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Stand scale effects of partial harvesting and clearcutting on small mammals and forest structure

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Abstract

Documenting responses of small mammals to alternative forestry practices (e.g., clearcutting versus partial harvesting versus no management) facilitates inferences about effects on wildlife communities. We compared abundances of small mammals (voles, mice, and shrews) during four summers among partially harvested mixed coniferous–deciduous stands (52–59% basal area removal, 15 m^2/ha live-tree residual basal area), regenerating commercial clearcuts (11–20-year-old), mature (>12 m tree height) mixed stands, mature deciduous, and mature coniferous stands. Partially harvested stands had significantly greater overall abundance of deer mice (*Peromyscus maniculatus*) than mature mixed stands, but abundances of red-backed voles (*Clethrionomys gapperi*) and short-tailed shrews (*Blarina brevicauda*) were not significantly different. Regenerating clearcut stands had significantly lower abundances of voles and mice relative to mature mixed stands, and ranked low in abundance of shrews. Mature coniferous stands also ranked low in relative abundance of shrews and had the lowest abundance of deer mice relative to other mature stand types. Mature deciduous stands ranked high in abundance of deer mice and had the greatest abundance of short-tailed shrews among all stand types. Despite reduced canopy closure, lower relative density of coniferous trees and saplings, and decreased basal area of deciduous trees and snags, partially harvested stands supported densities of mice and voles comparable to mature mixed-forest types. Forest harvesting practices that retain some structural attributes of mature forests may be beneficial to small mammals and associated predators that utilize mice, voles, and shrews as prey.

Keywords: *Blarina*; *Clethrionomys*; Clearcutting; Maine; Partial harvesting; *Peromyscus*; Small mammal

1. Introduction

The Acadian forest of eastern North America represents a transition zone between the temperate deciduous forest and the northern boreal forest (Seymour and Hunter, 1992) and encompasses parts of three northeastern US states and three Canadian provinces. Harvesting practices in the Acadian forest have shifted from an emphasis on clearcutting to partial harvesting throughout some jurisdictions during the past decade (Maine Forest Service, 2002). The Maine Forest Practices Act (Title 12 MRSA, Chapter 805) was passed in 1989, in part caused by a negative public perception of clearcutting (Bliss, 2000); this legislation created economic disincentives for large clearcuts, which accelerated the shift to partial harvesting. In Maine, partial harvesting (residual basal area >6.9 m^2/ha; including selection and shelterwood silvicultural systems) composed 97% of the total acreage harvested during 2001 (an increase of 27% in 10

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years), and was associated with a major decrease in clearcutting (residual basal area <6.9 m^2/ha) (Maine Forest Service, 2002). New Brunswick is also experiencing a gradual shift to partial harvesting, from only 8% of the area harvested in 1990 to 37% in 2000 (Canadian Council of Forest Ministers, 2002). Elsewhere within the Acadian region of Canada (e.g., Provinces of Nova Scotia, Quebec, Ontario, and Prince Edward Island), clearcutting composed 82% of all acres harvested during 2000, and the extent of clearcutting has not changed appreciably since 1990 (Canadian Council of Forest Ministers, 2002).

The effects of clearcutting on forest ecosystems have been questioned from the perspectives of biodiversity (Hunter, 1990), sustainability (Rowe, 1994), and aesthetics. Commonly perceived advantages of partial harvesting over clearcutting include enhanced habitat for wildlife and increased aesthetic values by maintaining some overstory cover. As a result, partial harvesting is being used increasingly to help meet ecological and economic objectives in managed forests, and may provide opportunities to extract timber while maintaining some structural features of mature forests (McComb et al., 1993).

Small rodents and insectivores are important components of forest ecosystems, and function as predators (Maxson and Oring, 1978), prey (Parker et al., 1983; Soutiere, 1979; Chubbs and Trimper, 1998; Dawson and Bortolotti, 2000), dispersers of seeds (Smith and Aldous, 1947; Ostfeld et al., 1997; Bermejo et al., 1998) and spores of hypogenous fungi (Maser et al., 1978; Kirkland, 1990). Small mammals (particularly voles) are also important herbivores and may significantly influence plant communities and communities of other herbivores. Therefore, small mammals have been used elsewhere as ecological indicators of the effects of forest management practices (Lautenschlager et al., 1997).

Use of partial harvest systems is increasing; however, ecological tradeoffs of partial-cut harvesting compared to clearcut logging have not been rigorously tested simultaneously within the same landscape. Previous studies have reported that partial harvesting increased abundance of small mammal populations or that abundances did not change (Campbell and Clark, 1980; Martell, 1983; Swan et al., 1984; Monthey and Soutiere, 1985). Red-backed voles increased with the number of years since mixedwood stands were selectively cut in Ontario, but were more abundant in uncut stands than in 4–16-year-old selection cuts (Martell, 1983). Partially harvested conifer stands with residual basal area of 22 m^2/ha had greater abundance of red-backed voles and deer mice relative to uncut softwood stands (Monthey and Soutiere, 1985). Similarly, red-backed voles increased after removal of 30% of stand volume (44 m^2/ha basal area) in British Columbia (Steventon et al., 1998). Although previous studies reported no declines in small mammal abundances after partial harvesting, basal areas in these studies were high, and thus do not represent the range of harvesting regimes currently practiced in the Acadian forest. It is unclear how small mammals respond to partial harvesting at lower residual basal areas.

The effects of clearcutting on small mammal abundance appears to be species- and area-specific; abundance of deer mice increased and red-backed voles declined in recent clearcuts in British Columbia (Steventon et al., 1998), and aggregate number of all small mammals were greater in clearcuts than in uncut stands in Maine (Monthey and Soutiere, 1985). In contrast, densities of small mammals were lower in clearcuts compared to uncut stands in Ontario (Martell and Radvanyi, 1977). For small mammals, the effects of clearcutting (e.g., Kirkland, 1977; Monthey and Soutiere, 1985; Clough, 1987; Potvin and Breton, 1997; Potvin et al., 1999) and uneven-aged partial harvesting (Campbell and Clark, 1980; Martell, 1983; Monthey and Soutiere, 1985; Steventon et al., 1998) on small mammals have been studied singularly, but relative densities have not been compared across a range of management scenarios from no management, medium intensity harvesting, to high intensity harvesting in mixed Acadian forests.

The continuum of forest practices has potential to alter habitat structure, which has been postulated to be the strongest habitat influence on small mammal diversity and abundance (Dueser and Porter, 1986). Small mammals often select habitat based on structure or volume of coarse woody debris (Miller and Getz, 1977; Kirkland, 1990; Nordyke and Buskirk, 1991), which provides cover for reproduction and feeding (Maser et al., 1978; Maser and Trappe, 1984), travel routes (Harris, 1984), substrate for fungal growth, and associated food and water (Maser et al., 1978). Forest harvesting practices that retain some structural attributes of mature forests may be beneficial to small mammals and associated predators such as American marten (Payer and Harrison, 2003), American kestrels (*Falco sparverius*) (Dawson and Bortolotti, 2000), and ospreys (*Pandion haliaetus*) (Chubbs and Trimper, 1998) that utilize small mammals as principal prey. We were thus interested in sampling a range of management practices to determine the effects of varying amounts of forest structure on small mammal populations.

We compared small mammal abundances and forest structure among even-aged commercial clearcuts, uneven-aged selection systems, and no management in multi-aged stands to better understand how the continuum of forest management approaches influences forest structure and the community of small forest mammals that are structurally dependent. We compared densities of red-backed voles (*Clethrionomys gapperi*), deer mice (*Peromyscus maniculatus*), and short-tailed shrews (*Blarina brevicauda*) among (1) mature (>12 m tree height, >50% stocking density) mixed coniferous–deciduous (25–75% coniferous or deciduous) stands with a past history of selective logging for large spruce (*Picea* spp.) and pines (*Pinus* spp.); (2) regenerating commercial clearcuts (11–20-year-old) in mixed stands followed by herbiciding to promote conifer regeneration; (3) partially harvested mixed stands where large conifers were selectively removed and a continuous spacing of residual trees was maintained; (4) mature deciduous and (5) mature coniferous stands. We also compared structural features of mature mixed-, partially harvested mixed-, and clearcut-stands to determine which within-stand structural variables helped explain observed differences in abundances of small mammals across the different silvicultural treatments.

2. Methods

2.1. Study area

Our study was conducted within two townships in the Acadian forest of northcentral Maine (T4 R11 WELS and T5 R11 WELS), Piscataquis County (460211.85 N, 690910.62 W). These townships were 134 km^2 in area and were managed for pulpwood and saw timber by Great Northern Paper Company, Inc., Millinocket, Maine. The study area had moderate topography with altitude ranging from 290 to 565 m. Approximately 56% of the area was silviculturally or commercially clearcut during 1974–1994. Most stands were commercially clearcut between 1976 and 1984 and trees were delimbed at the roadside. The seven clearcuts that we sampled were treated with glyphosate (Roundup^{TM}) 3–8 years post-harvest, and were not pre-commercially thinned prior to our study. These stands averaged 56 ha (33–89 ha) and had basal areas after harvesting from 0.81 to 2.44 m^2/ha. Regenerating clearcut stands were composed of young paper birch (*Betula papyifera*), red maple (*Acer rubrum*), balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), pin cherry (*Prunus pensylvanica*), and raspberries (*Rubus* spp.). There was no tree planting within regenerating clearcut stands.

The partially harvested stands comprised 850 ha. Harvesting occurred between 1992 and 1995, 52–59% of the basal area of these mixedwood stands was removed during harvesting, and residual basal areas averaged 13 m^2/ha (Fuller, 1999). One of the cuts was harvested with chain saws; the others were logged using single-grip harvesters that felled, delimbed, cross-cut, measured to length, piled logs at the felling site, and transported logs from the stand with forwarders.

Mature deciduous forest stands were composed of red maple, sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), paper birch, and yellow birch (*B. alleghaniensis*). Dominant species in mature coniferous stands included balsam fir, red spruce, and eastern white pine (*Pinus strobus*). Mature coniferous and mixed stands had been selectively harvested for large-diameter eastern white pine and red spruce prior to 1974. Coniferous stands typically occurred on sites with shallow glacial tills resulting in poorly drained soils. Deciduous and mixedwood stands occurred on better-drained soils, and deciduous species outcompeted spruce and fir as site drainage increased.

2.2. Study design

We compared abundances of deer mice, red-backed voles, and short-tailed shrews and vegetation and structural characteristics among five overstory types: partially harvested mixed, mature mixed, mature coniferous, mature deciduous, and regenerating clearcut stands (Table 1). The distribution of trap grids was

Table 1
Number of live-trap grids sampled for small mammal abundance among five overstory types during 1995–1998 in T4 R11 and T5 R11 WELS, northcentral Maine

Overstory type	Year[a]			
	1995	1996	1997	1998
Mature mixedwood	7[f]	7[f]	7[g]	7[g]
Regenerating clearcut[b]	7[f]	7[f]	2	2
Partially harvested mixedwood	0	0	7[g]	7[g]
Mature coniferous	2	2	2	2
Mature deciduous	2	2	2	2

[a] Statistical comparisons (within and between years) were conducted between overstory types with the same letter superscript.
[b] Regenerating clearcut grids sampled during 1997 and 1998 were a subset of the seven grids sampled during 1995 and 1996.

established to maximize power of statistical comparisons between clearcuts and mature mixed stands during 1995–1996, and partially harvested and mature mixed stands during 1997–1998, while evaluating relative differences in abundances across all five stand types.

We surveyed and statistically compared small mammal abundances among seven mature mixed and seven regenerating clearcut stands (harvested 1976–1984) surveyed during summers 1995 and 1996 and among seven mature mixed (the same stands that were surveyed during 1995–1996) and seven partially harvested mixed stands surveyed during summers 1997 and 1998 (Table 1). Further, we monitored abundances of small mammals within two mature deciduous and two mature coniferous stands from 1995 to 1998 as a relative benchmark of small mammal abundances compared to the mature mixed, clearcut, and partially harvested stands (Table 1). Finally, two of the clearcut stands included in the 1995–1996 comparisons were also surveyed in 1997–1998 to evaluate the relative rank of small mammal abundances within clearcuts relative to partially harvested stands (Table 1). Mature mixed coniferous–deciduous stands were chosen as the statistical benchmark for evaluating the effects of clearcutting and partial harvesting on within-stand vegetation and structural characteristics because the partially harvested stands that we studied were predominately mature, mixed stands prior to harvest, and because the landscape of the Acadian forest was historically dominated by mixed coniferous–deciduous stands. This study design allowed us to sample a continuum of forest practices from intensive clearcutting to partial harvesting to no management within mature mixed stands.

2.3. Small mammal trapping

Relative abundances of red-backed voles, deer mice, and short-tailed shrews were surveyed by live-trapping on grids that were positioned >100 m from the edge of stands. Grids were trapped for six consecutive 24 h periods during 27 June–4 August 1995, 25 June–25 July 1996, 22 June–28 July 1997, and during 21 June–31 July in 1998; four grids were sampled each week. Sampling was distributed so that no more than two mature mixed (1995–1998), partially harvested (1997–1998), or clearcut stands (1995–1996) were sampled during the same 6-day trapping session. Each trap grid contained 64 Bolton live traps (B.N. Bolton, Inc., Vernon, British Columbia) spaced 10 m apart in a 70 m $\times$ 70 m square grid (4900 m^2 total area). Traps were baited with a mixture of peanut butter and oats, and contained cotton balls for nesting material. Species and sex of each captured animal were recorded, and a numbered self-piercing ear tag (Model no. 1005-1; National Band and Tag Co., Newport, Kentucky) was affixed in the left ear of mice and voles. Captured animals were released at the trap site. Trapping and handling procedures were approved by the Institutional Animal Use and Care Committee, University of Maine. We followed safety guidelines for hantavirus pulmonary syndrome recommended by the United States Department of Health and Human Services (1993).

2.4. Small mammal abundances

Because mark-recapture population models are extremely sensitive to high mortality and low sample sizes (Otis et al., 1978; White et al., 1982; Menkens and Anderson, 1988a,b), we used the number of initial captures as an index of mice and vole abundance (Menkens and Anderson, 1988b). Abundance of short-tailed shrews was calculated as the number of traps per grid that captured shrews; 60–85% of shrews died in traps each year.

We used an analysis of variance (ANOVA) to compare abundance of small mammals between partially harvested mixed and mature mixed stands (1997,

1998) and between clearcut and mature mixed stands (1995, 1996), and to evaluate the interaction of year and stand type. We used a square root transformation (Zar, 1999) on abundance data when numbers of animals captured were distributed non-normally within a stand-type based on a Lilliefors test, or had unequal error variances (Levene's test) (Milliken and Johnson, 1992). If transformations did not result in normality, we used a Mann–Whitney test to compare the two overstory types within each year.

2.5. Structural differences among stand types

Sixteen trap stations were randomly selected from each of the small mammal grids ($n = 25$) for habitat sampling (400 sample plots). The area surrounding each trap station was divided in four quarters, and dbh of the closest tree (≥2 m height, ≥7.6 cm diameter, alive) and litter depth was measured in each quarter. The number of deciduous and coniferous trees and snags (≥7.6 cm dbh, ≥2 m in height), number of herbaceous and woody seedlings (<0.5 m height, <7.6 cm dbh), number of deciduous and coniferous saplings (<7.6 cm dbh, 0.5–1.5 m height, alive), number and volume of logs (<45° from horizontal, ≥1 m length, ≥7.6 cm diameter) and stumps (<2 m height, ≥7.6 cm diameter), and number of root masses (≥7.6 cm diameter at root collar) were also measured within a 10 m × 2 m rectangular plot centered on each trap station. Log volume was calculated using the equation for a frustum of a cone. Stump volume was calculated as a cylinder using mid-point diameter and height (Corn and Raphael, 1992). Percent live ground cover in a 2 m radius was ocularly estimated. Understory lateral foliage density was estimated using a 2.0 m cover pole (Griffith and Youtie, 1988) placed 10 m from the trap station. Visual obstruction (percent of 0.1 m bands ≥25% obstructed by vegetation) was recorded for each 0.5 m zone (0–0.5, 0.5–1.0, 1.0–1.5, 1.5–2.0 m) on the pole and the average was recorded. Basal area of snags and coniferous and deciduous trees was estimated using a 2 m^2/ha wedge prism (Avery and Burkhart, 2002). Percent canopy coverage from a spherical densiometer (Lemmon, 1956) was averaged among the four cardinal compass directions centered on each trap station.

We tested for differences in within-stand structural variables between mature mixed and partially harvested mixed stands after assessing normality of each habitat variable with Lilliefors test, and homogeneity of error variances with Levene's test (Milliken and Johnson, 1992). We square root transformed (Zar, 1999) non-normal variables, or those exhibiting heteroscedasticity to meet parametric assumptions. Next, we conducted univariate ANOVA's for each habitat variable and retained variables with $P \leq 0.10$. Remaining variables were used in a multivariate Hotelling's T^2 test (Rencher, 1995). Since we had more habitat variables (21) than grids sampled (14), we used the univariate ANOVA's to reduce the number of habitat variables to <14 to meet the requirement for the Hotelling's T^2 (Rencher, 1995). If the Hotelling's T^2 test suggested differences in at least one habitat variable between overstory types, we then used univariate F-tests with a Bonferroni-adjusted critical value of α/k (Rencher, 1995) to determine which habitat variables differed significantly between overstory types.

We were unable to test for differences between mature mixed and regenerating clearcut stands because the large differences in within-stand variables were not normally distributed. Therefore, we visually compared these two stand types by constructing box plots of coarse woody debris (density of logs, stumps, root masses), understory (density of coniferous and deciduous seedlings and saplings), overstory (basal area of deciduous and coniferous trees and snags), and closure (canopy closure, understory lateral foliage density) variables among mature mixed, partially harvested mixed, and regenerating clearcut stands.

3. Results

We captured 795 individual small mammals (red-backed voles, deer mice, masked shrews [*Sorex cinereus*], short-tailed shrews, and jumping mice [*Napaeozapus insignus*]) on 1849 occasions during 7616 trap-nights in 1995, 274 individuals a total of 700 times during 7601 trap-nights in 1996, 597 individuals on 1256 occasions during 7595 trap-nights in 1997, and 419 individuals a total of 778 times during 7589 trap-nights in 1998. Of the 13 grids that were sampled during all four years of the study, red-backed voles were the most abundant species (51–71% of all captures) (Table 2). Red-backed voles represented 56% of

Table 2
Average number of initial captures (S.E.) per live-trap grid (4900 m^2) among five stand types for three species of small mammals during July 1995–1998 in T4 R11 and T5 R11 WELS, northcentral Maine

Species group	Year	Partially harvested mixed ($n = 7$)	Mature mixed ($n = 7$)	Regenerating clearcut		Mature deciduous ($n = 2$)	Mature coniferous ($n = 2$)
				1995–1996 ($n = 7$)	1997–1998 ($n = 2$)		
Red-backed Voles	1995		27.6 (2.5)	11.9 (3.7)		24.5 (5.5)	13.5 (3.5)
	1996		16.3 (2.2)	2.3 (1.0)		8.0 (1.0)	7.5 (2.5)
	1997	22.1 (3.1)	23.0 (2.1)		5.0 (0.1)	14.0 (3.0)	11.5 (1.5)
	1998	12.4 (3.8)	15.4 (2.1)		2.5 (1.5)	2.5 (0.5)	7.0 (4.0)
DeerMice	1995		12.6 (2.4)	11.3 (4.2)		24.0 (2.0)	1.0 (1.0)
	1996		4.7 (0.8)	0.3 (0.2)		3.5 (0.5)	0.5 (0.5)
	1997	12.6 (3.7)	4.9 (1.1)		0.0 (0.0)	10.0 (7.0)	0.0 (0.0)
	1998	4.9 (1.2)	2.7 (0.4)		2.5 (2.5)	2.5 (0.5)	0.0 (0.0)
Short-tailed Shrews	1995		1.4 (0.5)	0.0 (0.0)		4.5 (1.5)	1.0 (1.0)
	1996		0.6 (0.3)	0.0 (0.0)		5.0 (1.0)	0.0 (0.0)
	1997	4.3 (1.4)	1.3 (0.5)		0.0 (0.0)	9.5 (3.5)	0.5 (0.5)
	1998	5.0 (1.6)	4.0 (1.6)		3.0 (1.0)	12.0 (4.0)	3.5 (1.5)

the total small mammals captured, followed by deer mice (22%), masked shrews (12%), short-tailed shrews (9%), and jumping mice (1%).

3.1. Small mammal abundances by stand type

Mature mixed stands had greater abundance of red-backed voles than the other three stand-types that were sampled during each of the 4 years (Table 2). Abundance of voles was greater ($F = 34.55, P \leq 0.001$) in mixed stands than in regenerating clearcut stands during 1995 and 1996 (Tables 2 and 3). Mixed stands also had greater abundance of deer mice than did regenerating clearcut stands during a year of low annual abundance (1996; $U = 49.00, P \leq 0.001$), but there was no difference between the two stand types during the year of highest overall abundance (1995; $U = 30.00, P = 0.48$) (Tables 2 and 3). Our evidence suggested that mature mixed stands may support slightly greater abundances of short-tailed shrews ($\bar{x} = 0.57$ captures per grid) than regenerating clearcut stands (no captures) during 1996 ($U = 35, P = 0.06$);

Table 3
Statistical comparisons (Analysis of Variance or Mann–Whitney U) of July abundance of three species of small mammals between mature mixed and regenerating Clearcut (1995, 1996) stands and between mature mixed and Partially Harv'ested mixed stands (1997, 1998) in T4 R11 and T5 R11 WELS, northcentral Maine

Comparison	Species group	Stand type		Year		Stand type × year	
		Test statistic	P	Test statistic	P	Test statistic	P
Mixed vs. Clearcut	Red-backed voles	$F = 34.55$	≤ 0.001	$F = 17.02$	≤ 0.001	$F = 0.12$	0.74
	Deer Mice[a]	$U = 30$ (1995), $U = 49$ (1996)	0.48 (1995), ≤ 0.001 (1996)	$U = 169.00$	≤ 0.001		
	Short-tailed shrews[a]	$U = 42$ (1995), $U = 35$ (1996)	0.01 (1995), 0.06 (1996)	$U = 114.50$	0.34		
Mixed vs. Partial harvest	Red-backed voles	$F = 0.45$	0.51	$F = 9.03$	0.01	$F = 0.14$	0.71
	Deer mice[b]	$F = 6.62$	0.02	$F = 7.15$	0.01	$F = 1.33$	0.26
	Short-tailed shrews	$F = 2.13$	0.16	$F = 1.57$	0.22	$F = 0.53$	0.47

[a] Mann–Whitney test (data transformations would not result in normality).
[b] Square root transformation.

however, our result is equivocal given potential for type II error. Abundances were also greater in mixed stands during 1995 $(U=42, P=0.01)$ (Tables 2 and 3).

Regenerating clearcuts had the lowest abundance of deer mice during 1996, and no deer mice were captured in the two clearcut stands sampled during 1997 (Table 2). Clearcut stands also had the lowest abundance of short-tailed shrews during both 1997 and 1998 (Table 2). No shrews were captured in clearcut stands during 1995–1997, and only six were captured during 1998. Abundance of voles was lowest in clearcut stands during all four years of the study.

Partially harvested mixed and mature mixed stands had similar abundances of red-backed voles $(F = 0.45, P = 0.51)$ and short-tailed shrews $(F = 2.13, P = 0.16)$ during 1997 and 1998 (Tables 2 and 3). However, partially harvested stands had greater abundance of deer mice $(F = 6.62, P = 0.02)$ than mature mixed stands, and mean numbers captured in partially harvested stands exceeded the values observed in all other stand types during both 1997 and 1998 (Tables 2 and 3).

Mature deciduous stands had the greatest abundance of short-tailed shrews during all four summers (Table 2). Deciduous stands maintained high abundances of deer mice during all 4 years, and had the greatest abundance of deer mice of all stand types during 1995 (Table 2). Deciduous stands had intermediate abundances of red-backed voles (Table 2).

Mature coniferous stands had the lowest abundance of deer mice during 1997–1998 (no captures), and low abundance of short-tailed shrews during 1995–1997 (Table 2). Coniferous stands ranked last or second to last in abundance of voles, mice, and shrews during all years except 1998 (Table 2).

3.2. Structural differences

Eleven of the original 21 within-stand variables (Table 4) did not differ $(P > 0.10)$ between mature mixed and partially harvested mixed stands; 10 significant variables (Table 5) were retained for analysis using Hotelling's multivariate T^2 test. The T^2 test suggested that at least one of the within-stand variables differed between the two overstory types (Wilk's Lambda $= 0.03, F = 9.57,\ 10,\ 3$ d.f., $P = 0.04$) (Table 5). Post-hoc univariate F-tests indicated that overhead canopy closure, density of coniferous trees, density of coniferous saplings, basal area of deciduous trees, and basal area of snags were greater (Bonferroni-adjusted $\alpha = 0.01$) in mature mixed than in partially harvested mixed stands (Table 5). There were no differences in coarse woody debris values including volume of stumps, density of snags, or in understory lateral foliage density between mature mixed and partially harvested mixed stands.

Partially harvested mixed stands had greater canopy closure (Fig. 1c), basal area of live coniferous and deciduous trees (Table 4) and snags (Fig. 1d), and density of coniferous trees and seedlings (Fig. 1a) than observed in regenerating clearcuts. However, understory lateral foliage density was similar between partially harvested and clearcut stands (Fig. 1c). Coarse woody debris variables including density of logs and root masses were similar between partially harvested and clearcut stands (Fig. 1b). Partially harvested stands had the lowest density of coniferous saplings and percent live ground cover compared to all other stands (Table 4). Partially harvested stands had a high volume of stumps; only regenerating clearcut stands had comparable volumes (Table 4). Average diameter of trees in partially harvested mixed stands was similar to diameters observed in mature mixed and mature deciduous stands, and was larger than diameters observed in mature coniferous stands (Table 4). Mature deciduous, coniferous, and mixed stands all had canopy closure >80% during the summer, and live-tree basal areas >30 m^2/ha, while partially harvested stands averaged only 64% canopy closure and 15 m^2/ha live-tree basal area.

Mature mixed stands had lower density of stumps than regenerating clearcut stands, but had similar densities of logs and root masses (Fig. 1b). Mixed stands also had lower values for understory lateral foliage density (Fig. 1c) and density of deciduous seedlings than regenerating clearcuts (Fig. 1a). Density of deciduous and coniferous trees and snags and canopy closure were all greater in mixed stands than in clearcuts (Table 4). Mixed stands had the greatest volume of down logs and density of deciduous trees of all overstory types (Table 4).

Regenerating clearcut stands ranked first in density of stumps, understory lateral foliage density, density of coniferous saplings, total density of coarse woody

Table 4
Mean values (range) for overstory, understory, and coarse woody debris variables observed during summer within 25 stands distributed among five stand types in T4 R11 and T5 R11 WELS, northcentral Maine, 1995–1998

Variable	Mature mixed ($n = 7$)	Partially harvested mixed ($n = 7$)	Mature deciduous ($n = 2$)	Mature coniferous ($n = 2$)	Regenerating clearcut ($n = 7$)
Density of down logs (#/ha)	2638 (1625–3688)	2674 (1563–4656)	1297 (1156–1438)	1078 (625–1531)	2571 (1188–4844)
Volume of down logs (m^3/ha)	98 (51–168)	80 (47–148)	59 (54–64)	38 (11–65)	55 (38–74)
Density of stumps (#/ha)	652 (313–1000)	674 (500–1031)	406 (344–469)	563 (531–594)	1326 (875–1813)
Volume of stumps (m^3/ha)	9.2 (2.6–16.0)	15.8 (9.3–24.3)	9.0 (6.3–11.8)	5.3 (3.5–7.3)	15.7 (10.4–23.7)
DBH[a] (cm)	19.8 (16.9–24.7)	19.2 (16.7–24.9)	20.4 (20.0–20.7)	15.4 (12.4–18.3)	2.2 (1.0–8.9)
Litter depth (cm)	3.0 (2.3–4.0)	3.1 (1.8–4.4)	3.6 (2.3–5.0)	0.6 (0.4–0.8)	2.9 (1.1–11.8)
Overhead canopy closure (%)	88 (85–92)	71 (55–82)	93 (91–94)	84 (80–89)	24 (2–71)
Understory lateral foliage density[b] (%)	42 (6–70)	62 (24–90)	60 (44–76)	32 (26–38)	70 (27–97)
Density of deciduous trees[c] (#/ha)	674 (500–1000)	424 (125–969)	641 (594–688)	16 (0–31)	0 (0–0)
Density of coniferous trees[c] (#/ha)	732 (500–1188)	250 (0–469)	297 (219–375)	1969 (1500–2438)	228 (0–1594)
Density of snags[d] (#/ha)	299 (156–438)	174 (31–250)	188 (188–188)	328 (156–500)	45 (0–281)
Density of deciduous saplings (#/ha) (0.5–1.5 m height)	7460 (875–9406)	3621 (63–13938)	15109 (14156–16062)	141 (31–250)	4406 (63–8000)
Density of coniferous saplings (#/ha) (0.5–1.5 m height)	1875 (1031–3438)	469 (0–1844)	1422 (719–2125)	3297 (1187–5406)	6808 (1813–17719)
Density of herbaceous seedlings (<0.5 m height) (#/ha)	27384 (7157–82719)	35522 (16031–50063)	22875 (15625–30125)	15125 (8094–22157)	56821 (39156–84313)
Density of woody seedlings (<0.5 m height) (#/ha)	38174 (15219–65406)	39938 (18500–59375)	52688 (46844–58531)	19297 (8813–39781)	22813 (11031–42750)
Basal area of live deciduous trees[c] (m^2/ha)	16.2 (11.4–26.5)	6.6 (4.2–9.6)	25.1 (24.1–26.1)	0.13 (0.0–0.30)	0.52 (0.0–1.5)
Basal area of live coniferous trees[c] (m^2/ha)	14.4 (7.0–26.8)	6.2 (3.3–13.4)	4.2 (3.8–4.6)	38.3 (31.8–44.9)	2.9 (0.6–7.8)
Basal area of snags[d] (m^2/ha)	3.9 (1.6–6.1)	1.8 (0.8–3.1)	1.6 (1.1–2.1)	4.9 (0.6–9.3)	0.23 (0.0–1.3)
Live ground cover (%)	17.7 (8.4–24.0)	17.6 (2.8–35.7)	34.2 (30.6–37.8)	84.4 (77.5–91.3)	50.7 (29.7–83.8)
Density of rootmasses (#/ha)	147 (31–219)	295 (0–813)	109 (94–125)	63 (31–94)	245 (31–500)
Total CWD density[e] (#/ha)	3732 (2500–5031)	3670 (2500–5031)	2000 (1781–2219)	2031 (1406–2656)	4188 (2594–6656)

[a] Average diameter (cm) at breast height of closest tree ($\geq$2 m height, $\geq$7.6 cm dbh, alive) in each quarter.
[b] Average of measures of visual obscurity in each of four height classes (0–0.5, 0.5–1, 1–1.5 and 1.5–2 m).
[c] Trees were defined as live stems $\geq$2 m height, $\geq$7.6 cm dbh.
[d] Snags were defined as dead stems $\geq$2 m height, $\geq$7.6 cm dbh.
[e] Number of snags + logs + stumps + root masses.

Table 5
Comparison (significant differences are depicted in italics) of within-stand habitat attributes sampled during summer between mature mixed ($n = 7$) and partially harvested mixed ($n = 7$) stands in T4 R11 and T5 R11 WELS, northcentral Maine

Variable	*F*	*P*[a]
Wilk's Lambda Multivariate *t*	9.57	0.04[b]
Overhead canopy closure (%)	22.57	*<0.001*
Density of coniferous trees (≥7.6 cm dbh, ≥2 m height) (#/ha)	14.41	*<0.001*
Density of coniferous saplings (0.5–1.5 m height, <7.6 cm dbh) (#/ha)	11.86	*<0.001*
Basal area of deciduous trees (≥7.6 cm dbh, ≥2 m height) (m^2/ha)	19.99	*<0.001*
Basal area of snags (≥7.6 cm dbh, ≥2 m height) (m^2/ha)	13.72	*<0.001*
Basal area of coniferous trees (≥7.6 cm dbh, ≥2 m height) (m^2/ha)	7.68	0.02
Volume of stumps (m^3/ha)	5.81	0.03
Density of deciduous trees (≥7.6 cm dbh, ≥2 m height) (#/ha)	3.88	0.07
Density of snags (≥7.6 cm dbh, ≥2 m height) (#/ha)[c]	4.96	0.05
Understory lateral foliage density (%)[d]	3.45	0.09

[a] *P*-value from univariate *F*-test, Bonferroni-adjusted $\alpha = 0.10/k = 0.01$.
[b] Wilk's Lambda *P*.
[c] Square root transformation used for statistical comparisons.
[d] Average of measures of visual obscurity in each of four height classes (0–0.5, 0.5–1, 1–1.5 and 1.5–2 m).

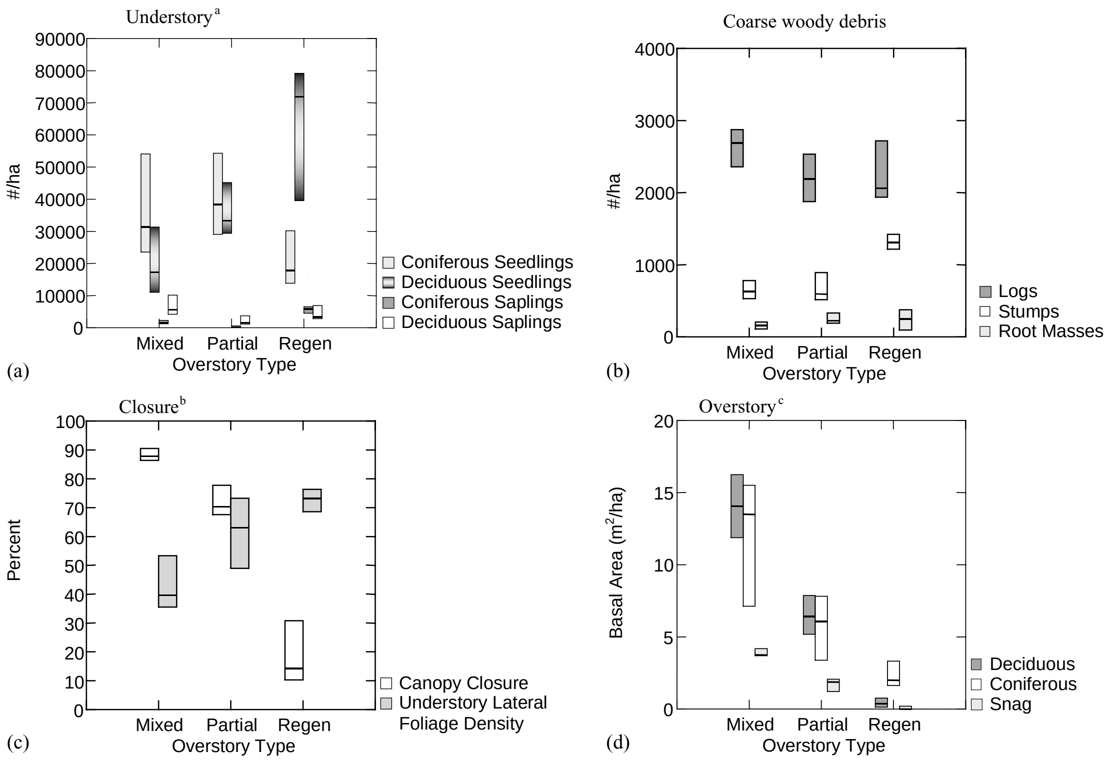

Fig. 1. Box plot indicating median values for understory, coarse woody debris, closure, and overstory variables measured on small mammal trap grids, T4 R11 and T5 R11, northcentral Maine. Horizontal line marks the median and boxes indicate the first and third quantiles. Superscripts: (a) Seedlings <0.5 m height, <7.6 cm dbh; Saplings 0.5–1.5 m height, <7.6 cm dbh. (b) Canopy closure (%), Understory lateral foliage density = average of measures of visual obscurity in each of four height classes (0–0.5, 0.5–1, 1–1.5 and 1.5–2 m). (c) Basal area of trees or snags ≥7.6 cm dbh, ≥2 m height.

debris, and density of root masses and logs (1997–1998 only) (Table 4). Regenerating clearcut stands had the lowest values for overhead canopy closure, density of deciduous and coniferous trees, density of snags, and basal area of snags and coniferous trees (Table 4).

Mature coniferous stands ranked lowest in density and volume of logs, volume of stumps, litter depth, understory lateral foliage density, density of herbaceous and woody seedlings, density of deciduous saplings, basal area of deciduous trees, and density of root masses, and ranked highest in percent live ground cover and density and basal area of snags and coniferous trees (Table 4).

Mature deciduous stands had the greatest litter depth, overhead canopy closure, density of deciduous saplings, density of woody seedlings, and basal area of live deciduous trees of all overstory types (Table 4). Deciduous stands ranked last in density of stumps and total density of coarse woody debris (Table 4).

4. Discussion

Despite reduced overhead canopy closure, density of coniferous trees and saplings, and basal area of snags and deciduous trees, partial harvesting did not reduce habitat quality for deer mice, red-backed voles, or short-tailed shrews relative to mature mixed-forest types. Monthey and Soutiere (1985) suggested that densities of small mammals may be greater in partially harvested stands than in uncut stands because of the positive effects of harvesting such as increased shelter created by logging residue, increased availability of tree seeds, and increased invertebrate prey populations. Total density of coarse woody debris was similar between mature mixed and partially harvested mixed stands, which likely provided small mammals with sufficient cover, travel routes, and substrate for fungal growth within the harvested stands. The reduced canopy closure in partially harvested stands promoted abundant understory vegetation, which probably benefited voles, mice, and shrews by providing more cover than is provided solely by coarse woody debris.

Abundance of short-tailed shrews in partially harvested mixed stands was >3 times greater than in mature mixed stands during 1997, but when shrew abundance increased in all overstory types during 1998, abundances were similar between the two stand types. Thus, partially harvested mixed stands may provide more consistent habitat features for shrews than mature mixed stands. Understory lateral foliage density was 20% greater in partially harvested stands than in mature mixed stands, which may have provided a moister microclimate for shrews.

Deer mice are considered habitat generalists (Dueser and Hallett, 1980); structural changes caused by partial harvesting did not reduce abundance of mice relative to mature mixed stands. In contrast to Vickery's (1981) finding that deer mice in Quebec were most common in stands with heavy ground cover (<2 m height) and mid-story cover, deer mice on our study area were most common in partially harvested stands. Those partially harvested stands had the least amount of live ground cover, and only moderate levels of sapling density. Apparently, abundant coarse woody debris and understory lateral foliage density can provide adequate structure for deer mice in stands (e.g., partially harvested stands) with low availability of live ground cover.

Density of red-backed voles has been positively correlated with coarse woody debris (Bowman et al., 2000), which provides travel corridors, shelter (Nordyke and Buskirk, 1991), and promotes growth of fungi, an important source of water and nutrients (Getz, 1968; Maser et al., 1978). We observed that abundant coarse woody debris and vertical and horizontal structure were associated with similar densities of voles in both partially harvested and mature mixed stands. Further, reproductive performance of voles (percent of captured females lactating) did not differ between partially harvested and mature mixed stands on our site (Fuller, 1999). Presence of red-backed voles in Maine was positively associated with density of logs (Lachowski, 1997), and logs were abundant in both our partially harvested and mature mixed stands. Finally, both mature mixed and partially harvested mixed stands had dense seedlings <0.5 m in height, which may provide voles with protection from predators (Monthey and Soutiere, 1985), as well as a humid microenvironment (Miller and Getz, 1977). Although mature and over-mature stands have been reported as supporting the greatest densities of red-backed voles (Nordyke and Buskirk, 1991), we conclude that partial harvesting in mixed coniferous–

deciduous stands does not reduce habitat quality for red-backed voles in eastern North America.

Our data do not support studies that report a positive relationship between clearcutting and abundance of small mammals (e.g., Kirkland, 1977, 1990; Martell, 1983; Monthey and Soutiere, 1985). Regenerating clearcut stands ranked lowest in abundance of red-backed voles, the most abundant species of small mammal on our study area. In contrast, Monthey and Soutiere (1985) documented that red-backed vole densities were greater in 9–18-year-old clearcuts than in partially harvested and uncut stands. Recovery of red-backed vole numbers after clearcutting has been postulated to occur from 1 to 3 years (Martell, 1983; Kirkland, 1990) and 9–30 years (Monthey and Soutiere, 1985; Mills, 1995) post-harvest; however, our 11–20-year-old clearcuts still did not provide quality habitat for voles relative to other stand types.

Kirkland (1990) suggested that small mammals respond positively to clearcutting because recently harvested sites have increased amount of herbaceous understory foliage. Our older clearcut stands had 60% greater density of herbaceous seedlings and had similar understory lateral foliage density compared to partially harvested stands; however, those clearcut stands maintained significantly lower densities of small mammals during our study.

Bowman et al. (2000) reported a positive relationship between red-backed vole density and coarse woody debris, but in another experimental study, presence of coarse woody debris in clearcut stands did not increase abundance of small mammals (Moses and Boutin, 2001). Similarly, abundant coarse woody debris in our clearcut stands also did not numerically benefit small mammals relative to the other four stand types, which had similar or lower volumes of coarse woody debris. We conclude that coarse woody debris is important for red-backed voles, but is not necessarily limiting in managed and unmanaged stands within the mesic Acadian forest.

Regenerating clearcuts on our study area did not provide adequate habitat for shrews. Short-tailed shrews have been documented to be absent from areas with low availability of food (Getz, 1961), and clearcutting has been documented to reduce arthropod abundance and diversity, in part, because of extreme moisture and temperature ranges (Vlug and Borden, 1973; Abbott et al., 1980; Blair and Crossley, 1988). Lower densities of arthropod prey could have reduced abundances of shrews in our 11–20-year-old clearcut stands.

Mature coniferous stands also had low abundance of short-tailed shrews. Shrews are active within the leaf litter, and our coniferous stands had the lowest litter depth of all stand types. Miller and Getz (1977) suggest that the compacted litter layer in coniferous stands prohibits shrews from moving easily under it, which may have resulted in reduced abundances on our study area. Additionally, short-tailed shrews are often associated with stands with dense herbaceous vegetation (Miller and Getz, 1977; Healy and Brooks, 1988; Kirkland, 1990), possibly because of the relationship between insect density and vegetation structure and diversity (Murdoch et al., 1972; Marques et al., 2000). Our coniferous stands had the lowest density of herbaceous seedlings (<0.5 m height) of all stand types. Thus, the combination of minimal leaf litter, few herbaceous seedlings, and potentially lower insect density and diversity probably created unfavorable conditions for short-tailed shrews in the coniferous stands on our study area.

Voles are often classified as residents of coniferous forest (Clough, 1987; Nordyke and Buskirk, 1991). However, we observed greater (>2 times) abundance of red-backed voles in mixed stands compared to coniferous stands. Abundance of voles did not differ among coniferous, deciduous, mixed, or open habitats in northwestern Maine (Richens, 1974), or among northern hardwoods, red maple, balsam fir, and red spruce–balsam fir overstory types in New Hampshire (DeGraaf et al., 1991). Although voles require humid microenvironments (Miller and Getz, 1977), they also require understory cover for protection from predators (Nordyke and Buskirk, 1991). Understory density was low (32%) in our coniferous stands, and may have contributed to the low abundance of voles. Thus, in the mixed forests of eastern North America, voles appear to be more generalist in habitat requirements and may reach their highest densities in mature mixed and partially harvested mixed stands. The mature coniferous stands on our study site were associated with poorly drained soils and supported low volumes of coarse woody debris and few seedlings <0.5 m in height. Better-drained soils typically supported mixed or deciduous stands. However, conifer stands occurring on higher quality sites (e.g., mixed stands treated with herbicides to reduce competing hardwoods) might support higher densities of voles.

Deciduous stands had the greatest abundance of short-tailed shrews and were the most stable habitat for shrews; population fluctuations were low in this habitat. Shrews require moist microenvironments to prevent water loss (Chew, 1951; Getz, 1961), and abundances have been positively correlated with dense ground vegetation and leaf litter (Miller and Getz, 1977; Kitchings and Levy, 1981; Adler, 1985), which was greatest in deciduous stands. Preference for deciduous stands over coniferous stands is well-documented in shrews (Richens, 1974; Monthey and Soutiere, 1985; DeGraaf et al., 1991), and moisture is the most important factor limiting their distribution (Getz, 1961). Deciduous stands with deep leaf litter probably provided increased soil moisture and increased the humidity, so that shrews were able to avoid desiccation, and contributed to the elevated densities that we documented.

5. Conclusions and management implications

Partially harvested mixed stands on our study area maintained summer densities of small mammals similar to mature mixed stands, and thus provided suitable habitat including structural features for mice, voles, and shrews. Our partially harvested stands retained some characteristics of mature stands, which likely benefited small mammals. The reduced overstory canopy in partially harvested stands promoted understory vegetation while maintaining many structural characteristics of mature forests. Retaining some large conifer seed-source trees that are old enough to produce abundant and reliable seed would be beneficial in increasing conifer regeneration (Smith et al., 1997). Damage to advance seedlings can be minimized by leaving residues on site to minimize damage and to provide nutrients and microhabitats for small mammals. Forest practices may be able to enhance the use of clearcut stands by small mammals by imitating structural characteristics found in partially harvested and mature stand types. On-site delimbing, slash management, and retention of scattered large trees and snags may increase structural complexity within clearcut stands and may functionally approach characteristics of partially harvested stands.

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