod richness was not associated with plant richness, and no model was found that adequately described arthropod richness.

Arthropod response to vertebrate community

Vertebrate access as a whole was positively associated with a 66% increase in herbivore abundance and a 40% increase in detritivore abundance (Table 2.4) but did not change the proportional abundances of arthropod families (perMANOVA $F =$

1.1906, $p > 0.1$) (Table 2.5). Rodent access decreased arthropod abundance (mixed effects model $p = 0.0443$) but had no association with the community structure of any arthropod guilds (Table 2.2). Burrower access increased arthropod abundance (mixed effects model $p = 0.0012$) (Table 2.3) and predators, and specifically Araneae, were negatively correlated with burrower access (Table 2.2). A separate glm modeled Araneae abundance to be negatively correlated with burrower access ($F = -0.7486$ on quasipoisson distribution, $p = 0.0422$) but not with the percent cover of gopher mounds ($F = 0.0307$, $p = 0.3276$).

In a NMS ordination, arthropod community composition was strongly correlated with both plant community and vertebrate access characteristics (Table 2.2, Figure 2.1). Starting with a matrix of 22 plots and 48 families, a 3-dimensional solution was selected with a final stress of 16.44 and final instability < 0.0001 . This solution accounted for 62.3% of the variation in arthropod community (Monte Carlo $p = 0.004$), with 19.6% of the variation represented by Axis 1, 19.1% by Axis 2, and 23.6% by Axis 3.

When plots excluding large vertebrates but not burrowers were examined, or when all plots were examined together, there was no evidence that the arthropod community was consistently impacted by vertebrate access (perMANOVA $p > .1$ for all). But when only plots that excluded burrowers were examined, there was suggestive evidence that burrower access impacted arthropod community as a whole (perMANOVA $p = 0.098$, Table 2.4). Burrowers altered arthropod community structure in a qualitatively different way than large herbivores, reflected in the NMS ordination by the associations of large vertebrates with axis 3 and burrowers with axis 1 (Figure 2.1).

Arthropod responses across the landscape

There was a high amount of variation in arthropod community composition between experimental blocks (perMANOVA $F = 1.3919$, $df = 10$, $p < .0001$), suggesting that arthropod families vary at large spatial scales across the landscape regardless of vertebrate access.

2.4 DISCUSSION

The top-down effect of vertebrates on plant composition is reflected in the arthropod community. In these experimental plots, vertebrate access was associated with a decrease in native plant cover (Seabloom et al. 2009), and the impacts of vertebrates and of exotic plants caused opposing changes in arthropod familial composition. Specifically, arthropod herbivores and detritivores responded positively to the shift from native to exotic plant cover in the presence of vertebrate herbivores. Many of the exotic plants in California's grasslands are annual grasses (Seabloom et al. 2006) which have a lower C:N ratios than native perennial grasses and are nutritious for herbivorous arthropods, resulting in greater abundances of herbivores (Borer et al. 2009). Increased insect herbivory accelerates nutrient cycling rates (Belovsky and Slade 2000) and can alter detritus nutrition (Belovsky and Slade 2002), which could act as the mechanism increasing detritivore abundance. The vertebrate-induced shift in plant community is thus changing arthropod composition via changes in the bottom-up nutrition of food sources.

Gophers and other burrowing vertebrates had a qualitatively different effect on the arthropod community than deer and other large vertebrates, which altered arthropod community via changes in the plant community. Burrowing vertebrates can alter arthropod community composition and increase arthropod abundance through changes in the plant community (Davidson et al. 2010, Bangert and Slobodchikoff 2006, Davidson and Lightfoot 2007), but the lack of correlation between burrower access

and vegetation characteristics in this study suggests that they are impacting the arthropod community via less direct means. Mound-constructing burrowers increase plant richness at the landscape scale, but decrease plant cover and height on their mound structures (Davidson and Lightfoot 2006) and introduce soil disturbance. The observed decrease in predatory arthropods, and specifically of Araneae, could reflect the simplified vegetation structure and decreased vegetation cover associated with gopher mounds, even though spiders did not show a direct correlation with the percent cover of gopher mound disturbance in a plot. Spiders increase in abundance with complex vegetation structure (Dennis et al. 2001), so the reduced cover and height of plants coupled with increased soil disturbance could decrease predatory arthropod abundance.

Arthropod community also responded to landscape-scale variation in plant community. Here, arthropod abundance decreased substantially with native plant richness. This could be a reflection of shifting plant functional guild composition with the transition from native to exotic plants. In California, a high proportion of exotic plant species are annual (Seabloom et al. 2006), and annual plants tend to support higher herbivorous arthropod fecundity than perennial plants (Borer et al. 2009). Additionally, predatory arthropods decreased in abundance with an increase in exotic plant richness, perhaps because of the relative structural simplicity of grasses which dominate a higher proportion of the exotic than native plant assemblage in California (Seabloom et al. 2006). A decrease in predator abundance could then release herbivores, resulting in proportionally greater herbivore abundances in plots with lower native plant richness.

Arthropod familial composition also reflects the negative correlation between oak canopy and exotic plant cover observed in this system (Seabloom et al. 2009), with different arthropod families correlated with exotic plants than with woody plant cover

(Figure 2.1). Oak recruitment is not limited here by the presence of vertebrate consumers (Seabloom et al. 2009), but long-term oak recruitment limitation could alter arthropod assemblages, especially when paired with increasing invasion by exotic plant species.

Arthropod abundance represents the amount of secondary biomass that can be supported by the primary producer community, while arthropod richness represents the number of niches available in the ecosystem. The correlation between plant and herbivorous arthropod richness is driven by the greater diversity of resources provided by a varied plant community (Haddad et al. 2009) but this correlation was not seen in our plots. Arthropod families can contain species that respond differently to plant composition and to vertebrate access (Davidson et al. 2010), and that coexist in the same plant community by partitioning food resources (Behmer and Joern 2008). Classifying our arthropod samples by family hides intrafamilial variation and likely masks the signals derived from shifts in plant community richness and composition. While there are few strictly monophagous arthropod herbivores (Novotny et al. 2002), many have at least a partially-specialist diet (Futuyma and Gould 1979) or are in different trophic subgroups: pollen feeders, for example, will have different plant community responses than vegetation chewers or seed herbivores.

Arthropods thus responded to both the vertebrate-induced plant community changes and to landscape-scale variation in the plant community. Effects generally spanned at least two arthropod trophic guilds; for instance, predatory arthropods decreased but total arthropod abundance increased with burrower access (i.e., a top-down response mediated via structural changes in the plant community), and herbivore and detritivore groups showed synchronous trends with large vertebrate access (i.e., from changes in plant and detritus nutrition). Arthropods appear to be responding to different vertebrate herbivore groups via different mechanisms. Large vertebrate access shifted

plant richness and composition (Seabloom et al. 2009), which alters the diversity of resources available to arthropods. Burrowing vertebrates affected arthropod community via shifts in plant structural composition. These different mechanisms indicate that impacts of vertebrate guilds on arthropod community are likely synergistic, and human-induced changes in the prevalence of any vertebrate group can have ecosystem-wide ramifications.

ACKNOWLEDGMENTS

We thank Eric W. Seabloom and the workers, volunteers and technicians of the Borer-Seabloom lab for collecting and sharing the plant and arthropod data used in this analysis. Bruce McCune provided valuable suggestions for the multivariate analyses, and Eric Seabloom and Lydia O'Halloran assisted with univariate statistics. David Maddison, Thomas Kaye and Barbara Bond provided valuable feedback on the manuscript. The data collection for this work was funded by the National Science Foundation (DEB 0235624, EF 0525666, DEB 0444217), the Integrated Hardwood Range Management Program, and by Oregon State University.

2.5 WORKS CITED

- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46.
- Arsenault, R., and N. Owen-Smith. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97:313-318.
- Bakker, E. S., H. Olf, and J. M. Gleichman. 2009. Contrasting effects of large herbivore grazing on smaller herbivores. *Basic and Applied Ecology* 10:141-150.
- Bangert, R. K., and C. N. Slobodchikoff. 2006. Conservation of prairie dog ecosystem engineering may support arthropod beta and gamma diversity. *Journal of Arid Environments* 67:100-115.

- Behmer, S. T., and A. Joern. 2008. Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proceedings of the National Academy of Sciences* 105:1977.
- Belovsky, G. E., and J. B. Slade. 2000. Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences of the United States of America* 97:14412-14417.
- Belovsky, G. E., and J. B. Slade. 2002. An ecosystem perspective on grasshopper control: possible advantages to no treatment. *Journal of Orthoptera Research* 11:29-35.
- Bigger, D. S., and M. A. Marvier. 1998. How different would a world without herbivory be? A search for generality in ecology. *Integrative Biology*:60-67.
- Borer, E. T., V. T. Adams, G. A. Engler, A. L. Adams, C. B. Schumann, and E. W. Seabloom. 2009. Aphid fecundity and grassland invasion: Invader life history is the key. *Ecological Applications* 19:1187-1196.
- Crawley, M. J. 1989. The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. Page Insect-Plant Interactions, E. A. Bernays, ed. CRC Press, Florida.
- Davidson, A. D., and D. C. Lightfoot. 2007. Interactive effects of keystone rodents on the structure of desert grassland arthropod communities. *Ecography* 30:515-525.
- Davidson, A. D., E. Ponce, D. C. Lightfoot, E. L. Fredrickson, J. H. Brown, J. Cruzado, S. L. Brantley, R. Sierra-Corona, R. List, D. Toledo, and G. Ceballos. 2010. Rapid response of a grassland ecosystem to an experimental manipulation of a keystone rodent and domestic livestock. *Ecology* 91:3189-3200.
- Dennis, P., J. Skartveit, D. I. McCracken, R. J. Pakeman, K. Beaton, A. Kunaver, and D. M. Evans. 2008. The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology* 45:279–287.
- Dennis, P., M. R. Young, and C. Bentley. 2001. The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. *Agriculture, ecosystems & environment* 86:39–57.
- Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thébault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522–538.

- Futuyma, D. J., and F. Gould. 1979. Associations of Plants and Insects in Deciduous Forest. *Ecological Monographs* 49:33-50.
- Gardner, S. M., M. R. Cabido, G. R. Valladares, and S. Diaz. 1995. The Influence of Habitat Structure on Arthropod Diversity in Argentine Semi-Arid Chaco Forest. *Journal of Vegetation Science* 6:349-356.
- Gómez, J. M., and A. González-Megías. 2002. Asymmetrical interactions between ungulates and phytophagous insects: being different matters. *Ecology* 83:203–211.
- Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. *The American Naturalist* 158: 17-35.
- Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, J. M. H. Knops, and D. Tilman. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12:1029-1039.
- Huntzinger, M., R. Karban, and J. H. Cushman. 2008. Negative effects of vertebrate herbivores on invertebrates in a coastal dune community. *Ecology* 89:1972–1980.
- Jonsson, M., D. Bell, J. Hjältén, T. Rooke, and P. F. Scogings. 2010. Do mammalian herbivores influence invertebrate communities via changes in the vegetation? Results from a preliminary survey in Kruger National Park, South Africa. *African Journal of Range & Forage Science* 27:39.
- Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* 2:286-293.
- Lindsay, E. A., and S. A. Cunningham. 2009. Livestock grazing exclusion and microhabitat variation affect invertebrates and litter decomposition rates in woodland remnants. *Forest Ecology and Management* 258:178–187.
- McCune, B., and J. Grace. 2002. *Analysis of Ecological Communities*. Mjmm Software Design.
- Murdoch, W. W., F. C. Evans, and C. H. Peterson. 1972. Diversity and Pattern in Plants and Insects. *Ecology* 53:819-829.

- Novotny, V., Y. Basset, S. E. Miller, G. D. Weiblen, B. Bremer, L. Cizek, and P. Drozd. 2002. Low host specificity of herbivorous insects in a tropical forest. *Nature* 416:841-844.
- Novotny, V., P. Drozd, S. E. Miller, M. Kulfan, M. Janda, Y. Basset, and G. D. Weiblen. 2006. Why Are There So Many Species of Herbivorous Insects in Tropical Rainforests? *Science* 313:1115 -1118.
- Ohgushi, T. 2005. Indirect Interaction Webs: Herbivore-Induced Effects Through Trait Change in Plants. *Annual Review of Ecology, Evolution, and Systematics* 36:81-105.
- Oksanen, J., F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens and Helene Wagner 2010. *vegan: Community Ecology Package*. R package version 1.17-2. <http://vegan.r-forge.r-project.org/>.
- Parker, J. D. 2006. Opposing Effects of Native and Exotic Herbivores on Plant Invasions. *Science* 311:1459-1461.
- Pringle, R. M., T. P. Young, D. I. Rubenstein, and D. J. McCauley. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proceedings of the National Academy of Sciences* 104:193.
- Rambo, J. L., and S. H. Faeth. 1999. Effect of Vertebrate Grazing on Plant and Insect Community Structure. *Conservation Biology* 13:1047-1054.
- Sarkar, D. 2008. *lattice: Lattice Graphics*. R package version 0.17-17.
- Schaffers, A. P., I. P. Raemakers, K. V. Sýkora, and C. J. F. ter Braak. 2008. Arthropod assemblages are best predicted by plant species composition. *Ecology* 89:782-794.
- Seabloom, E. W., E. T. Borer, B. A. Martin, and J. L. Orrock. 2009. Effects of long-term consumer manipulations on invasion in oak savanna communities. *Ecology* 90:1356-1365.
- Seabloom, E. W., J. W. Williams, D. Slayback, D. M. Stoms, J. H. Viers, and A. P. Dobson. 2006. Human Impacts, Plant Invasion, and Imperiled Plant Species in California. *Ecological Applications* 16:1338-1350.
- Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79:2057-2070.

Siemann, E., D. Tilman, J. Haarstad, and M. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist*:738–750.

Venables, W. N. and Ripley, B. D. 2002. *Modern Applied Statistics with S*. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.

Wimp, G. M., S. M. Murphy, D. L. Finke, A. F. Huberty, and R. F. Denno. 2010. Increased primary production shifts the structure and composition of a terrestrial arthropod community. *Ecology* 91:3303–3311.

Table 2.1 Number of arthropod families classified to each trophic group. The number in parentheses is the number of families remaining after rare families (occurring in only one plot) were removed from multivariate analysis. Groupings that contained only 1 or 2 families after rare families were removed were not considered in later analyses. The herbivore grouping contains all herbivore families, including those also classified more specifically by their type of herbivory.

Trophic classification	Number of families
Herbivore	12 (8)
Seed	3 (2)
Phloem	3 (2)
Vegetation	1 (1)
Pollen	1 (0)
Predator	9 (8)
Parasite	19 (5)
Omnivore	2 (1)
Detritivore	6 (6)
Fungivore	6 (1)

Table 2.2. Correlations of arthropod trophic groups and environmental components with NMS axes. The r-values, indicating the proportion of variance explained by each axis, are indicated for each trophic group and environmental component. R is shown rather than R^2 to indicate positive or negative relationships along the axis. Strong correlations (R-values that resulted in an R^2 greater than 0.2) are highlighted. For each component, the cumulative R^2 of the three NMS axes is shown to give an indication of overall fit with the ordination model. Araneae, though included in the Predator trophic group, is also listed separately because it represents a distinct phylogenetic group of arthropods whose responses to vegetational changes and vertebrate access have been previously studied.

		Correlations with NMS axes			
		Axis 1 r	Axis 2 r	Axis 3 r	Cumulative R^2
Trophic groups	Herbivores	0.005	-0.162	0.204	0.067
	Predators	0.166	-0.224	0.488	0.316
	Parasites	0.45	0.564	0.234	0.576
	Detritivores	0.347	0.453	-0.177	0.357
	Araneae	-0.219	-0.217	0.774	0.693
Environmental Components	Vertebrate Access	0.092	-0.45	-0.191	0.248
	Deer Access	-0.055	-0.523	-0.206	0.32
	Rodent Access	0.013	-0.044	-0.27	0.075
	Gopher Access	0.33	-0.067	-0.503	0.366
	Total cover	0.015	0.243	0.033	0.06
	Native cover	0.111	0.512	0.067	0.278
	Exotic cover	-0.125	-0.313	-0.03	0.115
	Woody cover	0.003	-0.441	0.354	0.321
	Total richness	-0.266	0.034	0.183	0.105
	Native richness	0.077	0.237	0.153	0.085
	Exotic richness	-0.45	-0.179	0.113	0.248
	Plant Biomass	0.366	-0.217	-0.061	0.185

Table 2.3. Correlations of arthropod community and arthropod trophic groups to vertebrate access and measures of plant community characteristics. Trophic group abundances used mixed effects modeling to determine how they changed in response to parameters after accounting for experimental block. Experimental block was included in these models because arthropod community can change across the landscape, and it was of interest to determine how each trophic group responded to parameters after accounting for landscape variation. Whole arthropod community measures were evaluated using generalized linear models (glm) for abundance and richness and linear models (lm) for evenness that did not take plot into account, as it was of interest to determine how the arthropod community directly responded to variation present in the environmental parameters. Each glm and lm started with all parameters, and the best-fitting model for each arthropod response was selected using AIC. Shaded values indicate parameter estimates with $p < 0.05$; and lightly shaded values $p < 0.10$.

Parameters	Whole arthropod community			Trophic group abundances			
	Abundance	Richness	Evenness	Herbivores	Predators	Parasites	Detritivores
Vertebrate access	-0.3757	0.0393	-	0.5105*	0.2256	0.1805	0.3359***
Plant biomass	0.0042	0.0014	-0.0127†	0.0048	-0.0040	-	-0.0173***
Total plant cover	0.0248*	-0.0013	-	-0.0061	-0.0052	0.0023	0.0081***
Native plant richness	-0.7744***	0.0570	-	0.1514	-0.1028	-0.2021	0.3373***
Exotic plant richness	0.1222	-	-0.0003†	0.0885	-0.3399*	-0.0954	-0.8657***

For each arthropod response variable, the parameter estimates (-, not included in final model) and their significance levels (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; †, $p < 0.1$) are given.

Table 2.4: The response of arthropod community abundance and richness to each set of vertebrates after accounting for plant richness and cover using mixed effects models. Responses were analyzed separately for each type of vertebrate exclosure, and numbers in parentheses indicate the number of paired fenced and unfenced plots used in each analysis. Upward-pointing arrows indicate a significant ($p < 0.05$) positive correlation between vertebrate access and arthropod abundance or richness, and downward-pointing arrows indicate a significant negative correlation. “0” represents a non-significant correlation in the mixed effects model.

	Arthropod Response	
	Abundance	Richness
Deer access (11)	0	0
Gopher access (6)	↑	0
Rodent access (3)	↓	0

Table 2.5. Results of perMANOVAs evaluating differences in proportional arthropod family abundances across vertebrate-exclusion fences. The cumulative effect of vertebrate exclusion on the arthropod community is assessed in the “all vertebrates” perMANOVA, which included all fence blocks, regardless of the types of vertebrates excluded. The effects of a specific subset of vertebrates are explored with the “gophers excluded” perMANOVA which used only the 6 blocks that excluded burrowing vertebrates, and the “gophers allowed” perMANOVA which used the 6 blocks that excluded large vertebrates but did not exclude burrowing vertebrates.

perMANOVA test	# Blocks	# families	Block F-ratio (df)	Fence F-ratio (df)
All vertebrates	11	46	1.3919*(10)	1.1906 (1)
Gophers excluded	6	34	1.7007* (5)	1.9344† (1)
Gophers allowed	6	33	1.4037* (5)	1.5665 (1)

For each test, the number of blocks (paired plots within and outside vertebrate fences), and the number of families, used in the analysis are included. The F-ratios, their significance levels (* $p < 0.001$, † $p < 0.1$), and the degrees for freedom (df) are given for each test.

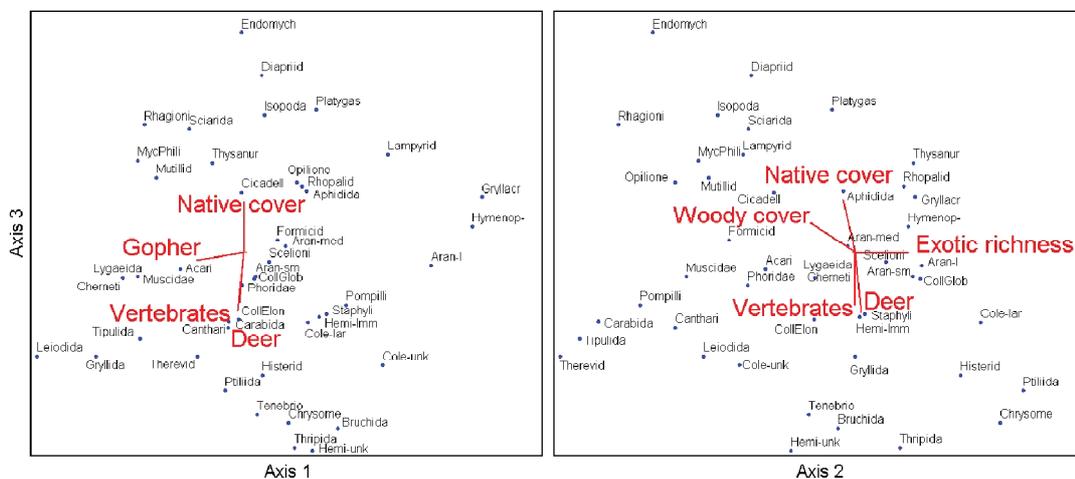


Figure 2.1. Ordination of plots in arthropod space based on the similarities in proportional arthropod familial abundances in each plot. Here, the arthropod families are plotted within 3-dimensional arthropod space. Axes 1 and 3 are plotted on the left, and axes 2 and 3 are plotted on the right. Vectors representing environmental factors strongly associated with each axis ($r > |0.20|$) have been overlain to show the association of ordination axes to environmental variables. Families along the same axes indicate their association with that environmental characteristic.

Chapter 3: Grassland arthropods are controlled by indirect interactions with vertebrate grazers and by nutritional quality of invasive plants

Kelly Anne Farrell and Elizabeth T. Borer

3.0 ABSTRACT

The invasion of non-native plant species worldwide causes dramatic changes in ecosystem processes such as nutrient cycling, litter decomposition, and biotic community composition. Many of these impacts are noticeable when exotic and native plants are of vastly different functional guilds, but fewer studies examine the bottom-up impacts of exotic versus native plant communities of similar diversity and functional guild composition. Grazing also causes shifts in plant community structure and biomass, but its indirect impacts on arthropod community structure have been little studied. Here we use a manipulative study to examine how two human-induced disturbances, the replacement of native perennial grasses by exotic annual grasses and the introduction of heavy cattle grazing, affect arthropod community structure in a California grassland. Arthropod richness, diversity, and abundance did not vary predictably between native perennial and exotic annual grass communities, though arthropods responded to plant community characteristics. In the presence of grazing, arthropod biovolume increased in annual grass treatments, which could trigger a positive-feedback cycle with vector-transmitted plant pathogens to further increase the prevalence of non-native annual grasses. Arthropod community was strongly affected by cattle grazing, which decreased the biovolume of predatory arthropods, causing a top-down increase in herbivorous arthropod biovolume. Grazing thus impacts plant composition both through the direct removal of biomass and increased species evenness, and through arthropod-mediated impacts. The effects of these two disturbances on the arthropod community could have far-reaching effects on ecosystem services provided by arthropods.

3.1 INTRODUCTION

Changes in arthropod communities due to human-induced disturbances can have sweeping ecosystem impacts: arthropods decrease grassland plant biomass (Coupe and Cahill Jr 2003), increase nutrient cycling (Belovsky and Slade 2002), are pollinators of many flowering plants, and can be vectors of human, livestock, and plant diseases. Through the intentional and incidental introduction of non-native plant species into grasslands, coupled with heavy agricultural and livestock use, many of the world's grasslands are composed of altered or degraded plant communities. While a number of studies investigate the impacts of grazing and invasion on grassland plant communities, few have examined multi-trophic effects of these disturbances or considered whether effects of these disturbances may be synergistic.

Vertebrate grazers, including cattle, can increase plant species richness and evenness in terrestrial systems (Hillebrand et al 2007), though their impacts on specific plant species may vary. Of the few studies that examine interactions among cattle and invertebrate assemblages, grazing tends to decrease arthropod biomass (Dennis et al 2008) and arthropod abundance (Rambo and Faeth 1999), but may have little impact on arthropod diversity (Rambo and Faeth 1999). In general, vertebrate herbivores have rarely been found to have consistent impacts on the abundance (Pringle et al 2007, Huntzinger et al 2008) or species richness (Bangert & Slobodchikoff 2006) of the arthropod community. However, when grazing is coupled with the introduction of invasive plants, it may compound effects on the arthropod community.

Past studies that have identified a shift in arthropod richness or abundance with plant invasion have hypothesized decreased plant diversity to be the causal mechanism (Simao et al. 2010). The well-established relationship between plant diversity and arthropod diversity (see Haddad et al. 2001, Siemann et al. 1998), or between plant functional group and arthropod richness (Haddad et al 2001) may be irrelevant,

however, if plant invasion alters plant species composition without changing the richness, evenness, or functional composition of the plant community.

In California, the focal region for our current study, 9.2 million hectares of grassland have been invaded by non-native grasses, their invasion facilitated by overgrazing and drought during the 19th century (see Barbour and Major 1977). In this region, grazing and invasion may act synergistically in altering grassland flora; vertebrate herbivores increase the proportion of highly-competent non-native hosts of barley yellow dwarf virus (BYDV) (Borer et al. 2009a), which allows further invasion by non-native grasses (Borer et al. 2007). Exotic annual grasses, which tend to have lower C:N ratios than perennial grasses (Borer et al. 2009b), and invest in fewer structural and chemical defenses, may be more palatable to vertebrate and invertebrate herbivores. Even though the replacement of native by exotic grass species may not change plant species richness in and of itself, as the identity of the dominant grass species within the community changes, plant community diversity and composition as a whole may also change (Miles and Knops 2009, Emery and Gross 2007), leading to changes in the arthropod community (Schaffers et al. 2008).

Here we experimentally examine arthropod richness, evenness, biomass, and compositional responses to two globally and regionally important alterations of the grassland biome, invasion and cattle grazing. We use an experimental manipulation of dominant grass species (native perennial mixture versus exotic annual mixture) crossed with cattle grazing to ask: (1) Does grazing alter characteristics of the arthropod community via changes in the plant community? (2) Does the provenance of the dominant plant community control the richness, evenness, biomass, or composition of the arthropod community? and (3) Does grazing interact with plant provenance to influence the arthropod community?

3.2 METHODS

To study the effects of plant composition and cattle grazing on grassland arthropods, we studied arthropod communities in a randomized factorial experiment (established by Katherine Suding and W. Stanley Harpole, UC Berkeley) at the Sierra Foothills Research Extension Center in Browns Valley, California, USA (39° 15' N, 121° 17' W) and managed by the University of California. The experiment was designed to determine the influence of grazing intensity as a driver of alternative vegetation states in California grasslands. It consisted of two experimental fields with different grazing and plant community histories that were tilled and solarized in October 2006 to remove vegetation and decrease soil seed bank and pathogens. We sampled arthropod communities from two of the four vegetation types within this experiment that were established between December 2006 and March 2007: (1) native perennial bunchgrasses planted as plugs (*Nassella pulchra*, *Elymus glaucus*, *Melica californica*) and (2) exotic annual grasses established by seeding (*Avena fatua*, *Bromus hordeaceus*, *Lolium multiflorum*). These were replicated with two blocks of each established on each pasture for a total of 4 blocks. Two years after establishment, a gradient of 6 grazing treatment levels was initiated, carried out with a combination of trampling by livestock and mechanical mowing. The most intensive grazing + mowing treatment, leaving approximately 200-300 pounds of residual dry matter per acre, was based on previous estimates made from intensively grazed rangeland bordering our research site. For logistical reasons, the highest grazing intensity was in the centermost plots, with decreased intensity moving outwards in both directions. This resulted in two mirror replicates within each vegetation block, with a total of eight 3m × 10m plots of each grazing × vegetation factorial manipulation (Figure 3.2).

We sampled arthropods from the ungrazed and heavily grazed plots in the native perennial bunchgrass and exotic annual grass treatments, after treatments had been in place for two years. The heavily grazed plots had been trampled in late March 2008

and 2009 when plants started flowering and in June 2008 when most plants were senescent. 40 – 42 cattle (up to one year old, Black Angus Mix, 900-1000lbs/head) were herded for 30-45 minutes during each trampling treatment. Additionally, plots were mowed to a height of 2 cm above the ground, and biomass removed, three times during 2008 (before each trampling treatment and additionally in late February, during early plant growth) and twice during 2009, before arthropods were sampled. This combination of trampling and mowing simulated, as closely as possible, the impacts of grazing within the spatial scale of the treatment plots.

In May 2009, arthropods were vacuum sampled using a method similar to that of Stewart & Wright (1995). A fine mesh bag, fitted into the suction tube of a gas-powered leaf blower, was used to “comb” vegetation from the bottom up within a 1m² quadrat for 30 seconds. At the end of the 30 seconds, the mesh bag was sealed before stopping the suction, ensuring that arthropods could not escape. Bagged insects were stored on ice, and frozen upon return to the laboratory. Two samples were taken from each plot and combined during analysis, to help account for any within-plot spatial variability in arthropod distribution. While this method of suctioning does not thoroughly sample large and mobile arthropods which can escape the open quadrat at the sound of the blower, it is effective for sampling many groups of small, vegetation-inhabiting arthropods. Importantly, it provides a uniformly biased estimate for comparing arthropod community change among plots from the same site.

In the lab, vegetation was removed from the samples and all arthropods visible at 10x magnification were identified to morphospecies, using a dissecting microscope to examine externally visible characters at up to 50x magnification. The first instance of each morphospecies was considered the primary voucher, photographed, and pinned. Subsequent individuals were identified using a digital library of photographed vouchers.

To quantify the response of trophic and taxonomic groups to treatments, morphospecies were classified to the lowest possible taxonomic rank. Using taxonomic keys and expert advice (see Appendix Table B.1), the majority of morphospecies were identified to family. We could not identify some individuals below suborder or order. Trophic status (herbivore, carnivore, parasitoid, detritivore) was assigned to each morphospecies, based on information in published keys and family accounts (Appendix Table B.1). Where ambiguity in the trophic classification for a morphospecies was possible, it was considered “varied” and omitted from the trophic analysis. For instance, if the lowest taxonomic identifier (e.g. family) contained both herbivores and carnivores within California, no trophic group was assigned for that morphospecies. With the exception of parasitoids and specimens collected as immatures, adult food source was used if known (Figure 3.1).

Arthropod biovolume, an estimate of body size and of the amount secondary production supported by the plant community, was estimated for all morphospecies. We use this measure as a surrogate for individual biomass. Up to three specimens of each morphospecies in each vacuumed sample, including the primary voucher, were measured for length and width to the nearest 0.1mm, and biovolume was calculated as $\pi r^2 \times \text{length}$, such that body volume was estimated to be cylindrical. The biovolume for each morphospecies was taken as the average of all measured individuals (Appendix Table B.1).

Arthropod abundance (total number of individuals), species richness, Shannon evenness, and total biovolume were calculated for each plot. For each, generalized linear models (glm) were used to test for effects of grazing treatment, grass treatment, experimental field, plant richness, plant evenness, plant biomass, and litter mass. The best fitting models were selected using the Akaike Information Criteria (AIC). Differences in plant species richness, evenness, biomass, and litter mass were

analyzed between grass treatments using t-tests and between grazing treatments using paired t-tests. All univariate statistics were performed in R (Version 2.8.1, R Foundation for Statistical Computing), using the MASS (Venables and Ripley 2002), lattice (Sarkar 2008), and vegan (Oksanen et al. 2010) packages.

To analyze the impacts of grazing on the arthropod community, we compared the abundances of each morphospecies in each plot. The data from one grazed annual plot was discarded because of insufficient labeling in the field. As a balanced design was needed, one randomly chosen ungrazed annual plot was also omitted from the analysis. Beginning with a matrix of 30 plots and 252 arthropod morphospecies, data were transformed by excluding morphospecies that occurred in fewer than 2 plots, resulting in a matrix of 30 plots and 179 morphospecies. This process decreases the noise generated by rare species while increasing the detection of patterns in community relationships (McCune and Grace 2002). We scaled the abundance of each morphospecies between 1 (its highest presence in any plot) and 0 (not occurring in a plot). This transformation is appropriate for data sets in which the abundance of one group may be drastically different than the abundance of another group; it prevents super-abundant taxa from masking patterns of less abundant taxa (McCune and Grace 2002, McCune personal communication). All multivariate analyses were conducted in PC-ORD (McCune and Medford 2010, version 6.243 beta).

Permutational-based multivariate analyses of variance (PerMANOVAs) were used to test for differences in arthropod morphospecies composition between treatments, using Sørensen distance measure after the methods of Anderson (2001). The experimental design prevented analysis of all variables at once. The impact of grazing was analyzed by conducting a perMANOVA comparing morphospecies composition in grazed and ungrazed paired plots, blocked by the grass treatment plot they occurred in. The impact of grass treatment was analyzed separately within grazed and ungrazed

treatments and was blocked by experimental field. In ungrazed plots, a matrix of 16 plots \times 138 relativized species abundances were analyzed to compare arthropod composition in annual and perennial plots. In grazed plots, an additional 2 plots were randomly discarded (because of missing samples) to create a balanced design, leading to a final matrix of 12 plots \times 122 relativized species abundances. Results were very similar when all grazed plots were included and with the 4 plots omitted.

We used a nonmetric multi-dimensional scaling (NMS) ordination with Sørensen distance measure to visualize the ways in which different environmental variables influenced the arthropod community composition. Ordinations plotted each plot's location in 179-dimensional morphospecies-space, with each axis representing the proportional abundance of a single morphospecies within a plot. Using a random starting configuration, 250 runs with real data, and 250 runs with randomized data, dimensions were collapsed into the smallest number of axes that adequately explained the data. Solution dimensionality was selected following the recommendation of PC-ORD combined with examination of a scree plot. Environmental characteristics of each plot were overlaid onto the final ordination, including treatments and plant characteristics, to find the correlations between the environmental variables and ordination axes.

Because the multivariate analyses identified a significant shift in the arthropod community with grazing, we tested whether closely related arthropod morphospecies could be treated as independent units within the analysis or whether phylogenetic groups were responding similarly and driving the trend. Using the program Mesquite (Maddison & Maddison 2010, version 2.74 (build 550)), a tree was built to reflect the phylogeny of morphospecies. The correlation of each morphospecies to grazing was mapped onto the tree (see Appendix Table B.1). We compared the number of squared changed steps in the observed data with the predictions of a null hypothesis in which

the correlation values were distributed randomly with respect to the phylogeny. This null hypothesis represents a phylogeny in which there is no historical, phylogenetically-driven response to grazing. Values to test the null hypothesis were generated by a permutation test, in which we randomly shuffled the correlation values among taxa 10,000 times.

3.3 RESULTS

27,927 arthropods representing 252 morphospecies were collected. Average specimen length was 0.6mm and the largest specimen was 11.5mm long. Hemipterans, including large numbers of cicadellids and aphids, were found in high abundance, as were collembolans. The most diverse group was the microhymenopteran parasitoids (70 morphospecies) (Appendix Table B.1).

The plant community responded in several ways to grass provenance and grazing treatments (Table 3.1). While overall plant species richness did not differ among grass provenance or grazing treatments (provenance t-test $p=0.1207$, grazing paired t-test $p=0.08844$), species evenness was lower in exotic annual than native perennial plots (t-test $p=0.00589$) and higher in grazed than ungrazed plots (paired t-test $p = 0.01941$). Plant litter was lower in grazed plots (paired t-test litter $p<0.01$), and plant biomass was lower in grazed plots, though not significantly so (paired t-test $p = 0.07$).

The arthropod community, as measured by aggregate variables, was influenced by the plant community (Table 3.2). First, arthropod abundance increased with the number of plant species in a plot (F-test $p = 0.042$) and arthropod evenness slightly but significantly decreased with increased plant richness (F-test $p= 0.024$). In addition, arthropod species richness increased with the evenness of the plant community (F-test $p = 0.024$) (Table 3.2). Although plant species evenness changed with both grazing and provenance treatments, neither treatment was significant in models of arthropod

aggregate variables; in fact, models were better-fitting when treatment terms were omitted (Table 3.2).

Total plot-scale arthropod biovolume (i.e. secondary production) was higher with grazing (F-test $p = 0.016$) and was higher in the exotic annual grass community compared to the native perennial grass community (F-test $p = 0.014$) (Figure 3.3). A significant interaction between the treatments revealed that biovolume was higher in exotic grass treatments only in the presence of grazing (Table 3.2). Individual trophic groups did not vary consistently with grass provenance treatments (F-test $p > 0.1$ for all) (Table 3.2). After accounting for plant community richness, evenness, and biomass, herbivorous arthropod biovolume increased and predatory arthropod volume decreased with grazing (F-test herbivores $p = 0.011$, predators $p = 0.0086$) (Table 3.2). The total biovolume of herbivorous arthropods in an ungrazed plot is estimated to be 60% lower than in a grazed plot while the biovolume of predatory arthropods is estimated to be 10.7 times higher in ungrazed plots than grazed plots. Neither parasitoid nor detritivore biovolume varied with grazing (F-test $p > 0.1$ for all).

The proportional representation of arthropod morphospecies within a plot (arthropod community) varied by experimental block (perMANOVA $F = 1.40$, $df = 14$, $p < 0.0001$) (Table 3.3). Grazing significantly altered arthropod community by differentially affecting the relative abundances of morphospecies (perMANOVA $F = 2.40$, $df = 1$, $p < 0.001$) (Figure 3.4). When morphospecies' correlations with grazing were plotted on a tree reflecting their phylogenetic relationships (Appendix Figure B.1), and the correlation values randomly permuted among the taxa, there was no indication that arthropod morphospecies were responding to grazing as phylogenetically related groups ($p = 0.40$) (Figure 3.5); rather, different morphospecies within the same higher-level classifications were responding independently. This allows us to more confidently treat even closely related

morphospecies as independent units in the analyses. There was no evidence that grass provenance impacted arthropod community in either grazed or ungrazed plots (perMANOVA $p > 0.1$ for all).

3.4 DISCUSSION

Arthropod responses to experimental manipulations of grass provenance and grazing clarified two key findings. First, the arthropod community composition was surprisingly invariant between plant communities dominated by native perennial grasses and exotic annual grasses, suggesting that arthropod community composition may be more strongly responsive to plant functional group than to specific composition within a functional group. In contrast, arthropod species richness was positively associated with plant species evenness, and arthropod abundance was positively correlated with plant species richness. Thus, it appears that plant community characteristics beyond the turnover of dominant species within a plant functional group are responsible for shifts in arthropod community. Second, the total biomass of predatory arthropods was reduced, and biomass of herbivorous arthropods increased, in the grazing treatments. This pattern is consistent with the effects of a top-down cascade, in which the reduction of predators would allow an increase in the numbers of their prey. Grazing therefore appears to reduce plant biomass by two means: by direct removal of plant biomass and by increased volume of herbivorous arthropods. Grazing can thus have larger top-down impacts on ecosystems than might be expected through direct impacts alone.

The composition of the arthropod community was relatively unresponsive to a complete replacement of the dominant native grasses by exotic annual grasses. The replacement of plant species within this functional group did not affect arthropod species richness, evenness, abundance, or the proportional representation of arthropod morphospecies. This could be, in part, because plant species richness did not vary

with provenance treatment; in past studies that have found a shift in arthropod species composition as a result of plant invasion, the invasion also caused decreased plant diversity (Simao et al. 2010, Spyreas et al. 2009). Although plant identity can be a strong driver of arthropod identity (Schaffers et al. 2008), the similar functional role of native and exotic grasses in this study could explain why the arthropod community did not vary with our treatments. This has not been supported in past studies, which found less diverse arthropod assemblages associated with exotic plants compared to their phylogenetically and functionally related congeners (Procheş et al. 2008, Harvey et al. 2010). However, those studies examined arthropod assemblages on individual native and exotic plant species, whereas we tested the arthropod response to the complete plant community. Also, this experimental manipulation of plant community prevented potential variability in arthropod community arising from different abiotic habitats (Procheş et al. 2008) or from different plant structure between congeners (Harvey et al. 2010).

The total biomass of arthropods responded directly to provenance treatments with increased biovolume in exotic annual plots compared to native perennial plots. Taken together with the lack of response in arthropod morphospecies composition, this suggests that plant replacement is causing a quantitative, rather than qualitative, change in the arthropod community. However, grass provenance is almost completely confounded by the life histories of the grasses in the two treatments: a high proportion of exotic grasses in California are annuals, including all the species used in this experiment, while the majority of native grasses are perennial (Barbour and Major 1977, Seabloom et al. 2003). Annual plants have less investment in structural defenses and a lower C:N ratio than their perennial counterparts, which likely explains the increase in arthropod biovolume in exotic annual grass treatments (Borer et al. 2009b). Neither the richness nor abundance of the arthropod community changed concurrently with the increased arthropod biovolume, further supporting increased

arthropod biomass as a response to the nutritional value of the plant community. Thus, secondary production of arthropods appears to be constrained by the efficiency with which these consumers access and convert primary production rather than by plant provenance, *per se* (Polis 1999).

There was no evidence of resource competition between herbivorous arthropods and cattle; rather, herbivorous arthropod biomass increased and predatory arthropod biomass decreased with grazing. The increase in herbivore biomass from grazing did not occur via bottom-up changes in plant species richness. Though grazing often increases plant richness in terrestrial systems (Rambo and Faeth 1999, Hillebrand et al. 2007), this effect was not seen here, possibly because of baseline habitat productivity (Schultz et al. 2011), or because the small spatial scale of treatments could facilitate continual colonization from surrounding plots. Instead, changes are consistent with the effects of a top-down cascade and may have been triggered by an increase in evenness and decrease in biomass within the plant community as a result of grazing. Predatory arthropod species composition and abundance is highly correlated with vegetation structure (Murdoch et al. 1972, Gardner et al. 1995, Haddad et al. 2009), with greater predator abundance and diversity associated with the taller, more complex vegetation structure of ungrazed habitats (Dennis et al. 2001). In this study, the greater plant species evenness and reduced litter and plant biomass associated with cattle grazing created a less complex habitat, which likely reduced the habitat use of arachnid and acarine predators, leading to an increase in the biomass of herbivorous arthropods. This herbivore release was great enough that, contrary to previous findings (Dennis et al. 2008), total arthropod biovolume increased with grazing.

Predator removal can have large negative impacts on producer biomass across productivity gradients and habitats (Borer et al. 2006); thus, grazing may decrease plant biomass both through direct removal of plant material and by initiating a top-

down release of herbivorous arthropods. Even in the absence of vertebrates, invertebrate herbivores can exert strong control on producer biomass (Bigger and Marvier 1998), and invertebrates also can affect the plant community through indirect means. For example, aphids and leafhoppers are the vectors of many plant diseases, which have been demonstrated to reverse the competitive dominance of hosts in this grassland system (Borer et al. 2007). Grazing may thus have a disproportionately dramatic impact on grassland plant communities through direct and indirect means mediated via the arthropod community.

Quantitative changes in the arthropod community observed with the introduction of annual grasses and grazing can lead to alterations of community dynamics and ecosystem functioning. The increase in herbivorous arthropod biomass with grazing could increase nutrient cycling rates (Belovsky and Slade 2002). It could also initiate a positive feedback cycle in vector transmitted plant disease; annual plants cause high fecundity in arthropod vectors (Borer et al. 2009b), (Malmstrom et al. 2005), increasing the prevalence of plant diseases that shift competitive dominance between plant species (Borer et al. 2007), further increasing the prevalence of annual host plants (Borer et al. 2009a). Also, carbon sequestration by grasslands is an important environmental service (Conant et al. 2001) that can be decreased by vertebrate grazing and by the increased herbivorous arthropod biovolume associated with grazing. Other types of ecosystem services that would be mediated by qualitative changes in the arthropod community may remain intact despite invasion, as neither arthropod richness nor arthropod community structure was altered by this disturbance. Pollination services, for instance, may be unimpacted by invasion since the morphospecies composition of the arthropod community remained unchanged across the grass composition treatments. The ranges of exotic plant species are predicted to increase as they overcome dispersal limitation (Seabloom et al. 2003), and much of the world's grasslands are expected to experience increased grazing intensity to meet

heightened demands (Conant et al. 2001). The far-reaching effects of human-induced disturbances on ecosystem services, then, will likely become more pronounced as these disturbances become stronger and more widespread.

ACKNOWLEDGEMENTS

The authors would like to thank the many individuals who contributed time and expertise towards the success of this analysis. Katherine Suding, W. Stanley Harpole, and Claudia Stein were generous in allowing us to sample arthropods from their experimental plots and for sharing their plant community data as well as for feedback on analyses and writing. David Maddison and Bruce McCune assisted with the multivariate and phylogenetic analyses and Eric Seabloom assisted with univariate analysis. Shawn Gerrity was instrumental in arthropod sampling, and numerous student workers and volunteers assisted in arthropod sorting and morphotyping: Jacky Schultz, Jonathan Truong, Rachel Steele, Rogelio Ayala, Kimberly Barrella, Chelsea Wolf, Caitlyn O'Mealy, Ron Lyons, Tiffany Mitchell, and Sierah Edwards. Danielle Lightle, Kojun Kanda, Samantha Colby, Christopher Marshall and David Maddison assisted with arthropod identification and trophic classification. David Maddison, Thomas Kaye and Barbara Bond gave valuable feedback on writing and analyses. The experiment was funded by USDA Managed Ecosystems Grant #2006-01350, and arthropod processing was funded by the University of California Integrated Hardwood and Range Management Program, Oregon State University Zoology Department, and the University of Minnesota.

3.5 WORKS CITED

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46.

- Arnett, Jr., R. H. 2000. American Insects: A Handbook of the Insects of America North of Mexico, Second Edition, 2nd edition. CRC Press.
- Arnett, Jr., R. H., M. C. Thomas, P. E. Skelley, and J. H. Frank. 2002. American Beetles, Volume II: Polyphaga: Scarabaeoidea through Curculionoidea, 1st edition. CRC Press.
- Arnett, Jr., R. H., and M. C. Thomas. 2000. American Beetles, Volume I: Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia, 1st edition. CRC Press.
- Arsenault, R., and N. Owen-Smith. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97:313-318.
- Bakker, E. S., H. Olf, M. Boekhoff, J. M. Gleichman, and F. Berendse. 2004. Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia* 138:91-101.
- Bakker, E. S., H. Olf, and J. M. Gleichman. 2009. Contrasting effects of large herbivore grazing on smaller herbivores. *Basic and Applied Ecology* 10:141-150.
- Bakker, E. S., M. E. Ritchie, H. Olf, D. G. Milchunas, and J. M. H. Knops. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters* 9:780-788.
- Bangert, R. K., and C. N. Slobodchikoff. 2006. Conservation of prairie dog ecosystem engineering may support arthropod beta and gamma diversity. *Journal of Arid Environments* 67:100-115.
- Barbour, M. G., and J. Major. 1977. Terrestrial vegetation of California. Wiley, New York.
- Behmer, S. T., and A. Joern. 2008. Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proceedings of the National Academy of Sciences* 105:1977.

- Belovsky, G. E., and J. B. Slade. 2000. Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences of the United States of America* 97:14412-14417.
- Belovsky, G. E., and J. B. Slade. 2002. An ecosystem perspective on grasshopper control: possible advantages to no treatment. *Journal of Orthoptera Research* 11:29-35.
- Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* 142:2401-2414.
- Bigger, D. S., and M. A. Marvier. 1998. How different would a world without herbivory be? A search for generality in ecology. *Integrative Biology*:60-67.
- Borer, E. T., B. S. Halpern, and E. W. Seabloom. 2006. Asymmetry in community regulation: effects of predators and productivity. *Ecology* 87:2813–2820.
- Borer, E. T., P. R. Hosseini, E. W. Seabloom, and A. P. Dobson. 2007. Pathogen-induced reversal of native dominance in a grassland community. *Proceedings of the National Academy of Sciences* 104:5473.
- Borer, E. T., C. E. Mitchell, A. G. Power, and E. W. Seabloom. 2009a. Consumers indirectly increase infection risk in grassland food webs. *Proceedings of the National Academy of Sciences* 106:503.
- Borer, E.T., V. T. Adams, G. A. Engler, A. L. Adams, C. B. Schumann, and E. W. Seabloom. 2009b. Aphid fecundity and grassland invasion: Invader life history is the key. *Ecological Applications* 19:1187-1196.
- Brusca, R. C., and G. J. Brusca. 1990. *Invertebrates*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Conant, R. T., K. Paustian, and E. T. Elliott. 2001. Grassland management and conversion into grassland: Effects on soil carbon. *Ecological Applications* 11:343-355.
- Connell, J. 1978. Diversity in tropical rain forests and coral reefs -- High diversity of trees and corals is maintained only in a non-equilibrium state. *Science* 199:1302-1310.

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

Crawley, M. J. 1989. The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. Page Insect-Plant Interactions, E. A. Bernays, ed. CRC Press, Florida.

Davidson, A. D., and D. C. Lightfoot. 2006. Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography* 29:755–765.

Davidson, A. D., and D. C. Lightfoot. 2008. Burrowing rodents increase landscape heterogeneity in a desert grassland. *Journal of Arid Environments* 72:1133–1145.

Davidson, A. D., and D. C. Lightfoot. 2007. Interactive effects of keystone rodents on the structure of desert grassland arthropod communities. *Ecography* 30:515–525.

Davidson, A. D., E. Ponce, D. C. Lightfoot, E. L. Fredrickson, J. H. Brown, J. Cruzado, S. L. Brantley, R. Sierra-Corona, R. List, D. Toledo, and G. Ceballos. 2010. Rapid response of a grassland ecosystem to an experimental manipulation of a keystone rodent and domestic livestock. *Ecology* 91:3189–3200.

Dennis, P., J. Skartveit, D. I. McCracken, R. J. Pakeman, K. Beaton, A. Kunaver, and D. M. Evans. 2008a. The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology* 45:279–287.

Dennis, P., M. R. Young, and C. Bentley. 2001. The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. *Agriculture, ecosystems & environment* 86:39–57.

Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thébault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522–538.

Firn, J., J. L. Moore, A. S. MacDougall, E. T. Borer, E. W. Seabloom, J. HilleRisLambers, W. S. Harpole, E. E. Cleland, C. S. Brown, J. M. H. Knops, S. M. Prober, D. A. Pyke, K. A. Farrell, J. D. Bakker, L. R. O'Halloran, P. B. Adler, S. L. Collins, C. M. D'Antonio, M. J. Crawley, E. M. Wolkovich, K. J. La Pierre, B. A. Melbourne, Y. Hautier, J. W. Morgan, A. D. B. Leakey, A. Kay, R. McCulley, K. F. Davies, C. J. Stevens, C. Chu, K. D. Holl, J. A. Klein, P. A. Fay, N. Hagenah, K. P. Kirkman, and Y. M. Buckley. 2011. Abundance of introduced species at home predicts abundance away in herbaceous communities. *Ecology Letters* 14:274-281.

Futuyma, D. J., and F. Gould. 1979. Associations of Plants and Insects in Deciduous Forest. *Ecological Monographs* 49:33-50.

Gardner, S. M., M. R. Cabido, G. R. Valladares, and S. Diaz. 1995. The Influence of Habitat Structure on Arthropod Diversity in Argentine Semi-Arid Chaco Forest. *Journal of Vegetation Science* 6:349-356.

Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystems processes : lessons from Florida. *Ecol Appl* 8:975-989.

Goulet, H., and J. T. Huber. 1993. Hymenoptera of the World: An Identification Guide to Families. Agriculture Canada.

Gómez, J. M., and A. González-Megías. 2002. Asymmetrical interactions between ungulates and phytophagous insects: being different matters. *Ecology* 83:203-211.

Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. *American Naturalist* 158:17-35.

Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, J. M. H. Knops, and D. Tilman. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12:1029-1039.

Harvey, K. J., D. R. Britton, and T. E. Minchinton. 2010. Insect diversity and trophic structure differ on native and non-indigenous congeneric rushes in coastal salt marshes. *Austral Ecology* 35:522-534.

Hillebrand, H., D. S. Gruner, E. T. Borer, M. E. S. Bracken, E. E. Cleland, J. J. Elser, W. S. Harpole, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and others. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences* 104:10904.

Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46:10-18.

Huntzinger, M., R. Karban, and J. H. Cushman. 2008. Negative effects of vertebrate herbivores on invertebrates in a coastal dune community. *Ecology* 89:1972–1980.

Jonsson, M., D. Bell, J. Hjältén, T. Rooke, and P. F. Scogings. 2010. Do mammalian herbivores influence invertebrate communities via changes in the vegetation? Results from a preliminary survey in Kruger National Park, South Africa. *African Journal of Range & Forage Science* 27:39.

Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* 2:286-293.

Levine, J. M., and C. M. D'Antonio. 2003. Forecasting Biological Invasions with Increasing International Trade. *Conservation Biology* 17:322-326.

Lindsay, E. A., and S. A. Cunningham. 2009. Livestock grazing exclusion and microhabitat variation affect invertebrates and litter decomposition rates in woodland remnants. *Forest Ecology and Management* 258:178–187.

Malmstrom, C. M., A. J. McCullough, H. A. Johnson, L. A. Newton, and E. T. Borer. 2005. Invasive annual grasses indirectly increase virus incidence in California native perennial bunchgrasses. *Oecologia* 145:153-164.

McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood. 1981. *Manual of Nearctic Diptera, Volume 1*. Agriculture Canada, Hull, Quebec, Canada.

- McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood. 1987. *Manual of Nearctic Diptera, Volume 2*. Agriculture Canada, Hull, Quebec, Canada.
- McCune, B., and J. Grace. 2002. *Analysis of Ecological Communities*. MjM Software Design, Glenden Beach, Oregon.
- Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative Effects of Grazing on Vegetation and Soils Over a Global Range of Environments. *Ecological Monographs* 63:327.
- Miles, E. K., and J. M. H. Knops. 2009. Shifting dominance from native C4 to non-native C3 grasses: relationships to community diversity. *Oikos* 118:1844–1853.
- Murdoch, W. W., F. C. Evans, and C. H. Peterson. 1972. Diversity and Pattern in Plants and Insects. *Ecology* 53:819-829.
- Novotny, V., Y. Basset, S. E. Miller, G. D. Weiblen, B. Bremer, L. Cizek, and P. Drozd. 2002. Low host specificity of herbivorous insects in a tropical forest. *Nature* 416:841-844.
- Novotny, V., P. Drozd, S. E. Miller, M. Kulfan, M. Janda, Y. Basset, and G. D. Weiblen. 2006. Why Are There So Many Species of Herbivorous Insects in Tropical Rainforests? *Science* 313:1115 -1118.
- Ohgushi, T. 2005. Indirect Interaction Webs: Herbivore-Induced Effects Through Trait Change in Plants. *Annual Review of Ecology, Evolution, and Systematics* 36:81-105.
- Oksanen, J., F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens and Helene Wagner 2010. *vegan: Community Ecology Package*. R package version 1.17-2. <http://vegan.r-forge.r-project.org/>.

- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1:3-19.
- Parker, J. D. 2006. Opposing Effects of Native and Exotic Herbivores on Plant Invasions. *Science* 311:1459-1461.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and Economic Costs of Nonindigenous Species in the United States. *BioScience* 50:53.
- Polis, G. A. 1999. Why Are Parts of the World Green? Multiple Factors Control Productivity and the Distribution of Biomass. *Oikos* 86:3-15.
- Pringle, R. M., T. P. Young, D. I. Rubenstein, and D. J. McCauley. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proceedings of the National Academy of Sciences* 104:193.
- Procheş, Ş., J. R. U. Wilson, D. M. Richardson, and S. L. Chown. 2008. Herbivores, but not other insects, are scarce on alien plants. *Austral Ecology* 33:691–700.
- Ramankutty, N., A. T. Evan, C. Monfreda, and J. A. Foley. 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles* 22:GB1003.
- Rambo, J. L., and S. H. Faeth. 1999. Effect of Vertebrate Grazing on Plant and Insect Community Structure. *Conservation Biology* 13:1047-1054.
- Ripple, W., and R. Beschta. 2004. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. *Forest Ecology and Management* 200:161-181.
- Sarkar, D. 2008. lattice: Lattice Graphics. R package version 0.17-17.
- Schaffers, A. P., I. P. Raemakers, K. V. Sýkora, and C. J. F. ter Braak. 2008. Arthropod assemblages are best predicted by plant species composition. *Ecology* 89:782–794.

Schmitz, O. J. 2009. Effects of predator functional diversity on grassland ecosystem function. *Ecology* 90:2339–2345.

Schuh, R. T., and J. A. Slater. 1995. *True Bugs of the World: Classification and Natural History*. Comstock Pub Assoc.

Schultz, N. L., J. W. Morgan, and I. D. Lunt. 2011. Effects of grazing exclusion on plant species richness and phytomass accumulation vary across a regional productivity gradient. *Journal of Vegetation Science* 22:130-142.

Seabloom, E. W., E. T. Borer, B. A. Martin, and J. L. Orrock. 2009. Effects of long-term consumer manipulations on invasion in oak savanna communities. *Ecology* 90:1356–1365.

Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences of the United States of America* 100:13384-13389.

Seabloom, E. W., J. W. Williams, D. Slayback, D. M. Stoms, J. H. Viers, and A. P. Dobson. 2006. Human Impacts, Plant Invasion, and Imperiled Plant Species in California. *Ecological Applications* 16:1338-1350.

Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79:2057–2070.

Siemann, E., D. Tilman, J. Haarstad, and M. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist*:738–750.

Simao, M. C. M., S. L. Flory, and J. A. Rudgers. 2010. Experimental plant invasion reduces arthropod abundance and richness across multiple trophic levels. *Oikos* 119:1553-1562.

Spyreas, G., B. W. Wilm, A. E. Plocher, D. M. Ketzner, J. W. Matthews, J. L. Ellis, and E. J. Heske. 2009. Biological consequences of invasion by reed canary grass (*Phalaris arundinacea*). *Biological Invasions* 12:1253-1267.

Stewart, A. J. A., and A. F. Wright. 1995. A new inexpensive suction apparatus for sampling arthropods in grassland. *Ecological Entomology* 20:98–102.

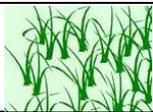
Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution* 19:46-53.

Triplehorn, C. A., and N. F. Johnson. 2004. Borror and DeLong's Introduction to the Study of Insects, 7th edition. Brooks Cole.

Venables, W. N. and Ripley, B. D. 2002. *Modern Applied Statistics with S*. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.

Wimp, G. M., S. M. Murphy, D. L. Finke, A. F. Huberty, and R. F. Denno. 2010. Increased primary production shifts the structure and composition of a terrestrial arthropod community. *Ecology* 91:3303–3311.

Table 3.1. Responses of the plant community to experimental treatments. A downward arrow indicates a decrease in that plant community variable in response to the treatment indicated; an upward arrow indicates an increase.

		Plant Community Response			
		Richness	Evenness	Biomass	Litter mass
Exotic grasses		0	↓ **	0	0
Grazing		0	↑ *	↓ †	↓ **

Arrows indicate a significant response to the treatment (**, $p < 0.01$; *, $p < 0.05$; †, $p < 0.1$). Plant community was compared between native perennial and exotic annual grass-dominated communities using a t-test, and between grazed and ungrazed treatments using paired t-tests.

Table 3.2. Results of linear model testing for significant impact of environmental parameters on arthropod diversity measures and biovolume of arthropod trophic guilds.

	Arthropod Diversity			Arthropod Biovolume					
	Abundance	Richness	Evenness	Total	Herbivore (ln herb)	Predator (ln pred)	Parasitoid	Detritivore	
Parameters	Exotic grasses (compared to Native)	-	-	-	348.4824*	0.4141	-0.8051	2.4307	0.5956
	Grazing	-	-	-	347.8504*	0.9091*	-2.3723**	1.2929	-1.5379
	Grass x Grazing interaction	-	-	-	418.9843*	0.6236	-1.9229*	0.5352	-0.3729
	Field/Block	-56.52***	-0.6416	0.0011*	-	0.0954***	-0.1388*	0.2498	-1.2271**
	Plant richness	30.87*	-	-0.0014*	-	-	-	-	-
	Plant evenness (Shannons)	-	30.6295*	-	-	-	6.2478**	-	-
	Plant biomass	-	-	0.00003	-0.4660	-	-	0.0118	-
	Litter mass	-	-	-	-	-	-0.0081†	-0.0198	-0.0449†
	F ratio (d.f.)	9.917(2,28)	4.897 (2,28)	3.665(3,27)	2.986(4,26)	5.836(4,26)	3.101(6,24)	1.224(6,24)	2.029(5,25)
Model p	0.0006	0.0150	0.02457	0.03736	0.0017	0.0216	0.3285	0.1090	
Adjusted R ²	0.3728	0.2062	0.2104	0.2094	0.392	0.2959	0.0430	0.1464	

Environmental parameters included experimental treatments and plant community measures. Each model started with all parameters, and the best-fitting model was selected using AIC. For each arthropod response variable, the parameter estimates (-, not included in final model) and their significance levels (***, p< 0.001; **, p<0.01; *, p< 0.05; †, p<0.1), and overall model statistics (F ratio with degrees of freedom, significance level, and R²), are given. (ln) natural log.

Table 3.3. Results of perMANOVAs evaluating differences in proportional morphospecies abundances between experimental treatments.

perMANOVA test	# plots	# morphos	Blocking F-ratio (df)	Treatment F-ratio (df)
Grazing	30	179	1.4012*(14)	2.4048*(1)
Grass in Ungrazed	16	138	1.7750 (1)	1.1931 (2)
Grass in Grazed	12	112	1.7110*(1)	0.9388 (2)

For each test, the number of plots, and the number of morphospecies, used in the analysis are included. The F-ratios, their significance levels (* $p < 0.001$), and the degrees for freedom (df) are given for each test. Paired grazing plots were evaluated with Field as a blocking factor to account for differences in baseline morphospecies' abundances between fields. Grass treatment was evaluated separately for grazed and ungrazed plots due to the complexity of the experimental design and were blocked by treatment block.

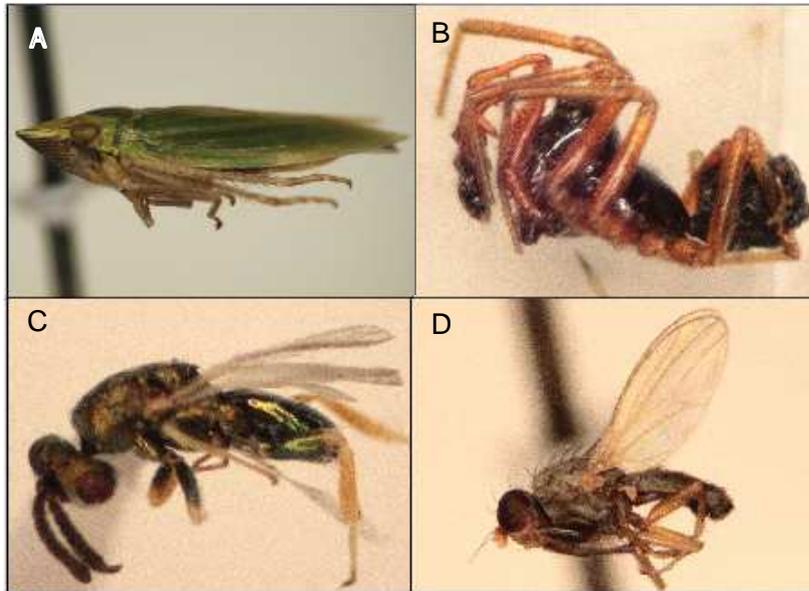


Figure 3.1. Examples of arthropod specimens from each trophic group: (A) an herbivore (Hemiptera: Auchenorrhyncha: Cicadellidae), (B) a predator (Araneae), (C) a parasitoid (Hymenoptera: Chalcidoidea), (D) a detritivore (Diptera: Heleomyzidae: *Trixoscelis*). 42 herbivorous, 29 predatory, 48 parasitoid, and 6 detritivorous arthropod morphotypes were identified in the experiment. 53 morphotypes had trophic preferences that were unknown or too varied to classify.

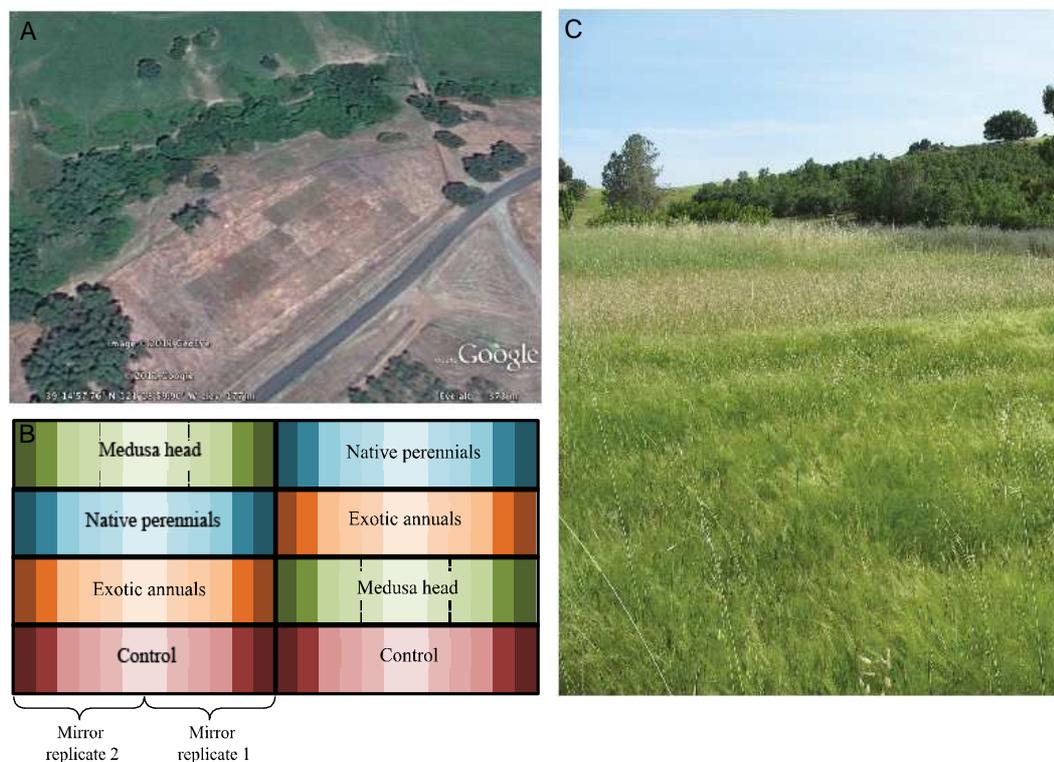


Figure 3.2. Plot experimental treatments. (A) A satellite photo of one of the experimental fields, taken June 2010, courtesy of Google Earth. (B) A diagram of the experimental setup of one of the fields. Plots were solarized in 2006, then planted with an exotic annual grass mixture, a native perennial grass mixture, an exotic Medusae head (*Taeneathrum caput-medusae*) grass monoculture, or left as a control in late 2006 and early 2007. Across these plantings, cattle herding and mowing were combined to create a gradient of grazing intensity, from heavy grazing at the centers of the plots (lightest color) to no grazing at the outside of the plots (darkest color). Two mirror replicates of each grass * grazing block were sampled, for a total of four samples from each grass*grazing combination in each field. (C) The vegetation differences between grass treatments were highly evident at the arthropod sampling date in May 2009.

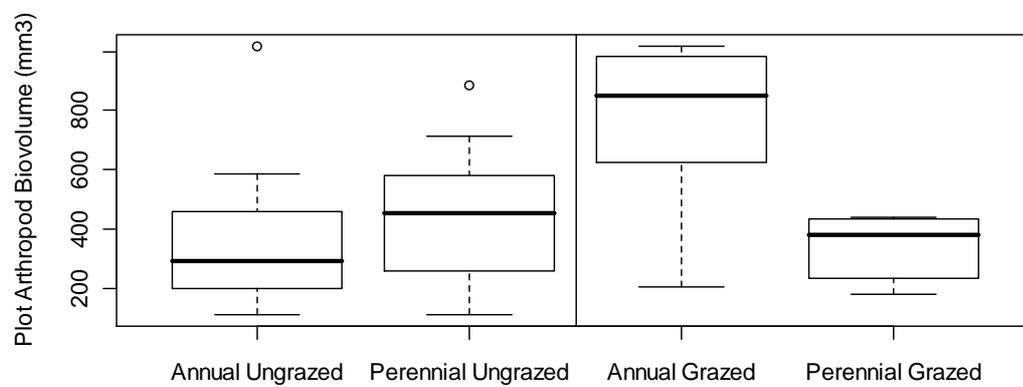


Figure 3.3. Response of total plot arthropod biovolume to grass provenance and grazing treatments.

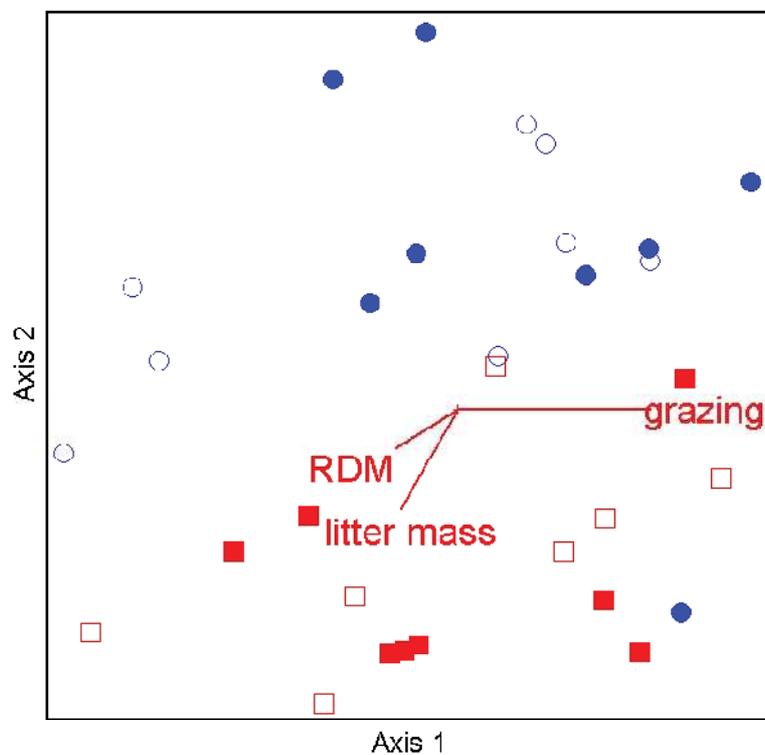


Figure 3.4. NMS ordination of plots in species space. Experimental field Scott5 is represented by red squares; field Scott14 by blue circles. Open shapes represent native perennial treatment plots; filled shapes represent exotic annual plots. Plots from the two fields were different from each other in the proportional representation of morphospecies they contained. Within both fields, grazing was negatively associated with litter mass and Residual Dry Matter (RDM), and was a strong predictor of arthropod assemblage. Arthropod assemblages from the two grass treatments were not distinct from each other.

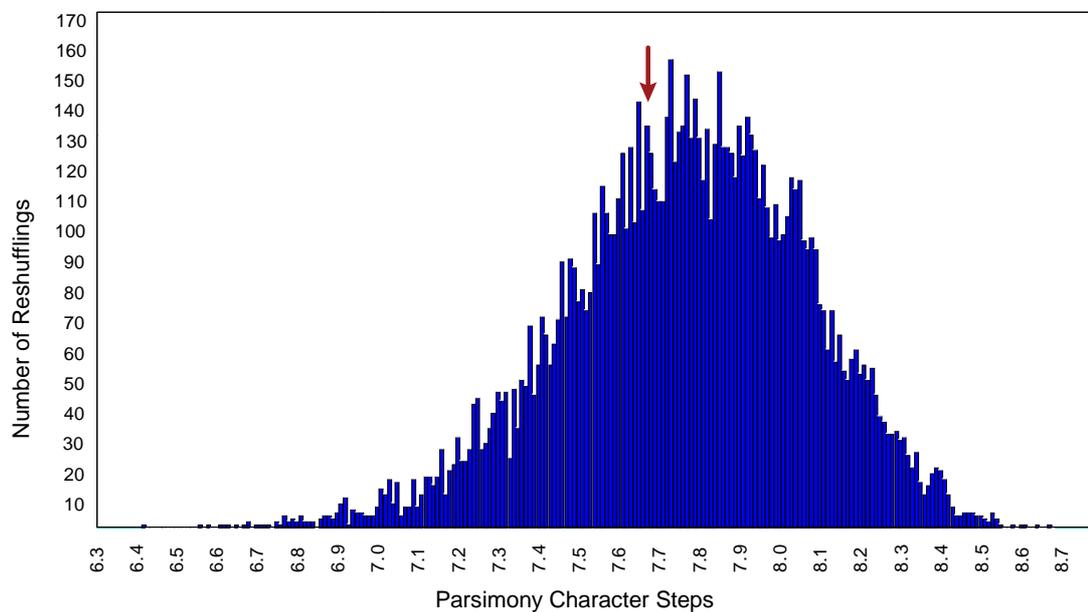


Figure 3.5. Number of squared changed steps as a result of reshuffling morphospecies correlations with grazing 10,000 times. Morphospecies' correlations with grazing were plotted on a tree reflecting their phylogenetic relationships and the correlation values reshuffled among the taxa. The number of squared change steps in the original phylogeny is indicated with an arrow; there is no indication that arthropod morphospecies responded to grazing as phylogenetically related groups ($p = 0.40$).

Chapter 4: General conclusions

In this thesis, I have explored the ways in which several types of human-induced disturbances can affect the arthropod community. I investigated two main themes in my research: (1) whether native and non-native vertebrate herbivores alter the arthropod community via changes in the plant community, and (2) how the invasion of non-native plants alters arthropod community composition.

Overall results suggest that vertebrate herbivores do alter the arthropod community. Whether their impacts cause bottom-up or top-down patterns in arthropod response depends on the types of modifications they cause in the plant community. Bottom-up increases in arthropod herbivore abundances are associated with shifting plant composition towards an annual-dominated, nutritious plant community. Top-down decreases in predator and increases in herbivore abundances were associated with reduced vegetation structural complexity caused by homogenization of the plant community or a shift towards structurally simple grasses. My findings also indicate that plant invasion alters the arthropod community by changing the relative abundance of nutrient-rich annual plants, rather than plant species identity within a functional guild.

I observed evidence of bottom-up changes in the arthropod community in both experiments. First, in the observational Hastings vertebrate exclosures described in Chapter 2, deer and other large vertebrate herbivores were positively associated with arthropod herbivore and detritivore abundances. Large vertebrates in that system are associated with a shift from native to exotic plant richness and cover (Seabloom et al. 2009), which increases the dominance of annual grasses. The increased nutrition associated with this change is likely the driver of observed increases in arthropod abundance with increasing exotic plant cover and vertebrate access.

In the Sierra Foothills grazing x plant provenance experiment described in Chapter 3, I also found evidence of bottom-up changes in the arthropod community. The exotic annual grass treatment supported greater arthropod biomass than the native perennial grass treatment even though it didn't shift the richness, evenness, or family-level composition of the arthropod community. This suggests that the nutrient composition of the annual grasses that drove the observed changes, rather than plant species identity.

The effect of annual grass treatment was only evident in the presence of grazing, suggesting a synergistic effect of the top-down effects of grazing and bottom-up effects of plant invasion. Grazing was associated with decreased plant evenness, and caused a decrease in predatory arthropods and increase in herbivorous arthropods. The homogenization of the plant community caused by grazing can decrease structural complexity, upon which spiders and other arthropod predators depend (Dennis et al. 2001). Because the top-down removal of predators and associated increase in herbivores often decreases producer biomass (Borer et al. 2006), this hints that grazing could decrease plant biomass both through direct removal and by triggering a top-down release of herbivorous arthropods. Moreover, herbivorous arthropods can increase the prevalence of vector-transmitted plant disease, which can shift competitive dominance between plant species (Borer et al. 2007), and accelerate the invasion of resistant annual grasses.

In the Hastings exclosures, gophers and burrowing mammals were associated with a decrease in predatory arthropod abundance but an increase in total arthropod abundance, also matching the pattern expected through top-down release. Since burrowing mammals decrease the vegetation structure associated with their mounds (Davidson and Lightfoot 2006) and predatory arthropods vary with vegetation structural complexity (Dennis et al. 2001), burrowers may have triggered a

qualitatively different impact on the arthropod community than large vertebrate herbivores.

Taken together, these results show that human alterations of different vertebrate guilds can impact the trophic structure of the arthropod community. Because arthropods mediate a number of ecosystem services, disturbances that alter arthropod assemblages can have far-reaching ecosystem impacts. By exploring the mechanisms by which manipulations of the vertebrate guild alter the arthropod community, this thesis can potentially inform managers of the types of constraints that must be overcome to restore function to degraded ecosystems, and demonstrates the importance of both consumer-prey interactions and diversity within trophic guilds.

Bibliography

- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46.
- Arnett, Jr., R. H. 2000. *American Insects: A Handbook of the Insects of America North of Mexico, Second Edition*, 2nd edition. CRC Press.
- Arnett, Jr., R. H., M. C. Thomas, P. E. Skelley, and J. H. Frank. 2002. *American Beetles, Volume II: Polyphaga: Scarabaeoidea through Curculionoidea*, 1st edition. CRC Press.
- Arnett, Jr., R. H., and M. C. Thomas. 2000. *American Beetles, Volume I: Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*, 1st edition. CRC Press.
- Arsenault, R., and N. Owen-Smith. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97:313-318.
- Bakker, E. S., H. Olf, M. Boekhoff, J. M. Gleichman, and F. Berendse. 2004. Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia* 138:91-101.
- Bakker, E. S., H. Olf, and J. M. Gleichman. 2009. Contrasting effects of large herbivore grazing on smaller herbivores. *Basic and Applied Ecology* 10:141-150.
- Bakker, E. S., M. E. Ritchie, H. Olf, D. G. Milchunas, and J. M. H. Knops. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters* 9:780-788.
- Bangert, R. K., and C. N. Slobodchikoff. 2006. Conservation of prairie dog ecosystem engineering may support arthropod beta and gamma diversity. *Journal of Arid Environments* 67:100-115.
- Barbour, M. G., and J. Major. 1977. *Terrestrial vegetation of California*. Wiley, New York.

- Behmer, S. T., and A. Joern. 2008. Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proceedings of the National Academy of Sciences* 105:1977.
- Belovsky, G. E., and J. B. Slade. 2000. Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences of the United States of America* 97:14412-14417.
- Belovsky, G. E., and J. B. Slade. 2002. An ecosystem perspective on grasshopper control: possible advantages to no treatment. *Journal of Orthoptera Research* 11:29-35.
- Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* 142:2401-2414.
- Bigger, D. S., and M. A. Marvier. 1998. How different would a world without herbivory be? A search for generality in ecology. *Integrative Biology*:60-67.
- Borer, E. T., B. S. Halpern, and E. W. Seabloom. 2006. Asymmetry in community regulation: effects of predators and productivity. *Ecology* 87:2813–2820.
- Borer, E. T., P. R. Hosseini, E. W. Seabloom, and A. P. Dobson. 2007. Pathogen-induced reversal of native dominance in a grassland community. *Proceedings of the National Academy of Sciences* 104:5473.
- Borer, E. T., C. E. Mitchell, A. G. Power, and E. W. Seabloom. 2009a. Consumers indirectly increase infection risk in grassland food webs. *Proceedings of the National Academy of Sciences* 106:503.
- Borer, E., V. Adams, G. Engler, A. Adams, C. Schumann, and E. Seabloom. 2009b. Aphid fecundity and grassland invasion: Invader life history is the key. *Ecological Applications* 19:1187-1196.
- Borer, E. T., V. T. Adams, G. A. Engler, A. L. Adams, C. B. Schumann, and E. W. Seabloom. 2009c. Aphid fecundity and grassland invasion: Invader life history is the key. *Ecological Applications* 19:1187-1196.

- Brusca, R. C., and G. J. Brusca. 1990. *Invertebrates*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Conant, R. T., K. Paustian, and E. T. Elliott. 2001. Grassland management and conversion into grassland: Effects on soil carbon. *Ecological Applications* 11:343-355.
- Connell, J. 1978. Diversity in tropical rain forests and coral reefs -- High diversity of trees and corals is maintained only in a non-equilibrium state. *Science* 199:1302-1310.
- Coupe, M. D., and J. F. Cahill Jr. 2003. Effects of insects on primary production in temperate herbaceous communities: a meta-analysis. *Ecological Entomology* 28:511–521.
- Crawley, M. J. 1989. The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. Page *Insect-Plant Interactions*, E. A. Bernays, ed. CRC Press, Florida.
- Davidson, A. D., and D. C. Lightfoot. 2006. Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography* 29:755–765.
- Davidson, A. D., and D. C. Lightfoot. 2008. Burrowing rodents increase landscape heterogeneity in a desert grassland. *Journal of Arid Environments* 72:1133–1145.
- Davidson, A. D., and D. C. Lightfoot. 2007. Interactive effects of keystone rodents on the structure of desert grassland arthropod communities. *Ecography* 30:515-525.
- Davidson, A. D., E. Ponce, D. C. Lightfoot, E. L. Fredrickson, J. H. Brown, J. Cruzado, S. L. Brantley, R. Sierra-Corona, R. List, D. Toledo, and G. Ceballos. 2010. Rapid response of a grassland ecosystem to an experimental manipulation of a keystone rodent and domestic livestock. *Ecology* 91:3189-3200.
- Dennis, P., J. Skartveit, D. I. McCracken, R. J. Pakeman, K. Beaton, A. Kunaver, and D. M. Evans. 2008a. The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology* 45:279–287.

Dennis, P., J. Skartveit, D. I. McCracken, R. J. Pakeman, K. Beaton, A. Kunaver, and D. M. Evans. 2008b. The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology* 45:279–287.

Dennis, P., M. R. Young, and C. Bentley. 2001a. The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. *Agriculture, ecosystems & environment* 86:39–57.

Dennis, P., M. R. Young, and C. Bentley. 2001b. The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. *Agriculture, ecosystems & environment* 86:39–57.

Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thébault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522–538.

Firn, J., J. L. Moore, A. S. MacDougall, E. T. Borer, E. W. Seabloom, J. HilleRisLambers, W. S. Harpole, E. E. Cleland, C. S. Brown, J. M. H. Knops, S. M. Prober, D. A. Pyke, K. A. Farrell, J. D. Bakker, L. R. O'Halloran, P. B. Adler, S. L. Collins, C. M. D'Antonio, M. J. Crawley, E. M. Wolkovich, K. J. La Pierre, B. A. Melbourne, Y. Hautier, J. W. Morgan, A. D. B. Leakey, A. Kay, R. McCulley, K. F. Davies, C. J. Stevens, C. Chu, K. D. Holl, J. A. Klein, P. A. Fay, N. Hagenah, K. P. Kirkman, and Y. M. Buckley. 2011. Abundance of introduced species at home predicts abundance away in herbaceous communities. *Ecology Letters* 14:274–281.

Futuyma, D. J., and F. Gould. 1979. Associations of Plants and Insects in Deciduous Forest. *Ecological Monographs* 49:33–50.

Gardner, S. M., M. R. Cabido, G. R. Valladares, and S. Diaz. 1995. The Influence of Habitat Structure on Arthropod Diversity in Argentine Semi-Arid Chaco Forest. *Journal of Vegetation Science* 6:349–356.

Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystems processes : lessons from Florida. *Ecol Appl* 8:975–989.

Goulet, H., and J. T. Huber. 1993. Hymenoptera of the World: An Identification Guide to Families. Agriculture Canada.

Gómez, J. M., and A. González-Megías. 2002a. Asymmetrical interactions between ungulates and phytophagous insects: being different matters. *Ecology* 83:203–211.

Gómez, J. M., and A. González-Megías. 2002b. Asymmetrical interactions between ungulates and phytophagous insects: being different matters. *Ecology* 83:203–211.

Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. *American Naturalist* 158:17-35.

Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, J. M. H. Knops, and D. Tilman. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12:1029-1039.

Harvey, K. J., D. R. Britton, and T. E. Minchinton. 2010. Insect diversity and trophic structure differ on native and non-indigenous congeneric rushes in coastal salt marshes. *Austral Ecology* 35:522-534.

Hillebrand, H., D. S. Gruner, E. T. Borer, M. E. S. Bracken, E. E. Cleland, J. J. Elser, W. S. Harpole, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and others. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences* 104:10904.

Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46:10-18.

Huntzinger, M., R. Karban, and J. H. Cushman. 2008. Negative effects of vertebrate herbivores on invertebrates in a coastal dune community. *Ecology* 89:1972–1980.

Jonsson, M., D. Bell, J. Hjältén, T. Rooke, and P. F. Scogings. 2010. Do mammalian herbivores influence invertebrate communities via changes in the vegetation? Results from a preliminary survey in Kruger National Park, South Africa. *African Journal of Range & Forage Science* 27:39.

Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* 2:286-293.

Levine, J. M., and C. M. D'Antonio. 2003. Forecasting Biological Invasions with Increasing International Trade. *Conservation Biology* 17:322-326.

Lindsay, E. A., and S. A. Cunningham. 2009. Livestock grazing exclusion and microhabitat variation affect invertebrates and litter decomposition rates in woodland remnants. *Forest Ecology and Management* 258:178-187.

Malmstrom, C. M., A. J. McCullough, H. A. Johnson, L. A. Newton, and E. T. Borer. 2005. Invasive annual grasses indirectly increase virus incidence in California native perennial bunchgrasses. *Oecologia* 145:153-164.

McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood. 1981. *Manual of Nearctic Diptera, Volume 1*. Agriculture Canada, Hull, Quebec, Canada.

McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood. 1987. *Manual of Nearctic Diptera, Volume 2*. Agriculture Canada, Hull, Quebec, Canada.

McCune, B., and J. Grace. 2002. *Analysis of Ecological Communities*. Mjm Software Design, Glenden Beach, Oregon.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative Effects of Grazing on Vegetation and Soils Over a Global Range of Environments. *Ecological Monographs* 63:327.

Miles, E. K., and J. M. H. Knops. 2009. Shifting dominance from native C4 to non-native C3 grasses: relationships to community diversity. *Oikos* 118:1844-1853.

Murdoch, W. W., F. C. Evans, and C. H. Peterson. 1972. Diversity and Pattern in Plants and Insects. *Ecology* 53:819-829.

- Novotny, V., Y. Basset, S. E. Miller, G. D. Weiblen, B. Bremer, L. Cizek, and P. Drozd. 2002. Low host specificity of herbivorous insects in a tropical forest. *Nature* 416:841-844.
- Novotny, V., P. Drozd, S. E. Miller, M. Kulfan, M. Janda, Y. Basset, and G. D. Weiblen. 2006. Why Are There So Many Species of Herbivorous Insects in Tropical Rainforests? *Science* 313:1115 -1118.
- Ohgushi, T. 2005. Indirect Interaction Webs: Herbivore-Induced Effects Through Trait Change in Plants. *Annual Review of Ecology, Evolution, and Systematics* 36:81-105.
- Oksanen, J., F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens and Helene Wagner 2010. *vegan: Community Ecology Package*. R package version 1.17-2. <http://vegan.r-forge.r-project.org/>.
- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1:3-19.
- Parker, J. D. 2006. Opposing Effects of Native and Exotic Herbivores on Plant Invasions. *Science* 311:1459-1461.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and Economic Costs of Nonindigenous Species in the United States. *BioScience* 50:53.
- Polis, G. A. 1999. Why Are Parts of the World Green? Multiple Factors Control Productivity and the Distribution of Biomass. *Oikos* 86:3-15.
- Pringle, R. M., T. P. Young, D. I. Rubenstein, and D. J. McCauley. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proceedings of the National Academy of Sciences* 104:193.
- Procheş, Ş., J. R. U. Wilson, D. M. Richardson, and S. L. Chown. 2008. Herbivores, but not other insects, are scarce on alien plants. *Austral Ecology* 33:691–700.

- Ramankutty, N., A. T. Evan, C. Monfreda, and J. A. Foley. 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles* 22:GB1003.
- Rambo, J. L., and S. H. Faeth. 1999. Effect of Vertebrate Grazing on Plant and Insect Community Structure. *Conservation Biology* 13:1047-1054.
- Ripple, W., and R. Beschta. 2004. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. *Forest Ecology and Management* 200:161-181.
- Sarkar, D. 2008. lattice: Lattice Graphics. R package version 0.17-17.
- Schaffers, A. P., I. P. Raemakers, K. V. Sýkora, and C. J. F. ter Braak. 2008. Arthropod assemblages are best predicted by plant species composition. *Ecology* 89:782–794.
- Schmitz, O. J. 2009. Effects of predator functional diversity on grassland ecosystem function. *Ecology* 90:2339–2345.
- Schuh, R. T., and J. A. Slater. 1995. *True Bugs of the World: Classification and Natural History*. Comstock Pub Assoc.
- Schultz, N. L., J. W. Morgan, and I. D. Lunt. 2011. Effects of grazing exclusion on plant species richness and phytomass accumulation vary across a regional productivity gradient. *Journal of Vegetation Science* 22:130-142.
- Seabloom, E. W., E. T. Borer, B. A. Martin, and J. L. Orrock. 2009. Effects of long-term consumer manipulations on invasion in oak savanna communities. *Ecology* 90:1356–1365.
- Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences of the United States of America* 100:13384-13389.

Seabloom, E. W., J. W. Williams, D. Slayback, D. M. Stoms, J. H. Viers, and A. P. Dobson. 2006. Human Impacts, Plant Invasion, and Imperiled Plant Species in California. *Ecological Applications* 16:1338-1350.

Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79:2057–2070.

Siemann, E., D. Tilman, J. Haarstad, and M. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist*:738–750.

Simao, M. C. M., S. L. Flory, and J. A. Rudgers. 2010. Experimental plant invasion reduces arthropod abundance and richness across multiple trophic levels. *Oikos* 119:1553-1562.

Spyreas, G., B. W. Wilm, A. E. Plocher, D. M. Ketzner, J. W. Matthews, J. L. Ellis, and E. J. Heske. 2009. Biological consequences of invasion by reed canary grass (*Phalaris arundinacea*). *Biological Invasions* 12:1253-1267.

Stewart, A. J. A., and A. F. Wright. 1995. A new inexpensive suction apparatus for sampling arthropods in grassland. *Ecological Entomology* 20:98–102.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution* 19:46-53.

Triplehorn, C. A., and N. F. Johnson. 2004. Borror and DeLong's Introduction to the Study of Insects, 7th edition. Brooks Cole.

Venables, W. N. and Ripley, B. D. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.

Wimp, G. M., S. M. Murphy, D. L. Finke, A. F. Huberty, and R. F. Denno. 2010. Increased primary production shifts the structure and composition of a terrestrial arthropod community. *Ecology* 91:3303–3311.

APPENDICES

Appendix A

Figure A.1: Histogram describing the plot occurrence of arthropod taxa in Hastings experimental plots. Almost half of observed taxa occurred in only one plot; 4 taxa occurred in all plots. One burrower-exclusion plot was located within a large-vertebrate exclusion plot; though both were never used in the same analysis, their arthropod assemblages are counted separately in this histogram.

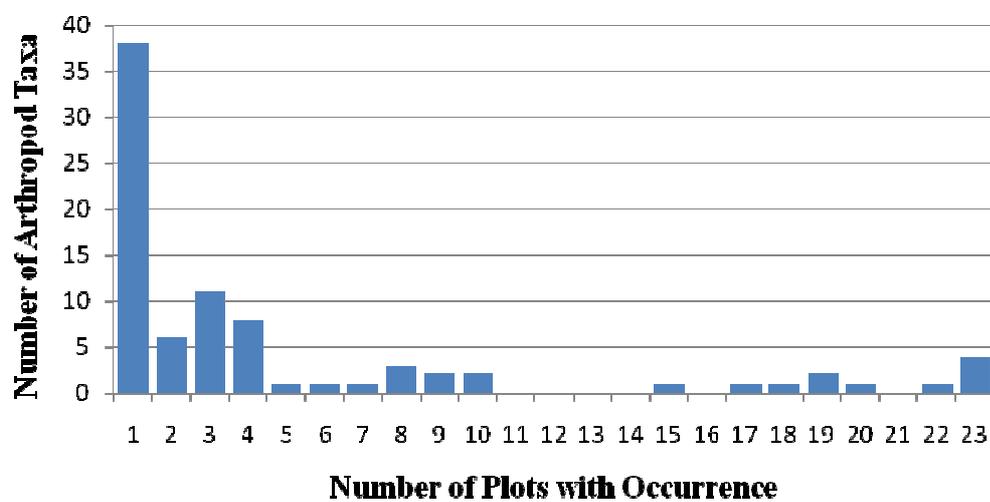


Table A.1: Table of arthropod taxa in Hastings native vertebrate exclosure experiment. All sampled taxa are displayed, but only taxa occurring in more than one plot were used in final community-level analyses. References used to determine trophic grouping are indicated with subscripts: 1, Schuh and Slater 1995; 2, Goulet and Huber 1993; 3a, Arnett, Jr. and Thomas 2000; 3b, Arnett, Jr. et al. 2002; 4a, McAlpine et al. 1981; 4b, McAlpine et al. 1987; 5, Arnett, Jr. 2000; 6, Triplehorn and Johnson 2004; 7, Brusca and Brusca 1990; 8, David Maddison, personal communication.

Taxon	Trophic group	Plots with occurrence	Total individuals
Acari	varied ₇	23	2897
Araneae- large	predator ₇	4	4
Araneae- medium	predator ₇	20	55
Araneae- small	predator ₇	22	194
Chelonethida	predator ₇	1	1
Coleoptera larvae	varied	9	17
Coleoptera- unknown	varied	3	3
Bruchidae	herbivore: seeds _{3b}	4	6
Cantharidae	herbivore: seeds _{3b}	3	4
Carabidae	varied ₈	8	49
Cleridae	varied _{3b}	1	1
Chrysomelidae	herbivore: vegetation _{3b}	2	2
Coccinellidae	predator _{3b}	1	1
Dascillidae	varied _{3b}	1	2
Elateridae	herbivore _{3b}	1	2
Endomychidae	fungivore _{3b}	2	2
Histeridae	predator _{3a}	4	5
Latridiidae	fungivore _{3b}	1	1
Lampyridae	predator _{3a}	3	3
Leiodidae	varied _{3a}	2	2
Mycetophagidae	fungivore _{3b}	1	1
Orsodacnidae	herbivore _{3b}	1	1
Phalacridae	fungivore _{3b}	1	1
Ptiliidae	fungivore _{3a}	3	3
Scaphidiidae	varied _{3a}	1	1
Staphylinidae	varied _{3a}	4	9
Tenebrionidae	varied ₈	10	28
Eosentomidae	fungivore ₅	1	1
Collembola- Globular	detritivore ₅	23	3855

Taxon	Trophic group	Plots with occurrence	Total individuals
Dermaptera- unknown	omnivore ₅	1	2
Forficulidae	omnivore ₅	1	4
Diplopoda	detritivore	1	1
Bibionidae	detritivore _{4a}	1	1
Muscidae	varied _{4b}	3	5
Mycetophilidae	varied _{4a}	4	7
Mydidae	varied _{4a}	1	1
Phoridae	varied _{4b}	17	45
Rhagionidae	predator _{4a}	3	4
Sepsidae	detritivore _{4b}	1	1
Sciaridae	detritivore _{4a}	10	18
Stratiomyidae	varied _{4a}	1	1
Therevidae	varied _{4a}	2	2
Tipulidae	varied _{4b}	2	4
Diptera- unknown	varied	1	1
Hemiptera immature	varied	8	10
Aphididae	herbivore: phloem ₅	9	11
Cicadellidae	herbivore: phloem ₅	18	50
Largidae	herbivore ₁	1	1
Lygaeidae	herbivore: seeds ₁	3	3
Miridae	varied ₁	1	2
Nabidae	predator ₁	1	1
Rhopalidae	herbivore ₁	4	6
Hemiptera- unknown	varied	4	4
Delphacidae	herbivore: phloem ₅	1	1
Diapriidae	parasitic ₂	7	12
Eulophidae	parasitic ₂	1	1
Formicidae	varied ₂	23	679
Halictidae	herbivore: pollen ₂	1	1
Ichneumonidae	parasitic ₂	1	1
Mutillidae	parasitic ₂	4	5
Mymaridae	parasitic ₂	1	1
Orussidae	parasitic ₂	1	1
Platygastridae	parasitic ₂	5	10
Pompilidae	parasitic ₂	3	3
Pteromalidae	parasitic ₂	1	1
Scelionidae	parasitic ₂	19	90

Taxon	Trophic group	Plots with occurrence	Total individuals
Hymenoptera- unknown	varied	3	3
Orthoptera immature	varied	1	1
Acrididae	herbivore: vegetation ₅	1	2
Gryllidae	omnivore ₅	6	12
Gryllacrididae	predator ₅	2	7
Tanaoceridae	herbivore: vegetation ₅	1	1
Orthoptera- unknown	varied	1	6
Chernetidae	predator ₇	3	3
Opiliones	omnivore ₇	8	21
Isopoda	detritivore	15	700
Pulicidae	parasitic ₅	1	1
Solpugidae	omnivore ₇	1	1
Thysanoptera	varied ₅	1	1
Phlaeothripidae	undetermined	1	1
Phloeothripidae	varied ₅	1	1
Thripidae	herbivore ₅	3	3
Thysanura	varied ₅	19	583

Appendix B

Table B.1: Table of arthropod morphospecies from Sierra Foothills grass provenance x grazing experiment, with grazing correlations. Arthropod taxa were identified by Kelly A. Farrell using keys in references 1-7 except where noted otherwise by subscripts. References used to determine trophic grouping are indicated with subscripts: 1, (Schuh and Slater 1995); 2, (Goulet and Huber 1993); 3a, (Arnett, Jr. and Thomas 2000); 3b, (Arnett, Jr. et al. 2002); 4a, (McAlpine et al. 1981); 4b, (McAlpine et al. 1987); 5, (Arnett, Jr. 2000); 6, (Triplehorn and Johnson 2004); 7, (Brusca and Brusca 1990); 8, David Maddison, personal communication; 9, Samantha Colby, personal communication; 10, crowd-sourced using the identification resource BugGuide.net; 11, Kojun Kanda, personal communication; 12, Danielle Lightle, personal communication. “*” preceding a trophic classification indicates that a larval foodsource is used though adults were collected.

Morphospecies	Order	Taxon	Trophic Grouping	Correlation with Grazing	Average Biovolume (mm ³)	Number of Individuals	Plots with Occurrence
104	Acarina	Ceratozetidae ₉		-0.1768	0.0188	1	1
903	Acarina			-0.2404	0.1117	3	2
906	Acarina			-0.1740	0.0061	139	3
911	Acarina	Mesostigmata ₉	predator ₉	0.2613	0.0393	14	5
904	Acarina	Prostigmata ₉	predator ₉	-0.3169	0.2068	3	3
907	Acarina	Prostigmata ₉	predator ₉	-0.2977	0.0503	208	11
908	Acarina	Prostigmata ₉	predator ₉	0.2208	0.1478	8	4
910	Acarina	Prostigmata ₉	predator ₉	-0.0738	0.0063	17	8
900	Acarina	Trombidiidae ₉	predator ₉	-0.2622	0.6413	68	10
901	Acarina	Trombidiidae ₉	predator ₉	0.4543	0.3058	615	28
902	Acarina	Trombidiidae ₉	predator ₉	-0.2497	0.0767	18	9
905	Acarina	Trombidiidae ₉	predator ₉	-0.0246	0.5737	42	11
912	Acarina	Trombidiidae ₉	predator ₉	-0.1092	0.1676	6	4
909	Acarina	Trombidiform ₉	predator ₉	0.1886	0.0251	1	1
800	Araneae		predator ₇	-0.2616	0.6362	6	5
801	Araneae		predator ₇	-0.0616	0.9385	32	14
802	Araneae		predator ₇	-0.1284	1.2704	9	6
803	Araneae		predator ₇	0.3485	1.1221	150	24
804	Araneae		predator ₇	-0.2543	43.8748	2	2
805	Araneae		predator ₇	-0.1188	0.2797	71	17
806	Araneae		predator ₇	-0.3633	0.6734	15	11
807	Araneae		predator ₇	-0.3494	0.5821	5	4

Morphospecies	Order	Taxon	Trophic Grouping	Correlation with Grazing	Average Biovolume (mm ³)	Number of Individuals	Plots with Occurrence
808	Araneae		predator ₇	0.1019	62.1910	5	5
809	Araneae		predator ₇	-0.2259	0.3011	4	2
810	Araneae		predator ₇	-0.1326	0.1747	96	13
811	Araneae		predator ₇	-0.1768	2.5133	1	1
812	Araneae		predator ₇	0.1886	19.7920	1	1
813	Araneae		predator ₇	0.2712	2.9845	2	2
814	Araneae		predator ₇	0.1197	3.8964	3	3
956	Collembola		detritivore ₅	0.1197	0.0265	3	3
1	Collembola	Sminthuridae	detritivore ₅	0.1915	1.7230	14005	31
2	Collembola	Sminthuridae	detritivore ₅	-0.1768	0.4712	3	1
958				-0.1806	0.0654	218	14
965				-0.1768	1.6965	1	1
10	Orthoptera	Acrididae	herbivore ₆	0.2465	39.2553	40	20
32	Thysanoptera	Thripidae	herbivore ₅	0.2320	0.4119	492	30
33	Thysanoptera			-0.3636	0.0515	34	12
950	Thysanoptera			-0.4343	0.2851	143	14
951	Thysanoptera			-0.3235	0.1251	817	28
953	Thysanoptera			0.2069	0.6671	12	3
30	Thysanoptera	Aeolothripidae		-0.0649	1.3404	220	27
31	Thysanoptera			-0.2421	3.5111	767	31
703	Hemiptera			0.2535	11.7286	48	9
711	Hemiptera			-0.1782	3.0240	5	3
733	Hemiptera			0.1197	1.2812	3	3
726	Hemiptera			0.1886	0.2011	1	1
734	Hemiptera			0.1886	3.3175	2	1
742	Hemiptera			0.2340	0.1402	12	10
743	Hemiptera			0.1886	168.5327	2	1
744	Hemiptera			0.1886	2.8510	1	1
723	Hemiptera	Anthocoridae		0.0093	3.2427	10	3
724	Hemiptera	Nabidae	predator ₁	-0.2543	25.0603	2	2
718	Hemiptera	Reduviidae	predator ₁	0.2727	0.9163	29	13
722	Hemiptera	Reduviidae	predator ₁	0.1886	63.9832	1	1
729	Hemiptera	Nabidae	predator ₁	0.1886	68.7632	1	1
725	Hemiptera	Lygaeidae	herbivore ₁	0.2712	2.5236	2	2
727	Hemiptera	Lygaeoidea	herbivore ₁	0.0809	20.7325	7	6
700	Hemiptera	Berytidae	herbivore ₁	0.2517	1.1573	56	13

Morphospecies	Order	Taxon	Trophic Grouping	Correlation with Grazing	Average Biovolume (mm ³)	Number of Individuals	Plots with Occurrence
707	Hemiptera	Berytidae	herbivore ₁	0.0227	4.9943	12	11
716	Hemiptera	Berytidae	herbivore ₁	-0.0600	0.0715	12	7
719	Hemiptera	Berytidae	herbivore ₁	0.3106	0.6160	6	3
732	Hemiptera	Berytidae	herbivore ₁	0.2959	0.6715	20	6
728	Hemiptera	Acanthosomatidae		-0.2543	42.2733	2	2
702	Hemiptera	Pentatomidae		-0.2600	8.7891	11	7
704	Hemiptera	Pentatomidae		-0.2854	49.7969	10	7
717	Hemiptera	Pentatomidae		0.3975	393.4428	4	4
720	Hemiptera	Pentatomidae		0.0891	43.9791	16	9
731	Hemiptera	Pentatomidae		-0.2404	571.8201	3	2
736	Hemiptera	Pentatomidae		0.1985	96.2042	5	3
710	Hemiptera	Pentatomidae		0.2370	32.6260	22	6
701	Hemiptera	Miridae		0.2127	7.7971	19	12
705	Hemiptera	Miridae		0.0658	37.8928	54	18
708	Hemiptera	Miridae		-0.0737	10.5371	22	10
712	Hemiptera	Miridae		-0.0249	20.2077	13	9
713	Hemiptera	Miridae		-0.4640	17.0846	22	15
714	Hemiptera	Miridae		-0.1576	18.2417	11	10
715	Hemiptera	Miridae		0.3324	25.7360	8	3
721	Hemiptera	Miridae		0.2305	9.1106	6	2
739	Hemiptera	Miridae		-0.1768	17.5207	1	1
741	Hemiptera	Miridae		0.1886	2.5447	1	1
709	Hemiptera	Miridae		-0.2543	6.9796	2	2
960	Hemiptera	Sternorrhyncha ₁₁	herbivore ₅	0.1886	0.1555	1	1
973	Hemiptera	Sternorrhyncha	herbivore ₅	-0.1768	0.1131	1	1
605	Hemiptera	Aleyrodidae	*herbivore ₅	0.2814	0.0731	35	12
609	Hemiptera	Psyllidae	herbivore ₅	-0.2922	0.6766	9	8
611	Hemiptera	Psyllidae	herbivore ₅	-0.1768	26.4648	1	1
600	Hemiptera	Aphididae	herbivore ₅	0.2955	0.5266	982	31
601	Hemiptera	Aphididae	herbivore ₅	-0.0300	0.5564	79	15
603	Hemiptera	Aphididae	herbivore ₅	0.2033	0.7474	34	17
610	Hemiptera	Coccoidea	herbivore ₅	-0.4252	0.2249	36	12
955	Hemiptera	Coccoidea	herbivore ₅	-0.2290	0.0194	34	15
969	Hemiptera	Coccoidea	herbivore ₅	0.0085	1.3085	2	2
521	Hemiptera	Cercopidae	herbivore ₅	-0.2543	4.3982	2	2
531	Hemiptera	Cercopidae	herbivore ₅	0.1886	2.7709	2	1

Morphospecies	Order	Taxon	Trophic Grouping	Correlation with Grazing	Average Biovolume (mm ³)	Number of Individuals	Plots with Occurrence
524	Hemiptera	Delphacidae	herbivore ₅	0.1634	3.3770	4	3
500	Hemiptera	Membracidae	herbivore ₅	-0.1443	122.2576	18	9
519	Hemiptera	Membracidae	herbivore ₅	0.1476	179.8387	7	3
502	Hemiptera	Cicadellidae	herbivore ₅	0.4921	13.4688	122	22
503	Hemiptera	Cicadellidae	herbivore ₅	0.0899	2.9836	46	14
504	Hemiptera	Cicadellidae	herbivore ₅	-0.1527	0.1636	47	19
505	Hemiptera	Cicadellidae	herbivore ₅	0.0124	2.8710	4	4
506	Hemiptera	Cicadellidae	herbivore ₅	-0.0527	7.8172	5	3
507	Hemiptera	Cicadellidae	herbivore ₅	0.2828	6.4191	41	11
508	Hemiptera	Cicadellidae	herbivore ₅	0.2266	0.3048	103	20
509	Hemiptera	Cicadellidae	herbivore ₅	-0.0986	1.7230	3	3
510	Hemiptera	Cicadellidae	herbivore ₅	-0.1235	11.7747	59	24
511	Hemiptera	Cicadellidae	herbivore ₅	-0.1719	11.1614	10	7
512	Hemiptera	Cicadellidae	herbivore ₅	0.4981	2.5133	29	16
513	Hemiptera	Cicadellidae	herbivore ₅	0.1886	0.5105	1	1
514	Hemiptera	Cicadellidae	herbivore ₅	0.2712	0.5890	2	2
515	Hemiptera	Cicadellidae	herbivore ₅	0.1363	0.5342	99	19
516	Hemiptera	Cicadellidae	herbivore ₅	0.1886	0.0440	1	1
517	Hemiptera	Cicadellidae	herbivore ₅	0.1357	0.2464	16	8
518	Hemiptera	Cicadellidae	herbivore ₅	0.1634	2.2774	4	3
520	Hemiptera	Cicadellidae	herbivore ₅	0.1197	3.6128	3	3
522	Hemiptera	Cicadellidae	herbivore ₅	-0.2543	2.5635	2	2
523	Hemiptera	Cicadellidae	herbivore ₅	0.0719	2.9103	9	7
525	Hemiptera	Cicadellidae	herbivore ₅	-0.1801	29.1912	4	4
526	Hemiptera	Cicadellidae	herbivore ₅	0.1886	12.3150	1	1
527	Hemiptera	Cicadellidae	herbivore ₅	0.1526	4.7393	39	7
528	Hemiptera	Cicadellidae	herbivore ₅	-0.0986	6.5531	3	3
529	Hemiptera	Cicadellidae	herbivore ₅	0.2894	6.7544	21	7
530	Hemiptera	Cicadellidae	herbivore ₅	0.1886	21.5592	1	1
501	Hemiptera	Cicadellidae	herbivore ₅	0.6069	3.1881	193	21
533	Hemiptera	Cicadellidae	herbivore ₅	0.1886	0.6786	1	1
106	Coleoptera	Chrysomelidae: Bruchinae _{8,11}	*herbivore _{3b}	0.2564	4.0901	3	2
101	Coleoptera	Lathridiidae _{8,11}	fungivore _{3b}	0.3570	0.6362	14	8
107	Coleoptera	Lathridiidae _{8,11}	fungivore _{3b}	0.1886	2.1901	2	1
109	Coleoptera	Anobiidae ₁₁		-0.1768	5.2025	1	1

Morphospecies	Order	Taxon	Trophic Grouping	Correlation with Grazing	Average Biovolume (mm ³)	Number of Individuals	Plots with Occurrence
103	Coleoptera	Corylophidae _{8,11}	fungivore _{3b}	0.1886	0.1963	1	1
111	Coleoptera			0.1886	5.5748	1	1
954	Coleoptera ₁₁			-0.1768	0.3848	2	1
963	Coleoptera ₁₁			-0.1768	0.0377	1	1
105	Coleoptera	Coccinellidae	predator _{3b}	-0.0928	56.0483	15	10
110	Coleoptera	Coccinellidae ₁₁	predator _{3b}	-0.1768	0.6220	1	1
108	Coleoptera	Coccinellidae ₁₁	predator _{3b}	0.0085	5.3093	2	2
100	Coleoptera	Melyridae: Dasytinae _{8,11}		-0.0696	5.7674	12	8
102	Coleoptera	Melyridae: Dasytinae _{8,11}		0.1019	23.1633	10	6
959	Neuroptera	Chrysopidae		0.1886	7.0686	1	1
964	Neuroptera	Hemerobiidae	predator ₅	-0.1768	1.2174	1	1
200	Lepidoptera		herbivore ₉	-0.1768	15.2681	2	1
962	Lepidoptera ₁₁		herbivore ₉	0.1886	0.5027	1	1
966	Lepidoptera ₁₁		herbivore ₉	0.1886	64.1120	3	1
972	Lepidoptera ₁₁		herbivore ₉	-0.1768	0.1979	14	1
305	Diptera			0.0085	0.4320	2	2
309	Diptera			0.4013	1.2017	22	13
313	Diptera			0.0099	0.2464	4	3
304.6	Diptera			-0.1768	0.1131	1	1
314	Diptera			0.1876	0.3334	8	3
319	Diptera			0.1886	0.1508	2	1
324	Diptera			-0.1768	0.0565	1	1
326	Diptera			-0.1768	2.6012	2	1
327	Diptera			-0.1768	0.5890	1	1
329	Diptera			-0.1768	0.8639	1	1
332	Diptera			-0.1768	0.4775	1	1
333	Diptera			0.1886	63.8136	1	1
317	Diptera			-0.3574	0.1764	12	7
321	Diptera			0.0437	0.0639	12	5
307	Diptera	Sciaridae	detritivore _{4a}	0.1272	0.1026	11	8
308	Diptera	Sciaridae	detritivore _{4a}	/	/	9	5
311	Diptera	Sciaridae	detritivore _{4a}	-0.1212	0.1372	15	7
316	Diptera	Chironomidae		-0.2625	0.4954	11	3
304	Diptera	Ceratopogonidae	predator ₁₀	0.1197	0.8294	6	4
310	Diptera	Ceratopogonidae	predator ₁₀	-0.2681	0.4506	21	6

Morphospecies	Order	Taxon	Trophic Grouping	Correlation with Grazing	Average Biovolume (mm ³)	Number of Individuals	Plots with Occurrence
312	Diptera	Ceratopogonidae : <i>Culicoides</i> ₁₀	predator ₁₀	-0.1514	0.6578	68	12
302	Diptera	Pipunculidae	parasitoid _{4b}	0.2564	8.5903	3	2
300	Diptera	Phoridae		0.2045	0.3147	24	14
322	Diptera	Phoridae		-0.2543	0.0798	2	2
318	Diptera	Muscidae		-0.2543	39.5608	4	2
325	Diptera	Tachinidae	*parasite _{4b}	-0.1768	31.7552	1	1
306	Diptera	Scathophagidae		-0.1582	0.3329	22	9
320	Diptera	Chloropidae		0.3381	4.4441	3	3
301	Diptera	Heleomyzidae: <i>Trixoscelis</i> ₁₀	*detritivore ₅	0.0531	14.6641	65	13
315	Diptera	Tephritidae		-0.0986	12.1857	3	3
323	Diptera	Simuliidae	predator _{4a}	0.0085	0.3519	2	2
499	Hymenoptera	Formicidae		/	/	2	2
427	Hymenoptera	Chrisidoidea ₁₂	parasitoid ₂	-0.0986	0.8508	3	3
303	Hymenoptera			0.0085	2.2117	2	2
429	Hymenoptera		parasitoid ₂	0.4391	0.1198	31	15
433	Hymenoptera		parasitoid ₂	-0.2543	0.2686	2	2
442	Hymenoptera		parasitoid ₂	0.1886	0.0079	1	1
467	Hymenoptera		parasitoid ₂	-0.1768	0.0628	1	1
4xy	Hymenoptera		parasitoid ₂	/	/	1	1
961	Hymenoptera			-0.1768	0.0377	1	1
414	Hymenoptera	Ceraphronidae ₁₂	parasitoid ₂	0.1634	0.1696	4	3
462	Hymenoptera	Diapriidae: <i>Ambositrinae</i> ₁₂	parasitoid ₂	0.0085	0.1272	2	2
454	Hymenoptera	Cynipoidea	herbivore ₂	0.1886	1.3085	1	1
458	Hymenoptera	Platygastroidea ₁₂	parasitoid ₂	0.0085	0.0503	2	2
416	Hymenoptera	Platygastridae ₁₂	parasitoid ₂	0.1151	0.0524	9	5
464	Hymenoptera	Platygastridae ₁₂	parasitoid ₂	0.1886	0.0173	2	1
445	Hymenoptera	Ichneumonoi- deae ₁₂	parasitoid ₂	-0.1436	0.5815	4	3
404	Hymenoptera	Ichneumonidae: <i>Phygadeuontini</i> ₁₀	parasitoid ₂	0.2712	0.4273	2	2
405	Hymenoptera	Brachionidae ₁₂	parasitoid ₂	-0.1475	0.3829	7	5
411	Hymenoptera	Brachionidae ₁₂	parasitoid ₂	-0.2543	1.4137	2	2
446	Hymenoptera	Brachionidae ₁₂	parasitoid ₂	-0.1768	0.0503	1	1
456	Hymenoptera	Brachionidae ₁₂	parasitoid ₂	0.1886	13.1193	1	1
459	Hymenoptera	Brachionidae ₁₂	parasitoid ₂	0.1886	0.0565	1	1
469	Hymenoptera	Vanhoriidae ₁₂	parasitoid ₂	0.1886	2.7709	1	1

Morphospecies	Order	Taxon	Trophic Grouping	Correlation with Grazing	Average Biovolume (mm ³)	Number of Individuals	Plots with Occurrence
4xx	Hymenoptera	Chalcidoidea	parasitoid ₂	/	/	1	1
400	Hymenoptera	Chalcidoidea	parasitoid ₂	0.0085	0.1979	2	2
401	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.1436	1.8064	4	3
402	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.3116	0.9702	8	3
406	Hymenoptera	Chalcidoidea	parasitoid ₂	/	/	1	1
406.3	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.1768	0.6676	1	1
407	Hymenoptera	Chalcidoidea	parasitoid ₂	0.2201	0.2575	32	20
408	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.1768	0.1131	1	1
417	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.1768	0.0565	1	1
418	Hymenoptera	Chalcidoidea	parasitoid ₂	0.2564	0.2545	3	2
419	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.1909	0.0638	6	3
423	Hymenoptera	Chalcidoidea	parasitoid ₂	0.1886	0.1272	1	1
424	Hymenoptera	Chalcidoidea	parasitoid ₂	0.0085	0.0834	2	2
425	Hymenoptera	Chalcidoidea	parasitoid ₂	0.3789	0.3598	39	11
426	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.0993	0.0740	8	6
428	Hymenoptera	Chalcidoidea	parasitoid ₂	0.2712	0.1424	2	2
437	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.1768	0.1272	1	1
449	Hymenoptera	Chalcidoidea	parasitoid ₂	0.2050	0.0914	4	4
451	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.1768	0.1367	4	1
457	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.0986	0.3016	3	3
460	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.1959	1.1027	10	2
461	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.1747	0.6414	11	3
450	Hymenoptera	Eurytomidae: <i>Sycophila</i> ₁₀	parasitoid ₂	-0.1768	0.5278	1	1
465	Hymenoptera	Chalcidoidea	parasitoid ₂	0.1886	4.2237	20	1
466	Hymenoptera	Chalcidoidea	parasitoid ₂	-0.1768	0.5781	2	1
468	Hymenoptera	Chalcidoidea	parasitoid ₂	0.1886	0.2969	2	1
452	Hymenoptera	Encyrtidae	parasitoid ₂	-0.1436	0.5701	4	3
406.2	Hymenoptera	Eulophidae	parasitoid ₂	-0.0291	0.2118	43	17
444	Hymenoptera	Eulophidae	parasitoid ₂	-0.1768	0.1979	1	1
448	Hymenoptera	Eulophidae	parasitoid ₂	0.1886	0.4775	1	1
415	Hymenoptera	Eupelmidae	parasitoid ₂	-0.1049	0.9480	13	8
440	Hymenoptera	Pteromalidae ₁₀	parasitoid ₂	-0.2970	0.7180	4	3
439	Hymenoptera	Torymidae ₁₀	parasitoid ₂	-0.2670	1.4434	9	5
412	Hymenoptera	Torymidae ₁₀	parasitoid ₂	-0.2294	2.4522	11	5
453	Hymenoptera	Torymidae	parasitoid ₂	-0.2543	0.3560	2	2

Morphospecies	Order	Taxon	Trophic Grouping	Correlation with Grazing	Average Biovolume (mm ³)	Number of Individuals	Plots with Occurrence
421	Hymenoptera	Trichogrammatidae ₁₂	parasitoid ₂	-0.3758	0.0487	41	14
432	Hymenoptera	Trichogrammatidae ₁₂	parasitoid ₂	-0.0214	0.0083	54	16
403	Hymenoptera	Aphelinidae ₁₂	parasitoid ₂	-0.0627	0.0482	14	10
409	Hymenoptera	Aphelinidae ₁₂	parasitoid ₂	0.3545	0.3534	7	4
420	Hymenoptera	Aphelinidae ₁₂	parasitoid ₂	0.0124	0.0440	4	4
410	Hymenoptera	Mymaridae ₁₂	parasitoid ₂	0.2128	0.0121	27	12
413	Hymenoptera	Mymaridae ₁₂	parasitoid ₂	-0.3588	0.0236	15	8
421.2	Hymenoptera	Mymaridae ₁₂	parasitoid ₂	0.0809	0.0305	7	6
430	Hymenoptera	Mymaridae ₁₂	parasitoid ₂	-0.0739	0.0356	8	4
431	Hymenoptera	Mymaridae	parasitoid ₂	0.0085	0.0134	2	2
434	Hymenoptera	Mymaridae ₁₂	parasitoid ₂	-0.2654	0.0276	10	7
435	Hymenoptera	Mymaridae ₁₂	parasitoid ₂	-0.2543	0.0534	2	2
436	Hymenoptera	Mymaridae ₁₂	parasitoid ₂	0.2561	0.1108	11	4
441	Hymenoptera	Mymaridae ₁₂	parasitoid ₂	-0.0736	0.0098	5	5
443	Hymenoptera	Mymaridae ₁₂	parasitoid ₂	0.1886	0.0157	2	1
447	Hymenoptera	Mymaridae ₁₂	parasitoid ₂	-0.2404	0.0157	3	2
455	Hymenoptera	Mymaridae ₁₂	parasitoid ₂	-0.1768	0.0503	1	1