

INTERACTIONS AMONG FIRE, ASPEN, AND ELK AFFECT INSECT DIVERSITY: REVERSAL OF A COMMUNITY RESPONSE

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Abstract. After a large crown fire in Arizona, we examined the direct and indirect effects of fire and herbivory (and their interaction) on the regeneration of aspen (*Populus tremuloides*) and arthropod species richness and abundance. We used elk exclosures covering 150 ha and other experiments to examine these interactions. Several major patterns emerged. First, in the absence of elk, there is a positive relationship between burn severity and the regeneration of aspens via asexual reproduction. Specifically, aboveground biomass of aspen resprouts was 10 times greater at sites of high burn severity than in sites of intermediate burn severity, and there was virtually no aspen regeneration without fire. Second, elk selectively browsed aspen ramets in high-severity burn sites two times more intensely than aspen ramets in intermediate-severity burn sites, largely negating the enhanced regeneration that would have otherwise occurred, thus resulting in three times greater regeneration in intermediate burn sites than in high burn sites. Third, fire and elk browsing had opposing impacts on an arthropod community composed of 33 taxa from 11 orders and 21 families. Fire severity alone showed no effect on arthropod richness and abundance; however, intermediate-severity fire and moderate levels of elk browsing resulted in 30% greater richness and almost 40% greater abundance. In contrast, high-severity fire and high levels of elk browsing resulted in 69% lower arthropod richness and 72% lower abundance. Fourth, the interaction of fire intensity and selective elk browsing resulted in four arthropod community types where the overall mosaic produced the greatest diversity. Our study demonstrates that patterns can completely reverse depending on the factors involved. This argues against a reductionist perspective and argues for studies incorporating greater complexity. At the very least, we need to be aware of such biases and consider how they may alter important decisions that affect basic ecological theory and management practices.

Key words: abundance; community ecology; direct and indirect interactions; diversity; fire; habitat mosaics; herbivory; species richness.

INTRODUCTION

The problem of scaling up from population- to community-level interactions is especially important to consider when unexpected outcomes emerge. Studies that incorporate greater complexity (incorporating aspects of time, space, and multiple factors) have demonstrated reversals in effects (e.g., a switch from a positive to negative effect; Brown et al. 1979, McNaughton 1983, Hunter 1987, Brown and Heske 1990), unexpected outcomes (Brown et al. 1979, McNaughton 1983, Brown and Heske 1990, Jones et al. 1998, Martinsen et al. 1998) or emergent properties. For example, after 11 yr of study, Brown et al. (1979) and Brown and Heske (1990) showed that kangaroo mice and ants compete for similar-sized seeds in the short term in desert grassland environments, thus having a negative effect on one another. However, in the longer term, the foraging of kangaroo mice increase the number of seeds used by ants and mice, thus actually facilitating ants, having a reversal in effect.

Similar to temporal effects, Jones et al. (1998) ex-

amined the multiple links between acorn abundance, gypsy moth outbreaks, and the risk of lyme disease. They demonstrated how acorn abundance affected mice and deer abundance, and indirectly negatively affected the abundance of gypsy moths through increased predation by mice. Also, because acorns are an important food item for mice and deer, an increase in acorn abundance increased the risk of lyme disease. Although such complex interactions between mammals, plants, and arthropods are probably common, relatively few studies have integrated multiple factors and documented the actual chains of interactions and their impacts on diverse organisms (Brown and Heske 1990, Hunter and Price 1992, Jones et al. 1998, Martinsen 1998). Similarly, we are aware of no studies of interactions of vertebrate and invertebrate herbivores that are triggered by forest fires.

Independently, fire and mammalian herbivory can have diverse consequences for communities and trophic levels through direct and indirect modification of bottom-up resources (Dannell and Huss-Danell 1985, Neuvonen and Danell 1987, Stein et al. 1992). By combining two factors in our study, we examined the effects of fire severity and elk browsing, as well as their in-

teraction on aspen regeneration and arthropod community structure. Specifically we examined links among aspen (*Populus tremuloides*), elk (*Cervus canadensis*), and a diverse group of arthropods that are directly and indirectly influenced by fire.

Aspen is a dominant montane and boreal forest species, which plays a complex role in supporting a diverse community (Bartos and Campbell 1998). As a major food and habitat source for a wide range of animals (Clausen et al. 1989, Basey et al. 1990, Kay 1990, Romme et al. 1995, Baker et al. 1997), aspen ultimately affect all trophic levels including fungi, arthropods, birds, and mammals (Johns 1993, Schieck et al. 1995, Berg, 1997, Merrill et al. 1998). However, since post-European settlement, aspen regeneration has declined across the western United States (Boyce 1989, Bartos et al. 1994, Romme et al. 1995, Baker 1997).

Several factors are known to contribute to the decline in aspen regeneration, principally fire suppression and mammalian herbivory (Jones and DeByle 1985, Cantor and Whitham 1989, Romme et al. 1995). In montane forests of the Southwest, natural disturbance through wildfire occurred every 5–7 yr at low to intermediate severity (Covington et al. 1997, Swetnam and Betancourt 1998), but this frequent fire regime has been virtually eliminated. Since post Euro-American settlement, fire suppression in the U.S. has been the preferred land management method (Covington et al. 1997, Swetnam and Betancourt 1998). As a result, fire frequency and severity have changed dramatically.

Because fire is not a uniform disturbance, forests can be maintained through attributes of both plant resistance and resilience. For example, because of the thickness of the bark, mature *Pinus ponderosa* is resistant to fire and can generally tolerate relatively high temperatures from moderate fires. Other tree genera, including *Populus*, *Salix*, and *Quercus*, are resilient and can tolerate low to intermediate temperatures, but die at high temperatures. These trees persist in forests by regenerating ramets that sprout from the rootstocks (Jones and DeByle 1985, Stein et al. 1992, Romme et al. 1995). Both resistance and resilience are important mechanisms for tolerating fire disturbance, maintaining a forest, and supporting dependent community members. However, young ramets, such as those regenerated by fire, are much more susceptible to mammalian herbivores than are large mature trees (Romme et al. 1995, Baker et al. 1997). The fact that fire directly affects aspen recruitment is well known, but how fire severity affects aspen recruitment and indirectly interacts with other factors such as elk browsing to affect aspen regeneration and arthropod community structure is much less understood.

Mammalian herbivory has diverse consequences for plants that affect basic properties of architecture (McNaughton 1983, Maschinski and Whitham 1989, Mopper et al. 1991, Hunter and Price 1992, Romme et al. 1995, Baker et al. 1997), phenology (Martinsen et al.

1998), and leaf quality (Lindroth 1989). Other studies show that even landscape level processes can be affected (Cantor and Whitham 1989, Campbell et al. 1994), and these may subsequently affect other dependent animal communities (Dannell and Huss-Danell 1985, Neuvonen and Danell 1987, Whitham et al. 1991, Hunter and Price 1992). For example, mammalian herbivory can modify plant architecture resulting in either compensatory growth (McNaughton 1983, Dannell and Huss-Danell 1985, Paige 1992, Martinsen et al. 1998) or reduced plant growth (Romme et al. 1995, McLaren 1996, Baker et al. 1997). Mammalian herbivory can either positively or negatively alter nutritional quality of plant resources (Dannell and Huss-Danell 1985, Neuvonen and Dannell 1987, Martinsen et al. 1998, Young and Okello 1998). Additionally, mammalian herbivory can structure plant community dynamics (Johnston and Naiman 1990, McInnes et al. 1992). Because direct and indirect effects of mammalian herbivory on plant architecture and quality are diverse, they are an important factor structuring arthropod communities and have consequences that are transferred to other trophic levels (Dannell and Huss-Danell 1985, Neuvonen and Danell 1987).

By using adjacent burned and unburned sites, as well as elk exclosures (browsed and unbrowsed), we extend previous work on the single factor effects of fire and elk browsing by integrating their individual and combined effects. Four hypotheses were tested. First, in the absence of elk browsing, aspen regeneration will be positively correlated with fire severity as predicted by previous studies. Second, in the presence of elk, aspen regeneration may shift such that peak regeneration is not associated with fire severity. Third, the interaction of fire severity and elk browsing will have variable effects for aspen regeneration that will differentially affect diverse arthropod species. Fourth, the interaction of fire severity and elk browsing will create a habitat mosaic in which each part of the mosaic supports a significantly different arthropod community.

METHODS

Hochderfer fire and elk exclosures

In 1996, the Hochderfer wildfire burned nearly 6640 ha of the Coconino National Forest on the San Francisco Peaks in northern Arizona. This fire burned at varying intensities from a very hot crown fire in the pure ponderosa pine stands to moderate and cool fires in mixed forest with aspen. Because aspen populations are declining in Arizona and across the West, in 1997 the United States Forest Service established and maintained two large elk exclosures to eliminate elk browsing and facilitate aspen regeneration. The forests in each exclosure sustained variable levels of burn intensity and each covered ~75 ha, which, prior to burning, supported numerous aspen stands intermixed among

stands of ponderosa pine. Such exclosures represent a powerful tool for examining complex interactions.

Having only two large exclosures, we felt it was important to understand possible effects of pseudoreplication. Inside the 150 ha of exclosures, meadow patches or ponderosa pine stands spatially separated our 15 sample aspen stands. Additionally, AFLP (amplified fragment length polymorphism) molecular analysis demonstrated that a single aspen stand contained at least four genets (B. Young, *unpublished data*). Thus, by having plots composed of different genets that are spatially separated by different vegetation types, our sample units are as independent as a reasonable investment of time and money could make them. Because no differences in dependent variables were detected, the two exclosures were generally uniform and thus representative of a larger landscape. By using mature aspen stands that had suffered variable levels of burning (e.g., unburned to high-severity burn), as well as elk exclosures that eliminate most browsing, we designed a 2-yr experiment to examine the individual and combined effects of fire severity and elk browsing on aspen regeneration and their associated arthropod community.

Aspen regeneration

To address the relationship between burn severity and aspen regeneration, 2 and 3 yr after the Hochderfer fire we randomly selected three subplots within our 15 stands (45 plots total) inside the forest service exclosures and quantified mature aspen mortality due to fire (burn severity) and counted resprouting ramets. The number of living mature aspen ramets out of the total number of mature ramets was surveyed on each plot. Additionally, the number of juvenile aspen ramets was also surveyed to determine the relationship between adult mortality and juvenile regeneration. However, due to the high density of juvenile ramets, these were counted from a single 1-m² plot in each of 45 plots. The level of burn severity was assessed based on the proportion of mature aspen trees that had been killed by fire. High burn-severity sites were characterized by 100% aspen mortality and intermediate-severity sites suffered ~50% mortality. Plots were 15 m long × 5 m wide, and had a southwesterly aspect. Due to unequal variances, the number of ramets that resprouted was square-root transformed and then regressed against mature aspen mortality.

Mammalian herbivory

To determine if burn severity indirectly affected levels of elk browsing through the response of juvenile aspen ramets, we quantified elk browsing in the high-severity burn zone and the intermediate-severity burn zone. Fifteen ramets were randomly chosen in three high and three intermediate-severity burned/browsed stands, for a total of 45 ramets in each treatment zone (90 ramets total). Elk browsing was quantified as the

percentage of shoots browsed out of the total shoots produced by a ramet. Because aspen regeneration is negligible in unburned stands, this zone was not used to quantify elk herbivory. These data were transformed (arcsine square-root) and analyzed using an independent samples *t* test.

In order to integrate the effects of both burn severity and elk browsing on aboveground aspen biomass, we collected aspen ramets from six randomly selected 1-m² plots (six inside and six outside the exclosure; 90 total plots were quantified) in each of 15 stands (three stands in the high-severity zone/unbrowsed, three stands in the high-severity zone/browsed, three in the intermediate-severity burn zone/unbrowsed, three in the intermediate-severity zone/browsed, and three in the unburned/browsed). All stands were separated spatially and likely to be genetically different. The aspen ramets were oven dried to a stable dry mass at 70°C for 24 h and weighed. Because assumptions of normality and equal variances were met, we used a two-factor ANOVA to analyze these data.

Arthropod communities

In the summer of 1998, we quantified the effects of burn severity and elk browsing on arthropod diversity by visually surveying ramets in high and intermediate-severity burn zones, both inside and outside of the elk exclosures. Using the same 1-m² plots described in *Methods: Mammalian herbivory*, we surveyed all arthropods on the tallest ramet ($n = 72$ total ramets; 18 ramets per treatment). Because aspen regeneration was negligible, we were unable to quantify arthropod diversity in unburned stands.

Additionally, in June of 1999, we simulated natural levels of elk browsing by manually cutting shoots (Edenius et al. 1993, Hjalten et al. 1993) to experimentally examine how elk browsing affects arthropod communities. By simulating elk browsing we sought to examine the alternative hypothesis that elk selectively foraged among ramets taking only the best and avoiding inferior ramets. This hypothesis was important to address because inherent differences among ramets might result in different arthropod communities, independent of elk herbivory.

Arthropod species richness and abundance were quantified by visually censusing the entire ramet in each treatment category (i.e., high-severity burn zone/unbrowsed, high-severity zone/browsed, intermediate-severity burn zone/unbrowsed, and intermediate-severity burn zone/browsed) to give a ramet-level estimate of diversity (Wimp and Whitham 2001). We excluded unburned stands from this analysis because aspen regeneration was nearly zero. In our surveys in 1999, we identified all arthropods to order and family. Within families, morphologically distinct taxa were considered to be separate species. In our experimental surveys in 1999, 11 orders, 21 families, and 33 taxa were identified (Table 1). Our classifications were then

TABLE 1. Arthropod community found on observational and experimental trees.

Taxonomic group	Family (Genus species)	Guild	Abundance	Primary zone
Acarina 1		predator	1	NP
Acarina 2		gall maker	3	NP
Araneidae 1	Salticidae	predator	2	Mbr
Araneidae 2	Salticidae	predator	1	NP
Coleoptera	Coccinellidae 1	predator	1	NP
	Coccinellidae 2	predator	1	NP
	Curculionidae 1	free feeding	11	Mubr
	Curculionidae 2	free feeding	2	NP
Diptera	Surphidae	predator	2	Mbr
Hemiptera	Miridae 1	free feeding	2	NP
Homoptera	Aphidae 1 (<i>Chaitophorous populicola</i>)	free feeding	123	Hubr/Hbr
	Aphidae 2	free feeding	369	Mbr
	Aphidae 3	gall maker	7	Hubr
	Cercopidae 1	free feeding	8	All
	Diaspididae	free feeding	1	NP
	Cicadellidae 1	free feeding	4	Hubr/Mbr
	Cicadellidae 2	free feeding	28	All
	Cicadellidae 3	free feeding	3	NP
	Formica 1	predator	136	All
	Formica 2	predator	1	NP
Hymenoptera	Tenthredinidae (<i>Phyllocolpa bozemanii</i>)	gall maker	42	NP
		leaf roller	4	Hubr/Mubr
Lepidoptera	Geometridae 1	leaf chewer	1	NP
	Gelechiidae 1	leaf miner	2	Hubr
	Gracilariidae (<i>Lithocolletis tremuloidiella</i>)	blotch mine	11	Mubr/Mbr
	Lasiocampidae	tent maker	4	NP
		free feeding	1	NP
	Tortricidae	leaf tier	7	Mubr/Mbr
		free feeding	5	Mubr/Mbr
	Sphingidae	free feeding	2	NP
Neuroptera	Chrysopidae	predator	3	Mbr
Thysanoptera	Thripidae 1	free feeding	10	Hubr
	Thripidae 2	free feeding	4	Mbr
Gastropoda		herbivore	4	All

Notes: The "primary zone" is the zone where the greatest abundance of a particular taxa occurred. Zones are heavy burned/unbrowsed (Hubr), heavy burned/browsed (Hbr), moderate burn/unbrowsed (Mubr), and moderate burn/browsed (Mbr). In some cases taxa occurred in all zones (All), or with no particular pattern (NP).

used in analyses of richness, abundance, and community composition. Both arthropod species richness and abundance met assumptions of normality and equal variances, and were analyzed with a two-way ANOVA to determine the effects of fire, browsing, and the interaction of burn severity and elk browsing on overall arthropod diversity.

Nonmetric multidimensional scaling

In addition to the above analyses of arthropod communities, we examined how the composition of the arthropod community was affected by both burn severity and level of herbivory using NMDS (nonmetric multidimensional scaling) techniques developed in the program, DECODA (Minchin 1987a, b). Potential dif-

ferences between groups were analyzed using an analysis of similarity (ANOSIM) test (Faith et al. 1987, Minchin 1987a, b, Kantvilas and Minchin 1989, Oksanen and Minchin 1997). NMDS is an ordination technique that provides an accurate representation of community composition (e.g., community composition = combined arthropod richness and abundance; Minchin 1987a, b). Although originally developed for community vegetation analyses, it has also been used in analyses of arthropod communities and plant defensive chemistry (e.g., Dungey et al. 2000, Bailey et al. 2001). This method of analysis also allowed us to determine if arthropod community composition (using combined species richness and abundance/ramet) differed significantly among groups.

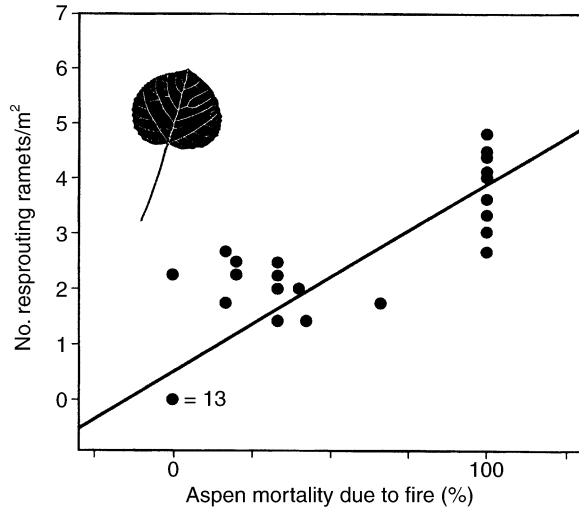


FIG. 1. The densities of aspen ramet resprout increase with the amount of mature aspen mortality due to fire ($r^2 = 0.678$, $P < 0.0001$). Forty-five plots of 10×5 m were censused. Each point represents a single transect except in unburned sites where one point represents 13 transects.

RESULTS

Interactions of fire and elk

In the absence of elk herbivory, there was a positive relationship between burn severity (i.e., percentage of adult aspen mortality) and the number of ramets that resprouted from aspen roots three growing seasons after the fire ($r^2 = 0.671$, $P < 0.0001$; Fig. 1). This relationship demonstrated two patterns that were important to the following studies. First, fires can trigger massive aspen regeneration. For example, in 14 of 15

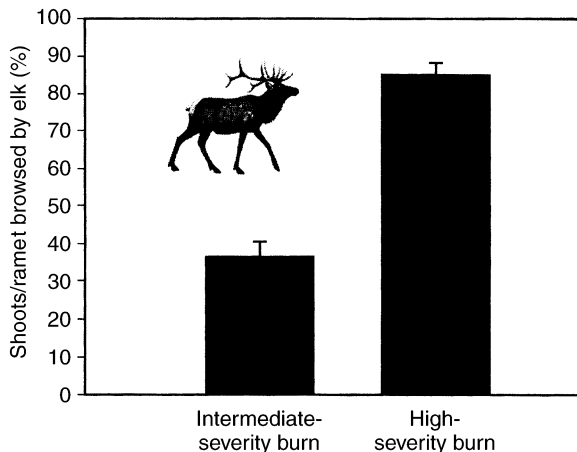


FIG. 2. Elk browse 85% of young aspen shoots in high-severity burn sites and only 36% of the shoots in intermediate burn sites (mean herbivory ± 1 SE, 84.7 ± 3.73 and 36.4 ± 4.30 , respectively; $t = 8.445$, $P < 0.0001$). Forty-five ramets were randomly selected in intermediate- and high-severity burn zones. Herbivory was calculated as the percentage of shoots browsed out of the total available (means ± 1 SE are shown).

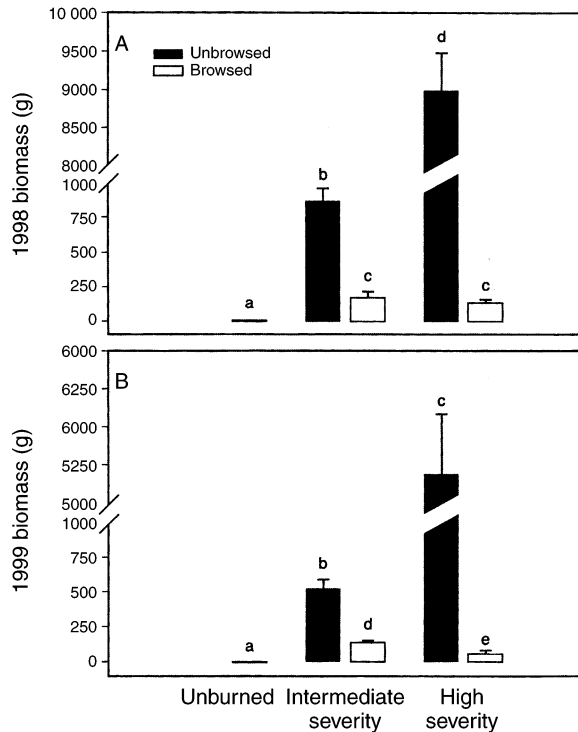


FIG. 3. In both (A) 1998 and (B) 1999, burn severity and browse intensity interact to effect overall aboveground biomass. Ninety total plots were quantified ($n = 18$ plots in each treatment; means ± 1 SE are shown).

stands that were not burned, no resprouting occurred. However, at all burned stands, aspen regeneration occurred. This effect of burning is well supported in the literature (Romme et al. 1995, Baker et al. 1997), but these studies did not examine the effects of burn severity. Second, intermediate burns also triggered sprouting (i.e., 2–6 ramets/m²), but less than severe burns, which killed the aboveground portions of all aspens (i.e., 6–25 ramets/m²). Having demonstrated that the number of ramet resprouts per m² increased with burn severity, we then sought to determine if elk exhibited a preference for stands with high burn severity where forage was most abundant.

Consistent with this hypothesis, we found that outside the exclosures, elk selectively browsed in stands that experienced a high-severity burn, and also produced the highest levels of aspen resprout. In high burn-severity stands, where aspen ramet biomass was greatest, elk browsed 85% of the young aspen shoots, compared to only 34% of aspen shoots per ramet in intermediate burn-severity stands, where aspen ramet biomass was intermediate ($t = 8.45$, $P < 0.0001$; Fig. 2). Such selective browsing suggested that elk might have a greater negative effect on aboveground biomass in high-severity burn stands than in intermediate-severity burn stands.

Burn severity and elk browsing interacted to significantly affect overall aboveground biomass (1998,

TABLE 2. Means \pm 1 SE and results of a two-way ANOVA on the dependent variables.

Source of variation	Year	Unbrowsed		Browsed		Unburned
		Intermediate-severity burn	High-severity burn	Intermediate-severity burn	High-severity burn	
Biomass (g)	1998	861.77 \pm 99.69	8966.6 \pm 497.11	172.48 \pm 37.77	135.3 \pm 19.47	0 \pm 0
	1999	527.12 \pm 61.12	5186.2 \pm 402.54	136.64 \pm 14.09 ^a	57.0 \pm 6.83 ^a	0.33 \pm 0.33
Arthropod richness (observed)	1999	3.29 \pm 0.318	3.47 \pm 0.438	4.71 \pm 0.41	1.11 \pm 0.20	
Arthropod richness (experimental)	1999	3.0 \pm 0.28	3.29 \pm 0.41	4.52 \pm 0.378 ^b	1.7 \pm 0.25 ^b	
Arthropod abundance (observed)	1999	5.0 \pm 0.69	6.35 \pm 1.15	7.93 \pm 0.96	1.78 \pm 0.34	
Arthropod abundance (experimental)	1999	4.47 \pm 0.53	5.52 \pm 0.92	7.12 \pm 1.05 ^c	1.94 \pm 0.4 ^c	

Note: Within a row, entries with the same superscript letter were found to be significantly different from each other by a one-way ANOVA following a significant fire \times browse interaction.

$F_{1,144} = 315.21$, $P < 0.0001$; 1999, $F_{1,72} = 177.99$, $P < 0.0001$; Fig. 3, Table 2) such that net aspen biomass was greatest in intermediate burn stands. In the absence of elk, high-severity burn stands had ~ 10 times greater aboveground biomass than intermediate-severity burn stands (mean biomass \pm 1 SE, 5186 g/m² \pm 402.54 and 527.12 \pm 61.12, respectively). However, in the presence of elk, selective browsing reduced aboveground biomass by 90-fold in the high-severity burn stands, and by only 4 fold in intermediate-severity burn stands (57.0 g/m² \pm 6.83 and 136.64 \pm 14.09, respectively).

The effects of burn severity and elk browsing on aboveground biomass were consistent in both 1998 and 1999, which suggests that these patterns are general. However, aboveground aspen biomass decreased from 1998 to 1999. We attributed this result to a corresponding change in ramet density between those years (J. Bailey and T. Whitham, *unpublished data*). In conclusion, when elk were absent, high-severity burn stands had the greatest aspen regeneration (e.g., 1999, 9.8 \times greater than intermediate burn stands and 15 000 \times greater than unburned stands/browsed). However, when elk were present, their selective browsing altered the outcome so that the greatest aspen regeneration was in the intermediate-burn stands (e.g., 1999, 2.4 \times greater than high-severity burn stands and 414 \times greater than no-burn stands). This result demonstrates the direct effects a mammalian herbivore can have on plant biomass and regeneration. Because other studies have demonstrated the indirect effects of mammalian herbivory on arthropod communities, we predicted that elk would have similar effects. These are examined in the following section.

Arthropod community responses

In 1999, fire severity and elk browsing interacted to significantly affect arthropod species richness on aspen ($F_{1,66} = 9.11$, $P < 0.004$). Fig. 4A shows four major effects of this interaction on species richness (Table 2). First, in the absence of elk browsing, arthropod species richness was not different between high and interme-

diatese burn stands. Second, due to the selective browsing of elk in high-severity burn stands, arthropod richness declined by 68% relative to controls that suffered no browsing. Third, fire severity and elk browsing exhibited a significant interaction effect such that the greatest arthropod richness is found at intermediate burn stands that had been browsed. Fourth, when browsed and unbrowsed stands were combined, intermediate burn sites had the highest net species richness.

Because our results, from inside and outside of the enclosure, could potentially stem from some innate differences among stands, in 1999 we also experimentally simulated natural levels of elk browsing with clipping experiments. Relative to our enclosure treatments that eliminated elk, this simulated herbivory experiment resulted in very similar patterns ($F_{1,66} = 13.44$, $P < 0.006$; Fig. 4B). These data eliminated potential stand effects as an alternative hypothesis. Most importantly, they show that the combined effects of fire severity and elk browsing interacted to positively affect arthropod richness under one set of circumstances and negatively under other circumstances.

In 1999, fire severity and elk browsing also interacted to significantly affect total arthropod abundance ($F_{1,66} = 8.614$, $P < 0.005$). Fig. 5A shows four major effects on total arthropod abundance (Table 2). First, in the absence of elk, arthropod abundance did not differ between high-severity burn stands and intermediate-severity burn stands. Second, high levels of elk browsing in the high-severity burn stands negatively affected arthropod abundance by 72% relative to the controls without elk. Third, intermediate levels of elk browsing in the intermediate-severity burn stands increased arthropod abundance over unbrowsed ramets in these stands. Fourth, when browsed and unbrowsed stands were combined, the intermediate-burn stands had the highest net total arthropod abundance.

In 1999, the reciprocal clipping experiments showed significant and similar patterns in total arthropod abundance to those in the enclosure experiment ($F_{1,66} = 10.51$, $P < 0.002$; Fig. 5B). These experimental results

TABLE 2. Extended.

Herbivory			Fire			Interaction		
df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
1, 144	154.83	0.000	2, 144	430.99	0.000	1, 144	315.21	0.000
1, 72	241.5	0.000	2, 72	83.21	0.000	1, 72	177.99	0.000
1, 66	13.67	0.000	1, 66	6.33	0.014	1, 66	9.11	0.004
1, 66	5.13	0.027	1, 66	2.46	0.122	1, 66	13.44	0.006
1, 66	6.43	0.014	1, 66	1.734	0.192	1, 66	8.614	0.005
1, 66	1.99	0.163	1, 66	3.492	0.066	1, 66	10.51	0.002

also eliminated potential stand effects as an alternative hypothesis. Furthermore, they again showed that the combined effects of fire severity and elk browsing interacted to affect arthropod abundance positively under one set of circumstances and negatively under other circumstances.

Using NMDS ordination techniques, we found that arthropod community composition differed significantly by burned and browsed condition. The NMDS

showed that arthropod communities associated with all four possible stand conditions (i.e., high-severity burn/unbrowsed, high-severity burn/browsed, intermediate-severity/unbrowsed, intermediate-severity burn/browsed) differed significantly from each other (Fig. 6, ANOSIM: $r = 0.212$, $P \leq 0.001$; Table 3). This suggests that the interaction of fire severity and

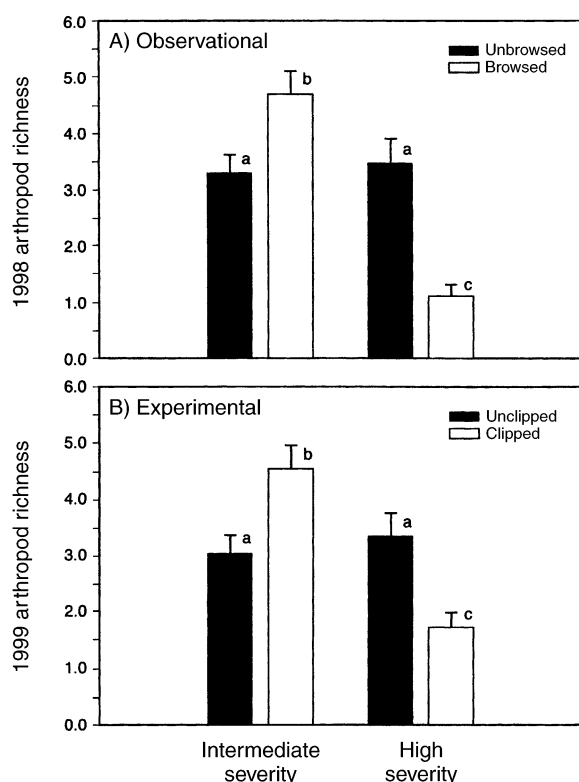


FIG. 4. Burn severity and elk browsing interact to affect arthropod richness. Panel (A) shows observational data of arthropod species richness taken from inside and out of the exclosures. Panel (B) shows experimental clipping data of arthropod species richness where unbrowsed ramets were clipped to simulate natural levels of elk browsing (means + 1 SE are shown).

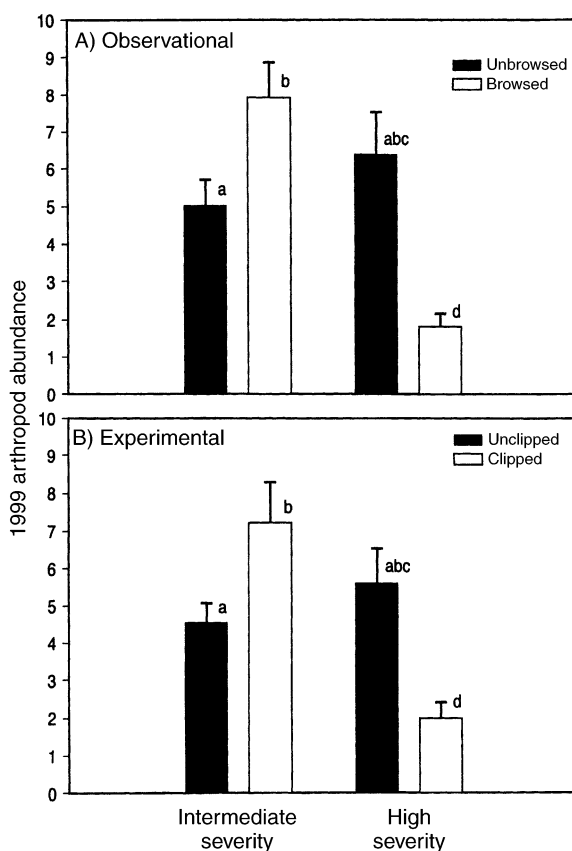


FIG. 5. Burn severity and browsing intensity interact to affect arthropod abundance. Panel (A) shows observational data of arthropod abundance taken from inside and out of the exclosures. Panel (B) shows experimental data of arthropod abundance where unbrowsed ramets were clipped to simulate natural levels of elk browsing (means + 1 SE are shown).

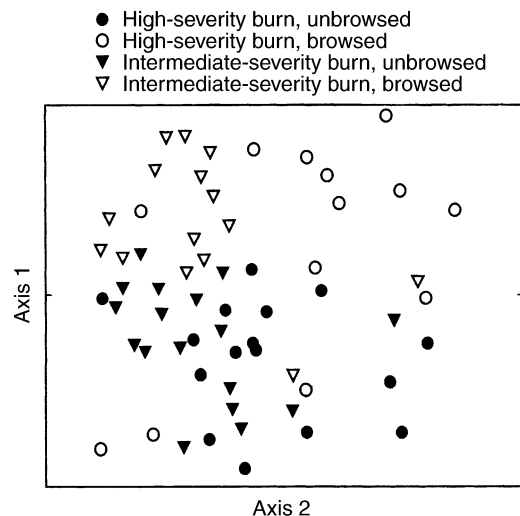


FIG. 6. NMDS (nonmetric multidimensional scaling) ordination using 33 different species of arthropods distributed across four different treatments of aspens (i.e., high burn and unbrowsed by elk, high burn and browsed, intermediate burn and unbrowsed, intermediate burn and browsed) shows that the arthropod communities associated with each treatment type are significantly different. Each symbol represents the community of arthropods on a single aspen ramet.

elk browsing support four different arthropod communities.

Furthermore, because many common species affect other community members (Wimp and Whitham 2001) and higher trophic levels, we examined how burn severity and elk browsing affected the distribution of the four most common species in our communities. Fig. 7 (A and B, $P < 0.05$) demonstrates, both observationally and experimentally, how the distribution of four common herbivores were affected by fire and herbivory. Specifically, this figure shows that individual insects are sensitive to differences in plant architecture or quality due to the direct or indirect effects of burn severity and elk browsing. For example, one free-feeding aphid species was 92% more abundant in high-severity burn stands (on both the browsed and unbrowsed ramets; Aphidae 1, $\chi^2 = 89.6$, $\chi^2 = 20.5$, respectively). In contrast, Gracilariidae larvae (i.e., blotch miner) were 73% more abundant in intermediate-severity burn stands (on both the browsed and unbrowsed ramets; $\chi^2 = 5.32$, $\chi^2 = 4$, respectively). Other species responded differently to elk herbivory. *Phyllocolpa* (leaf edge galler) was

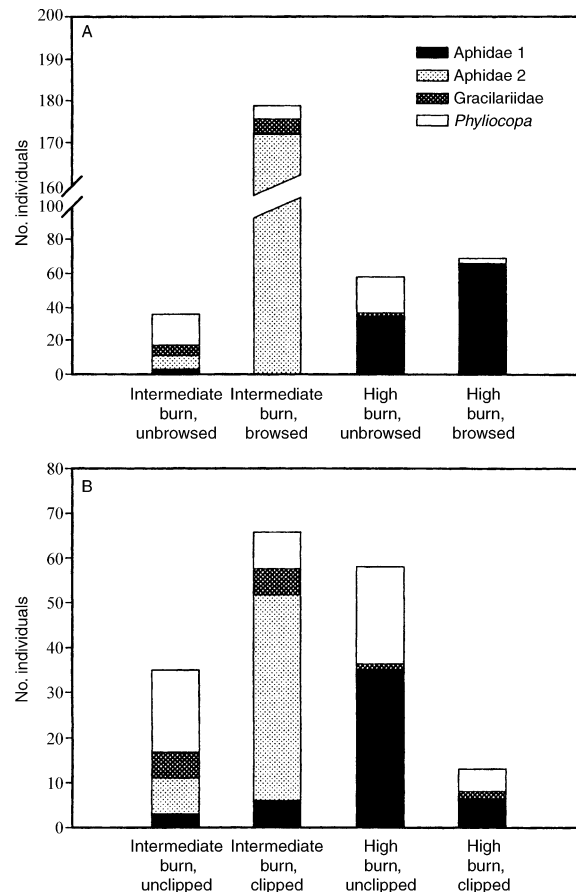


FIG. 7. Burn severity and browsing intensity interact to affect the distribution and abundance of the four most common herbivores. Panel (A) shows observational data taken from inside and outside the enclosures. Panel (B) shows experimental data where unbrowsed ramets were clipped to simulate natural levels of elk browsing (means are shown).

76% more abundant on unbrowsed ramets (both high-severity and moderate-severity sites; $\chi^2 = 27.94$, $\chi^2 = 13.0$, respectively), and a second species of free-feeding aphid (Aphidae 2) only occurred in the moderate severity and browsed stands ($\chi^2 = 478.8$, $\chi^2 = 107.48$, respectively).

DISCUSSION

Fire and aspen regeneration

Fire is a natural process involved in regeneration of many forests and grasslands (Jones and DeByle 1985,

TABLE 3. Nonmetric multidimensional scaling arthropod community ordination results.

Treatment	High-severity burn		High-severity burn and browse		Intermediate-severity burn	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
High-severity burn and browse	0.1807	0.002				
Intermediate-severity burn	0.1156	0.005	0.2378	$\ll 0.001$		
Intermediate-severity burn and browse	0.3524	$\ll 0.001$	0.1938	0.002	0.2838	$\ll 0.001$

Notes: Overall differences of the groups: Anosim, $R = 0.212$, $P < 0.00001$.

Stein et al. 1992, Romme 1995) and has been shown to enhance overall system productivity (Stein et al. 1992, Vinton et al. 1993, Singer and Harter 1996). However, fire can have variable effects on forest systems. For example, when catastrophic fires kill all aboveground biomass, subsequent forest regeneration is typically a single-aged stand (Smiris et al. 1998). In contrast, intermediate- to low-severity fires reduce fuel loads and thin forest stands. This can increase overall stand productivity and create mixed-aged stands (Jones and DeByle 1985), which diversify habitat and enhance overall diversity (Schieck et al. 1995, Berg 1997). Our data indicate that aspen regeneration varies greatly as a function of burn severity. In the absence of elk, sites with a high burn severity regenerate by vigorously producing ramets that sprout from living aspen root systems in which the crowns were killed by fire. Sites with intermediate burn severity show significantly less regeneration and sites with no burning exhibited virtually no ramet production. However, there were no unburned stands within our exclosures, and we were unable to address the regeneration of aspen in both unburned and unbrowsed stands.

There are two likely explanations for this pattern of regeneration, which are not mutually exclusive. First, we propose a differential resource allocation hypothesis that is dependent upon which structures survive the fire (Schier and Johnston 1971). In high-severity fires, which kill mature trees, all of the resources stored in the roots are committed to resprout growth. If the mature tree is not killed, the resources remaining in the roots are allocated to a damaged crown as well as resprout growth. And, in the absence of fire, few resources are normally allocated to asexual reproduction. Second, we propose that release from competition after high-severity fire favors early successional species such as aspen (Jones and Trujillo 1975). High-severity fires can eliminate mature trees (Campbell et al. 1977), thereby eliminating competition and increasing light penetration and soil temperature of the forest floor. Thus, high-severity fires should be a better mechanism for an early successional species like aspen that can sucker from the living rootstock to rapidly occupy new habitat (Jones and Trujillo 1975). In contrast, intermediate-severity fires, which eliminate understory growth (herbaceous and small trees), should be a better mechanism for maintaining climax species such as ponderosa pine (Jones 1974).

Switches and reversal of effects

Reversals in the sign of an effect are the result of an interaction of two or more factors. Although rarely studied, similar reversals have been found in other systems, which examine the effects of plant-herbivore interactions (Hunter 1987), keystone species (Brown et al. 1979, Brown and Heske 1990), mutualisms (Johnson et al. 1997), and plant development (Kearsley and Whitham 1998). For example, Hunter (1987) demon-

strated that early spring defoliation of *Quercus ruber* negatively affects growth and survival of one common late-season caterpillar, but positively affects the abundance and distribution of three other common late-season caterpillars. Also, Brown et al. (1979) and Brown and Heske (1990) demonstrated how ants and rodents compete for grassland seeds in the short term, but facilitate one another in the long term, due to their combined effects in maintaining grassland habitat.

In our study, fire directly affected aspen regeneration through variation in burn severity and indirectly affected stand regeneration through herbivore preference. Because fire generally increases the productivity of vegetation, dominant herbivores should respond to fire (Price 1991, Stein et al. 1992). In fact, many studies have shown mammalian and insect herbivore preference for previously burned vegetation (MacCracken and Viereck 1990, Stein et al. 1992, Vinton et al. 1993, Romme et al. 1995, Baker 1997). When elk were present, they browsed aspen shoots more intensively in the high-severity burn zone, where regeneration was greatest, than in the intermediate-severity burn zone. After three years, cumulative effects of less mammalian browsing in the intermediate-burn zone resulted in significantly greater aspen biomass in the intermediate-burn zone. Therefore, when elk were present at these densities, the zone of maximum aspen regeneration actually switched. In the absence of elk, aspen regeneration was 10 times greater in high-burn sites than in intermediate-burn sites (Fig. 3). However, in the presence of elk, aspen regeneration was three times greater in intermediate-burn sites than in high-burn sites (Fig. 3). These results demonstrate that the zone of maximum aspen regeneration can switch depending upon single- or multiple-factor analysis, such as fire, elk browsing, and time.

Not only did the sites of maximum aspen regeneration switch depending upon the interaction of fire and herbivory, so did arthropod richness and abundance. In the absence of elk browsing, arthropod richness and abundance were the same between burn zones (Figs. 4 and 5). When elk were present, there was a disproportionate increase of 77–78% for arthropod species richness and abundance in intermediate-severity burn sites where aspen biomass had been reduced by up to 76%. Dannell and Huss-Danell (1985) also found that moderate browsing of birch shoots by moose positively affected diversity of arthropods by decreasing the C:N ratio and increasing overall food quality. High-severity burn sites also demonstrated disproportional changes in the arthropod community. Reduction of aspen biomass by 99% resulted in only 68–72% lower richness and abundance. These data suggest the arthropod community response was not a simple consequence of the change in plant biomass due to elk browsing, but may be related to resource quality and apparency of aspen.

By categorizing species interactions as being positive, neutral, or negative we limit our perspective on

an organism's role in its community. Our study, as well as others, demonstrates that patterns can completely reverse through time or space, or depending on the number of factors involved. We predict that as the number of factors in studies increase (i.e., incorporate greater complexity), the probability of interaction effects and pattern reversals that are detected will also increase. Furthermore, by increasing the number of factors in our studies and focusing on the biological interactions which occur, unexpected properties of the systems are likely to emerge.

Habitat mosaics, diversity, and trophic level implications

Fire is a natural disturbance with highly variable effects on vegetation, and which creates a mosaic of habitat types. Habitat mosaics increase the complexity of landscape structure and effectively increase diversity on all trophic levels (Janzen 1987, Martinsen et al. 1998, Natuhara et al. 1999). However, because of landscape fragmentation, most land reserves in the United States are too small to effectively maintain natural disturbance regimes (Noss 1987).

Our data showed that the combination of all levels of fire and browsing affected aspen regeneration differently and supported four different arthropod communities on aspen. Thus, when the mosaic of habitat types created by these combinations of fire and browsing are added together, diversity should be greatest. Although we did not find that individual arthropod species were exclusively found in any single habitat type, we found their abundances differed dramatically across the mosaic. For example, we found that the abundance of two species of aphids, a leaf roller, and a leaf miner varied across the aspen habitat types created by the interaction of fire and elk browsing (Fig. 7). The altered distribution of these common herbivores demonstrates the sensitivity of important arthropods to direct and indirect effects mediated by a plant, much like the results of Hunter (1987). Because these arthropods are limited in their distributions and can affect other community members, the loss of a habitat type due to fire suppression or by heavy browsing can result in trophic level effects (Power 1990, Waltz and Whitham 1997).

The overall community effects of the mosaic are likely to be greatest if keystone species or ecosystem engineers are affected (Paine 1966, 1969, Jones et al. 1997). For example, we found that the leaf galler, *Phyllocopa bozemanii*, was three times more abundant on unbrowsed ramets than browsed. Because leaf galling insects modify the environment and create shelters for other organisms, they have potential to be ecosystem engineers and keystone species. For example, Martinsen et al. (2000) found that the habitat created by the leaf roller, *Anacampsis niveopulvella*, supported four times more species that reached seven times greater abundance than adjacent controls that had no leaf rolls. Even different guilds of arthropods showed positive

responses to rolled leaves. Shoots with leaf rolls contained seven times as many species of predators and 17 times as many predators as controls. Similarly, shoots with leaf rolls contained four times as many species of herbivores and seven times as many herbivores as controls.

Management implications

Variation in natural disturbance regimes can have opposing effects in the same system. For managers, it is important to understand the effects of variation on a particular system. In the southwestern U.S., past fire-management practices have altered stand structure, composition, and productivity, which has resulted in changes to the historic fire frequency and an increase in extreme fire intensity. Also, ungulate populations have risen dramatically, largely due to current management practices (Romme et al. 1995, Baker et al. 1997) and a lack of natural predators.

Our data argue that the combination of high burn severity and elk browsing result in the lowest aspen regeneration and the lowest arthropod diversity, and these are probably the most common conditions over the western U.S. landscape. Because aspen stands represent islands of diversity in montane forests (Johns 1993), by managing for high-severity fires and large ungulate herds, we virtually eliminate aspen habitat and the ecological processes that would normally occur therein. Our findings also demonstrate that, in the field, major ecosystem traits such as diversity and regeneration can reverse depending on complex interactions that are not often integrated in single experiments. Designing such complexity into experiments may avoid inappropriate or costly management decisions.

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