

Fuel reduction treatment and wildfire influence on carabid and tenebrionid community assemblages in the ponderosa pine forest of northern Arizona, USA

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Abstract

We investigated the response of community assemblages of carabids (Coleoptera: Carabidae) and tenebrionids (Coleoptera: Tenebrionidae) from June to August in 2003 and 2004 on ponderosa pine forest stands of various conditions that were created by fuel reduction treatments (thinning, and thinning plus prescribed burning) and wildfires between 1987 and 1996 in northern Arizona. We found that richness and abundance increased for carabids but decreased for tenebrionid significantly from June (the driest season of the year) to August (wet monsoon season of the year), a temporal partition for ecological niches in ponderosa pine forests. For both taxa, wildfire burned stands had the highest species richness and diversity; whereas the thinned stands had the highest species evenness. Both fuel reduction treatment and wildfire resulted in significantly different community assemblages of carabids and tenebrionids compared to unmanaged stands. Results showed that carabids from the genera of *Amara*, *Anisodactylus*, *Cicindela*, *Harpalus*, *Radine*, and tenebrionids in the genus of *Eleodes* were ecological indicators for wildfire stands. However, *Synuchus dubius*, and *Coelocnemis* spp.1 were indicator species for thinned stands, and unmanaged stands, respectively. We concluded that the richness and diversity of both taxa tended to increase after fuel reduction treatment and wildfire, and that some species from both taxa were suitable as ecological indicators for the structural change of ponderosa pine forests. Creating a mosaic of heterogeneous landscape through mechanical fuel reduction treatments is an important management strategy to maintain high invertebrate species diversity in ponderosa pine forest ecosystems in the southwestern US.

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1. Introduction

Prior to Euro-American settlement in late 1800s, ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) forests of the southwestern U.S. were park-like with abundant understory grasses and a variety of forbs, and dominated by frequent, low-intensity surface fires (Weaver, 1951; Cooper, 1960; Biswell, 1972; Covington and Moore, 1994a,b; Moore et al., 1999; Swetnam et al., 1999). However, anthropological disturbances after settlement, such as overgrazing, logging, and fire suppression, as well as climate changes resulted in dramatic structural changes in ponderosa pine forest ecosystems (Cooper, 1960; Covington and Moore, 1994a,b; Fulé et al., 1997;

Covington et al., 2001; Barton, 2002 and references therein; Farnsworth et al., 2003; www.eri.nau.edu). The contemporary conditions of ponderosa pine forests are characterized by overstocked small diameter trees, stagnant in growth and nutrient cycling (Kaye and Hart, 1998; Kaye et al., 1999), water stressed, susceptible to bark beetle attacks (Feeney et al., 1998), and at high risk to catastrophic or stand replacing wildfires (Covington and Moore, 1994a; Covington et al., 1994, 1997). Therefore, management intervention is urgently needed to bring ponderosa pine forests within the natural range of variability in order to improve ecosystem function and sustain forest ecosystem services and high productivity.

Ecological restoration is defined as a process of assisting the recovery and management of ecological integrity. Ecological integrity includes maintaining a critical range of variability in biodiversity, ecological processes and structures, regional and historical context, and sustainable cultural practices (The Society

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for Ecological Restoration, Tucson, Arizona, USA, <http://www.ser.org>). Although this definition is also commonly cited by others (van Diggelen et al., 2001; Swart et al., 2001; Young et al., 2005), we want to point out that this is an arguable definition because some important issues, such as the scale and type of restoration, techniques used to achieve the goals, and methods for evaluating the success of restoration are not specified. Considering the complexity of ecological restoration that is the assemble of practices involved in the participation of human and natural science, technologies, politics, economics, and cultural dimensions (Higgs, 2005), it is difficult to have one definition for ecological restoration that can fit for all situations. Therefore, we are not surprised about the numerous comments on the definition of ecological restoration (Higgs, 1997, 2005; Swart et al., 2001; Davis and Slobodkin, 2004); however, discussions on the definition of ecological restoration are beyond our scope of this study. Some techniques used to restore the degraded ponderosa pine forest ecosystems in northern Arizona include thinning overstocked stands, removal of invasive species, seeding with native plant species, and reintroducing low-intensity surface fire regimes (www.eri.nau.edu). However, the selection of appropriate restoration techniques will depend on the complex context of management goals and constraints of the particular ecosystems under management (Moore et al., 1999).

Over the past 10 years, several ecological restoration research projects have been conducted in ponderosa pine forests of northern Arizona. Such projects include Gus Pearson Natural Area Restoration (Kaye et al., 1999; Covington et al., 2001), Mt. Trumbull Wilderness Restoration (Fulé et al., 2001; Waltz et al., 2003), Flagstaff Urban and Wildland Interface (UWI) Project (Meyer and Sisk, 2001; Meyer et al., 2001; Farnsworth et al., 2003; www.eri.nau.edu), Chimney Springs Restoration (www.gffp.org/non_forest.htm), and the Stand Treatment Impacts on Forest Health (STIFH) Project (Bailey et al., 2000). Moreover, as a part of nationwide Fire and Fire Surrogate (FFS) research network (www.fs.fed.us/ffs), three study sites were established in the ponderosa pine forests of northern Arizona in 2000. The overall purpose of FFS research is to monitor and assess the ecological consequences of fuel reduction treatments throughout several major fire prevalent forest ecosystems in the United States.

A complete ecological restoration research project includes three basic steps: (1) determining management goals; (2) implementing treatments; and (3) monitoring and assessing the status and process of restoration treatments. It is necessary to develop a suite of suitable biotic and abiotic response measures/variables in order to adequately monitor the impacts of restoration treatments. Because invertebrate insects are an important component in terrestrial ecosystems with high diversity and abundance (Borrer et al., 1989; Price, 1997), and high sensitivity to the changes of physical and chemical aspects of the environment over time and space (Danks, 1992), they are commonly used as indicators of ecosystem structural changes (Faith and Walker, 1996; Oliver and Beattie, 1996; Kitching et al., 2000; Similä et al., 2002; Longcore, 2003; Andersen et al., 2004; Vanbergen et al., 2005).

Among the insects, ground beetles (Coleoptera: Carabidae) are well studied (Holmes et al., 1993; Butterfield et al., 1995; Jukes et al., 2001; Thomas et al., 2001; Eyre et al., 2003; Heyborne et al., 2003; Irmiler, 2003; Vanbergen et al., 2005). This is because carabids are abundant, exhibit high species diversity, and are functionally important (as predators) in ecosystems (Thiele, 1977; Niemelä et al., 1993; Samways, 1994). Moreover, carabids are taxonomically stable and easy to collect with standardized methods, such as pitfall trapping (Niemelä et al., 1993; Jukes et al., 2001; Villa-Castillo and Wagner, 2002). Carabids were used to monitor structural changes created by fuel reduction treatments, such as thinning, and thinning plus prescribed burning in ponderosa pine forests of northern Arizona (Villa-Castillo and Wagner, 2002). Further, some other invertebrate insects including bark beetles (Sánchez-Martínez and Wagner, 2002), butterflies (Meyer and Sisk, 2001; Waltz and Covington, 2004), and ants (Stephens, 2004) were also employed for similar purposes. Insect taxa and their community assemblages were indicators of the various environmental (microclimate) conditions created by fuel reduction treatments in the ponderosa pine forest ecosystems of northern Arizona.

Darkling beetles (Coleoptera: Tenebrionidae) have not been included in studies in ponderosa pine forests of northern Arizona despite their abundance and co-occurrence with carabids in the ponderosa pine forests. Tenebrionids are the fifth largest family of beetles with more than 1000 species in North America, particularly in arid and semi-arid terrestrial ecosystems (Borrer et al., 1989). They are common ground dwelling beetles in ponderosa pine forests and are frequently caught in the same pitfall traps with carabids (Zhong Chen personal observations). In addition, they are quite mobile presumably for the purpose of seeking food, mates, or other resources as well as suitable habitats (Doyen and Tschinkel, 1974). Consequently, we were interested in whether tenebrionids were suitable ecological indicators as was the case for carabids.

As part of an ongoing Stand Treatment Impacts on Forest Health (STIFH) Project (Bailey et al., 2000), we are evaluating the impacts of fuel reduction treatments that included thinning (TH), thinning plus prescribed burning (TB), and wildfires (WF) on the community assemblages of both carabids and tenebrionids by using a retrospective approach. The thinning, and thinning plus prescribed burning are typical silvicultural approaches employed by forest land managers to reduce the fuel load and hence the risk of wildfire and increase aesthetics (Smith et al., 1996). Assessing the diversity of carabids and tenebrionids as a surrogate for invertebrate biodiversity and their possible mechanistic links with the structural change, productivity, sustainability, and mosaic habitat heterogeneity of ponderosa pine forests allows us to assess the long-term ecological consequences of these silvicultural fuel reduction treatments and wildfires in a relatively short timeframe. We hypothesize that both carabids and tenebrionids are suitable ecological indicators for the ponderosa pine forest conditions.

2. Methods

2.1. Study site

Our study was conducted in the Coconino National Forest near Flagstaff, Arizona, which is located within the largest continuous portion of the 16.2 million hectares of ponderosa pine forest in North America (Farnsworth et al., 2003). The ponderosa pine stands that our study encompassed ranged in elevation from approximately 2000–2500 m, and are dominated by ponderosa pine species mixed with a few other sparsely distributed woody plants, such as gambel oak (*Quercus gambelii* Nut.) and alligator juniper (*Juniperus deppeana* Steud.). Summers in northern Arizona are typically warm and dry in June and early July, followed by monsoon rainfall from mid-July through September. The annual mean temperature and precipitation over the past 50 years (1953–2003) was 7.7 °C and 543 mm, respectively, and the mean summer (June to August) air temperature is 17.4 °C (<http://www.wrcc.dri.edu>).

2.2. Experimental design

Based on the history of forest restoration practices and wildfires, four types of stands that represented various disturbance legacies were selected: (1) unmanaged or control (UN, stands dominated by even aged pole size trees, no management taken during past 30 years, high fuel load and lack of significant understory vegetation cover, lowest disturbance); (2) thinned only (TH, 30% basal area removed between 1987 and 1993, and at least 50% of basal area came from diameter class 30 cm, light disturbance); (3) thinned plus prescribed broadcast burned (TB, similar to thinned stands but with broadcast burning within 3–4 years after thinning, intermediate disturbance); and (4) wildfire burned (WF, >90% basal area consumed during wildfire in 1996, severe disturbance) (Bailey et al., 2000). Detailed descriptions of the criteria for selecting the stands are available elsewhere (Bailey et al., 2000). Sixteen of these stands, approximately 20–40 ha in size, located within a radius of 32 km from Flagstaff, northern Arizona were randomly selected in 1997 for this study; each stand was 1–30 km apart and represented one of the above four types (treatments): UN, TH, TB and WF. This retrospective study resulted in a completely randomized experimental design with four replications for each treatment. Ten permanent plots (20 m × 20 m) were established within the center of each stand along a 150–200 m grid depending on the total size of the stand, and each plot was located at least 50 m away from the forest edge.

2.3. Sampling

Pitfall traps were used to collect the ground dwelling arthropods on the above 16 stands during the summer months (June, July, and August) in both 2003 and 2004. We set up one trap per plot; each trap was located in the NE corner of a permanent plot and approximately 15 m away from its center. In total, 160 pitfall traps (1 trap/plot × 10 plots/stand × 16 stands) were located.

The pitfall traps were plastic cups, approximately 10 cm × 8 cm (wide × depth). Two stacked cups were buried about 1 cm below the soil surface: the bottom cup remained in place to minimize disturbance during sampling; whereas the upper cup was for trapping ground dwelling arthropods. Approximately, 150–250 ml of water (depending on 3-day precipitation forecast in monsoon seasons to avoid overflow) plus a few drops of unscented detergent was added into each upper cup. Previous research in these stands showed that a 3-day trapping regime generated sufficient numbers of ground beetles (Villa-Castillo and Wagner, 2002). The collected ground dwelling insects were transported to the laboratory within 6–8 h, cleaned with water and then transferred into vials containing 70% ethanol for temporary storage. Carabids and tenebrionids were sorted, mounted, and identified within 2–3 months after being collected. Carabid identification was based on Lindroth (1969), Ball and Bousquet (2001), and voucher specimen by Villa-Castillo and Wagner (2002) in the Forest Entomology Laboratory of the School of Forestry at Northern Arizona University (NAU). The identification of tenebrionids was based on Aalbu et al. (2001) and voucher specimen in the Museum of the Biology Department at NAU. We identified all beetles to the species level except in a few cases where beetles were identified to the genus level. These species were assigned morphospecies names.

2.4. Statistical analysis

2.4.1. Species diversity and distribution pattern

To compare the differences in species diversity among “treatments” and between two taxa, we first combined samples for each taxon over 3 months from 10 plots within each stand in 2003 and 2004. This generated a data set with 64 records (2 taxa × 4 treatments × 4 replications × 2 years). The analysis of species diversity measures at a stand level for each taxon each year was performed with PC-ORD (McCune and Mefford, 1999). They included: (1) species richness, S; (2) species evenness, E; (3) Shannon diversity index, H; and (4) Simpson diversity index, D. Then, a three-way analysis of variance (ANOVA) that included three main factors (taxa, year, and treatment), and their interactions was performed with SAS (2000) to determine differences in species diversity measures due to taxa, year of sampling, treatment, and their interactions at a significant level of $\alpha = 0.05$.

Temporal variation refers to the differences in species diversity and abundance among three separated sampling periods (June, July, August) within and between years. Finally, because ANOVA overall did not show significant differences in species diversity measures between years (except for the marginally significant differences in Simpson diversity index, D), we further pooled data from both years to compare the temporal distribution of carabids and tenebrionids.

2.4.2. Community assemblages

Analyses of carabid and tenebrionid community assemblage data were performed with PC-ORD software (McCune and Mefford, 1999). Here, we emphasized the differences in

community species assemblages among ponderosa pine stands of various conditions or “treatments” but not among the months of samplings (i.e. temporal variation) because understanding the impacts of fuel reduction treatments on the distribution of carabids and tenebrionids is more pertinent to our research questions. First, an ordination method of non-metric multi-dimensional scaling (NMS) was used to explore the distribution of carabid and tenebrionid community among the 16 stands over two-dimensional scales. NMS, an iterative ordination method based on the ranked distances between sample units, is especially appropriate for data of non-normal distributions (McCune and Mefford, 1999). Then, two-dimensional graphs based on the NMS results were used to display the relationships among stands of different treatments. After that, a multi-response permutation procedure (MRPP) was used to test whether a priori groups (“treatments”) differed in their position in a multi-dimensional space (McCune and Mefford, 1999). The MRPP is a non-metric procedure for testing the hypothesis of no differences between two or more groups of entities. It has the advantage of not requiring assumptions, such as multivariate normality and homogeneity of variance that seldom occur in ecological community data (McCune and Mefford, 1999). Finally, if an overall MRPP test was significant among groups or “treatments” (e.g. $P < 0.05$), a pair-wise test was applied to determine which two groups differed significantly. However, since we have six possible pair wise comparisons for the means from four groups simultaneously, we used a Bonferroni correction to adjust the α -value that we would accept as indicating significant differences (an adjusted α -value equals to the original α level divided by the number of outcome measures, i.e. $0.05/6 = 0.0083$ for multiple comparisons).

2.4.3. Indicator species analysis

Indicator species analysis (Dufréne and Legendre, 1997) is a method to determine the contribution of a given species to the community assemblage based on its indicator value, which is based on information regarding the relative abundance of a species in a particular group (treatment), and the faithfulness of occurrence of that species in a particular group (McCune and Mefford, 1999). The indicator value of a species ranges from zero (no indication, e.g. that species occurs in all stands of all groups/treatments) to 100 (perfect indication, e.g. that species occurs only in stands of one particular group/treatment). The P -value of the maximum indicator value of a given species in the assemblage is obtained by using a random permutation procedure Monte Carlo test (McCune and Mefford, 1999). The statistical significance of such maximum indicator values were further determined by Monte Carlo tests with the number of permutations $n = 1000$ with the time of a day as a random number.

3. Results

3.1. Species diversity and distributional patterns

A total of 152 individuals including 18 carabid species in 2003 and 175 individuals of 14 species in 2004 were collected;

whereas 270 individuals including 18 tenebrionid species in 2003, and 271 individuals of 23 species in 2004 were collected. In terms of species abundance, carabid species from the genera *Amara*, *Anisodactylus*, *Carabus*, *Cyclotrachelus*, *Cymindis*, *Harpalus*, *Rhadine*, and *Synuchus* had at least 10 individuals over two years. Overall, the abundance of *Amara latior*, *A. obesa*,

Table 1

Carabid and tenebrionid beetles collected by using pitfall traps from June to August of 2003 and 2004 in the ponderosa pine forests of northern Arizona

Taxa	Species	Code	Abundance	
			2003	2004
Carabidae	<i>Agonum placidum</i>	AGPL	1	5
	<i>Agonum</i> spp.1	AGSP1	1	0
	<i>Amara latior</i>	AMLA	4	0
	<i>Amara obesa</i>	AMOB	6	5
	<i>Amara quenseli</i>	AMQU	13	28
	<i>Amara</i> spp.	AMSP	0	3
	<i>Anisodactylus anthracinus</i>	ANAN	0	9
	<i>Anisodactylus</i> spp.1	ANSP1	36	0
	<i>Anisodactylus</i> spp.2	ANSP2	15	0
	<i>Anisodactylus</i> spp.3	ANSP3	1	0
	<i>Carabus taedatus agassii</i>	CATA	12	17
	<i>Cicindela punctulata</i>	CIPU	5	4
	<i>Cicindela purpvrea audubonii</i>	CIPUA	2	2
	<i>Cyclotrachelus constrictus</i>	CYCO	0	29
	<i>Cymindis arizonensis</i>	CYAR	2	9
	<i>Discoderus parallelus</i>	DIPA	1	0
	<i>Harpalus amputates</i>	HAAM	12	9
	<i>Harpalus retractus</i>	HARE	25	0
	<i>Harpalus</i> spp.	HASP	0	19
	<i>Harpalus</i> spp.1	HASP1	1	0
	<i>Rhadine</i> spp.	RHSP	7	6
	<i>Synuchus dubius</i>	SYDU	8	30
		Subtotal		152
Tenebrionidae	<i>Coelocnemis magna</i>	COMA	28	16
	<i>Coelocnemis</i> spp.1	COSP1	0	42
	<i>Coelocnemis</i> spp.2	COSP2	0	3
	<i>Darkling beetle</i> spp.1	DBSP1	1	0
	<i>Darkling beetle</i> spp.2	DBSP2	1	0
	<i>Darkling beetle</i> spp.3	DBSp3	2	0
	<i>Darkling beetle</i> spp.4	DBSP4	0	1
	<i>Darkling beetle</i> spp.5	DBSP5	0	5
	<i>Darkling beetle</i> spp.6	DBSP6	0	4
	<i>Eleodes carbonaria</i>	ELCA	14	36
	<i>Eleodes dissimimilis</i>	ELDI	39	10
	<i>Eleodes extricates</i>	ELEX	5	41
	<i>Eleodes hispilabris</i>	ELHI	19	0
	<i>Eleodes nigrina</i>	ELNI	7	3
	<i>Eleodes obscura sulcipennis</i>	ELOBS	8	9
	<i>Eleodes</i> spp.1	ELSP1	6	4
	<i>Eleodes</i> spp.2	ELSP2	31	5
	<i>Eleodes</i> spp.3	ELSP3	21	15
	<i>Eleodes</i> spp.4	ELSP4	75	2
	<i>Eleodes</i> spp.5	ELSP5	0	8
	<i>Eleodes</i> spp.6	ELSP6	0	2
	<i>Eleodes</i> spp.7	ELSP7	0	2
	<i>Eleodes</i> spp.8	ELSP8	0	2
<i>Eleodes sulcipennis</i>	ELSU	1	44	
<i>Ipthimus laevis</i>	IPLA	2	4	
<i>Ipthimus lewisi</i>	IPLA	1	2	
<i>Neobaphion planipennis</i>	NEPL	9	11	
	Subtotal		270	271

Table 2
Analysis of variance on beetle species diversity measures at the stand level

Source	DF	Diversity measures							
		S ^a		E		H		D	
		F	P	F	P	F	P	F	P
Taxa	1	10.53	0.0021	11.94	0.0012	23.61	<0.0001	26.39	<0.0001
Year	1	0.01	0.9085	3.51	0.0670	3.42	0.0706	5.04	0.0294
Treatment	3	25.44	<0.0001	6.73	0.0007	17.88	<0.0001	14.22	<0.0001
Taxa ^a Year	1	0.22	0.6422	2.73	0.1051	0.57	0.4545	1.22	0.2742
Treatment ^a Year	3	2.87	0.0458	0.72	0.5467	1.09	0.3640	1.01	0.3977
Taxa ^a Treatment	3	1.26	0.2984	5.92	0.0016	4.49	0.0074	7.16	0.0005

Significant differences consistent across all measures are bold.

^a S-species richness, E-species evenness, H-Shannon diversity index, and D-Simpson diversity index (McCune and Mefford 1999).

A. quenseli, *A. spp.*, *Anisodactylus anthracinus*, *Anisodactylus spp.1*, *Anisodactylus spp.2*, *Anisodactylus spp.3*, *Carabus taedatus audubonii*, *Cyclotrachelus constrictus*, *Cymindis arizonensis*, *Harpalus amputatus*, *H. retractus*, *H. spp.1*, *H. spp.2*, *Rhadine spp.*, and *Synuchus dubius* accounted for approximately 93% of total species abundance each year (Table 1). However, approximately 44% of carabid species in 2003, and 21% of carabid species in 2004 were uncommon with less than 5 individuals caught. On the other hand, eight *Eleodes* species (*E. carbonaria*, *E. dissimilis*, *E. extricatus*, *E. hispilabris*, *E. spp.2*, *E. spp.3*, *E. spp.4*, and *E. sulcipennis*) had at least 10 individuals in abundance in either 2003 or 2004. Overall, *Eleodes* species accounted for 84% and 79% of the total number of individuals collected in 2003 and 2004, respectively (Table 1). Further, only 8 carabid species and 15 tenebrionid species were collected in both 2003 and 2004, indicating a high turnover of species occurrence for both taxa (Table 1).

Analyses of variance (ANOVA) on diversity measures (richness, S; evenness, E; Shannon diversity index, H; and Simpson diversity index, D) showed that consistent significant differences occurred between the two taxa and among various forest stand conditions (Table 2). The interactions between year and taxa, and between year and treatment overall had no significant influence on species diversity measures except for marginal effects on S ($P = 0.0458$) (Table 2), which indicated that the patterns of differences in species diversity measures between two taxa and among four structural conditions of ponderosa pine forest were similar in both 2003 and 2004. In contrast, the interaction between treatment and taxa had significant effects on the measures of E, H, and D ($P \leq 0.0074$), but not on S (Table 2), meaning that the differences in species diversity between two taxa depended on the stand structural conditions. For example, tenebrionids had slightly greater species richness than the carabids across four types of stands

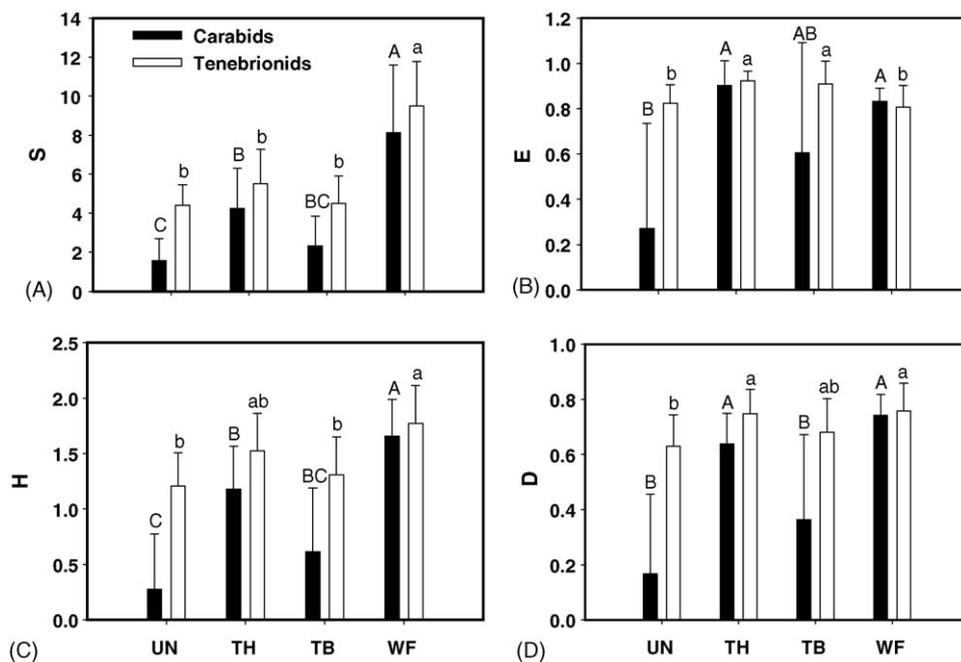


Fig. 1. Mean diversity measures (+1S.D.): S-species richness (A), E-species evenness (B), H-Shannon diversity index (C), and D-Simpson diversity index (D) for species community assemblages of carabids (solid bars) and tenebrionids (open bars) of stands under contrasting stand conditions of UN-unmanaged, TH-thinned only, TB-thinned followed by prescribed burned, and WF-wildfire burned. Data were collected over two consecutive years from 2003 to 2004 in ponderosa pine forests of northern Arizona. Bars with different letters denote a significant difference at the $\alpha = 0.05$.

consistently but it was not the case for other measures where tenebrionids and carabids had similar E on thinned stand (Fig. 1B), and similar E, H, and D on the wildfire burned stands (Fig. 1B–D). The mean measures of S, E, H, and D over all stands (mean \pm S.D.) for carabids ($n = 29$) were 4.28 ± 3.41 , 0.669 ± 0.394 , 0.976 ± 0.687 , 0.496 ± 0.305 , respectively; whereas the measures of S, E, H, and D for tenebrionids ($n = 32$) were 5.97 ± 2.79 , 0.865 ± 0.095 , 1.451 ± 0.385 , 0.704 ± 0.115 , respectively. This indicates that tenebrionids had overall greater species diversity measures than carabids.

Carabids had the highest species richness (S) and Shannon diversity index (H) for the WF stands, followed by TH, TB, and UN stands (Fig. 1A and C). While the tenebrionids had the highest S in the WF stands, their S and H were essentially the same among TH, TB, and UN stands (Fig. 1A and C). On the other hand, the evenness (E) and Simpson diversity index (D) measures for carabids were the highest in both WF and TH stands but the lowest in UN stands (Fig. 1B and D). As for the tenebrionids, their highest E occurred in both TH and TB stands (Fig. 1B) but the highest D in both TH and WF stands (Fig. 1D). Moreover, the WF stands had the highest abundance of carabids and tenebrionids in both 2003 and 2004. For example, 106 out of 152 carabids, and 114 out of 270 tenebrionids occurred in WF stands in 2003; and 112 out of 175 carabids and 163 out of 271 tenebrionids occurred in WF stands in 2004. That is, the abundance of both taxa from WF stands alone accounted for approximately 40–70% of the total number of individuals sampled.

Temporally, both species richness and abundance steadily increased for carabids but tended to decrease for tenebrionids from June (the driest season of the year) to August (mid monsoon season of each year). Carabid species richness was 8, 9, and 12 in June, July, and August of 2003, respectively; while it was 6, 14, and 17 in June, July, and August of 2004, respectively. Carabid species richness in August accounted for approximately 67% and 81% of total carabid species richness in 2003, and 2004, respectively. In contrast, the species richness of tenebrionids was 13, 15, and 8 in June, July, and August of 2003, respectively; and it was 20, 16, and 9 in June, July, and August of 2004, respectively. Tenebrionid species richness in June accounted for approximately 72% and 87% of total tenebrionid species richness in 2003 and 2004, respectively. The species abundance of both taxa showed a similar temporal distribution as species richness (data not shown). The mean species richness and abundance of carabids and tenebrionids each month over two years ($n = 32$) also showed similar temporal distribution as above: the mean species richness and abundance overall was highest in June for tenebrionids and in August for carabids (Fig. 2A and B).

3.2. Community assemblages

Since there was overall no significant interaction between treatment and year for the species diversity measures except for the marginally significant difference in the species richness (S) for both taxa ($P = 0.0458$) (Table 2), data from 2003 and 2004 were combined for community species assemblages for both

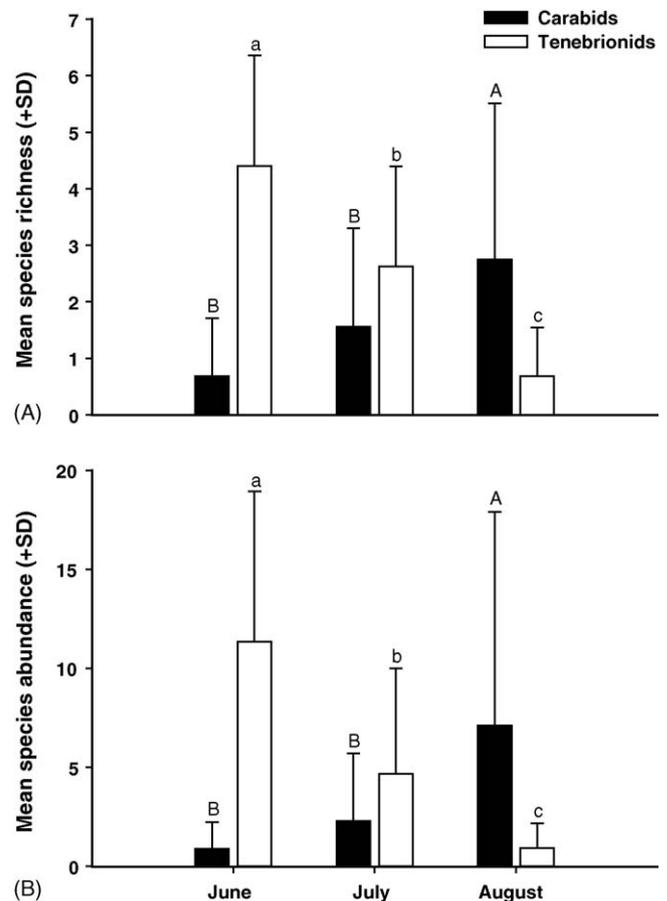


Fig. 2. Mean (+S.D.) species richness (A) and species abundance (B) per month pooled over all stands of various stand conditions in two consecutive years from 2003 to 2004 for carabids (solid bars) and tenebrionids (open bars) on ponderosa pine forests in northern Arizona. Bars with different letters denote significant differences at $\alpha = 0.05$.

taxa. Ordinations of carabid and tenebrionid community assemblages at two-dimensional scales showed that wildfire (WF) stands were clearly separated from all other stand types for both taxa (Fig. 3A and B). That is, the WF stands had significantly different community species assemblages from all other stand conditions. Subsequent multi-response permutation procedures demonstrated that there existed overall significant differences in both carabid and tenebrionid community assemblages among stands of different conditions ($P \leq 0.006$) (data not shown). The following pair-wise MRPP showed that WF stands had a marginally significant difference in the community assemblages of carabids ($P \leq 0.012$) but significant difference in the community assemblages of tenebrionids ($P \leq 0.007$) compared to these in the UN, TH, and TB stands (Fig. 3A and B; Table 3). In addition, the community assemblages of carabids were quite similar among the UN, TH and TB stands ($P \geq 0.149$) (Table 3). Finally, the community assemblages of tenebrionids were significantly different between the UN and TB, and between TB and TH stands ($P = 0.006$); however, the community assemblages of tenebrionids in UN and TH stands were only slightly different ($P = 0.059$) based on a conservative adjusted significant level (Fig. 3B; Table 3).

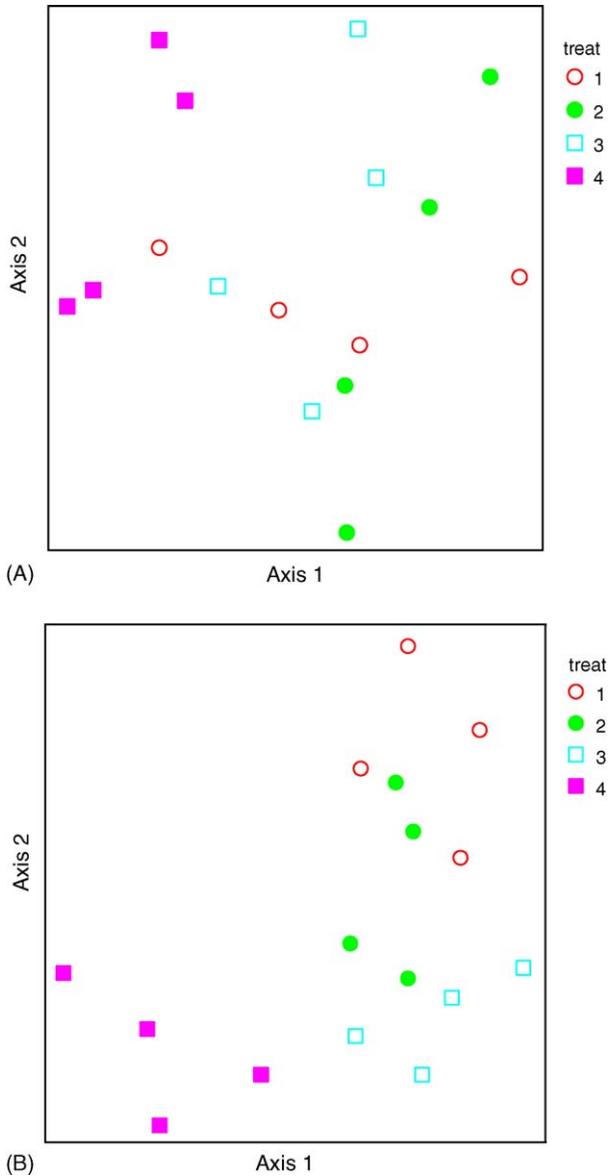


Fig. 3. Ordination of stands contrasting by stand condition: (1) UN (open circle); (2) TH (solid circle); (3) TB (open square); and (4) WF (solid square) (see the definition of treatments in Fig. 1) for carabids (A) and tenebrionids (B).

Table 3
Multi-response permutation procedure (MRPP) comparison of beetle assemblages among stands of different types/treatments based on combined data set of 2003 and 2004

Pair-wise comparison	Carabids				Tenebrionids			
	<i>T</i>	δ	<i>A</i>	<i>P</i>	<i>T</i>	δ	<i>A</i>	<i>P</i>
TB vs. WF	-3.433	13.106	0.227	0.009	-3.753	15.328	0.213	0.007
TH vs. WF	-3.075	16.245	0.152	0.012	-3.839	16.078	0.212	0.006
UN vs. WF	-3.388	13.296	0.222	0.009	-4.132	16.366	0.257	0.006
TB vs. TH	-2.128	7.659	0.098	0.039	-1.594	7.265	0.074	0.066
UN vs. TB	-0.116	4.710	0.003	0.425	-3.865	7.553	0.238	0.006
UN vs. TH	-0.925	7.849	0.045	0.149	-1.746	8.303	0.082	0.059

Treatment: UN-unmanaged, TH-thinned only, TB-thinned followed by broadcast burned, and WF-wildfires burned. *t*-test statistics = (observed-expected)/standard deviation of expected; δ , the weighted mean within-group distance = $\sum c_i x_i$ ($c_i = n_i/N$, where n_i is the number of items in the group i and N is the total number of items); *A*, the chance-correlated within-group agreement, = $1 - (\text{observed } \delta / \text{expected } \delta)$; *P*, the proportion of these that is smaller than the observed δ , = $(1 + \text{number of small } \delta) / \text{total number of possible } \delta$ s. The *P*-value associated with *T*, is determined by numerical integration of the Pearson type III distribution (McCune and Mefford, 1999).

3.3. Indicator species analysis

The results of the Monte Carlo test for the significance of maximum indicator value for both taxa each year are summarized in Table 4. Most indicator species were associated with the wildfire (WF) stands but varied over years. For example, carabids *Anisodactylus* spp.1, *Cicindela punctulata*, *Harpalus retractus*, *H. spp.1* and *Rhadine* spp. were indicators for WF stands in 2003 but others, such as *Amara obsesa*, *A. quenseli* were indicators for WF stands in 2004. In contrast, all tenebrionid indicator species for the WF stands were from the genus *Eleodes*. Except for *Eleodes carbonaria*, which was an ecological indicator in both 2003 and 2004, other *Eleodes* were indicator species in either 2003 (*E. hispilabris*, *E. spp.4*) or 2004 (*E. obscura sulcipennis*, *E. sulcipennis*, *E. spp.1*, *E. spp.2*, *E. spp.5*) (Table 4).

Indicator species also existed for other forest stand conditions. For example, the *S. dubius* was an indicator species for the thinned (TH) stands in 2004; *Coelocnemis* spp.1 was an indicator for the unmanaged (UN) stands in 2004. However, no indicator species occurred in thinned plus burned (TB) stands (Table 4). Overall, the WF stands had both different community assemblages of carabids and tenebrionids and some indicator (or unique) species compared to the other stands. Except for the *Rhadine* spp. and *Eleodes* spp.4, the observed indicator value for these indicator species was greater than 75 (100 means perfect indication) (Table 4).

4. Discussion

4.1. Temporal variation in beetles

Tenebrionids demonstrated dramatic temporal variation but in the opposite direction to the carabids. That is, tenebrionid species richness and abundance decreased from June to August as precipitation increased. This different temporal variation in species richness and abundance may allow them to effectively avoid interspecific competition for similar ecological niches in ponderosa pine forests. Also, because tenebrionids and carabids occupy different trophic levels in the food web: the former are

Table 4
Indicator species analysis results for carabids and tenebrionids

Taxa	Species	Year	Maxgrp	Observed indicator value (IV)	IV from randomized groups		P
					Mean	Standard deviation	
Carabids	AMOB	2003	–	–	–	–	–
		2004	WF	100.0	28.6	14.01	0.004
	AMQU	2003	–	–	–	–	–
		2004	WF	100.0	32.9	16.38	0.004
	ANSP1	2003	WF	83.8	41.9	14.60	0.005
		2004	–	–	–	–	–
	CIPU	2003	WF	75.0	25.4	15.16	0.028
		2004	–	–	–	–	–
	HARE	2003	WF	81.5	39.1	17.43	0.040
		2004	–	–	–	–	–
	HARSP1	2003	WF	80.0	34.4	15.56	0.025
		2004	–	–	–	–	–
	RHSP	2003	WF	62.5	27.3	13.68	0.042
		2004	–	–	–	–	–
	SYDU	2003	–	–	–	–	–
2004		TH	75.0	36.5	14.84	0.025	
Tenebrionids	COSPI	2003	–	–	–	–	–
		2004	UN	76.5	31.0	10.89	0.003
	ELCA	2003	WF	92.9	31.8	15.28	0.007
		2004	WF	75.0	37.2	11.28	0.007
	ELHI	2003	WF	75.0	23.5	11.49	0.025
		2004	–	–	–	–	–
	ELOBSU	2003	–	–	–	–	–
		2004	WF	75.0	27.0	14.81	0.034
	ELSU	2003	–	–	–	–	–
		2004	WF	100.0	28.1	15.08	0.003
	ELSP1	2003	–	–	–	–	–
		2004	WF	75.0	24.5	14.14	0.003
	ELSP2	2003	–	–	–	–	–
		2004	WF	75.0	23.1	14.05	0.019
	ELSP4	2003	WF	42.7	33.5	4.39	0.042
2004		–	–	–	–	–	
ELSP5	2003	–	–	–	–	–	
	2004	WF	100.0	27.4	14.0	0.003	

The abbreviation of beetles was given in Table 1. Only those that showed significant indication for stand types/treatments using Monte Carlo tests were listed.

detritivores whereas the latter are predaceous, such temporal partitioning of ecological niches is presumably beneficial to tenebrionids. Further, we noted that both carabids and tenebrionids showed a high turnover of presence between years. For example, the similarity of tenebrionid species composition between 2003 and 2004 was 68%, meaning that 32% of species did not occur in both years.

4.2. Population fluctuation

We observed that populations of carabids and tenebrionids we sampled varied substantially from populations in our previous studies (Villa-Castillo and Wagner, 2002). It is common to collect thousands of arthropod individuals by using

pitfall traps. For example, after three sampling seasons, 7822 individuals of 51 carabid species were collected in coniferous plantations across different bioclimatic zones in Britain (Jukes et al., 2001). However, we caught less than 180 individuals of about 20 species of carabids each year in 2003 and 2004. One interesting question is if this small number was due to a light sampling intensity of 3 days each month. We noted that sampling for 3 days per month actually provided a good number of individuals in a previous study conducted by Villa-Castillo and Wagner (2002), in which the number of individuals of carabids collected in pitfall traps was 919, 1125, and 551 in 1998, 1999, and 2000, respectively; totally represented 20 species of 15 genera (Villa-Castillo and Wagner, 2002). Consequently, the difference between the sampling period of

1998–2000 and 2003–2004 is species abundance but not richness.

So why did carabid species abundance drop dramatically from more than 550 per year in the period of 1998–2000 to less than 180 per year in the period of 2003–2004, considering the fact that the same sampling approach was used? This phenomenon is likely due to a change in annual precipitation in northern Arizona. Annual precipitation was about 693 mm in 1998, approximately 26% greater than annual mean precipitation; however, the annual precipitation in 1999–2003 was below the average. In 2002, the annual precipitation was barely 59% of the annual mean precipitation, which is an extremely low historical record. The annual precipitation in 2004 was approximately 9% more than the average; but 55% of annual precipitation occurred between September and December, and only 6.3% between June and August. In fact, no carabids showed up under the extreme drought in 2002 in our ponderosa pine sampling (Zhong Chen personal observations). Although the mechanisms responsible for this remarkable population fluctuation remain unknown, high soil moisture seems favorable to carabids.

4.3. Carabid and tenebrionid community structure under various stand conditions

Why did wildfire stands have different community species assemblages and higher diversity for both taxa when compared to other forest stand types? Perhaps the heterogeneous environments created by wildfires may explain this. Heterogeneity is important to species richness of all taxa although different taxa are related to different measures for the heterogeneity, such as structure and composition (Watts and Gibbs, 2002). Generalist predators like carabids may be less affected by the composition change of local invertebrate assemblages caused by forest structural change (Oliver et al., 2000). Although carabids are active predators, their distributions depend to a considerable extent on the environmental variables, such as moisture, soil, density, altitude, as well as prey abundance (Thiele, 1977; Butterfield et al., 1995). It seems that wildfire stands created overall favorable environments for the carabids, such as abundant prey that is further related to the occurrence of abundant ground herbaceous vegetation in this treatment. In addition to the abundant food sources, a higher soil surface temperature due to high radiation energy may also explain why wildfire stands had different tenebrionid community assemblages than other forest stand types. Because wildfire stands had unique community species assemblages of both carabids and tenebrionids, it is not surprising that most carabid and tenebrionid ecological indicator species occurred in wildfire stands.

Our results clearly support our hypothesis that both carabids and tenebrionids are suitable ecological indicators of ponderosa pine forest structural changes, most evidenced by the occurrence of indicator species in the wildfire stands. While wildfire dramatically affected community assemblage of carabids and tenebrionids, silvicultural fuel reduction treatments did not cause a pronounced shift in their community assemblage, particularly

for the carabids. Fuel reduction treatments consistently increased species richness and Shannon diversity measurements for carabids, indicating that carabids may be more useful than tenebrionids as indicators for such treatments.

A clear result from this study is that each of the four forest conditions we surveyed provided habitat for some species of beetles. No single forest condition can be labeled as optimum in providing habitat. If our management goal is to provide for the greatest diversity of carabids and tenebrionid populations then we must create a heterogeneous landscape of varying disturbance levels. At the scale relevant to these beetles, some severely burned sites in a larger landscape may be important to maintain a diverse community.

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