

Small mammals in young forests: implications for management for sustainability

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Abstract

Small mammals have been proposed as indicators of sustainability in forests in the Pacific Northwest and elsewhere. Mammal community composition and species abundances purportedly result from interactions among species, forest-floor characteristics, large coarse woody debris, understory vegetation, and overstory composition. Coarse woody debris is thought to be particularly important because of its diverse ecological functions; covers from 10 to 15% have been recommended based on retrospective studies of forests and small mammals. Unfortunately, ecological correlations are not necessarily indicative of causal relationships and magnitudes depend on composition of finite, usually non-random, cross-sectional samples. Retrospective studies must be replicated to confirm relationships. We conducted a large-scale, cross-sectional survey of 30- to 70-year-old coniferous forests in western Washington to determine if previously reported relationships would hold with an unrelated, larger sample. Coarse woody debris cover was $8.3 \pm 0.6\%$ ($O \pm S.E.$, $n = 8$ blocks of forest, range 4-13%). Understory cover was too low ($18 \pm 8\%$ for shrubs) to allow examining interactions between understory and coarse woody debris. Overstory composition covaried with coarse woody debris. One or two of four statistically extracted habitat factors (overstory composition, herbaceous cover, abundance of *Acer circinatum*, and abundance of *Acer macrophyllum*) accounted for 18-70% of variance in abundance of 11 mammal species. Our results support hypotheses that: (1) biocomplexity resulting from interactions of decadence, understory development, and overstory composition provides pre-interactive niche diversification with predictable, diverse, small-mammal communities; (2) these communities incorporate numerous species and multiple trophic pathways, and thus, their integrity measures resiliency and sustainability. © 2000 Elsevier Science B.V All rights reserved.

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1. Introduction

Growing demand world-wide for forest management transcends timber and wildlife management and addresses values related to biodiversity and sustainability (Reid and Miller, 1989; Goodland, 1995; Folke et al., 1996; Kohm and et

al., 1996; Kohm and Franklin, 1997; Costanza et al., 2000). People are demanding ecologically based forest management (Hunter, 1990; Swedish National Board of Forestry, 1990; Plochman, 1992; Ray, 1996; Kennett, 1998). But, we have little experience in intentionally managing ecosystems simultaneously for diverse values, including wood, water, fish, wildlife, highly varied recreation, economic activity in local communities, revenues for schools and roads, assimilation of anthropogenic emissions and by-products (e. g., carbon sequestration), biotic

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integrity, biodiversity, open space, esthetics, and other abstract values (hereafter, ecosystem management, sensu Carey et al., 1999b). Ecosystem management entails more than extracting a commodity, reestablishing a stand of commercially valuable trees, or providing a prescribed number of snags for cavity-using wildlife. It entails managing ecological systems for resiliency (resistance to disturbance, see Folke et al. (1996) for a discussion) and general sustainability (social, economic, and environmental, see Goodland (1995) for a review) by emphasizing management of processes, rather than structures, measurement of outcomes and comparison of outcomes to predictions, and provision for readjustment of goals, procedures, and actions (Harwell et al., 1999). Guidance for managing non-timber structures, ecosystem processes, and biocomplexity is limited (Carry, 2000).

Historical management in the Pacific Northwest (see Curtis et al. (1998) for a review) generally has been low intensity management of extensive areas (hereafter, extensive management) or high intensity management of plantations (hereafter, plantation management). Until recently, extensive management included clearcutting, prescribed burning to reduce residual organic matter, regeneration of a new stand by volunteer seedlings, protection from forest fires, and salvage of timber killed by windthrow or disease. Biological legacies (live trees, snags, coarse woody debris, and understory plants from the preceding stand) were retained only haphazardly. Sometimes, trees were left to ensure a seed source; sometimes, seedlings were planted. Planting of *Pseudotsuga menziesii* seedlings has been de rigueur for only about 20 years; thus, most second-growth stands >40 years old arose from seed. Sometimes, pre-commercial thinning and commercial thinning were used to control the density of growing stock. It is now routine to retain some live trees and coarse woody debris and to plant seedlings. Plantation management included site preparation, planting genetically selected stock, chemical control of vegetation competing with crop trees, pre-commercial thinning, fertilization, pruning, and commercial thinning. Specific combinations of practices and rotation lengths depended on markets, site quality, and landowner objectives. Plantation management was not the norm and was (and is) more common on private lands than on public lands.

Nonetheless, substantial information exists upon which to base ecosystem management. The Pacific Northwest has seen two decades of intensive research on how individual species such as the spotted owl (*Strix occidentalis*) relate to forests (Forsman et al., 1984; Carey et al., 1990, 1992) and forested landscapes (Carey et al., 1992; Carey and Peeler, 1995). How plant, fungal, and animal communities vary among physiographic provinces and in response to environmental gradients, natural disturbance regimes, and developmental processes in forests regenerating after natural disturbance have been documented (Franklin et al., 1981; Ruggiero et al., 1991; Franklin, 1993a; Carey, 1998). Development of biotic communities after timber harvest has been studied intensively (Carey, 1988, 1995, 1998, 2000; Carey et al., 1991, 1999a-c, 2000; Rosenberg and Anthony, 1992, 1993; Carey and Johnson, 1995; Hayes et al., 1995, 1997; Hagar et al., 1996; Colgan et al., 1999; Butts and McComb, 2000). Efforts to develop new management systems have drawn from these, and other, retrospective, correlational studies (Carey and Curtis, 1996; Franklin et al., 1997; Curtis et al., 1998; Carey et al., 1999b).

The accumulated studies of diverse species and biotic communities also provide a basis for choosing species or species groups to be monitored under ecosystem management. It seems reasonable to assume that forest-floor processes are fundamental to resiliency and sustainability and that we should focus in part on these processes in formulating new monitoring systems (Folke et al., 1996; Freedman et al., 1996). But which, and how many processes are important? What structures are important in conditioning the processes? How can effectiveness be measured? These are unanswered questions (Vogt et al., 1999). Decadence and its products of snags, fallen trees, canopy gaps, decayed wood, litter, and humus have long been recognized as fundamental, not only to biological activity in the soil and support of complex plant, fungal, and invertebrate communities (see Harmon et al. (1986) and Freedman et al. (1996) for reviews; Amaranthus et al., 1994; Johnson, 1996; Perry, 1998; Ponge et al., 1998; Siitonen et al., 2000), but also to the small mammals that inhabit the forest floor (Hamilton and Cook, 1940; Elton, 1966; Carey and Johnson, 1995; Carey et al., 1999a; see Bowman et al. (2000) for a review). Similarly, the role of canopy gaps in

development of understories, midstories, and spatial heterogeneity in vegetation is now well recognized as contributing to system productivity, diversity, and resiliency (Canham et al., 1990; Lertzman et al., 1996; Tilman, 1999). Decadence and development of spatial heterogeneity results in pre-interactive niche diversification (expansion of niche space within a community) that provides for diverse small-mammal communities (Carey et al., 1999a,b). Niche separation among small mammals has been hypothesized to represent capitalization on diverse trophic pathways in the forest floor. Thus, the biotic integrity of the forest-floor (Soricidae – Talpidae – Muridae) and arboreal-rodent (Sciuridae) communities has been related to ecological function and resiliency (Carey, 1995, 2000; Carey and Johnson, 1995; Carey et al., 1999a,b). Small-mammal communities have potential as indicators of forest-floor function because they disseminate seeds, spores, and propagules of vascular plants, bryophytes, fungi, and lichens; physically mix soil, decomposed organic matter, and litter; regulate some invertebrate populations; and provide prey for terrestrial and avian predators. On the Olympic Peninsula of Washington, Carey (1995) found significant positive correlations with coarse woody debris for *Sorex trowbridgii*, *Clethrionomys gapperi*, and *Peromyscus maniculatus* in managed stands (5-16% cover; the latter two species had stronger simultaneous relationships with shrub cover than with woody debris) and for *Neurotrichus gibbsii* in both managed and old-growth stands (5-24% cover), but not for *Peromyscus keeni* (positive relationship with shrubs), *Microtus oregoni* (positive relationship with herbaceous understory), *Sorex monticolus* (no predictors found), or *Sorex vagrans* (no predictors found). Carey and Johnson (1995) concluded that 15-20% cover of coarse woody debris, well distributed over the forest floor, would be adequate for most functions associated with small mammals in *Tsuga heterophylla* forests, but that 51% cover would not be adequate. They also suggested that variable-density thinning should be used to promote spatial heterogeneity in understory vegetation in even-aged forests, given correlational evidence for various relationships between small mammals and different types of understory vegetation (see also Carey, 1995).

Although there is substantial information on the importance of coarse woody debris to diverse taxa and

ecological processes in Pacific Northwest forest ecosystems (Harmon et al., 1986; Ruggiero et al., 1991; Freedman et al., 1996), only a few reports address the amount of coarse woody debris that is necessary to support complete small-mammal communities or other ecosystem functions (e.g., Tallmon and Mills, 1994, Klamath Mountains, California; Amaranthus et al., 1994, Klamath Mountains, Oregon; Carey and Johnson, 1995, Olympic Peninsula, Washington; Lee, 1995, Puget Trough, Washington; Carey et al., 1999a, Coast Ranges, Oregon; Butts and McComb, 2000, western Oregon; Carey, 2000, Puget Trough, Washington). Carey et al. (1999a) concluded that $\geq 10\%$ cover of coarse woody debris is needed to ensure high prey populations for mustelids and owls in *P. menziesii* forests in southwestern Oregon. Reports of correlative relationships between small mammals and coarse woody debris from outside the region have been accumulating since Hamilton and Cook (1940) and Elton (1966) (see Loeb (1999) and Bowman et al. (2000) for reviews).

Less attention has been paid to amounts of understory needed to maintain various trophic pathways because understory development is often a by-product of management for high quality timber (Carey, 2000). New studies, however, suggest that plant species composition and spatial arrangement of plant growth forms are important (Carey, 1995; Carey et al., 1992, 1999a,b; Carey and Johnson, 1995). Conventional thinning may produce undesirable, unintended consequences for plant communities and small mammals (Carey, 2000; Thysell and Carey, 2000; Wilson and Carey, 2000). Thus, there is a need not only for experimental studies to test hypotheses about the roles (cause and effect relationships) of coarse woody debris, but also for additional studies to confirm or refute the correlational relationships between coarse woody debris, vegetation structure and composition, and small mammals. How can we move forward in developing information on small mammals as indicators of managerial effectiveness? In the short term, previous retrospectives can be supported or detracted by additional cross-sectional studies and, in the long term, hypotheses can be tested in formal manipulative experiments.

Our goals for this study were: (1) to select numerous 30- to 70-year-old second-growth conifer forests across the Olympic National Forest on the Olympic

Peninsula, Washington, that could be used in prospective experimental tests of hypotheses about coarse woody debris and spatial heterogeneity (treatments now in progress); (2) to describe the current conditions with respect to coarse woody debris, understory vegetation, and small mammals in replicate plots in each forest; (3) to examine relationships among small mammals, woody debris, and vegetation within a retrospective, quasi-experimental design (Cook and Campbell, 1979; Hoaglin et al., 1991). Here, we report the results of the large-scale, cross-sectional survey of second-growth forests and small-mammal communities.

2. Methods

We studied extensively managed second-growth coniferous forests on the non-reserved area of the Olympic National Forest (Fig. 1). The forest encircles the Olympic Mountains on the Olympic Peninsula of northwestern Washington, which is bounded on the west

by Pacific Ocean, on the north by Straits of Juan de Fuca, on the east by Hood Canal and Puget Sound, and on the south by Chehalis River Valley and Coast Ranges (Henderson et al., 1989). The Olympic Mountains have ridges that rise 1200-1500 m above sea level and peaks of 2100-2420 m. The physiography of the peninsula results in sharp gradients of precipitation (80 cm/yr near Quilcene in the northeastern rain shadow to 340 cm/yr at Quinalt on the southwest, near the Pacific Coast) with January minimum temperatures of 1°C at low elevations dropping sharply to -2.5°C at moderate elevations (Franklin and Dymess, 1973). Thus, even in the relatively narrow elevational band we sampled (125-550 m), forests were variously dominated by *P. menziesii*, *T. heterophylla*, and *Picea sitchensis* (dry to wet on the moisture gradient) with *T. heterophylla* present on most sites and *Thuja plicata* occasionally abundant (Table 1). Wet sites tend to accumulate organic matter because of wind-dominated disturbance regimes and formation of mor and duff mull soils; dry sites have fire-dominated disturbance

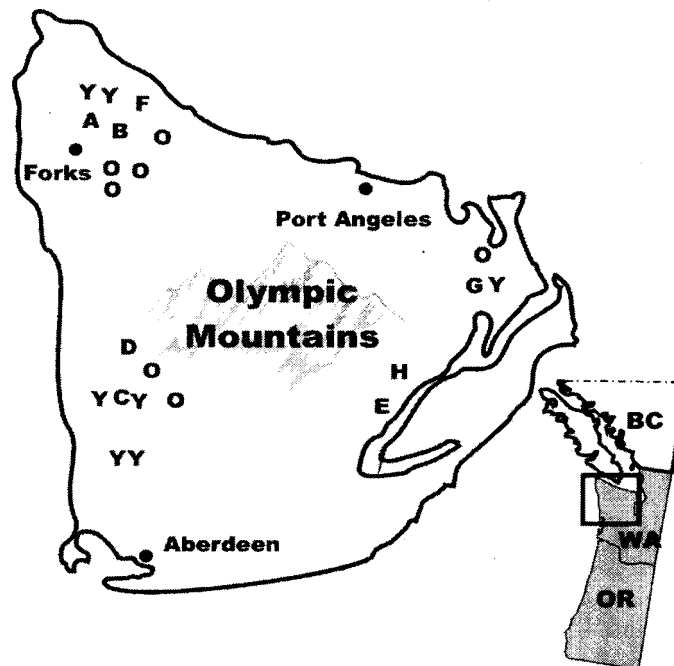


Fig. 1. Location on the Olympic Peninsula, Washington, of eight blocks (A-H) totaling 37 plots of second-growth forests, 34-62 years old, studied during 1994-1998 and the old (O) and young (Y) stands studied by Carey and Johnson (1995) to which they were compared.

Table 1

Forest age, elevation, mean annual precipitation, percent of area covered by pools of water following periods of heavy rain in winter and spring, and number of plots for study blocks (letters A–H) on the Olympic Peninsula, Washington, 1994–1998

Site name	Letter ^a	Plots, <i>n</i>	Elevation (m)	Annual precipitation (cm)	Pools of water (%)	Forest age (yr)
Snow white	G	5	550	260	6	62
Triton	E	5	400	305	1	62
NF Fulton	H	5	500	350	6	55
Eats	C	5	125	385	30	39
Bait	D	5	275	345	14	34
Clavicle	B	4	475	210	2	47
Fresca	A	4	150	210	1	46
Rail	F	4	275	115	1	45

^a Letter indicates rank order on a complex moisture, temperature, overstory-composition, coarse woody debris gradient and serves as the site identification in text, tables, and figures; the gradient ranges from wet sites dominated by *T. heterophylla* and *P. sitchensis* with high woody debris loads to dry sites dominated by *P. menziesii* with high shrub cover and low coarse woody debris loads.

regimes and duff mull or mull soils (Henderson et al., 1989). Parent material was generally of glacial origin (outwash, alluvium, till, or moraine) and sites were well drained except for sites C (Eats) and D (Bait) which were moderately well-drained alpine till, but still tended to form vernal pools as a result of heavy winter precipitation.

2.1. Study area selection

With assistance from Olympic National Forest personnel, we identified eight blocks of coniferous forest that met the following criteria: (1) 30- to 70-years old, (2) large enough to install four or more plots, each ≥ 5.6 ha, (3) plots within a block had similar tree species and understory composition and disturbance (natural and management) histories, (4) plots were not immediately adjacent to a major change in forest condition (≥ 100 m from old growth or stands ≤ 15 years old), (5) plots could be laid out so that trapping grids in adjacent plots were ≥ 80 m apart, (6) each block could support a commercial thinning operation (tree size and area size sufficient), (7) the block was not administratively constrained from future harvesting activities, and (8) plots were not bisected by streams (although streams could, and did, occur between plots in a block). Blocks had to be representative of the types of stands that would be managed in the future and could not duplicate the stand- and site conditions sampled by another block selected for this study. Each block had four or five plots; there were 37 plots overall. All plots were even-aged and in the stem exclusion stage of forest

development (Oliver and Larson, 1996).

2.2. Plot establishment and vegetation data

We used a laser range finder to survey a 200 m x 280 m (5.6 ha) sampling grid of 10 m intervals in each plot and mapped vegetation and site features on the resulting 560 10-m x 10-m grid cells. We chose the minimum grid size that, based on our experience (e.g., Carey et al., 1980, 1999a,c; Carey, 1995; Carey and Johnson, 1995), would incorporate a small-mammal community and the fine-scale environmental variation associated with managed stands in the Pacific Northwest (Carey et al., 1999a). We chose a rectangular, rather than square, grid to avoid incorporating riparian areas within grids. We described each grid with variables previously suggested as important influences on small-mammal communities in the Pacific Northwest (see papers in Ruggiero et al., 1991; Carey and Johnson, 1995; Wilson and Carey, 2000). Rock outcrops, talus slopes, and standing water during the winter and spring were recorded as present or absent in each cell. We counted conifer stumps and snags >50 cm in diameter and deciduous snags >15 cm in diameter. We recorded vegetation by cover class (0-trace, 5-20%, $>20\%$) and type (ericaceous shrubs; non-ericaceous shrubs; low shrubs, forbs, and grasses; and ferns) and calculated prevalences as the percentage of sub-plots with $>20\%$ cover of a particular life form. In addition, we used 39 10-m line intercepts to determine shrub cover. We recorded percent cover

of herbaceous plants on three 0.1-m² sub-plots per 10-m line (117 nested sub-plots/plot). We used line intercepts along grid lines (1440 m/grid, length based on a pilot study) to precisely estimate cover of coarse woody debris >10 cm in diameter at interception. We measured trees and tree-form shrubs >5 cm dbh on 5.6-m-radius sub-plots. We counted trees, measured their diameters on 6-8 variable-radius prism plots, and calculated basal areas (m²/ha). We calculated relative density, a measure of crowding among trees for each plot by dividing basal area by the square root of quadratic mean diameter (Curtis, 1982). We measured heights of dominant trees and extracted increment cores to estimate their ages.

2.3. Trapping and trapping data

We overlaid a 96-station (8 x 12) trapping grid with stations 20-m apart in the central portion of the surveyed grid such that exterior trap stations were ≥ 30 m inside the plot boundary. We set two 7.6 cm x 8.9 cm x 22.9 cm metal box traps, baited with peanut butter and oats, at each station for two four-night trapping periods separated by three nights for three summers (June-September) during 1994-1998 (170,496 trap nights in total). This procedure has been shown to be effective in sampling the eight species composing the forest-floor small-mammal community on the Olympic Peninsula (Carey and Johnson, 1995; Carey et al., 1999d; Wilson and Carey, 2000). We marked with ear tags and released alive mice (primarily *P. maniculatus* and *P. keeni*) and voles (*C. gapperi* and *M. oregoni*). Most shrews (Soricidae) and moles (Talpidae) died in the traps. We used the number of individuals of each species (also known as the minimum number known to have been alive) to calculate catch per 100 trap nights (CPUE) corrected for sprung traps and total captures (Nelson and Clark, 1973). We used CPUE averaged over 3 years to calculate rank abundances for community structures and, transformed as $\ln(\text{CPUE} + 1)$, in regressions with habitat variables. A natural log transform was used because small-mammal CPUE variances are often proportional to mean CPUE (heteroscedasticity); I was added to avoid mathematical problems associated with values of 0 (Carey and Johnson, 1995).

2.4. Data analysis

We compared community structure among blocks (A-H) and between these blocks and those old-growth and second-growth forests studied by Carey and Johnson (1995). Community structure was defined as octave-scale rankings based on dividing the CPUE for each species by the total CPUE. The scale ranged from 1 to 6 corresponding to midpoint percentages of 2, 4, 8, 16, 32, and 64% of total CPUE. The theoretical basis for using this scale in describing biotic communities was presented by Preston (1948, 1981) and was applied to small-mammal communities by Carey and Johnson (1995). We considered differences in ranks to be biologically significant because a major reappportionment of individuals among species is necessary for ranks to change with samples of the size we took (675-2400 individuals captured per block), even with CPUE variances proportional to mean CPUE. Total relative abundances among blocks were calculated by dividing each block total (across species) CPUE by the lowest block CPUE (i.e., setting the lowest value to 1.0). A relative evenness index was calculated by dividing sum of octave scores in second-growth blocks by the sum of octave scores for old-growth communities studied by Carey and Johnson (1995); all evenness comparisons were based on octave scores derived from averages with large sample sizes and similar distributions of individuals among species.

Species presence and absence were used to calculate probability of occurrence for each species in each block (occasions present divided by plot times years sampled). All species we analyzed are consistently present ($\geq 80\%$ of the time) in natural forest communities (Carey and Johnson, 1995) but may be absent or infrequent in some managed forests (Carey and Johnson, 1995; Wilson and Carey, 2000). Thus, we constructed a scale of likelihood of occurrence. We arbitrarily defined species as having a high likelihood of occurrence for probabilities ≥ 0.80 , a low frequency of occurrence for probabilities < 0.80 , and at risk of local (i.e., 5-25 ha scale) extirpation for probabilities < 0.50 (more likely to be absent than present).

We calculated a simple habitat complexity index (0-100) by comparing values from our blocks to old growth communities studied by Carey and Johnson (1995) for five variables putatively important to small

mammals: number of dominant/codominant canopy species, prevalence of tall (>2 m) shrubs, prevalence of shrubs <2 m, prevalence of herbaceous plants, and cover of coarse woody debris. Each block value was divided by the corresponding old-growth value, the quotients were summed, and the sum was divided by 5 and multiplied by 100 to produce a mean percent old-growth complexity. We calculated Pearson product moment correlations among the complexity index values and four measures of mammal community structure: changes in rank differences from old growth, evenness based on ranks, ranked abundances, and number of species with low frequencies of occurrence (probability of occurrence <0.80).

Factor analysis with varimax rotation and Kaiser normalization was used to determine principal components of variation among mammal communities on plots and among habitat variables on plots. Factors with eigenvalues >1 were extracted and scree plots were used to choose the number of factors we would examine (SPSS, 1998; Carey et al., 1999a). We used plots as observations because we selected blocks to represent locations arrayed across the gradient of broad scale environmental conditions that existed on Olympic Peninsula (Fig. 1) and plots within blocks to examine the range of conditions within geographical locations. Our observations, however, were confined to second growth subject to future active management. Thus, our sample is not necessarily representative of all second growth on the Olympic Peninsula, and certainly not representative of all second growth in the Pacific Northwest. Factor analysis of habitat variables allowed us to describe quantitatively the important sources of environmental variation in our samples. Knowing these sources of variation is important because small mammals respond to multiple environmental factors (Carey and Johnson, 1995; Carey et al., 1999a; Carey, 2000), but in specific samples only to factors with biologically significant variance in abundance. In addition, the prevailing environmental factor may or may not be limiting to particular species; a statistically secondary factor may be more influential. Factor analysis of small-mammal abundances provided us with equivalent sources of variation in our small-mammal data set, allowing us to examine the response of communities to environmental variation. Habitat variables and extracted factors were related to mammal species abundances and extracted factors; only correlations significant at $P < 0.01$ ($n = 37$ plots in

eight areas) are reported, unless otherwise noted. Relationships between species abundances ($\ln(\text{CPUE} + 1)$), habitat factors, and habitat elements were explored using all-possible subsets regression, forced-variable stepwise regression, and stepwise regression with Mallows's C_p , adjusted R^2 , and tests of statistical significance for improvements in R^2 and differences of coefficients from zero. Final regressions were conducted with habitat factors only and evaluated on the basis of statistical significance, biological relevance, and parsimony (Analytical Software, 1996; SPSS, 1998).

3. Results

3.1. Nature of the habitat space

Overstory composition differed among study sites from wet forests dominated by *P. sitchensis* (block A) to dry forests dominated by *P. menziesii* (blocks G and H; Tables 1 and 2). Factor analysis produced four significant components of variance in habitat data. The first component accounted for 33% of variance and represented a gradient from dry *P. menziesii* forest with high shrub cover and low coarse woody debris to *T. heterophylla* and *P. sitchensis* forests with high basal area, little understory, and abundant coarse woody debris. Prevalence of forbs and grasses increased from A to H, but remained <10%. Prevalence of ericaceous shrubs was significantly correlated (r) with abundance of one species of ericaceous shrub, *Gaultheria shallon* (0.71); the tree species *P. menziesii* (0.68), *T. heterophylla* (-0.48), and *P. sitchensis* (-0.48); prevalence of ferns (0.55); and total shrub cover (0.55). Thus, overstory composition, shrub cover, and coarse woody debris loads were interrelated. The second, third, and fourth factors explained 15, 14, and 10% of the variance, respectively, and represented gradients in abundance of high herbaceous cover in conjunction with *Alnus rubra* ($r = 0.44$) and *P. sitchensis* ($r = 0.50$); non-ericaceous shrubs (primarily *Acer circinatum*, $r = 0.83$, abundant only in C and F, also associated with *A. rubra*, $r = 0.44$); and occurrence of *Acer macrophyllum* (abundant only in E).

All plots were over- (RD > 7) to fully (RD 7) stocked with trees (Table 2). Wet forests had the highest relative densities, basal areas, and shade-

Table 2

Vegetative characteristics of eight second-growth study blocks (A-H) and old growth (OG) and second growth (SG) studied by Carey (1995) and Carey and Johnson (1995) on the Olympic Peninsula

Characteristic	OG	SG	A	B	C	D	E	F	G	H
Dominant species ^a	Ts, Ab	Ps, Ts	Ts-Pi	Pi-Ts	Ts	Ts-Ps	Ts-Ps	Ps-Ts	Ps	Ps
QMD ^b (cm)										
\bar{x}	71	42	34	44	22	27	40	45	45	30
S.E.	7	4	3	9	3	2	4	2	1	1
Basal area (m ² /ha)										
\bar{x}	na	na	64	79	48	63	63	46	45	45
S.E.	na	na	8	7	2	5	6	1	3	3
Trees/ha										
\bar{x}	na	na	588	837	1790	1095	856	360	709	1317
S.E.	na	na	64	205	236	134	176	25	113	451
Relative density ^c	na	na	11	12	10	12	7	7	7	8
CWD > 10 cm (% cover) ^d										
\bar{x}	13	8	10	11	13	7	10	8	4	4
S.E.	4	1	2	2	1	1	1	1	<1	1
Snags > 50 cm dbh (No. ha ⁻¹)										
\bar{x}	24	3	10	14	9	4	10	6	1	4
S.E.	3	1	2	5	1	1	3	2	<1	1
Stumps > 50 cm dbh (No. ha ⁻¹)										
\bar{x}	na	na	72	77	69	146	88	55	45	96
S.E.			5	9	4	13	9	4	10	11
Herb patches (% of plot)										
\bar{x}	46	46	8	3	<1	4	40	11	38	32
S.E.	15	12	2	2	<1	2	10	2	6	10
Shrub patches for shrubs <2 m tall										
\bar{x}	42	42	4	0	<1	4	43	15	17	64
S.E.	8	12	2	0	<1	2	8	7	3	13
Shrub patches for shrubs >2 m tall										
\bar{x}	33	14	5	4	29	<1	8	21	<1	5
S.E.	6	5	2	2	5	<1	6	10	<1	2

^a Ab, *Abies amabilis*; Pi, *P. sitchensis*; Ps, *P. menziesii*; Ts, *T. heterophylla*.

^b Quadratic mean diameter, at 1.3 m measured (dbh).

^c A measure of crowding of trees; basal area divided by the square root of quadratic mean diameter.

^d Percent cover of coarse woody debris >10 cm in diameter.

tolerant trees; thus, understory development was exceptionally low. Coarse woody debris averaged $8.3 \pm 0.6\%$ (block O \pm S.E.) but was scarce ($\leq 4\%$ cover) only on the driest portion of the gradient in the two areas of *P. menziesii*-dominated canopies. In *T. heterophylla* blocks, coarse woody debris cover was $\geq 10\%$ (the lower desirable limit suggested by Carey and Johnson (1995)) in all but area D. In dry forests, where RD = 7-8, shrubs

were more prevalent (1564% of sites covered by patches of shrubs) than in wet forests. In summary, four areas (A-C, E) had abundant coarse woody debris; three areas had abundant herbaceous understories (E, G, H); only two areas had abundant low shrubs (E, H); another two had abundant tall shrubs (C, F). Complexity values ranged from 34 to 78% of that in old growth and were lowest in the youngest block (D),

Table 3

Species comprising $\geq 1\%$ of individuals captured and their octave-scale relative abundances (RA; 1: 1–3% of captures, ..., 6: >48% of captures) on the Olympic Peninsula in the Olympic Habitat Development Study (HD), 1994–1998, and in old-growth (OG) forests and second-growth (SG) forests studied by Carey and Johnson (1995) and their food habits, use of the forest floor, and important habitat elements (van Zyll de Jong, 1983; Nowak, 1991; Carey and Johnson, 1995; Verts and Carraway, 1998; Wilson and Ruff, 1999), CWD: coarse woody debris

Species	OG, RA	SG, RA	HD, RA ^a	HD, n ^b	Food habits	Vertical distribution	Important habitat elements
<i>S. trowbridgii</i> , Trowbridge's shrew	5	5	5	3222	Small arthropods, slugs, snails, conifer seed	Burrows in soil organic layers beneath litter	Thick organic layer, dry soil, high ground and canopy cover, CWD, <i>P. menziesii</i>
<i>P. keeni</i> , northwestern deer mouse	4	4	4	2186	Seeds, nuts, fruits, fungi, insects	Forest floor to canopy	Old growth, tall layered canopy, patchy dense shrubs, edges
<i>S. monticolus</i> , montane shrew	4	4	4	1648	Soft-body invertebrates, conifer seed, fungi, lichens	Burrows in surface litter and debris	Mesic sites, dense understory, CWD in winter, acidic soils, <i>T. heterophylla</i>
<i>C. gapperi</i> , southern red-backed vole	3	4	4	1243	Omnivore, opportunistic	Burrows beneath rocks, CWD, roots	Mesic sites, litter, CWD, patchy dense shrubs, moss
<i>N. gibbsii</i> , shrew-mole	3	3	3	997	Earthworms, insects	Burrows beneath litter	Leaf litter, humus, CWD, loose soil, shrub or grass cover, <i>A. macrophyllum</i> , <i>A. rubra</i>
<i>M. oregoni</i> , creeping vole	3	3	1	227	Green vegetation, fungi	Burrows in soil and under litter, logs, and roots	Xeric sites within mesic conifer forest, herbaceous ground cover
<i>S. vagrans</i> , vagrant shrew	2	2	1	172	Generalist, invertebrates	Does not burrow, on surface litter	Wet, mossy forest, <i>T. plicata</i> , <i>A. rubra</i> , rich, and basic soils, wet meadows
<i>P. maniculatus</i> , deer mouse	2	2	2	522	Seeds, nuts, fruits, fungi, insects	Soil to lower canopy	Long-tailed subspecies inhabit forests, CWD, shrubs

^a Other captures: *G. sabrinus* (250), *T. townsendii* (88), *M. erminea* (74), *Tamiasciurus douglasii* (27), *S. cinereus* (13), *Sorex bendirii* (12), *Zapus trinotatus* (12), *Scapanus orarius* (10), *Sorex palustris* (2), *Neotoma cinerea* (1).

^b Number of individuals captured.

34-year old with high relative density of trees and low coarse woody debris (Tables 2 and 3). Complexity values were not highly correlated with either age or tree size in our second-growth stands.

3.2. Captures of small mammals

We captured 11,170 animals of 18 species 19,625 times in 37 grids in eight blocks each trapped during three summers. Eight species each composed with >1% of captures; these eight species were the species characteristic of the upland forest-floor small-mammal community (Table 3). In addition, we caught significant numbers of two squirrel species – 250 *Glaucomys sabrinus* and 88 *Tamias townsendii* – and 74 weasels, *Mustela erminea*. *S. trowbridgii* were numerically dominant; *P. keeni*, *S. monticolus*, and *C. gapperi* were next most abundant, followed by *N. gibbsii*, then *P. maniculatus*. *M. oregoni* and *S. vagrans* were relatively few in most communities. *Sorex cinereus* were caught only occasionally (13 captures).

A gradient in abundance of *S. trowbridgii*, *N. gibbsii*, *S. monticolus*, and *P. maniculatus* accounted for 41% of the variance in mammal abundance. Total

abundances were highly and positively correlated with abundances of the three numerically dominant species on this gradient ($r = 0.80$ for *S. trowbridgii*, 0.77 for *S. monticolus*, and 0.73 for *N. gibbsii*). Correlations with *S. trowbridgii* were 0.54 and 0.58 for *N. gibbsii* and *S. monticolus*, respectively; 0.60 between *N. gibbsii* and *P. maniculatus*; and 0.57 between *N. gibbsii* and *S. monticolus*. A bipolar gradient contrasting abundance of *C. gapperi* and *P. keeni* accounted for 13% of variance ($r = -0.47$) in mammal abundance; a gradient of increasing abundances of *S. vagrans* and *S. cinereus* ($r = 0.62$) for 13%; and a bipolar gradient contrasting *C. gapperi* with *M. oregoni* for 8% (no significant Pearson product moment correlation).

Community structure and mammal abundance varied among study areas. When compiled over blocks, community structure differed from those in previously studied old growth and second-growth forests – *M. oregoni* and *S. vagrans* composed much less of the entire community (Tables 3 and 4). Compared to old growth, communities in our blocks had lower total relative abundances, less evenness, reduced importance of 3-5 species (with summed deviations from rank-

Table 4

Community evenness, species importance (differences in octave-scale rankings), and relative abundance of small mammals in old growth (OG) and second growth (SG) (Carey and Johnson, 1995) and in eight blocks (A–H) of second growth on the Olympic Peninsula, 1994–1998

Study	Octave rank		Differences from old-growth octave rank							
	OG	SG	A	B	C	D	E	F	G	H
<i>S. trowbridgii</i>	5	5	-1	0	0	0	0	0	0	0
<i>P. keeni</i>	4	4	1	0	1	1	-2	0	-3	-2
<i>S. monticolus</i>	4	4	0	0	-1	0	0	0	0	0
<i>C. gapperi</i>	3	4	-2	0	-1	-1	0	-2	1	2
<i>N. gibbsii</i>	3	3	-1	-1	-1	0	1	-1	0	0
<i>M. oregoni</i>	3	3	-2	-2	-2	-2	-2	1	-2	-2
<i>S. vagrans</i>	2	2	-1	1	-1	-1	-1	-1	-1	-1
<i>P. maniculatus</i>	2	2	1	-1	0	0	1	0	-1	-1
Sum of deviations	na	1	-5	-3	-5	-3	-3	-3	-6	-4
Evenness	26	27	21	24	21	23	24	23	21	23
Relative abundance ^a	6.6	2.0	1.0	1.8	2.6	1.7	3.0	1.4	2.3	2.1
Species <80% frequent	0	3	3	1	2	3	2	4	3	2
Habitat complexity index ^b	100	70	46	40	58	34	78	58	40	64

^a Relative abundances between (Carey and Johnson, 1995) OG and SG are not fully comparable with this study (A–H) due to difference in study design and trapping methodology.

^b An index of relative (to old growth) complexity based on overstory composition, patchiness of tall shrubs, patchiness of short shrubs, patchiness of herbaceous plants, and cover of coarse woody debris.

Table 5

Mean (S.E.) number of individuals caught per 100 trap nights (averaged over all years and plots for each block) of small-mammal species in eight blocks (A–H) of second-growth coniferous forests on the Olympic Peninsula, Washington, USA, 1994–1998

Species	A	B	C	D	E	F	G	H
<i>S. trowbridgii</i>	0.58 (0.13)	2.12 (0.42)	2.37 (0.19)	1.8 (0.10)	3.20 (0.08)	1.47 (0.38)	3.05 (0.29)	2.10 (0.17)
<i>P. keeni</i>	1.46 (0.19)	1.09 (0.19)	3.54 (0.17)	2.07 (0.28)	1.14 (0.22)	0.78 (0.18)	0.37 (0.07)	0.59 (0.11)
<i>S. monticolus</i>	0.52 (0.16)	0.76 (0.24)	0.99 (0.19)	0.79 (0.17)	1.57 (0.15)	1.06 (0.17)	1.54 (0.03)	1.08 (0.14)
<i>C. gapperi</i>	0.08 (0.05)	0.65 (0.20)	0.44 (0.17)	0.24 (0.12)	0.82 (0.44)	0.05 (0.03)	1.73 (0.42)	2.07 (0.26)
<i>N. gibbsii</i>	0.10 (0.04)	0.23 (0.13)	0.29 (0.05)	0.54 (0.11)	2.29 (0.28)	0.16 (0.03)	0.62 (0.11)	0.66 (0.14)
<i>P. maniculatus</i>	0.34 (0.06)	0.15 (0.04)	0.46 (0.07)	0.26 (0.03)	0.86 (0.17)	0.15 (0.03)	0.13 (0.02)	0.20 (0.05)
<i>M. oregoni</i>	0.05 (0.03)	0.15 (0.10)	0.17 (0.03)	<0.01 (0.01)	0.01 (0.01)	0.75 (0.21)	0.02 (0.01)	0.09 (0.05)
<i>S. vagrans</i>	0.03 (0.02)	0.41 (0.23)	0.07 (0.05)	0.04 (0.01)	0.08 (0.03)	0.04 (0.01)	0.21 (0.05)	0.03 (0.01)
<i>S. cinereus</i>	0.01 (0.01)	0.03 (0.03)	0.00 (0.00)	0.01 (0.01)	0.02 (0.01)	0.00 (0.00)	0.02 (0.01)	0.00 (0.00)
<i>G. sabrinus</i>	0.32 (0.06)	0.34 (0.10)	0.00 (0.00)	0.17 (0.06)	0.09 (0.03)	0.35 (0.04)	0.02 (0.01)	0.07 (0.02)
<i>T. townsendii</i>	0.00 (0.00)	0.00 (0.00)	<0.01 (0.01)	<0.01 (0.01)	0.00 (0.00)	0.12 (0.02)	0.13 (0.06)	0.19 (0.06)

orders ranging from –3 to –6), and 1–4 more species of low frequency of occurrence (Table 4). Total CPUE ranged from 0.0 to 7.3 individuals/species and 3.2 to 9.5 individuals/block (Table 5). Relative evenness ranged from 66 to 75% of that in old growth. *S. trowbridgii*, *P. keeni*, and *S. monticolus* had high (>0.80) likelihoods of occurrence in any given block in any given year (probability of occurrences averaged 0.95–1.00). For other species, probabilities of occurrence were more variable (0.07–1.00) with mean (across blocks) probabilities for *S. vagrans* = 0.43, *M. oregoni* = 0.59, *N. gibbsii* = 0.71, *C. gapperi* = 0.73, and *P. maniculatus* = 0.83. *M. oregoni* was more likely to be absent than present (probability of occurrence <0.50) in sample communities from blocks D, E, and G; *S. vagrans* in samples from C, D, and F; and *N. gibbsii* and *C. gapperi* in samples from F. Compared to old growth, *P. keeni* assumed increased importance in sample communities from blocks A, C, and D (peaking in C) and decreased in importance in E (where *N. gibbsii* assumed greater importance) and G and H (where *C. gapperi* was most abundant). *M. oregoni* achieved much greater importance and abundance in F than in other blocks.

T. townsendii were not caught in A, B, and E, more likely to be absent than present in samples from C and D (probability of presence in both = 0.07), and regularly caught in G (0.40), H (0.60), and F (0.67). *G. sabrinus* was absent from C, rare in F (0.20), and common only in A (0.92), B (1.00), and F (1.00), averaging 1.5–1.7 individuals/plot/yr. *M. erminea* were caught occasionally on all plots.

3.3. Mammal diversity and abundance

Habitat complexity was highly correlated with the total relative abundance of mammals in the forest-floor mammal community in old-growth and second-growth samples ($r = 0.80$, $n = 10$, $P < 0.01$). Total relative abundance was negatively correlated with the number of species occurring at low frequencies (probability of occurrence <0.80) in each community ($r = -0.77$, $n = 10$, $P = 0.01$). Evenness was highly correlated with summed deviations from species ranks in old growth ($r = 0.97$, $n = 10$, $P < 0.01$) – the more species with decreased importance in the community, the less even the distribution of individuals over species. Thus, it appears that as total habitat space (defined by various dimensions, either extracted factors or habitat elements) decreased from old growth to second growth, complexity inextricably decreased, total abundance of mammals decreased, evenness decreased, and more species became at risk of local extirpation.

S. trowbridgii was positively correlated (0.47) with vegetation factor I (*P. menziesii* and shrubs), total percentage of area covered by dense vegetation (0.51), and prevalence of ferns (0.57), but not with coarse woody debris (vegetation cover and coarse woody debris were negatively correlated in our sample, $r = -0.47$). Two factors, *P. menziesii* shrubs and abundance of *A. macrophyllum*, accounted for 32% of the variance in abundance of *S. trowbridgii* (Table 6). Thus, the importance of associations with

Table 6

Standardized coefficients for habitat factors identified by stepwise regression as having high predictive value for small mammals captured in 37 plots in eight blocks of second-growth forest on the Olympic Peninsula, Washington, USA, 1994–1998, and *F*-values with *P* < 0.01

Species	PSME/shrubs (+) — TSHE/CWD (–)	Habitat factor ^a			Statistics	
		Herbaceous cover	<i>A. circinatum</i>	<i>A. macrophyllum</i>	<i>R</i> ²	<i>F</i>
<i>S. trowbridgii</i>	+0.48			0.30	0.32	7.7
<i>P. keeni</i>	–0.60		0.54		0.65	30.1
<i>S. monticolus</i>	+0.62				0.39	21.8
<i>C. gapperi</i>	+0.60				0.36	18.8
<i>N. gibbsii</i>	+0.47			0.45	0.42	12.0
<i>M. oregoni</i>		0.31			0.11	3.6 ^b
<i>S. vagrans</i>		0.84			0.70	80.1
<i>P. maniculatus</i>				0.59	0.34	17.8
<i>S. cinereus</i>		0.54			0.29	13.6
<i>T. townsendii</i>	+0.57				0.32	16.0
<i>G. sabrinus</i>	–0.42				0.18	7.5

^a Mathematically extracted plant community gradients of *P. menziesii* and shrubs vs. *T. heterophylla* and coarse woody debris; herbaceous understory in conjunction with *A. rubra* or *P. sitchensis*; non-ericaceous shrubs, primarily, *A. circinatum* and *A. macrophyllum*.

^b *P* = 0.07.

vegetation cover and *P. menziesii* (Table 3) were confirmed. *P. keeni* was negatively correlated with vegetation factor 1 (–0.53), thus associated with *T. heterophylla* (0.47) and coarse woody debris (0.49), and positively correlated with factor 3, *A. rubra* (0.59) and non-ericaceous shrubs, especially *A. circinatum* (0.53). Factors 1 (*T. heterophylla* coarse woody debris) and 3 (*A. circinatum*) accounted for 65% of the variance in abundance of *P. keeni*. The associations with factors 1 and 3 are new discoveries, but help explain the association of *P. keeni* with old-growth forests: multi-species canopies with annual conifer seed fall, coarse woody debris as den sites, and *A. circinatum*, *A. rubra*, and shade-tolerant *T. heterophylla* providing foliage height diversity (layering in canopies, Table 3), as well as the former providing high-food-quality samaras that are easily handled and stored. *S. monticolus* was also positively correlated with factor 1 (which alone explained 39% of the variance in its abundance); this was not consistent with the suggested association with *T. heterophylla* (Table 3), but did correspond with the suggested association with dense understory vegetation. *C. gapperi* was positively correlated with the *P. menziesii* shrub pole of habitat factor 1 (0.63), basal area of *P. menziesii* (0.53), and prevalences of ferns (0.58) and ericaceous shrubs (0.56), but negatively correlated (–0.54) with *T. heterophylla*. Factor 1 alone explained 36% of the variance in *C. gapperi* abundance. Again

association with patchy, dense shrubs prevailed over association with coarse woody debris in a sample where the two habitat elements were negatively correlated. *N. gibbsii* was positively correlated with factor 1 (0.40) and factor 4 (0.47), *A. macrophyllum*, which explained 42% of variance in abundance. *N. gibbsii* reached its peak abundance (four times greater than in other areas) in E, the only area with significant amounts of *A. macrophyllum* (coarse woody debris cover was 10%), and abundance was positively correlated with abundance of ferns (0.70), confirming the association in Table 3. *M. oregoni* was more than four times more abundant in F than elsewhere; F was relatively xeric, had moderate prevalences of herbaceous cover (often associated with *M. oregoni*, Table 3) and shrubs (particularly the deciduous *Vaccinium ovatum*, *r* = 0.51 with *M. oregoni*), but exceptionally low abundances of *C. gapperi*. Areas with high cover of herbaceous plants (E, G, H) also were relatively xeric with moderate to high covers of shrubs, moderate to low cover of coarse woody debris, and abundant *C. gapperi*. The regression of *M. oregoni* with factor 2 (herbaceous cover) explained only 11 % of variance in abundance (*P* = 0.07). Thus, the habitat relationships of *M. oregoni* (Table 2) may be tempered by abundance of the other vole in the community (*C. gapperi*) in the absence of physical partitioning of the forest floor by coarse woody debris. Other species

positively correlated with factor 1 were *T. townsendii* (0.56) and *S. vagrans* (0.85). Factor 1 explained 32% variance in abundance of *T. townsendii*. *S. vagrans* was also positively correlated with herbaceous cover (0.77) and *A. rubra* (0.61), factor 2, which explained 70% of the variance in its abundance, as suggested in Table 3. *S. cinereus* was positively correlated with *S. vagrans* (0.62) and herbaceous cover (0.46); factor 3 accounted for 29% of its variance in abundance. *P. maniculatus* was positively correlated with factor 4 (0.60) and directly with the abundance of *A. macrophyllum* (0.52) and had positive Spearman rank correlation with coarse woody debris (0.47, $n = 37$, $P < 0.01$). In this case, association with coarse woody debris overwhelmed association with shrubs, an unexpected result. The best predictor of *P. maniculatus* was factor 4, *A. macrophyllum*, which produces large seeds of high food quality easily accessible in a lightly constructed samara.

4. Discussion

Following clearcutting and extensive management for 34-62 years, ecosystem structure (physical attributes of the habitat) and composition of the vegetation community were simplified (i.e., complexity was low) relative to natural forests. This simplification resulted in some naturally common species having lowered probabilities of occurrence, some species being placed at risk of local extirpation, and lower total abundance of small mammals. Total abundance of small mammals was correlated highly not only with the numbers of the three dominant species of small mammals but also with habitat complexity, suggesting that as conditions improved for the dominant species in our study plots, complexity also increased and provided for increased total habitat space, increased dimensions within the habitat space, and concomitant increases in subordinate species. Increased abundance of dominant mammal species in a constant habitat space would be expected to result in decreased abundance of other community members, given strong natural history documentation of interspecific competition and our factor analysis of mammal species abundances demonstrating two bipolar gradients of species abundance. Thus, enriched mammal communities (in terms of species composition, species density, relative abundances of species, and total

density of small mammals) in areas fixed in size and nominal seral stage were not simply a summation of the responses of individual species to one or more elements of the habitat important to each particular species, but also to overall complexity (multidimensionality) and its mediating effect on interspecies competition. This is the emergent property of pre-interactive niche diversification, a phenomenon that can lead to increased carrying capacity for all members of the community (Hutchinson, 1958, 1978; Odum, 1969; Carey et al., 1999a).

The influence of interspecific interactions on portions of the total available habitat space actually occupied by small mammals has been thoroughly documented for squirrels (e.g., Heller, 1971; States, 1976; Carey et al., 1980, 1992), rodents (Morris and Grant, 1972; Grant, 1972, 1978; Hawes, 1975; Carraway and Verts, 1985), and insectivores (Hawes, 1977; van Zyll de Jong, 1983; Churchfield, 1990, 1994; Shvarts and Demin, 1994; George, 1999), but see Dueser et al. (1989) for a critical review of the experimental basis for claims about competition. Competition is common among *M. oregoni*, *P. maniculatus*, *C. gapperi*, and *Microtus townsendii* (Carraway and Verts, 1985). *C. gapperi* is known to be both intra- and interspecifically aggressive (Merritt, 1981). *P. maniculatus* and *P. keeni* have been shown to occupy discrete topographic positions in contiguous coniferous forests (Sheppe, 1961) or to occupy deciduous (*A. rubra* and *Salix spp.*) and coniferous forests mutually exclusively (Dalquest, 1948). *M. oregoni* has been credited with extirpating local populations of *P. maniculatus* in coastal British Columbia (Petticrew and Sadleir, 1974). Grant (1972) experimentally demonstrated competitive exclusion among *Clethrionomys*, *Microtus*, and *Peromyscus* with outcomes conditioned by type of environment. He also reviewed pertinent literature and concluded that competitive interactions for space is a general phenomenon among rodent species.

The role of structural elements in mediating competition is not uncommon. For example, large coarse woody debris partitions food and space between *Cervus elaphus* and *Odocoileus hemionus* on the Olympic Peninsula (Leslie et al., 1984), rock outcrops obstruct visual contact, reducing agonistic interactions, and facilitating coexistence of *Spermophilus*

lateralis and *Tamias minimus* in the Rocky Mountains (Carey et al., 1980), and tree species architecture enables separation of foraging niches, increased total density, and increased species density for cavity-using birds in the Oregon Coast Ranges (Carey et al., 1991). Vegetation arrangement may also mediate predation. For example, spatial heterogeneity in vegetation structure aids *S. occidentalis* in foraging (Carey et al., 1992) and understory structure may determine foraging suitability for various species of *Mustela* (Wilson and Carey, 1996). Dense understory vegetation, coarse woody debris, and litter are all thought to provide small mammals with some protection from predation to the extent of even conditioning their behavior (e.g., see Harestad (1991) for a discussion of overhead cover and *T. townsendii*).

Composition of the vegetation community can influence small mammals (Carey, 1995; Carey and Johnson, 1995; Carey et al., 1999a). Our results suggest that the occurrence in coniferous forests of deciduous species such as *A. macrophyllum* and *A. circinatum*, that bear numerous large seeds of high food value that are easily handled and stored by small mammals (Martin et al., 1951, Burns and Honkala, 1990), can be an especially important component of complexity. Maintaining a variety of seed, fruit, and nut-bearing deciduous shrubs and trees in conifer forests can help ameliorate the effects on vertebrate seed predators (including small mammals) of the conifer anti-seed-predator strategy of simultaneous cone crop failures (Smith, 1970).

Thus, increasing complexity of the environment through increasing horizontal and vertical heterogeneity in vegetation structure, species diversity in vascular plant composition, and forest-floor structure with coarse woody debris may simultaneously (1) increase multidimensional habitat space (Carey et al., 1999a), (2) reduce frequencies and intensities of interspecies interactions (Grant, 1972; Carey et al., 1980), (3) increase or maintain the already high abundance and diversity of seed fall, fungal fruiting bodies, and invertebrates characteristic of mesic, temperate coniferous forests (Church field, 1990), and (4) allow not only coexistence, but abundance of potentially competing species within communities (Carey and Johnson, 1995, this study). As a result of this complexity, Pacific Northwest forests support the greatest diversity of shrews in North America (Rose, 1994) and our results

(Carey and Johnson, 1995; Wilson and Carey, 2000, this paper) of 6-7 species regularly occurring on forested plots of <6 ha is comparable to the nine species reported from various vegetation cover types in Siberia (Sheftel, 1994; Shvarts and Demin, 1994). This coexistence of numerous potentially competing species based on biocomplexity in homogeneously diverse biotopes (Hutchinson, 1978) differs from the three patterns of coexistence postulated by Grant (1972): fine-scale spatial segregation based on habitat types with small areas of overlap; large-scale selection of markedly different habitat types (e.g., grassland vs. shrub-land vs. forest); and coexistence without interaction.

4.1. Species accounts

We found that *P. keeni*, the small mammal most commonly reported as associated with old-growth forests in Washington (West, 1991; Carey and Johnson, 1995; Songer et al., 1997), is not only more widespread, but also more routinely sympatric with *P. maniculatus* in westernmost Washington than described historically (Dalquest, 1948; Sheppe, 1961; Petticrew and Sadleir, 1974) or recently (Songer et al., 1997; Lomolino and Perault, 2000). Both species occur throughout the stages of forest development and both are most abundant in complex stages, but *P. keeni* is particularly influenced by the degree of dominance of *T. heterophylla* in the canopy with strong positive correlations with woody debris and midstory hardwoods like *A. circinatum*. Correlations between *P. keeni* and coarse woody debris may reflect the role of decaying fallen trees as nurse logs for *T. heterophylla* (Bums and Honkala, 1990), but most likely, in this data set, the correlation represents the positive response of mice to large numbers of stumps of old-growth trees that provide them with den sites (Wilson and Carey, 2000). *P. keeni* reached maximum abundance on moist sites on the southwestern Olympic Peninsula (blocks C and D) with especially high numbers of large stumps which provide den sites, *A. circinatum* which provide high quality food, and *T. heterophylla* which produce seed annually. Excessive moisture has its drawbacks, however. Even though block D had more stumps than block C, it had lower *P. keeni* populations – 30% of D was covered by standing water in winter and spring, whereas only

14% of C was covered with water. *P. keeni* was markedly reduced in community importance in the dry second-growth *P. menziesii* forest on the eastern Olympic Peninsula, where Songer et al. (1997) found it in abundance in old-growth forests of multiple conifer species, including *P. menziesii* and *T. heterophylla*. *P. keeni* was virtually absent in dry *P. menziesii* second-growth forest in the Puget Trough where *P. maniculatus* was fifth ranked in abundance (Wilson and Carey, 2000). *P. keeni* was absent from prairie-*Quercus garryana*-*P. menziesii* ecotones in the Puget Trough, where *P. maniculatus* and *S. vagrans* dominated the small-mammal community (Wilson and Carey, in press).

N. gibbsii is the small mammal most often reported as tied to old growth in both Washington and Oregon, although the relationship is relatively weak (Aubry et al., 1991). The basis for its putative association with old growth is the abundant coarse woody debris there, even though *N. gibbsii* seems to be more associated with high organic matter content in the soil than with the physical structure of large fallen trees (Terry, 1981; Aubry et al., 1991; Carey and Johnson, 1995; Verts and Carraway, 1998). Decaying fallen trees, however, through the action of wood-boring beetles and termites, are the source of much soil organic matter and sites of accumulation of organic matter inhabited by diverse invertebrates and fungi (Maser and Trappe, 1984; Harmon et al., 1986). *N. gibbsii* burrows deep into the soil where there is much organic matter, whereas *S. trowbridgii* forages among the litter and moss, *S. monticolus* forages in coarse debris, and *S. vagrans*, a non-burrower, forages in open areas and stands of *A. rubra* where water tables are high and numbers of *S. trowbridgii* low - a fine partitioning of resources within the same local habitat (Terry, 1981). In her study, Terry (1974) found the abundance of *N. gibbsii* to be positively correlated with depth of duff and organic matter. All these insectivores also eat seeds of conifers (e.g., *T. heterophylla*, *P. menziesii*, *P. sitchensis*); *N. gibbsii* exhibited preferences for *P. sitchensis* and *P. menziesii*. The three burrowing species showed a wide range of acceptance for other seeds including those of *G. shallon* and *Vaccinium parvifolium* (ericaceous shrubs) and a variety of herbs and fungi. All readily consumed a variety of soft forms of various insects and smaller hard-bodied insects. *N. gibbsii*, however, consumed larger seeds, insects, and slugs that the soricids could not or would not

consume (Terry, 1974). Churchfield (1994) noted that, in general, shrews are wide spectrum feeders but that the diet of each species tends to be dominated by a few major prey items that are common and abundant, a quantitative rather than qualitative specialization. However, Carraway and Verts (1994) demonstrated that differentiation in size of mouthparts and musculature of soricids in western North America was correlated with size and hardness of prey and therefore, presumably, with efficiency of handling and consuming prey of different sizes and hardness. *N. gibbsii*, at 9 g, is the largest of the insectivores we studied, considerably larger compared to *S. monticolus* (6.9 g), *S. trowbridgii* (5.3 g), and *S. vagrans* (4.1 g) (Carey and Johnson, 1995). Seeds of *A. macrophyllum* dwarf those of the conifers in these forests. However, among the limited number of studies of the diet of *N. gibbsii*, there is no compelling evidence that this insectivore actively seeks out and consumes seeds of *A. macrophyllum*. The association of *N. gibbsii* with *A. macrophyllum* sites with deep loamy soils that allow deep burrows and that support earthworms (its documented favorite food) is commonly accepted (Verts and Carraway, 1998). Nevertheless, it appears that a diversity of seed-bearing canopy and understory species, which also produce organic litter, and the accumulation of decaying fallen trees (that provide organic matter to the soil and habitat for diverse invertebrates and fungi), in close spatial conjunction allows coexistence, even abundance, of mammalian species that overlap substantially in morphology, diet, and space. More spatially simple and uniform environments can cause coarse-scale partitioning of habitats and reduced community diversity (Grant, 1972; Terry, 1974, 1981; Haves, 1977) and, presumably, reduced system stability and resiliency (Tilman, 1999).

In our forests, *N. gibbsii*, *S. trowbridgii*, and *S. monticolus* increased from areas of high coarse woody debris to areas of high understory cover (our first habitat factor), but *S. vagrans* increased along the herbaceous cover *A. rubra* gradient (factor 2). *S. vagrans* reportedly favors wooded and open grassy areas on well drained to moist sites and commonly occurs with, and always outnumbers, *S. cinereus* (van Zyll de Jong, 1983). Carey and Johnson (1995) found the abundances of *S. vagrans* and *M. oregoni* positively correlated with one another and with herbaceous

cover, as we found in this study, but they did not find any *S. cinereus*. Wilson and Carey (2000, in press) neither found *S. cinereus* in second-growth *P. menziesii* in the Puget Trough nor did West (1991) report *S. cinereus* in natural young, mature, and old-growth forests in the Southern Washington Cascade Range.

G. sabrinus and *T. townsendii* are indicators of ecological productivity (production of seeds, fruits, and truffles) and are important prey for vertebrate predators in Pacific Northwest conifer forests (Carey et al., 1999a,b). The two squirrel species were absent from five of our eight study sites. Their rarity supports the conclusions of Carey (1995, 2000), Carey et al. (1992, 1999a), and Colgan et al. (1999) that competitive-exclusion stage forests may not support prey populations adequate to sustain *S. occidentalis* and other vertebrate predators. However, in three of the eight blocks, *G. sabrinus* densities ($\approx 0.6 \text{ ha}^{-1}$, assuming plots sampled $\approx 8 \text{ ha}$ based on previous estimates of *G. sabrinus* movements) over 3 years were similar to mean densities ($\approx 0.5 \text{ ha}^{-1}$) previously reported by Carey (1995) for old-growth forests on the Olympic Peninsula. All the three blocks (A, B, F) were on the northwest corner of the Olympic Peninsula. Our data were not sufficient to explain why *G. sabrinus* were abundant in some blocks but not in others. Our sampling grids were much smaller than recommended for *G. sabrinus* (Carey, 1995), and squirrels may have been using our plots as only a part of their home ranges. However, relatively high densities of *G. sabrinus* are found occasionally in second-growth stands across the Pacific Northwest, especially in stands with significant numbers of mature *A. macrophyllum*, *Arbutus menziesii*, and other deciduous trees (Carey et al., 1992; Rosenberg and Anthony, 1992; Carey, 1995, 2000, in press; Carey and Peeler, 1995). Carey (1995) suggested that, on the Olympic Peninsula, *G. sabrinus* occurred in high densities where there were >5 large snags/ha (as in these three blocks), multiple canopy species (all three blocks), and cover of ericaceous shrubs > 12% (only in one of the three blocks). However, total shrub cover was 36% in block F, and mapping revealed that captures of *G. sabrinus* were all in or immediately adjacent to patches of *A. circinatum*. Other blocks had all the three characteristics but did not support high densities of flying squirrels. Surprisingly, two of the three blocks with high densities were *P. sitchensis* – *T. heterophylla* associations; Carey

(1995) found no *G. sabrinus* in the one old-growth *P. sitchensis*–*T. heterophylla* stand he studied (in the southwestern Olympic Peninsula). The abundance of *T. townsendii* is closely tied to shrubs (Harestad, 1991; Sutton, 1993; Carey, 1995; Hayes et al., 1995) and that explains its low abundance in many of our plots, but not its absence from block E, which had high shrub cover.

Two species not found in Washington have been associated with old-growth forests in western Oregon – *Arborimus longicaudus* (Corn and Bury, 1986) and *Clethrionomys californicus* (Mills, 1995; Tallmon and Mills, 1994). The former is associated with large trees with deep canopies (Gillesberg and Carey, 1991) and its northern distribution is curtailed by the Columbia River; it has no ecological equivalent in Washington. *C. californicus* is associated with large, decaying logs and hypogeous fungi (Hayes and Cross, 1987; Tallmon and Mills, 1994) in various stages of conifer forest (Aubry et al., 1991; Carey and Johnson, 1995) and is separated from its congener, *C. gapperi*, by the Columbia River to the north and the Western Cascades to the east. *C. gapperi* seems to be much more of a generalist than *C. californicus* (West, 1991; Carey and Johnson, 1995).

4.2. Implications for conservation

Our study areas did not lend themselves well to quantifying relationships among coarse woody debris, understory vegetation, and small mammals. There was too much coarse woody debris in the absence of understory vegetation and too little range in coarse woody debris where other habitat elements were present. Rarely will wild vertebrates adhere to Liebig's "law of the minimum" (i.e., be restricted by one and only one limiting factor). Rather, their responses are multifactorial, more in accord with Shelford's "law of tolerance" that suggests as more than one factor approaches a limiting value the effects on the animal are multiplicatively negative (Odum, 1971, pp. 106107; Sugihara, 1980). The inverse of Shelford's law would predict that as multiple habitat factors are increased above critical thresholds, a "release" of species or community responses results in synergistic, non-linear (multiplicative) increases in species abundances, essentially an emergent property of ecosystems.

Although we can neither confirm or refute recommendations about how much coarse woody debris is needed for small-mammal community diversity, we believe that our results support the conclusions of Carey (1995), Carey and Johnson (1995), and Carey et al. (1999a) about the importance of habitat complexity at the appropriate ecological scale in maintaining diverse, resilient mammal communities. Carey et al. (1999a) found that spatial heterogeneity in vegetation at the 0.5 ha scale had profound influence on squirrel communities, suggesting fine-scale (within stand or within landscape unit) heterogeneity is more important to small mammals than nominal seral stage at a coarse (e.g., landscape) scale. In a modeling exercise, Carey et al. (1999b) demonstrated the importance of the internal complexity of landscape units to maintain a fully functional dynamic landscape mosaic. Thus, we argue that (1) complexity in forest ecosystems is a result of forest developmental processes that include small and intermediate disturbances and competition, inhibition, and facilitation (e.g., Whittaker, 1969; Bormann and Likens, 1979; Carey et al., 1999a; Tilman, 1999; Bergeron, 2000; Coomes and Grubb, 2000); (2) complexity can be produced naturally and stochastically or intentionally through management (Carey et al., 1999b); (3) processes of disturbance, niche diversification, and predation seem to be responsible for the development of complex small-mammal communities (Paine, 1966; Petraitis et al., 1989; Carey et al., 1992, 1999a; Carey, 1995; Carey and Johnson, 1995); (4) thus, the integrity of small-mammal communities is a measure of managerial effectiveness in creating complex forest ecosystems (Carey and Johnson, 1995; Carey et al., 1999b; Wilson and Carey, 2000, this paper); (5) increased complexity leads to increased stability (*sensu* resilience) in ecological systems (May, 1973; van Voris et al., 1980; Tilman, 1999).

Our results, however, seem to contradict those of Mills (1995), Songer et al. (1997), and Lomolino and Perault (2000) who suggested that clearcutting is equivalent to deforestation and creates forest remnants in a fragmented landscape, and that principles of reserve design, including connecting corridors, may be necessary to offset the results of logging if viable populations of small mammals, such as *P. keeni* and *C. californicus*, are to be maintained. We found *P. keeni* as a community dominant in forests as young as 34 years, and Carey and Johnson (1995) and Wilson and

Carey (2000) found *P. keeni* in forests 40-70 years old. Studies in Oregon (Aubry et al., 1991; Carey and Johnson, 1995) found a similar occurrence of *C. californicus*. Our results and those of Carey and Johnson (1995), Carey et al. (1999b) and Wilson and Carey (2000) do suggest that simplification of forest ecosystems through management aimed simply at wood products can have negative effects on *P. keeni* to the point of local extirpation. Maintenance of large proportions of landscapes in clearcuts and simplified competitive-exclusion stages with short rotations (Carey and Curtis, 1996) may compound effects of habitat destruction and further decrease habitat quality because of fragmentation of suitable habitats. Clearcuts, however, usually develop rapidly into forests. Thus, local effects of forest fragmentation (if at all separable from localized catastrophic destruction of habitat) would be short-lived (Bayne and Hobson, 1998) and probably insignificant in landscapes of units managed under rotations averaging >90 years, particularly if stands were managed intentionally for biodiversity (Carey et al., 1999b).

Our cross-sectional survey of second-growth forests, a previous comparison of second-growth forests with old-growth forests (Carey, 1995; Carey and Johnson, 1995), and a recent comparison of second-growth forests managed under different strategies (Carey, 2000; Wilson and Carey, 2000) all contrast markedly with old growth-clearcut comparisons that led others (Mills, 1995; Songer et al., 1997; Lomolino and Perault, 2000) to conclusions about dangers of forest fragmentation. Studies of closed-canopy second-growth forests often do not support absolutely the purported effects of fragmentation of old-growth forests on small mammals (Carey, 1995, 2000; Carey and Johnson, 1995; Carey et al., 1999a,b; Wilson and Carey, 2000) or birds (Carey, 1988; Carey et al., 1991; Haveri and Carey, 2000). These studies do suggest that management can homogenize and simplify (reduce decadence, amounts of coarse woody debris, variety of tree species, diversity and abundance of understory vegetation, and spatial heterogeneity) forest ecosystems. We found local extirpations of a number of species and particularly absence of *G. sabrinus* and *T. townsendii* in multiple plots. These absences raise questions about long-term viability of these species in managed landscapes. Management-

induced homogeneity and simplification (1) is a real danger to diversity, resiliency, and susceptibility to invasions of exotic plants (Carey, 1998; Carey et al., 2000; Halpern et al., 1999; Heckman, 1999; Thysell and Carey, 2000), (2) may result in small-mammal communities non-supportive of predators populations (Carey et al., 1992; Carey and Peeler, 1995), and (3) may produce environments inhospitable to specific species with concomitant fragmentation effects on those species (Gillesberg and Carey, 1991; Carey et al., 1992, 1999c; Ryan and Carey, 1995). Thus, we conclude that active management for complexity on long rotations may be necessary for conservation of the diverse values attributed to forests (Carey and Curtis, 1996; Carey et al., 1999a,b,d). Our results also suggest that monitoring of selected vertebrate communities can provide effective measurements of ecosystem health (Franklin, 1993b).

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