Effects of a stand-replacing fire on small-mammal communities in montane forest

Rafał Zwolak and Kerry R. Foresman

Abstract: Wildfire, ubiquitous and recurring over thousands of years, is the most important natural disturbance in northern coniferous forest. Accordingly, forest fires may exert a strong influence on the structure and functioning of small-mammal communities. We compared the composition of rodent and shrew communities in burned and unburned patches of a Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) – western larch (*Larix occidentalis* Nutt.) forest in western Montana, USA. Trapping was conducted during two consecutive summers after a wildfire. Four trapping sites were sampled in areas that burned at high severity and two in unburned forest. Small-mammal communities in burned sites were characterized by strong numerical dominance of deer mice (*Peromyscus maniculatus* (Wagner, 1845)) and greatly reduced proportion of southern red-backed voles (*Clethrionomys gapperi* (Vigors, 1830)) and red-toothed shrews (genus *Sorex* L., 1758). Relatively rare species such as northern flying squirrels (*Glaucomys sabrinus* (Shaw, 1801)) and bushy-tailed woodrats (*Neotoma cinerea* (Ord, 1815)) were largely restricted to unburned areas. The numbers of chipmunks (genus *Tamias* Illiger, 1811) were similar in burned and unburned areas. Rodent diversity was higher in unburned forest, but only during the 1st year after fire. Overall, the fire shifted small-mammal communities away from more specialized red-backed voles and shrews and towards greater abundance of generalist deer mice.

Résumé : Les feux de brousse, qui se produisent partout et se multiplient au cours des millénaires, constituent la perturbation naturelle la plus importante dans la forêt boréale de conifères. En conséquence, les feux de forêt peuvent avoir une forte influence sur la structure et le fonctionnement des communautés de petits mammifères. Nous comparons la composition des communautés de rongeurs et de musaraignes dans des taches incendiées et intactes d'une forêt de sapins de Douglas (*Pseudotsuga menziesii* (Mirbel) Franco) et de mélèzes occidentaux (*Larix occidentalis* Nutt.) dans l'ouest du Montana, É.-U. Nous avons fait du piégeage pendant deux années consécutives après un incendie de forêt. Quatre sites d'échantillonnage se trouvaient dans des zones sévèrement incendiées et deux dans une forêt intacte. Les communautés de petits mammifères des sites incendiés se caractérisent par une dominance numérique importante des souris à pattes blanches (*Peromyscus maniculatus* (Wagner, 1845)) et une proportion fortement réduite de campagnols à dos roux (*Clethrionomys gapperi* (Vigors, 1830)) et de musaraignes (genre *Sorex* L., 1758). Les espèces relativement rares, telles que les écureuils volants (*Glaucomys sabrinus* (Shaw, 1801)) et les rats sylvestres gris (*Neotoma cinerea* (Ord, 1815)), sont généralement restreintes aux zones intactes. Les densités de tamias (genre *Tamias* Illiger, 1811) sont les mêmes dans les zones incendiées et intactes. La diversité des rongeurs est plus grande dans la forêt intacte, mais seulement durant la première année suivant le feu. En résumé, le feu a comme conséquence de modifier les communautés de petits mammifères d'une prédominance de campagnols à dos roux et de musaraignes plus spécialisés vers une abondance accrue des souris à pattes blanches plus généralistes.

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Introduction

Over the past few decades, the understanding that recurring disturbance is critical for shaping the structure and function of biological systems has developed into a major ecological paradigm (White and Pickett 1985; Willig and Camillo 1991). In northern coniferous forests, the most important natural disturbance is fire (Ahlgren and Ahlgren 1960; Hansson 1992; Hunter 1993). Fires have been shaping coniferous forest ecosystems for thousands of years (Wein and MacLean 1983; Agee 1993). Nevertheless, most research on the effects of forest disturbances on wildlife has focused on logging and other anthropogenic events, perhaps because natural disturbances such as fire are extremely variable both in space (patchiness) and in time (unpredictability), and thus are difficult to study. However, fire represents an integral part of an ecosystem that can strongly influence its productivity, diversity, and stability (Kilgore 1987). Furthermore, the number and area of wildfires across North America has strongly increased in recent years, partly because of the accumulation of fuels resulting from decades of fire suppression policy (Schoennagel et al. 2004). Consequently, fires have become the focal issue in forest management (National Fire Plan 2000, Healthy Forest Initiative 2002, Healthy Forest Restoration Act 2003 — cf. Bury 2004) and insights into the effects of fire on wildlife are important for the evaluation of proposed management (Bury 2004).

Because of their abundance and strong ecological interactions, small mammals are important to forest ecosystems

R. Zwolak[1] and K.R. Foresman. Health Sciences Room 104, Division of Biological Sciences, The University of Montana, Missoula, MT 59812, USA.

[1]Corresponding author (e-mail: rafal.zwolak@mso.umt.edu).

(e.g., Maser et al. 1978; Ostfeld et al. 1996). However, very little research has been conducted on the impact of natural disturbances on small mammals in coniferous forest, and a large part of current knowledge comes from studies on the consequences of human-related disturbances such as logging (e.g., Hayward et al. 1999; Sullivan and Sullivan 2001; Klenner and Sullivan 2003; Fuller et al. 2004; Pearce and Venier 2005), clear-cutting followed by burning (e.g., Halvorson 1982; Martell 1984; Sullivan and Boateng 1996; Sullivan et al. 1999), or fuel reduction (Converse et al. 2006a, 2006b). In the present study, we compare small-mammal communities in unburned and severely burned montane forest, focusing on differences in species composition, diversity, and overall abundance of rodents and shrews. Fire-associated changes in small-mammal communities likely depend on time since fire (Smucker et al. 2005), fire characteristics (e.g., severity, size, and timing), and burned forest type (e.g., species composition and age). Thus, we quantified the vegetation condition in areas trapped, with emphasis on those variables that are considered important for small mammals. To our knowledge, this is the first small-mammal study on the effects of wildfire in a Douglas-fir (*Pseudotsuga menziensii* (Mirbel) Franco) – western larch (*Larix occidentalis* Nutt.) forest.

Materials and methods

Study site

The study area, Boles Meadow (47°60′N, 113°45′W), is located in the Seeley valley in west-central Montana (USA), approximately 40 km northeast of Missoula. The topography is hilly, with mean elevation of 1766 m (minimum 1547 m, maximum 1942 m) and mean slope of 13% (SD 6%). The dominant tree species are Douglas-fir and western larch. In August 2003, 4468 acres of forest at Boles Meadow burned in a wildfire caused by a lightning strike. Fire removed all organic material across relatively extensive areas, creating a large-scale mosaic consisting of large, severely burned patches interspersed with smaller areas that burned with lower severity. In May 2004, we selected six study sites: four (F1–F4) within areas burned with very severe, stand replacement fire and two unburned areas (C1 and C2) within intact forest (the number of sites in burned and unburned forest was unequal because the study design was chosen for a related investigation of the effects of expected salvage logging). At each site, a 1 ha small-mammal trapping grid and three pitfall arrays were constructed. In May 2005, the grids were enlarged to 1.44 ha. The grids were placed more than 0.2 km from the edge of the burn and at median distance of 2.18 km from one another (maximum distance 5 km). Investigated sites were located at elevations ranging from 1721 m (F4, measured in the center of grid) to 1869 m (C1). All sites were located on south aspects except for F4, which was located on a north aspect.

Habitat sampling

We visually estimated percent vegetation cover in 1 m radius circles centered at randomly selected trapping stations within each small-mammal trapping site. In 2004, we examined 10 circles per grid. In 2005, we estimated vegetation cover and additionally measured the volume of coarse

woody debris (CWD, defined as downed logs ≥7.5 cm in diameter and ≥0.5 m in length) in twenty-eight 1 m radius circles per grid. Volume of each piece of CWD was calculated as $\pi \times h \times r \times p$, where h is the length of a CWD fragment contained within the circle, and r and p are radii at the ends of the CWD piece within the circle. The volume of all CWD within a circle was pooled.

Presence or absence of canopy cover was measured using a moosehorn densiometer (Bonham 1989) along two perpendicular transects per grid that crossed at the center of the grid. In 2004, transects were 90 m long. In 2005, transects were lengthened to 110 m after the grids were enlarged. After the enlargement, the grid centers changed, therefore the transect location changed from year to year. The presence or absence of canopy was recorded at 1 m intervals. Furthermore, we counted trees (>2.5 m in height) within 1 m on both sides of the transects and classified them as either dead or alive. Data from both transects within a grid were pooled and results were expressed as number of stems per hectare.

All vegetation variables were measured in both 2004 and 2005. However, except for changes in the percent vegetation cover (see the Results section), the changes between years were negligible. Therefore, with the exception of vegetation cover, we pooled the data from both years.

Small-mammal trapping

Capture, handling, and marking of all species followed the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). In 2004, each of the six grids consisted of 100 trapping stations arranged in a 10 × 10 square at 10 m spacing. In 2005, the grids were enlarged to 144 trap stations (12 × 12 square). One folding Sherman™ live trap was placed at each station. To protect captured animals from sun and rain, the traps were placed inside open-ended waxed milk cartons or covered with foam sheets. The traps were baited with oats and examined twice daily (morning and evening). A piece of carrot and polyester bedding were placed inside each trap to minimize trapping effects such as mass decline and reduced survivorship (Pearson et al. 2003). Captured rodents were identified to species, weighed, sexed, and individually marked by toe-clipping or ear-tagging (species the size of chipmunks (genus *Tamias* Illiger, 1811) or larger). We did not attempt to distinguish red-tailed chipmunks (*Tamias ruficaudus* (A.H. Howell, 1920)) and yellow-pine chipmunks (*Tamias amoenus* J.A. Allen, 1980) in the field, but in 2005, hair samples were collected from some individuals and their species was determined via genetic analyses (Good et al. 2003).

Pitfall trapping

To increase the chances of capturing shrews, each live-trapping grid was supplemented with three Y-shaped arrays of pitfalls and drift fences. Each array consisted of four pitfalls (one at the end of each arm and one in the center) connected with 5 m sections of drift fence made of heavy-duty plastic sheeting. The pitfall arrays were smaller versions of the design proposed by Kirkland and Sheppard (1994). The arrays were inspected once a day. Most shrews were found dead, collected, and classified to species through skull and dental examination. Shrews found alive were marked by

toe-clipping and released. Their species was classified as "unknown".

Timing of trapping

Livetrapping and pitfall-trapping were conducted every 3rd week for 4 consecutive nights and days. In total, there were eight such trapping sessions per site: four in the summer of 2004 and four in 2005. The only exception was site F3, which was operated for only the first three trapping periods in 2005.

For logistic reasons, trapping sessions could not be conducted at the same time at all sites. To provide valid comparisons between burned and unburned sites, we divided the sites into two sets, each consisting of one unburned and two burned areas. Sites within each set were trapped concurrently. Trapping at sites C1, F1, and F3 began 1 June in 2004 and 31 May in 2005. Trapping at sites C2, F2, and F4 began 8 June in 2004 and 7 June in 2005.

Diversity index

We quantified small-mammal diversity using the Simpson index: $1 - D = 1 - \sum p_i^2$, where p is the proportion of ith species among all species captured at a given site. This index was chosen because it de-emphasizes rare detections such as captures of vagrant animals and is easier to interpret and more robust than other widely used indices (Feinsinger 2001; Magurran 2004). Ninety-five percent confidence intervals (95% CI) for the Simpson index were calculated on the basis of the approach presented in Grundmann et al. (2001), and differences were considered significant when the 95% CI did not overlap.

Statistical analysis

At several trapping sites, most sampling circles did not contain any vegetation or any CWD, thus the data on these variables could not be normalized. Therefore, we used the Mann–Whitney U test to analyze the differences in vegetation cover and CWD between burned and unburned study sites.

In most sampling occasions, small mammals were captured in numbers too small to use abundance estimators (e.g., Pollock et al. 1990). Thus, we used the number of unique individuals captured as an index of abundance. As recommended by McKelvey and Pearson (2001), the chosen method was applied to all compared data.

The difference in the number of individuals captured in burned and unburned areas was tested with the goodness-of-fit χ^2 test or, if less than five animals were captured in either burned or unburned area, Fisher's exact test (Fisher 1922). If the result was not significant, the goodness-of-fit χ^2 test was used to examine if there were differences among particular sites. We used the same procedure to test the hypothesis that the proportion of a given species differs between burned and unburned areas. Significant results were indicated by $P < 0.05$.

Results

Vegetation sampling

Tree density averaged 2256 (SE = 456.0) stems/ha in unburned sites and 2038 (SE = 280.7) stems/ha in burned sites.

All trees on the burned sites were killed by fire, whereas in unburned areas only 12% of trees were classified as dead (none of these were killed by fire). Consequently, canopy cover at burned areas (13%, SE = 2.1%) was greatly reduced when compared with unburned sites (55%, SE = 6.8%).

Understory vegetation in both unburned areas was dominated by common beargrass (*Xerophyllum tenax* (Pursh) Nutt.) and huckleberry (genus *Vaccinium* L.). Most of the vegetation in burned areas consisted of heartleaf arnica (*Arnica cordifolia* Hook.), fireweed (*Epilobium angustifolium* subsp. *angustifolium* L.), and beargrass.

During the first summer after the fire, vegetation cover in burned areas was drastically reduced relative to unburned areas (Mann–Whitney U test, $P < 0.0001$). Median percentage vegetation cover in burned sites ranged from 0.5% to 4%, whereas in unburned areas it ranged from 28% to 33% (Fig. 1). In 2005, median vegetation cover in burned areas increased (Mann–Whitney U test, $P < 0.001$), ranging from 2.5% to 31.5%. The fastest regeneration rate occurred at F4, the only north-facing study site. Increase in vegetation cover, however, occurred not only in the burned areas (where it was expected as a result of succession), but also in unburned sites (to 50% at C1 and 62.5% in C2). Still, this increase was not significant (Mann–Whitney U test, $P = 0.113$). In 2005, the differences in vegetation cover between burned and unburned sites, although smaller, remained highly significant (Mann–Whitney U test, $P < 0.001$).

Fire did not appear to have reduced the amount of CWD (Fig. 2). In fact, the burned areas contained more CWD than the unburned areas (Mann–Whitney U test, $P = 0.036$).
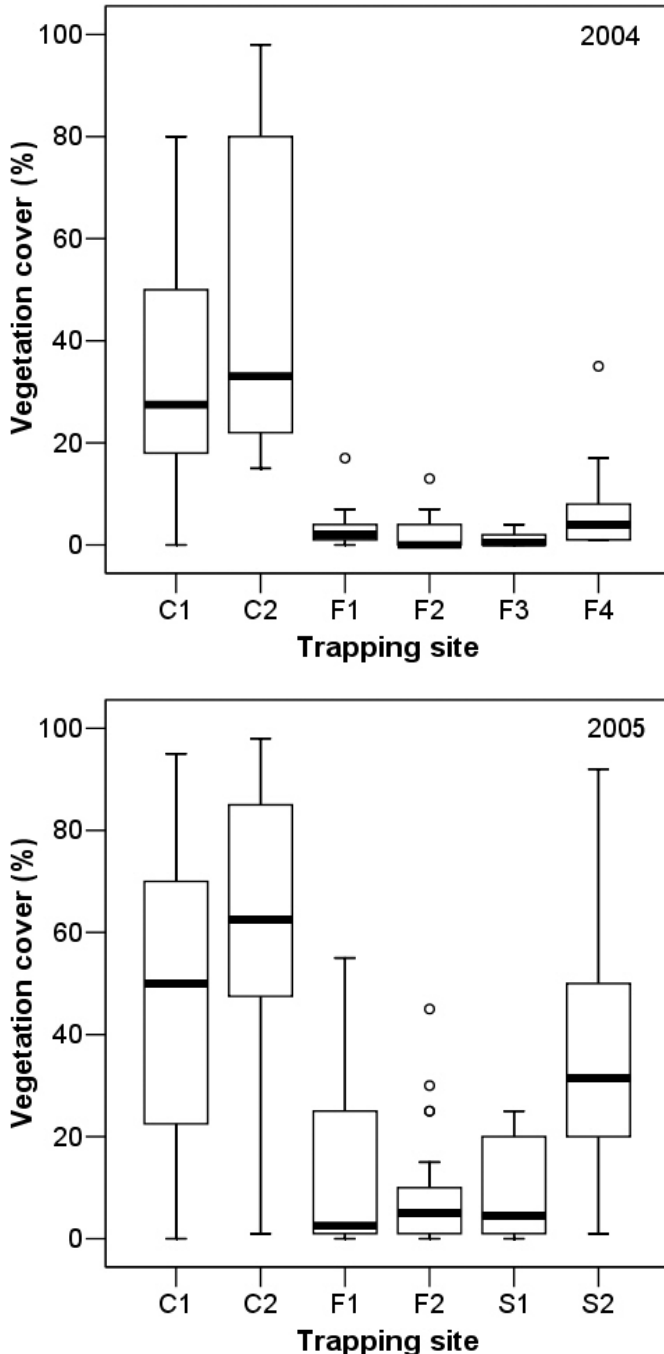
Rodent communities

Relative abundance

Overall, 738 individuals representing 12 species of rodents were caught (Table 1): 10 species were captured in live traps and an additional 2 species, western heather vole (*Phenacomys intermedius* Merriam, 1889) and northern pocket gopher (*Thomomys talpoides* (Richardson, 1828)), were found in pitfall traps. During the 1st year after fire, the relative abundance of rodents differed among sites ($\chi^2_{[5]} = 13.96$, $P = 0.016$, $n = 464$), but not between burned and unburned sites ($\chi^2_{[1]} = 1.81$, $P = 0.18$, $n = 464$). In the 2nd year after fire, even though we enlarged every grid by 44% (see Materials and methods above), the number of rodents caught was lower at each trapping site (Table 1). During that 2nd year, the relative abundance of rodents was higher in unburned than in burned sites ($\chi^2_{[1]} = 14.45$, $P < 0.001$, $n = 274$).
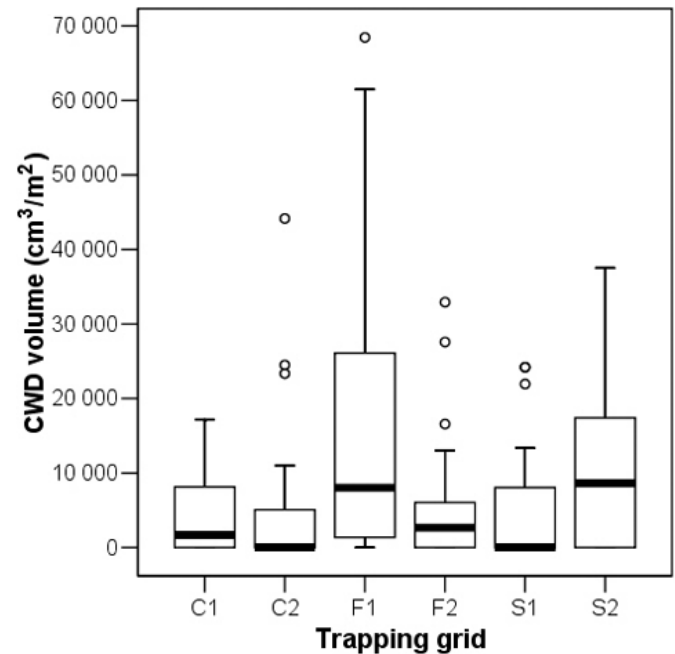
Community composition

Deer mice (*Peromyscus maniculatus* (Wagner, 1845)) were invariably the most numerous species in each burned site both years after fire. In 2004, this species represented 64.7% of individual rodents captured in burned sites and 22.7% of those in unburned sites ($\chi^2_{[1]} = 69.40$, $n = 464$, $P < 0.001$). Similarly, in 2005 deer mice accounted for 61.4% of individuals captured in burned areas, but only 6.6% of rodents in unburned forest ($\chi^2_{[1]} = 86.91$, $P < 0.001$, $n = 274$).

Fig. 1. Boxplots of percent vegetation cover in 1 m radius circles centered on randomly selected trapping stations in 2004 ($n = 10$ circles per each trapping site) and 2005 ($n = 28$ circles per each trapping site). Boxes denote 25th, 50th, and 75th percentiles, whereas whiskers denote the farthest data points within 1.5 interquartile range and open circles denote data points outside of the 1.5 interquartile range.

Fig. 2. Volume of course woody debris (CWD) within 1 m radius circles centered on randomly selected trap stations (28 circles per each trapping site). See Fig. 1 for the explanation of boxplots.

burned sites was significantly different (63.6% vs. 8.5%, $\chi^2_{[1]} = 93.13$, $P < 0.001$, $n = 274$).

The proportion of chipmunks did not differ consistently between small-mammal communities in burned and unburned areas. One year after fire, chipmunks represented 32.5% of all individuals captured. This proportion differed among sites ($\chi^2_{[5]} = 12.72$, $P = 0.026$, $n = 151$), but not between burned and unburned areas ($\chi^2_{[1]} = 0.45$, $P = 0.50$, $n = 464$). Two years after fire, chipmunks accounted for 20.1% of individuals captured. Again, this proportion differed among sites ($\chi^2_{[5]} = 15.30$, $P = 0.009$, $n = 55$), being higher in burned sites (26.1%) and lower in unburned sites (12.4%). This difference is significant ($\chi^2_{[1]} = 7.96$, $P = 0.005$, $n = 274$) and largely driven by the high number of chipmunks captured at site F4 (Table 1).

Genetic analyses of hair samples collected in 2005 revealed the presence of two species of chipmunks, *T. amoenus* and *T. ruficaudus*. Among 14 sampled individuals, 9 were identified as *T. amoenus* (4 found in unburned and 5 in burned sites) and 5 were identified as *T. ruficaudus* (burned areas only). The difference in species composition between burned and unburned sites was not significant (Fisher's exact test, $P = 0.221$).

The proportion of bushy-tailed woodrats (*Neotoma cinerea* (Ord, 1815)) was higher in unburned areas than in burned areas (Fisher's exact test — 2004: $P < 0.001$; 2005: $P = 0.024$). However, this result should be interpreted with caution, because this species was captured almost exclusively at site C2. Likewise, flying squirrels (*Glaucomys sabrinus* (Shaw, 1801)) represented a higher proportion of the small-mammal communities in unburned areas and lower in burned areas (Fisher's exact text; 2004: $P = 0.001$; 2005: $P < 0.001$), but occurred mainly at C2.

Other species, such as montane voles (*Microtus montanus*

Southern red-backed voles (*Clethrionomys gapperi* (Vigors, 1830)) were abundant in unburned sites, but disappeared almost entirely from the burned sites. In 2004, red-backed voles accounted for 31.2% of individuals captured in unburned areas, but only 2.2% of those captured in burned areas ($\chi^2_{[1]} = 84.60$, $P < 0.001$, $n = 464$). Also in 2005, the proportion of red-backed voles in burned and un-

Table 1. Number of different individuals of rodent species captured at unburned (C) and burned (F) trapping sites during the summer of 2004 and 2005.

Species	C1 2004	C1 2005	C2 2004	C2 2005	F1 2004	F1 2005	F2 2004	F2 2005	F3 2004	F3 2005	F4 2004	F4 2005
Peromyscus maniculatus	17	1	15	7	51	29	59	25	59	18	40	22
Clethrionomys gapperi	29	50	15	27	1	4	5	1	—	—	1	8
Tamias amoenus and *Tamias ruficaudus*	39	13	10	2	28	9	34	9	14	2	26	20
Neotoma cinerea	—	—	8	7	—	—	—	—	—	—	1	—
Glaucomys sabrinus	—	3	7	9	—	—	—	—	—	—	—	1
Microtus montanus	—	—	—	—	—	—	—	—	—	—	—	3
Spermophilus lateralis	—	—	—	—	—	—	—	—	—	—	2	1
Spermophilus columbianus	—	—	—	—	1	—	—	—	—	—	—	—
Tamiasciurus hudsonicus	—	2	—	—	—	—	—	—	1	—	—	—
Thomomys talpoides	—	—	—	—	—	—	—	—	—	—	—	1
Phenacomys intermedius	1	—	—	—	—	—	—	—	—	—	—	—
Total	86	69	55	52	81	42	98	35	74	20	70	56

Table 2. Number of different individuals of four species of shrews captured at unburned (C) and burned (F) trapping sites during summer 2004 and 2005.

Species	C1 2004	C1 2005	C2 2004	C2 2005	F1 2004	F1 2005	F2 2004	F2 2005	F3 2004	F3 2005	F4 2004	F4 2005
Sorex cinereus	7	14	9	16	—	1	1	3	—	—	—	4
Sorex hoyi	—	—	3	1	—	—	—	—	1	—	—	—
Sorex vagrans	2	1	—	—	—	2	—	1	—	—	—	1
Sorex monticolus	—	1	1	1	—	1	—	1	—	—	—	—
Unknown	4	7	2	1	—	—	2	1	1	2	—	2
Total	13	23	15	19	0	4	3	6	2	2	0	7

Note: Shrews found alive were marked and released. In these individuals, species remained unidentified.

(Peale, 1848)), golden-mantled ground squirrels (*Spermophilus lateralis* (Say, 1823)), Columbian ground squirrels (*Spermophilus columbianus* (Ord, 1815)), red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)), northern pocket gophers, and western heather voles (Table 1), were not captured frequently enough to justify statistical comparisons.

Shrew communities

Overall, we captured 94 shrews (Table 2). In both years, we found four species: masked shrew (*Sorex cinereus* Kerr, 1792), pygmy shrew (*Sorex hoyi* Baird, 1857), vagrant shrew (*Sorex vagrans* Baird, 1857), and montane shrew (*Sorex monticolus* Merriam, 1890). In 2004, we captured 28 shrews in 2 unburned sites, but only 6 shrews in 4 burned sites ($\chi^2_{[1]} = 34.62$, $P < 0.001$, $n = 34$). In 2005, the number of different shrews captured equaled 42 in unburned sites and 19 in burned sites ($\chi^2_{[1]} = 34.77$, $P < 0.001$, $n = 61$). The lower overall abundance of shrews in burned sites was primarily caused by the low numbers of masked shrew. This species accounted for 82.1% of all identified shrews captured in unburned sites, but only 56.3% in burned sites ($\chi^2_{[1]} = 4.63$, $P = 0.032$, $n = 72$).

Small-mammal diversity

One year after fire, diversity ($1 - D$) at site C2 was significantly higher than in other areas (Fig. 3). Diversity in burned sites was significantly lower than that in both unburned sites. However, 2 years after fire the difference between burned and unburned areas was no longer consistent. Diversity at sites C2 and F4 was significantly higher than in other sites, whereas diversity at F3 was significantly lower than that at any other site (Fig. 3).

Discussion

Our study documents considerable differences in the composition of small-mammal communities soon after severe, stand-replacement forest fire that are consistent with expectations based on habitat associations of these species (e.g., Pearson 1999; Foresman 2001; Pearce and Venier 2005). When compared with small-mammal communities in unburned forest, those in burned sites were distinguished by much higher proportion of deer mice, substantially lower proportion of red-backed voles and shrews, and almost complete absence of relatively rare species such as bushy-tailed woodrats and flying squirrels. These characteristics were mostly consistent across burned sites and between years. In 2004, the diversity of rodent communities in burned areas was considerably lower than in unburned areas, but this effect disappeared during the 2nd year after fire. On the contrary, the relative abundance of rodents in burned and unburned sites differed during the 2nd, but not the 1st year after fire.

An increase in deer mice has been reported after very different disturbances in coniferous forest: wildfire (Krefting and Ahlgren 1974; Koehler and Hornocker 1977; Crête et al. 1995), prescribed fire (Bock and Bock 1983), logging

Fig. 3. The complement of Simpson index ($1 - D$, estimate ± 95% CI) of the rodent communities at different trapping sites in summer 2004 (1 year after fire) and 2005 (2 years after fire). Indices with nonoverlapping 95% CI are marked with different letters.
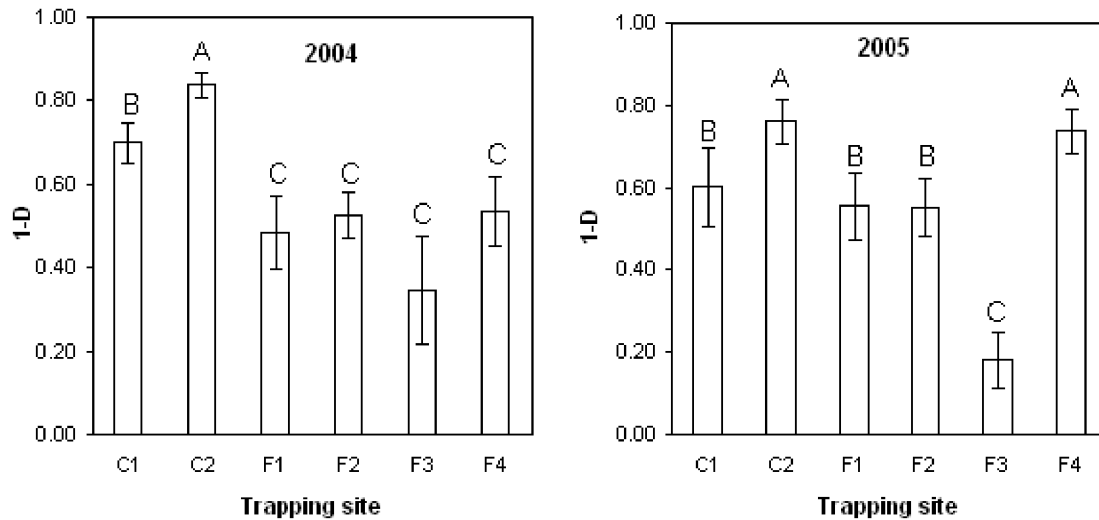
(e.g., Martell 1983; Kirkland 1990; Walters 1991; Pearce and Venier 2005), and clear-cutting followed by burning (Ahlgren 1966; Halvorson 1982; Martell 1984; Sullivan et al. 1999). The most frequently invoked explanations of this pattern increase involve (*i*) the increase in food resources in burned forests (insects and (or) seed, e.g., Ahlgren 1966) and (*ii*) the creation of dispersal and (or) population sinks in disturbed areas (Buech et al. 1977; Sullivan 1979; Martell 1984; Walters 1991, but see Tallmon et al. 2003).

The avoidance of burned areas by some species of small mammals, including red-backed voles, bushy-tailed wood-rats, and flying squirrels, can be attributed to three main factors: (1) reduction in food resources, (2) increased exposure to predation, and (3) distance of the burned plots to potential sources of colonists (>200 m) in unburned forest. The strong decline in red-back voles has been reported after various disturbances that result in decreased cover — wildfire (Krefting and Ahlgren 1974; Buech et al. 1977), logging followed by burning (Halvorson 1982; Martell 1984; Walters 1991), and clear-cutting (Campbell and Clark 1980; Martell 1982) — although this response may be dependent on the size of disturbed patches (Hayward et al. 1999). The avoidance of burned areas by flying squirrels could also result from their affinity to dense canopy cover for locomotion (Lehmkuhl et al. 2006).

There was no consistent difference in the overall proportion of chipmunks (*T. amoenus* and *T. ruficaudus*) between burned and unburned areas. Both species of chipmunks prefer areas with well-developed understory (e.g., Foresman 2001). Therefore, their abundance after high-intensity fire is surprising and may suggest that beneficial effects of fire such as increased availability of seed (Ahlgren 1966) could compensate for the loss of cover.

Data on the responses of shrews to disturbance is very limited because they are rarely caught both in snap traps and regular live traps. Moreover, different species of shrews are usually pooled together and treated as identical. In 3 out of 5 studies on clear-cutting in coniferous forest reviewed by Kirkland (1990), the abundance of shrews increased after the disturbance. Kirkland (1990) suggested that shrews, as sec-

ondary consumers, may be less affected by the changes in plant communities. In the present study, however, the abundance of shrews was greatly reduced in burned areas. This effect seemed to be driven by the decrease in masked shrew, a species that numerically dominates shrew communities in unburned forest. Similarly, in one of the few studies comparing the responses of different species of shrew to disturbances, Spencer and Pettus (1966) found that the proportion of masked shrew is lower in shrew communities in clearcuts. On the other hand, Crête et al. (1995) and Pearce and Venier (2005) did not detect any change in the abundance of masked shrews after wildfire and clear-cutting, respectively, in boreal forest.

The lower abundance of shrews in burned vs. unburned forest could have been caused by the intensity of fire that completely removed not only the vegetation cover, but even the litter layer, and by the subsequent changes in the microclimate. Following tree and shrub destruction, burned forest is much drier than unburned forest (Bendell 1974). Since shrews have high water requirements and are strictly insectivorous, this change may affect them directly or indirectly by changing the abundance of their prey (Kirkland 1991; McCay and Storm 1997).

Conclusions

Our study contributes to the growing body of evidence on the role of disturbances in shaping ecosystems, creating habitat heterogeneity, and modifying animal communities. Fire-created mosaic of burned and intact forest supports divergent small-mammal communities.

Small-mammal communities in burned forest do not contain unique, fire-dependent species, unlike those of plants, insects, or birds. However, the dramatic change in abundances coupled with complete disappearance of some species creates a distinctive community composition that may allow some species to benefit in the short term after fire. Thus, disturbance may contribute to the maintenance of overall diversity across a longer successional span of time.

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