

# Response of ground-dwelling spider assemblages to prescribed fire following stand structure manipulation in the southern Cascade Range<sup>1</sup>

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**Abstract:** We assessed spider (Arachnida: Araneae) responses to prescribed fire following stand structure treatments in ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) stands in the Cascade Range of California. Stands were logged or left untreated to create three levels of structural diversity. We logged one treatment to minimize old-growth characteristics (low diversity) and one to enhance old-growth characteristics (high diversity) and we used unlogged Research Natural Areas (RNAs) as old-growth, highest-diversity reference stands. We conducted low-intensity prescribed fire on half of each plot following harvest. Spider assemblages in unburned, logged stands were similar to one another but diverged from those in RNAs, with increased abundance, species richness, and diversity in more structurally diverse stands. Prescribed fire, which altered habitat in the organic soil layer where many spiders forage, resulted in altered spider assemblages and population declines in most plots. Fire generally reduced spider species richness, evenness, and diversity. Several taxa were potential indicators of fire and old-growth structure, and we discovered one species and one genus that were previously unknown. There was evidence that old-growth characteristics intensified the effects of fire on spider abundance. This outcome probably results from the deep litter layers in high-diversity stands and RNAs, which constituted greater fuel loads than low-diversity stands.

**Résumé :** Nous avons évalué la réaction des araignées (Arachnida : Araneae) au brûlage dirigé à la suite de traitements visant à modifier la structure du peuplement dans des peuplements de pin ponderosa (*Pinus ponderosa* Dougl. ex P. & C. Laws.) situés dans la chaîne des Cascades en Californie. Les peuplements furent récoltés ou ne furent pas traités afin de créer trois niveaux de diversité structurale. Un traitement visait à réduire au minimum les caractéristiques de vieille forêt (faible diversité), un autre visait à accentuer les caractéristiques de vieille forêt (forte diversité) et des zones naturelles de recherche non exploitées qui ont été utilisées comme peuplements témoins de vieille forêt avaient la plus forte diversité. Nous avons effectué un brûlage dirigé de faible intensité dans la moitié de chacune des parcelles après la récolte. Les assemblages d'araignées dans les peuplements récoltés non brûlés étaient semblables mais différaient de ceux des peuplements témoins. L'abondance ainsi que la richesse et la diversité en espèces étaient plus grandes dans les peuplements avec la plus forte diversité structurale. Le brûlage dirigé, qui a altéré l'habitat dans l'horizon organique du sol où plusieurs araignées se nourrissent, a modifié les assemblages d'araignées dont la population a diminué dans la plupart des parcelles. Le feu a généralement réduit la richesse, l'équitabilité et la diversité des espèces. Plusieurs taxons étaient des indicateurs potentiels du feu et d'une structure de vieille forêt et nous avons découvert une espèce et un genre jusqu'à maintenant inconnus. Il y avait des indices que les caractéristiques de vieille forêt accentuent les effets du feu sur l'abondance des araignées. Ceci est probablement le résultat de l'épaisse couche de litière qui constitue une charge de combustibles plus importante dans les peuplements avec une forte diversité et les peuplements témoins que dans les peuplements avec une faible diversité.

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## Introduction

Spatial and stand structural patterns of forests in the northwestern United States have been drastically modified since presettlement times (Hessburg et al. 2000; Taylor and Skinner 2003), rendering them more susceptible to widespread wildfire and insect outbreaks (Hessburg et al. 2005).

Land management agencies have responded by applying stand structure modifications (thinning) and prescribed fire to create more fire- and insect-resistant stands and to approximate the more open and structurally diverse stands that existed when European immigrants first colonized the Pacific Northwest. Little is known, however, about the impact of such treatments on the biodiversity and function of im-

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portant forest biotic communities, particularly the soil and litter fauna (Freckman 1994; Moldenke et al. 1999). There is growing evidence that, collectively, spiders (Arachnida: Araneae) are important in stabilizing populations of other arthropods, including pest insects (Coyle 1981), so forest management practices may have unintended consequences if impacts for ground-dwelling arthropods are not taken into consideration. There is, therefore, an acute need for replicated, controlled experiments to elucidate the consequences of habitat modification for structurally complex faunal assemblages, particularly those of spiders (Wise 1993).

Spiders are generalist predators with a diet limited almost exclusively to arthropods, principally insects but including other spiders (Wise 1993; Foelix 1996). As a group, spiders are megadiverse and have worldwide distribution, occupying almost all terrestrial habitats (Coddington and Levi 1991); most individual species, however, are locally adapted to microhabitats (Foelix 1996). The habitat requirements of spider species are thought to be driven both by microclimate and by the spatial characteristics of the habitat because of the influence of habitat architecture on the development of specialized predatory adaptations by spiders (McIver et al. 1992). For example, bolas spiders (Araneidae), which lure and snare male moths by synthesizing the female moths' sex pheromones and then swinging a baited line of silk from understorey vegetation, occupy an extremely narrow stratum of vegetation (Yeargan 1994). Spitting spiders (Scytodidae) are slow-moving nocturnal hunters that catch their prey by spraying adhesive silk from modified venom glands in a zig-zag pattern to immobilize their prey (Li et al. 1999). Such highly specialized predatory adaptations are myriad among Araneae, so spider species are expected to reflect habitat architecture more reliably than many other arthropod groups. Indeed, spiders have been reported to be very sensitive to habitat structure, in particular the understorey vegetation that provides the architectural framework of their habitats (Halaj et al. 2000; Work et al. 2004). Spider communities have been shown to assemble, whether through immigration or in situ speciation, into "ecomorphs" that reflect narrow habitat adaptation with a single ecomorph of each type, indicating a high level of resource partitioning (Gillespie 2004). Stand structure and prescribed fire modify both microclimate and habitat structure for epigeic organisms, so spider assemblages might be expected to be sensitive to habitat modification and therefore to be good indicators of disturbance or specific habitats such as late successional stands. For example, Buddle (2001) demonstrated that there are distinctive spider assemblages in down woody material, both with and without bark, and the adjacent forest floor. Although the ecology of soil- and litter-dwelling spiders is generally poorly known, there is evidence that they are strongly territorial (Coleman and Crossley 1996), further suggesting that they may prove to be good indicators of forest disturbance. Indicators of this type may serve as useful surrogates for assessment of adequacy of conservation strategies and status of ecosystem recovery following disturbance (McIver et al. 1992). Ecological indicators, i.e., indicators that demonstrate the effects of environmental change on biotic systems (Pearce and Venier 2006), are especially useful because they provide some predictability about ecosystem stresses caused by forest management prac-

tices. Such indicators are best derived from randomized, replicated, and controlled prospective studies, which are rare. Most past studies have necessarily relied on retrospective and (or) chronosequence studies because of the expense and logistical difficulty of large-scale forest management manipulations, with a few noteworthy exceptions such as the EMEND study in northern Alberta, Canada (Work et al. 2004), and the EVO project in Finland (Vanha-Majamaa et al. 2007).

The study of spider response to silvicultural treatments such as thinning and prescribed fire is in its infancy, particularly with respect to interior ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) forests. For example, it may seem intuitively obvious that retention patches might provide refugia for recolonization of treated plots following harvesting or prescribed fire, but results have been ambiguous in some cases (Matveinen-Huju et al. 2006) and responses from different geographic areas have yielded contradictory results. We know of no published results, in fact, for biological indicators of effects of forest management on the spider fauna of interior ponderosa pine forests, and such indicators of disturbance are highly desirable because they can serve as surrogate measures of long-term sustainability of forest management (Brennan et al. 2006). As such, they may help land managers predict the outcome of treatments such as prescribed fire and various tree-retention harvesting plans for soil arthropods. Interior ponderosa pine forests (SAF forest type 237) (Barrett et al. 1980), which are characterized by short growing seasons with limited summer precipitation, represent the most extensive forest type in North America, ranging from west-central Mexico to southern British Columbia (Oliver and Powers 1998). Considering the extent and value of this forest type, it is prudent to assess impacts and determine reliable indicator species that are specific to this geographic region before initiating large-scale silvicultural treatments.

To that end, we chose to incorporate an analysis of ground-dwelling pitfall-trapped spiders, as well as other forest floor arthropods, as part of a large-scale interdisciplinary study initiated at Blacks Mountain Experimental Forest (BMEF) in Lassen County, California (Oliver and Powers 1998). This study, conducted in the southern Cascade Range, California, presented a rare opportunity to examine the effects of stand structure manipulations and prescribed fire on these arthropod assemblages. This study represents one of the few replicated and controlled prospective studies to examine the effects of common silvicultural practices on forest understorey flora and fauna, particularly for interior pine forests.

In our study, we explicitly tested the hypotheses that (1) differences in stand structural diversity did not affect spider assemblages and (2) low-intensity prescribed fire did not affect spider assemblages in this interior pine forest. We furthermore assessed treatment effects on the total soil arthropod assemblage, including beetles, mites, and springtails, as possible explanatory variables in the discussion. We also analyzed spider assemblage responses to prescribed fire and changes in stand structure to determine whether any species might serve as ecological indicators (*sensu* Pearce and Venier 2006) of sustainable management of this forest type. North American forests are increasingly being managed for multiple benefits, including biodiversity conservation, so re-

sults from this study may have wide application for management of western pine forests.

## Materials and methods

### Treatments

A detailed description of treatments is presented in the Establishment Report for BMEF (Oliver 2000). Study plots were established at BMEF, Lassen National Forest, roughly 60 km east of Redding, California (elevation 1700–2100 m). Soils are mostly shallow, stony loams over lava bedrock. The climate is typical of the southern Cascade Range with short, dry summers and cold, moderately wet winters; most precipitation occurs as snowfall (Oliver 2000). The forest is dominated by ponderosa pine with some Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), especially at lower elevations, with increasing proportions of white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) and incense-cedar (*Libocedrus decurrens* Torr.) (syn. *Calocedrus decurrens* Torr.) at higher elevations. Much of the native old-growth forest had been removed from BMEF during the 1930s and 1940s, but remnants remained in four, roughly 50 ha Research Natural Areas (RNAs) (Oliver 2000). The RNAs represent undisturbed late successional forest that, until 1997, experienced fire exclusion as a by-product of local forest management practices.

The BMEF study design incorporated two treatments: stand structure diversity and prescribed fire (Table 1). Twelve plots averaging roughly 100 ha in size (hereafter referred to as units) were selected and then stand structure treatments (high- versus low-diversity stand structure) were randomly assigned to those units and harvesting was conducted to create high (HD) and low (LD) stand structural diversity units. LD treatments were intended to create a single, continuous canopy layer with few snags per hectare and with evenly spaced trees of similar size. HD treatments were harvested to create stands with multiple canopy layers, many large, old trees, many large snags, dense clumps of smaller trees, and many small canopy gaps and forest floor openings (Oliver 2000). This harvesting was done in a series of three temporal blocks (four units per block) in 1996, 1997, and 1998. Each unit was then split into two plots, one scheduled to be treated with low-intensity prescribed fire the year following the harvest and the other left unburned. It was impossible to design a truly randomized study including units of true old-growth stand structure because of past harvesting history, but the four RNAs were used as reference stands for late successional stand characteristics. These RNAs were the most structurally diverse of the three types of stands, with many large, old trees, many large snags, very uneven spacing, and very deep litter layers. The RNAs were not logged, but at the time of sampling, one had been burned under a low-intensity fire prescription. The prescribed burn scheduled for 1998 was delayed until late 1999 because of logistical problems, so arthropod sampling was complete before the prescribed fire treatments began that year, resulting in an unbalanced design that was accommodated in the statistical analysis. All units, including the four RNAs, were permanently marked in a grid with numbered brass disks at 100 m intervals for spatial referencing of collected data.

**Table 1.** Summary of recent treatment history at Blacks Mountain Experimental Forest.

Block	Unit	Structure	Harvest year	Fire year
<b>1</b>	<b>38</b>	<b>HD</b>	<b>1996</b>	<b>1997</b>
<b>1</b>	<b>39</b>	<b>LD</b>	<b>1996</b>	<b>1997</b>
<b>1</b>	<b>41</b>	<b>HD</b>	<b>1996</b>	<b>1997</b>
<b>1</b>	<b>43</b>	<b>LD</b>	<b>1996</b>	<b>1997</b>
2	42	HD	1997	1999
2	44	LD	1997	1999
2	47	HD	1997	1999
2	45	LD	1997	1999
3	48	HD	1998	2000
3	40	LD	1998	2000
3	49	HD	1998	2000
3	46	LD	1998	2000
	RNA A		Not harvested	Not burned
	RNA B		Not harvested	1999
	<b>RNA C</b>		Not harvested	<b>1997</b>
	RNA D		Not harvested	Not burned

**Note:** Boldface indicates units where prescribed fire was incorporated before sampling in 1999. HD, high stand structural diversity; LD, low stand structural diversity; RNAs, very high diversity, undisturbed reference stands.

### Sampling

A 1 ha subplot was chosen at random on each split plot of each of the 12 logged units and on each of the four RNAs for collection of sifted litter and pitfall trap samples (28 subplots in total). Subplots were deliberately located near roads because of the need to transport heavy soil samples for a related study of soil/litter microarthropods (Camann et al. 2008) but were chosen at random from among those roadside sites in each treated unit or RNA. In no case were transects closer than 100 m to any road. We installed five tree-centered transects at random on each subplot for microarthropod sampling of sifted litter, and we placed a pitfall trap (Lemieux and Lindgren 1999) 1 m east of the eastern end of each of those transects. All trapping methods introduce bias into arthropod sampling (Green 1999), but pitfall traps are the most efficient and widely used single approach for sampling forest floor arthropods (Oliver and Beattie 1996a; Work et al. 2002). Indeed, Scharff et al. (2003) reported 92% overlap in species identified by two radically different methods (an intensive 3-day hand-sampling and a 2-year-long biweekly pitfall trapping effort); the number of rare species was essentially the same for the two sampling approaches. Churchill and Michael Arthur (1999) found that pitfall traps captured 94% of species, whereas sweep nets caught only 25% and visual searches caught 41% of species. Given the usual resource limitations, we concluded that there is sufficient evidence that our 10 cm diameter traps were the most efficient single sampling method (Oliver and Beattie 1996a; Work et al. 2002).

We used tree-centered transects because soil fauna tend to be clustered where nutrients are most abundant, in the litter layers above tree roots (Walter and Proctor 2004). Collection cups were filled to a height of 20 cm with a 50:50 blend of propylene glycol and distilled water to minimize predation of trapped arthropods. Trapped arthropods were collected at five intervals, once every 3 weeks from 7 July 1999 to 9 October 1999. This sampling approach, with re-



petitive sampling in localized areas, has been shown to yield greater spider species richness, especially of covert and cryptic species, than less frequent sampling over wider areas (Dobyns 1997). Collected specimens were placed in 70% ethanol and kept under refrigeration until they were sorted and identified.

### Identification

A lighted magnifying ring was used to separate trapped arthropods into several broad categories including mites, springtails, beetles, spiders, and “other arthropods.” These were counted and stored in 70% ethanol and refrigerated. Counts for all spiders (including immatures), mites, beetles, and springtails were summarized for use as potential explanatory variables (i.e., prey base) in the analysis of adult spider response to treatments. Adult spiders were subsequently identified to species where possible using either a Wild M5 or a Leica MZ16 microscope and original species descriptions or keys in the most recent taxonomic revisions. Immature spiders were not treated in the subsequent species-level analysis because many of them cannot be identified with certainty and their presence in pitfall traps can be skewed by maternal behavior (e.g., Li et al. 1999), making ecological interpretation difficult. For example, female wolf spiders often carry their brood for an extended period after the spiderlings hatch; the capture of a single brood-carrying female spider in a pitfall trap would seriously skew the abundance data for that species. Unidentifiable morphospecies, new species, and new genera were treated as operational taxonomic units in the analysis; there is considerable evidence that identification to morphospecies is taxonomically sufficient for assessment of assemblage richness and turnover (Oliver and Beattie 1996b; Pik et al. 1999). Voucher specimens were sent to the California Academy of Sciences, San Francisco, California, except for new genera and species, which were sent to specialists for further taxonomic work. Mites (Arachnida: Acari), springtails (Hexapoda: Collembola), and beetles (Hexapoda: Coleoptera) from these samples have not all been identified to species level, so those results are analyzed as broad classifications to assess the impact of treatments on total arthropod biomass as a possible explanatory variable in the discussion.

### Statistical analysis

Responses (counts) of the “coarse-sorted” material that was identified only to the level of order (mites, spiders, beetles, and springtails) were analyzed using the overdispersed Poisson model for randomized block, split plots from the family of the generalized mixed models (McCulloch and Searle 2001). This model was used to determine prescribed fire and stand structural diversity treatment effects on mean abundance of these broad arthropod categories. These were also compared with the four reference RNA units. The model is as follows:

$$[1] \quad E(\text{count}_{ijkl} | \text{Bl}_k, \text{Pl}(\text{Bl})_{ijkl}) = e^{D_i + F_j + D^*F_{ij} + \text{Bl}_k + \text{Pl}(\text{Bl})_{ijkl}}$$

where  $e$  is Napier’s constant  $\approx 2.7183$ ,  $D_i$  is the stand structural diversity treatment (fixed effect),  $i = 1, 2$  (1, 2, 3 including RNA),  $F_j$  is the prescribed fire treatment (fixed effect),  $j = 1, 2$ ,  $D^*F$  is the diversity  $\times$  fire interaction (fixed effect),  $\text{Bl}_k$  is the block effect due to different treatment ap-

plication time on a block of experimental units (random effect),  $k = 1, 2, 3, 4$ ,  $\text{Pl}_l$  is the main plot unit (random effect),  $l = 1, 2, 3, 4$ , and the vertical bar means “conditioned to the random effects...”

The counts conditioned to the random effects are assumed to have the Poisson distribution with the expected value defined by the model (above). The random effects are assumed to be normally distributed. The parameters of the model were estimated using SAS version 9.1.3 (GLIMMIX procedure) (SAS Institute Inc. 2005). The null hypotheses of no difference in the assemblage responses under the stand structural diversity treatments and (or) under the prescribed fire treatment were tested at an experimentwise error rate of  $\alpha = 0.05$  (Bonferroni-adjusted cutoff points).

We used PC-ORD (McCune and Grace 2002) to calculate the effects of treatments on spider assemblages (i.e., the subset of samples that represent mature spiders identified to morphospecies) applying multiresponse permutation procedures (MRPP), indicator species analysis, and analysis of indices of species richness, evenness, and diversity. MRPP is a nonparametric procedure equivalent to MANOVA for testing the hypothesis of no difference between two or more groups of species under different treatment regimes (McCune and Grace 2002). Unless otherwise indicated,  $\alpha = 0.05$  was chosen as the experimentwise error rate for testing the pairwise comparisons and the Bonferroni approach was used to adjust the individual  $\alpha$  levels.

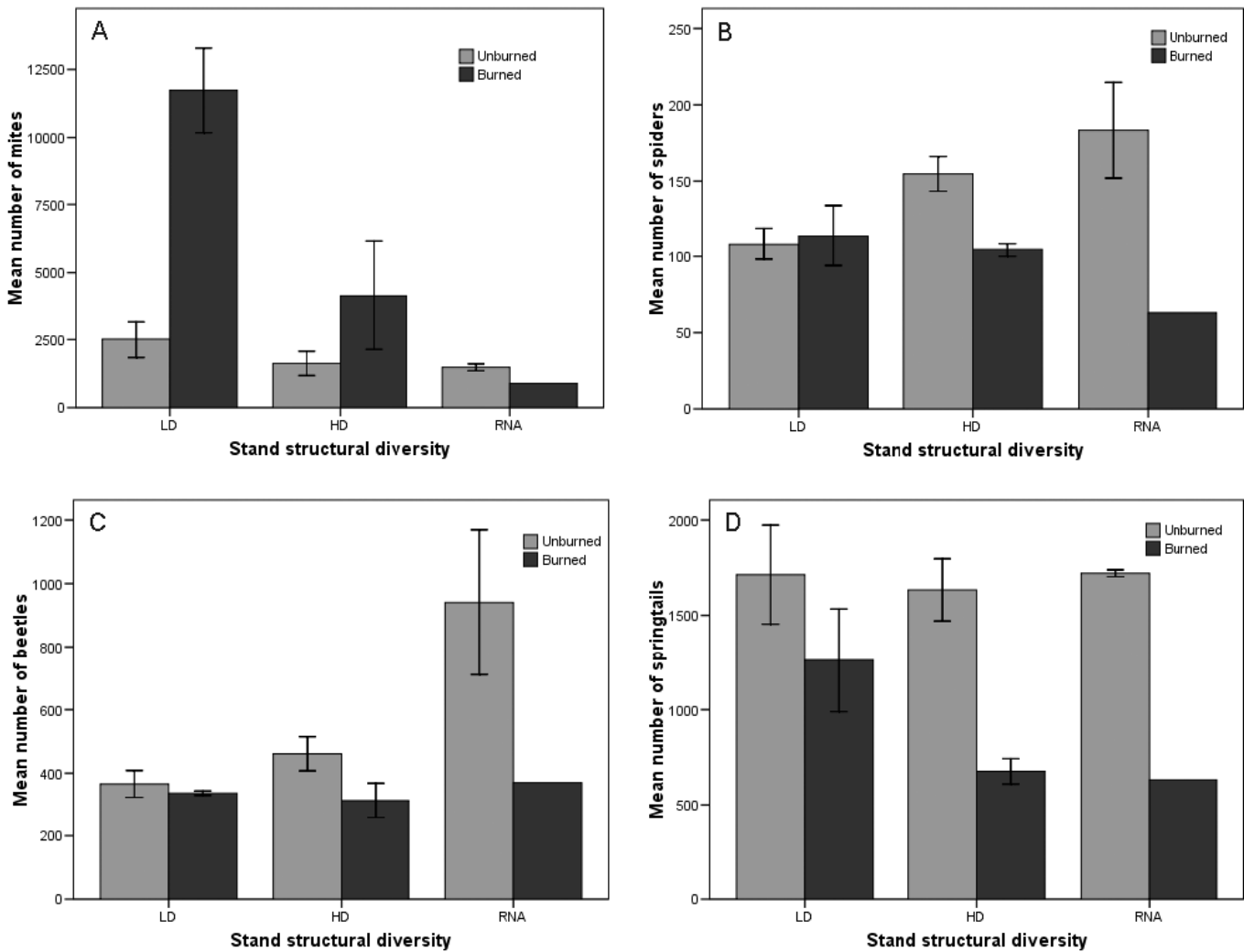
We calculated mean species richness of spiders with and without prescribed fire using first-order jackknife estimation (Palmer 1990) and we assessed spider assemblage heterogeneity with the Shannon–Weiner index. We determined spider assemblage dominance/evenness change using Pielou’s  $J$  as a measure of evenness (Pielou 1969) and we used species–area curves and jackknife estimates of total species richness (Heltshel and Forrester 1983) to evaluate adequacy of sampling and to estimate total assemblage size. We based species–area curve estimates on mean richness obtained by 500 random subsamplings from the spider abundance data at each possible subsample size.

We performed multivariate indicator species analyses to determine whether there were characteristic postfire taxonomic complexes (Dufrêne and Legendre 1997). We conducted significance testing of species indicator values by recording the proportion of 1000 randomized Monte Carlo tests of significance in which the trial indicator value equalled or exceeded the maximum observed indicator value and we evaluated assemblage similarities using MRPP with Sorensen, relative Sorensen, and Euclidean distances (Zimmerman et al. 1985). We used three distances because there is little ecological basis for selecting one distance measure over another; Sorensen and relative Sorensen are semimetric distances that are measured along the edges of the species space (city-block distance) and have been shown to work well empirically. The Euclidean distance is a metric distance with useful mathematical properties. Within-group heterogeneity was quantified with chance-corrected within-group agreement statistics ( $A$ ) (McCune and Grace 2002).

### Results

All together, we collected 3519 spiders in pitfall traps

**Fig. 1.** Total arthropod abundance (with standard error bars) ((A) mites, (B) spiders, (C) beetles, and (D) springtails) in pitfall-trapped samples (including immatures), Blacks Mountain Experimental Forest, 1999. The burned RNA has no error bar because it was not replicated at this sampling interval.



(Fig. 1B). Of these, we identified 642 adult spiders to the level of morphospecies (Table 2; Fig. 2A), with 81 spider species in 56 genera and 18 families represented in the 1999 samples (Table 2). In addition to the spider fauna, we trapped 12 320 beetles, 42 703 springtails, and 74 960 mites (Fig. 1). Beetle identifications are underway for future analysis, but mite and springtail populations are more accurately assessed using Berlese funnel treatment of litter samples, so mite and springtail counts from these pitfall traps will only be used as a rough guide to total arthropod fauna (i.e., prey base for spiders) in the treated plots.

**Total arthropod counts**

For all four broad taxonomic categories (mites, spiders, beetles, and springtails) (Fig. 1), the *F* statistic for a Type III test of the fixed effects for the stand diversity – prescribed fire interaction was significant (mites:  $p < 0.0001$ , beetles:  $p = 0.0191$ , spiders:  $p = 0.0044$ , springtails:  $p < 0.0001$ ). Several trends are apparent. First (Fig. 1A; Table 3), the numbers of mites significantly increased following the burn for LD and HD stands but not RNAs. Second (Fig. 1B; Table 3), the

burn did not significantly reduce spider numbers in LD plots but did so in both the HD plots and the RNAs. Third (Fig. 1C; Table 3), beetle numbers were significantly reduced by the burn at the higher levels of stand diversity but not in LD plots. Fourth (Fig. 1D; Table 3), numbers of springtails were significantly reduced by the burn at all levels of stand structure. Reductions in numbers of beetles, springtails, and spiders following the burns appeared to be directly proportional to stand structural diversity, whereas increases in mite numbers appeared to be inversely proportional to stand structural diversity (Fig. 1).

**Adult spider counts (identified to morphospecies)**

Seventy-eight spider taxa were identified to morphospecies in our analysis, with several showing value as indicator species for burned (i.e., fire history) and old-growth forest stands (stand structural diversity) (Table 2). Species–area curve analysis (Fig. 3) indicates that we sampled nearly three fourths of the true number of species at BMEF susceptible to pitfall trapping, suggesting that sampling was probably adequate (Buddle et al. 2005) (first-order jackknife estimates

**Table 2.** Maximum indicator values (IV), types, and probabilities ( $p$ ) for spiders from Blacks Mountain Experimental Forest in burned (B) and unburned (U) plots in each of three stand structural diversity treatments, Blacks Mountain Experimental Forest, 1999 (dashes indicate nonsignificant indicator values).

Family code	Genus	Species	Total adults/juveniles	IV, type (B/D)	IV ( $p$ )	Mean number of spiders per subplot					
						HD, B	HD, U	LD, B	LD, U	RNA, B	RNAs, U
Agele	<i>Hololena</i>	<i>nedra</i>	1/0	—	—	0	0	0.50	0	0	0
Amaur	<i>Zanomys</i>	<i>kaiba</i>	3/0	—	—	1.00	0	0.50	0	0	0
Antro	<i>Antrodiaetus</i>	<i>montanus</i>	4/0	—	—	1.00	0	1.00	0	0	0
	<i>Atypoides</i>	<i>gertschi</i>	3/0	—	—	0.50	0.20	0	0	0	0
Corin	<i>Phrurotimpus</i>	<i>mateonus</i>	11/0	—	—	0.50	0.20	0	0.40	2.00	0.70
Dicty	<i>Blabomma</i>	sp.	68/5	65.7, B	0.048	9.00	1.00	3.00	1.80	9.00	2.30
	<i>Cicurina</i>	<i>sierra</i>	5/0	—	—	0.50	0.10	0.50	0.20	0	0
	<i>Cicurina</i>	<i>utahana</i>	8/0	—	—	1.00	0.30	1.50	0	0	0
	<i>Cicurina</i>	sp.	3/0	—	—	0.50	0	0.50	0	1.00	0
	<i>Dictyna</i>	<i>subpinicola</i>	14/0	—	—	1.50	0.10	0	0.20	6.00	0.70
	<i>Dictyna</i>	sp.	1/0	—	—	0	0.10	0	0	0	0
	<i>Emblyna</i>	<i>peragrata</i>	2/0	—	—	0	0	0	0.10	1.00	0
	<i>Callilepis</i>	<i>eremella</i>	106/0	—	—	10.50	2.80	12.50	1.80	5.00	3.00
Gnaph	<i>Callilepis</i>	sp.	0/4	—	—	0	0	0	0	0	0
	<i>Gnaphosa</i>	<i>muscorum</i>	5/0	—	—	1.00	0.10	0	0.10	0	0.30
	<i>Gnaphosa</i>	sp.	0/1	—	—	0	0	0	0	0	0
	<i>Haplodrassus</i>	<i>eunis</i>	6/0	—	—	1.00	0.10	0.50	0	1.00	0.30
	<i>Micaria</i>	<i>deserticola</i>	1/0	—	—	0	0	0	0.10	0	0
	<i>Micaria</i>	<i>porta</i>	3/0	40.0, B	0.026	1.00	0	0.50	0	0	0
	<i>Micaria</i>	<i>pulicaria</i>	3/0	—	—	0	0	0.50	0	2.00	0
	<i>Micaria</i>	<i>utahna</i>	1/0	—	—	0	0.10	0	0	0	0
	<i>Sergiolas</i>	<i>columbianus</i>	2/0	—	—	0	0	0.50	0	0	0.30
	<i>Sergiolas</i>	<i>montanus</i>	4/0	—	—	0.50	0	0.50	0.10	1.00	0
	<i>Zelotes</i>	<i>fratris</i>	104/0	38.7, B	0.010	12.50	3.10	7.50	1.80	3.00	4.00
	<i>Zelotes</i>	<i>puritanus</i>	29/0	—	—	1.00	0.40	4.50	1.10	1.00	0.70
	<i>Zelotes</i>	<i>tuobus</i>	1/0	—	—	0.50	0	0	0	0	0
	<i>Zelotes</i>	<i>viola</i>	8/0	—	—	0	0.10	1	0.50	0	0
	Hahni	<i>Hahnia</i>	<i>arizonica</i>	8/0	—	—	0	0.70	0	0	0
<i>Hahnia</i>		<i>sanjuanensis</i>	4/0	—	—	0.50	0	0	0	2.00	0.30
Linyph	<i>Genus nova</i>	nova species	0/16	—	—	0.50	0.20	0.50	0.30	0	0
	<i>Agyneta</i>	nova species	39/0	—	—	6.00	0.60	2.00	0.20	5.00	3.30
	<i>Ceratinella</i>	<i>brunnea</i>	2/0	—	—	0	0.10	1.00	0	0	0
	<i>Ceratinops</i>	<i>inflatus</i>	4/0	—	—	0.50	0	0	0.20	1.00	0
	<i>Coreorgonal</i>	<i>monoceras</i>	3/0	—	—	0	0.20	0	0	0	0.30
	<i>Coreorgonal</i>	sp.	1/0	—	—	0	0	0	0	0	0.30
	<i>Disembolus</i>	<i>kesimbus</i>	1/0	—	—	0	0	0	0	1.00	0
	<i>Disembolus</i>	sp.	1/0	—	—	0	0.10	0	0	0	0
	<i>Erigone</i>	<i>aletris</i>	1/0	—	—	0	0	0	0	1.00	0
	<i>Helophora</i>	<i>reducta</i>	1/0	—	—	0.50	0	0	0	0	0
	<i>Linyphantes</i>	sp.	2/0	—	—	0	0.10	0	0	1.00	0
	<i>Meioneta</i>	sp.	1/0	—	—	0	0	0	0.10	0	0
	<i>Microneta</i>	<i>viaria</i>	5/0	—	—	0	0	1.00	0.10	0	0.70
	<i>Neriere</i>	<i>litigiosa</i>	3/0	—	—	1.50	0	0	0	0	0
	<i>Neriere</i>	<i>radiata</i>	1/0	—	—	0	0	0	0	0	0.30
	<i>Oreonetides</i>	<i>filicatus</i>	1/0	—	—	0	0	0.50	0	0	0
	<i>Pityohyphantes</i>	<i>brachygynus</i>	3/0	—	—	0	0.10	0	0	1.00	0.30
	<i>Pityohyphantes</i>	<i>pallidus</i>	1/0	—	—	0	0	0	0	1.00	0
	<i>Pocadicnemus</i>	<i>nroccidentalis</i>	1/0	—	—	0	0.10	0	0	0	0
	<i>Tachygyna</i>	<i>nr. sonoma</i>	1/0	—	—	0	0	0.50	0	0	0
<i>Tapinocyba</i>	<i>nr. simplex</i>	12/0	—	—	2.00	0.30	0.50	0.10	1.00	0.67	
Liocr	<i>Genus</i>	sp.	10/0	—	—	0.50	0.30	1.00	0.20	2.00	0
	<i>Agroeca</i>	<i>ornata</i>	2/0	—	—	0	0.10	0	0	0	0.30
	<i>Hesperocranium</i>	<i>rothi</i>	2/0	—	—	0	0.20	0	0	0	0
Lycos	<i>Alopecosa</i>	<i>kochii</i>	12/36	—	—	0	0.10	1.50	0.40	0	1.30
	<i>Pardosa</i>	<i>altamontis</i>	2/0	—	—	0	0	0	0.20	0	0
	<i>Pardosa</i>	<i>nigra</i> group	84/7	77.8, B	0.004	10.50	2.30	5.00	1.70	6.00	2.33
	<i>Pardosa</i>	<i>ramulosa</i>	1/0	—	—	0	0	0	0	1.00	0
	<i>Genus</i>	sp.	7/15	—	—	2.00	0.20	0	0	0	0.30
Nesti	<i>Nesticus</i>	<i>silvestrii</i>	4/0	—	—	1.00	0.10	0.50	0	0	0

**Table 2** (concluded).

Family code	Genus	Species	Total adults/juveniles	IV, type (B/D)	IV ( <i>p</i> )	Mean number of spiders per subplot					
						HD, B	HD, U	LD, B	LD, U	RNA, B	RNAs, U
Oonop	<i>Orchestina</i>	<i>moaba</i>	3/0	—	—	1.00	0	0.50	0	0	0
Oxyop	<i>Oxyopes</i>	<i>scalaris</i>	1/0	—	—	0	0	0.50	0	0	0
Philo	<i>Philodromus</i>	<i>speciosus</i>	1/0	—	—	0	0	0	0.10	0	0
	<i>Thanatus</i>	<i>formicinus</i>	7/0	—	—	1.00	0.10	0	0.20	0	0.70
Pholc	<i>Pholcophora</i>	<i>americana</i>	4/0	—	—	0.50	0.10	0	0.20	0	0
Salti	<i>Habronattus</i>	<i>americanus</i>	32/4	—	—	2.50	0.20	9.50	0.60	0	0
	<i>Habronattus</i>	<i>jucundus</i>	4/0	51.3, D	0.067	0.50	0	0	0.10	1.00	0.30
	<i>Habronattus</i>	<i>oregonensis</i>	6/0	—	—	0.50	0.30	0	0.20	0	0
Theri	<i>Phidippus</i>	<i>johnsoni</i>	3/0	—	—	0	0.10	0.50	0.10	0	0
	<i>Crustulina</i>	<i>sticta</i>	1/0	—	—	0	0	0	0.10	0	0
	<i>Euryopis</i>	<i>formosa</i>	13/0	55.6, D	0.026	1.00	0.30	1.00	0	0	2.00
Thomi	<i>Lasaeola</i>	<i>prona</i>	2/0	—	—	0	0.10	0.50	0	0	0
	<i>Steatoda</i>	<i>albomaculata</i>	12/0	38.3, B	0.028	3.50	0.10	2.00	0	0	0
	<i>Theridion</i>	<i>micelbacheri</i>	1/0	—	—	0	0.10	0	0	0	0
	<i>Thymoites</i>	<i>camano</i>	1/0	—	—	0	0	0	0.10	0	0
	<i>Bassaniana</i>	<i>utahensis</i>	1/0	—	—	0	0	0	0	1.00	0
Thomi	<i>Xysticus</i>	<i>locuples</i>	4/0	—	—	1.00	0	0.50	0.10	0	0
	<i>Xysticus</i>	<i>montanensis</i>	68/0	76.3, B	0.005	6.50	1.90	7.00	1.70	1.00	1.30

**Note:** Agele, Agelenidae; Amaur, Amaurobiidae; Antro, Antrodiaetidae; Corin, Corinnidae; Dicty, Dictynidae; Gnaph, Gnaphosidae; Hahni, Hahniidae; Linyph, Linyphiidae; Liocr, Liocranidae; Lycos, Lycosidae; Nesti, Nesticidae; Oonop, Oonopidae; Oxyop, Oxyopidae; Philo, Philodromidae; Pholc, Pholcidae; Salti, Salticidae; Theri, Theridiidae; Thomi, Thomisidae; LD, low stand diversity; HD, high stand diversity; RNAs, Research Natural Areas; B, burn indicator; D, stand structural diversity indicator.

indicate that the true number is approximately 111 species). One of the genera sampled is a new genus in the family Linyphiidae (Thomas R. Prentice, Department of Entomology, University of California, Riverside, California, personal communication), and a previously undescribed species of *Agyneta* was also found (Table 2).

MRPP analysis of treatment effects indicates that stand structural diversity was reflected in spider assemblages, but although there was a trend toward increasing complexity of assemblage in more structurally diverse stands, the association between stand structural diversity treatments and spider community structure only approached significance (Table 4). The HD and LD treatments were clearly not significantly different from one another in terms of spider assemblages, but there was a trend toward increasing divergence when either the LD or the HD treatments were compared with the RNAs; depending on the distance measure used, the difference between LD and RNA was significant at  $\alpha$  (experimentwise error rate) = 0.10 (Table 4).

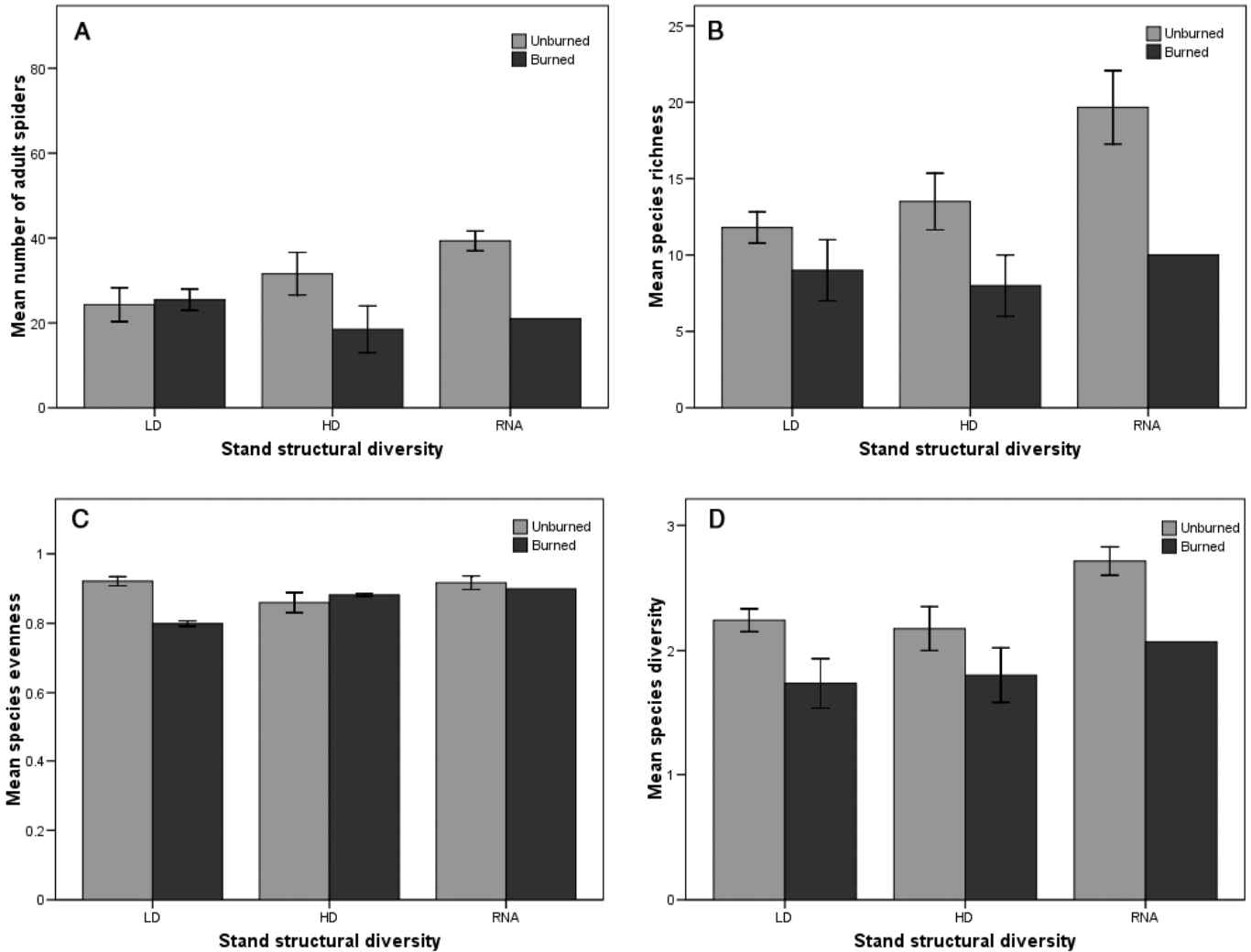
Prescribed fire, on the other hand, had a clear impact on spider assemblages (Table 4; Fig. 2). Spider assemblages in burned and unburned plots were significantly different from one another ( $p < \alpha = 0.05$ ) for all measures of distance except in the case of Euclidean distance for the HD stands (Table 4). Reductions in spider abundance and species richness were proportionately greater in the RNA (highest structural diversity stand) than in the HD and LD stands (Figs. 2A and 2B). We were not able to make pairwise comparisons using RNAs because of the lack of replication of the burn at this time.

**Discussion**

The analysis of total arthropod abundance (Fig. 1; Table 3) indicates that, with the exception of mites, prescribed fire

significantly reduced total numbers of arthropods, which are the prey base for spiders, for 2 years following the burn. In the case of spiders (Fig. 1B) and beetles (Fig. 1C), abundance was positively correlated with stand structural diversity before the burn and was reduced to a greater extent by the burn in HD than in LD stands, probably because these two highest structural diversity stands had the highest fuel loads. Springtails had equivalent levels of abundance in LD, HD, and RNA plots before the burns but suffered greater reduction in abundance in the higher-diversity treatments (HD and RNA) than in the LD plots. Mites, on the contrary, responded positively to prescribed burn in the two logged treatments, with significant differences between burned and unburned plots in both LD and HD stands; numbers in burned and unburned RNAs were probably not significantly different, but the lack of a true replicate makes it impossible to test that difference. Camann et al. (2008) reported that Berlese-extracted mites sampled on the same plots 1 year earlier than our study showed population declines in most acarine orders. Prostigmata, however, increased in the LD plots in that study and were unaffected in the RNA. We speculate that by 1999, some of the mycophagous Prostigmata and Astigmata, which feed on fungal spores and hyphae (Walter and Proctor 2004), had shown a functional response to the decaying woody material resulting from the prescribed burn. In addition, rapidly moving predaceous Mesostigmata and Prostigmata (Adl 2003) may have been sampled more frequently in pitfall traps (used in this study) than in sifted litter samples (used in Camann et al. 2008) because the former trap type tends to bias sampling toward more active taxa. Indeed, tydeid mites were the most abundant family among prostigmatids in their sampling 1 year earlier on the same plots, and there was no difference in tydeid abundance between burned and unburned plots (Camann et al. 2008). It is unlikely that Oribatei represent

**Fig. 2.** Mean (A) abundance, (B) species richness, (C) species evenness, and (D) species diversity (with standard error bars) of spiders identified to morphospecies (immatures excluded) in pitfall-trapped samples, Blacks Mountain Experimental Forest, 1999.



**Table 3.** Multiple comparisons for responses of total arthropod counts including the RNAs, responding to stand structural diversity, and prescribed burn treatments, Blacks Mountain Experimental Forest, 1999.

Treatment	Comparison	<i>p</i>			
		Mites	Spiders	Beetles	Springtails
Unburned + burned	HD vs. LD	0.014	0.314	0.584	0.030
Unburned + burned	HD vs. RNAs	0.249	0.945	0.063	0.233
Unburned + burned	LD vs. RNAs	0.681	0.482	0.134	0.878
Low diversity	B vs. U	<0.0001	0.405	0.672	<0.0001
High diversity	B vs. U	<0.0001	0.0001	0.0009	<0.0001
RNAs	B vs. U	0.311	0.003	0.055	0.014
Unburned	HD vs. LD	0.083	0.017	0.286	0.831
Unburned	HD vs. RNAs	0.582	0.0130	0.003	0.662
Unburned	LD vs. RNAs	0.962	0.421	0.015	0.731
Burned	HD vs. LD	0.003	0.633	0.990	0.0004
Burned	HD vs. RNAs	0.110	0.114	0.813	0.030
Burned	LD vs. RNAs	0.474	0.18159	0.818	0.583

**Note:** Responses are significant at  $0.05/3 = 0.0167$  (Bonferroni's adjustment) for an experimentwise error rate = 0.05 (cutoff point). LD, low stand structural diversity treatment; HD, high stand structural diversity treatment; RNAs, Research Natural Areas; B, burned treatments; U, unburned treatments.

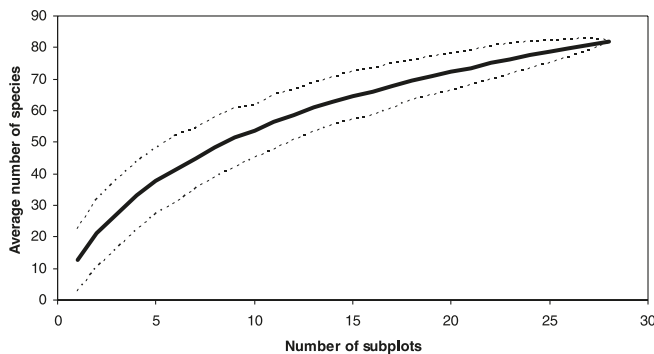


**Table 4.** Multiple comparison statistics for MRPP procedures analyzing adult spider assemblages from Blacks Mountain Experimental Forest, 1999.

Comparison	Probabilities ( <i>p</i> ) associated with different MRPP distance measures		
	Sorensen	Relative Sorensen	Euclidean
U LD vs. U HD	0.901	0.912	0.478
U HD vs. U RNA	0.377	0.242	0.482
U LD vs. U RNA	0.142	0.091	0.122
<b>B HD vs. U HD</b>	<b>0.004</b>	<b>0.007</b>	<b>0.081</b>
<b>B LD vs. U LD</b>	<b>0.005</b>	<b>0.004</b>	<b>0.004</b>

**Note:** B, burned; U, unburned; LD, low diversity; HD, high diversity; RNAs, Research Natural Areas. The burn comparisons are indicated by bold. It was not possible to conduct pairwise testing for the burned RNA unit, since it was not replicated.

**Fig. 3.** Spider species–area curve for 700 samples taken from both unburned and postfire units in Blacks Mountain Experimental Forest during 1999. The solid line represents the mean number of species in 500 random subsamples of size *x*. The broken lines represent species confidence intervals  $\pm 2.0$  SD from the mean. The first-order jackknife estimate indicates that the true number of species is approximately 111.



much of the mite biomass seen in our 1999 samples, since that mite suborder consists mostly of univoltine, slow-moving, and slow-recruiting species (Adl 2003). Prescribed burns result in the rapid release of nutrients into the forest soil and may, like air pollution, have increased the level of both nutrients and fungal hyphae in the forest soil (Horvath et al. 2005), thereby stimulating recovery of mycophagous mites. Horvath et al. (2005) found that prey availability as well as habitat structure and air pollution contributed to spider assemblage structure in a European forest, so the beginning recovery of a prey base (mites) 2 years following the prescribed burn at BMEF may signal the initiation of recovery at higher trophic levels. The positive response of some mite groups is promising because, as primary and secondary heterotrophs, they constitute an important food resource for small Scydmaenidae and other Staphylinoida (Coleoptera) that are characteristic predators in this forest floor ecosystem. Future sampling will be required to assess this possibility.

The relatively strong response to low-intensity prescribed fire, in terms of both total arthropod abundance and spider assemblages, provides something of a cautionary tale. These samples were taken nearly 2 full years following the prescribed burn in 1997, suggesting that recovery of most ar-

thropods, with the exception of some rapidly recruiting mite groups, is slow in this cool and dry interior pine forest. Our results concur with those of Buddle et al. (2006), who found that faunal succession after clear-cutting in an aspen–spruce forest seemed to progress more rapidly than after wildfire. This result is not surprising inasmuch as manipulation of stand structure (i.e., harvesting of trees) has less drastic an effect on epigeic spider habitat than does prescribed fire. This outcome may be widespread, considering the large geographic extent of this pine type, which ranges from Mexico to Canada (Oliver and Powers 1998).

Eight spider taxa were shown to be significant indicator species in this study, six for burns and two for stand structural complexity (Table 2). *Blabomma* sp. Prentice, (Dictynidae), *Micaria porta* Platnick & Shadab (Gnaphosidae), *Zelotes fratris* Chamberlin (Gnaphosidae), the *Pardosa nigra* group (Lycosidae), *Steatoda albomaculata* de Geer (Theridiidae), and *Xysticus montanensis* Keyserling (Thomisidae) all responded positively to the prescribed burns. The *Pardosa nigra* group consists of *Pardosa mackenziana* (Keyserling), *Pardosa uncata* (Thorell), *Pardosa dorsalis* Banks, and *Pardosa dorsuncata* Lowrie and Dondale, females of which are nearly indistinguishable from one another; males, which we did not collect, are necessary for definitive species determinations. Several other studies (Koponen 1993; Larrivee et al. 2005; Buddle et al. 2006) indicate that burned sites are generally characterized by open-habitat, non-web-building species such as gnaphosids, lycosids, and thomisids. Our finding that these taxa appear to be postburn specialists at our study site, as well, suggests that prescribed fire or other disturbance may be important for the maintenance of their local populations. Moretti et al. (2004) reported similar results for two European species of *Zelotes*. Gnaphosids (“cursorial spiders”), lycosids (“wolf spiders”), and thomisids (“crab spiders”) are active and mobile hunters, so it is understandable that they were able to repopulate the burned plots, especially since sampling took place nearly 2 years after the prescribed burn, which was patchy enough to provide refugia for recolonization. The web-builders in the families Theridiidae and Dictynidae appear to be a bit of an anomaly as indicators of past burns; further sampling will be needed to confirm these results. We found two taxa that were significant indicators of old-growth stand characteristics, *Habronattus jucundus* (Peckham and Peckham) (Salticidae) and *Euryopis formosa* Banks (Theridiidae), but their relationships with stand structure were not as strong as those of the indicators of past burns.

We were not surprised to find a trend toward a positive correlation between stand structural diversity and complexity of spider assemblages, since most are habitat specialists *par excellence* (McIver et al. 1992; Gillespie 2004). We therefore expected that more structurally diverse stands might provide more niches for ecomorph specialization (Matveinen-Huju et al. 2006). Oxbridge et al. (2005) found that habitat structural characteristics such as litter depth and understorey vegetation were positively correlated with species richness, and they recommended maintenance of a mosaic of tree age classes to support spider biodiversity. Varady-Szabo and Buddle (2005) found that spider assemblages in logs were distinctly different from those of the forest floor, and those in logs had higher species diversity and abundance as well. Similarly, Barbaro et al. (2005) found

that habitat spatial heterogeneity enhanced spider diversity, and our results confirm the findings from South America (Baldissera et al. 2004), Europe (Barbaro et al. 2005; Horvath et al. 2005; Oxbrough et al. 2005), interior Canada (Larrivee et al. 2005), and Australia (Harris et al. 2003) that suggest that spider assemblages are reliable predictors of habitat complexity. Larrivee et al. (2005) found that ground-living spider assemblages in boreal forests respond very differently to clearcuts and fires, and they recommended modifications of forestry practices to create disturbances that are more similar to natural wildfires, which, over the long term, enhance habitat mosaics.

The discovery of a new species in the genus *Agyneta* is not surprising, since these spiders are very small and the taxonomy of the group is poorly understood. Much more important, however, is the discovery of the linyphiid species that belongs to a new, yet-to-be named genus. To our knowledge, this is the first time this species has been uncovered and it is helping to define the species limits of the new genus that is being erected where other previously named species were misplaced in other genera. The Blacks Mountain species is a valuable intermediate link between two other species groups in this new, unnamed genus.

Buddle et al. (2005) emphasized the importance of using taxon sampling curves in comparative biodiversity research with forest arthropod assemblages, since inadequate sampling can seriously bias the results. Our species–area curves for five samples, taken during a single season over an approximately 4000 ha experimental forest, indicate that we captured three fourths of the true number of ground-dwelling spider species in that ecosystem, suggesting that the sampling effort was adequate. We recommend future sampling and analysis, however, considering concerns about biodiversity conservation in this widespread, yet little-studied forest type. Such sampling would provide a rare opportunity to assess recovery over time in a controlled, randomized, and replicated study. Additional sampling might also provide the opportunity to confirm or refute the trends that we saw for several apparent indicator species and perhaps to allow extrapolation to similar spider guilds in other interior pine sites in North America. To meet Pearce and Venier's (2006) criteria for good ecological indicators, those species must be easily sampled, be easily and reliably identified, be functionally significant, and respond to disturbance in a consistent manner. The species that we identified in this study as significant indicators clearly meet the first three criteria; only repeated sampling will reveal whether their functional response to the treatments at BMEF is consistent over time. This is, to our knowledge, the first such analysis of response of spider assemblages in the interior pine type and may serve as a useful baseline for future work.

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