



Effects of vertebrate herbivores and shrub characteristics on arthropod assemblages in a northern Arizona forest ecosystem

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ABSTRACT

Large herbivores have potential to affect invertebrate community structure through numerous processes, but little work has been done to evaluate the relative importance of direct and indirect factors. In this study, we measured arthropod community assemblages on *Ceanothus fendleri* A. Gray (Fendler's ceanothus) plants that were growing inside and outside of 4-m² exclosures. We used univariate analyses and structural equation modeling (SEM) to evaluate relationships within this herbivore–plant–arthropod system in ponderosa pine (*Pinus ponderosa* Laws.) forests of northern Arizona, USA. Results showed that individual arthropod abundance, family diversity, family richness, and functional group richness were significantly greater on plots where *C. fendleri* plants were protected from large ungulate herbivores (e.g., mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus nelsoni*)) than on unprotected plots in each of the three study years. Results also indicated the following: (1) arthropod abundance was significantly greater on protected plants than unprotected plants; (2) rarefaction curves suggested arthropod family richness was similar between protected and unprotected plants in two of the three years when scaled by number of individuals but the estimated total richness was consistently higher on protected plants; (3) arthropod abundance was directly affected by protection from herbivores, plant stem length, and number of flowers; (4) arthropod family richness was related to the number of individuals collected and affected by stem length. Results from this study illustrate that arthropod communities are directly affected by foraging vertebrate herbivores as well as indirectly affected through complex plant-mediated factors in this model system. Protection of preferred forage plants such as *C. fendleri* from ungulate herbivores can potentially increase diversity of arthropod assemblages in these forests, help conserve biological diversity, and enhance ecosystem restoration efforts.

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1. Introduction

Large herbivores often play a central role in determining the structure and functioning of ecosystems through direct and indirect effects of numerous activities including foraging, deposition of nutrients in dung and urine, and trampling of vegetation and soils. Herbivores such as deer (*Odocoileus* sp.) and elk (*Cervus* sp.) can affect survival, growth, and reproduction of individual plants and thereby influence plant community composition (Roininen et al., 1997; Dennis et al., 1998; Rambo and Faeth, 1999; Rooney and Waller, 2003; Huffman and Moore, 2003; Goheen et al., 2007). These effects on vegetation may cascade through ecosystems, impacting dynamics of other taxa such as invertebrates and their associated food webs (Siemann et al.,

1998). For example, decreases in invertebrate abundance may directly result when herbivores consume these organisms in the process of foraging (Polis et al., 1989). In addition, invertebrates may be indirectly affected through changes in the structure, quantity, or quality vegetation (Stewart, 2001; Barrett and Stiling, 2007). Variations in arthropod assemblages are ultimately likely to cascade through larger food webs (Danell and Huss-Danell, 1985; Bailey and Whitham, 2003; Rooney and Waller, 2003). To date, much research has addressed large herbivore effects on invertebrates by isolating and analyzing the factors individually (Rooney and Waller, 2003). Few studies have used multivariate approaches to examine herbivore–plant–invertebrate systems and analyze multiple interactions. In this study, we modeled relationships of an herbivore–plant–arthropod system in ponderosa pine (*Pinus ponderosa* Laws.) forests of Arizona that were undergoing ecological restoration.

Ponderosa pine forests of the southwestern United States suffered widespread exclusion of natural surface fires in the late

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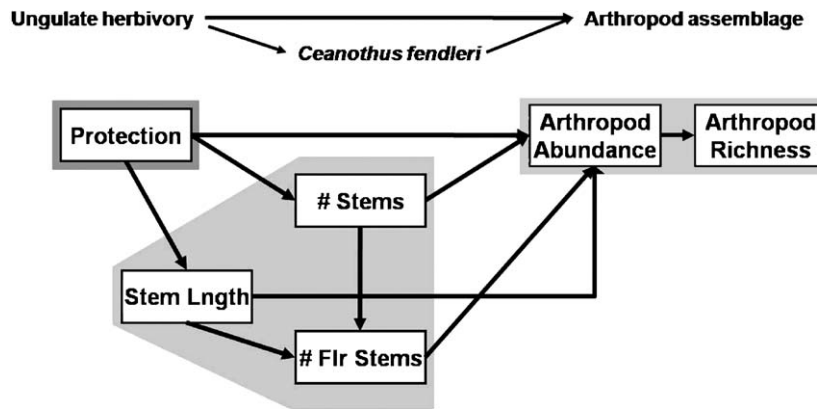


Fig. 1. Conceptual model of how ungulate herbivory may indirectly and directly affect arthropod community assemblages by browsing a common shrub (*Ceanothus fendleri*). All pathways were hypothesized to be positive relationships. This model illustrates the initial multivariate model that we evaluated using structural equation modeling.

19th century as a result of intensive livestock grazing of fine surface fuels of mainly grasses and forbs (Covington and Moore, 1994; Fulé et al., 1997). Fire exclusion and reduced competition with grasses in the understory favored tree seedling establishment and allowed for unprecedented tree regeneration pulses (Mast et al., 1999). Resulting dense forest conditions have led to numerous conservation concerns including reduced production and richness of understory plant communities and degradation of habitat quality for vertebrate and invertebrate species dependent on understory communities (Covington and Moore, 1994; Waltz and Covington, 2004). In addition, Rocky Mountain elk (*Cervus elaphus nelsoni*) were introduced in the early 20th century to replace Merriam's elk (*Cervus elaphus merriami*), which were extirpated by uncontrolled hunting before 1910 (Allen, 1996; Truett, 1996). Concurrent with elk reintroduction and management, predator control activities eliminated important large carnivores in the region, such as wolves (*Canis lupus* ssp.) and brown bears (*Ursus arctos* ssp.), by the mid 1900s (Brown, 1983). Rocky Mountain elk have subsequently become widespread and numerous in the forests of the Southwest (Allen, 1996). Overuse of forage resources in some locations suggests that elk herbivory may be exacerbating understory community degradation. Research on experimental restoration treatments suggests that thinning overstory trees and reintroducing low severity fire increases understory production as well as invertebrate diversity (Waltz and Covington, 2004; Laughlin et al., 2006; Moore et al., 2006). Protecting preferred forage species from large herbivores during the forest restoration process can allow plants to capitalize on increased resource levels after tree thinning and increase size, complete life cycles, and increase reproduction (Huffman, 2003). These changes can in turn have effects on arthropod populations. In this study, we modeled the relative importance of protection from large herbivores and plant characteristics on arthropod abundance and family richness. We selected *Ceanothus fendleri* Gray (Rhamnaceae; Fendler's ceanothus) as our model system.

C. fendleri is a semi-evergreen, nitrogen fixing shrub found in ponderosa pine forests throughout the Rocky Mountains and southwestern United States. In predominately herbaceous understories, the woody growth form of *C. fendleri*, being taller and more persistent than co-occurring grasses and forbs, can enhance structural heterogeneity and habitat diversity. High-protein content and palatability of the leaves of *C. fendleri* encourage year-round browsing by elk, deer, and leporids (Conard et al., 1985). Seeds, flowers, and other vegetative parts provide resources for various other animals including invertebrates (Huffman, 2006). Because of its common occurrence in these forests and its

importance to both ungulate herbivores and arthropods, *C. fendleri* provided a model system for studying large herbivore–invertebrate relationships.

In this study, we used structural equation modeling (SEM) to investigate the relative importance of causal factors influencing arthropod abundance and family richness. Evaluating hypotheses that partition direct and indirect effects requires an analytic framework that is designed to model multivariate relations between system components (Grace, 2006). SEM is an extension of regression and path analysis that can be used to model multivariate relations and to evaluate multivariate hypotheses (Bollen, 1989). The use of SEM has gained favor in recent years due to its potential to increase understanding of complex systems (Shipley, 2000; Grace, 2006). In turn, resulting information can be used to improve effectiveness of resource conservation efforts. In this study, we asked the following specific research questions: (1) Are arthropod abundance and family richness on *C. fendleri* positively related to protection of plants from large ungulate herbivores? (2) Does protection of *C. fendleri* from ungulates increase diversity of arthropod functional groups? (3) Are direct effects of protection more important in determining arthropod abundance and richness than indirect effects? (4) Is aerial stem length more important in affecting changes in arthropod assemblage than number of stems or number of flowering stems? To answer these questions, we developed a theoretical model of hypothesized causal relationships among variables in this ungulate herbivore–plant–arthropod system (Fig. 1).

2. Methods

2.1. Study site

This study was conducted on the Fort Valley Experimental Forest (35° 16' N, 111° 41' W) within the Coconino National Forest, 15 km NW of the city of Flagstaff in northern Arizona. Elevation of the study site ranged from 2225 to 2380 m, with gentle rolling topography and southerly slope gradients less than 15%. Annual precipitation averages 520 mm, which falls in late summer as rain from monsoonal thunderstorms and in winter as snow. Soils are of basalt and volcanic origin and consist of a complex of fine, montmorillonitic, frigid Typic Argiborolls and mollic Eutroboralfs (Covington et al., 1997). Overstory vegetation was nearly pure ponderosa pine with an understory dominated by grasses, mainly *Festuca arizonica*, *Muhlenbergia montana* and *Elymus elymoides*; a variety of forbs, and a few shrubs such as *C. fendleri* and *Rosa woodsii*. Domestic livestock were not present on the site and large

herbivores included mule deer (*Odocoileus hemionus*) and Rocky Mountain elk. Although wolves and brown bears were no longer present, mountain lions (*Puma concolor*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), and bobcats (*Felis rufus*) were other potential predators occurring at the study site.

In 1998–1999, experimental ecosystem restoration treatments were implemented at the study site. Treatments included thinning trees in experimental forest units (14–16 ha in size) from approximately 1490–1040 trees ha⁻¹ before treatment to 240–140 trees ha⁻¹ post-treatment. Large and old trees (e.g., ≥35.7 cm in diameter measured at 1.37 m above ground) were retained, along with a limited number of smaller trees (for details regarding treatment prescriptions, see Fulé et al., 2001). Experimental units were burned with prescribed fire in 2000–2001. These treatments were designed to address undesirable ecological conditions arising from high tree densities, which in turn developed as a result of early intensive livestock grazing and fire exclusion (Moore et al., 1999).

2.2. Experimental design

Our study was part of a larger experiment, initiated in 1999 to examine responses of *C. fendleri* to experimental forest restoration treatments (Huffman, 2003). For purposes of the experiment, *C. fendleri* plots were established in three of the experimental forest units described above. Sixty *C. fendleri* shrubs were located within each of the three forest units for a total of 180 plants. Shrubs were groups of 1–25 upright stems and generally covered an area less than 2 m². Centered on each shrub, we established a 1-m² sample plot. In each forest unit, 30 plots were randomly selected for protection from large herbivores. Exclosures 4 m² in area and 1.4 m in height were constructed around shrubs selected for protection. A large mesh size of 5 cm × 10 cm and open tops on the exclosures allowed entry of small animals including birds and invertebrates but excluded large ungulate herbivores. Exclosures were constructed after overstory trees were thinned in 1999.

2.3. Plant and arthropod sampling

As part of the long-term study, yearly data from 1999–2004 were collected on the number of flowering stems, total number of stems and average stem lengths on *C. fendleri* plots. In June of years 2002, 2003, and 2004, we used sweep nets (39 cm diameter) to sample invertebrate assemblages on the plots. In 2002, we sampled all plots with live shrub individuals in two of the three forest units ($n = 52$). In 2003 and 2004, we randomly selected 10 plots from each group, (protected and unprotected) within each of the three forest units ($n = 30$). At each plot, nets were swept five times through the plant stems at approximately 20–50 cm above the ground. For plots with the majority of stems shorter than 50 cm, invertebrates were collected with aspirators in addition to sweep nets; overall arthropod individuals collected with aspirators represented very minor contributions to samples. Plot samples were fumigated in jars containing ethyl acetate, and then transferred to collection vials containing 70% isopropyl alcohol. Samples were transported back to the lab where samples were sorted. Insect arthropods were identified to family using Borror et al. (1989). Báldi (2003) has shown that family diversity is a good surrogate measure of species diversity, particularly for large arthropod groups (e.g., Coleoptera and Diptera). Specimens that were difficult to identify were sent to the USDA Systematic Entomology Laboratory in Beltsville, MD. The only non-insect arthropods captured in this study were in the order Araneae and we did not attempt to identify these families. For analysis of functional richness, we assigned insect arthropod families to functional groups (e.g., predator, pollinator, herbivore, parasitoid,

omnivore, detritivore, scavenger, or unknown). We based this categorization on general ecological information provided by Borror et al. (1989); however, we acknowledge that some families may represent multiple functional groups. All Araneae were considered predators.

2.4. Univariate analyses

We analyzed effects of ungulate herbivory on arthropod communities by comparing protected and unprotected plots in terms of arthropod abundance (total individuals), family richness, family diversity, functional group richness, and abundance of individuals within functional groups. For each of the three study years, variables were compared using a Wilcoxon two-sample nonparametric test with JMP-IN 5.1 software (SAS, 2004). We did not analyze time effects on dependent parameters since sample plots were randomly selected each year and therefore were not suitable for repeated measures analysis. To calculate family diversity, we used Shannon's diversity index (H') where: $H' = -\sum p_i \log_e p_i$ and p_i is the proportion of the total number of arthropods represented by family i divided by the total number of arthropods (Price, 1997). To account for relationships between family richness and number of individuals captured, we compared Coleman rarefaction curves (Coleman, 1981), plotted for protected and unprotected plots in each of the three study years, as suggested by Gotelli and Colwell (2001). In addition, we estimated total family richness using the Michaelis–Menten function (Colwell and Coddington, 1994). These analyses were performed using EstimateS, Version 8.0 (Colwell, 2006).

2.5. Structural equation modeling

To examine the relative importance of herbivore protection and plant characteristics on arthropod assemblages, we used observed variable SEM (Bollen, 1989). We examined bivariate plots for the presence of outliers, evidence of skewness or kurtosis, and nonlinear relationships. We acknowledge that not all causal processes that act in this system are represented in Fig. 1. Rather, our objective was to determine whether the data were consistent with the expectations of the proposed model. Ultimately, the goal was to arrive at a model consistent with the data using the fewest modifications of the initial hypothesized model as possible, thereby preserving the ability to draw inferences from model parameters. The final structural equation model describes a covariance structure that is consistent with the covariance structure of the dataset; theory, then, guides our interpretation of the mechanistic nature of the directional paths.

Our initial model included squared terms of arthropod abundance and shrub stem length because bivariate scatter plots indicated second-order polynomial relationships to other variables in the model. However, only significant squared terms were retained in the final model. Robust maximum likelihood solution procedures were used and we relied on chi-square goodness of fit measures to evaluate model adequacy (note that large P -values (>0.05) imply no statistical difference between model and data). The degrees of freedom when using robust maximum likelihood estimators are estimated according to a formula given in the Mplus Technical Appendices (Muthen and Muthen, 2005). Residuals and modification indices were also examined to determine if there were obvious model-data discrepancies. Analyses were performed using Mplus software (Muthen and Muthen, 2005). For simplicity, we evaluated the model using data collected in 2003, which was a nearer-normal year for spring precipitation (53% of 30-year average, January–June) compared to 2002 (12% of average) and 2004 (44% of average) (WRCC, 2007). Finally, we calculated the standardized 'direct' and 'indirect' effects, the sum of which equals

the 'total effects' of a factor on a response (Grace, 2006). Coefficients were standardized by converting them into units of standard deviations. Indirect effects equal the total sum of the products of all path coefficients from a predictor to richness. Direct effects are the individual coefficients in the model. Total effects are a simple summary of the complex relationship between the factors and arthropod family richness and they provide a calculation of the net effect (i.e., strength and sign) of a relationship. Standardized direct, indirect, and total effects range from -1 to +1.

3. Results

3.1. Comparison of protected and unprotected plots

A total of 13 orders and 65 families were collected during the three-year period (Appendix A). Families in the Coleoptera, Diptera, Hemiptera, Homoptera, and Hymenoptera orders were found in each of the three sample years on plots protected from large ungulate herbivores. Similarly, Diptera, Homoptera, and Hymenoptera were found on unprotected plots each year. Of the five most abundant families collected in each of the three years, protected and unprotected plots had 2–3 of these in common (Table 1). In all years, individual arthropod abundance, family diversity, family richness, and functional group richness were significantly greater on protected plots than on unprotected plots (Table 2). Herbivore arthropods were the most abundant and frequent functional group, comprising on average 63% of the individuals captured and occurring on more than 50% of the plots. In this functional group, sapsuckers in the orders Homoptera (Auchenorrhyncha and Sternorrhyncha suborders) and Hemiptera, and chewers in the order Coleoptera, were consistently abundant (Table 1). Predators were second most abundant followed by omnivores, pollinators, and parasitoids, respectively. Twenty percent of the arthropods were identified as having a strong relationship with flowers, either as pollinators or florivores. Herbivores and omnivores were more abundant on protected plots than unprotected plots in all three years. Predator and parasitoid arthropods were more abundant on protected plots in 2003 and 2004, while pollinators were more abundant on protected plots only in 2003 (Table 2).

Rarefaction curves showed no difference in family richness between protected and unprotected plots at similar numbers of captured arthropod individuals in 2002 and 2003 (Fig. 2). In 2004,

family richness was significantly greater on protected plots than unprotected plots when scaled by number of individuals captured. Total estimated family richness in all three study years was higher on protected plots than unprotected plots (Fig. 2).

Arthropod family richness exhibited significant bivariate relationships with all five factors tested in the model (Fig. 3). Richness exhibited nonlinear positive relationships with arthropod abundance and number of flowering stems, and richness exhibited positive linear relationships with number of stems, stem length, and protection from herbivores (Fig. 3).

3.2. Structural equation model

The initial model (Fig. 1) described the multivariate relations in the data well ($\chi^2 = 6.2$, 3 d.f., $P = 0.10$). Inclusion of a direct path from protection to arthropod family richness was not significant, despite the significant univariate relationship (Fig. 3). However, the addition of a pathway from stem length to arthropod family richness was significant and this final model fit the data well (Fig. 4; $\chi^2 = 5.8$, 3 d.f., $P = 0.12$). Evaluations of standardized total effects (Table 3) suggest that protection from ungulate herbivory indirectly increased arthropod family richness (standardized total effects coefficient = 0.56).

The SEM analysis yielded the following three results: (1) arthropod family richness was indirectly affected by protection from browsing of *C. fendleri*, (2) arthropod family richness exhibited a positive yet nonlinear relationship with arthropod abundance and was weakly positively affected by stem length, (3) arthropod abundance was influenced most strongly by a direct, positive effect of protection from browsing and secondarily by indirect effects through changes in structural characteristics (stem length and number of flowering stems) of *C. fendleri*.

4. Discussion

4.1. Effects of ungulate herbivory on arthropod assemblages

In each of the three years of our study, we found greater arthropod abundance and family richness on shrubs that were protected from ungulates. Rarefaction curves showed that high observed family richness on protected plots was related to greater numbers of arthropod individuals collected on these plots compared with unprotected plots. Indeed, when scaled by number

Table 1

Mean number of individuals and functional groups for the five most abundant arthropod families captured on *Ceanothus fendleri* plots protected and unprotected from large herbivores in 2002, 2003, and 2004. Standard error of the mean shown in parentheses.

Year	Protected				Unprotected			
	Order	Family	Function ^a	Abundance	Order	Family	Function	Abundance
2002	Auchenorrhyncha ^b	Psyllidae	Herbivore (ss)	1.51 (0.048)	Auchenorrhyncha ^b	Psyllidae	Herbivore (ss)	0.31 (0.017)
	Coleoptera	Chrysomelidae	Herbivore (c)	0.31 (0.015)	Araneae	n.i.	Predator	0.06 (0.004)
	Hymenoptera	Formicidae	Omnivore	0.23 (0.018)	Coleoptera	Chrysomelidae	Herbivore (c)	0.04 (0.004)
	Hemiptera	Miridae	Herbivore (ss)	0.12 (0.007)	Hymenoptera	Colletidae	Pollinator	0.04 (0.005)
	Araneae	n.i.	Predator	0.10 (0.006)	Diptera	Bombyliidae	Pollinator	0.02 (0.003)
2003	Coleoptera	Tenebrionidae	Herbivore (c)	2.23 (0.124)	Sternorrhyncha ^b	Cicadellidae	Herbivore (ss)	0.57 (0.041)
	Diptera	Empididae	Predator	1.53 (0.098)	Collembola	Sminthuridae	Detritivore	0.23 (0.037)
	Collembola	Sminthuridae	Detritivore	1.37 (0.149)	Diptera	Bombyliidae	Pollinator	0.17 (0.025)
	Diptera	Bombyliidae	Pollinator	1.20 (0.090)	Hymenoptera	Formicidae	Omnivore	0.13 (0.011)
	Hemiptera	Miridae	Herbivore (ss)	1.03 (0.053)	Hemiptera	Rhopalidae	Herbivore (ss)	0.10 (0.010)
2004	Hymenoptera	Formicidae	Omnivore	1.60 (0.066)	Hymenoptera	Formicidae	Omnivore	0.37 (0.040)
	Sternorrhyncha ^b	Cicadellidae	Herbivore (ss)	0.77 (0.040)	Auchenorrhyncha ^b	Psyllidae	Herbivore (ss)	0.17 (0.025)
	Hemiptera	Miridae	Herbivore (ss)	0.67 (0.031)	Araneae	n.i.	Predator	0.07 (0.008)
	Araneae	n.i.	Predator	0.47 (0.041)	Collembola	Sminthuridae	Detritivore	0.07 (0.008)
	Auchenorrhyncha ^a	Psyllidae	Herbivore (ss)	0.43 (0.026)	Thysanoptera	Thripidae	Herbivore (ss)	0.07 (0.008)

^a For herbivores, (ss): sapsuckers and (c): chewers.

^b Suborder of Homoptera.

Table 2
Mean (and standard error (SE)) of arthropod abundance (no. individuals per plot), family richness (no. families per plot), diversity (Shannon's H'), functional group richness (no. functional groups per plot), and abundance within functional groups (no. per plot) on protected and unprotected *Ceanothus fendleri* plots in 2002, 2003 and 2004. Wilcoxon two-sample tests indicated that protected plots had significantly ($P < 0.001$) larger values than unprotected plots for all variables shown below except those indicated with "ns" (non-significant; $P > 0.05$).

Year	Treatment	n	Arthropod abundance	Family richness	Family diversity (H')	Functional group richness	Assemblage composition				
							Herbivore	Predator	Omnivore	Pollinator	Parasitoid
2002	Protected	52	2.70 (0.44)	1.43 (0.17)	0.31 (0.05)	1.06 (0.11)	2.17 (0.38)	0.13 (0.05) ns	0.24 (0.13)	0.06 (0.03) ns	0.05 (0.03) ns
	Unprotected	52	0.52 (0.16)	0.35 (0.11)	0.06 (0.03)	0.31 (0.09)	0.38 (0.13)	0.06 (0.03) ns	0.00 (0.00)	0.06 (0.03) ns	0.02 (0.02) ns
2003	Protected	30	15.76 (2.97)	6.83 (0.98)	1.48 (0.17)	2.90 (0.30)	8.18 (1.52)	2.80 (0.63)	0.7 (0.25)	3.12 (0.95)	0.66 (0.24)
	Unprotected	30	1.87 (0.54)	1.30 (0.03)	0.26 (0.09)	0.83 (0.14)	1.30 (0.41)	0.12 (0.06)	0.13 (0.06)	0.25 (0.19)	0.00 (0.00)
2004	Protected	30	7.60 (1.01)	4.77 (0.44)	1.31 (0.11)	2.53 (0.21)	3.98 (0.62)	0.98 (0.27) ns	1.6 (0.36)	0.01 (0.07)	0.20 (0.08)
	Unprotected	30	0.83 (0.29)	0.50 (0.13)	0.09 (0.04)	0.40 (0.11)	0.33 (0.15)	0.06 (0.05) ns	0.37 (0.22)	0.00 (0.00)	0.00 (0.00)

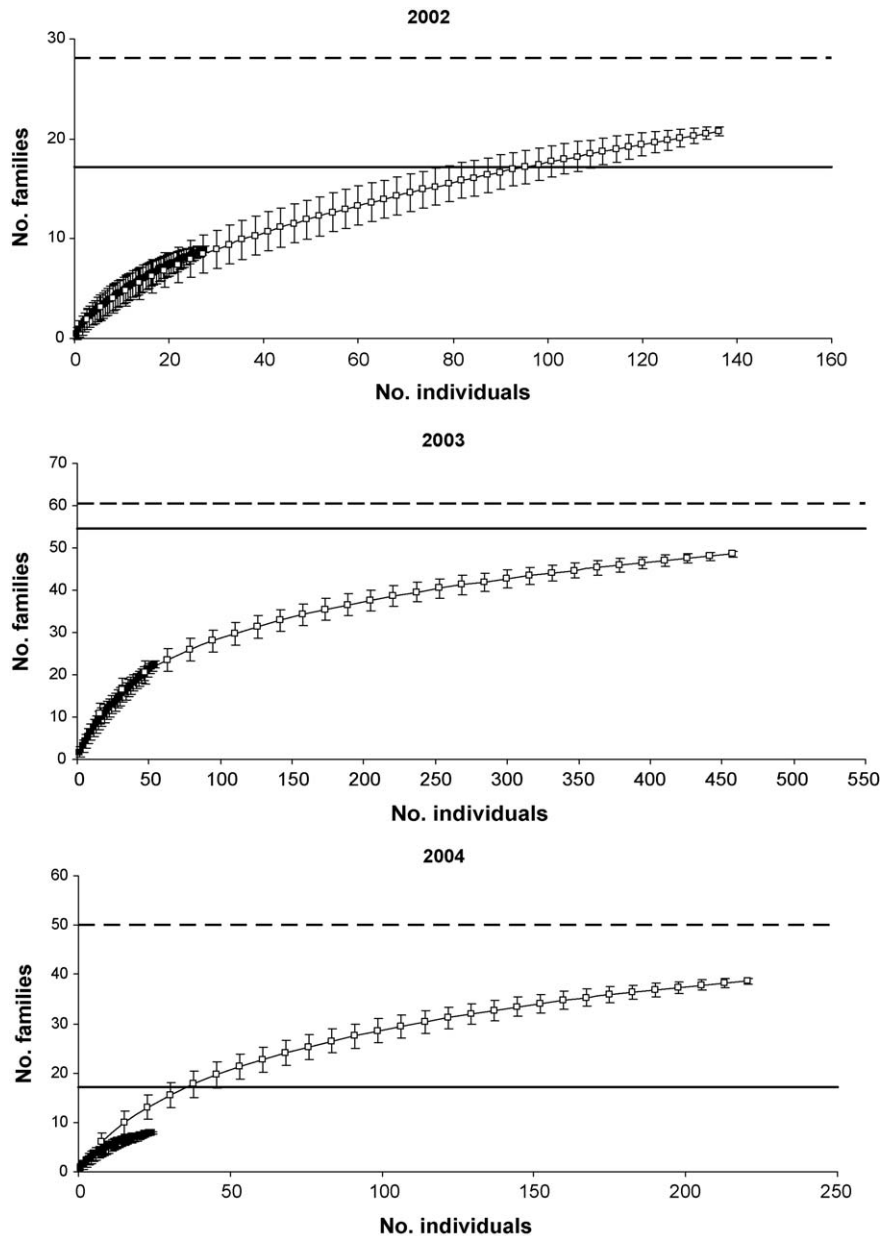


Fig. 2. Rarefaction curves showing estimated relationship between arthropod family richness and number of individuals for protected (open symbols) and unprotected (closed symbols) *C. fendleri* plots in three sample years. Horizontal lines indicated estimated total richness for the two groups (protected is dashed line; unprotected is solid line).

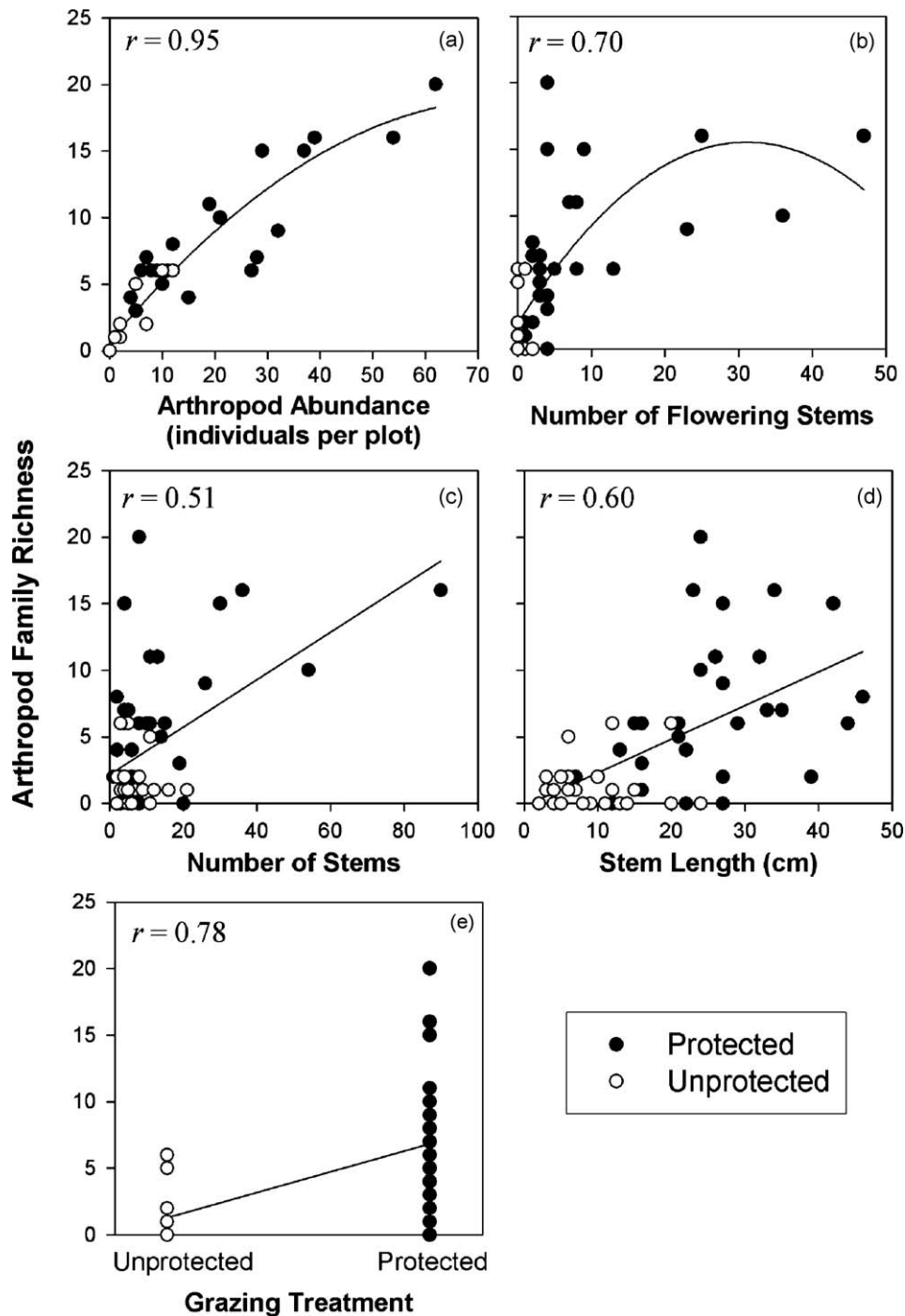


Fig. 3. Bivariate relationships between arthropod family richness and arthropod abundance (a); number of flowering stems (b); number of stems (c); mean stem length (d), and ungulate protection treatment (e). Note that symbols are coded to illustrate whether the plots were protected or not. All relationships are highly significant ($P < 0.05$).

of arthropod individuals collected, observed family richness was greater on protected plots only in 2004. However, estimated total richness was higher for protected plots in all years. These results suggest that, in addition to number of individuals occurring, arthropod family richness was also affected by differences in plant characteristics between protected and unprotected plots. Because we did not identify arthropods below the level of family, species richness was likely underestimated in this study. However, general patterns we found regarding family richness are likely to hold true at finer taxonomic resolution (Báldi, 2003).

Numerous factors influence plant responses to herbivory, and these responses may indirectly affect arthropod communities. In

some cases, herbivory can stimulate flower production or enhance plant growth. For example, Paige and Whitham (1987) reported increased flower production of *Ipomopsis aggregata* after experimental clipping as well as natural herbivory by deer and elk. Similarly, Throop and Fay (1999) found that browsed *Ceanothus herbaceus* produced a greater number of inflorescences than unbrowsed plants on a tallgrass prairie site. In contrast, intensive herbivory on other species can reduce growth and reproduction. For example, Huffman and Moore (2003) found that unprotected *C. fendleri* plants had significantly shorter aerial stems, fewer stems, and lower rates of flowering than protected plants in the first few years following implementation of ponderosa pine forest restora-

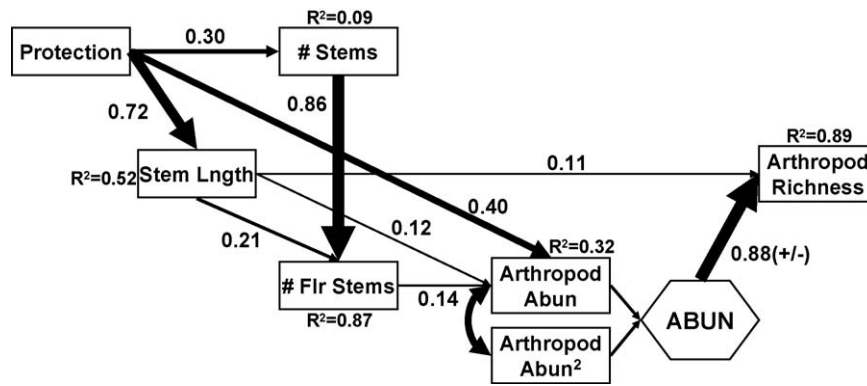


Fig. 4. Final structural equation model with standardized path coefficients ($\chi^2 = 5.8$, 3 d.f., $P = 0.12$). The size of the arrows is proportional to the strength of the paths.

tion treatments. Similar results have been described for other ecosystems. Stein et al. (1992) noted that elk completely consumed *Salix lasiolepis* resprouts after plants were experimentally burned. Strohmeier and Maschinski (1996) reported both wild and domestic herbivores reduced total shoot length and number of branches of *S. arizonica*. This indicates that indirect effects on arthropods, as mediated by plant characteristics, are dependent upon intensity of vertebrate herbivory.

In other forest ecosystems, intense ungulate herbivory has been shown to have strong indirect effects on arthropod community characteristics (see Stewart, 2001 for a review). In our study, protected plots had a greater number of arthropod functional groups, and thus apparently more complex arthropod food webs, than unprotected plants. Resources provided by the plant host attract and sustain primary arthropod consumers as well as detritivores, which in turn provide resources for secondary arthropod consumers. These effects have potential to cascade through the ecosystem and influence food web dynamics at coarser scales. For example, at another forested study site in the southwestern U.S., insectivorous birds were found to benefit from increased insect diversity on aspen (*Populus tremuloides*) trees that were protected from elk herbivory (Bailey and Whitham, 2003). Still further, such herbivore-induced changes in arthropod communities may ultimately affect basic ecosystem function as arthropods represent significant pathways for energy transfer and material flow (Kim, 1993).

4.2. Herbivore–plant–arthropod relationships

Our model explained 89% of the variation in arthropod richness by differentiating direct and indirect relationships with factors that may be driving arthropod community diversity. Arthropod family richness increased asymptotically with number of arthropods captured (Gotelli and Colwell, 2001). Our model showed 32% of the variation in arthropod abundance was explained by the combined influence of flowering stems, stem length, and protection from browsing. A factor affecting both arthropod abundance and

richness was stem length. The plant vigor hypothesis (Price, 1991) predicts greater insect herbivory on faster growing plant modules or those that have grown fast enough to become relatively large (Price, 1991; Cornelissen et al., 2008). Although plant vigor may have influenced patterns observed in this study, we did not assess plant growth rates, nor did we analyze a reduced model that only included herbivorous arthropods. Future work could directly explore relationships between plant growth rates and arthropod assemblage characteristics. In addition, the larger size of the plant likely makes it more apparent and easier to locate on the landscape by arthropods.

Numbers of stems and stem length positively affected number of flowering stems. In turn, number of flowering stems and stem length showed similar importance in affecting arthropod abundance. This indicates that abundant and diverse host resources are as important in this system as plant module size in attracting or sustaining arthropod populations (Lawton, 1983). In our study, 20% of the sampled arthropods were either considered pollinators or their diet consisted mainly of flower parts. Marques et al. (2000) found that 32% of the variation in arthropod herbivores was explained by flower biomass alone. Surprisingly, the number of flowering stems in our study was not significantly related to arthropod family richness.

Direct effects of plant protection from ungulates showed the strongest influence on arthropod abundance. It is well known that arthropods living in fruits, flowers, leaves and seeds can be consumed as larger vertebrates forage (Polis et al., 1989; Gomez and Gonzalez-Megias, 2002; Bonal and Munoz, 2007). Our results support those of other studies which have documented such direct effects to be quite large (60–80% of the population in one study) and detrimental to the arthropod community (Gomez and Gonzalez-Megias, 2002).

4.3. Implications

Complex ecological relationships can be better understood through the use of multivariate techniques such as SEM. Our model indicated that large herbivores affected diversity of arthropod assemblages directly, as well as indirectly through variations in *C. fendleri* characteristics. Although beyond the scope of our study, it is plausible that large herbivore effects on arthropod assemblages may in turn cascade through the ecosystem and influence other functional properties (see Hooper et al., 2005 for a review). These effects may constrain efforts to reestablish structural characteristics and functional properties in degraded ecosystems (Opperman and Merenlender, 2000). Prior to Euro-American settlement, Merriam's elk was thought to be a locally uncommon species in northern Arizona and New Mexico (Allen, 1996; Truett, 1996). Elk populations were historically limited by forage conditions, weather patterns, water availability, Native American hunters,

Table 3

Standardized direct, indirect, and total effects of factors influencing arthropod family richness. These standardized coefficients range from -1 to $+1$ (see Section 2 for more details).

Factors	Direct	Indirect	Total
Protection		0.56	0.56
#Stems		0.11	0.11
#Flowering stems		0.12	0.12
Stem length	0.11	0.13	0.24
Arthropod abundance	0.88		0.88

and large predators such as wolves and brown bears (Brown, 1983; Truett, 1996). Since their reintroduction in the early 20th century, populations of elk in northern Arizona have grown to about 30,000 adults (Ballard et al., 2000). Elk at our study site were not limited by large predators, and water catchments occur at various locations on the landscape. Ballard et al. (2000) concluded that elk survival rates in northern Arizona suggested expanding populations. In contrast, mule deer populations, after increasing in the early to mid 1900s, have recently declined (Clements and Young, 1997). Management actions that reduce intensive ungulate herbivory during the early stages of forest restoration when forage resources are limited may help to conserve biological diversity and ecological integrity. Although protection of plants by using fenced exclosures may be impractical, other techniques such as manipulation of water sources and strategic location of natural impediments (e.g., tree falls, thinning debris) may prove to be effective approaches for controlling herbivore movement and related browsing impacts on desirable species (Reynolds, 1966; Severson and Medina,

1983). Additionally, reintroduction of large carnivores such as wolves may help restore food web complexity and biodiversity in these ecosystems (Ripple and Beschta, 2004). Further work that examines ungulate herbivore effects on multitrophic interactions and ecosystem function will help land managers formulate sound approaches for restoration and stewardship of these forests.

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Appendix A. Mean number (and standard error) of arthropod individuals captured on protected and unprotected *Ceanothus fendleri* plants during 2002, 2003, 2004

Order	Family ^a	2002		2003		2004	
		Protected	Unprotected	Protected	Unprotected	Protected	Unprotected
Araneae	n.i.	0.10 (0.01)	0.06 (0.01)	0.36 (0.02)	0.03 (0.01)	0.50 (0.04)	0.07 (0.01)
Auchenorrhyncha ^b	Aphididae	0	0	0.07 (0.01)	0	0.13 (0.01)	0
Sternorrhyncha ^b	Cicadellidae	0	0	0.63 (0.04)	0.56 (0.04)	0.8 (0.04)	0
Auchenorrhyncha ^b	Psyllidae	1.50 (0.05)	0.31 (0.02)	0.43 (0.05)	0.03 (0.01)	0.4 (0.03)	0.20 (0.03)
Coleoptera	Anthribidae	0	0	0.03 (0.01)	0.03 (0.01)	0.03 (0.01)	0
Coleoptera	Bruchidae	0	0	0.17 (0.03)	0.03 (0.01)	0.10 (0.02)	0
Coleoptera	Cerambycidae	0	0	0.13 (0.01)	0.03 (0.01)	0.03 (0.01)	0
Coleoptera	Chrysomelidae	0.31 (0.02)	0.04 (0.004)	0.40 (0.03)	0	0.20 (0.02)	0
Coleoptera	Cleridae	0	0	0	0.03 (0.01)	0	0
Coleoptera	Curculionidae	0	0	0.10 (0.10)	0	0.10 (0.01)	0
Coleoptera	Histeridae	0	0	0.33 (0.04)	0	0.20 (0.02)	0
Coleoptera	Melandryidae	0	0	0.03 (0.01)	0	0	0
Coleoptera	Mordellidae	0	0 (0.0)	0.07 (0.01)	0	0.20 (0.03)	0
Coleoptera	Phalacridae	0	0	0	0	0.03 (0.01)	0
Coleoptera	Tenebrionidae	0	0	2.20 (0.12)	0.06 (0.01)	0.07 (0.01)	0
Collembola	Sminthuridae	0	0	1.40 (0.20)	0.233 (0.04)	0.10 (0.01)	0.07 (0.01)
Diptera	Bombyliidae	0	0.02 (0.003)	1.20 (0.10)	0.16 (0.02)	0	0
Diptera	Cecidomyiidae	0.02 (0.003)	0	0.07 (0.01)	0	0	0
Diptera	Chloropidae	0	0	0.27 (0.01)	0	0	0
Diptera	Culicidae	0	0	0.03 (0.01)	0	0	0
Diptera	Dolichopodidae	0	0	0.07 (0.01)	0	0.07 (0.01)	0
Diptera	Empididae	0	0	1.50 (0.10)	0.03 (0.01)	0.23 (0.01)	0
Diptera	Muscidae	0	0	0.03 (0.01)	0	0.03 (0.01)	0
Diptera	Otitidae	0	0	0.03 (0.01)	0	0	0
Diptera	Phoridae	0	0	0.03 (0.01)	0.03 (0.01)	0.07 (0.01)	0.04 (0.01)
Diptera	Pipunculidae	0	0	0.03 (0.01)	0	0	0
Diptera	Scathophagidae	0	0	0.03 (0.01)	0	0	0
Diptera	Scatopsidae	0	0	0.10 (0.01)	0	0	0
Diptera	Tachinidae	0	0	0.50 (0.04)	0	0	0
Diptera	Tephritidae	0	0	0.03 (0.01)	0	0	0
Hemiptera	Alydidae	0.02 (0.003)	0	0	0	0	0
Hemiptera	Anthocoridae	0	0	0.80 (0.05)	0.03 (0.01)	0.03 (0.01)	0
Hemiptera	Berytidae	0	0	0.03 (0.01)	0	0	0
Hemiptera	Cimicidae	0	0	0.20 (0.03)	0	0	0
Hemiptera	Lygaeidae	0	0	0	0.03 (0.01)	0	0
Hemiptera	Miridae	0.12 (0.01)	0	1.00 (0.05)	0	0.70 (0.03)	0.04 (0.01)
Hemiptera	Nabidae	0	0	0.10 (0.01)	0	0.07 (0.01)	0
Hemiptera	Pentatomidae	0	0	2.00 (0.07)	0	0	0
Hemiptera	Reduviidae	0	0	0.07 (0.01)	0	0	0
Hemiptera	Rhopalidae	0.06 (0.005)	0	0.20 (0.03)	0.01 (0.01)	0.03 (0.01)	0
Hemiptera	Thyreocoridae	0.02 (0.003)	0	0.10 (0.01)	0	0	0
Hemiptera	Tingidae	0	0	0	0	0.07 (0.01)	0
Hymenoptera	Andrenidae	0	0	0.10 (0.01)	0	0	0
Hymenoptera	Apidae	0	0	0	0	0	0
Hymenoptera	Braconidae	0.06 (0.01)	0	0	0	0.07 (0.01)	0
Hymenoptera	Chalcididae	0	0	0.03 (0.01)	0	0	0
Hymenoptera	Colletidae	0.04 (0.004)	0.04 (0.01)	0.83 (0.05)	0.03 (0.01)	0	0

Appendix A (Continued)

Order	Family ^a	2002		2003		2004	
		Protected	Unprotected	Protected	Unprotected	Protected	Unprotected
Hymenoptera	Cynipidae	0	0	0	0	0.03 (0.01)	0
Hymenoptera	Encyrtidae	0.02 (0.003)	0	0	0	0.10 (0.01)	0
Hymenoptera	Eurytomidae	0.02 (0.003)	0	0	0	0	0
Hymenoptera	Formicidae	0.24 (0.02)	0	0.70 (0.05)	0.13 (0.01)	1.60 (0.07)	0.40 (0.04)
Hymenoptera	Halictidae	0.02 (0.003)	0	0.13 (0.01)	0	0.07 (0.01)	0
Hymenoptera	Perilampidae	0	0.02 (0.003)	0	0	0	0
Hymenoptera	Scelionidae	0	0	0.50 (0.03)	0.03 (0.01)	0	0
Hymenoptera	Sphecidae	0	0	0.017 (0.02)	0	0.07 (0.01)	0
Hymenoptera	Tiphidae	0	0	0	0.03 (0.01)	0	0
Lepidoptera	Geometridae	0.02 (0.003)	0	0	0	0.20 (0.01)	0
Lepidoptera	Heterocera	0.04 (0.004)	0	0	0	0	0
Lepidoptera	Pyrilidae	0	0	0.03 (0.01)	0	0	0
Neuroptera	Chrysopidae	0	0	0.03 (0.01)	0	0	0
Neuroptera	Myrmeleontidae	0.02 (0.003)	0	0	0	0.03 (0.01)	0
Orthoptera	Acrididae	0	0.02 (0.003)	0.13 (0.01)	0.03 (0.01)	0.03 (0.01)	0
Phasmida	Heteronemiidae	0.04 (0.004)	0	0	0	0.07(0.01)	0
Phasmida	Phasmatidae	0	0	0.03 (0.01)	0	0	0
Thysanoptera	Aeolothripidae	0	0.02 (0.003)	0	0.03 (0.01)	0	0
Thysanoptera	Thripidae	0	0	0.20 (0.02)	0.06 (0.01)	0.40 (0.04)	0.07 (0.08)

^a n.i.: Family not identified.

^b Suborder of Homoptera.

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