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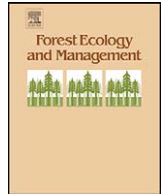
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Review

A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals

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ABSTRACT

Wildfires and timber harvest are two of the most prevalent disturbances in North American forests. To evaluate and compare their impact on small mammals, I conducted meta-analyses on (1) the effect of stand-replacement wildfires and several types of forest harvest (clearcutting followed by burning, clearcutting, and uniform partial harvest) on the abundance of deer mice (*Peromyscus maniculatus*) and red-backed voles (*Myodes gapperi*), (2) the impact of clearcutting and partial harvest on a broader array of small mammal species, and (3) the responses of small mammals to recent and older clearcuts (i.e. less than 10 years vs. 10–20 years after harvest). In coniferous and mixed forest, all disturbances except for partial harvest triggered significant increases in the abundance of deer mice and declines in red-backed voles. The increase in deer mice after wildfire was stronger than after clearcutting and marginally stronger than after clearcutting and burning. The abundance of red-backed voles was greatest in undisturbed or partially harvested stands, intermediate after clearcutting, and lowest after wildfire or clearcutting and burning. While the positive effect of clearcutting on deer mice did not persist beyond 10 years after disturbance, the negative effect on red-backed voles was similar between recent and older clearcuts. In deciduous forest, clearcutting did not result in a consistent change in abundance of deer mice and red-backed voles. For other small mammals, recent clearcutting tended to increase the abundance of yellow-pine chipmunks (*Tamias amoenus*), and meadow and long-tailed voles (*Microtus pennsylvanicus* and *Microtus longicaudus*). Woodland jumping mouse (*Neozapus insignis*), masked shrew (*Sorex cinereus*), and short-tailed shrew (*Blarina brevicauda*) did not show consistent response to timber harvest. Overall, the impact of different disturbances on the abundance of small mammals (i.e. positive or negative) appears to be species-specific, but disturbance type may influence the magnitude of this effect. Disturbance types can be ranked from severe to mild in terms of small mammal responses. The effects of forest harvest on small mammals are not equivalent to those of wildfire.

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1. Introduction

The structure and function of North American forests have been shaped by natural disturbance, predominantly wildfire (Attiwill, 1994). Repeated fire cycles have occurred in many North American forests for thousands of years (Hansson, 1992) and forest vertebrates show evidence of adaptation to this disturbance (Bunnell, 1995). Currently, forest harvest (mostly in the form of clearcutting) has replaced fire as the primary disturbance in many American forests, causing concerns about loss of biodiversity and resilience of forest ecosystems (Toman and Ashton, 1996; Simberloff, 1999; Drever et al., 2006). While it is widely accepted that conservation of biodiversity should be one of the primary objectives of forest management (Kohm and Franklin, 1997), the means to achieve this goal remain contentious (see e.g. Simberloff, 1999).

In recent years, the idea that carefully planned clearcuts could emulate and substitute for natural disturbances (Hunter, 1993) has gained remarkable popularity among foresters, researchers, and policymakers and is promoted as a way to integrate timber production with conservation of biodiversity (Ehnes and Keenan, 2002; Perera et al., 2004). Still, several researchers have pointed out considerable differences in ecological consequences of fire and logging (e.g. McRae et al., 2001; Hébert, 2003; Schieck and Song, 2006; Bergeron et al., 2007; Thiffault et al., 2007).

Harvest with retention of green trees (hereafter “partial harvest”) has emerged as a common group of methods to increase ecological sustainability of timber production (Work et al., 2003). Traditionally, the primary goal of partial harvest was to improve postharvest stand regeneration (e.g. shelterwood or selection systems, Nyland, 2002), but currently it is often used to maintain “environmental values associated with structurally complex forests” and to increase the similarity between natural and anthropogenic disturbances (variable retention harvest systems, Franklin et al., 1997). However, empirical evidence supporting this use of partial harvest remains scant (Simberloff, 2001; Schulte et al., 2006; Tappeiner et al., 2007).

In this study, I used small mammals as a model to (1) test the ecological premise of emulation silviculture, (2) assess conservation benefits provided by partial harvest, and (3) analyze the impacts of clearcutting on wildlife through a temporal perspective. To achieve these objectives, I conducted a meta-analysis on the changes in the relative abundance of small mammals after wildfire and several types of forest harvest: clearcutting, clearcutting followed by burning, and partial harvest.

Small mammals represent the majority of mammalian species in North American forests, play important roles in the forest food web (e.g. Maser et al., 1978; Ostfeld et al., 1996; Jones et al., 1998; Tallmon et al., 2003), and are considered indicators of forest-floor function (Carey and Harrington, 2001). A relative profusion of small mammal studies enables the use of meta-analytic approach, which offers improved control over type II statistical errors (Arnqvist and Wooster, 1995). Furthermore, by synthesizing results of studies conducted on different species, in different areas, and within different timeframes, the scope of inference in meta-analysis can be considerably greater than in the standard single-study approach (Osenberg et al., 1999). Finally, meta-

analyses are thought to be more informative and objective than qualitative reviews (Arnqvist and Wooster, 1995).

My study consisted of three analyses. First, I compared the effects of stand-replacement wildfires and several types of forest harvest (clearcutting followed by burning, clearcutting, and partial harvest) on the abundance of the two most commonly investigated species, deer mice (*Peromyscus maniculatus*) and red-backed voles (*Myodes gapperi*). This comparison addressed the question of whether anthropogenic disturbances emulate natural ones. Second, I quantified the impact of clearcutting and partial harvest on the abundance of a broader array of small mammal species: yellow-pine chipmunk (*Tamias amoenus*), deer mouse, red-backed vole, woodland jumping mouse (*Neozapus insignis*), meadow and long-tailed vole (*Microtus pennsylvanicus* and *Microtus longicaudus*), masked shrew (*Sorex cinereus*), and short-tailed shrew (*Blarina brevicauda*). This analysis measured relative severity of these types of harvesting techniques according to their influence on small mammals. Third, I examined the temporal dynamics of the effects of clearcutting on all of the above species except yellow-pine chipmunk and long-tailed vole. The goal of the third analysis was to identify species with ephemeral and long-lasting responses to this disturbance. Together, these analyses assessed whether natural and anthropogenic disturbances could be ranked from mild to severe in terms of small mammal response, or whether species/disturbance relationships were unique and idiosyncratic.

2. Methods

2.1. Source data

The data set used in this meta-analysis consisted of studies reporting the effects of wildfire, clearcutting followed by prescribed burning, clearcutting, and partial harvest on the abundance of North American small mammals (rodents or shrews). The analyzed studies were published between 1970 and 2008. I identified relevant publications by searching online databases of Agricola and the Web of Science (conducted in April 2008) using the following search words: *forest* and (*logging* or *harvest** or *clearcut** or *fire* or *wildfire* or *burn**), and (“*small mammals*” or *rodent** or *mice* or *mouse* or *vole** or *shrew**), and searching bibliographies of the studies that I retrieved.

I selected studies that reported the abundance of small mammals in disturbed and matching undisturbed (control) forest. Because the abundance of small mammals tends to fluctuate from year to year, I included only studies where trapping was conducted simultaneously on disturbed and undisturbed plots. When pre-disturbance data were available, they were examined only qualitatively to ensure that control plots were sufficiently similar to those that became disturbed.

I selected research papers where estimates or indices of abundance were derived from trapping and presented in text, tables, or bar charts. When the same results were presented in several papers, I used the most inclusive version. I did not use live-trapping studies where the number of captures rather than the number of different individuals captured was used. I excluded studies where abundances of related species were pooled because species within the same genus are known to react differently to

forest disturbance (e.g. Songer et al., 1997). To avoid confounding effects of patch configuration and edge effects, I did not use data from studies on strip clearcutting, patch clearcutting (clearcuts less than 2 ha), or other logging practices such as aggregated retention harvest (Franklin et al., 1997) that create small-scale mosaic of undisturbed and disturbed forest.

2.2. Calculation of effect sizes

Evaluating small mammal abundance requires considerable trapping effort. Therefore most studies in the data set were either unreplicated or contained only 2–3 replicates in each treatment. Furthermore, standard deviations could not be extracted from most of the studies. Thus, I could not apply commonly used effect sizes that are based on standard deviation and often require sample size greater than 5 or 10 (Rosenberg et al., 2000). Instead, I used the relative abundance index (RAI) developed by Vanderwel et al. (2007):

$$\text{RAI} = \frac{N_{\text{disturbed}} - N_{\text{undisturbed}}}{N_{\text{disturbed}} + N_{\text{undisturbed}}}$$

where $N_{\text{disturbed}}$ and $N_{\text{undisturbed}}$ are the abundance reported for disturbed and undisturbed sites, respectively. When needed, I standardized abundances to account for the difference in trapping effort between disturbed and undisturbed sites. The relative abundance index ranges from +1 (species found in disturbed sites only) to –1 (species found only in undisturbed sites).

I selected only those studies where at least 10 individuals were captured in at least one site category (disturbed or undisturbed). To avoid potential bias, I did not use any other inclusion criteria based on study quality (Englund et al., 1999). To take into account differences in sampling intensity among studies, the effect sizes were weighted (Hunter and Schmidt, 1990) by the \log_{10} of the total number of individuals used to calculate given RAI (i.e. the sum of different individuals captured in disturbed and undisturbed sites). I chose this conservative weighting scheme because the number of different individuals used to calculate RAI ranged from 10 to 4004.

Some studies did not provide the number of individuals captured or information sufficient to calculate it. In such cases, I tried to contact the corresponding author. For studies where this information proved impossible to obtain, I included only those where in at least one site category standard error of the abundance did not exceed the value of the mean. For such studies, I assumed the lowest acceptable number of captures, thus their weight equaled $\log_{10}(10) = 1$.

Studies were divided according to (1) the type of disturbance, (2) time since disturbance, and (3) forest type (coniferous, mixed, and deciduous). For each study, I calculated one effect size per species per category (disturbance type, time, and forest type), using abundances averaged across years and replicates.

Disturbances included stand-replacement wildfire, clearcutting followed by broadcast burning, clearcutting, and uniform partial harvest. The last category was the most varied. It included harvest labeled as shelterwood (e.g. Waters and Zabel, 1998), diameter-limit cut (e.g. Ford and Rodrigue, 2001), basal area retention harvest (e.g. Elliot and Root, 2006), or single-tree selection (e.g. Klenner and Sullivan, 2003). The abundance of different types of uniform partial harvest and therefore low numbers of studies investigating each type made it impossible to compare particular prescriptions of partial harvest. Instead, I tested the general strategy of retaining green trees after logging. Most studies on partial harvest included in this analysis were conducted after removal of 30–60% of basal area (range 29–79%; restricting the analysis to 30–60% of basal area removed did not influence the overall pattern).

Time since disturbance was divided into two categories: early (<10 years after disturbance) and late (10–20 years after

disturbance). All studies used in comparisons 1 (wildfire and forest harvest) and 2 (clearcutting vs. partial harvest) represented early (<10 years) effects of disturbance on small mammals. Ultimately, small mammal responses are related to the structure of regenerating habitat rather than time since disturbance (Monamy and Fox, 2000) but only the later information was reported widely enough to be used in this analysis. Studies reporting a single measure of abundance from a period covering two of the above categories were assigned on the basis of greater overlap (e.g. 8–14 years after logging were assigned to the “10–20 years after” category). Time was calculated since the most recent disturbance (e.g. the date of broadcast burning rather than the date of prior clearcutting). I excluded data collected within the first 3 months since the disturbance to avoid confounding effects of disturbances on habitat with their direct effects on small mammals.

Overall, 56 studies satisfied all the above-listed criteria (see Appendix 1).

2.3. Statistical analysis

To analyze species-specific changes in abundance after forest disturbances, I used linear models with RAI as the response variable and disturbance type (comparison 1), small mammal species and harvest practice (comparison 2), or small mammal species and time category (comparison 3) as explanatory variables.

In each analysis, normal distribution of errors was assured by examining Q–Q plots and conducting Shapiro–Wilk tests (all p -values were > 0.1). Examination of residuals revealed mild nonconstant variance. p -Values of less than 0.05 were considered “significant” and those between 0.1 and 0.05 “marginally significant”. All analyses were conducted in R (Ihaka and Gentleman, 1996).

Initial data analysis suggested that for deer mice and red-backed voles, the effects of harvest differed between deciduous and coniferous/mixed forests. Therefore, for these two species, data from deciduous forests were not included in comparisons 1–3 below, but were analyzed separately.

3. Results

3.1. Comparison 1: short-term (0–9 years) effects of wildfire and forest harvest in coniferous and mixed forest on deer mice and red-backed voles

Deer mice increased in response to all forest disturbances, but the strength of this response depended on the type of disturbance (Fig. 1). The response to wildfire was stronger than to any other disturbances: clearcutting followed by burning ($t_{3,41} = -2.02$, $p = 0.05$), clearcutting ($t_{3,41} = -3.78$, $p = 0.0005$), or partial harvest ($t_{3,41} = -4.54$, $p < 0.0001$). The effects of partial harvest did not differ from those of clearcutting ($t_{3,41} = 1.27$, $p = 0.212$).

Red-backed voles decreased in response to all disturbances with the exception of partial harvest (Fig. 1). The effects of clearcutting followed by burning were not significantly different from those of wildfire ($t_{3,32} = 0.68$, $p = 0.498$). The decline in abundance after wildfire was stronger than after clearcutting ($t_{3,32} = -2.20$, $p = 0.034$). For red-backed voles, the impact of clearcutting was significantly different than that of partial harvest ($t_{3,23} = -2.74$, $p = 0.01$).

3.2. Comparison 2: short-term effects of clearcutting and partial harvest

Yellow-pine chipmunks, deer mice, and both *Microtus* species were significantly more abundant and red-backed voles were significantly less abundant in clearcuts relative to undisturbed

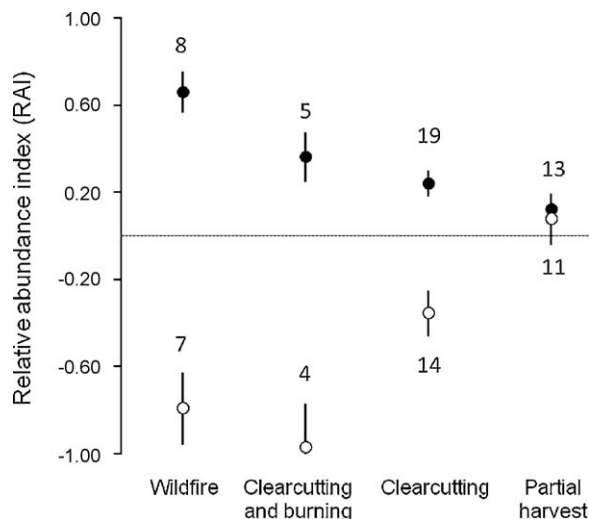


Fig. 1. The abundance of deer mice, *Peromyscus maniculatus* (filled circles) and red-backed voles, *Myodes gapperi* (open circles) after stand-replacement wildfire and three types of timber harvest relatively to undisturbed forest. Positive values of the relative abundance index (RAI) indicate higher abundance in harvested than in undisturbed forest, whereas negative values mean lower abundance in harvested forest. Bars represent standard errors; numbers denote sample sizes.

areas (Table 1). Partial harvest significantly increased the abundance of yellow-pine chipmunks and marginally significantly increased abundance of *Microtus* species (Table 1). The responses of other species to either type of forest harvest were not statistically significant and in general, small mammal species responded in a similar way to clearcutting and partial harvest. Other than the red-backed vole (comparison 1 above), only the meadow vole showed some evidence of a difference in the response to clearcutting and partial harvest ($t_{15,117} = -1.79$, $p = 0.076$).

Table 1
Abundance of small mammals in clearcut and partially harvested forest, 1–9 years after disturbance. Positive values of the relative abundance index (RAI) indicate higher abundance in harvested than in undisturbed forest, whereas negative values mean lower abundance in harvested forest. *p*-Values concern the hypothesis that RAI equals 0.

Species	Harvest type (sample size in parenthesis)	RAI (SE)	t-Value	p-Value
Meadow vole	Clearcutting (11)	0.72 (0.12)	6.14	>0.0001
	Partial harvest (5)	0.33 (0.19)	1.77	0.080
Long-tailed vole	Clearcutting (4)	0.68 (0.17)	3.92	0.0001
	Partial harvest (4)	0.37 (0.20)	1.83	0.070
Yellow-pine chipmunk	Clearcutting (3)	0.67 (0.21)	3.26	0.001
	Partial harvest (5)	0.47 (0.17)	2.68	0.008
Deer mouse	Clearcutting (19)	0.24 (0.08)	2.93	0.004
	Partial harvest (13)	0.12 (0.10)	1.23	0.221
Masked shrew	Clearcutting (12)	0.12 (0.11)	1.02	0.309
	Partial harvest (4)	0.18 (0.20)	0.89	0.374
Short-tailed shrew	Clearcutting (11)	-0.08 (0.12)	-0.63	0.521
	Partial harvest (7)	0.05 (0.15)	0.32	0.748
Woodland jumping mouse	Clearcutting (6)	-0.07 (0.17)	-0.42	0.678
	Partial harvest (3)	0.09 (0.26)	0.53	0.724
Red-backed vole	Clearcutting (14)	-0.35 (0.09)	-3.77	0.0003
	Partial harvest (11)	0.08 (0.10)	0.75	0.453

Table 2
Abundance of small mammals in clearcut areas relative to undisturbed forest 10–20 years after disturbance. *p*-Values concern the hypothesis that the relative abundance index (RAI) equals 0.

Species (sample size in parenthesis)	RAI (SE)	t-Value	p-Value
Woodland jumping mouse (6)	0.33 (0.19)	1.75	0.082
Meadow vole (4)	0.25 (0.23)	1.13	0.262
Masked shrew (7)	0.10 (0.15)	0.63	0.530
Short-tailed shrew (10)	-0.08 (0.13)	-0.61	0.542
Deer mouse (7)	-0.05 (0.14)	-0.38	0.702
Red-backed vole (8)	-0.30 (0.13)	-2.36	0.020

3.3. Comparison 3: long-term effects of clearcutting

10–20 years after clearcutting, the abundance of deer mice and meadow voles was no longer higher than in undisturbed forest (Table 2). For both of these species, the short-term and the long-term responses to clearcutting were marginally different (deer mouse: $t_{11,103} = 1.80$, $p = 0.074$; meadow vole: $t_{11,103} = 1.86$, $p = 0.066$). There was some indication that at this stage the abundance of woodland jumping mice may be higher in clearcuts than in undisturbed forest, but the evidence was inconclusive (Table 2). The short- and long-term responses of this species did not differ significantly ($t_{11,103} = -1.52$, $p = 0.131$). Red-backed voles were negatively affected by clearcutting even in the long-term (Table 2). There was no difference between the short-term and long-term response of this species ($t_{11,103} = -0.35$, $p = 0.725$). Shrews did not show significant long-term response to clearcutting (Table 2) nor any difference between short- and long-term effects (short-tailed shrew: $t_{11,103} = 0.03$, $p = 0.976$; masked shrew: $t_{11,103} = 0.09$, $p = 0.926$).

3.4. Effects of clearcutting in deciduous forest on the abundance of deer mice and red-backed voles

Due to the small number of studies conducted in deciduous forest (six for each species), only the short-term effects of clearcutting on deer mice and red-backed voles could be analyzed statistically. In contrast to coniferous and mixed forests, clearcutting in deciduous forests did not affect the abundance of these species relative to undisturbed areas (deer mouse: RAI = -0.02, SE = 0.12, $p = 0.88$; red-backed vole: RAI = 0.15, SE = 0.21, $p = 0.49$). The differences between responses in deciduous versus coniferous/mixed forests were marginally significant (deer mouse: $t_{23} = 1.84$, $p = 0.078$; red-backed vole: $t_{18} = -2.06$, $p = 0.054$).

4. Discussion

4.1. Emulating wildfire with clearcuts: insights from small mammal responses

The current study indicates that the effects of clearcutting are milder than those of stand-replacement wildfires, at least for the two most common small mammals: red-backed voles, which tended to decline in abundance after disturbances, and deer mice, which tended to increase. These responses are consistent with habitat associations of these species. Disturbed stands are more xeric and offer less cover than intact forest. Open, xeric microhabitats are preferred by deer mice (Pearson et al., 2001; Fuller et al., 2004; Kaminski et al., 2007; Zwolak, 2008), but avoided by red-backed voles (Yahner, 1986; Pearson, 1994; Morris, 1996).

So far, emulation of natural stand-replacing disturbances with clearcuts focused mainly on imitating the shape and size distribution of fires (Hunter, 1993). However, if there are intrinsic differences in local habitat quality between wildfire-burned and

clearcut stands (as suggested by the response of small mammals), adjusting the shape and size of clearcuts is unlikely to be successful in mimicking the effects of fires. Therefore, emulation of stand-replacing natural disturbance through clearcutting may be problematic.

Contrary to stand-replacement wildfires, clearcutting does not remove herbs and shrubs. In order to produce early seral forest floor conditions, foresters sometimes combine clearcutting with slash burning (Kimmins, 2004). In the case of red-backed voles, the effects of clearcutting followed by burning did not differ from those of wildfire. For deer mice, the effects of these two disturbances were marginally different. Thus, although the small number of available studies on clearcutting followed by burning precludes firm conclusions, it appears that the severity of this disturbance is similar or slightly lower than that of stand-replacing wildfire. However, the popularity of this practice has declined since 1970s (Agee, 1997), in part because public perceives it as a too severe disturbance (Kimmins, 2004). Finally, mimicking the severity of stand-replacement fires may not be considered practical by foresters. For example, severe disturbances cause strong increases in deer mouse abundance, often resulting in intense seed predation and potentially slower reestablishment of commercially valuable stand (Gashwiler, 1967; Sullivan, 1979; Sullivan and Sullivan, 1982; Zwolak, 2008).

Harvest that retains residual structures such as snags and logs, also included in the broad concept of emulation forestry (Franklin et al., 1997; Beese et al., 2003), is unlikely to increase the similarity between the effects of wildfire and forest harvest because effects of the former on small mammals appear to be more, not less severe. The management implications of this analysis are profound: managers need to pay more attention to managing for the maintenance of naturally disturbed (burned) forest conditions because acceptable forms of artificial disturbance are not a good substitute.

Studies on other taxa yield similar results. Buddle et al. (2005) found considerable differences between clearcutting and wildfire in the succession rate of arthropod communities. They concluded that the effects of wildfire were more severe than those of clearcutting. Bird communities also differ between stands disturbed by wildfire and forest harvest (Schieck and Song, 2006). These differences are very pronounced during the first 10 years after disturbance, tapering off afterwards. However, in contrast to arthropods or birds, there are no fire-dependent species among small mammals in North American forests.

4.2. Responses of small mammals to clearcutting and partial harvest

Most small mammal species analyzed either did not show a consistent response to clearcutting of coniferous and mixed forest (masked and short-tailed shrews, woodland jumping mouse) or increased in abundance relative to undisturbed stands (non-forest species: meadow and long-tailed vole and generalist species: yellow-pine chipmunk, and deer mouse). Only the abundance of red-backed voles significantly declined after clearcutting. Interestingly, an earlier analysis of published studies concluded that red-backed voles tend to increase after clearcutting in coniferous forest (Kirkland, 1990). However, this conclusion was based on the vote-counting method (comparing the number of significant and non-significant results), which currently is considered unreliable and prone to bias (Hunter and Schmidt, 1990; Osenberg et al., 1999).

As expected, the effects of partial harvest tended to be less pronounced than those of clearcutting. However, the response to these two harvest practices was significantly different only for the red-backed vole, while in the meadow vole the difference approached significance. While this result indicates that leaving

green trees does not provide major gains for most small mammal species, conservationists and practitioners are concerned mainly about clearcutting-sensitive species. The response of red-backed voles suggests that green tree retention represents an efficient strategy to mitigate the impact of forest harvest on species that tend to decline in abundance after stand-replacement disturbances.

The value of green tree retention is particularly important given that the negative effects of clearcutting on red-backed voles are long-lasting. The red-backed vole was the only analyzed species that expressed a significant long-term response to forest harvest. This result corroborates findings of recent field studies: St-Laurent et al. (2008) concluded that stands of 3 m in height (i.e. 14–17 years after harvest), considered “regenerated” under the legislation of some Canadian provinces, do not maintain abundance of red-backed voles similar to those of unharvested mature forest.

Red-backed voles have been proposed as an indicator of mature forest (Nordyke and Burskirk, 1988; McLaren et al., 1998; see also Pearce and Venier, 2005 for critical evaluation). This analysis shows that this role may be played in coniferous and mixed forests only. In deciduous forests, the abundance of red-backed voles tended to be similar between clearcuts and mature forests. This pattern of red-backed vole responses could be caused by the difference in microclimate: deciduous forests often grow in more humid regions than coniferous forests (Holdridge, 1967). Clearcuts are dryer than intact stands (Tappeiner et al., 2007), thus many conifer clearcuts may be too dry for red-backed voles (D.E. Pearson, *personal communication*), which are known for their high moisture requirements (Getz, 1962). Alternatively, the different effects of clearcutting on red-backed voles in deciduous and coniferous forest may be related to the intensity of postharvest treatments. Red-backed voles strongly prefer structurally complex microhabitats (Pearson, 1994). In deciduous clearcuts, where the risk of fires is lower, dense logging slash is often left on site. In coniferous clearcuts, slash is usually removed or piled, thus they lack structural complexity (D.E. Pearson, *personal communication*).

Competition with red-backed voles could explain why deer mice increase in abundance in coniferous but not deciduous clearcuts (Crowell and Pimm, 1976; Schulte-Hostedde and Brooks, 1997; although Morris, 1983, 1996; Wolff and Dueser, 1986 did not find evidence of competition between these two species). In addition, deer mice prefer open microhabitats (Pearson et al., 2001; Fuller et al., 2004; Kaminski et al., 2007; Zwolak, 2008; but see Goodwin and Hungerford, 1979; Morris, 2005), which are created in greater abundance by clearcutting in coniferous forest than in deciduous forest, as discussed above. Unfortunately, not enough studies reported information on postharvest conditions to test this hypothesis statistically.

Alternatively, the patterns of red-backed vole and deer mouse response to forest harvest could be caused by changes in predatory pressure. Little is known about the effects of forest disturbances on the numbers and activity of predators (Fisher and Wilkinson, 2005), but if predation was driving disturbance-related changes in rodent abundance, it would almost certainly do it through changes in survival. However, most studies conclude that the survival of red-backed voles (Von Trebra et al., 1998; Sullivan and Sullivan, 2001; Hadley and Wilson, 2004) and deer mice (Von Trebra et al., 1998; Zwolak, 2008; Zwolak and Foresman, 2008; but see Tallmon et al., 2003) does not differ between disturbed and undisturbed stands. Moreover, even though these two species share their most important predators (such as weasels and owls: Merritt, 1981; Kaufman and Kaufman, 1989), their responses to disturbances in coniferous forest are very different. Thus, predation is unlikely to explain the impact of harvest and other forest disturbances on red-backed voles and deer mice.

For other investigated species forest type did not influence the effects of forest harvest in any perceptible way. This is in agreement with the statement that when assessing the effects of forest harvest, for many species of small mammals “it is apparently not necessary to make a major distinction between coniferous and deciduous forests” (Kirkland, 1990), at least until more studies are conducted and higher resolution can be achieved. Not surprisingly, *Microtus* species, associated with grassy habitats and rarely caught in closed forest, increased after forest harvest. The increase also occurred in yellow-pine chipmunk, a generalist species found mostly in open, dry areas and brushy habitats (Foresman, 2001). In the long-term, woodland jumping mice also appeared to be positively affected by clearcutting, perhaps because of their association with abundant herbaceous cover that develops after canopy is removed (Miller and Getz, 1977; Kaminski et al., 2007). Masked and short-tailed shrews did not respond to forest harvest, possibly because these generalist insectivores, as secondary consumers, are not directly affected by changes in plant communities and vegetation structure (Kirkland, 1977). Still, our understanding of ecological mechanisms that determine shrew and other small mammal responses to forest harvest is rudimentary (Ford et al., 2000).

4.3. Limits of the study

I analyzed the effects of forest harvest on common species with high reproductive rates and “fast” life histories. As a caveat, rare, less resilient forest species that are of primary management concern may respond differently to forest harvest. On the other hand, it is common species that determine ecosystem functions (Gaston and Fuller, 2007), thus even relatively small changes in small mammal abundance and species composition might influence important ecological processes in forest ecosystems. For example, small mammals influence the abundance of trees and other forest plants through consumption of seeds and seedlings (Ostfeld et al., 1997; Tallmon et al., 2003; Zwolak, 2008), contribute to the regulation of insect populations (Andersen and Folk, 1993; Jones et al., 1998), and serve as prey for endangered species of forest vertebrates (Forsman et al., 2004).

Because of the relatively small number of analyzed studies, I treated uniform partial harvest as a single management approach and evaluated the overall strategy of retaining green trees. Still, it could be revealing to compare the effects of different types of partial harvest on small mammals. Such an analysis will certainly be possible in the future, when more field studies are conducted on this subject.

Finally, the majority of studies retrieved in my search were conducted in western and northern montane and boreal communities, and in eastern temperate/Appalachian systems (Appendix 1). Therefore, my results are more representative for these regions, and less for e.g. pine-dominated forests in the South.

5. Conclusions

The results of this study demonstrate that the qualitative responses of small mammals to disturbance are species-specific, but relatively consistent across fires and different cutting regimes. However, the type of disturbance strongly influences the magnitude of that response. According to their effects on small mammals, disturbances can be ranked from mild (partial harvest), through moderate (clearcutting) to severe (stand-replacement wildfire). As found with other taxa, the effects of forest harvest on small mammals are not equivalent to those of wildfire, thus, mimicking natural disturbances with anthropogenic ones (the premise of emulation forestry) appears problematic. On the other hand, green tree retention seems to provide an efficient method of

minimizing post-logging changes in small mammal communities. Given that we do not know which aspects of natural disturbance regimes are important for maintaining biodiversity (Simberloff, 2001), mitigating the impacts of forest harvest through legacy retention (Franklin et al., 1997) and allowing the occurrence of natural disturbances (Hutto, 2009) may represent a better strategy of biodiversity protection than trying to mimic the extent and severity of wildfires.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2009.05.033.

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