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Legacy Retention Versus Thinning: Influences on Small Mammals

Abstract

Management strategies for promoting late-seral attributes in second-growth forest need evaluation for their efficacy in maintaining biodiversity, including complete forest-floor, small-mammal communities. Two common strategies in the Pacific Northwest are (1) management with thinnings to promote large trees with developed understories and (2) retention of legacies, defined as live trees, logs, and snags from the preceding forest, at harvest, followed by protection but not thinnings of the new stand. We compared small-mammal communities resulting from >65 yr of application of these strategies in the Puget Trough, Washington. We also compared these communities with the small-mammal communities found in old-growth, naturally young, and extensively managed forests elsewhere in western Washington. Forests managed with thinnings had 1.5 times the individual mammals and 1.7 times the mammal biomass of forests managed with legacies of coarse woody debris and snags—differences similar to those between old-growth and naturally young forest (1.2 times more individuals in old-growth) and old-growth and extensively managed forest (1.6 times more individuals in old-growth). Management strategy had a profound impact on community structure, with the Columbian mouse (*Peromyscus oreas*), the small mammal most associated with old growth, much reduced in Puget Trough forests (absent from most stands) and the creeping vole (*Microtus oregoni*) (a species commonly associated with early seral stages, but found in all seral stages in Washington) third-ranked in thinned stands but seventh ranked in legacy stands. The montane shrew (*Sorex monticolus*) was second-ranked, after Trowbridge's shrew (*S. trowbridgii*), in marked contrast to codominance by the southern red-backed vole (*Clethrionomys gapperi*), *S. monticolus*, and *P. oreas* in old growth. Thus, neither strategy produced communities typical of late-seral forests.

Introduction

Harvest of Pacific Northwest old growth has raised questions concerning the ability of younger, managed stands to adequately sustain wildlife diversity and abundance (Meslow et al. 1981; Carey 1989; Thomas 1991; Carey et al. 1992). Ecologists warned decades ago that harvest-regenerated, densely stocked, unthinned, coniferous forests and forests lacking snags and coarse woody debris were detrimental to small-mammal populations (Hamilton and Cook 1940). Clearcutting in the Pacific Northwest created extensive tracts of forest with various levels of these conditions. Second-growth stands often have few old, large, snags, logs, and trees (hereafter referred to collectively as legacies), reduced vertical and horizontal heterogeneity in vegetation structure, and diminished ecological function (Carey et al. 1996*b*).

The rate of clearcutting in the Pacific Northwest has slowed during the past decade (McGinnis et al. 1997), and new forestry techniques presumed to have fewer esthetic and ecological drawbacks have emerged (Franklin 1989; Hansen et al. 1995; Carey et al. 1996*a*; Curtis and Carey 1996). Two of the most commonly recommended (and potentially opposing) alternatives for managing Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests are multiple thinnings and legacy retention (snags, logs, live trees) at harvest (Franklin et al. 1981; Carey and Curtis 1996; Carey et al. 1996*a*; Hayes et al. 1997; Tappeiner et al. 1997). Management by thinning combines multiple commercial thinnings with long rotations to produce stands with large contemporary trees and developed understories. As these stands mature, they are hypothesized to develop the functions and processes of late-seral forest (Weigand et al. 1993) and accrue commercial value as timber (Perry 1998). Legacy retention emphasizes retaining biologically significant structures (logs, snags, live trees) and intact patches of forest floor at final harvest to provide structures and sources for colonization of the new stand by organisms of limited mobility. Harvest under legacy management systems leaves standing trees—both healthy and decadent, in patches or singly—up to 30% of the stand basal area although standard guidelines have not been set (Franklin et al. 1997). Thinning is precluded under this management strategy. The resulting closed-canopy stands inoculated with snags, logs, and older trees are hypothesized to foster biodiversity similar to a late-seral forest

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(Hopwood 1991; Franklin 1993; Franklin et al. 1997). Both of these strategies have been suggested in forest management literature and in habitat conservation plans (e.g., FEMAT 1993). However, the long-term ecological effects of these techniques are virtually unknown.

We compared small-mammal communities resulting from 65 years of application of the two strategies to second-growth stands in the Puget Trough of Washington. First, we examined small-mammal abundances. Because small mammals are generally more abundant in old growth than in extensively managed second growth (Carey and Johnson 1995), we were interested in the relative potential of thinning versus retention of old, large, snags, logs, and live trees to produce abundances of small-mammals in second growth. Only species with niche dimensions (Carey 1981; Carey et al. 1999*a*) affected by thinning or legacy retention would be expected to be influenced by the two management strategies. We hypothesized that the shrew-mole (*Neurotrichus gibbsii*) and Trowbridge's shrew (*Sorex trowbridgii*) would be more numerous under legacy management and its concomitant retention of coarse woody debris, and that deer mice (*Peromyscus maniculatus*) and creeping voles (*Microtus oregoni*) would be more abundant under thinning management and its resulting understory development (Carey and Johnson 1995). Of particular interest was the Columbian mouse (*P. oreas*), a species tied to old growth (West 1991; Carey and Johnson 1995; Songer et al. 1997). The Columbian mouse seems associated with tall understory and, perhaps, shade-tolerant midstories; we expected this mouse to be more abundant in the thinned forest. Although the mycophagous southern red-backed vole (*Clethrionomys gapperi*) is positively correlated with both coarse woody debris and shrubs (Carey and Johnson 1995), we expected higher abundances under legacy management because of the fungal-food resources associated with coarse woody debris (Maser et al. 1978). In addition to examining abundances, we calculated reproductive statistics to ensure we did not confound abundances with variation in population demographics (Van Horne 1983).

Second, we compared diversity and community structure (species rank abundances) under thinning and legacy management to diversity and structure in old-growth, naturally young, and extensively managed forests in the adjacent physiographic provinces (Olympic Peninsula and southern Washington Cascades)–no data on small mammals in old-growth or naturally young forests in the Puget Trough were available. We used these comparisons to evaluate the likelihood that either active management strategy would produce complete communities with abundant small mammals.

Methods

Study Area

Our study sites were on the Fort Lewis Military Reservation, 30 km northeast of Olympia in Thurston County, Puget Trough Physiographic Province, Washington (Franklin and Dyrness 1973). Due to its extensive forest cover and strategic location between the large federal land holdings on the Olympic Peninsula and in the Cascade Range, Fort Lewis was named a Designated Conservation Area for the Northern Spotted Owl (Lujan et al. 1992). The area is composed of about 6,000 ha of second-growth Douglas-fir stands with various management histories. Large tracts of homogeneous stands and the U.S. Army's desire to reconcile land management objectives for timber with conservation of threatened species made the area ideal for comparing forests of differing management histories (Carey et al. 1999*b*).

We had four study sites. Two sites were managed by thinning and two were managed by legacy retention without thinning. Each site had four stands. We randomly selected two stands per site. Stands were separated by a minimum of 200 m within study sites and we considered stands independent because the number of forest-floor small-mammal movements between stands was negligible. All study sites were seed-regenerated after clearcutting and dominated by second-growth Douglas-fir. Trees were fewer and larger, understory more abundant, and coarse woody debris less in thinned stands than in legacy stands (Carey et al. 1999*b*).

Thinned sites were clearcut ~1927 and thinned 45 years and 62 years after clearcutting. Commercial thinning operations removed subordinate, merchantable live, dead, and diseased trees, and salvageable fallen trees. Each thinning removed 17.5 - 33.8 m^3/ha. Few snags and scant coarse woody debris remained. Thinning produced large (52-cm dbh) Douglas-fir, a low shrub layer typified by salal (*Gaultheria shallon* Pursh), and a patchy herbaceous layer. Stand condition resembled the understory reinitiation stage described by Carey and Curtis (1996).

Sites managed with legacy retention were clearcut ~1937, and numerous large trees, snags, logs, and stumps were left on site following harvest. The stand was left to reestablish and grow naturally resulting in heavy stocking with small-diameter Douglas-fir. The forest floor had moderate accumulations of dead, small-diameter trees from the current cohort of trees and large coarse woody debris from the original old-growth forest. Shrub height was low (<0.5 m) and moss was more extensive than herbaceous ground cover. Later (ca. 1981), a small number of standing legacy trees that projected above the canopy and were deemed a hazard to military aircraft were felled and left on the forest floor. Stand development closely resembled the competitive-exclusion stage (Carey and Curtis 1996).

Sampling Procedures

In each stand we established a 10 x 10 trapping grid with 20-m spacing between grid points. Each trapping grid encompassed 4 ha. We visually estimated cover of down wood and low vegetation on 4-m-radius plots (50-m^2) centered on grid points (n = 100 plots per stand). We estimated percent cover for small woody debris 5-15 cm in diameter; coarse woody debris > 15 cm in diameter; herbs, including ferns; and shrubs; and shrub height <2 m. Plots encompassed 13% of each grid. Additional sampling included 15 variable-radius prism plots (basal area factor 30 English) to determine tree dbh for each grid (Carey et al. 1999*b*).

Two Sherman live traps (Sherman Co., Tallahassee, Fl.), one large (7.6 cm x 8.9 cm x 22.9 cm) and one small (5.1 cm x 6.4 cm x 16.5 cm), were placed at least 1 m apart within 2 m of each grid point. Traps were checked and treadle tension was adjusted daily to ensure that traps operated freely and could capture even the lightest insectivores (<4 g). Traps were baited with a mixture of peanut butter, whole oats, and molasses. Polyester batting was placed in each trap to provide thermal insulation and bedding material for trapped animals. We recorded species, age, sex, reproductive status, weight (g), and capture status (new capture or recapture) for each captured mammal. We recorded all sprung traps. A single Monel eartag (National Band and Tag Co.) was attached to the right ear of mice, voles, and squirrels. Insectivores were not marked because most died as a result of trapping. We used tail length to distinguish between species of *Peromyscus*. *Peromyscus* with tails >96 mm were designated as Columbian mice, and shorter-tailed animals were designated as deer mice (Allard et al. 1987). Classification of mice and voles as adult or young was based on weight and external criteria indicative of reproductive condition (McCravy and Rose 1992). Mice and voles in breeding condition or showing signs of past breeding were classified as adults. Otherwise, deer mice that had not attained the brownish pelage of adults, and deer mice and voles < 15 g, were considered to be young of the year. Each animal that died was collected for necropsy to confirm species, sex, and reproductive status. Morphology of the median tine (Carraway 1995), tail length, and pelage characteristics were used to identify shrew species. Shrew age (adult or young) was determined by the amount of tooth wear on incisors and unicuspids (Rudd 1955; Hawes 1977). Where necropsy samples allowed, mean litter size was determined by species for each management strategy. Taxonomy and nomenclature follow Jones et al. (1992).

All grids were trapped for forest-floor small mammals during three consecutive summers (1992-1994). Repeated sampling was undertaken because we expected significant interannual fluctuations in mammal populations. We selected summer trapping (mid-July to mid-August) to coincide with peak numbers of forest-floor small mammals and to allow data collection on multiple age and breeding classes. We trapped small mammals in two consecutive trapping sessions of eight nights each; one-half the stands under each management strategy were trapped in each session.

Data Analysis

We calculated descriptive statistics to determine the need for transformations and appropriateness of parametric tests. Summary statistics of means and standard errors are reported. The biological significance of test results was evaluated when statistical significance was $P \leq 0.05$. We used arcsine square root transformations for habitat variables (except dbh) and performed t-tests using four samples per management strategy (Bonham 1989; Carey and Johnson 1995). The forest-floor small-mammal community was defined as the assemblage of mice (*Peromyscus maniculatus* and *oreas*), voles (*Clethrionomys gapperi* and *Microtus oregoni*), shrews (*Sorex trowbridgii, S. monticolus, S. vagrans*), and shrew-moles (*Neurotrichus gibbsii*) that normally occur on upland sites and that we caught regularly in our traps. We excluded the marsh shrew (*S. bendirii*) because it is primarily associated with damp areas (Ingles 1965) and the Pacific jumping mouse (*Zapus trinotatus* Rhoads) because it is associated with meadows (Ingles 1965) and riparian areas (Doyle 1985). Moles (*Scapanus spp.*) were excluded because they were not routinely captured by our traps.

The sampling unit was the stand, and the primary response variable was animal abundance by species by year. We assumed that probability of capture was equal between management strategies. For each species we calculated total individuals captured per 100 trap nights (CPU) corrected for traps sprung by any cause (Nelson and Clarke 1973; Carey et al. 1999*a*). We used a transformed measure [ln (CPU + 1)] to compare species abundances (Carey and Johnson 1995) between management strategies and among years with a simple factorial ANOVA with a year x management strategy interaction (Norušis 1993). One could argue repeated-measures ANOVA was appropriate here; we conducted such an analysis and found comparable results. Tukey's honestly significant difference test was used for post hoc multiple comparisons among years (SPSS 1997). We also plotted mean annual CPU for each species by management strategy. We then inspected plots for synchrony in annual fluctuations (Boonstra et al. 1998) among species and between management strategies.

Because density has been questioned as an appropriate indicator of habitat quality (Van Horne 1983), we determined demographic statistics for each population based on sex ratio, age ratio, and the proportion of the population composed of reproductive females. We used these vital rates to determine if we were dealing with source populations which are self replacing and sink populations which are receptacles of the surplus from nearby sources. We counted females showing signs of lactation, pregnancy, or estrus to determine the proportion of the population composed of reproductively active females. Mann-Whitney U tests were used to determine if there were significant rank differences in species age ratio, sex ratio, or proportion of the population composed of reproductive females between thinned and legacy treatments. For each species, we multiplied number of individuals caught (Krebs 1966) by mean body-mass and used a Mann-Whitney U test to determine if there were significant differences in biomass between management strategies.

To compare small-mammal community diversity—species richness and evenness—between management strategies and across the three years of our study, we used the Shannon index. We calculated an index value for each stand by year ($n = 24$), then found the mean index value for each of our eight stands. We used the eight Shannon index values, four per management strategy, in a t-test (Magurran 1988).

Inter-regional Comparisons

We compared small-mammal community structure on our sites to those found in old-growth and young forests on the Olympic Peninsula and the southern Washington Cascades. The effect of stand conditions on species abundances were not directly comparable between regions due to differences in trapping methods and significant interannual variation in animal abundances. However, the index of abundance (CPU) based on individual captures and relative frequencies served as corrective factors allowing us to generate regional small-mammal community structures by ranking adequately sampled species by abundance (Carey et al. 1991, Carey and Johnson 1995). In Puget Trough forests, CPUs were derived as stated above. In the southern Washington Cascades, CPU was derived by taking the mean of two years' (1984 -1985) combined snap trap and pitfall trap data presented by West (1991). Olympic Peninsula CPUs were taken directly from snap trap data, 1987 -1989, presented by Carey and Johnson (1995).

Results

Habitat Attributes of Management Strategies

Commercially thinned stands had trees with significantly larger diameters ($t = -15.50$, $df = 6$, $P < 0.001$) and significantly taller shrubs ($t = -4.10$, $df = 6$, $P = 0.006$) than legacy stands (Table 1). Herb cover ($t = -2.35$, $df = 6$, $P = 0.057$) and shrub volume ($t = -2.36$, $df = 6$, $P = 0.056$) were marginally greater under the thinning management

TABLE 1. Mean, range, and 95% confidence interval (CI) of habitat values for stands managed by retaining logs, snags, and residual trees from the previous stand and stands managed by thinning in the Puget Trough, Washington, 1992-1994.

	Legacy stands n = 4			Thinned stands n = 4		
Habitat feature[1]	Mean	Range	CI	Mean	Range	CI
Dbh trees (cm)	35	29-37	29-42	52	48-60	43-61
SWD (%)[2]	3	2-5	1-5	1	<1-2	0-2
CWD (%)[3]	6	5-9	3-10	1	<1-2	1-2
Herb cover (%)	4	2-7	1-7	10	5-16	2-18
Shrub cover (%)	16	12-20	10-21	21	13-27	10-32
Shrub height (%)[4]	23	20-26	19-27	32	28-36	26-37

[1] Stand values based on 100 sampling points per stand.

[2] Forest floor small woody debris <15 (cm) and > 5 (cm) in diameter.

[3] Forest floor coarse woody debris >15 (cm) in diameter.

[4] Shrub height expressed as % of 2 m.

strategy. However, mean shrub cover did not differ significantly ($t = -1.28$, $df = 6$, $P = 0.249$) between management strategies. Legacy stands had a significantly greater cover of coarse woody debris ($t = 5.41$, $df = 6$, $P = 0.002$) and small woody debris ($t = 3.70$, $df = 6$, $P = 0.010$) than thinned stands.

Mammal Abundance and Distribution

We caught 4,280 individual small mammals of 16 species (Table 2). Six species, Trowbridge's shrew, montane shrew (*S. monticolus*), southern red-backed vole, deer mouse, creeping vole, and shrew-mole accounted for 94% of total individuals trapped, and each of these species composed at least 3% of the individual small mammals trapped per management strategy. Trowbridge's shrew was the most numerous species under both strategies and occurred in every stand every year, as did montane shrews, red-backed voles, and deer mice. We caught 1.4 times as many individual small mammals in thinned stands as in legacy stands (Table 2). Contrary to our predictions, however, we found no difference in the abundances of red-backed voles, Trowbridge's shrews, and shrew-moles between strategies (Table 3). No species was statistically more abundant in the legacy stands. As we predicted, deer mice and creeping voles, and montane shrews as well, were more abundant in thinned stands. We had not expected to catch many squirrels, so we made no predictions. Never less, Northern flying squirrels (*Glaucomys sabrinus*) were captured four times more frequently in legacy stands than in thinned stands; however Townsend's chipmunks (*Tamias*

TABLE 2. Total individuals captured in 4 young stands managed by retaining logs, snags, and residual trees from the previous forest and 4 managed by repeated thinnings, Puget Trough, Washington, 1992-1994.

Species	Legacy retention	Intensive thinning	Total
Sorex trowbridgii	640	596	1236
Sorex monticolus	376	557	933
Clethrionomys gapperi	266	317	583
Peromyscus maniculatus	110	308	418
Microtus oregoni	51	407	458
Neurotrichus gibbsii	201	178	379
Sorex vagrans	57	31	88
Peromyscus oreas	6	12	18
Tamias townsendii	21	75	96
Glaucomys sabrinus	22	5	27
Mustela erminea	5	15	20
Mustela sp.	2	2	4
Peromyscus sp.	3	3	6
Scapanus orarius	1	1	2
Sorex bendirii	3	1	4
Mus musculus	2	0	2
Zapus trinotatus	0	3	3
Sorex sp.	1	1	2
Tamiasciurus douglasii	0	1	1
Total individuals	1767	2513	4280
Sprung traps[1]	1229	1709	2938
Trap nights	19200	19200	38400
CPU[2]	10	15	12

[1] Sprung traps includes repeat captures.

[2] Catch per 100 trap-nights, corrected for traps closed by any cause (Nelson and Clarke 1973).

TABLE 3. Results from an analysis of variance of small mammal abundances (ln [CPU + 1]) by management, year, and management x year interaction in 4 stands managed for logs, snags, and carried over residual trees, and 4 stands managed with repeated thinning, Puget Trough, Washington, 1992–1994.

Species	Legacy		Thinned		Management			Year			Year x management		
	$\bar{x}$	(se)	$\bar{x}$	(se)	*F*	df	*P*[1]	*F*	df	*P*[1]	*F*	df	*P*[1]
Sorex trowbridgii	1.52	(.05)	1.49	(.05)	0.2	1, 23	0.690	0.3	2, 23	0.761	0.01	2, 23	0.994
Sorex monticolus	1.12	(.06)	1.42	(.08)	11.3	1, 23	0.003	3.8	2, 23	0.041	0.1	2, 23	0.868
Clethrionomys. gapperi	0.88	(.09)	1.00	(.11)	0.9	1, 23	0.360	4.0	2, 23	0.036	2.9	2, 23	0.084
Neurotrichus gibbsii	0.72	(.09)	0.65	(.11)	0.2	1, 23	0.658	1.2	2, 23	0.314	0.6	2, 23	0.565
Peromyscus maniculatus	0.43	(.10)	0.98	(.11)	78.1	1, 23	0.000	49.3	2, 23	0.000	6.9	2, 23	0.006
Microtus oregoni	0.23	(.07)	1.16	(.11)	69.1	1, 23	0.000	5.8	2, 23	0.012	0.1	2, 23	0.945
Sorex vagrans	0.26	(.06)	0.15	(.05)	2.5	1, 23	0.133	5.3	2, 23	0.016	0.02	2, 23	0.982
Peromyscus oreas	0.03	(.02)	0.06	(.03)	0.7	1, 23	0.409	0.2	2, 23	0.835	0.2	2, 23	0.838

[1] Bold type indicates significance at $P \leq 0.05$.

townsendii) were >3 times more abundant in the thinned stands. Coast moles (*S. orarius*) and marsh shrews were captured infrequently under both management strategies. We captured the house mouse (*Mus musculus*) only in legacy stands and jumping mice only in thinned stands.

We did not predict that some usually common species would be absent from some stands. Creeping voles were absent from one legacy stand in 1992 and two in 1993. Shrew-moles were absent from one legacy stand in 1993. The vagrant shrew composed 3% of total individuals under legacy management and 1% under commercial thinning, and was absent from two thinned stands during 1992 and one thinned stand during 1993. Columbian mice were trapped only in the same two stands, one in each strategy, each year, except that a single Columbian mouse was captured on a second thinned grid during 1993. Columbian mice were restricted in distribution within the two occupied stands, occupying the same area from year to year.

Temporal Variation in Small-Mammal Abundance

Deer mice varied among years differently between management strategies (significant interaction effect) (Table 3). Deer mice, creeping voles, montane shrews, vagrant shrews, and shrew-moles all attained their highest mean abundance during 1994 under both management strategies (Figure 1). The highest mean abundance of red-backed voles in thinned stands also occurred during 1994 (Figure 1). Deer mice and vagrant shrews were more abundant in 1994 than in 1992, and deer mice were more abundant in 1992 than in 1993. During years with low mean abundance in legacy stands, confidence intervals encompassed 0 for creeping voles and approached 0 for deer mice, suggesting extirpations were possible (Figure 1). Similarly, confidence intervals for vagrant shrews encompassed 0 under each management strategy during years of low mean-abundance.

Population Structure and Biomass

Reproductively active females were ≤37% of individual captures for any species under both management strategies (Table 4). Necropsy of 1,226 animals from legacy stands yielded 27 pregnant females and necropsy of 1,422 animals from thinned stands yielded 69 pregnant females. Pooled data showed no significant differences in litter sizes between strategies (Mann-Whitney U test, $P \geq 0.15$; Table 4). We lacked sufficient samples to determine litter sizes for deer mice, Columbian mice, and shrew moles. We found greater proportions of adults in Trowbridge's shrew populations in thinned stands than in legacy stands (Table 4); however, the magnitude of the difference was small. There were no significant differences between management strategies in population sex ratios or proportions of reproductively active females for any species (Table 4). Total small-mammal biomass was 1.7 times as great in thinned stands as in legacy stands (Table 5).

Community Structure and Diversity

Small-mammal communities developed under the two strategies were dominated numerically by Trowbridge's shrews and montane shrews.

TABLE 4. Small mammal abundance, litter size, and Mann-Whitney U tests (*P*) for the effects of forest management strategy on population proportion of reproductively active females, sex ratio, and age ratio in four 4-ha sampling plots in each of two forests on Fort Lewis, Washington, 1992–1994.

		CPU[2]		Litter size[3]		Rpro-fem[4]			Sex M:F			Age A:Y		
Species	Mgmt[1]	$\bar{x}$	(se)	$\bar{x}$	(se)	$\bar{x}$	(se)	(*P*)	$\bar{x}$	(se)	(*P*)	$\bar{x}$	(se)	(*P*)
C. gapperi	L	1.5	(0.2)	2.4	(0.5)	0.20	(0.04)	0.36	2.9	(0.6)	0.45	5.2	(0.9)	0.21
	T	1.9	(0.3)	2.5	(0.2)	0.25	(0.04)		2.4	(0.4)		7.2	(1.0)	
M. oregoni	L	0.3	(0.1)	2.0	(1.0)	0.17	(0.08)	0.06	0.8	(0.2)	0.16	3.6	(1.4)	0.31
	T	2.4	(0.4)	2.5	(0.1)	0.33	(0.03)		1.4	(0.1)		4.8	(1.1)	
P. maniculatus	L	0.6	(0.2)	...	...	0.20	(0.05)	0.33	1.6	(0.2)	0.28	1.4	(0.3)	0.07
	T	1.8	(0.3)	...	...	0.26	(0.03)		2.1	(0.3)		2.4	(0.3)	
S. trowbridgii	L	3.6	(0.2)	3.0	(0.0)	0.20	(0.03)	0.69	1.2	(0.1)	0.42	0.5	(0.0)	0.01
	T	3.5	(0.2)	4.0	...	0.17	(0.02)		1.4	(0.1)		0.7	(0.0)	
S. monticolus	L	2.1	(0.2)	3.9	(0.3)	0.16	(0.02)	0.23	2.5	(0.4)	0.31	1.9	(0.3)	0.95
	T	3.3	(0.3)	3.6	(0.3)	0.19	(0.02)		1.8	(0.1)		1.9	(0.1)	
N. gibbsii	L	1.1	(0.2)	...	...	0.19	(0.03)	0.90	1.3	(0.3)	0.31	3.3	(1.2)	0.55
	T	1.1	(0.2)	3.0	...	0.20	(0.05)		1.5	(0.3)		2.1	(0.5)	
S. vagrans	L	0.3	(0.1)	4.0	(1.0)	0.32	(0.09)	0.93	1.0	(0.1)	0.78	1.2	(0.2)	0.90
	T	0.2	(0.1)	3.0	...	0.37	(0.14)		0.8	(0.1)		1.2	(0.2)	
P. oreas	L	0.03	(0.0)	...	...	0.25	(0.25)	1.00	0.00	...	0.08	0.7	(0.7)	0.6
	T	0.1	(0.0)	...	...	0.25	(0.16)		1.8	(0.7)		1.5	...	

[1] Management strategy, (L) retention of legacies of large logs, dead trees, and live trees and (T) thinning.

[2] Catch per 100 trap-nights corrected for traps closed by any cause (Nelson and Clarke 1973).

[3] Mean number of fetuses per female for each management strategy; of 2648 necropsies, 96 were pregnant females.

[4] Proportion of individuals captured that were reproductively active females, either in estrus, pregnant, lactating, or post lactating.

Community structure, however, differed significantly between the two strategies (Figure 2), with creeping voles being third ranked in thinned stands, but seventh ranked in legacy stands. Shrew-moles assumed greater importance in legacy communities than in thinned communities but were not significantly different in abundance between strategies. Community structure based on biomass (Table 5) differed from structure based on abundance. In thinned stands, the three common rodents—creeping vole, red-backed vole, and deer mouse—superseded the common shrews—Trowbridge's shrew and montane shrew—when community structure was based on biomass. In legacy stands, however, only red-backed voles superseded Trowbridge's shrew in biomass rank (Table 5). Deer mice, creeping voles, and montane shrews were significantly more abundant numerically and in biomass in thinned stands compared to legacy stands.

The same eight species composed the small-mammal communities in both legacy and thinned stands; only six species, however, occurred consistently in thinned stands and only five species in legacy stands (Figure 1). According to the Shannon index, the greater number of individuals in the thinned stands were more evenly distributed over species (H' = 1.68) than in the legacy-stand small-mammal communities (H' = 1.53) ($t = -2.44$, $df = 6$, $P = 0.051$).

Discussion

Small-Mammal Communities

Overall, the same species composed the forest-floor small-mammal communities in the thinned stands, legacy stands, old-growth and naturally young forest in the Southern Washington Cascades, and old-growth and extensively managed second-growth forests on the Olympic Peninsula (Figure

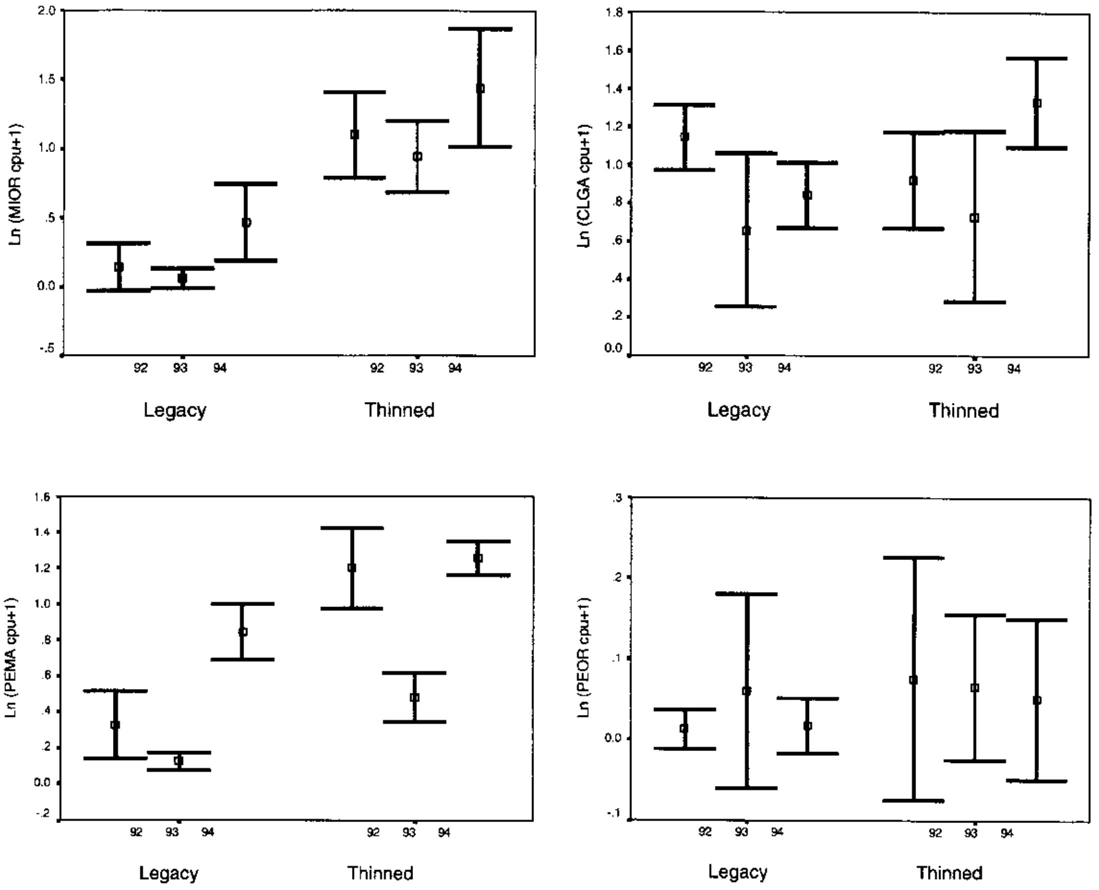
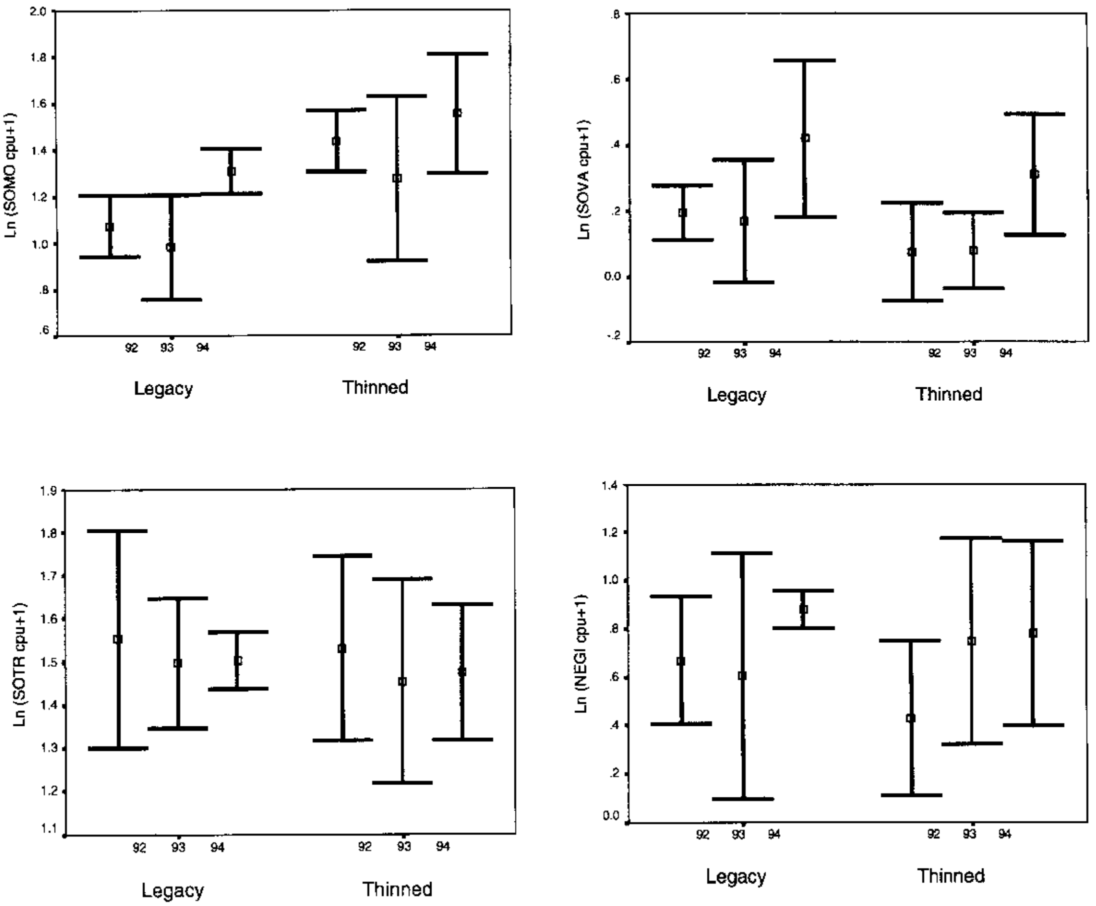


Figure 1. Error bars of small mammal abundance [Ln (CPU+1) ± 2*SE*] by year and management strategy in forest managed with letters of genus and species: *Clethrionimys gapperi, Microtus oregoni, Neurotrichus gibbsii, Peromyscus maniculatus,*

2). Although thinned stands had greater abundance, biomass, and diversity of small mammals than legacy stands, neither management strategy produced environments that consistently supported complete small-mammal communities when compared to old-growth forests in neighboring physiographic provinces. Small mammals were 1.2 and 1.6 times as abundant in old-growth as in natural young or managed young forest in the southern Washington Cascades and on the Olympic Peninsula, respectively (Carey and Johnson 1995). This difference was comparable to the differences that we found between thinning and legacy management strategies. Because small mammals feed widely on truffles (Ure and Maser 1982), invertebrates, and seeds (Gunther et al. 1983), the reported depression of these food resources in certain young managed forests (Buchanan et al. 1990; Carey 1991; Estrada-Venegas 1995; North et al. 1997) may result in low numbers of small mammals in young stands. Limitations could be especially severe during winter when truffle biomass and other foods are at seasonal lows (North et al. 1997). We hypothesize that this diversity of food sources underlies the structure and abundance of forest-floor small-mammal communities and that neither management by thinnings nor management with legacies provided that diversity of food sources.

Of three species primarily responsible for the differences between small-mammal communities in legacy and thinned stands, two had niches strongly associated with understory vegetation (creeping vole and deer mouse, Carey and Johnson



legacies and forest managed with thinning, Puget Trough, Washington. Taxa are identified by alpha codes comprised of first 2
P. oreas, Sorex monticolus, S. trowbridgii, S. vagrans.

1995), and one with the soil-layer litter (montane shrew, Hawes 1977). Thinned stands had greater shrub volumes and herbaceous cover than legacy stands. No forest-floor small-mammal species achieved significantly greater abundance under legacy management, an unexpected result that suggests (1) that statistical correlations between shrew-moles and coarse woody debris (Carey and Johnson 1995) do not represent a direct cause and effect relationship and (2) a second hypothesis that there may be some substitutability in providing protective cover and organic inputs to the forest floor between dense low understory vegetation and coarse woody debris. Furthermore, stumps and logs in legacy stands may have been unable to attain their full potential as habitat elements because of poor understory development—covers of both coarse woody debris and understory vegetation were low compared to old-growth forests. Carey and Johnson (1995) found that abundances of most small mammals were correlated with both understory vegetation and coarse woody debris. The distribution of patches of dense understory vegetation was more important than mean abundance and that mammal species responded differently to different kinds of vegetation. Carey et al. (1999*a*) hypothesized that a synergistic response of small mammals occurs when a diversity of vegetation site-types (discrete repeatable associations that differ in composition and structure) in the understory and coarse woody debris are arrayed in close juxtaposition in a fine-scale mosaic. This synergy is due, in part, to pre-interactive

TABLE 5. Distribution of small mammal biomass in four 4-ha sampling plots in each of 2 forest tracts on Fort Lewis, Washington, 1992-1994; forest managed with retention of legacies[1] (L) or managed with intensive thinning (T).

Species	Forest	Mnka[2]		Mean Body Mass (g)		Mean Stand Biomass (g)		
		x̄	(se)	x̄	(se)	x̄	(se)	*P*
Clethrionomys gapperi	L	22.2	(3.2)	15.8	(0.2)	351	(50)	0.377
	T	26.4	(4.0)	15.8	(0.3)	417	(65)	
Microtus oregoni	L	4.3	(1.5)	14.4	(1.4)	61	(22)	0.000
	T	33.9	(5.4)	14.3	(0.3)	485	(75)	
Peromyscus maniculatus	L	9.2	(2.5)	14.4	(0.7)	133	(32)	0.001
	T	25.7	(4.0)	14.5	(0.3)	373	(56)	
Sorex trowbridgii	L	53.3	(3.4)	4.4	(0.0)	235	(15)	0.427
	T	49.7	(3.4)	4.4	(0.0)	219	(14)	
Sorex monticolus	L	31.3	(2.5)	5.6	(0.1)	175	(15)	0.008
	T	46.4	(4.1)	5.7	(0.1)	265	(26)	
Neurotrichus gibbsii	L	16.8	(2.5)	7.2	(0.1)	121	(19)	0.802
	T	14.8	(3.3)	7.7	(0.1)	114	(25)	
Sorex vagrans	L	4.8	(1.2)	3.7	(0.1)	18	(5)	0.177
	T	2.6	(0.9)	4.0	(0.1)	10	(4)	
Peromyscus oreas	L	0.5	(0.3)	14.6	(2.8)	7	(7)	0.406
	T	1.0	(0.5)	17.7	(8.5)	18	(9)	
Mean stand biomass	L	...	...	...	...	1101	(14)	0.000
	T	...	...	...	...	1901	(23)	
Mean biomass / hectare	L	...	...	...	...	275		
	T	...	...	...	...	475		

[1] Logs, snags, and residual trees from the previous stand.

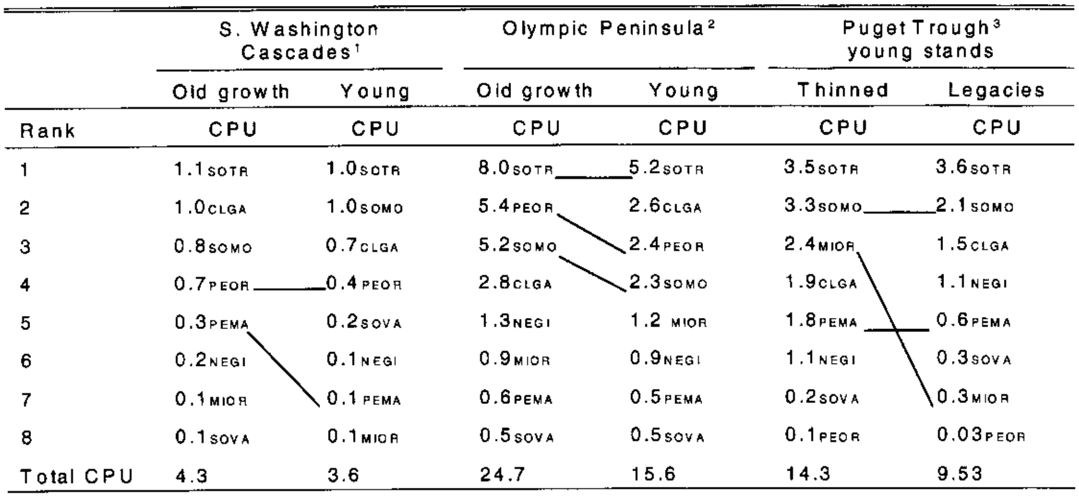
[2] Minimum number known alive.

[3] Significance of Mann-Whitney U tests for differences between species man biomass between management treatments L and T.

niche diversification that promotes high abundances and diversity in the forest-floor small mammal community. Our results support this third hypothesis. Contrary to observed patterns of forest-floor small mammals, flying squirrels were more abundant in legacy stands; this result was confirmed by sampling aimed specifically at squirrels, as was the greater abundance of chipmunks in thinned stands (Carey 2000).

Species Responses to Management Strategies

Four common species—Trowbridge's shrew, vagrant shrew, shrew-mole, and red-backed vole–were equally abundant under the two management strategies. Critical niche dimensions for these species may be more directly tied to biological activity at the soil-litter interface than to either understory vegetation or woody legacies in the forest environment. Montane shrews were more abundant in thinned stands than legacy stands and in old growth more than second growth on the Olympic Peninsula. Montane shrews forage for invertebrates within unconsolidated soil organic layers (Terry 1974) and prefer *mor* humus (organic litter distinct from mineral soil) over *moder* humus (netlike structure of organic and mineral particles) (Hawes 1977). High shrub volume and deciduous litter in the thinned sites could have enhanced *mor* humus development and fostered greater invertebrate diversity and abundance thus benefiting montane shrews. We did not measure



	S. Washington Cascades[1]		Olympic Peninsula[2]		Puget Trough[3] young stands	
	Old growth	Young	Old growth	Young	Thinned	Legacies
Rank	CPU	CPU	CPU	CPU	CPU	CPU
1	1.1 SOTR	1.0 SOTR	8.0 SOTR	5.2 SOTR	3.5 SOTR	3.6 SOTR
2	1.0 CLGA	1.0 SOMO	5.4 PEOR	2.6 CLGA	3.3 SOMO	2.1 SOMO
3	0.8 SOMO	0.7 CLGA	5.2 SOMO	2.4 PEOR	2.4 MIOR	1.5 CLGA
4	0.7 PEOR	0.4 PEOR	2.8 CLGA	2.3 SOMO	1.9 CLGA	1.1 NEGI
5	0.3 PEMA	0.2 SOVA	1.3 NEGI	1.2 MIOR	1.8 PEMA	0.6 PEMA
6	0.2 NEGI	0.1 NEGI	0.9 MIOR	0.9 NEGI	1.1 NEGI	0.3 SOVA
7	0.1 MIOR	0.1 PEMA	0.6 PEMA	0.5 PEMA	0.2 SOVA	0.3 MIOR
8	0.1 SOVA	0.1 MIOR	0.5 SOVA	0.5 SOVA	0.1 PEOR	0.03 PEOR
Total CPU	4.3	3.6	24.7	15.6	14.3	9.53

[1] Four night snap-trap session combined with 30-34 night pitfall-trap session per year.

[2] Four night snap-trap session per year.

[3] Eight night live-trap session per year.

Figure 2. Small mammal community structures listed from most to least abundant species for the southern Washington Cascade Range, 1984-1985 (West 1991); the Olympic Peninsula, Washington, 1987-1989 (Carey and Johnson 1995); and the Puget Trough, Washington, 1992-1994. Lines connect species with significantly different abundances between stand types within a region ($P \leq 0.05$). Note low numerical importance of *P. oreas* in Puget Trough communities. Taxa are identified by alpha code comprised of first 2 letters of genus and species: *Clethrionomys gapperi, Microtus oregoni, Neurotrichus gibbsii, Peromyscus maniculatus, P. oreas, Sorex monticolus, S. trowbridgii, S. vagrans.*

depth, successional stage, or quality of organic litter (Shaw et al. 1991) under our two management strategies, but understanding litter layers might be key to understanding patterns of abundance of small mammals. Our fourth hypothesis is that the soil-litter interface is a key element in structuring small-mammal communities.

Coarse woody debris cover was significantly lower in thinned stands than in legacy stands and very low in abundance compared to natural stands (West 1991, Carey and Johnson 1995). However, the 1-2% cover of coarse debris in thinned stands represented a minimum 400 m^2 of coarse woody debris per stand. In a companion telemetry study (S. Wilson, unpublished data) of deer mice, Columbian mice, and red-backed voles, nearly all individuals in thinned stands used stumps and logs as denning or resting sites. It appears that stumps and logs, even in low densities, are an important resource for small mammals and the value of these legacies to small mammals may be bolstered by understory vegetation. Our fifth hypothesis is that the fungal and invertebrate activity supported by downed wood (Harmon et al. 1986), and its protective cover (Hayes and Cross 1987), may help to maintain minimum carrying capacities in stands managed with legacies for those small mammals not directly reliant on herbs, shrubs, or invertebrates associated with understory plants (Tallmon and Mills 1994, Carey and Johnson 1995).

Columbian mice were rare. This mouse has been related to diverse understories, midstories including shade-tolerant trees, coarse woody debris, and tall canopies (Dalquest 1948, West 1991, Carey and Johnson 1995)—but the determinants of Columbian mouse abundance remain unknown. Certainly there is a greater overall abundance and variety of seeds, fruits, and nuts in forests with complex canopies. Deer mice for example, are known to consume fruits, seeds, and invertebrates (Van Horne 1982, Gunther et al. 1983) and montane shrews are known to consume conifer seed (Gunther et al. 1983). Greater shrub prevalence

(Carey and Johnson 1995) plus greater canopy tree species richness producing more abundant and varied conifer seed may account for greater abundances of a number of species in old growth. Our study sites had monospecific canopies without midstories; legacy sites had sparse to moderate understories. Thus, low abundances of the habitat-generalist deer mouse (Baker 1968) in legacy stands was not surprising. In a companion study (S. Wilson, unpublished data), we found fluorescent pigment trails (Lemen and Freeman 1985) on the forest floor and in branches of fruiting salal suggesting that deer mice were able to exploit the additional resources provided by the greater shrub volume in thinned stands. The relative abundances of deer mice in our thinned stands were large compared to small-mammal communities in other regions. Deer mice may replace Columbian mice as the dominant forest mouse in rapidly changing, simply structured, early seral environments (Songer et al. 1997). However, low abundances of Columbian mice in young forests on the Olympic Peninsula and the southern Washington Cascades were not accompanied by a reciprocal increase in deer mice (West 1991; Carey and Johnson 1995).

Vagrant shrews were very low in abundance on our study sites–but were low in abundance elsewhere as well (Carey and Johnson 1995). Low abundances of creeping voles in legacy stands is easily explained by low amounts of herbaceous vegetation there (Carey and Johnson 1995). Creeping voles reach peak densities in clearcuts and old fields (Dalquest 1948, Hooven 1973). High relative abundances of creeping voles on thinned sites were probably due to lingering effects of disturbance on the understory—numerous weedy species were abundant in thinned stands but rare or absent from legacy stands (Carey et al. 1999*b*, Thysell and Carey 2000).

Implications

Repeated thinning fostered development of understory vegetation on our sites and in forests of similar age and management history in western Oregon (Bailey and Tappeiner 1998). Because understory vegetation is 1) responsive to management and 2) seemed to have a large influence on *Peromyscus* and *Microtus* abundance, thinning has potential to remedy low small-mammal abundance in young managed forest. Conventional thinnings result in systematically spaced trees and dense low understories dominated by a few native plants; development of shade-tolerant regeneration may be precluded; and vegetation-site type diversity reduced (Thysell and Carey 2000). Variable-density thinning (Carey 1995; Carey and Curtis 1996; Carey et al. 1999*a,b*) manipulates spatial heterogeneity in the canopy to produce diverse understories. Combining vegetation management with management of decadence, including retention of woody legacies (Carey et al. 1996*b*; Carey et al. 1997; Carey et al. 1999*a*) could provide markedly greater benefits than either strategy we examined here.

Without intentional management of forest processes, including decadence (Carey 1999*a*), timber harvesting can lead to a decline in legacies, simplification of stand structure, and lowered habitat quality with consequences for trophic webs (Spies and Cline 1988; Halpern and Spies 1995; Carey and Curtis 1996; Harmon et al. 1996; Carey et al. 1999*a*; Carey et al. 1999*b*). Future tests of small mammals should consider the effects of stand structure and canopy heterogeneity on forest floor processes.

Limitations

It is possible that population density may be a misleading indicator of habitat quality (Van Horne 1983), but our demographic data did not indicate that was the case in our study. Population structures for most species were similar under each management strategy and we believe that abundance was an appropriate indicator of small-mammal habitat quality.

Temporal variation in species abundances can confound or obscure effects of treatment and comparisons among studies. We observed a simultaneous increase in the abundances of five species between 1993 and 1994. Only deer mice showed an interactive effect between year and management strategy. One or more extraneous factors, such as weather, conifer seedfall (Gashwiler 1979; Sullivan 1979; Gunther et al. 1983), or invertebrate outbreak (Elkinton et al. 1996) appeared to affect animal abundance across the entire study area. Unfortunately, we cannot identify the cause.

But, given our three years of data from four sampling units per management strategy, and given parallels with other retrospective studies, we have confidence in our findings as they apply to our study areas and in general to second-growth Douglas-fir forests. Our sites did not include the full range of habitat variability in western Washington forests and our results should be applied cautiously to other forests of different location, age, and composition. Our ability to detect a continuous response to legacies and understory vegetation was constrained because we tested only two levels of each. We observed small-mammal communities only during summer, and our results may not hold for other seasons.

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