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Forest Ecology and Management 152 (2001) 13-30

Forest Ecology
and
Management

www.elsevier.com/locate/foreco

Experimental manipulation of spatial heterogeneity in Douglas-fir forests: effects on squirrels

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Received 1 April 2000; accepted 24 July 2000

Abstract

Squirrel communities simultaneously composed of abundant populations of *Glaucomys*, *Tamias*, and *Tamiasciurus* are: (1) a result of high production of seeds and fruiting bodies by forest plants and fungi and complexity of ecosystem structure, composition, and function; (2) indicative of high carrying capacity for vertebrate predators and (3) characteristic of old, natural forests in the Pacific northwest, USA. I hypothesized that silvicultural manipulation of canopies of second-growth forests could result in spatial heterogeneity that would reproduce the biocomplexity and plant-fungal productivity associated with high squirrel populations. I predicted that accelerating biocomplexity would require ≥ 20 years, but short-term effects of induced heterogeneity would be apparent in 5 years: initial decreases followed by increases in *Glaucomys* populations, nonlinear increases in *Tamias* populations, and little change in *Tamiasciurus* populations. If my predictions proved accurate, confidence in long-term predictions would be enhanced. I chose 16 13-ha stands with two different management histories for a randomized block experiment and began measuring squirrel populations in 1991. Variable-density thinnings were implemented in spring 1993. Fall and spring populations were measured through fall 1998. Populations responded as predicted, except for a treatment-management history interaction. Previous conventional thinnings altered ecosystem function such that low *Glaucomys* populations failed to respond to treatment. Variable-density thinning, in conjunction with retention of biological legacies and management of decadence, could possibly accelerate biocomplexity in second-growth forest that mimics that in old, natural forests. Published by Elsevier Science B.V.

Keywords: Biocomplexity; Forest ecology; *Glaucomys*; Silviculture; *Tamias*; *Tamiasciurus*; Squirrels

1. Introduction

A salient feature of old, natural, temperate and tropical forests is spatial heterogeneity that results from a history of disturbances ranging from catastrophic to local in scale, e.g. fires, windstorms, volcanic eruptions, disease epidemics, individual tree death, and individual tree fall (Franklin et al., 1987; Petraitis et al., 1989; Canham et al., 1990; Lertzman et al., 1996;

Nicotra et al., 1999). This spatial heterogeneity exists in the vertical (foliage height and life-form diversities), horizontal (light, moisture, and nutrient availability, canopy gaps, and patchy understories), and temporal dimensions (a shifting, more or less steady-state, mosaic) within biotic communities (Bormann and Likens, 1979; Spies and Franklin, 1989; Carey et al., 1999a). Heterogeneity at a scale appropriate to a particular ecological system can result in emergent properties resulting from synergism among system components (Odum, 1969), such as: (1) increased habitat breadth (diversity of vegetation site types. Whittaker et al., 1973) and pre-interactive niche diversification (increased

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multidimensional niche space allowing coexistence of species with similar life histories and resource utilization, Hutchinson, 1958, 1965, 1978) within communities (Whittaker et al., 1973; Whittaker and Goodman, 1979; Carey et al., 1999a); (2) increased diversity of species and complexity of habitats across communities (Whittaker, 1975; Tilman, 1999) and (3) permeability for dispersal and recolonization across shifting, steady-state, landscape mosaics (Pickett and Thompson, 1978; Carey et al., 1999b).

Traditional forest management often results in simplified forest ecosystems with loss of tree species diversity and habitat elements for vertebrates and invertebrates, such as dead trees (Perry, 1994, p. 557; Spence et al., 1999; Carey et al., 1999b); decreased biocomplexity, biodiversity, and resiliency (Canham et al., 1990; Franklin, 1993; Tilman, 1999; Carey, 2000); globalization of flora and increased invasibility for exotic plants (Heckman, 1999; Tilman, 1999; Thysell and Carey, 2000a); fragmentation of old, natural forest by simplified second-growth forests with concomitant negative effects on biological diversity and dispersal-colonization processes (Harris, 1984; Carey et al., 1992, 1999b); and reduced function, e.g. site productivity and carbon sequestration (Harmon et al., 1996; Ponge et al., 1998; Vogt et al., 1999). I reported that even new approaches to forest management can lead to homogeneity and reduced biocomplexity (Carey, 2000). But I also hypothesized that silviculture could be used in second-growth forest to achieve the same spatial heterogeneity that arises in natural ecosystems by emulating intermediate and small-scale disturbances, but in a shorter period than is required under natural conditions, ≥ 100 -200 years, depending on the nature of the catastrophic regenerative disturbance that originated the stand, particularly the degree of retention of biological components from the preceding forest (Carey et al., 1999c; Carey, 2000). Intermediate disturbances, either natural or silvicultural, however, potentially have widespread effects, not only over geographic areas but also across life forms and taxa. Short-term effects may differ significantly from long-term effects. Postulated benefits of manipulation of spatial heterogeneity are long-term-perturbations, by definition, disruptive of ecosystem processes in the short-term. To evaluate the effects of managerially induced heterogeneity on biocomplexity and biodiversity,

various response variables are required, many of which relate to the productivity and integrity of key biotic communities (Carey et al., 1999b, c). A key community in many forest ecosystems that is especially responsive to environmental conditions is the arboreal mammals (e.g. Carey, 1995; Pausas et al., 1997; Wauters and Dhondt, 1998; Taulman et al., 1998; Reunanen et al., 1999). For example, in the Pacific northwest, USA, the biomass of tree squirrels is a good measure of the carrying capacity of forests for predators; the reproductive activity of ectomycorrhizal fungi, trees, and shrubs (i.e. the production of truffles, seeds, and berries); spatial heterogeneity in canopy and understory; abundance of coarse woody debris; and potential for dissemination of fungal spores and propagules of mosses and lichens (for review see Carey, 2000). Indeed, various taxa of gliding tree squirrels now are threatened because of land management practices in China (Beijing, Yunnan), Finland, Himalayas, Malaysia, Nepal, Pakistan, Sumatra, Thailand, and USA (southeast and west) (Nowak, 1991).

In 1991, I began an experiment to accelerate development of late-seral conditions in young (55-65-year-old), managed Douglas-fir (*Pseudotsuga menziesii*) forest in the Puget Trough of Washington, USA (Carey et al., 1999c). I made the following predictions about the short-term (≤ 5 years) consequences of removing trees to produce a mosaic of various densities of trees within forest stands that would mimic the spatial patterns in old-growth Douglas-fir. The purpose of removing trees was not to create openings, but rather, by removing subordinate and codominant trees ('thinning from below'), to create a mosaic at a scale (0.2 ha patches) that, in conjunction with the low sun angles of the Pacific northwest, would produce a highly variable environment in the understory. The degree of thinning would not be enough to prevent future canopy closure; indeed, a subsequent thinning was planned for 10 years after the first (Carey et al., 1999c). My predictions were the following.

1. Killing and removing 30-40% of the trees (20-30% of the basal area) would: (a) reduce production of fungal sporocarps (truffles, a major food source for squirrels) by ectomycorrhizal fungi associated with those trees and total truffle production in the

production in the stand for 1-3 years until the remaining trees were able to capitalize on the newly available light, water, and nutrients through crown and root development; (b) disrupt canopy connectivity, destroy established canopy travel ways used by squirrels, damage some den trees, and change arrangement of habitat elements, placing squirrels in unfamiliar environments and increasing their susceptibility to predation by weasels (*Mustela* sp.), the major terrestrial predators of squirrels in the area; (c) have little immediate effect on seed production by retained dominant and codominant conifers except perhaps increasing the vulnerability of these trees to windstorms; increased physiological activity by trees that would stimulate seed (and truffle production) would be somewhat delayed because of the age of the trees to be retained and the size of live crowns (restricted by crowding) at time of thinning and (d) immediately damage existing understory, but quickly stimulate further development of understory plant communities.

2. Three species of indigenous squirrels would each respond differently in the short-term to remove trees and the collateral damage to plants, fungi, and other habitat elements: (a) populations of the principal mycophagist, the northern flying squirrel (*Glaucomys sabrinus*), would decline in response to decreased truffle production, mechanical destruction of den trees, and increased predation, but recover within 5 years as truffle production increased and travel ways and den sites were reestablished; (b) populations of the more sedentary and territorial conifer-seed specialist, the Douglas' squirrel (*Tamiasciurus douglasii*), would decline slightly because of mechanical destruction of den trees or remain the same and (c) populations of the semiarbooreal Townsend's chipmunk (*Tamias townsendii*), which eat conifer seed, fungal sporocarps, and the seeds and fruits of understory plants, would increase in abundance in response to increasing ground cover (protection from predation) and increasing seed and fruit production by shrubs in response to increased light levels.

In the long-term (10-20 years), the canopy would become more complex, canopy travel ways would be redeveloped by squirrels, and growth and

vigor of dominant and codominant trees would increase with concomitant increases in seed (Eis et al., 1965) and sporocarp production (for a review of the complex influences on truffle production see Colgan et al., 1999). Understory development would progress: (1) with concomitant increases in seed and fruit production, diversity of understory plant associations (increased habitat breadth), and abundance of understory plants (woody and herbaceous) but; (2) unevenly in vertical and horizontal dimensions. Populations of all three squirrels would increase.

My short-term predictions now have been evaluated. Colgan et al. (1999) confirmed short-term deleterious effects of the variable-density thinnings on truffle production (1 (a)). Carey et al. (1999c) documented the physical effects of the tree removal, including resistance to high (≥ 130 km/h) winds (1 (b) and (c)) and minor loss of den trees (Carey et al., 1997). Wilson and Carey (1996) documented heavy predation (1 (b)) on flying squirrels by weasels. Others reported on short-term effects on plants (1 (d); Thysell and Carey, 2000b in litt.) and forest-floor small mammals (Carey and Wilson, 2000 in litt.). In this paper, I report on the responses of the three squirrels over 8 years, 3 years pre-treatment and 5 years post-treatment (2 (a-c)).

2. Methods

After extensive surveys of study areas in western Oregon and Washington (Thomas et al., 1993), I contacted private and public landowners in western Washington and inspected the areas they had available for study and experimentation. I was particularly interested in homogeneously treated blocks of forests that would allow replication of experimental treatments. I found both a suitable study area and interested managers on Fort Lewis Military Reservation in Thurston County, Washington. The 6000-ha study area is just south of the Nisqually river and has low relief (100-140 m), precipitation averaging 91 cm per year, mild climate (minimum in January, temperatures range from 0 to 2.5°C), and second-growth Douglas-fir stands of various management histories. Its isolation from old-growth Douglas-fir forest eliminated potentially confounding effects of adjacency to old forest.

2.1. Experimental design

I chose four large management blocks ≤ 4 km apart and demarcated four 13-ha stands in each, ≥ 80 m apart. Stand size was more a result of past management, particularly road networks, than marked variation in vegetation. Eight of the 16 stands, two in each block, were randomly assigned for treatment with variable-density thinning. Each stand was subdivided by an 8 x 8 surveyed grid with grid points 40 m apart and a 40-m buffer around the grid. Grid points were used as sampling points for trapping squirrels and reference points for other sampling not reported here, e.g. vascular plants, truffles, and invertebrates. The 49 0.16-ha grid cells were used as treatment subplots to which various thinning intensities were randomly assigned. The buffers were lightly thinned (Carey et al., 1999c). Pre-treatment data were collected during 1991-1993; spatial heterogeneity was induced through variable-density thinning in spring, 1993. Squirrel responses were measured through 1998.

2.2. Historical management of experimental blocks

Two blocks were clear-cut ~ 1927 and thinned twice conventionally (light thinnings with approximately equal spacing between trees) before the age of 60 years and >10 years before this study (hereafter referred to as thinned blocks). Standing and fallen dead trees had been removed during cuttings. Coarse woody debris was scarce. Few trees (live or dead) from the preceding forest had been retained (<1 per ha combined). All the stands were well stocked (224-236 stems per ha) with large Douglas-fir (averaging 58-63 cm diameter at breast height, dbh). Understory cover (e.g. *Gaultheria shallon*, *Polystichum munitum*, *Pteridium aquilinum*, and *Rubus ursinus*) was high (87-89%). No significant regeneration of shade-tolerant conifers was found.

Two blocks were clear-cut ~ 1937 , but many live and dead trees had been retained from the preceding stand (hereafter referred to as legacy blocks). No further manipulation of stands had been undertaken except that a few retained old-growth trees that projected well beyond the canopy and that appeared to be hazards to helicopters had been felled and left on the forest floor 10 years before our study. Forest floors had several kinds of

several kinds of coarse woody debris: tall stumps of old-growth trees (averaging 48 per ha); old well-decayed, fallen trees (5.0-9.5% cover); a few lightly to moderately decayed felled old-growth trees; and abundant (2-4% cover) fallen small-diameter trees that had died from suppression or root rot (*Phellinus weirii*). Understory ranged from absent to moderate cover of salal (*Gaultheria shallon*) and other shrubs, averaging 17-19% cover with highest cover in pockets of root-rot infestation where most trees were dead or had reduced foliage. Many residual large snags (3.5 per ha) and large live trees (2.7 per ha) were still standing. Contemporary Douglas-fir were small (43 ± 2 cm dbh) and crowded (598-642 stems per ha). No shade-tolerant regeneration was found.

The 16 stands exemplified conditions found in present day forested landscapes in the Pacific northwest and managed under long (>60 years) rotations – intensive management for high-quality timber and extensive management with biological legacies retained from preceding stands. They were past the common harvest age for industrial forest lands (40-50 years) and approaching the age (>70 years) at which forests are commonly harvested on public lands (Carey et al., 1999b; Carey, 2000).

2.3. Experimental treatment

I designed an experimental variable-density thinning to create spatial heterogeneity in canopies of second-growth stands that would be similar to canopy heterogeneity that produced understory heterogeneity in old-growth forests. Understory heterogeneity is highly correlated with simultaneous high abundances of northern flying squirrels, Douglas' squirrels, and Townsend's chipmunks (Carey, 1995; Carey et al., 1999a). Variable-density thinning creates heterogeneity by: (1) removing sub-ordinate trees, and if necessary, codominant trees to reach a specified level of intertree competition for space and (2) varying the degree of retained competition among 0.16 ha subplots with the objective of reducing competition for light, moisture, nutrients, and space to an extent that these resources became available spatially in various amounts to other vegetation. Spacing among trees and size of subplots were derived empirically from comparative studies of

old- and second-growth forests (Carey, 1995; Carey et al., 1999a,c). The number of subplots was determined by the size of stands and was not an experimental criterion other than the requirement that the experiment be conducted on an operational and ecologically valid scale. Stand size in landscapes dominated by natural disturbance regimes in the Pacific northwest is a function of topography, the more dissected the topography, the smaller the homogeneous vegetation units. Most of the Pacific northwest is mountainous, and detailed examination of topography and vegetation in large landscapes has revealed mean stand sizes of 15-18 ha for young forests (Carey and Peeler, 1995); thus, our stand size was realistic.

For the measure of competition I used to determine the number of trees to remove was relative density (RD), the ratio of basal area to the square root of quadratic mean dbh, which is based on the relation of quadratic mean diameter, stem density, basal area, and intercrown competition of Douglas-fir (Curtis, 1982). RD ranges from 0 (no trees) to a species-specific biological maximum (14 for Douglas-fir); excessive crown restriction and suppression mortality occurs with $RD > 7$. My first decision was how to deal with existing canopy openings caused by root rot. Reconnaissance mapping revealed that $\leq 15\%$ of the area of any stand had reduced canopy density due to root rot. I decided to treat root-rot pockets by removing all trees with visibly reduced vigor ≤ 10 m from the edge of distinguishable pockets of infestation. This removal resulted in an $RD \approx 2$. Then, I randomly assigned thinnings to subplots until each treated stand had 15% of its area in $RD \approx 2$. The remaining subplots were assigned RD of six (light thinning) and four (heavy thinning) in about equal ratios. Buffers were assigned light thinnings. Post-thinning assessment revealed that operational errors by the contract logger (failure to fell trees in isolated subplots) resulted in an average of 14% of subplots retaining pre-thinning stocking of $RD \approx 8$. I considered the results to be a fully acceptable application of variable-density thinning to achieve the study goals of creating a mosaic of well-dispersed patches of various stocking of dominant trees with heavy and light stocking in ratio of 1:2. Hereafter, I refer to experimentally treated stands as legacy mosaics (from legacy blocks) or thinned mosaics (from thinned blocks) and experimentally untreated stands as legacy controls and thinned controls.

2.4. Response variables and analysis of outcomes

My study differed from a conventional randomized block design in that I was not interested especially in the values of the response variables (abundances) at any single point. Rather, I wanted to determine if the patterns in changes in abundances of the three species of squirrels over time in treated versus control stands were as I predicted they would be. I did not expect immediate responses to treatment to be sustained over time; rather the expected responses were: (1) no reaction to slight decrease followed by a slight increase for the Douglas' squirrel; (2) a non-linear increase in abundance of Townsend's chipmunk and (3) a decrease followed by a recovery of northern flying squirrels. I also recorded captures of the primary predator of flying squirrels and chipmunks in these second-growth forests-weasels (*Mustela* sp.) (Wilson and Carey, 1996).

Field experiments conducted outside a laboratory, such as mine, are confounded by historical and concomitant uncontrolled factors and thus are considered quasi-experiments (Cook and Campbell, 1979; Hoaglin et al., 1991; Johnson, 1999). I expected variation in populations in both treated and untreated stands owing to uncontrollable confounding factors (e.g. weather, predation, annual variation in food supply). Even though my study was large (real-world scale), replicates were few compared with requirements of determining normality and homoscedasticity; therefore, I did not analyze data with repeated measures analysis of variance.

Given strong similarities among stands within legacy blocks and within thinned blocks but strong differences between legacy stands and thinned stands (Carey et al., 1999c; Thysell and Carey, 2000a), I considered pooling the four blocks into two groups of samples. To determine if pooling was warranted, I: (1) diagrammatically compared variation in species abundances in pre-treatment and late (≥ 4 years) post-treatment samples for legacy mosaics, legacy controls, thinned mosaics, and thinned controls to assess homogeneity in response within pooled groups (E.D. Ford, personal communication) and (2) conducted an exploratory split-plot analysis of variance to look for contraindications to pooling, incorporating four blocks, two treatments (control, mosaic), two periods (pre-treatment and

post-treatment with two to three repeated samples each), interactions terms, and stands as covariates (Analytical Software, 1996) and a post-hoc analysis using Scheffe and Waller-Duncan homogeneous subsets (SPSS, 1997). Because abundances were essentially counts, some counts were zero, and variances of abundance seemed to be proportional to the size of the mean, I used the transformation $\ln(\text{ICPUE} + 1)$, where ICPUE is the number of individual captured per unit effort (100 trap nights) (Carey et al., 1991a; Carey, 1995, 2000).

After pooling blocks by management history, I calculated long-term mean abundances for legacy and thinned blocks using data from 13 sampling periods over 8 years for four control stands per pooled block; these means, then, served as a reference point against which populations responses to manipulation of spatial heterogeneity can be evaluated absolutely. I present box and whisker (median, quartiles, and two ranges) plots over 13 sampling periods that compare graphically relative differences between mosaic stands and controls, before and after treatment. I used Mann-Whitney tests to determine if treated and untreated stands, grouped by management history, differed within sampling periods. In all box and whisker presentations, separation of the 75% quartile (box top) of a box of a lower abundance from the 25% quartile (box bottom) of a box of higher abundance was statistically significant at $P < 0.05$ (Mann-Whitney test). Plots, sample sizes, means, standard errors, and 95% confidence intervals provide visual and numeric descriptions of the magnitude of change in species populations, and thus are superior to typical presentations of complex test statistics (Yoccoz, 1991; Cherry, 1998; Johnson, 1999).

As separate measures of demographic performance of the species in treated versus control stands, I examined: (1) differences in proportions of the fall adult populations that were females with external anatomical evidence of pregnancy or lactation (Carey, 1995) and (2) the proportions of total fall populations that were newly recruited, nulliparous females <1-year-old. Proportions were calculated by minimum number of individuals known to be alive.

2.5. *Sampling procedures and data generation*

Squirrels were trapped and captured data were analyzed following Carey et al. (1991a). I placed two Tomahawk 201 traps at each station

(one on the ground and one 1.5 m high in a tree; a total of 2048 traps); baited them with peanut butter, molasses, and oats, and left them open for two four-night periods separated by three nights in fall 1991, spring and fall 1992, fall 1993, and spring and fall 1995-1997, and fall 1998 (13 trapping periods totaling ~135,000 trap nights). I did not sample during spring 1993, because of disruption caused by logging; spring sampling was discontinued 5 years after treatment (1997). The effectiveness of these procedures has been demonstrated for northern flying squirrels and Townsend's chipmunks and have been widely used for Douglas' squirrels (Carey et al., 1991a; Carey, 1995, 2000). Trapping in 1991, however, was too late in the fall to trap Townsend's chipmunks.

I used ICPUE as an index to a species' abundance within a trapping grid with effort calculated as number of total trap nights minus one-half the numbers of sprung, but empty traps and traps containing animals (Nelson and Clark, 1973; Carey et al., 1991a, 1999a). This metric avoids multiplicative errors to estimate density that arise from mark-recapture calculations and estimates of mean maximum distances moved (MMDM) between subsequent recaptures (Skalski and Robson, 1992). And it reduces errors in estimating population size from simple counts that arise from reductions in trapping effort caused by wind, rain, and animals closing traps (Nelson and Clark, 1973). Number of individuals captured is a good predictor of population size (as estimated from various mark and recapture analyses) of flying squirrels and chipmunks over a wide range of densities in the Pacific northwest with $R^2 = 0.84$, slope = 1.1, and intercept = 0.0 for flying squirrels and $R^2 = 0.99$, slope = 1.1, and intercept = 0.0 for chipmunks in southwestern Oregon (Carey et al., 1991a) and $R^2 = 0.82$, slope = 1.16, and intercept = 1.07 for flying squirrels and $R^2 = 0.99$, slope = 1.07, and intercept = 0.0 for chipmunks, in the retrospective (baseline) phase of this study (Carey, 2000). Relatively few Douglas' squirrels were captured and recaptured in previous studies, and their densities have not been calculated by mark and recapture methods (Carey et al., 1991a; Carey, 1995, 2000). ICPUE can be a misleading index of density if a species exhibits significant differences in MMDM among sampling grids; therefore, I calculated MMDM and

tested for differences using 95% confidence intervals generated from marginal means estimated by a general linear model incorporating management history (blocks 1 and 2 versus 3 and 4), experimental treatment (experimentally thinned or not), and history by treatment interaction. Interspecific comparisons of abundance also can be misleading if species differ in MMDM; thus I calculated 95% confidence intervals by species.

3. Results

3.1. Capture data

I captured 3183 individual squirrels 8032 times in 13 trapping periods (Table 1). Differences among species in MMDM were not statistically significant (Table 1), the 95% confidence interval of 100-116 m for flying squirrels overlapped those for Townsend's chipmunks (89-106 m) and Douglas' squirrels (67- 100 m). Intraspecific confidence intervals overlapped considerably among treatment-history groups. This failure to demonstrate differences in MMDM between treatments and among species, however, could be artifactual because recaptures were often too few to reliably estimate MMDM especially for Douglas' squirrels and for flying squirrels in mosaic stands; 74% of Douglas' squirrel estimates, 34% of flying squirrel estimates, and 8% of chipmunk estimates had sample sizes too low for accurate estimation of MMDM. I caught 21 long-tailed weasels (*Mustela frenata*),

12 ermine (*M. erminea*), and two weasels unidentified as to species. Twenty weasels (14 long-tailed) were caught in the legacy forest; 13 weasels (eight ermine) were caught in the thinned forest. Captures ranged from two to seven weasels per year (4.4 ± 0.6 weasels) for 1992-1998 with lowest captures (two weasels) the year of thinning (1993) and peak captures (seven weasels) the year after variable-density thinning.

3.2. Pooling blocks

Preliminary analyses offered few contraindications to pooling blocks by management history. Comparison of pairs of stands from the two blocks in each treatment group (Fig. 1) revealed no consistent differences in patterns of response. Split-plot analysis of variance with four blocks showed no effect of treatment ($F = 2.27$, $df = 1, 82$; $P = 0.23$) and strong block effects ($F = 1027.74$, $df = 3, 82$; $P < 0.01$) for flying squirrels with legacy blocks and thinned blocks in different homogeneous Waller-Duncan subsets ($P < 0.05$; Scheffe $P = 0.11$). Douglas' squirrels also showed no effect of treatment ($F = 3.25$, $df = 1, 82$; $P = 0.17$) and strong block effects ($F = 171.5$, $df = 3, 82$; $P < 0.01$), also with blocks falling into homogeneous Waller-Duncan subsets reflecting management history ($P < 0.05$; Scheffe $P = 0.06$). Chipmunks, however, showed effects of both treatment ($F = 9.48$, $df = 1, 66$; $P = 0.05$) and blocks ($F = 37.26$, $df = 3, 66$; $P < 0.01$) with legacy blocks grouped and thinned

Table 1
Squirrel mark and recapture statistics for 13 trapping periods in 16 stands, 1991-1998, Fort Lewis, Washington

Statistic	<i>Glaucomys sabrinus</i>	<i>Tamias townsendii</i>	<i>Tamiasciurus douglasii</i>
Total captures and recaptures (<i>N</i>)	1720	5722	590
Total individuals captured (<i>N</i>)	1019	1786	378
Individuals captured/stand/period			
O \pm S.E.	4.9 \pm 0.3	9.3 \pm 0.5	1.8 \pm 0.1
Range	0-21	0-34	0-12
Mean maximum distance moved between subsequent recaptures			
Number of estimates (<i>N</i>)	138	177	55
O \pm S.E. (m)	108 \pm 4	94 \pm 3	83 \pm 8
Naive density (individuals per ha) ^a	0.3 \pm 0.0	0.7 \pm 0.0	0.1 \pm 0.0

^a Individuals captured divided by area sampled calculated as the square of the grid width plus the mean maximum distance moved between subsequent recaptures.

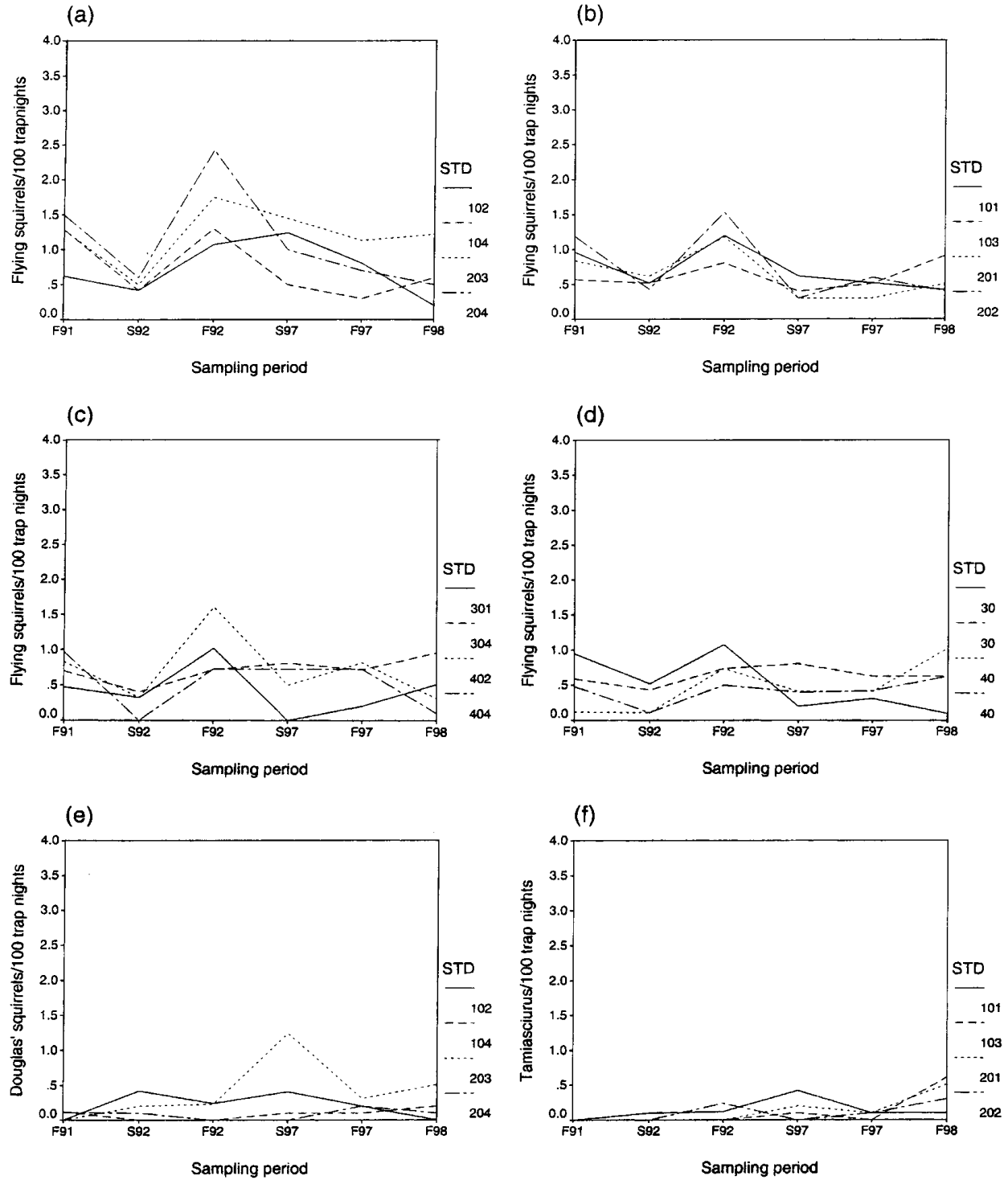


Fig. 1. Pre-treatment (fall 1991-1992) and 5-6 years post-treatment (spring 1997-fall 1998) abundances (individuals captured/100 trap nights) of northern flying squirrels (*Glaucomys sabrinus*) in experimentally manipulated and control stands: (a) legacy controls; (b) legacy mosaics; (c) thinned controls; (d) thinned mosaics, and Douglas' squirrels (*Tamiasciurus douglasii*) in; (e) legacy controls; (f) legacy mosaics; (g) thinned controls; (h) thinned mosaics, and Townsend's chipmunks (*Tamias townsendii*) in; (i) legacy controls; (j) legacy mosaics; (k) thinned controls and (l) thinned mosaics. Stand numbers reference paired stands in different blocks (100, 200, 300 and 400 s).

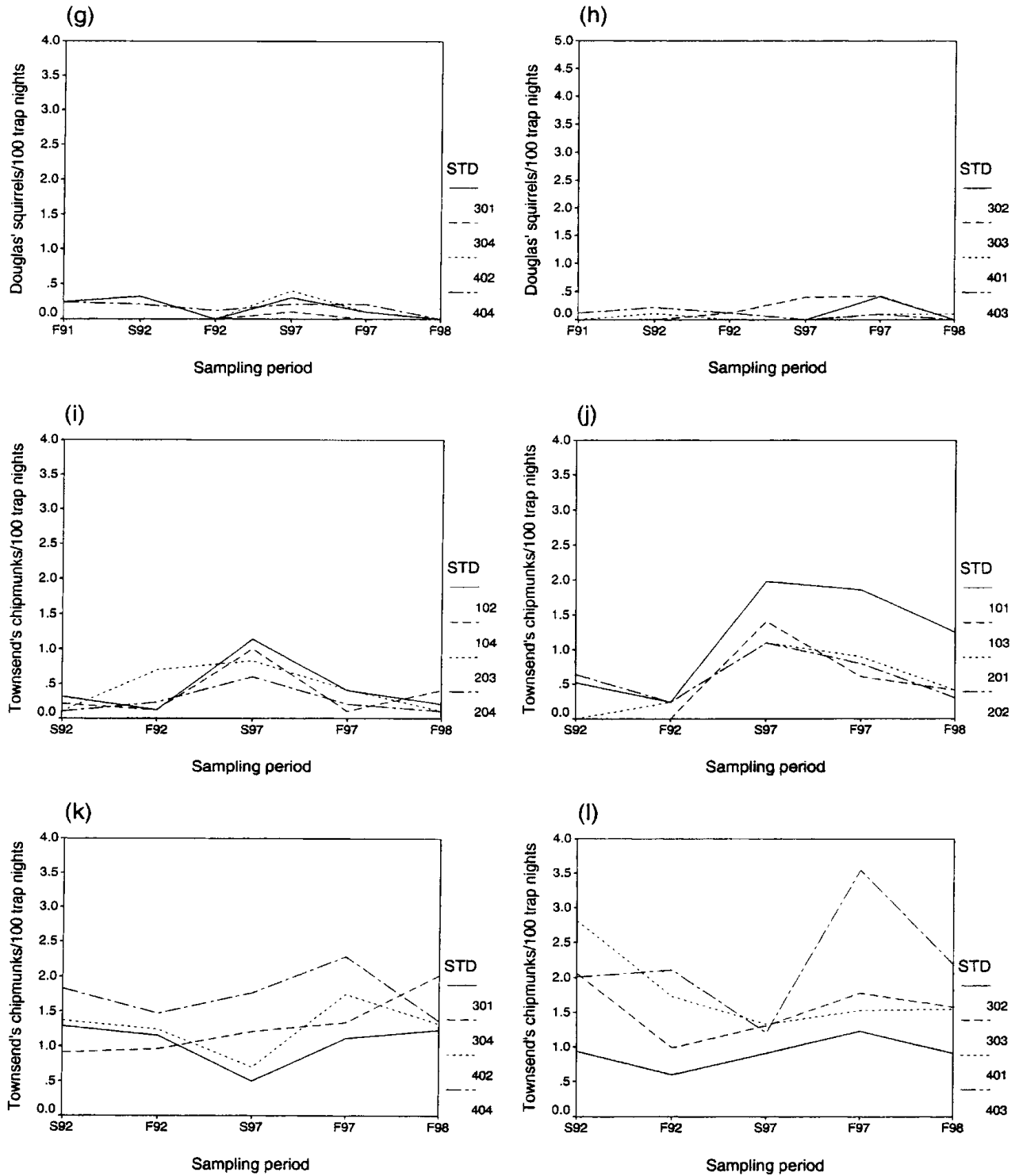


Fig. 1. (Continued).

Table 2

Carrying capacities (based on 12 or 13 sampling periods in 8 years in eight control stands of two different management histories, 1991-1998) and abundances in experimentally treated stands for three seasons (spring 1997, fall 1997 and 1998) >5 years after treatment for northern flying squirrels (*Glaucomys sabrinus*), Douglas' squirrels (*Tamiasciurus douglasii*), and Townsend's chipmunks (*Tamias townsendii*) on Fort Lewis, Washington

Species	Management history	95% Confidence interval for carrying capacity (mean individuals/100 trap nights)				95% Confidence interval >5 years post-treatment abundance (mean individuals/100 trap nights)			
		<i>n</i>	Lower bound	Mean	Upper bound	<i>n</i>	Upper bound	Mean	Lower bound
Flying squirrel	Legacy	52	0.68	0.82	0.97	3	0.57	0.48	0.39
	Thinned	56	0.42	0.51	0.60	3	0.60	0.50	0.40
Douglas' squirrel	Legacy	56	0.19	0.27	0.34	3	0.39	0.21	0.03
	Thinned	56	0.10	0.13	0.17	3	0.27	0.13	0.00
Townsend's chipmunk	Legacy	52	0.15	0.33	0.41	3	1.48	1.01	0.54
	Thinned	52	1.26	1.44	1.63	3	1.83	1.59	1.35

discrete in Waller-Duncan subsets ($P < 0.05$) and blocks grouped by management history in Scheffe subsets ($P < 0.05$).

3.3. Block and treatment effects

Stand management history affected flying squirrel mean abundances in control stands (Table 2 and Fig. 2). Eight-year (13-period) average abundance ($O \pm S.E.$ individuals captured/100 trap nights) for flying squirrels was 0.82 ± 0.07 in legacy controls and 0.51 ± 0.05 in thinned controls (Table 2). There was treatment-history interaction with abundances in legacy mosaics significantly lower than in legacy controls for seven periods after treatment but only two of 10 post-treatment estimates differed between thinned mosaics and thinned controls. Significant annual variation in abundance occurred in both control and mosaic stands, including decreased population abundances in both legacy controls and legacy mosaics more than 5 years after treatment compared with pre-treatment abundances. As predicted, flying squirrel abundance in legacy mosaics dropped below the 8-year mean in legacy controls (0.82) and pretreatment control levels immediately after treatment in winter 1993 and did not recover to match mean control values until fall 1997 (Fig. 1 a). The mean of period-mean abundances for the three periods sampled more than 5 years after treatment (spring 1997, fall 1997 and 1998) was less than the 8-year mean for controls (Table 2); the 95% confidence interval for fall 1998 ($O \pm S.E. = 0.56 \pm 0.12$), however, overlapped the confidence

interval for the 8-year mean. Flying squirrel abundances in thinned mosaics were less than abundances in thinned controls only in fall 1994, spring 1996, and fall 1996 (Fig. 1b), but remained lower than 8-year mean for legacy controls in all post-treatment periods. Box plots (and Mann-Whitney tests) showed no significant differences among legacy and thinned blocks, mosaic and control stands, or years for percentages of the fall populations ($n =$ fall populations with sufficient captures to estimate percentages) that were nulliparous young females ($19 \pm 2\%$, $n = 120$) and breeding adult females ($41 \pm 3\%$, $n = 113$).

Eight-year mean abundances for chipmunks were 1.4 ± 0.09 in thinned controls and 0.3 ± 0.4 in legacy controls (Table 2 and Fig. 3), a pattern opposite of that of flying squirrels. Chipmunks also exhibited annual variation in abundance. Chipmunk populations responded positively to treatment in legacy mosaics but not in thinned mosaics. As predicted, chipmunks in legacy mosaics began increasing 1 year after treatment (fall 1994) and exceeded populations in legacy controls in the three periods 5 years after treatment. In thinned blocks, populations in mosaics exceeded control populations only in fall 1996. Box plots showed no block, period, or treatment differences in percentages of the fall populations that were nulliparous young females ($25 \pm 2\%$, $n = 110$) and breeding adult females ($25 \pm 2\%$, $n = 100$).

Douglas' squirrel populations were the lowest of the three species (Fig. 4). Long-term mean

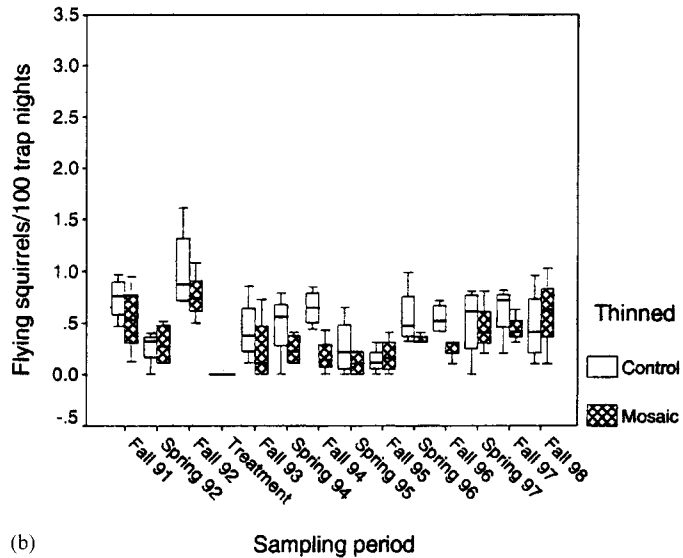
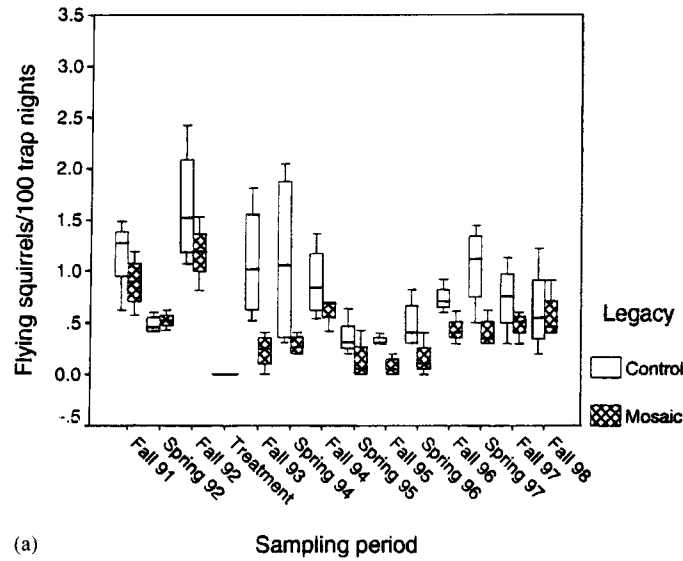


Fig. 2. Flying squirrel (*Glaucomys sabrinus*) abundances in fall and spring sampling periods in: (a) legacy stands and (b) thinned stands before and after manipulation of spatial heterogeneity with variable-density thinning in period 4 (spring 1993, no data collected) in the Puget Trough, Washington, fall 1991–1998; non-overlap of boxes indicates statistically significant differences ($P < 0.05$, Mann-Whitney tests).

Abundances were 0.27 ± 0.04 in legacy controls and 0.13 ± 0.02 in thinned controls. There were no apparent effects of treatment on Douglas’ squirrels. Percentages of fall populations, that were nulliparous young females, were $27 \pm 3\%$ ($n = 90$), and breeding adult females were $39 \pm 5\%$ ($n = 74$).

4. Discussion

4.1. Predictions about squirrels

Evaluation of experimental outcomes of long-term experiments are aided by explicit a priori rationale and predictions (for this study see Carey et

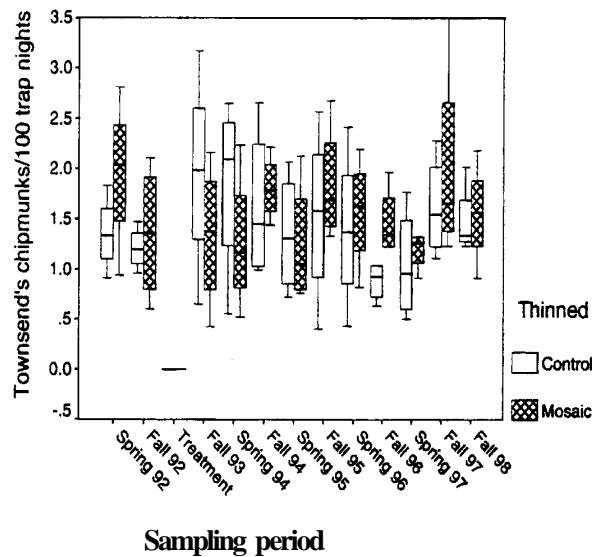
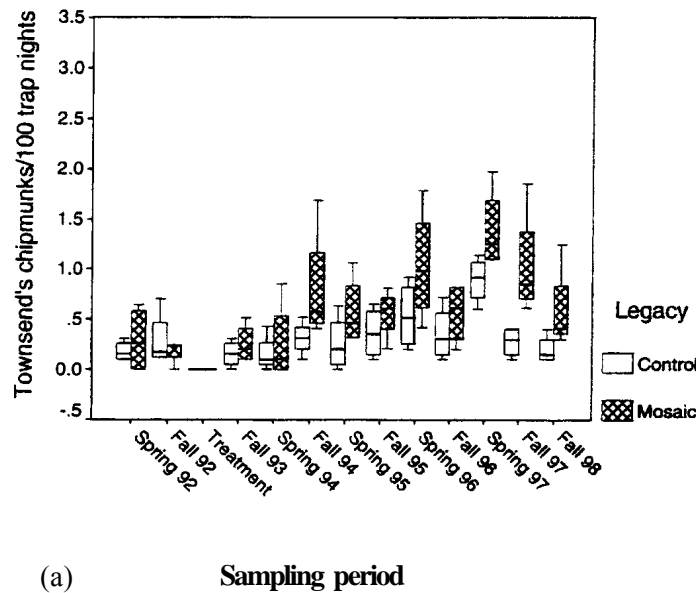


Fig. 3. Townsend's chipmunk (*Tamias townsendii*) abundances in spring and fall sampling periods in: (a) legacy stands and (b) thinned stands before and after manipulation of spatial heterogeneity with variable-density thinning in period 4 (spring 1993, no data collected) in the Puget Trough, Washington, spring 1992–fall 1998; non-overlap of boxes indicates statistically significant differences ($P < 0.05$, Mann-Whitney tests).

al., 1999c) and computer simulations of putative processes that produce predicted outcomes (for this study see Carey et al., 1999b). Because manipulative experiments of forest ecosystems are expensive, long-term, and unwieldy, matching observed outcomes to predicted outcomes over time can provide useful insights into ecosystem processes and implications for management. Population decreases, followed by recovery to control

levels, of flying squirrels in the legacy mosaics is my most significant finding. This finding supports variable-density thinning as an aide to restoring late-seral forest conditions (large trees, complex understories) in second-growth forests without significant long-term negative effects on the main prey of the threatened spotted owl (*Strix occidentalis*). But it also suggests caution in simultaneous widespread application of variable-density

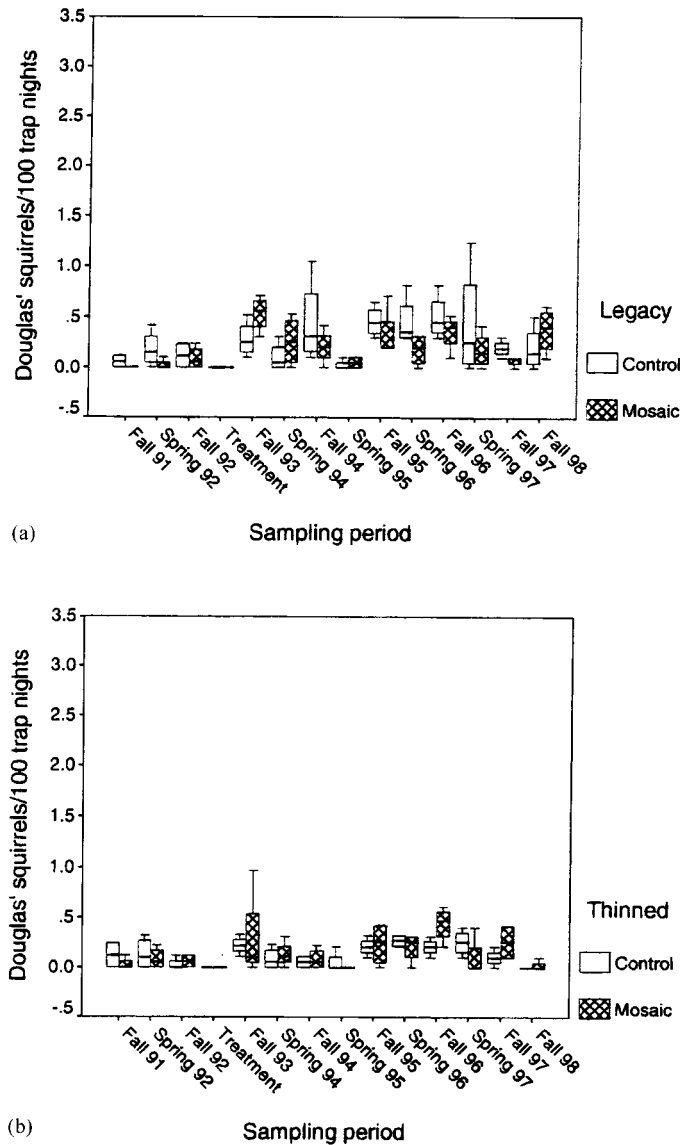


Fig. 4. Douglas' squirrel (*Tamiasciurus douglasii*) abundances in fall and spring sampling periods in: (a) legacy stands and (b) thinned stands before and after manipulation of spatial heterogeneity with variable-density thinning in period 4 (spring 1993, no data collected) in the Puget Trough, Washington, fall 1991-1998; non-overlap of boxes indicates statistically significant differences ($P < 0.05$, Mann-Whitney tests).

thinning in areas that might be crucial to the survival of particular owls. It remains to be seen if flying squirrels will increase to and beyond pre-treatment levels as predicted. The failure of flying squirrels to decrease in abundance after experimental manipulation in the previously thinned stands was unexpected. Tree crowns in the previously thinned forest were already relatively well separated, and flying squirrel populations were already low (Carey,

2000); thus the effect of any additional canopy disruption on flying squirrel populations was hard to detect.

I had not predicted treatment-history interaction; in hindsight, I should have. The understory development in previously thinned stands provided for many, but not all, of the projected short-term benefits of manipulation of spatial heterogeneity to Townsend's chipmunk, i.e. stimulating

development of existing understory to provide protective overhead cover and food in the form of fruits, seeds, and nuts. Thus, the failure of Townsend's chipmunk to rapidly increase in abundance in previously thinned stands is understandable. The rapid increase in chipmunks in legacy stands was as predicted by me and others, such as Harestad (1991), who experimentally demonstrated selection of protective cover by chipmunks.

The response of Douglas' squirrels was as expected, no measurable change. Douglas' squirrels quickly respond reproductively to increasing conifer seed availability on an annual basis and emphasize stable populations by strongly defending territories large enough to allow caching of food in sufficient quantities to allow survival during years of low cone crops (Smith, 1970). Seedfall is abundant in Douglas-fir only sporadically, about every 7 years (Hermann and Lavender, 1990). Significant increases in food production for Douglas' squirrels would develop with increased understory diversity of seed (e.g. *Acer* sp.) and nut-bearing (*Corlyus cornuta*) deciduous shrubs and trees and shade-tolerant conifers (e.g. *Tsuga heterophylla* or *Abies grandis*).

4.2. Demographic data

My other demographic measures did not contradict conclusions implied by population size (Maguire, 1973; Whittaker and Goodman, 1979); rather proportions of fall adult populations of northern flying squirrels that were breeding females were higher, and densities lower, than previously reported for old-growth forests in Washington and, especially, Oregon (Carey, 1995; Villa et al., 1999). Females in the low-density Puget Trough populations matured at an earlier age, and a greater proportion of mature females bred, but survivorship was lower for all age classes than in high-density populations in Oregon old-growth. The Puget Trough squirrels apparently were responding to relatively harsh environments with extraordinarily low carrying capacities (Carey, 1995, 2000) with increased reproductive effort that could aid in recolonizing habitat of extirpated populations or replacing adults in high-turnover populations. Truffle biomass was low in control stands, about 65% of what would be found in western hemlock (*Tsuga heterophylla*) old-growth in

Washington and only 10-20% of the biomass in Douglas-fir old-growth in Oregon (Colgan et al., 1999). In 3 years after variable-density thinning, truffle biomass in treated stands was one-half that in controls. Predation was high with 32% of radiocollared flying squirrels killed by Weasles in winter (1992, 1993) before thinning; subsequently, winter mortality averaged 25-58% (Wilson and Carey, 1996). Oregon old-growth squirrels had responded to apparently stable, high carrying capacities by adopting a strategy that emphasized high density and survivorship and minimizing energy diverted into reproduction. Spotted owls may consume the bulk of flying squirrels newly recruited into old-growth populations (Forsman et al., 1994). Whereas spotted owls occasionally (e.g. in selected stands in breeding years) may reduce flying squirrel populations in old-growth by 50% (Carey et al., 1992), populations rarely fall to the levels measured in the Puget Trough (this study), where predation by spotted owls is absent but predation by weasels evidently is severe (Wilson and Carey, 1996). Comparable data on the Townsend's chipmunk and Douglas' squirrels have not been published, although Puget Trough chipmunk populations also had higher proportions of females breeding than in old-growth forests in Washington (Carey, 1995).

4.3. Vegetation development

Conventional thinning produced understories in the thinned blocks that lacked the habitat breadth (vegetation site-type diversity) favored by flying squirrels (Carey, 1995; Carey et al., 1999c). It remains to be seen if my experimental manipulation of spatial heterogeneity can overcome the management history that favored homogeneous, dense, low understory (Thysell and Carey, 2000a). Of particular interest will be whether or not a shade-tolerant midstory will develop, even with underplanting of shade-tolerant trees in heavily thinned areas. Shade-tolerant midstory conifers may control understory light levels even more than overstory conifers do, and are major determinants of understory heterogeneity (Carey et al., 1999a). Recruitment of shade-tolerant trees into the overstory may be necessary to restore canopy connectivity in multiply thinned

stands, as Douglas-fir does not have the capacity to develop wide enough crowns to fill canopy gaps between mature trees (J.F. Franklin, personal communication). The conventionally thinned stands also lacked coarse woody debris and other legacies important to fungi and squirrels (Carey et al., 1999a), the lack of which may have contributed to low flying squirrel populations in multiply thinned stands. It remains to be seen if continued understory development in close spatial conjunction with coarse woody debris in legacy stands will have synergistic effects on chipmunk and flying squirrel populations and raise their populations beyond those in the thinned stands and up to levels in Douglas-fir old-growth (Carey, 1995, 2000).

4.4. Synergy

An important feature of late-seral forests is synergy that arises from close spatial juxtaposition of various habitat elements in a mosaic of varying vegetation structure. Many of these elements are low in abundance in second-growth forests. An example of this synergy is pre-interactive niche diversification (Hutchinson, 1958, 1978), diversification that promotes simultaneously high populations of diverse vascular plants (Canham et al., 1990; Spies and Franklin, 1991; Carey et al., 1999a), ectomycorrhizal fungi (Perry et al., 1989; Colgan et al., 1999), cavity-using birds (Carey et al., 1991b), arboreal sciurids (Carey, 1995; Carey et al., 1999a), forest-floor small-mammal communities (Carey and Johnson, 1995), and other life forms (Carey et al., 1996) that together form an unexpectedly high abundance of prey for terrestrial and avian predators (Carey et al., 1992, 1999a,b,c). Recent research has shown that traditionally managed forests (e.g. Perry, 1998; Curtis and Carey, 1996; DeBell et al., 1997) and forests managed under new strategies (Franklin, 1993; Franklin et al., 1997; Carey, 2000) may not achieve the various emergent properties necessary for sustainable production of the multiple ecologic and economic benefits desired by society. In this paper, I focused on one aspect of forest ecosystems — spatial heterogeneity in the canopy that promotes heterogeneity in habitat breadth (understory structure and composition) (Carey et al., 1999a). Management of decadence (decay in live trees, standing dead trees, and fallen trees and accumulation of dead biomass in soil organic matter, litter, fine woody debris, and coarse

woody debris; Harmon et al., 1986) is equally important (Carey et al., 1999a). Extension of rotation length (Curtis and Carey, 1996), active riparian management (Reeves et al., 1995; Carey et al., 1999b), and variable-retention harvest methods (Franklin et al., 1997) are key landscape management tactics that maintain diversity through undisturbed refugia and permeability (for gene flow, immigration, emigration, and recolonization by species of limited mobility) through minimizing inhospitable competition-exclusion stages and maximizing diverse late-semi stages (Carey et al., 1999b).

4.5. Scope and limitations

I studied populations of three species of squirrels in one age class of Douglas-fir forest in the Puget Trough of Washington; the magnitude of effects I recorded should not be extrapolated to forests of markedly different character (e.g. age classes or seral stages) or in different settings (e.g. physiographic provinces or vegetation zones). Distant areas would not contain the same species of squirrels, and other species of arboreal rodents and marsupials will have unique niches; nevertheless, arboreal mammals, collectively, would provide useful guidance in developing ecological forest management systems. I studied the responses of squirrels for only 6 years post-treatment; insufficient time had elapsed for the full projected responses of the plant, fungal, and animal communities to occur. Prospective experiments in manipulating forest ecosystems at real-world scales take decades, if not a century, to fully evaluate (Carey et al., 1999c). Although, many of my predictions were confirmed and, thus, my confidence in out-year predictions increased, some predictions did not come true, and I have not demonstrated that projected out-year benefits of manipulating spatial heterogeneity are certain.

5. Conclusions

Management for spatial heterogeneity with variable-density thinning on a ≈ 0.2 ha scale, retaining 1:1-2:1 ratios of relative densities of RD 6 and 4 with $\leq 15\%$ of the stand in patches of RD 2

and 8, may help accelerate development of the later-seral forest characteristic of niche diversification in second-growth Douglas-fir forests. Success in achieving niche diversification may depend on degree of legacy retention, effective management of decadence, and supplementing existing natural vegetation with underplanting of shade-tolerant conifers in natural or created gaps (Carey and Curtis, 1996; Carey et al., 1999c). Negative short-term effects on flying squirrels (primary prey for spotted owls and many mustelids) should be expected, and widespread simultaneous application of variable-density thinnings to forest stands making up habitat conservation areas should be avoided. As predicted, prey-base populations (total biomass of squirrels) should be enhanced within 5 years. Repeated conventional thinnings (with even spacing) do not hold this promise and may place a stand on an undesirable trajectory of forest development with reduced understory diversity (Carey et al., 1996, 1999c; Carey, 2000; Thysell and Carey, 2000a). Withdrawing a forest from active management after clearcutting, even with substantial legacy retention, may not achieve multiple ecosystem management goals either (Carey, 2000; Haveri and Carey, 2000; Wilson and Carey, 2000, this study). Active management beginning at the time of regeneration harvest might reduce the short-term impacts of variable-density thinning and decreased canopy connectivity later in the life of the stand. Variable-density thinning alone may not meet multiple goals; extended rotations (≥ 130 years), legacy retention, and variable retention harvest systems may be necessary for effective landscape management.

Acknowledgements

This research was supported by the USDA National Research Initiative, US Army, Fort Lewis, and the Ecosystem Processes Research Program, Pacific Northwest Research Station, USDA Forest Service. I thank Todd Wilson and Bruce Haveri for assistance in data analysis and in the field. I also thank Greg Braden, Stacey Brewster, Regine Carey, Dave Johnson, Charley Knox, Angela Lovato, Lisa Villa, Suzanne Wilson, and Laurie Wunder for assistance in the field. I thank Bob Curtis, Dean DeBell, Jerry Franklin, and Connie Harrington for

numerous useful discussions. I thank John Hayes, Chris Maguire, and John Marzluff for reviews of an earlier manuscript; E. David Ford provided a cogent statistical review.

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