

# INDUCED SPATIAL HETEROGENEITY IN FOREST CANOPIES: RESPONSES OF SMALL MAMMALS

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**Abstract:** We hypothesized that creating a mosaic of interspersed patches of different densities of canopy trees in a second-growth Douglas-fir (*Pseudotsuga menziesii*) forest would accelerate development of biocomplexity (diversity in ecosystem structure, composition, and processes) by promoting spatial heterogeneity in understory, midstory, and canopy, compared to typical managed forests. In turn, increased spatial heterogeneity was expected to promote variety in fine-scale plant associations, foliage height diversity, and abundance of small mammals. Three years following treatment, understory species richness and herb cover were greater with variable-density thinning than without. Midstory and canopy species did not have time to develop significant differences between treatments. Variable-density thinning resulted in larger populations of deer mice (*Peromyscus maniculatus*), a species associated with understory shrubs; creeping voles (*Microtus oregoni*), a species associated with herbaceous vegetation, and vagrant shrews (*Sorex vagrans*), a species usually associated with openings but common in old growth. No forest-floor small-mammal species, including those associated with old-growth forest, declined in abundance following variable-density thinning. Annual variation in population size was not related to treatment. Variable-density thinning may accelerate the development of biocomplexity in second-growth forest by promoting spatial heterogeneity and compositional diversity in the plant community, increasing diversity and abundance of small mammals, and similarly affecting other vertebrate communities. When combined with long rotations, legacy retention, and management for snags and coarse woody debris, variable-density thinning has broad applicability to enhance biodiversity in managed Douglas-fir forests across the Pacific Northwest.

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Public forests are expected to provide a sustainable flow of commodities, revenues to landowners, economic support to local communities, habitat for wildlife and plants, recreational and spiritual opportunities, and clean air and water (Goodland 1995, Daily and Ehrlich 1996, Folke et al. 1996). Conversion of old growth to managed forest, especially through even-aged management systems, has raised questions about the ability of second-growth forests to continue to provide diverse goods and services (e.g., Harris 1984, Harmon et al. 1996, Carey et al. 1999b). Forests managed for timber often are intentionally restricted in structure, composition, and longevity—managed on short rotations for a single-tree species, 1 age cohort, and reduced diversity and abundance of other vegetation (Perry 1994). Old-growth forests, with their long histories of small (e.g., tree fall) and large (e.g., fire and windstorm) disturbances, are spatially heterogeneous and diverse in composition (Spies and Franklin 1989, Lertzman et al. 1996). Such biocomplexity, defined as diversity in ecosystem structure, composition, and processes (including tree size, snags, coarse woody debris, soil organic matter, and spatial

heterogeneity at a fine scale; tree species, vascular plant life forms, soil flora and fauna, and vertebrates; and soil food webs, trophic pathways, and habitat breadth) contributes to productivity, resilience to perturbation, resistance to invasion, and niche diversification (Heljden et al. 1998, Carey et al. 1999a, Tilman 1999). Forest ecosystem management that goes beyond timber management will be required to develop biocomplexity (Franklin 1993a, Carey et al. 1999b). Otherwise, multiple-rotation forests will become increasingly biologically simplified with corresponding declines in habitat quality for wildlife (Perry 1994:557, Carey et al. 1999b), ecosystem function (Canham et al. 1990, Franklin 1993b, Tilman 1999), site productivity, watershed quality, and carbon sequestration (Harmon et al. 1996, Ponge et al. 1998, Vogt et al. 1999).

Variable-density thinning has been suggested as a management tool to accelerate the development of biocomplexity in managed forest stands (Carey 1995, Hagar et al. 1996). Thinning to various densities (with corresponding differences in canopy cover) to create a mosaic of patches (e.g., about 40 x 40 m or 1,600 m<sup>2</sup> each) has been

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hypothesized to promote processes associated with natural development of diverse fine-scale plant associations, foliage height diversity, and horizontal vegetation patchiness that have concomitant effects on soil and vertebrate communities (Carey et al. 1996, 1999a,b,c). Variable-density thinning, in conjunction with management for decadence and long rotations, shows promise in developing complex forests that produce diverse products and services (Carey et al. 1999b).

Forest-floor small mammals serve as prey for reptiles, carnivores, hawks, and owls (Verts and Carraway 1998); consume invertebrates, vegetation, fruits, and seed (Terry 1974, Gunther et al. 1983); and disperse fungal spores (Maser et al. 1978). Forest-floor small mammals generally are more abundant in complex, natural forest than in simplified, managed forest (Carey and Johnson 1995, Wilson and Carey 2000). Studies have demonstrated species-specific short-term (<5 yr) effects of clearcutting and other harvest methods on small mammals (Hooven and Black 1976, Gunther et al. 1983, Songer et al. 1997, Von Trebra et al. 1998). Partial harvest or thinning (Hagar et al. 1996, Steventon et al. 1998, Carey 2000, Wilson and Carey 2000) and herbicide application (Cole et al. 1998, Sullivan et al. 1998) also influence the abundance of small-mammal populations. Thus, Carey and Johnson (1995) and Carey et al. (1999b) suggested that achieving small mammal abundances and community structure similar to those in resilient old-growth forests could serve as 1 of several measures of success of forest ecosystem management.

Neither the effects of variable-density thinning on ecosystem function nor the utility of the small-mammal community as an environmental barometer have been experimentally demonstrated; however, vertebrate communities have been used as measures of ecosystem and landscape function in models incorporating variable-density thinning (e.g., Carey et al. 1999b). Here, we present the results of a replicated, controlled experiment on the effects on forest-floor small mammals of creating a vegetation mosaic with variable-density thinning.

Our study objectives were to determine responses of small-mammal populations to vegetation changes induced by variable-density thinning during the first 4 years following thinning. Based on Carey and Johnson (1995), we hypothesized that experimentally induced spatial heterogeneity in canopy cover would increase population sizes of small mammals associated with understory shrubs and herbaceous vegetation in the short-term - deer mouse, creeping vole, and vagrant

shrew and eventually produce small-mammal communities with the same species, species rank-order abundance, and overall abundance (herein referred to as biotic integrity) as small-mammal communities in old-growth forests. We expected to see a more pronounced response to variable-density thinning in closed-canopy stands with moss-dominated understories than in stands previously thinned with even spacing between trees and with developed low understories.

## STUDY AREA

Our study areas were 30 km southeast of Olympia, Washington, USA, on Fort Lewis Military Reservation in the Puget Trough physiographic province (Franklin and Dyrness 1988). Topography was level to gently rolling, and elevation ranged from 100 m to 143 m. Precipitation, mostly rain, averaged 91 cm per year, with wet falls, winters, and springs and dry summers. Vegetation was typical of the drier portions of the Western Hemlock (*Tsuga heterophylla*) Zone with Douglas-fir predominant in forest cover (Franklin and Dyrness 1988). We selected 4 study areas from the 6,000-ha Rainier Training Area to be used as blocks in our randomized blocks experiment (Carey et al. 1999d). All blocks were composed of even-aged stands of Douglas-fir that had regenerated from natural seeding following clearcutting in the 1920s and 1930s. All were in the late competitive-exclusion to early understory reinitiation stages of forest development and all lacked significant shade-tolerant regeneration (Carey et al. 1999d). All blocks were past the usual harvest age for industrial forest lands but exemplified conditions commonly found in present-day forested landscapes managed under long (>60 yr) rotations, and were approaching the age at which forests are commonly harvested under even-aged management on public lands (Carey et al. 1999d, Carey 2000). Within each block, we delineated 4 13-ha stands for a total of 16 stands. Stands were separated  $\geq 80$  m and blocks by  $\leq 4$  km (Carey et al. 1999d). During trapping, we recorded no movements of small mammals among stands. Significant differences occurred both within and among blocks in topography, vegetation, and abundance of vertebrate species, although stands within blocks were more similar than stands among blocks (Carey et al. 1999d, Carey 2000, Haveri and Carey 2000, Thysell and Carey 2000, Wilson and Carey 2000).

Before our experiment, 2 blocks had been managed for high-quality timber with 2 conventional (thinning from below and with even spacing between trees), commercial thinnings and removal of merchantable dead and defective trees. Coarse woody debris >10 cm in diameter was scarce (<3% cover), but understory cover (shrubs, ferns, and forbs) was high (>85%). Commercially thinned stands were well-stocked ( $\geq 225$  stems/ha) with large (approx. 60 cm dbh) Douglas-fir (Carey et al. 1999d).

In the other 2 blocks, a variety of biological legacies (large live, dead, and fallen trees and their associated biota) had been retained during the regeneration harvest, but no further management had been undertaken prior to our experiment, other than felling of a few residual trees that overtopped the canopy and posed danger to low-flying aircraft. Among these legacy stands, low shrub cover varied from 17 to 31% with moderate shrub cover associated with canopy gaps formed by root rot (*Phellinus weirii*) infestations. Coarse woody debris was moderately abundant and structurally varied: tall stumps (>1 m) of old-growth trees (approx. 48/ha); old well-decayed, fallen trees (approx. 8% cover); a few lightly to moderately decayed felled old-growth trees; and abundant fallen small-diameter trees that had died from suppression or root rot (approx. 3% cover). Legacy stands had numerous residual large snags (approx. 3.5/ha) and large live trees (approx. 2.7/ha), but contemporary Douglas-fir were small (approx. 43 cm dbh) and crowded ( $\geq 600$  stems/ha).

## METHODS

### Experimental Design

We used experimental variable-density thinning to create spatial heterogeneity in second-growth Douglas-fir forest canopies in a randomized blocks experiment. We based the scale and intensities of thinning subtreatments on empirical data collected in old-growth forests; our goal was to begin to replicate the spatial heterogeneity found in natural forest canopies (Carey and Johnson 1995, Carey et al. 1999a,d). Our intent was not to test the effects of subtreatments, rather, we were interested in the stand-wide response of small mammals to increasing understory development and species richness resulting from spatial heterogeneity in the tree canopy.

In each block, we randomly chose 2 stands for variable-density thinning (hereafter, mosaics) and 2 for

no thinning (hereafter, controls). In the center of each stand, we laid out an 8 x 8 reference grid with 40-m spacing, creating 64 reference points and 49 0.16-ha cells; each grid was surrounded by a 40-m buffer. Reference grids served as templates for application of variable-density thinning. Controls were not controls in the sense that we expected them to remain static; rather, they represented continuously developing homogeneously spaced stands of trees resulting from management without thinning (but with self-thinning) and management with conventional thinning. This design resulted in 8 replicates each of experimental treatment and control.

Variable-density thinning of even-aged stands is best described in terms of relative density (Curtis 1982). Relative density (RD) is an index of competition among trees and is based on the square root of the quadratic mean diameter at breast height, stem density, basal area, and inter-crown competition of Douglas-fir (Curtis 1982). Relative density for Douglas-fir ranges from 0 (no trees) to a biological maximum of 14; excessive crown competition with suppression mortality occurs with  $RD > 7$ .

We conducted a reconnaissance survey of the resulting grid cells and found root rot forming small gaps; 0-15% of the area of each stand had reduced canopy density due to root rot. We designed a root-rot treatment that produced an  $RD = 2$  and assigned that treatment to 15% of the area of all treated stands (using random assignment to cells when root rot was not evident). We randomly treated the remaining cells to achieve a ratio of 2:1 of moderately closed ( $RD = 6$ ) and moderately open ( $RD = 4$ ) 0.16-ha patches of canopy, well-interspersed across the stands. Buffers between treated stands were lightly thinned ( $RD = 6$ ). Implementation of this design produced a 2:1 ratio of lightly thinned ( $RD > 4.75$ ) to heavily thinned ( $RD < 4.75$ ) grid cells as suggested by Carey et al. (1999a). Experimental thinning was accomplished by a commercial operation in spring 1993 with all merchantable thinned trees removed. Thinning reduced tree density in legacy stands from an average of  $454 \pm 11$  trees/ha ( $RD = 7.4 \pm 0.2$ ) to an average  $291 \pm 9$  trees/ha ( $RD = 4.8 \pm 0.1$ ) a reduction of 30% of basal area. In the previously conventionally thinned stands, variable-density thinning reduced tree density from an average ( $\pm$  SE) of  $203 \pm 5$  trees/ha ( $RD = 7.8 \pm 0.2$ ) to an average of  $147 \pm 4$  trees/ha ( $RD = 4.7 \pm 0.1$ ) a reduction of 24% of basal area (see Carey et al. 1999d for further details and outcomes of

implementing stand thinnings).

### Sampling Vegetation

We sampled vegetation during July and August 1996, the fourth summer following experimental variable-density thinning. We ocularly estimated species-specific cover on an octave scale as recommended by Gauch (1982) on 6 5.6-m-radius plots in controls and 18 plots in mosaics. We summed covers of individual species into composite variables representative of vegetative life-forms (ferns, herbs, trailing vines and half-shrubs, low shrubs, and tall shrubs) and total vegetative cover. We calculated total plant species richness from plot data. Additional vegetation data were collected by Carey et al. (1999d) and reported by Thysell and Carey (2000, 2001).

### Sampling Small Mammals

We targeted 8 species identified by Carey and Johnson (1995) as characteristic of upland small-mammal communities in Washington: southern red-backed vole (*Clethrionomys gapperi*), creeping vole, deer mouse, Keen's mouse (*Peromyscus keeni*), shrew mole (*Neurotrichus gibbsii*), montane shrew (*S. monticolus*), Trowbridge's shrew (*S. trowbridgii*), and vagrant shrew. We considered other species captured in our traps, including moles (Talpidae, except *Neurotrichus*), squirrels (Sciuridae), and weasels (Mustelidae), as incidental captures of species not adequately sampled by our methods or as species primarily associated with habitat features outside our sites—the Pacific jumping mouse (*Zapus trinotatus*), house mouse (*Mus musculus*), and marsh shrew (*Sorex bendirii*).

We established a 10 x 10 small-mammal trapping grid with 20-m spacing in the central portion of each reference grid. We placed 1 large (7.6 cm x 8.9 cm x 22.9 cm) and 1 small (5.1 cm x 6.4 cm x 16.5 cm) Sherman live trap (use of trade names is for information only and does not constitute an endorsement of any product by the U.S. Department of Agriculture)  $\leq 2$  m from each grid point,  $>1$  m apart, and not in contact with the same physical structure (e.g., log or stump). We trapped small mammals 3 and 4 years after thinning, in 1996 and 1997. Because of the large effort required to check 3,200 traps/day, we divided our trapping into 2 successive sessions between mid July and mid-August, during the presumed annual peak of small-mammal abundance (Hamilton 1942). One control and 1 mosaic from each block were trapped during each session

to avoid bias due to timing of trap ping. Within each session, we opened traps for 4-night periods separated by a 3-night hiatus (a total of 51,200 trap nights). We baited all trap, with a peanut butter-oats-molasses mixture and a carrot slice and added polyester batting for bedding. We checked traps daily for captures, bait, and function. Treadles were set to capture the lightest insectivores (approx. 4 g). We re-corded species, mass, sex, age, and reproductive condition of each mammal captured and marked rodents with 1 Monel eartag and released them alive. We released live insectivores without tagging; few insectivores, however, survived trapping. Dead animals, mostly insectivores, were collected for necropsy to verify field evaluation of species, sex, age, and reproductive status. All collected specimens were deposited in the Charles R. Conner Museum, Washington State University, Pullman, USA. Scientific and vernacular names for mammals follow Jones et al. (1997).

### Data Analysis

We used t-tests to compare vegetation cover values between controls and mosaics. For mosaics, we used weighted means to account for the distribution of vegetation plots among RD classes and the relative abundance of RD classes within stands (Snedecor and Cochran 1967). We used actual post-treatment data on retained RD (Carey et al. 1999d) to determine weights. For controls, we simply used the mean value of vegetation plots. Based on consultations with statisticians (T. Max and K. Hyer, Pacific Northwest Research Station, U.S. Forest Service, personal communication), we used split-plot univariate analysis of variance (ANOVA; Kuehl 1994) to test for differences in small mammal abundance and population demographics attributed to treatment, year, or a treatment-by-year interaction. We accepted  $P \leq 0.05$  as a traditional limit for statistical significance. However, we considered  $P \leq 0.10$  to indicate marginally significant differences when differences also seemed biologically significant and risk of Type II error was low (Yoccoz 1991, Cherry 1998, Johnson 1999). All tests were conducted in SPSS (Norulsi 1993).

Annual variation in small-mammal populations can be large, presumably in response to complex climatological and demographic interactions, and population estimates are expected to vary from year to year (i.e., estimates taken in successive years are not necessarily repeated estimates of the same population size). However, one could argue that such estimates are

not independent and the year effects were not randomly assigned, thus repeated measures ANOVA also would have been appropriate (E. D. Ford, University of Washington, Seattle, personal communication). This kind of conundrum is common in field experiment (e.g., Cook and Campbell 1979), but, here, interpretation of study results would not change with the ANOVA model used (e.g., Carey 2000, Wilson and Carey 2000). In our design, the variable-diversity thinning treatment was the whole-plot factor and year was the split-plot factor. Prior to analysis, numbers of individuals captured, or the minimum numbers known alive (Krebs 1966), were converted to an index of abundance, catch per 100 trap-nights (CPU) corrected for sprung trap (Nelson and Clark 1973) for our primary response variable. Preliminary tests of CPU ANOVA produced residual plots indicative nonlinear relationships and unequal variances for 6 of our 8 target species; thus, we transformed CPU by  $\ln(\text{CPU} + 1)$  and used  $\ln(\text{CPU} + 1)$  subsequent ANOVA for all 8 species (Sabina and Stafford 1990, Carey 1995, Carey and Johnson 1995, Carey et al. 1999a, Wilson and Carey 2000).

Understanding both numerical and structure demographic responses is important when examining effects of environmental variation and forest management on mammals (Maguire 1973; Van Horne 1981, 1983). Therefore, we used demographic measures (based on counts of individuals in our split-plot ANOVA model to determine whether the internal structure of populations influenced by effects of treatment, year, or their interaction.

Because many of our target species (deer mouse, creeping vole, red-backed vole) are known to have multiple litters and may breed in their birth-year (Kenagy and Barnes 1988), while others (shrews) may have more than 1 litter but are less likely to breed in their birth-year (Hawes 1977), determination of species-specific population processes of age-class survival, birth, death, and growth rates would require multiple samples per year (Lewellen and Vessey 1998). Instead, we derived estimates of 4 population parameters based on the relative abundances of age, sex, and breeding-classes. We viewed sex ratio (males/females) as an index to differential trappability and space use because males generally move farther and are more active than females (Verts and Carraway 1998, Aars and Ims 1999). We used age ratio (adults/all individuals) to identify habitat conditions that might function as sinks for dispersing animals (Van Horne 1981, 1983). We used fecundity ratio (female young/ breeding females) to represent reproductive attainment. We used breeding ratio (breeding females/all individuals) as an index of current production and as an indicator of the progression of the breeding season.

## RESULTS

### Vegetation

Three years following treatment, mosaics had significantly greater plant species richness and greater herb cover than controls (Table 1).

Table 1. Characteristics of understory vegetation in 8 variably thinned (mosaic) and 8 control stands, Puget Trough, Washington, USA, 1996.

Characteristic	Treatment				Independent sample <i>t</i> -test		
	Mosaic		Control		<i>t</i>	df <sup>a</sup>	<i>P</i>
	$\bar{x}$	SE	$\bar{x}$	SE			
Species richness	27	2	19	1	-4.050	14	0.001
Total cover	110	15	90	11	-1.055	13	0.311
<i>Gaultheria shallon</i>	23	3	27	6	0.734	14	0.475
<i>Polystichum munitum</i>	11	4	12	4	0.201	14	0.843
<i>Pteridium aquilinum</i>	12	3	5	1	-1.821	9	0.102
<i>Rubus ursinus</i>	8	2	3	1	-2.152	8	0.065
Ferns	24	7	18	5	-0.668	14	0.515
Herbs	27	2	15	2	-4.334	14	0.001
Trailing shrubs	15	4	9	1	-1.522	8	0.166
Low shrubs	28	3	35	6	1.100	14	0.290
Tall shrubs	16	3	13	3	-0.837	14	0.417

<sup>a</sup> df < 14 indicates Welch's approximate *t* was used due to unequal sample variances.

**Table 2.** Numbers of individuals of small mammal species captured in 8 control and 8 variably thinned (mosaic) stands in Puget Trough, Washington, USA, 1996–1997.

Species	Control		Mosaic	
	1996	1997	1996	1997
<i>Clethrionomys gapperi</i>	249	159	178	132
<i>Glaucomys sabrinus</i>	9	10	5	2
<i>Microtus longicaudus</i>	0	0	2	1
<i>Microtus oregoni</i>	130	52	261	145
<i>Mus musculus</i>	2	1	0	4
<i>Mustela erminea</i>	14	6	9	6
<i>Neurotrichus gibbsii</i>	34	54	16	42
<i>Peromyscus keeni</i>	24	19	3	0
<i>Peromyscus maniculatus</i>	177	64	298	93
<i>Scapanus orarius</i>	1	1	0	1
<i>Sorex bendirii</i>	1	2	2	7
<i>Sorex monticolus</i>	221	218	217	213
<i>Sorex trowbridgii</i>	215	440	213	380
<i>Sorex vagrans</i>	11	9	61	84
<i>Tamias townsendii</i>	42	17	65	49
<i>Tamiasciurus douglasii</i>	6	1	0	0
<i>Zapus trinotatus</i>	2	1	12	8
Total individuals	1,138	1,054	1,342	1,167
Catch per 100 trap-nights	9.1	8.4	10.9	9.3

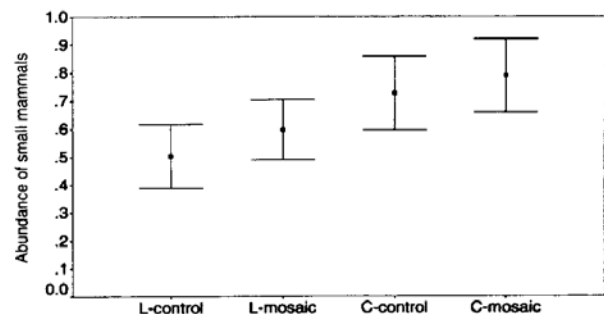
Cover of California blackberry (*Rubus ursinus*) and brackenfern (*Pteridium aquilinum*) were greater in mosaics, but with marginal statistical significance (Table 1). These differences were primarily due to growth of existing perennials and to rapidly colonizing herbs that responded positively to altered environmental conditions associated with opening the canopy and with forest floor disturbance. Other species and life-form groups did not develop appreciable differences between treatments (all  $P > 0.17$ ; Table 1).

### Small Mammal Abundance

We captured 4,701 individuals of 16 native and 1 introduced species of mammals during 1996–1997 (Table 2). The 8 target species comprised 94% of the total number of individuals captured. Conventionally thinned blocks had more individuals of these 8 species than legacy blocks; red-backed voles, creeping voles, and deer mice were most abundant in conventionally thinned blocks (Fig. 1, Table 3). Mosaics had 15% more individuals of the target species in 1996 and 10% more individuals in 1997 than controls; creeping voles, deer mice, and vagrant shrews were most abundant in mosaics (Fig. 1, Tables 2 and 3). Differences in total abundance of the target species between years

were not significant ( $F = 1.2$ ,  $df = 1;246$ ,  $P = 0.27$ ), and no year-by-treatment interaction occurred ( $F = 0.001$ ,  $df = 1;246$ ,  $P = 0.97$ ; Tables 2 and 3). But total abundance of target species differed among blocks ( $F = 82.06$ ,  $df = 1;3$ ,  $P = 0.002$ ) and between mosaics and controls ( $F = 31.8$ ,  $df = 1;3$ ,  $P = 0.01$ ). As predicted, increased spatial heterogeneity resulted in larger populations of small mammals associated with understory shrubs (deer mouse), herbaceous vegetation (creeping vole), and open canopies (vagrant shrew; Fig. 2b,d,h). Deer mice were 1.5 times as abundant, creeping voles >2 times as abundant, and vagrant shrews 6 times as abundant in mosaics as in controls. Furthermore, the increase in abundance of creeping voles in mosaics compared to controls was more striking in the legacy blocks—that had little preexisting understory vegetation—than in conventionally thinned blocks (Fig. 2b). Vagrant shrews, however, were relatively low in abundance overall and varied in abundance between years (Tables 2 and 3). We had not expected to catch many squirrels in our small traps, but we captured twice as many northern flying squirrels (*Glaucomys sabrinus*) in controls as in mosaics and 1.6 times more Townsend's chipmunks (*Tamias townsendii*) in mosaics than in controls (Table 2).

There were no significant treatment-by-year interactions for individual species, which suggested that differences in annual measures of abundance were related to external environmental factors and not to treatment (Table 3).



**Fig. 1.** Mean and 95% confidence intervals for combined abundance (In [individuals caught/100 trap nights + 1]) of the 8 most common small mammal species (*Clethrionomys gapperi*, *Microtus oregoni*, *Neurotrichus gibbsii*, *Peromyscus keeni*, *Peromyscus maniculatus*, *Sorex monticolus*, *Sorex trowbridgii*, and *Sorex vagrans*) in stands with old-growth legacies and no thinning (L-control), legacies and experimental variable-density thinning (L-mosaic), no legacies and conventional thinning (C-control), and no legacies, conventional thinning, and experimental variable-density thinning (C-mosaic) in the Puget Trough, Washington, USA, 1996–1997.

Species	Block (df = 3;22)		Treatment (df = 1;22)		Year (df = 1;22)		Treat X Year (df = 1;22)	
	F	P	F	P	F	P	F	P
<i>Clethrionomys gapperi</i>	16.11	0.024	3.50	0.158	8.16	0.009	0.80	0.380
<i>Microtus oregoni</i>	6.82	0.075	55.66	0.005	11.35	0.003	0.01	0.920
<i>Neurotrichus gibbsii</i>	1.02	0.493	2.65	0.202	7.08	0.014	0.10	0.756
<i>Peromyscus keeni</i>	1.05	0.483	1.60	0.295	0.04	0.852	0.06	0.814
<i>Peromyscus maniculatus</i>	7.61	0.065	10.10	0.050	38.74	0.000	0.46	0.505
<i>Sorex monticolus</i>	3.57	0.162	0.00	0.961	0.67	0.422	0.29	0.866
<i>Sorex trowbridgii</i>	0.24	0.866	0.59	0.497	31.30	0.000	0.47	0.501
<i>Sorex vagrans</i>	1.58	0.359	8.87	0.059	0.26	0.614	0.69	0.414

direction of significant species-specific variation in annual abundance was the same for both mosaics and controls (Table 2), and total captures were greater in 1996 than 1997 in each (Table 2). Three rodent species (creeping vole, deer mouse, and southern red-backed vole) were significantly more abundant in 1996; whereas, 2 insectivore species (shrew mole and Trowbridge's shrew) were significantly more abundant in 1997 (Table 3). Because of pronounced annual variation in abundance for some species, community structure differed between years under both treatments. Trowbridge's shrew was the most numerous small mammal under both treatments in 1997; however, during 1996, the red-backed vole was the most numerous species in controls and the deer mouse was the most numerous in mosaics.

### Population Structure

Over all species combined, we captured 1.4 times as many males as females (Table 4). Males were more numerous in controls than in mosaics and during 1996 than in 1997. Males were a higher proportion of the population for deer mice during 1997 ( $F_{1,19} = 7.00$ ,  $P = 0.016$ ), Trowbridge's ( $F_{1,22} = 24.6$ ,  $P < 0.001$ ) and montane shrews ( $F_{1,22} = 13.3$ ,  $P = 0.001$ ) during 1996, and montane shrews in controls in both years ( $F_{1,22} = 11.2$ ,  $P = 0.044$ ). However, captures of female montane, vagrant, and Trowbridge's shrews equaled or exceeded captures of males in mosaics during 1997, which suggested that (1) sex ratio did not reflect only greater movements by males; (2) male movements may have equilibrated with female movements in high-quality habitat in 1997; and (3) mosaics may support populations with greater reproductive potential than controls.

Similarly, the proportion of montane shrew females

breeding was 62% higher in mosaics ( $F_{1,22} = 13.8$ ,  $P = 0.034$ ) and overall 26% higher in 1997 than in 1996 ( $F_{1,22} = 4.3$ ,  $P = 0.049$ ). Deer mouse fecundity was 34% higher in mosaics ( $F_{1,19} = 7.3$ ,  $P = 0.074$ ), but creeping vole fecundity was 79% higher in controls ( $F_{1,17} = 10.2$ ,  $P = 0.05$ ). Thus, reproductive performance of the species differed although abundance of both increased in mosaics, which may indicate a density-dependent feedback on fecundity in creeping voles. A higher proportion of adults in deer mouse (28% higher;  $F_{1,22} = 6.44$ ,  $P = 0.019$ ), southern red-backed vole (12% higher;  $F_{1,22} = 20.0$ ,  $P \leq 0.001$ ), Trowbridge's shrew (28% higher;  $F_{1,22} = 20.4$ ,  $P = 0.001$ ), and vagrant shrew (63% higher;  $F_{1,16} = 5.4$ ,  $P = 0.034$ ) populations occurred in 1996 than in 1997; however, no differences due to treatment were observed.

## DISCUSSION

### Disturbance, Heterogeneity, and Biocomplexity

We predicted that small mammals would respond positively to inducement of spatial heterogeneity into forest canopies because (1) disturbance in previously unthinned stands would produce quick invasion by herbaceous plants, germination of seeds in the soil seed bank, and increased growth of existing shrubs and ferns (Thyssel and Carey 2000, 2001), thereby increasing diversity and abundance of food and cover; (2) disturbance in conventionally thinned stands would increase growth and fruiting of existing low vegetation (Thyssel and Carey 2000), again increasing food; (3) heterogeneity in the canopy would increase diversity of vegetation site types

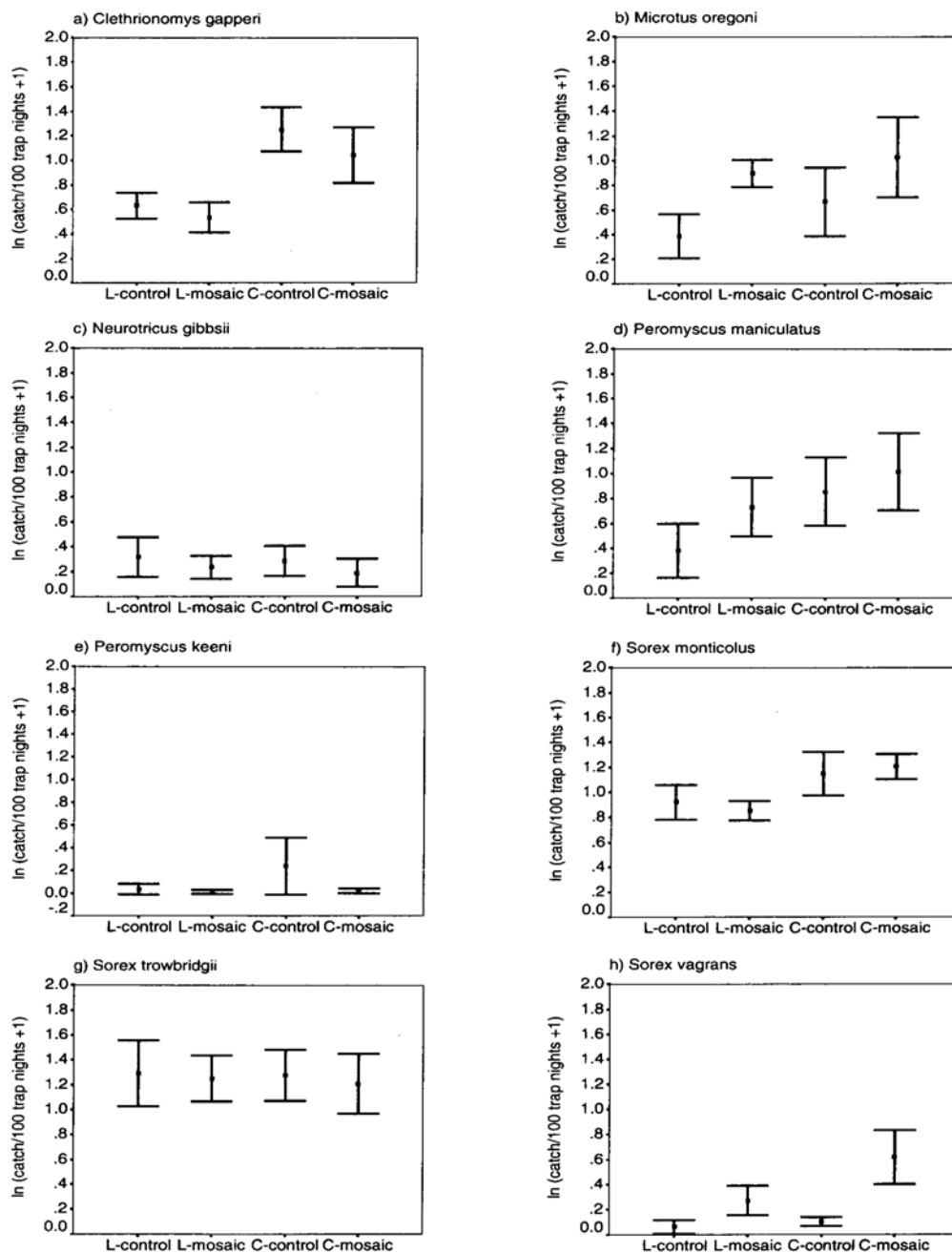


Fig. 2. Mean and 95% confidence intervals for abundances ( $\ln$  [individuals caught/100 trap nights + 1]) of small mammal species in stands with old-growth legacies and no thinning (L-control), legacies and experimental variable-density thinning (L-mosaic), no legacies and conventional thinning (C-control), and no legacies, conventional thinning, and experimental variable-density thinning (C-mosaic) in the Puget Trough, Washington, USA, 1996-1997: (a) southern red-backed vole (*Clethrionomys gapperi*), (b) creeping vole (*Microtus oregoni*), (c) shrew mole (*Neurotrichus gibbsii*), (d) deer mouse (*Peromyscus maniculatus*), (e) Keen's mouse (*Peromyscus keeni*), (f) montane shrew (*Sorex monticolus*), (g) Trowbridge's shrew (*Sorex trowbridgii*), and (h) vagrant shrew (*Sorex vagrans*).



Table 4. Number of male and female small mammals captured in 16 experimental stands in the Puget Trough, Washington, USA, 1996–1997.

Species	Numbers caught		Sex ratio (M/F)
	Male	Female	
<i>Clethrionomys gapperi</i>	428	288	1.5
<i>Microtus oregoni</i>	338	241	1.4
<i>Neurotrichus gibbsii</i>	71	51	1.4
<i>Peromyscus keeni</i>	30	15	2.0
<i>Peromyscus maniculatus</i>	373	257	1.5
<i>Sorex monticolus</i>	500	306	1.6
<i>Sorex trowbridgii</i>	647	526	1.2
<i>Sorex vagrans</i>	78	76	1.0

that contribute to biocomplexity and niche diversification (Carey et al. 1999a); and (4) in stands with old-growth legacies, the combination of large live trees, snags, and decaying logs, increased growth of the current even-aged cohort of trees, and a rapidly developing, complex understory and midstory would hasten niche diversification, allowing coexistence of simultaneously high populations of potentially competitive species (Carey et al. 1999a,b; Carey 2000, 2001; Carey and Harrington 2001). Sufficient time has not passed since experimental manipulation to fully evaluate these predictions; i.e., too little time has passed to allow midstory development (Thysell and Carey 2001).

Four years after treatment, total abundance of small mammals increased. Late-seral species, including the shrew mole, montane shrew, Trowbridge's shrew, red-backed vole, and Keen's mouse (West 1991, Carey and Johnson 1995, Songer et al. 1997) did not decrease in abundance, thus allaying fears that potentially sensitive small-mammal species might suffer short-term negative effects due to the mechanical disruption of thinning (Carey 2001). However, variable-density thinning did not produce small-mammal communities of the same structure and composition found in old-growth forests (Table 5; West 1991, Carey and Johnson 1995, Songer et al. 1997). Trowbridge's shrew, the montane shrew, and the southern red-backed vole had equivalent importances (rankings) in small-mammal communities in old growth and the experimental stands. Keen's mouse was either absent or in much-reduced abundance compared to old growth, and the deer mouse assumed greater importance in managed forest communities. The creeping vole and vagrant shrew also assumed higher importance, whereas the shrew mole decreased in importance compared to old growth.

The ecological conditions that allow coexistence of the deer mouse and Keen's mouse in high numbers are not fully understood but appear to be related to forest development, especially tall shrubs, deciduous shrubs and trees, midstory development, and coarse woody debris (West 1991, Carey and Johnson

Table 5. Small mammal community structure measured as octave-scale ranked abundances of species (ranks 0–6 with midpoints of 0, 2, 4, 8, 16, 32, and 64% of catch per unit effort) in old-growth forests on the Olympic Peninsula, 1987–1989, and Washington Cascade Range, 1984–1985, and second-growth forests historically managed with retention of old-growth trees and logs (Legacy) or conventional thinning (Con-thin) and experimentally treated with variable-density thinning to create heterogeneity (mosaics) or left to develop naturally (controls), Puget Trough, Washington, USA, 1996–1997.

Species	Olympic old growth <sup>a</sup>	Cascade old growth <sup>b</sup>	Puget Trough second-growth experimental stands			
			Legacy control	Legacy mosaic	Con-thin control	Con-thin mosaic
<i>Sorex trowbridgii</i>	5	5	5	5	5	5
<i>Peromyscus keeni</i>	4	4	1	1	2	1
<i>Sorex monticolus</i>	4	4	4	4	4	4
<i>Clethrionomys gapperi</i>	3	4	4	3	4	4
<i>Microtus oregoni</i>	3	3	3	4	3	4
<i>Peromyscus maniculatus</i>	1	3	3	4	4	4
<i>Neurotrichus gibbsii</i>	2	2	2	2	2	1
<i>Sorex vagrans</i>	1	1	1	2	1	3

<sup>a</sup> Adapted from Carey and Johnson (1995).

<sup>b</sup> Adapted from West (1991) as reported by Wilson and Carey (2000).

1995), and possibly to landscape conditions, including corridors, habitat contiguity, and edge effects (Songer et al. 1997). Research indicates that the presence of several particular species of trees, especially western hemlock, vine maple (*Acer circinatum*), and bigleaf maple (*A. macrophyllum*), not only adds to biocomplexity but also is an important determinant of the abundance of Keen's mouse (Carey and Harrington 2001). The vagrant shrew and creeping vole apparently responded positively to increases in herbaceous vegetation, whereas the shrew mole might not have responded to perturbation in the previously thinned stands simply because of the low abundance of coarse woody debris, and, thus, decreased in importance as other species increased in abundance.

We predicted that small-mammal populations in legacy stands would show a larger positive response to increased spatial heterogeneity than populations in conventionally thinned stands. This prediction proved correct for the creeping vole but not for the deer mouse, which increased even in conventionally thinned stands where deer mouse populations were already large (Wilson and Carey 2000). Total small-mammal abundance increased with number of thinnings and consequent increased plant species richness and understory cover. Legacy controls had the fewest animals—creeping voles were particularly restricted there because of the lack of herbaceous ground cover—while conventionally thinned stands that were experimentally thinned (thinned a total of 3 times) had the most animals (Fig. 1). The predictions of Carey and Johnson (1995)—that deer mice and creeping voles would increase with increasing cover of shrubs and herbaceous plants, respectively—are borne out by our study, as is the converse, that these species would be expected to decrease in abundance as the canopy closed in early seral stages and to remain low as long as competitive-exclusion stages persisted (Carey et al. 1999b).

Although Carey and Johnson (1995) did not report significant predictors for vagrant shrews other than a positive correlation with creeping voles, others found vagrant shrews to be most abundant in open areas dominated by herbaceous vegetation (Newman 1976, Hawes 1977, Terry 1981, Cole et al. 1998, Carey and Harrington 2001). The modest increase in vagrant shrew abundance on our treated sites was most likely stimulated by the patchy openings in the forest canopy. Variable-density thinning thus accelerated a mosaic of understory conditions and significantly increased the number of deer

mice, creeping voles, and vagrant shrews across a range of preexisting forest conditions as represented by our blocks while simultaneously creating a vegetation mosaic.

The increases we observed in small-mammal abundances were consistent with the creation of a mosaic of light, moisture, and temperature conditions leading to a more diverse and abundant understory plant community (Carey et al. 1999d). Numerous ecological benefits accompany increased small-mammal abundance, which include improved prey availability for reptiles, carnivores, and raptors; intensified dispersion of spores of fungi symbiotic with trees across the forest floor; and higher consumption rates of invertebrate pests, including Douglas-fir beetles (*Dendroctonus pseudotsugae*). Conventional thinning had apparent long-term (>10 yr) negative effects on northern flying squirrels and positive effects on Townsend's chipmunks (Carey 2000, Wilson and Carey 2000). Flying squirrel populations were further reduced by variable-density thinning in the short term (our study), but appeared to recover after 5 years while Townsend chipmunk populations increased further (Carey 2001).

We observed significant annual variation in abundance for 5 of 8 common small-mammal species. The direction of annual variation in species abundances was the same for controls and mosaics for all 5 species. Trowbridge's shrew was overall the most abundant species. However, in 1996, when captures of Trowbridge's shrew were relatively low, other species achieved numerical dominance—the red-backed vole in controls and the deer mouse in mosaics. No consistent negative ramifications of induced spatial heterogeneity on population stability were apparent. None of our demographic results indicated negative effects due to spatial heterogeneity; e.g., we found higher ratios of males to females in controls than in mosaics and greater population sizes in mosaics.

### Scope and Limitations

We studied small mammals in 1 age class of Douglas-fir forest in 1 physiographic province. Thus, the results of our study should be applied with caution to forests of different ages and in markedly different locations. Nevertheless, inferences from experimental studies are particularly valuable in the formulation of management methods and are more reliable and generalizable than cross-sectional surveys or ecological

correlations. Our experiment (Carey et al. 1999d), fully replicated, seems to be the first experiment to evaluate the efficacy of manipulating spatial heterogeneity to influence positively a carefully chosen array of life forms, such as vascular plants (Thysell and Carey 2000, 2001), fungi (Colgan et al. 1999), small mammals (our study), arboreal rodents (Carey 2000, 2001), and wintering birds (Haveri and Carey 2000). In addition, our experimental results support ecological correlations reported from previous, widespread cross-sectional surveys of natural and managed forests (e.g., Carey 1995, 2000; Carey and Johnson 1995; Carey et al. 1999a; Wilson and Carey 2000, Carey and Harrington 2001; ).

The induction of spatial heterogeneity in managed forests as a method of accelerating development of late-seral forest characteristics is as yet unproven ecologically and its social acceptability is unknown. Many of the expected structural, spatial, and synergistic properties will take decades to emerge. Because of the short elapsed time (3-4 yr) between treatment and measurement of effects for this report, the full projected benefits of variable-density thinning (Carey et al. 1999d) did not have time to develop. However, the changes we observed in the understory plant community following variable-density thinning, as compared to those following conventional thinning, seem to better mimic gap formation and promote heterogeneity in understory development (see also Thysell and Carey 2000, 2001).

Whereas variable-density thinning has been implemented on operational scales by the U.S. Army, Olympic National Forest, and Washington Department of Natural Resources (Carey, personal observations), it has not been evaluated economically in the field. But Lippke et al. (1996), using simulation models, predicted superior economic returns with ecosystem management based in part on variable-density thinning and long rotations. Thinning trials in the Pacific Northwest have developed reliable methods for producing large trees (Worthington and Staebler 1961, Worthington 1966), and there is indication that multi-species stands with multilayer canopies can be developed through thinning (Curtis and Marshall 1993:83, Maguire and Bennett 1996). If our predictions and those of others (e.g., Curtis 1995, Curtis and Carey 1996, Lippke et al. 1996, Carey et al. 1999b) hold true, long rotations combined with management of decadence and spatial heterogeneity could be advantageous for cost-effective timber production as well as providing an opportunity to manage for biotic integrity at the ecosystem and landscape scales.

## MANAGEMENT IMPLICATIONS

The short-term responses of small mammals to variable-density thinning provide support for the use of variable-density thinning to accelerate development of late-seral conditions in second-growth forests. Similar results have been obtained for various biotic communities, including soil food webs (Carey et al. 1996), hypogeous fungi (Colgan et al. 1999), vascular plants (Thysell and Carey 2001), wintering birds (Haveri and Carey 2000), and arboreal rodents (Carey 2001). Conventional thinnings might benefit bats (Humes et al. 1999), some small mammals (Carey 2000, Wilson and Carey 2000), birds (Hagar et al. 1996, Haveri and Carey 2000), and deer (Conroy et al. 1982). But conventional thinnings with even-spacing of trees might have negative effects on spotted owl prey (Waters and Zabel 1995, Carey 2000), fail to provide for the biotic integrity of small-mammal communities (Wilson and Carey 2000), decrease the abundance of amphibians (Grialou et al. 2000), and lead to homogenization and globalization of understory flora (Thysell and Carey 2000). Similarly, shelterwood harvests (timber harvests that leave a sparse overstory to be removed when regeneration is achieved) also have negative effects on spotted owl prey (Waters and Zabel 1995), although Von Trebra et al. (1998) found no effects on small mammals (but see the critique by Smith 1999 and rebuttal by Sullivan et al. 1999). Conventional thinnings are designed to (1) forestall mortality of trees due to crowding and remove subordinate, dying, and defective trees (thus decreasing snag production and coarse woody debris recruitment); (2) favor commercially valuable species (resulting in reduced tree species diversity); (3) maintain stocking at levels that maximize wood production (and concomitantly minimize solar energy diverted to understory development); and (4) maintain even spacing to produce an even-aged crop of trees of similar size and quality (and, inadvertently, a homogeneous understory often dominated by aggressive clonal species). All these goals are aimed at timber and fiber production and reduced biocomplexity. Even variable-density thinning with marking guidelines to promote species diversity, however, is not adequate for ecological restoration.

Management for spatial heterogeneity should be used in a management system that includes

(1) retention of biological legacies of large, live trees; large, dead, trees; coarse woody debris; and even intact patches of forest; (2) management of decadence to ensure cavity tree, snag, and coarse woody debris recruitment; (3) promotion of tree species diversity in the canopy, midstory, and understory (including deciduous species and shade-tolerant conifers in conifer forests); and (4) rotations >130 years (Carey 1995, Carey and Johnson 1995, Fra-nklin et al. 1997, Carey et al. 1999a,b,c). Variable-density thinning should not be standardized for systematic application; the approach must be tailored to site to achieve biocomplexity and biodiversity goals. For example, on the Olympic Peninsula, C. A. Harrington and A. B. Carey (Carey, unpublished data) implemented a variable-density thinning experiment using a variant called "thinning with skips and gaps" that allows protection of existing snags and reduces susceptibility of windthrow in dense, 40-70-year-old stands in an area of high frequency of windstorms. The long-term postulated effects of variable-density thinning (Carey et al. 1999d) have not been proven.

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