



Response of forest soil Acari to prescribed fire following stand structure manipulation in the southern Cascade Range (1).(Report).Michael A. Camann, Nancy E. Gillette, Karen L. Lamoncha and Sylvia R. Mori. *Canadian Journal of Forest Research* 38.5 (May 2008): p956(13). (9313 words)

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Abstract: We studied responses of Acari, especially oribatid mites, to prescribed low-intensity fire in an east side pine site in the southern Cascade Range in California. We compared oribatid population and assemblage responses to prescribed fire in stands that had been selectively logged to enhance old growth characteristics, in logged stands to minimize old growth characteristics, and in undisturbed forest reference stands. Low-intensity prescribed fire altered habitat characteristics within the organic layer of forest soil. Acarine populations declined following prescribed fire, and oribatid losses accounted for two thirds of that decline. Individual oribatid species responded differently to prescribed fire, with a few populations increasing after fire but most declining. The prescribed fire also altered oribatid assemblages, reducing species richness and species diversity and modifying assemblage dominance relationships. We also identified several oribatid taxa that were potential indicator species of fire effects upon forest soil fauna. Finally, our results suggested that oribatid responses to fire were intensified by stand alteration and especially by removal of old growth structural characteristics. Decline in oribatid abundance, species richness and diversity, and loss of equilibrium dominance relationships was greatest in the low structural diversity plots.

Resume : Nous avons etudie les reponses des acariens, en particulier celles des oribates, au brulage dirige a faible intensite dans une pinede exposee a l'est et situee dans la partie sud de la chaine des Cascades en Californie. Nous avons compare les reponses des populations et des assemblages d'oribates au brulage dirige dans des peuplements qui avaient fait l'objet d'une coupe selective visant a ameliorer les caracteristiques de vieille foret, dans des peuplements coupes de manie re a minimiser les caracteristiques de vieille foret et dans des peuplements temoins en foret non perturbee. Le brulage dirige a faible intensite a altere les caracteristiques d'habitat dans la couche de matiere organique du sol forestier. Les populations d'acariens ont diminue a la suite du brulage dirige, en particulier celles des oribates dont les pertes representaient les deux tiers de cette diminution. Chaque espece d'oribates a reagi differemment au brulage dirige : certaines populations ont augmente apres feu mais la majorite d'entre elles ont diminue. Le brulage dirige a aussi altere les assemblages d'oribates en reduisant la richesse et la diversite specifiques et en modifiant les relations de dominance entre les assemblages. Nous avons aussi identifie plusieurs taxons d'oribates qui pourraient servir d'especes indicatrices des effets du feu sur la faune du sol forestier. Finalement, nos resultats indiquent que la reponse des oribates au feu a ete amplifiee par l'altere ration du peuplement, en particulier l'elimination des caracteristiques structurales de vieille foret. Le declin de l'abondance, de la richesse et de la diversite specifiques des oribates, ainsi que la disparition de l'equilibre des relations de dominance, etaient maximales dans les places-echantillons ou la diversite structurale etait faible.

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Introduction

Microarthropods, particularly Oribatei (Arachnida: Acari), dominate forest soil faunas. Their communities are often hyperdiverse, with local assemblages exceeding scores of species (Hansen and Coleman 1998; Lamoncha and Crossley 1998). Oribatid mites, whose life history characteristics constrain their recovery from disturbance, appear to be ideal for assessing

disturbance effects on forest soils (Crossley et al. 1997).

Soil oribatids provide crucial ecosystem services (Wallwork 1983; Kaneko et al. 1998). They indirectly regulate litter decomposition and nutrient mineralization rates in forest soils (Crossley 1977; Seastedt 1984; Hooper et al. 2000), and litter decomposition is slowed when soil microarthropods are excluded (Harding 1967). The question of top-down versus bottom-up regulation of decomposition by soil microarthropods has been much debated, but evidence exists for both means (Klironomos and Kendrick 1995; St. John et al. 2006; Wardle 2006). There is, nevertheless, strong support for the hypothesis that increased soil arthropod biodiversity enhances decomposition (Hattenschwiler and Tiunov 2006; Lenoir et al. 2007). Disturbances that reduce oribatid numbers or alter their assemblages thus may affect litter decomposition and nutrient mobilization (Seastedt and Crossley 1980; Abbott and Crossley 1982).

Forest management practices can modify the quality of the soil and litter habitat (Vose et al. 1999; Hattenschwiler and Tiunov 2006). For example, partial canopy removal affects forest floor microclimate by increasing insolation, reducing litter inputs, and altering soil and litter moisture levels. Clear-cutting can affect litter arthropod assemblage structure, litter decomposition, and soil nutrient cycling for a decade or more (Seastedt and Crossley 1981). Fire can also affect soil arthropods both directly, through incineration, and indirectly, by changing soil moisture and temperature, decreasing aboveground litter inputs, increasing belowground inputs (decaying roots), destabilizing nutrient cycling, and affecting other litter biota. Most studies of fire effects on soil fauna have focused on catastrophic wildfires, which cause much direct mortality (Sgardelis and Margaris 1993; Paquin and Coderre 1997). Fire exclusion has significantly altered the structure of many western forests, often increasing their risk of catastrophic wildfire (Taylor and Skinner 2003; Hessburg et al. 2005). Low-intensity prescribed fire, which usually produces mosaics of forest floor patches ranging from completely unaffected to completely incinerated (Vose et al. 1999), is an effective means of reducing this risk, but the effects of prescribed fire on soil and litter microarthropod communities are poorly understood.

The need for this information is particularly acute in the western US, where the use of prescribed fire is increasing but the soil microarthropod fauna is poorly characterized (Price 1973). Research in other regions suggests that fire may have persistent effects on soil biota, but the climate and fire history regimes in those areas are quite different from those of the interior Pacific Northwest. Vlug and Borden (1973), for example, noted diminished soil mite densities following slash burning in British Columbia, but the sites represented a relatively mesic coastal forest with deep humus accumulations. Crossley et al. (1997) found that a prescribed stand-replacing fire in the southeastern Appalachian Mountains reduced oribatid populations to 28% of their preburn abundance over 2 years, and taxonomic richness declined by 30%. These studies, however, reflect relatively mesic climatic conditions.

Western interior forests differ substantially from southeastern and coastal northwestern forests. In contrast with the mesic climates and deep humus layers of southern Appalachian and western coastal forests, interior pine forests of western North America receive nearly all their precipitation during the winter, as snow. Summers are hot and dry, with historically frequent wildfire that limits accumulation of woody debris, removes small trees, and creates forest openings (Oliver 2000). Litter and humus layers are often thin, with volcanic soils of comparatively recent origin. Forest stands are relatively open, with greater insolation and wind penetration and consequently greater evaporative losses. These characteristics should, in theory, favor a soil fauna that is relatively fire tolerant.

We tested the hypotheses that fire and stand structure have no effect on soil oribatid assemblages, by comparing soil arthropod assemblages in burned and unburned split-plots in the southern Cascade Range of California, both in unaltered interior ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) forest and in stands selectively logged to create two standardized stand structures. Our objectives were to characterize the responses of soil Acari, especially Oribatei, to low-intensity fire in dry, interior forests of the western US and to determine whether stand complexity influences

mite assemblage responses to prescribed fire. We hypothesized that oribatid response and recovery would be adversely affected by prescribed fire and changes in stand structure.

Materials and methods

Study site

We established study plots at Blacks Mountain Experimental Forest (BMEF), Lassen National Forest, near Redding, California (1700-2100 m a.s.l.). Soils are mostly shallow stony loams over lava bedrock, and the climate is typical of the southern Cascade Range, with short, dry summers and cold, moderately wet winters. Most precipitation falls as snow, with mean annual precipitation of 46.2 cm measured from 1935 to 1953 (Hallin 1959). The forest stands are dominated by ponderosa pine with some Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), especially at lower elevations, and increasing proportions of white fir (*Abies concolor* (Gord. & Glend.) Lindl.) and incense cedar (*Libocedrus* [= *Calocedrus*] *decurrens* (Torr.) Florin) at higher elevations (Society of American Foresters forest cover type 231, Barrett et al. 1980). This forest type occurs over a wide geographic range, from central Mexico to southern British Columbia (Oliver and Ryker 1990; Oliver and Powers 1998). Much of the old growth forest was removed during the 1930s and 1940s, but remnants remained in four research natural areas (RNAs) (Oliver 2000). The RNAs represent undisturbed, late successional forest that, until 1997, experienced fire exclusion as a byproduct of local forest management. Litter depths range from essentially 0 cm to a mean of 8 cm (Alexander 1993), but are highly variable depending on harvesting intensity and canopy and understory plant composition. Recently harvested plots showed evidence of mixing of the O horizon with mineral soil. Litter is obviously a heterogeneous environment for soil organisms, with clear resource partitioning by soil fauna (Anderson 1978), and ordinarily this heterogeneity should be accounted for in sampling. We did not have sufficient resources to stratify and sample different layers; however, the litter layers at our sample sites, which were under the drip line of trees of a standard size, were sufficiently uniform that this did not pose a problem.

Treatments

We used a split-plot design with 12 treatment plots of at least 100 ha each and 4 RNA reference plots of approximately 50 ha each (Table 1). The treatment plots were aggregated into three blocks of four plots each. Two plots in each block were selectively logged to reduce stand density while maintaining old growth characteristics of high structural diversity (HSD), such as multiple canopy layers, an abundance of large snags, many large old trees, and many small canopy gaps and forest floor openings. The other two plots were selectively logged to minimize old growth characteristics, creating low structural diversity (LSD) plots of intermediate age with a single-layered, evenly spaced, continuous canopy retaining few snags. One half of each plot (i.e., each split-plot) was subjected to low-intensity prescribed fire in the fall. The RNAs were not logged, but two were burned under similar fire prescriptions.

In summary, the complete study design included six unburned HSD split-plots, six burned HSD split-plots, six unburned LSD split-plots, six burned LSD split-plots, two unburned RNA plots, and two burned RNA plots (Table 1). All treatments were randomly assigned except the RNAs, which were constrained by the management history of the site. The RNAs therefore served as undisturbed reference stands rather than as true controls. Harvesting per se was not intended to be uniform, but was designed to create uniform residual stands. Prescribed fire was applied 1 year after harvest, and arthropod sampling began after snowmelt 8 months later.

The treatment plots were segregated into three blocks of four plots because the logistics of applying the full treatment regime prevented all treatments being completed in a single year. Thus, the first block, which consisted of four treatment plots, was selectively harvested in 1996, and its split-plots and one RNA plot were burned in 1997. A second RNA plot was left unburned to serve as an untreated reference.

Soil arthropod sampling

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We established a 1 ha subplot ("study plot"), placed at random, within each split-plot and RNA. Five 25-36 cm diameter at breast height (DBH) ponderosa pines were randomly chosen within each of these 28 study plots. An 8.0 m east-west transect was centered at each tree, and four litter samples were collected at 1.0 m intervals from the base of the bole to the approximate east and west drip lines. 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). East and west transect samples were pooled for each tree, resulting in four composite samples for each transect and each sampling date.

Samples consisted of all loose soil and litter down to hard mineral soil, enclosed by a 30.5 cm cylinder. We initially sampled cores of mineral soil as well, but abandoned that effort when repeated samples yielded few arthropods. We measured litter thickness, recorded a visual (presence or absence) assessment of litter incineration for each sample, then sieved the litter sample through 0.64 cm mesh to remove coarse debris. Sieved samples were stored on ice for up to 3 days and then transported to Placerville, California, for Berlese extraction of arthropods into 70% ethanol. Acari were sorted to suborder, and oribatids were determined to the lowest practical taxon, usually to species or morphospecies, in the entomology laboratory at Humboldt State University in Arcata, California.

We collected samples in June, August, and October 1998, but preliminary analyses suggested that the June 1998 samples had by far the greatest abundance and richness of mites. This manuscript describes the June 1998 results from block 1, with 400 samples (200 pooled) from two HSD plots, two LSD plots, and two RNAs (Table 1), representing analyses of the first fauna sampled after the complete treatment regime was applied.

Data analyses

We compared mean abundance of acarine suborders from burned and unburned split-plots within and among stand structure treatments and with reference RNA plots. We made similar comparisons for each individual oribatid taxon to assess the significance of prescribed fire effects on abundance and frequency. We used mixed models to account for fixed and random effects using either general linear models for continuous responses or overdispersed Poisson generalized linear models (McCulloch and Searle 2001) for counts. Minimum Akaike Information Criterion was used to select appropriate models from a set of candidates. The general linear model for the response was

$$[1] \text{ response} = \text{predictors} + [\epsilon]_{\text{sub}.u} + [\gamma]_{\text{sub}.s(u)} + [\delta]_{\text{sub}.t[s(u)]} + [\lambda]_{\text{sub}.r(u,s,t)}$$

where the best predictors were usually treatments (diversity and fire status), litter thickness, and fire status x litter thickness, $[\epsilon]$ was the random effect due to plot ($u = 1, 2, 3, 4$), $[\gamma]$ was the random effect due to subplot nested within plot (split-plot) ($s = 1, 2$), $[\delta]$ was the random effect due to transect nested within split-plot ($t = 1, 2, \dots, 25$), and $[\lambda]_{\text{sub}.r}$ was the residual error ($r = 1, 2, 3, 4$; pooled composites / transect). All random effects and residual errors are assumed to be independent and normally distributed. The overdispersed Poisson model for the expected count response was

[2] [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]

using the same predictors as in eq. 1 and defining the random effects $[\epsilon]$, $[\gamma]$, and $[\delta]$ as above. The corresponding models for the burned and unburned RNAs were

$$[3] \text{ response} = \text{predictors} + [\epsilon]_{\text{sub}.u} + [\delta]_{\text{sub}.t(u)} + [\lambda]_{\text{sub}.r(u,t)}$$

and

[4] [MATHEMATICAL EXPRESSION NOT REPRODUCIBLE IN ASCII]

respectively. Mixed effects regressions were fit using the R lme (linear mixed-effects models) and R glmmPQL Linear (generalized mixed-effects models) statistical estimation functions (Ihaka and Gentleman 1996; Venables and Ripley 2002; R Development Core Team 2005). We used the generalized linear model for mixed effect models to examine relationships between species abundance and litter thickness and between litter thickness and fire coverage.

We compared mean species richnesses of oribatid mites with and without prescribed fire, and assessed oribatid assemblage heterogeneity using Brillouin indices (Magurran 1988; Krebs 1999). We used rarefaction to determine whether observed differences in species richness were attributable to sample size differences. We compared taxonomic richness using overdispersed Poisson generalized linear models and assessed oribatid assemblage dominance and evenness directly using nonparametric comparisons of mean proportions of oribatid abundance accounted for by the five most numerically dominant taxa, and also by linear mixed effects models of Camargo's evenness index, which is relatively unaffected by rare species (Camargo 1995). We used Kruskal-Wallis rank sum tests and pairwise Wilcoxon rank sum tests (with Bonferroni corrections) for nonparametric comparisons.

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We also looked for changes in assemblage dominance rank structure following prescribed fire, assessing both differences in rank proportion and species occupancy using multiple sample dominance-rank coefficients calculated for each taxon from a matrix of species ranks. The dominance-rank index, [D.sub.r], varies from 0 to 1, with [D.sub.r] equal to 1 for any species that is top ranked in every sample and [D.sub.r] equal to 0 for any species absent from all samples (McCune and Grace 2002). It integrates species dominance across multiple samples, while avoiding species rank inflation when a few samples have atypically high abundances.

We used species-area curves, first-order jackknife estimates of total species richness (Palmer 1990), and abundance-based coverage estimates (ACE) (Colwell 2005) of total richness to evaluate sampling sufficiency and estimate assemblage size. Both species-area curves and ACE estimates were based on mean species richness obtained by 500 random subsamples from the oribatid abundance data at each possible subsample size.

We identified ecological gradients and sample relationships with nonmetric multi-dimensional scaling (NMS) of oribatid abundance vectors using Sorensen (Bray-Curtis) distance, with species scores calculated by weighted averaging (Minchin 1987). We used multivariate indicator species analyses to detect characteristic postfire taxonomic complexes (Dufrene and Legendre 1997) and ran 10 000 randomized Monte Carlo trials of the indicator analyses to assess the probability of Type I error when comparing indicator values (IV). We used multiple response permutation procedures (MRPP) with rank-transformed Sorensen distances (Zimmerman et al. 1985) to evaluate within-group assemblage heterogeneity and to relate observed assemblages to fire coverage. We quantified within-group heterogeneity using chance-corrected within-group agreement statistics (McCune and Mefford 1999; McCune and Grace 2002). We conducted indicator species analyses and MRPP using PC Ord (McCune and Mefford 1999); all other analyses (except ACE, as noted above) were performed with functions written in R (R Development Core Team 2005).

Results and discussion

Low-intensity fire reduced mean litter thickness in the harvested plots and in the burned RNAs (Fig. 1), and this difference was highly significant for the RNAs. The effect was even more apparent when HSD and LSD data were pooled, so that the effects of fire were not distinguished from stand structural treatments ($p = 0.019$, unburned versus burned split-plots). Mean litter thickness and the number of scorched samples per transect were correlated ($p < 0.001$, [r.sup.2] = 0.53).

Mite suborder analyses

In the June 1998 samples, 148 505 Acari were collected. Of these, 58 516 were oribatid mites, 9 546 were mesostigmatid mites, 55 872 were prostigmatid mites, and 24 571 were either astigmatid mites or hypopi. The latter were not included in subsequent analyses. Total mite abundance declined slightly in all burned plots, from 795 [+ or -] 78 to 621 [+ or -] 59 mites ($p = 0.15$ for fire alone, $p = 0.001$ for reduced litter thickness, and $p = 0.02$ for fire x litter thickness). When the harvested plots were considered separately from the RNAs, only litter thickness appeared to be a significant predictor of acarine abundance ($p = 0.01$ and $p = 0.07$ in the pooled treatment plots and the RNAs, respectively).

Oribatid mites

Oribatid mites experienced greater proportional population reduction than did other mite suborders, declining by 53% in burned split-plots and accounting for 68% of the total acarine decline. Mean oribatid abundance declined significantly in the burned split-plots, but the burned HSD split-plots contributed relatively little to that decline (Fig. 2a). Declines were steep in burned split-plots of LSDs and RNAs, but much of this effect resulted from reduced litter thickness.

Mesostigmatid mites

Mean mesostigmatid mite abundance declined by 52% in the pooled treatment burned split-plots (Fig. 2b, $p = 0.02$ for fire, $p < 0.001$ for litter thickness, and $p < 0.001$ for fire x litter thickness). As with oribatids, mesostigmatid decline was most pronounced in the burned LSD split-plots, intermediate in the RNAs, and least evident in the HSD plots. While low-intensity fire and reduced litter thickness were both good predictors of mesostigmatid population decline in the RNAs and in the pooled HSD and LSD treatments, neither was a good predictor in the LSD treatment alone, where the effect was most pronounced ($p = 0.27$ for fire, $p = 0.83$ for litter thickness, and $p = 0.82$ for fire x litter thickness).

Prostigmatid mites

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Prostigmatids accounted for 38% of all mites sampled and were the least affected by fire. Of the prostigmatids, Tydeidae were most abundant and their mean abundance in the combined unburned split-plots did not differ from the combined burned split-plots (Fig. 2c). Prostigmatid abundance declined somewhat in the burned HSD split-plots, primarily owing to reduced litter thickness ($p < 0.004$ for fire and $p = 0.03$ for fire x litter thickness). It increased in both of the burned LSD split-plots. None of the prostigmatid populations in the burned split-plots differed significantly from the population in the unburned RNAs, the least disturbed reference plot in the study.

Positive Oribatei population responses to prescribed fire

Seven species were more frequent in one or more of the burned split-plots, and the abundance of immatures also increased in most burned split-plots. Several such increases were inconsistent across plots, but two positively responding oribatid species were significant fire indicators (Table 2). *Aphelacarus acarinus* was more frequently sampled in all of the burned split-plots and in the burned RNAs. Nearly absent in one unburned LSD split-plot, it increased 100-fold and made up one third of the oribatid mites in the corresponding burned split-plot. *Nortonella gildersleeveae* was also more abundant in all of the burned split-plots, especially in the pooled LSD samples. Seemingly tolerant of low-intensity fire, it was a significant fire indicator species (Table 2).

Negative Oribatei population responses to prescribed fire

As noted above, a few oribatid populations increased in burned split-plots, but most populations declined, yielding a net reduction of oribatid abundance in the burned split-plots (Fig. 3).

Twenty-four taxa declined markedly in samples from one or more of the burned split-plots and many were significant indicator species in unburned split-plots (Table 2). Eight oribatid species experienced significant population change in the burned RNAs, 15 species in at least one burned split-plot from the HSD treatment plots, and 27 oribatid species in at least one of the LSD treatment plots. Twelve oribatid populations differed significantly in both burned LSD split-plots, while only four differed in both burned HSD split-plots. Most of these differences were conspicuous declines.

Oppia parviaures was the most abundant oribatid in the unburned split-plots. Although its response to fire was not completely consistent, it was, overall, a significant indicator species for mite assemblages from unburned split-plots and from the less-disturbed RNAs. Likewise, *Oppiella nova* populations declined in every burned split-plot, especially the burned LSD split-plots, where it declined by nearly 93% ($p = 0.17$). It was a significant and effective indicator species of unburned split-plots, as well as the RNAs.

The species complex *Suctobelbella* spp. also declined in all of the burned split-plots, especially in HSD split-plots and RNAs. *Suctobelbella* spp. population decline was least apparent in burned LSD split-plots because few *Suctobelbella* spp. occurred in any LSD plots. *Suctobelbella* spp. was nonetheless a significant indicator taxon for oribatid assemblages from unburned split-plots and from HSD mite assemblages (Table 2).

Cultoribula vtouri abundance declined with prescribed fire in all but one LSD split-plot, from which it was absent entirely, and *Ceratozetes cuspidatus* abundance also declined in all but one HSD split-plot. Both *C. vtouri* and *C. cuspidatus* were significant indicator species of oribatid assemblages from unburned treatments (Table 2).

Of the remaining oribatids that declined in burned split-plots, an unidentified *Zachvatkinibates* sp. is of interest because it declined only in HSD split-plots and was a strong indicator of oribatid assemblages in unburned split-plots and in untreated RNAs (Table 2).

Effects of prescribed fire on Oribatei assemblages

Burned split-plots were distinguished from unburned split-plots by extent of litter scorching, increased oribatid assemblage evenness, and proportional abundance of *A. acarinus* in the burned split-plots (Fig. 4). Most other measures of community structure were higher in unburned split-plots, for example, oribatid abundance, species richness, and assemblage heterogeneity, as was litter thickness. The strong association of several dominant taxa with unburned split-plots noted above was also apparent in the correlations between those taxa and the distributions of transects within the ordination space. The first and second NMS axes extracted 63% and 18% of the variance from the distance matrix, respectively (cumulative [$r_{sup.2}$] = 0.81 on two axes, stress = 10.4).

We identified 51 620 oribatid mites in 60 species or morphospecies, which compares well with the jackknife (70 [+ or -] 5 species) and ACE (66 species) estimates of species richness for the combined samples. Our analyses suggest that a few oribatid species were undetected; when the expected number of species and (or) octave was extrapolated along a truncated log normal distribution, it included six undetected species beyond the veil line, which is identical to the ACE estimate.

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The reduced oribatid species richness observed in the pooled stand structure treatment burned plots was indistinguishable from the interpolated species richness at similar sample sizes when all samples from each fire treatment were pooled (Fig. 5a). This outcome was not troublesome because the reduced sample size itself was attributable largely to thermal mortality, litter consumption, and other effects of fire. However, species richness declines in the two stand structure treatments and the RNAs exceeded the interpolated richness loss (Fig. 5b). The latter analysis included both burned and unburned split-plots within each treatment category, so it

averaged the effects of both the stand structure modification and subsequent fire impacts on oribatid assemblages.

Oribatid species richness declined in the burned split-plots and in the RNAs (Fig. 5c, $p = 0.003$ for the burned split-plots and $p < 0.001$ for the RNAs). The mean numbers of species in the HSD split-plots declined from 13 [+ or -] 0.7 species in the HSD unburned split-plots to 9 [+ or -] 1 species in the burned split-plots ($p = 0.12$ for fire and $p < 0.001$ for reduction in litter thickness in the burned split-plots). The actual total species richness was slightly higher in the burned HSD split-plots (45 species, Table 3) than in the corresponding unburned split-plots (42 species), but this difference was small and may be attributable to interaction between increased patchiness and infrequent taxa distributions in the burned split-plots. The burned LSD split-plots experienced the greatest species loss, declining by >50%, from 16 [+ or -] 0.8 species to 7 [+ or -] 0.7 species in the burned split-plots ($p = 0.10$ for fire and $p < 0.001$ for litter loss). The decline in oribatid species richness was lowest in the RNAs, where it dropped from 16 [+ or -] 1 species in the unburned RNAs to 11 [+ or -] 2 species in the burned RNAs ($p < 0.001$ for fire and $p = 0.001$ for litter thickness).

Oribatid assemblage heterogeneity also declined in the burned split-plots, but not significantly in the burned RNAs (Fig. 5d). Mean Brillouin diversity declined from 1.65 [+ or -] 0.04 species in the unburned pooled stand structure treatment split-plots to 1.07 [+ or -] 0.07 species in the burned split-plots ($p = 0.003$ and $p < 0.001$ for reduced litter thickness). Oribatid assemblage heterogeneity declined the most in the LSD plots.

Oribatid assemblage evenness increased in most burned split-plots, but the impact of fire on community evenness was greatest in LSD split-plots (Fig. 6a, $p = 0.2$ for fire and $p = 0.04$ for decreased litter thickness). The effect of fire was better supported in pooled treatment split-plots ($p = 0.05$ for fire and $p < 0.001$ for reduced litter thickness). This result highlights a trend toward much stronger statistical support with only a few additional replicates, but replication was at the level of plot treatments (harvesting and fire), making increased replication prohibitive.

Assemblage dominance relationships were quite different in the burned and unburned split-plots (Table 4), with a significant decline in the mean proportion of several taxa that dominated assemblages in unburned split-plots. Interestingly, the five most numerically dominant taxa were identical in both HSD plots, and most occupied similar proportional dominance ranks in both plots (except *O. nova*, which was ranked higher in HSD plot 41). Although LSD plots and the RNAs were slightly less consistent in their dominance patterns, prescribed fire nonetheless caused significant rank reductions for most previously dominant taxa.

While there were many instances of taxonomic exchange among the top five dominance ranks in the burned split-plots, the overall assemblage dominance shifts were subtle (Fig. 6b). The dominance-rank index [D.sub.r] declined from 0.25 [+ or -] 0.06 in the unburned split-plots to 0.19 [+ or -] 0.05 in the burned split-plots (Fig. 6c, $p = 0.004$, paired sample Wilcoxon rank sum test). This likely corresponded to the "unseating" or rank reduction of several species that were quite dominant in the unburned split-plots. For example, *O. parviaures* was the highest ranking oribatid in the unburned split-plots, making up 31% of the total abundance with a [D.sub.r] equal to 0.54, but it slipped to third rank in burned split-plots with a [D.sub.r] equal to 0.22. *Oppiella nova*, second-ranked in unburned split-plots with [D.sub.r] equal to 0.47, declined to sixth rank in burned split-plots with a [D.sub.r] equal to 0.12.

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At the same time, proportional abundance of a few oribatid species either consistently increased with fire or their decline in burned split-plots was apparently limited by fire tolerance (Table 4). For example, *A. acarinus* was the most numerically abundant and first-ranked oribatid species in the burned split-plot from LSD plot 39, accounting for 35% of the total abundance. In burned split-plot 41, the most abundant species were *Joshuella* sp. nr. *striata* and *A. acarinus*, accounting for 24%

and 14% of oribatid abundance, respectively. *Aphelacarus acarinus* was the fourth-ranked oribatid species in the burned RNA C. *Propelops* sp. was the second most abundant oribatid species in burned split-plots from plots 38, 39, and 43. In terms of [D.sub.r] exchanges, *A. acarinus* increased overall from 26th ranked ([D.sub.r] = 0.02) to fourth ranked ([D.sub.r] = 0.2) and *Propelops* sp. increased from fourth ranked ([D.sub.r] = 0.24) to second ranked ([D.sub.r] = 0.34) (after immature oribatids, which increased their relative abundance in most burned split-plots).

Oribatid assemblage organization was distinct in unburned and burned split-plots in every treatment plot and between the RNA (MRPP, $p < 0.001$ for homogeneity of within-group average distance in each instance; Table 5). Within-group assemblage homogeneity was least in the burned RNAs. However, it must be noted that oribatid assemblages were distinct in all paired comparisons of unburned split-plots within stand structure treatments, suggesting that there was little homogeneity of oribatid assemblage organization in stand structure replicates.

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MRPP also revealed that the extent of prescribed fire affected oribatid assemblages. Thirty-two percent of the samples from burned split-plots had no scorched quadrats; whereas, 25% had one scorched quadrat and both quadrats were scorched in the remaining 43%. Mean within-group distances were indistinguishable from between-group distances for samples having no scorched quadrats and for samples with a single scorched quadrat ($p = 0.58$, MRPP), but samples with two scorched quadrats differed from both ($p < 0.001$, MRPP).

Conclusions

Several major patterns of disturbance response were apparent in forest soil Acari at BMEF, even 8 months following application of low-intensity fire. Mite abundance was reduced, especially the Oribatei. Oribatid assemblage structure was modified--often simplified and with altered dominance relationships. Population and assemblage demographic structure changed as immature mite dominance increased. Several of these responses were strongest in the LSD treatment plots. Many oribatid species responded consistently and predictably to fire.

Prescribed fire clearly altered forest soil habitat. Sixty-eight percent of samples in burned transects were scorched, so transient high temperatures presumably caused some immediate arthropod mortality. Crossley et al. (1997) reported similar rapid mortality following prescribed fire in North Carolina. At BMEF, litter and woody debris were consumed in a mosaic, reflecting local fire intensity. There was significant reduction in mean thickness of organic detritus in the burned split-plots. Fire coverage explained more than half of the variation in litter depth and changes in oribatid assemblage organization were correlated with patterns of fire coverage.

Acari mean abundance declined by 35% in the burned split-plots and oribatid, mesostigmatid, and hypopi and (or) astigmatid mite populations remained depressed the following season. Prostigmatids either escaped short-term mortality or recovered relatively quickly. The latter seems reasonable, since oribatids and prostigmatids are equally vulnerable to fire. Most tydeids, overwhelmingly dominant in our prostigmatid samples, are fungivores adapted for rapid response to resource availability. They are also quite mobile, increasing the possibility of rapid recruitment by migration. Crossley et al. (1999) observed high prostigmatid mortality immediately following prescribed fire in North Carolina, but essentially complete recovery in 2 years. Our data suggest that, if affected, prostigmatid mites were capable of full recovery within months.

Oribatei experienced the greatest loss of proportional abundance, accounting for roughly two-thirds of the acarine decline. Their sensitivity to fire and the longevity of their response confirms our assumption that they are ideal bioindicators of prescribed fire effects on forest soil microfauna. Our experience in this regard at BMEF corroborates that of other workers.

Prescribed fire did not reduce the abundance of all oribatid species. Several species--17% of those whose populations changed significantly in at least one burned split-plot--responded positively to

fire, either by escaping short-term mortality or by recovering rapidly. *Aphelacarus acarinus* increased numerically in every burned split-plot and proportionally in most. This response might have resulted from fire tolerance, but *A. acarinus* must also have recruited successfully during the postfire recovery period because populations increased numerically as well as proportionally. We do not know whether this increase was in direct response to fire, for example, by suppression of otherwise abundant acarine competitors, or whether it represented tolerance for altered abiotic conditions in burned habitats. Since periodic fire was historically common in the interior ponderosa pine forest (Taylor and Skinner 2003), we surmise that these positively responding taxa would increase following natural low-intensity fire. While it remains to be seen how persistent their responses are, it is likely that some, especially *A. acarinus*, might serve as bioindicators of natural fire regimes, particularly during the immediate postfire interval. This possibility begs further investigation.

[GRAPHIC OMITTED]

Several oribatid species that were very abundant in the unburned split-plots were conspicuously reduced in burned split-plots, particularly *O. parviaures*, *O. nova*, *Suctobelbella* sp. a, *Zachvatikinabates* sp., and *Eobrachychthonius latior*. They were among the most dominant oribatid species in the unburned split-plots, so natural fire regimes might also reduce their dominance in forest oribatid assemblages, at least in the immediate aftermath of fire. If the natural fire return interval exceeds the postfire recovery interval, we might expect oribatid assemblages strongly dominated by these taxa to occur later in the fire cycle.

The net effects of prescribed fire on oribatid populations at BMEF were reduction of oribatid abundance and increased proportions of immature mites. There were at least five times as many declining populations as there were populations responding positively to prescribed fire. This was generally consistent with the effects of prescribed fire noted elsewhere, but the decline in oribatid abundance and species richness was apparently less pronounced at BMEF than has been reported in the southern Appalachians, at least in the short term. Crossley et al. (1997) noted a 72% decline in oribatid abundance and 30% loss of species richness over 2 years following prescribed fire at Wine Spring, North Carolina, while we found 50.5% reduction in oribatid abundance and only 9% decline in species richness. However, microarthropod sampling at Wine Spring was conducted twice, at 1 month and 2 years following prescribed fire, while we first sampled roughly 8 months after the treatment split-plots were burned. Oribatid decline at BMEF may yet be continuing, or the pattern of oribatid decline and recovery at Wine Spring might differ from that at BMEF. Wikars and Schimmel (2001) reported a delayed decline in mite abundance 60 days following fire, and Webb (1994) reported a 15 year postfire recovery period for oribatid mites in a British heathland. We are presently analyzing data from an additional year of sampling to assess potential recovery at BMEF.

Oribatid species assemblage organization changed in most burned split-plots following prescribed fire. Species richness and diversity declined in most split-plots and assemblage evenness increased. Finally, some of our data suggested that the effects of prescribed fire were least intense in stands retaining old growth characteristics and more intense in stands of LSD. There was little evidence supporting significant homogeneity of oribatid assemblages in the unburned split-plots from the replicate stand structure treatments, especially in the HSD treatment plots where differences were most pronounced. Nevertheless, the decline in oribatid abundance and species richness was consistently greatest in the burned LSD split-plots, suggesting some homogeneity of post-treatment oribatid response to additional disturbance. These results were consistent with the report of Paquin and Coderre (1997), who noted increased severity of fire effects on soil macroarthropod populations following deforestation. The number of oribatid populations that were significantly affected by prescribed fire was greatest in the LSD treatment plots, intermediate in the HSD treatment plots, and least in the RNAs. Oribatid populations were also three times as likely to respond to prescribed fire in both of the LSD treatment plots as in both of the HSD treatment plots, again, usually declining. The number of taxa responding to prescribed fire was also least in the burned RNAs, intermediate in the HSD treatment plots, and greatest in the LSD treatment plots, where nearly three times as many species responded significantly to prescribed fire as in the

burned RNAs. In all but a few instances, these included the most numerically dominant Oribatei.

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Assemblage level responses to prescribed fire were also greatest in the LSD treatment plots. Oribatid species richness was the only indicator of assemblage structure that declined significantly after prescribed fire in the HSD treatment plots. Neither taxonomic richness nor assemblage heterogeneity declined significantly in the burned RNAs, and oribatid evenness actually increased. Conversely, species richness and assemblage heterogeneity declined in both burned LSD split-plots. Overall, changes in oribatid species richness were easier to tie to differences in stand structure and the interaction between stand structure and fire than to fire alone.

Oribatid assemblage heterogeneity declined in burned stands lacking old growth structure, despite increased assemblage evenness. Reduced stand complexity and canopy structure apparently diminished the tolerance of oribatid assemblages for further disturbance, perhaps because of increased insolation, wind penetration, and drying following partial canopy removal. We saw strong correlations between reduced mite abundance and litter loss in the burned split-plots. Such corollary effects of reduced litter thickness might well have been exacerbated in the harvested treatment plots generally, and in the more open LSD treatment plots in particular. Other perturbations that might have affected soil microarthropod fire response include changes in litterfall, increased amounts of postharvest coarse debris (and fuel) in the LSD treatment plots, and changes in winter precipitation accumulation and melting regimes. These issues must be examined in greater detail if we are to fully understand the dynamics of soil microarthropod fire response and recovery in managed forests.

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Fundamental questions also remain regarding the functional consequences of the changes in acarine abundance and organization that we saw. Oribatida are presumed to be generalists (Rusek 1975), and as such, should not be severely impacted as long as sufficient refugia are available for recolonization following disturbance. Oribatid mites clearly evolved with natural wildfire, so we expect some degree of resilience to such a low-intensity prescribed fire. The relative microhabitat specializations of individual mite species are poorly understood, though, (Walter and Proctor 2004), so it is difficult to predict the functional impacts of the mite assemblage shifts seen in our study. We recommend future sampling to assess recovery over time. The BMEF project represents a rare opportunity for such replicated, controlled, and long-term study.

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Table 1. Summary of the treatment history at Blacks Mountain Experimental Forest (BMEF).

Plot	Structure	Harvest year	Fire year
Block 1			
38 (a)	HSD	1996	1997
39 (a)	LSD	1996	1997
41 (a)	HSD	1996	1997
43 (a)	LSD	1996	1997
Block 2			
42	HSD	1997	1999
44	LSD	1997	1999
47	HSD	1997	1999
45	LSD	1997	1999
Block 3			
48	HSD	1998	2000
40	LSD	1998	2000
49	HSD	1998	2000
46	LSD	1998	2000
RNA			
RNA A	Old growth	Not harvested	Not burned
RNA B	Old growth	Not harvested	1999
RNA C (a)	Old growth	Not harvested	1997
RNA D (a)	Old growth	Not harvested	Not burned

Note: Treatment plots were numbered and RNAs were lettered. HSD, high structural diversity; LSD, low structural diversity.

(a) Plots included in the present study.

Table 2. Observed maximum indicator values (IV) for oribatid species with at least one IV having $p < 0.05$.

Taxon	Observed max. IV			Unburned	Burned
	HSD	LSD	RNA		
Aphelacarus acarinus					41 ***
Verachthonius sp. a				17 **	
Verachthonius sp. b				8 **	
Brachychthonius bimaculatus			25 ***		
Brachychthonius sp. a				19 **	
Sellnickochthonius rostratus				13 ***	
Eobrachychthonius latior		28 **		30 ***	
Liochthonius brevis				16 *	
Eueremaues alvordensis			29 **		
Nortonella gildersleeveae					31 **
Epidamaeus sp.			31 *	51 ***	

Quadroppia sp. a		41 ***	43 ***
Oppiella nova		46 ***	76 ***
Oppia parviaures		42 **	68 ***
Tectocepheus velatus			43 **
Ramusella manifera			12 **
Cultoribula vtouri			35 ***
Zachvatkinibates sp.		29 *	47 ***
Ceratozetes cuspidatus			25 **
Pilogalumna sp.		35 ***	32 **
Gymnodamaeus sp		12 *	12 *
Eueremaeus stiktos	20 **		23 ***
Charassobatidae sp.	8 *		
Oribatella sp. a			12 **
Oribatella dentaticuspis	27 **		27 ***
Jacotella enoplura		42 **	
Micropoppia minus		22 **	19 *
Galumna sp.	27 ***		
Suctobelbella sp. a	29 *		64 ***
Eremaeus sp.		10 *	
Maculobates sp. b			21 **
Tectocepheus sp. b	8 *		

Note: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; where p is the proportion of randomized Monte Carlo trials having trial indicator values equal to or exceeding the maximum observed IV. Observed IV having $p > 0.05$ were omitted. HSD, high structural diversity; LSD, low structural diversity; RNA, research natural area.

Table 3. Oribatei taxonomic richness and assemblage diversity in unburned and burned split-plots and RNAs.

	[S.sub.obs]	[??]
Unburned split-plots		
HSD	42	44.85[+ or -]2.69
LSD	51	58.60[+ or -]4.39
RNA	38	43.70[+ or -]4.82
Pooled	55	63.92[+ or -]4.48
Burned split-plots		
HSD	45	52.60[+ or -]4.39
LSD	36	46.45[+ or -]7.34
RNA	31	35.75[+ or -]4.04
Pooled	50	57.93[+ or -]5.36
All plots	60	69.95[+ or -]5.08
	[[bar.S].sub.obs]	[??]
Unburned split-plots		
HSD	18.45[+ or -]0.91	1.85[+ or -]0.06
LSD	23.70[+ or -]1.02	2.04[+ or -]0.05
RNA	14.70[+ or -]1.03	1.37[+ or -]0.10
Pooled	14.80[+ or -]0.48	1.62[+ or -]0.04
Burned split-plots		
HSD	14.40[+ or -]0.87	1.75[+ or -]0.08
LSD	9.75[+ or -]1.12	1.43[+ or -]0.08
RNA	10.60[+ or -]1.27 **	1.25[+ or -]0.17 **
Pooled	8.60[+ or -]0.62 **	1.13[+ or -]0.07 **
All plots	10.79[+ or -]0.44	1.38[+ or -]0.04

Note: [S.sub.obs], observed species richness; [??], first-order jackknife estimate of species richness; [[bar.S].sub.obs], mean number of species per sample; [??], mean Brillouin diversity index; HSD, high structural diversity; LSD, low structural diversity; RNA,

research natural area. Values are means [+ OR -] 1 SE, with relative p values for the difference of means in burned split-plots indicated by asterisks. *, p < 0.05; **, p < 0.01.

Table 4. Mean frequency of occurrence of the five most dominant oribatid taxa.

Rank	Unburned split-plot Taxon	Frequency
Split-plot 38		
1	<i>Oppia parviaures</i>	0.24 [+ or -] 0.033a
2	<i>Oppiella nova</i>	0.19 [+ or -] 0.031ac **
3	Immature oribatids	0.12 [+ or -] 0.02 bcd **
4	<i>Suctobelbella</i> spp.	0.12 [+ or -] 0.026bcde **
5	<i>Zachvatikinabates</i> sp.	0.12 [+ or -] 0.029bcde **
Split-plot 41		
1	<i>O. nova</i>	0.28 [+ or -] 0.055a **
2	<i>O. parviaures</i>	0.24 [+ or -] 0.040ac **
3	<i>Zachvatkinibates</i> sp.	0.12 [+ or -] 0.028bde **
4	Immature oribatids	0.08 [+ or -] 0.014bdef *
5	<i>Suctobelbella</i> spp.	0.07 [+ or -] 0.013bdef **
Split-plot 39		
1	Immature oribatids	0.22 [+ or -] 0.028a
2	<i>O. parviaures</i>	0.21 [+ or -] 0.048ac **
3	<i>Propelops</i> sp.	0.18 [+ or -] 0.038ace
4	<i>Eobrachychthonius latior</i>	0.04 [+ or -] 0.025bdfg **
5	<i>Oribatella dentaticuspis</i>	0.04 [+ or -] 0.013bdfg **
Split-plot 43		
1	<i>O. parviaures</i>	0.31 [+ or -] 0.034a **
2	<i>O. nova</i>	0.17 [+ or -] 0.034bc **
3	Immature oribatids	0.13 [+ or -] 0.029bce **
4	<i>Suctobelbella</i> spp.	0.10 [+ or -] 0.022bdeg **
5	<i>Tectocephus velatus</i>	0.04 [+ or -] 0.010bdfg **
RNA D		
1	<i>O. nova</i>	0.32 [+ or -] 0.061a **
2	<i>O. parviaures</i>	0.31 [+ or -] 0.057ac *
3	Immature oribatids	0.07 [+ or -] 0.015bde **
4	<i>Propelops</i> sp.	0.05 [+ or -] 0.014bdeg
5	<i>Quadroppia</i> sp.	0.03 [+ or -] 0.011bdfg *
Rank	Burned split-plot Taxon	Frequency
Split-plot 38		
1	<i>Propelops</i> sp.	0.23 [+ or -] 0.048a **
2	Immature oribatids	0.22 [+ or -] 0.027ac **
3	<i>O. parviaures</i>	0.18 [+ or -] 0.042ace
4	<i>Aphelacarus acarinus</i>	0.06 [+ or -] 0.038bdfg
5	<i>O. nova</i>	0.05 [+ or -] 0.014bdfh **
Split-plot 41		
1	Immature oribatids	0.35 [+ or -] 0.083a *
2	<i>Propelops</i> sp.	0.12 [+ or -] 0.041bc
3	<i>A. acarinus</i>	0.12 [+ or -] 0.050bcd
4	<i>Jacotella enoplura</i>	0.09 [+ or -] 0.047bcde
5	<i>Joshuella</i> sp. nr. <i>striata</i>	0.08 [+ or -] 0.039bcde
Split-plot 39		

1	Immature oribatids	0.30	[+ or -]	0.048a
2	Propelops sp.	0.15	[+ or -]	0.036bc
3	A. acarinus	0.14	[+ or -]	0.050bce **
4	Jacotella enoplura	0.10	[+ or -]	0.037bceg
5	Oribatula tibialis	0.07	[+ or -]	0.053bdfh

Split-plot 43

1	Immature oribatids	0.28	[+ or -]	0.032a **
2	Propelops sp.	0.19	[+ or -]	0.046bc **
3	A. acarinus	0.12	[+ or -]	0.041bce **
4	O. parviaures	0.07	[+ or -]	0.032bdef **
5	O. nova	0.07	[+ or -]	0.026bdef **

RNA C

1	Immature oribatids	0.25	[+ or -]	0.045a **
2	O. parviaures	0.16	[+ or -]	0.038ac *
3	T. velatus	0.10	[+ or -]	0.052bce
4	O. nova	0.07	[+ or -]	0.033bdef **
5	A. acarinus	0.06	[+ or -]	0.024bdef **

Note: Frequency values are means [+ or -] 1 SE. Asterisks indicate significant differences between means in unburned and burned split-plots (Wilcoxon rank sum test). Lowercase letters indicate differences in within-group dominance ranks ($p < 0.05$). In each split-plot, dominant taxa with different letters in the same column occurred at significantly different mean frequencies within that split-plot. RNA, research natural area.

Table 5. Results of multiple response permutation procedures (MRPP) analyses of oribatid assemblages.

Split-plots	HSD	LSD	RNA
HSD	0.436 (0.127) **	0.485 *	0.489ns
LSD	0.463 **	0.421 (0.159) **	0.475 **
RNA	0.475 **	0.478 **	0.450 (0.099) **

Note: Observed [Δ] is shown with the probability of obtaining [Δ] [less than or equal to] [Δ].sub.obs] summarized by asterisks as in previous tables. Low p values suggest significant differences between oribatid assemblages. Values in boldfaced type on the diagonal are within-treatment comparisons between assemblages from unburned and burned split-plots. Lower triangle values compare assemblages in unburned split-plots, while those in the upper triangle compare assemblages from burned split-plots. Values in parentheses are the within-group homogeneity parameter A (chance-corrected within-group agreement) for within-treatment comparisons on the diagonal. HSD, high structural diversity; LSD, low structural diversity; RNA, research natural area.

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