Supplement to
The Journal of Wildlife Management
Vol. 63, No. 1, January 1999

WILDLIFE MONOGRAPHS

(ISSN:0084-0173)

A Publication of The Wildlife Society

ECOLOGICAL SCALE AND FOREST DEVELOPMENT: SQUIRRELS, DIETARY FUNGI, AND VASCULAR PLANTS IN MANAGED AND UNMANAGED FORESTS

by

ANDREW B. CAREY, JANET KERSHNER,
BRIAN BISWELL, AND LAURA DOMINGUEZ DE TOLEDO

NO. 142 **JANUARY 1999**

WILDLIFE MONOGRAPHS Roy L.

Kirkpatrick, *Editor*
Department of Fisheries and Wildlife Sciences,
Virginia Polytechnic Institute and State University,
Blacksburg, VA 24061

The Wildlife Society believes that increased awareness and appreciation of wildlife values is an important objective. Society publications are one means of doing this.

Wildlife Monographs was begun in 1957 to provide for longer papers than those normally accepted *for The Journal of Wildlife Management.* There is no set schedule for publication. Individual issues of *Wildlife Monographs will* be published as suitable manuscripts are accepted and processed and when financing has been arranged.

Each *Monograph is* sponsored financially by organizations or institutions interested in publication of the information contained therein. Usually, the sponsor is the organization that conducted the original research, but others interested in disseminating the information may assist in defraying *Monograph* costs. The sponsors pay for printing and distribution of each *Monograph,* and The Wildlife Society provides skilled editors to assist *Monograph* authors and assures wide distribution through its worldwide mailing list to a select group of knowledgeable wildlife scientists, libraries, and others, and to members and subscribers who receive *The Journal of Wildlife Management.*

There is a perpetual need for additional funds to sponsor publication of worthwhile manuscripts in *Wildlife Monographs. Any* contribution will be accepted with gratitude by The Wildlife Society. Memorial funds collected to honor and perpetuate the names of deceased members of the profession probably could be put to no better use.

This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

PRINTED
IN
U.S.A

This study was supported by
U.S.D.I. BUREAU OF LAND MANAGEMENT
Roseburg District and Oregon State Office
and
U.S.D.A. FOREST SERVICE

Pacific Northwest Research Station
Publication costs were provided by
U.S.D.A. FOREST SERVICE
Pacific Northwest Research Station
and
Ecological Foundations of Biodiversity Research Team

FRONTISPIECE. A northern flying squirrel consumes a truffle from the forest floor (photo by Wes Colgan III).

ECOLOGICAL SCALE AND FOREST DEVELOPMENT: SQUIRRELS, DIETARY FUNGI, AND VASCULAR PLANTS IN MANAGED AND UNMANAGED FORESTS

ANDREW B. CAREY
Pacific Northwest Research Station, U.S. Forest Service, 3625 93rd Avenue S.W., Olympia, WA 98512-9193, USA

JANET KERSHNER
Pacific Northwest Research Station, U.S. Forest Service, 3625 93rd Avenue S.W., Olympia, WA 98512-9193, USA

BRIAN BISWELL
Pacific Northwest Research Station, U.S. Forest Service, 3625 93rd Avenue SW, Olympia, WA 98512-9193, USA

LAURA DOMINGUEZ de TOLEDO
Instituto Multidisciplinario de Biologia Vegetal, Universidad Nacional de Córdoba, Casilla de Correo 495-5000, Córdoba, Argentina

Abstract: Understanding ecological processes and their spatial scales is key to managing ecosystems for biodiversity, especially for species associated with late-seral forest. We focused on 2 species of squirrel (Sciuridae: northern flying squirrel, *Glaucomys sabrinus,* and Townsend's chipmunk, *Tamias townsendii*) in a cross-sectional survey of managed and natural stands in southwestern Oregon during 1985-89. We measured vegetation and abundances of squirrels at >2,000 points in 19 stands in 3 seral stages. We described the diets of the squirrels in the stands. We analyzed data at point, stand, and stage scales to identify key processes contributing to biodiversity and scales at which emergent properties (synergistic effects) appeared.

Four factors (crown-class differentiation, decadence, canopy stratification, and understory development) accounted for 63% of variance in vegetation structure. Decadence contributed to variation mostly in late-seral forest. Within stands, most habitat variables were poorly correlated. Across stands many variables were highly correlated, suggesting forests developed emergent properties above the point level but at or below stand level (16 ha). Plant species composition was summarized by 21 vegetation site types. Stands had 7-19 site types arrayed in fine scale (point and groups of points 40 m apart). Site types were used to measure habitat breadth (within-stand heterogeneity resulting from disturbance and forest development). Vegetation structure varied on a 0.5-ha scale. Stand-level characteristics were more influential than nominal seral stage for a variety of organisms. Late-seral forests were more moist and complex with greater habitat breadth than 40-70-year-old managed stands.

Structural factors, moisture-temperature gradient values (MGV), and habitat breadth were used to describe the habitat space potentially available to squirrels. Correlations between squirrels and habitat variables within stands were low. Linear regressions explained <20% of the within-stand variance in squirrel captures, but logistic regressions correctly classified 74 and 88% of the points according to usage (used, not used) by flying squirrels and chipmunks, respectively. Compared to available habitat space, the realized habitat of flying squirrels had high decadence and complex canopies. The realized habitat of chipmunks had complex canopies and large, dominant trees. Overall, chipmunks were less selective than flying squirrels and used 83% of the habitat space compared to 59% by flying squirrels. Among stands, variance in carrying capacity of flying squirrels was best explained (70%) by decadence, habitat breadth, and MGV. For chipmunks, decadence and canopy stratification provided the best model (72% of variance explained). Both squirrels had mycologically diverse diets; richness was correlated with decadence and canopy stratification. Major dietary fungi were associated with woody debris. Flying squirrels had higher carrying capacities and overlap among foraging patches of individuals, but smaller foraging patches, in late-seral forest than in managed stands. Squirrels were more abundant in late-seral forest than in managed forests. Abundance in some stands deviated markedly from the stage mean-stand character was more influential than nominal seral stage.

The 4 structural factors each represented an important ecological process; decadence and canopy stratification apparently had profound influences on other life forms. Carefully timed variable-density thinnings could accelerate crown-class differentiation, canopy stratification, and understory development and increase habitat breadth. Management of decadence is more problematic and may require various interventions, including inducing decay in live trees, conserving biological legacies from previous stands, and ensuring recruitment of coarse woody debris.

WILDLIFE MONOGRAPHS 142,1-71

Key words: ecological scale, forest development, *Glaucomys sabrinus,* habitat, northern flying squirrel, Oregon, *Tamias townsendii,* Townsend's chipmunk.

CONTENTS

INTRODUCTION

Squirrels (Sciuridae) in the Pacific Northwest are of a size (85-200 g) easily handled by many predators but are larger than most small mammals; thus, they are an important prey to several predators (Carey 1991). The 125-g nocturnal northern flying squirrel (*Glaucomys sabrinus*) is the primary prey for the spotted owl (*Strix occidentalis*) and an important prey of other strigid and mustelid predators in the Pacific Northwest (Carey et al. 1992, Wilson and Carey 1996). The flying squirrel also consumes and disseminates spores of ectomycorrhizal fungi that are symbiotic with Pinaceae and essential to tree growth. Townsend's chipmunk (*Tamias townsendii*), 85-g and diurnal, is prey for mustelids and disseminates fungal spores. The chipmunk has a broader niche than the flying squirrel and consumes seeds and fruits as well as fungal sporocarps (Sutton 1993). Because squirrels specialize on fruiting bodies of fungi and plants, their collective biomass can be construed as an index to ecological productivity as well as a correlate of the carrying capacity of forests for owls and mustelids (Carey et al. 1992, 1996*a*; Carey 1995).

Squirrels can be construed as good indicators of function in Pacific Northwest forest ecosystems. Knowledge of the characteristics of their habitat and the scale at which they integrate habitat elements can be useful in designing silvicultural systems for forest ecosystem management and for efforts to create or restore habitat for threatened species such as the spotted owl (Carey 1995). The response of squirrel populations to regional variation in late stages of forest development is well documented (Carey 1995, Waters and Zabel 1995, Zabel et al. 1995). Thus, we know these animals are more abundant in Oregon than in Washington and more abundant in old growth than in young, closed-canopy, competitive-exclusion-stage forests. Although considerable information about forest ecosystems in the

Pacific Northwest has been accumulated since Franklin et al. (1981) subjectively described the ecological characteristics of old-growth forests (*see* Ruggiero et al. 1991), questions about spatial scales of organization of natural and managed forest communities have not been addressed.

Our goal was to describe the responses of vascular plants, fungi in squirrel diets, and squirrels (flying squirrels and chipmunks) to environmental variation at various scales in a southwestern Oregon landscape. First, we asked if there was evidence of differential use by squirrels of stands within the landscape and of microhabitats within stands. Then, we asked how much variation in use of sites can be explained by the composition and structure of vegetation at (1) grid points (trap stations 40 m apart), (2) groups of points representing foraging patches and home ranges, (3) stands (100 grid points, 16 ha) supporting populations, and (4) gradients among stands-the habitats, or arrays of communities, occupied by species within the landscape (Whittaker et al. 1973). For each species of squirrel, we defined (1) a multidimensional space of habitat potentially available to the species by reducing numerous direct measures of vegetative structure and composition to a few major factors through multivariate analyses (Hutchinson 1958, Whittaker et al. 1973); (2) a multidimensional realized habitat space (space actually used by the species) based on use of points within the potentially available space; (3) the species' response surface ("habitat") within the space based on minimally sufficient regressions of abundance on factors (Maguire 1973); and (4) carrying capacities associated with the response surface based on maximum achieved densities in stands and regression on habitat factors. Finally, we asked if the taxonomic composition of fungal spores in fecal pellets of squirrels differed with environmental factors. After we identified the factors and habitat elements that were correlates of the abundance of chipmunks and flying squirrels, we related these factors and elements to numerous species and to management of forests for biodiversity.

Acknowledgments.—We thank our numerous field assistants, particularly those who persevered through multiple seasons of sampling: G. Bekker, B. R. Casler, G. S. Center, and A. M. Gillesberg. Useful reviews of various drafts were provided by M. P. Amaranthus, D. E. Capen, J. S. Hatfield, J. P. Hayes, D. B. Ransome, and T. A. Spies.

STUDY AREA

Our study area was the southern Coast Ranges Physiographic Province and immediately adjacent parts of the Klamath Mountains Province and Umpqua River Valley margins in Douglas and Coos counties, Oregon-the terminus of the Western Hemlock (*Tsuga heterophylla*) Zone and its transition to the Mixed Conifer Zone and Mixed Conifer-Mixed Evergreen Zone (Franklin and Dyrness 1973), also known as the Transition Life Zone (Bailey 1936). The area is edaphically and topographically diverse (elevation range 70650 m) with mild, wet, winters and hot summers (min. temperatures from -2.5 to +2.5 C in winter; max. temperatures of 22-27 C in summer; and 100-160 cm annual precipitation). The return interval for widespread, catastrophic fires is 250-350 years; locally intense fires occur at 10-50year intervals (Juday 1977). The Transition Life Zone differs from the Western Cascades, Southern Washington Cascades, Northern Cascades, and Olympic Peninsula provinces of the Pacific Northwest in having younger old-growth forests with less coarse woody debris and less accumulation of soil organic matter (Spies and Franklin 1991). The convergence of different physiographic provinces, vegetation life zones, high fire activity, and timber harvesting produced a landscape of high floristic, fungal, and faunal diversity (Franklin and Dyrness 1973, Ruggiero et al. 1991, Carey et al. 1992, Carey 1995). In the Pacific Northwest, the area is unique for its concentration of arboreal mammals and high carrying capacity for spotted owls, which specialize in preying on arboreal rodents (Carey et al. 1992). Flying squirrels averaged 1.9/ha in late-seral, natural forest and 0.9/ha in managed

Table 1. Age, plant community structure, and dominant species in old-growth (OG), niche-diversification (ND), and competitive-exclusion (CE) stands in southwestern Oregon, 1985—90.

Stand name	Age (yr)	Trees/ha		Cover (%)				
		Live	Dead	Overstory	Midstory	Shrub layer	Ground cover	Coarse woody debris
OG04	350	257	52	49	36	26	52	10
OG05	350	305	40	38	42	19	52	8
OG07	210	698	62	60	26	32	17	7
OG17	300	554	0	38	49	19	52	8
OG20	280	439	28	34	58	27	44	8
OG22	300	387	43	32	57	32	44	7
OG23	210	498	24	50	34	22	35	6
OG46	330	428	67	54	43	35	28	9
ND42	120	391	136	52	59	11	40	22
ND44	100	405	24	41	51	30	58	6
ND45	100	335	53	54	35	49	33	8
CE61	60	641	134	63	13	42	11	4
CE62	60	331	46	56	20	34	62	6
CE64	40	743	79	61	32	49	5	6
CE70	55	499	155	63	5	20	32	9
CE71	50	596	173	61	12	17	33	6
CE72	60	740	107	63	10	54	7	2
CE73	60	650	87	63	12	44	10	2
CE75	50	423	207	63	12	35	34	4

[a] Species acronyms are the first 2 letters of the genus and species (*see* Table 2).

forest (Carey et al. 1992, Carey 1995). Townsends chipmunk densities were similar: 1.9/ha in late-seral forest and 1.0/ha in managed forest (Carey 1995).

We preferentially selected 19 stands, 40—350 years old, that we believed spanned the range of variation in closed-canopy forests common in the southern Coast Ranges (Table 1, Fig. 1). We could not take a random sample of stands because (1) a complete inventory of stands was not available, (2) we were studying an actively managed landscape and we wanted to avoid the effects of ongoing harvest operations, (3) not all stands were accessible (landowner permission unobtainable), and (4) we wished to study stands for ≥3 years and many stands >40 years old were scheduled for imminent harvest. Preferential selection has advantages over random selection when only a limited sample can be taken—the sample may better represent the range of natural variation. Unknown biases may be present, however, and the scope of inference (probabilities associated with statistics) is limited to the sample. Levels of statistical significance cannot be precisely estimated, but statistical results should be conservative because variances should be overestimated (Gauch 1982). Our sample contained substantial variation in age, geographic location, elevation, vegetation structure, vegetation composition, and coarse woody debris (Table 1, Fig. 1).

METHODS

Sampling Stands

We defined stands as homogeneous units of vegetation that originated after a catastrophic disturbance (fire or clearcutting); did not differ markedly in elevation, aspect, slope, slope position, vegetation structure, and vegetation composition; and occupied sites of about 20 ha (Carey and Peeler 1995). We identified stands by examining aerial photos and inventory records of landowners and on-the-ground reconnaissance. We categorized stands into stages of forest development based on age, canopy appearance, degree of retention of biological legacies (live trees, snags, and coarse woody debris of the preceding stand), and understory development (Carey et al. 1996*a*). We categorized the stands floristically into vegetation site types (point scale), community

Table 1. Extended.

Species[a]			
Overstory	Midstory	Shrub layer	Ground cover
PSME, TSHE, THPL	TSHE, THPL	VAOV, TSHE, RHMA	POMU, OXOR, BENE
PSME, TSHE, THPL	TSHE	VAOV, TSHE, ACCI	POMU, OXOR, litter
PSME, ARME, TSHE	TSHE, PSME, LIDE	VAOV, LIDE, GASH	litter, POMU, moss
PSME, TSHE, THPL	TSHE, THPL, PSME	GASH, TSHE, THPL	litter, moss, GASH
PSME, ABGR, LIDE	ABGR, ACMA, THPL	GASH, COCO, ABGR	BENE, POMU, litter
PSME, ABGR	ABGR, TSHE, PSME	GASH, ACCI, HODI	BENE, POMU, forbs
PSME, ARME, LIDE	PSME, ARME, LIDE	PMSE, HODI, RHDI	litter, forbs, grass
PSME	TSHE, THPL, PSME	GASH, ACCI, TSHE	BENE, POMU, litter
PSME, TSHE	TSHE, PSME	VAPA, GASH, RHMA	POMU, BENE, OXOR
PSME, THPL, ABGR	ABGR, ACMA, PSME	HODI, COCO, GASH	litter, POMU, moss
PSME	ACMA, TSHE, PSME	GASH, ACCI, HODI	POMU, BENE, litter
PSME, ARME, CACH	PSME, CACH	GASH, VAOV, COCO	litter, moss
PSME	TSHE, ACMA, ACCI	GASH, HODI, BENE	POMU, forbs, OXOR
PSME	UMCA, CONU, LIDF	VAOV, ACCI, RHMA	litter, moss, POMU
PSME, TSHE	TSHE, PSME	GASH, HODI, COCO	POMU, litter, moss
PSME	ARME, PSME	GASH, HODI, COCO	BENE, moss, POMU
PSME, ARME, CACH	PSME	GASH, VAOV, RHMA	litter, POMU
PSME, ARME, CACH	ACMA	GASH, VAOV, HODI	litter, moss, POMU
PSME, ACMA	ACMA	HODI, GASH, COCO	BENE, POMU, moss

types (stand scale), and vegetation zone—Western Hemlock Zone, Mixed Conifer Zone, Zone, Mixed Conifer Zone, and Transition Life Zone—(Whittaker 1975). The landscape was composed primarily of 4 of the 8 stages described by Carey and Curtis (1996):

1. Ecosystem initiation—recent clearcuts and shrub and sapling stands.
2. Late competitive exclusion and early understory reinitiation (hereafter combined and referred to as competitive exclusion [CE] because few of the stands were understory reinitiation)—originated by clearcutting (40-70-yrold, second-growth, closed-canopy stands of trees generally 20-50 cm dbh).
3. Niche diversification (ND)—wildfire-regenerated stands of trees 80-120years old (generally 50-75-cm dbh) with developed understories and remnant old-growth structures (large live trees, snags, and coarse woody debris).
4. Old growth (OG)—dominant trees >200 years old and >75 cm dbh.

We searched for stands representative of competitive-exclusion, niche-diversification, and old-growth stages; niche-diversification stands were least common. We refer to niche diversification and old growth collectively as late-seral forest.

We located stands that appeared to be >16-ha and surveyed a sampling grid with 40-m horizontal spacing within the stand. Spacing between grid points was based on previous studies of forest mammal communities (Carey et al. 1981, 1991*a*). Initially some grids had >100 points, but after describing vegetation, we found that stands were rarely. large enough to encompass a grid with >100 points with a 40-m buffer. Usually aspect or slope position changed enough to result in obvious changes in plant communities. Thus we standardized our sampling to 100-point grids (16 ha). Five stands, however, were too narrow or too small for square 100 point (10 X 10) grids, and we surveyed rectangular grids or small grids: ND44 (7 x 15), CE62 (8 x 13), CE72 (8 x 8), CE73 (7 x 9), and CE75 (7 x 9). The 3 smallest grids were trapped briefly and used only in describing

Table 2. Frequency of occurrence of taxa composing ground, shrub, midstory, and overstory cover in 1,789 plots in 8 competitive-exclusion, 3 niche-diversification, and 8 old-growth stands in southwestern Oregon, 1986-87.

Cover category and Latin name	Common name	Acronym[a]	Occurrence (%)
Ground cover			
Rhus diversiloba	Pacific poison oak	RHDI	<1
Whipplea modesta	Whipple vine	WHMO	<1
Symphoricarpos mollis	creeping snowberry	SYMO	1
Linnaea borealis	northern twinflower	LIBO	1
Oxalis oregana	Oregon oxalis	OXOR	9.4
Berberis nervosa	oregongrape	BENE	23.6
Polystichum munitum	western swordfern	POMU	36.0
Shrub layer			
Thuja plicata	western redcedar	THPL	1.5
Vaccinium parvifolium	red huckleberry	VAPA	1.9
Pseudotsuga menziesii	Douglas-fir	PSME	1.9
Rhododendron macrophyllum	Pacific rhododendron	RHMA	3.5
Tsuga heterophylla	western hemlock	TSHE	3.8
Corylus cornuta	California hazel	COCO	5.9
Acer circinatum	vine maple	ACCI	8.0
Holodiscus discolor	creambush oceanspray	HODI	10.1
Vaccinium ovatum	evergreen huckleberry	VAOV	13.0
Gaultheria shallon	salal	GASH	36.1
Midstory			
Taxus brevifolia	Pacific yew	TABR	<1
Corylus cornuta	California hazel	COCO	1.2
Acer circinatum	vine maple	ACCI	2.2
Libocedrus decurrens	California incense-cedar	LIDE	2.1
Umbellularia californica	California-laurel	UMCA	2.7
Cornus nuttallii	Pacific dogwood	CONU	2.7
Castanopsis chrysophylla	golden chinkapin	CACH	2.8
Arbutus menziesii	Pacific madrone	ARME	3.7
Alnus rubra	red alder	ALRU	<1
Lithocarpus densiflorus	tanoak	LIDF	<1
Acer macrophyllum	bigleaf maple	ACMA	8.0
Thuja plicata	western redcedar	THPL	8.9
Abies grandis	grand fir	ABGR	10.2
Pseudotsuga menziesii	Douglas-fir	PSME	15.4
Tsuga heterophylla	western hemlock	TSHE	22.9
Overstory			
Pinus lambertiana	sugar pine	PILA	<1
Castanopsis chrysophylla	golden chinkapin	CACH	1.7
Acer macrophyllum	bigleaf maple	ACMA	2.2
Abies grandis	grand fir	ABGR	2.3
Libocedrus decurrens	California incense-cedar	LIDE	3.0
Thuja plicata	western redcedar	THPL	3.2
Tsuga heterophylla	western hemlock	TSHE	4.9
Arbutus menziesii	Pacific madrone	ARME	9.2
Pseudotsuga menziesii	Douglas-fir	PSME	86.9

[a] Species acronyms are the first 2 letters of the genus and species.

the potential habitat space. All stands, regardless of size, were in a context of stands of similar age and structure. Apsect changes, streams, logging roads, and property boundaries (that determined cutting-unit boundaries) created the discontinuities that resulted in the small stands. Even small stands, however, showed fine-grained heterogeneity with differing, but recurring, vegetation site types; i.e., they were "homogeneously diverse" (Hutchinson 1978:159). Several stands had clearcuts adjacent to 1 side. To avoid the pseudoreplication of sampling the same stand with >1 grid, grids were separated by >1 km or by changes in aspect or slope that resulted in noticeable differences in vegetation. Study stands were scattered over, 1,500 km^2.

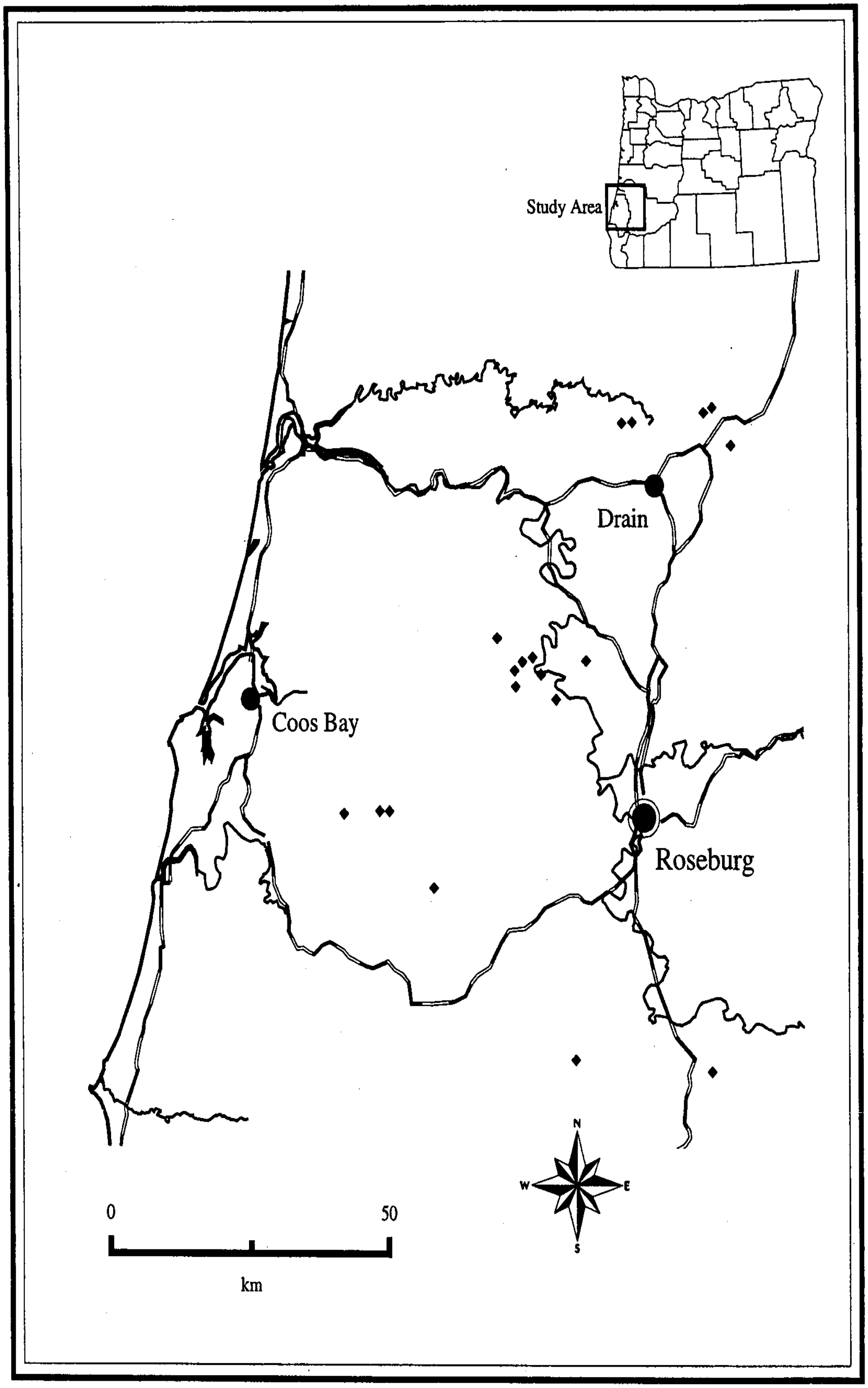


Fig. 1. Locations of study stands (black diamonds) in southwestern Oregon, 1985-89.

Sampling Vegetation

Our objectives in sampling vegetation were to (1) describe the composition and structure of each stand (Table 1), (2) quantify within-stand heterogeneity, (3) quantify differences among stages of development (competitive exclusion, niche diversification, and old growth), (4) classify vegetation communities, (5) describe environmental gradients, and (6) quantify attributes thought to be important to flying squirrels and chipmunks and useful as predictors of squirrel abundance (large trees, large snags, coarse woody debris, foliage-height diversity, and shrub cover—*see* Carey 1995).

We sampled the vegetation around each grid point by using 2 nested plots. We chose variables and categories based on previous widespread sampling of vegetation and birds in the southern Coast Ranges (Carey et al. 1991*b*). On 10.6-m-radius plots (350 m^2), we recorded the following canopy features: (1) counts of trees by life form (deciduous and conifer) and dbh class (10-50 cm, >50 cm, and >100 cm); (2) counts of snags in 4 classes defined by dbh (10-50 cm, >50 cm) and height (<15m, ≥ 15m); and (3) total canopy cover and cover by dominant and codominant species. These plots, however, were too small to accurately estimate numbers of trees >100 cm dbh.

On 5.6-m-radius plots (100 m^2), we measured the percentage of cover by vegetation and by the dominant and the codominant species in each of 3 layers: (1) forest floor (<0.5 m; generally forbs, ferns, grasses, and half-shrubs), (2) shrub layer (0.5-2 m; shrubs and seedlings), and (3) midstory (>2-m subcanopy; tall shrubs, saplings, suppressed trees, shade-tolerant trees). We recorded litter (leaves, needles, and twigs, and branches <10 cm in diameter) and moss as if they were species of plants when they were dominant (and <12% cover) or codominant (and >6% cover) features of the forest floor. Litter and moss were later combined to represent a measure of open forest floor (little protective cover for squirrels). We recorded percent cover of fallen trees ≥10 cm dbh by decay class. Decay classes were (1) little decay (bark, branches, and wood intact), (2) moderately decayed (bark sloughing; wood showing cubical rot), and (3) well decayed (bole compressed; no bark; wood powdery). Covers were summed over decay classes to obtain a measure of total coarse woody debris. If >2 species of a life form were present in a layer and no species was clearly dominant or codominant, we recorded the categories of grass, forbs, ferns, shrubs, and trees as if they were species. Generally, plot sizes were small enough that 1-2 species dominated each layer. Midstory layers in competitive exclusion were generally subordinate or suppressed trees of the dominant species or of pioneer species. Deciduous trees often were in the midstory of competitive-exclusion stands. In old-growth stands, midstory trees often were a second age class (cohort) composed of ≥1 species of shade-tolerant trees. We measured nested plots at 2,107 grid points.

All percent covers were estimated by eye and recorded on an octave scale with midpoints of 0, 2, 4, 8, 16, 32, and 64% and category ranges of 0, trace-2.9, 3.0-5.9, 6.0-11.9, 12.0-23.9, 24.0-47.9, and ≥48.0%. Preston (1981) reported the ecological relevance of the octave scale in studies of commonness and rarity of species. We chose the octave scale also to (1) allow fine discrimination of covers of low values, (2) allow easier estimation of the relation of area covered to area of plot, (3) more finely divide the ranges of covers often found in the understories of forested environments, (4) concentrate effort at levels that seem more biologically important (i.e., the difference between 60 and 100% seems less important than the differences between 0 and 40%), (5) reduce rounding errors associated with estimates based on divisions of 5's and 10's, and (6) reduce interobserver variability, which seems greatest at values around 50% (*see* Bonham 1989 for a discussion of alternative scales for cover estimation). Observers were trained in groups and with silhouette diagrams showing percent covers of clumped and randomly distributed particles (Terry and Chilingar 1955) to further reduce variability among observers. We defined cover as the vertical projection of foliage on to the ground (or sky) and viewed from above (or below); we did not project crowns horizontally—gaps in foliage were not included in cover estimates (Bonham 1989). Thus, cover >48% is dense. Because the maximum value recorded was 64%, values >60% represent near complete closure for tree canopies. Canopy-cover values in competitive exclusion were skewed toward 64%, providing little discrimination between grid points in young stands. Our tree counts, however, did measure variation in canopy cover among points, assuming growth form is essentially the same among well-stocked, even-aged stands of Douglas-fir (*Pseudo tsuga menziesii*). The octave scale worked well for other layers. Coarse woody debris (fallen tree) covers were skewed towards the low, more precise end of the scale (≤16%). In retrospect, even the low end of the scale should have been more precise given the economic impacts associated with management recommendations. Costs increase sharply with 1% increments in cover equivalent to 2-3 large (>50 cm dbh) trees/ha. Thus, pragmatically, there is a huge difference between 8% and 16%.

Our values for canopy cover may not be comparable to those of other investigators. Definitions of canopy cover vary widely (Bonham 1989) and it is our experience that few investigators explicitly define, in their reports, how they measured cover. It appears that canopy-cover estimates often include crown projection and the subordinate and midstory vegetation we placed in our midstory class. Our cover estimates for the 4 layers are not additive because there is overlap in the foliage cover among the layers. Likewise, our cover estimates cannot be compared to leaf area because of horizontal overlap of leaves. Indeed, our cover estimates do not demonstrate fully the differences between old-growth and second-growth canopies because these canopies differ markedly in depth (Franklin et al. 1981). The estimates are most useful in comparing coverages among plots and groups of plots, calculating indices of foliage-height diversity, and describing the process of forest development.

Sampling Squirrels

We sampled squirrels with the methods of Carey et al. (1991*a*). Two wire box traps were placed at each grid point. One trap was placed 1.5 m high in the largest tree <5 m from the grid point. The other was placed on the ground, near a fallen tree, underneath shrubs, or at the base of a live tree. Each trap was covered with a 3.8-L (1-gallon) waxed paper carton and woody debris to provide stability and shelter from wind and rain. A waxed paper nest box with nonabsorbent batting was placed in each trap to provide additional protection from cold temperatures. Traps were baited with a peanut butter, molasses, and oat mixture as an attractant and as food for captured animals. Traps were adjusted to spring with a light pressure, crisp release, and quick fall of the door. Bait and adjustment were checked daily.

Initially, traps were opened for 8 consecutive nights. High rates of recapture stressed squirrels, resulting in hypothermia and sometimes death. Predation on squirrels by mustelids increased with consecutive trap nights also (Wilson and Carey 1996). Subsequently, we opened traps on Monday and closed them on Friday (4 nights open) for 2 consecutive weeks. If captures were high and weather inclement, we reduced trap nights to 3/week to further reduce stress on captured animals. Captured animals were handled by using wire mesh and cloth cones (Carey et al. 1991a) to reduce stress and injury to the animals. We placed numbered ear tags in both ears of each squirrel at first capture. We recorded tag numbers, age, sex, weight, and reproductive condition of each captured animal and then released the animal at the point of capture. Pilot studies (Carey et al. 1991*a*) showed that trap success was high after fall rains and before summer drought; therefore, we trapped in spring and fall (Table 3). We do not know why trap success was particularly high during rainy periods with mild temperatures, but these periods coincide with high production of the sporocarps of ectomycorrhizal fungi (truffles), the major food of the northern flying squirrel and an important food of Townsend's chipmunk (Maser et al. 1986, Luoma 1991, Carey 1995). Presumably, trap success is enhanced by the animals' intensive on-the-ground foraging for truffles. Thus, our results apply to spring and fall; we do not know their applicability to summer or winter. Truffle supply presumably is reduced in cold winters and dry summers, and foraging site selection may be more pronounced in those seasons than in spring and fall. Telemetry studies in the Puget Trough of Washington, however, demonstrate little seasonal differences in foraging site selection (A. B. Carey, coauthor, unpubl. data).

Initially, our plans were to sample equal numbers of natural (niche-diversification and old-growth) and managed (competitive-exclusion) stands for 5 consecutive years; however, changes in timber harvest plans and funding circumvented our plans. Thus, the number of seasons and years of sampling differed among stands (Table 3).

Dietary Analysis

We collected fecal pellets from the anus (to avoid contamination of pellets by wind-born spores) of each animal that defecated while being handled. During preliminary analyses of pellets we found that pellets from animals recaptured within a trapping period were contaminated with the bait used in traps. Consequently, we limited our analysis of pellets to those obtained from animals at their first capture within a trapping period (and thus avoided pseudoreplication as well). Because not all animals defecate at first capture and densities of squirrels were low, we were limited in the number of pellets we could collect in any 1 stand in 1 trapping period (6-8 nights). Pellets were analyzed microscopically (400X) for fungal spores, fungal hyphae, plant material (moss, lichen, fern sporangia, pollen, leaf fragments, seeds of monocots and dicots), and insects following the procedures developed by McIntire and Carey (1989) to be adequate to inventory taxa present in samples (i.e., examining ≥50 microscope fields/sample). In 1986, some flying squirrel samples were analyzed with 50 fields (Carey 1995); all other samples were analyzed with 75 fields to ensure that rare items were found—but the 1986 samples with fewer fields examined were more diverse, which suggests little gain from the extra effort. Fungal spores were recorded by the most specific taxon possible (generally genus or family; Castellano et al. 1989) and as present or absent in each field. Percent frequencies (% of fields) were calculated for fungal taxa. Relative densities were calculated for the major food groups (spores, hyphae, plants, insects) by summing the percent frequencies and dividing the percent frequency of each food group by the total. Taxonomic richness (total no. of taxa, taxa occurring in >80% of stands within a stage, and mean taxa/stand within stages) and diversity (Shannon-Wiener Index) were calculated for fungal taxa. We used a bootstrapping program (Raphael 1991) to estimate species richness for each collection of fecal samples (stand X season) and constructed overall taxa accumulation curves to determine the minimum collection size per stand per sampling period needed to detect all taxa present in the diets of the squirrel populations. Taxa accumulation curves for 00 pseudoreplications of collections of 1-29 samples reached asymptotes for both flying squirrels and chipmunks at 7 samples. From a total collection of 158 flying squirrel samples (12 stands) and 244 chipmunk samples (13 stands), we found collections adequate (≥7 samples) for computing diets for flying squirrels (7-10 samples) and chipmunks (9-20 samples) in 11 stands in spring 1986 and 10 stands in spring 1988 (a total of 14 stands in the spring: OG 4, 5, 17, 20, 22, 46; ND 42, 44, 45; and CE 61, 62, 64, 70, 71). We had adequate data for chipmunks from fall 1986 (OG 17, 20, 22, 46) to compare fall and spring diets in old growth.

Analysis of Vegetation Data

We developed a flowchart for data analysis that would meet our objectives of describing our sample points, stands, and stages and relating vegetation structure and composition to site selection by, and abundance of, squirrels (Fig. 2). In addition to descriptive statistics, our exploratory analyses encompassed both parametric and nonparametric paths and univariate and multivariate statistics. We adopted a multi-faceted approach because we were dealing with measures of proximate (vs. ultimate) factors of the environment and indices rather than absolute measures of activity and abundance of squirrels. Even though our analyses entailed functional redundancy in a statistical sense, the parallel

Table 3. Trap nights and captures/100 trap nights of *Glaucomys sabrinus* and *Tamias townsendii* in southwestern Oregon in spring and fall, 1985–89.

Stand name	Number of trap nights										Captures/100 trap nights			
	1985	1986		1987		1988		1989			*Glaucomys*		*Tamias*	
	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Total	$\bar{x}$	SE	$\bar{x}$	SE
OG04		1,200	1,400	1,600						4,200	3.4	2.5	7.9	4.2
OG05	1,440	1,440	1,400	1,600						5,880	1.9	1.4	9.1	5.1
OG07								1,600	1,600	3,200	1.3	1.9	5.7	5.9
OG17						1,600	1,600	1,600	1,600	6,400	5.1	2.2	7.8	3.6
OG20	4,400	4,400	1,400	1,400		1,600	1,600	1,600	1,600	18,000	3.1	1.1	5.8	1.8
OG22	3,168	1,440	1,600	1,600	1,600	1,600	1,600	1,600	1,600	15,808	6.3	1.7	6.4	1.7
OG23							1,600	1,600	1,600	4,800	0.6	0.8	7.0	3.6
OG46		800	1,600	1,600		1,600	1,600	1,600	1,600	10,400	3.7	1.2	5.4	1.9
ND42	960	1,000	1,400	1,600		1,600				6.560	6.3	2.3	7.3	3.5
ND44						1,680		1,680		3,360	1.9	2.5	7.6	5.9
ND45		800		1,600		1,600		1,600		5,600	3.9	2.7	7.5	3.3
CE61	2,016	1,275	1,600	1,600						6,491	1.2	1.1	3.9	4.0
CE62						1,664		1,664		3,328	3.6	3.3	5.6	4.9
CE64	1,200	1,200	1,600	1,600						5,600	4.8	2.3	3.9	2.2
CE70		1,400	1,600	1,600		1,600		1,680		7,880	2.2	1.0	3.4	1.9
CE71		882	1,400	1,600		1,600				5,482	1.2	0.9	3.4	2.5

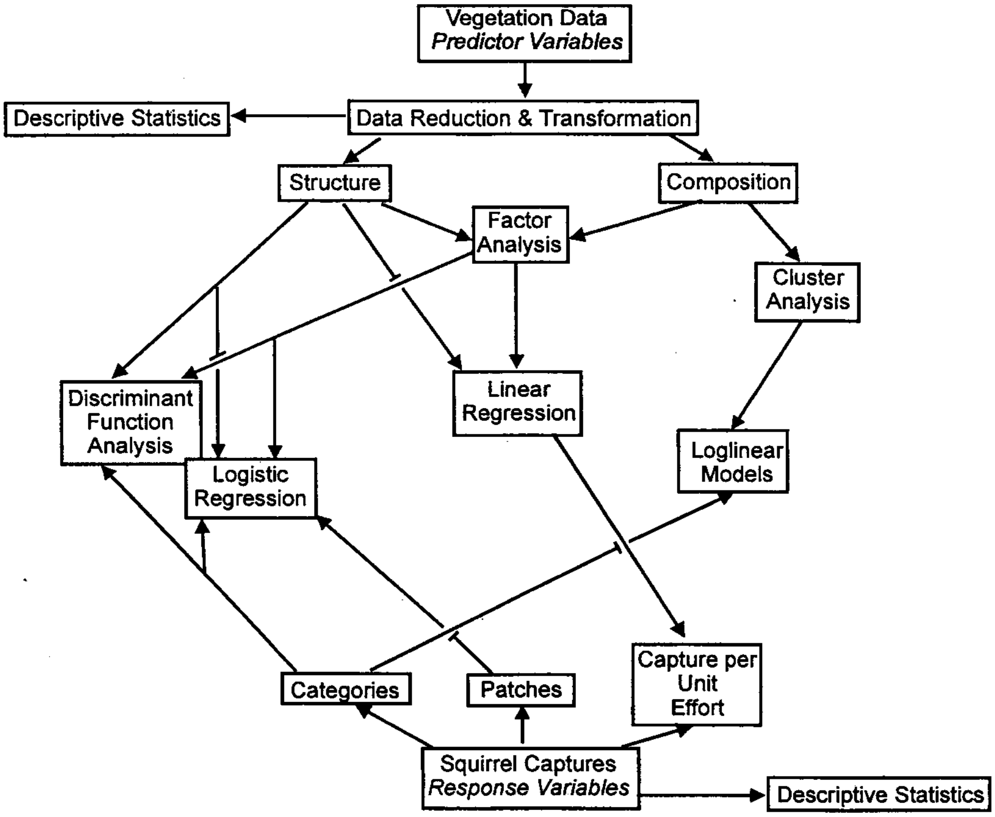


Fig. 2. Flowchart for use of data in statistical analyses.

the parallel paths entailed rescaling of the proximate variables and the animal responses. We thought that using multiple procedures would result in a heuristic set of analyses highlighting internal consistencies and inconsistencies and insight into the nature of both predictor and response variables.

Preliminary Analyses.—Data were collected from 2,107 nested plots during 1986-88. All data were used in cluster analysis of vegetation composition and structure. Large grids were reduced to 10 X 10 grids and data from the excess plots were not included in subsequent analyses, leaving observations on 1,789 plots. Observations were collected for 33 variables at each plot. We recorded 67 categories of cover (including 53 categories of plants): 15 in the ground layer (8 species plus moss, grass, forbs, shrubs, litter, and bare soil), 18 in the shrub layer (16 species plus trees and shrubs), 21 in the midstory (20 species plus shrubs), and 13 in the overstory (12 species plus trees). Some species occurred in up to 3 layers, but were treated as separate species for cluster analysis. Cover categories (15 species) occurring with <1% frequency were dropped from all analyses except cluster analysis (Table 2).

Frequency distributions, box-and-whisker plots, and summary statistics for each variable were compiled by stand, stage, and all stands combined. Histograms and Kolmogorov-Smirnov goodness-of-fit tests were used to determine departures from normality (Zar 1984). We report standard deviations (SD) when describing the distribution of observations in a sample and standard errors (SE) when describing the precision of sample statistics (Zar 1984). For nonnormally distributed variables and variables with outliers, logarithmic and square-root transformations were used successfully to reduce the number of outhers and skewness. Frequency distributions, scatter plots, histograms, and standard scores (>3.0) were used to identify errors in data entry and extreme values (Tabachnik and Fidell 1989). Frequencies of occurrences of structural (nonspecies) variables and correlations among variables were used to determine if rare or highly correlated variables should be dropped or combined to reduce redundancy in the data set and to avoid singularity of matrices. New variables resulting from combining height or diameter categories included the total number of medium (10-50 cm dbh) snags, total number of large (>50 cm dbh) snags, total number of live deciduous trees, total number of large (>50 cm dbh) live coniferous trees, and total number of live coniferous trees (>10 cm dbh). This procedure reduced both the total number of variables and departures from normality. Foliage-height diversity was calculate for each point by using the Berger-Parkei Index (*BPI*) (Magurran 1988, Carey et al. 1991*b*):

$$BPI = 1 \div d$$

Where

$d = C_{\max} \div C$,

$C =$ total cover, and

$C_{\max} =$ cover in the densest layer.

Stand-level prevalences of dense shrubs and midstory (percentages of stations >24% cover, Carey 1995) and overstory cover (≥32%) were calculated. We used these prevalences as measures of abundance of high cover at the stand level and to separate plots into 2 groups to determine scale of change in vegetation structure. We treated rows and columns of grids as 360-m-long transects and calculated distances between changes (low to high or high to low) in structure. We also examined correlations between rows and columns to determine if within-stand heterogeneity was indicative of environmental gradients or random variation. Rows generally ran along topographic contours and columns up and down slopes. All correlations between variables reported in this paper were significant at $P < 0.05$ unless stated otherwise.

Cluster Analysis.—Our objective was to determine if there was a discrete set of clusters of plots that represented vegetation site types making up plant communities in response to the north-south, moisture-temperature gradient influencing forest composition regionally in the Pacific Northwest (Franklin and Dyrness 1973) or that were associated with the chronosequence of the stands we studied (40-330 yr). If such a set existed, we would be able to examine the influence of plant species composition on squirrel abundance, either independent of the stage of forest development or in interaction with stage of forest development. Cluster analysis, like other multivariate methods, is a way to reduce redundancy in large sets of data in order to facilitate understanding of complex relationships (Gauch 1980). Program COMPOSE (Mohler 1987) was used to condense and format our matrix of 2,107 plots and 53 species. We used COMPCLUS (Gauch 1979) (a rapid, nonhierarchial clustering program for large data sets) for our analysis. Cover values were transformed to octave categories as defined by Gauch (1982). The intermediate distance measure was chosen for the analysis. In phase 1 of COMPCLUS, we used iteration (100 random choices of radii) to choose a target cluster number. Replicate clusterings were performed and results were compared through cross-tabulations of plots among clusters. The final target number was 35 clusters. More consistent and repeatable clusters were obtained with 53 species than with the 33 species that occurred in >5% of plots. We used the results from analysis of 53 species.

In phase 2, the number of small clusters (few plots) was minimized by incrementally (0.1 increments) increasing the minimum radius. Discriminant function analysis was used to assign outlying points to the large clusters. For use in subsequent analyses, mean cluster values were based on 1,789 plots. We used canonical analysis of discriminance and detrended correspondence analysis to identify gradients among the clusters (Pielou 1984). We interpreted the ordinations by positions of plant species on gradients and descriptions of the ecologies of species in Franklin and Dyrness (1973) and Spies and Franklin (1991). The first detrended correspondence analysis axis was interpreted as a moisture-temperature gradient, and values (MGV) were used in subsequent analyses.

We calculated 3 measures of diversity of plant communities within stands (Pielou 1977, Magurran 1988): (1) site-type richness (no. of types), (2) diversity (Brillouin's index, H_{B} = [In $N!$ — Σln $n_i!$] ÷ N for N total observations and n observations in the i different site types), and (3) evenness (E = [H_{B}] ÷ [H_{Bmax}]). We also calculated habitat breadth of stands by dividing the 0 ± 2 SD by the range of MGV Habitat breadth is a measure of the proportion of the total across-all-stands axis occupied by the statistically central 95% of the grid points in the stand. We measured the ecological distance (differences in MGV) at adjacent grid points (by rows and columns) to estimate the variance of distances (s^2) and divided this number by the mean dis tance as a measure of contagion $_{\mathrm{(IDCA)}}$ orgrain ($I_{\mathrm{DCA}} = s^2 \div 0$). In other words, if like site types are clustered because of strong, localized, moisture-temperature gradients, topography, or edaphic features, contagion would be high ($I_{\mathrm{DCA}} > 1$). If arrangement of site types reflects variability in local (among grid point) microclimate and light as a result of small-scale canopy variation due to competition among trees and stochastic processes leading to tree fall, then the distribution of distances would be uniform (I_{DCA} near 0). Significance of I_{DCA} was tested with $x^2 = I_{\mathrm{DCA}}\,(n - 1)$, 99 df; $x^2 > 130$ indicates significant contagion and $x^2 < 74.2$ indicates significant uniformity at $P < 0.05$. Values of x^2 between 74.2 and 130 indicate no statistically significant departures from random distributions. Vegetation patterns, however, usually are the result of a combination of stochastic, physiographic, and biotic influences (e.g., canopy closure).

The value of measures of habitat breadth and contagion lies in the presumptions that site-type clusters represent a moisture-temperature gradient and that clusters adjacent on the gradient have less difference among them than clusters selected from across the gradient. If this were true, measures of diversity and evenness could be misleading because they incorporate only types and not relative differences among types. Thus, we believed the best measure of within-stand diversity would be either mean MGV distance between adjacent grid points or habitat breadth. If site types were clumped in distribution, then H_{B} and E would be of greater interest than if site types were uniformly distributed.

Factor Analysis.—We used factor analysis with varimax rotation and Kaiser normalization (Norusis 1990) to identify principal components of the variance in our data that might reflect important ecological gradients in our study area. We used varimax rotation (maximizing the variance of squared loadings for each factor), because it is purported to give a clearer separation of factors than other methods (Kim and Mueller 1978). Nichols (1977) suggested that interpretation of factors should be limited to the first 3 or 4 factors. Factors with eigenvalues > 1 were extracted and a scree plot was used to set the number of factors to include in our model (Norusis 1990). Factor analysis of structural variables generally produced 4 interpretable factors. Because factor analysis uses only shared variance (whereas principal component analysis uses the variance of all observed variables), variance due to error and variance unique to each variable is eliminated. Exploratory factor analysis summarizes data by grouping together variables that are correlated. Factors, therefore, are orthogonal and unrelated to one another (Tabachnik and Fidell 1989). Variables were assigned to 1 factor each, based on maximum loading. Interpretation of factors was based on sign and strength of the variable loadings. We included 11 structural variables (vegetation cover by layer, foliage-height diversity, fallen trees, snags, conifers, and deciduous trees), 33 species variables (variables occurring at <5% of grid points were excluded), and a combined data set in a series of factor analyses. Four factors from analysis of vegetation structure and MGV were used to define a habitat "hypervolume" (Hutchinson 1958, Whittaker et al. 1973) of the data set. Factor analysis of species variables and combined species-structure data sets added little beyond detrended correspondence analysis; some minor compositional gradients were identified. We also performed factor analysis of structural variables for each stand, on the set of competitive-exclusion stands, and on the set of late-seral (niche-diversification and oldgrowth) stands to determine which factors were common to all 3 scales and if different factors were operating within stands and within seral stages than over the chronosequence.

Analysis of Mammal Data

Data collected were (1) captures and identity (tag no.) of flying squirrels, chipmunks, and other animals and (2) numbers of traps sprung (closed but empty) and open (and empty) by trap station (2 traps/ grid point) by day in multiple trapping periods (seasons and years). Thus, we had a choice of several dependent variables for flying squirrels and chipmunks; these could be (1) total captures (including repeated captures of the same individual), (2) total captures per unit effort of trapping (TCPUE), (3) total individuals captured, (4) total individuals captured per unit effort (ICPUE), and (5) presence-absence (species captured or not). At the stand level, we also estimated mean maximum distance moved by individuals within a 2-week trapping period. Thus, we could use mark-recapture analysis to estimate population size and mean maximum distance moved to estimate area sampled to obtain estimates of density.

Presence-absence could be biased if trapping effort was low and differed among grid points and stands, but trapping effort was substantial and repeated over seasons. The cumulative proportion of grid points used in stands increased asymptotically with number of trap nights to 3,0006,000 trap nights—except CE61 did not show an asymptote with 6,500 trap nights and 27% of points used. Even after 18,000 trap nights in the most trapped old-growth stand, no captures of flying squirrels were recorded at 50% of the grid points, no chipmunks at 31% of the grid points, and neither species at 19% of the grid points. Presence-absence is a definition of realized habitat space (i.e., separates grid points that are used from those not used), whereas captures per unit effort (CPUE) is an index to activity and habitat quality. Presence-absence with large trapping effort may not be as subject to sampling error as CPUE. Thus, we used presence-absence as the dependent variable in discriminant function analysis with habitat factors and in logistic regression with habitat elements.

Assuming that CPUE contains information about the relative value of a grid point or stand as habitat, we conducted a second analysis with CPUE as the dependent variable in multiple linear regression. When the probability of capture at a grid point is a function of trap effort, overall population density, behavioral factors, and time (day, season, and year), the ability of habitat variables to explain variance in CPUE is reduced. Because trapping effort (no. of traps opened X no. of nights/period summed over trapping sessions) differed among stands and numbers of captures and sprung traps differed among stations, we calculated effort as suggested by Nelson and Clarke (1973): effort = total trap nights - 0.5 X [no. of sprung traps + no. of captures of all species]. We used 100 trap nights as the unit of effort. Total captures (TCPUE) may be a biased estimator of abundance because the behavior of some individuals may change after first capture—they may become trap-happy or trap-shy (White et al. 1982). Carey et al. (1991a) examined our data for behavioral and other effects on probability of capture at the stand (population) level through program CAPTURE (Otis et al. 1978). They found 72% of the stand-level data sets for flying squirrels showed no behavioral effects and concluded that flying squirrels became neither trap-happy nor trap-shy. Initial probabilities of capture (0.51 ± 0.03) were reasonably homogeneous and not significantly different from probabilities of recapture (0.50 ± 0.03). The data for Townsend's chipmunks, however, indicated reasonably homogeneous initial probabilities of capture (0.66 ± 0.03), but trap-happiness with probabilities of recapture of 0.79 ± 0.03 (46% of the sets showed behavioral effects). Thus, we decided to use TCPUE for flying squirrels and ICPUE for chipmunks. We used the same measures at the stand level (rather than densities) because densities incorporate multiplicative sampling errors from model choice, calculations of population size, and methods for estimating area sampled. Catch indices, with their inherently smaller sampling error, are preferable to densities for determining animal responses to habitat factors when capture probabilities are homogeneous among populations (Skalski and Robson 1992). Thus, CPUE's reflect activity at grid points and activity at the stand level; they estimate density only imperfectly (Carey et al. 1991*a*). We used ln(CPUE + 1) in regression analyses. We included all grid points and mean (over seasons and years) CPUE's for analysis of grid points within stands. For analysis of among-stand variation, we eliminated stands that (1) were trapped in only 1 season (<3,000 trap nights), (2) had <100 grid points, and (3) had truncated trapping sessions (<6 nights/session). Three competitive-exclusion stands (72, 73, 75) met all 3 criteria; the remainder of the stands met none of the criteria.

There is another potential pitfall in using capture data at the grid point and stand level. Traps at the periphery of a trapping grid may catch more animals than traps in the interior of the grid because of reduced influence of surrounding traps. We tested for edge effect by examining captures across 3 embedded sets of traps for each stand (exterior, penultimate, and interior grid lines) by using Kruskal-Wallis tests with $\alpha = 0.05$ (White et al. 1982). We found 6 of 19 grids showed edge effects for the northern flying squirrel and 14 of 19 for Townsend's chipmunk (even after using ICPUE). Thus, edge effect seemed to be a nonrandom, serious, systematic effect for chipmunks, but not for flying squirrels. Edge effects were almost exclusive to the exterior traps, and differences in captures were up to 5-fold for chipmunks. There seemed no seral stage bias to the edge effect; 3 of 5 grids without edge effect were the 3 small grids in competitive exclusion (72-75) where (1) statistical power was low due to lower than average sample size, (2) length of edge was less, and (3) depth of grid was less (entire grids may have had edge effect). Thus, edge effect was contributing positive bias to traps at exterior grid points for captures of chipmunks. The effect of this bias would be to add undue weight to particular trap stations and increase the error term (decrease variance explained) in regression of ICPUE on habitat variables. Thus, we removed the exterior trap lines (and the small grids) from the data sets for regression analysis.

At the stand level, mean maximum distances moved showed that activity areas of both species exceeded distance between grid points by a factor of 2-3 (80-120 m vs. 40 m between grid points) and that the mean maximum distances moved were higher in competitive-exclusion stands than in old-growth stands (Carey et al. 1991*a*)—grids in competitive-exclusion stands sampled larger areas than equivalent-sized grids in old growth (a positive bias in CPUE for competitive-exclusion stands). Because of the area-sampled bias in young stands and because spotted owls preyed on the flying squirrels in our lateseral stands (Carey et al. 1992), we conducted a second regression analysis of the influence of mean habitat factors on flying squirrel and chipmunk abundance. We assumed that the abundance of squirrels was a function of carrying capacity, temporal variation in carrying capacity, and temporally varying density-dependent predation. Predation was heavier in late-seral stands than in competitive-exclusion stands. Predation differed markedly among stands, seasons, and years (Carey et al. 1992, Carey and Peeler 1995) and might have reduced population levels, in some sampling periods, below the carrying capacity determined by habitat factors (Carey et al. 1992, Carey 1995). Predation by weasels (*Mustela* spp.) also was heavier in our late-seral stands than in our competitive-exclusion stands (Wilson and Carey 1996). Thus, we concluded that mean abundance (CPUE averaged over sampling periods) might not be the best measure of carrying capacity. Rather, maximum recorded density for each stand might better represent potential carrying capacity. We chose density over CPUE because of the correction for area sampled and because we were trying to estimate a population parameter rather than a measure of foraging activity. We used maximum densities based on a modified Lincoln-Peterson estimator and adding one-half the mean maximum distance moved to the periphery of the grid to estimate area sampled (Carey et al. 1991*a*). Maximum densities were well distributed among years (4-6/yr) and between seasons (12 of 19 in spring), with no indication of confounding effects due to year or season.

Habitat Analyses

We used discriminant function analysis with factor variables and logistic regression with original variables to define realized habitats based on species presence and absence (caught at a point or not caught at a point). We identified foraging patches (flying squirrels) and home ranges (chipmunks) for squirrels with ≥3 captures within a sampling period with the inclusive boundary strip method (Stickel 1954) wherein areas of use are defined by polygons connecting points midway between used and unused trap stations. We compared foraging patch and home range characteristics (mean factor and moisture—temperature gradient values) by stand among 3 consecutive springs (1986—88: 148 flying squirrel foraging patches in 3 old-growth, 2 niche-diversification, and 3 competitive-exclusion stands; 424 chipmunk home ranges in 6 old-growth, 3 niche-diversification, and 6 competitive-exclusion stands) and found no differences (Kruskal Wallis tests, $P > 0.05$). Then, we combined data sets by stand and compared foraging patches and home ranges to randomly selected patches of the same size and shape and to randomly selected points of the same number to determine if sets of points used by individuals in the spring differed from randomly selected points with and without spatial constraints. We considered the results of Wilcoxon matched paired sign rank tests to be significant at $P < 0.05$ (within stand comparisons) if a discernable pattern of proportion of contrasts with significant differences appeared in respect to seral stages. We used simple-linear and multiple regression to model the response to habitat descriptors in terms of habitat (ln[CPUE + 1]) and carrying capacity (maximum seasonal density). Simple-linear and step-wise multiple regressions were exploratory; final models were based on all-possible-subsets regression.

Preliminary Analyses.—The purposes of the preliminary analyses were (1) to explore relations among variables (predictive value and multicollinearity) and stands, (2) to determine which transformations would be useful to achieve normality in independent variables and standardized residuals, (3) to determine which observations (grid points or stands) might be outliers and if deleting outer trap lines had positive effects on residuals, and (4) to search for nonlinear relations. Residuals in regressions using data from grid points showed departures from normality due to points with no captures. We therefore eliminated points with no captures from point-level regression analyses. The resulting regressions model responses only within the realized habitat space. All regressions reported were significant at $P < 0.05$ and had normally distributed residuals as evidenced by plots of the predicted values against the residuals and normal probability plots of standardized residuals.

Independent variables were directly measured structural habitat variables and variables derived from direct measures (means, sums, and indexes), 4 new variables obtained through factor analysis, and 1 measure of position on the complex moisture—temperature gradient (MGV) derived from detrended correspondence analysis of vegetation clusters. Observations were used for among-grid-point analyses and means for among-stand analyses. Variable-stand relations include (1) among-grid points within stands, (2) among-grid points across competitive-exclusion stands, (3) among-grid points across late-seral (niche-diversification and old-growth) stands, (4) among-grid points across all stands, (5) among stands within seral stage, and (6) among stands across seral stages.

Final Regression Analyses.—Final equations were chosen based on (1) biological relevance of predictor variables, (2) parsimony (using the fewest possible variables to obtain a model with good fit and normally distributed residuals), (3) avoidance of overfitting models (using too many variables for the no. of observations), (4) statistical significance of the model and variable coefficients, and (5) consistency of variable selection by 2 procedures-stepwise and all-possible-subsets (Draper and Smith 1981).

RESULTS

Potential Habitat Space

Structure.—The 1,789 plots from the 19 stands (8 old growth, 3 niche diversification, 8 competitive exclusion) were distributed normally (Fig. 3) with respect to total cover of fallen trees (0 = 7.6%, SD = 10.0%, mode = 4%), foliage-height diversity (0 = 2.4, SD = 0.59), and total number of trees per plot (0 = 17.3, SD = 8.7). The distribution of plots by shrub-cover class was logarithmic (0 = 29.2%, SD = 25.0%, median = 16%, mode = 64%). The distribution of plots by numbers of snags and for the components (decay classes) of coarse woody debris exhibited logarithmic declines. Large snags averaged 0.5/plot (SD = 1.0, median = 0); total snags were 2.8/plot (SD = 3.2, median = 2).

Numbers of large (>50 cm dbh) trees increased with stand age (Spearman's rank correlation adjusted for ties, $r_s = 0.80$), but with substantial variability reflecting retention of old-growth trees in younger stands (Table 4). Abundance of large snags was low and variable (again reflecting variable retention of old-growth legacies) in young stands and increased with age in old-growth stands (r_s = 0.67); ND42 had exceptionally large numbers of large residual snags (0 ± SD = 73 ± 51/ha). Total cover of fallen trees showed the same pattern (r_s = 0.67). Cover of fallen trees was 1.6 times greater in late-seral forest (0 = 9.1 ± 1.4%, mode = 8%) than in competitive-exclusion stands (4.9 ± 0.9%, mode = 6%). Shrub cover was variable and not significantly correlated with age. Overstory cover decreased and midstories developed after 100 years (Table 1). Midstory cover increased with age (r_s = 0.75). Foliage-height diversity increased with age (r_s = 0.53) and was positively correlated (r_s = 0.76) with midstory cover.

Old-growth and niche-diversification stands did not differ in density of large conifers, foliage-height diversity, midstory cover, numbers of medium-dbh conifers, or medium-dbh snags (Table 4). Niche-diversification stands had the greatest large-snag density of the 3 stages (1.1 ± 0.8 snags/plot), and old-growth stands had the greatest coarse woody debris cover (9.6 ± 1.9%). Competitive-exclusion stands had the least foliage-height diversity, midstory, coarse woody debris, and large conifers and had the most medium conifers and medium snags (Tables 1, 4; Fig. 4). Thus, late-seral stands were structured differently from competitive-exclusion stages (Table1, Fig. 4). Competitive exclusion had foliage cover concentrated in the canopy—with little midstory, moderate cover of herbaceous vegetation, and heavy shrub cover—whereas late-seral forest (niche diversification and old growth) had less dense canopies, more developed midstories, nearly equivalent shrub layers, and heavier herbaceous cover.

Structural Spatial Scales.—Scale of heterogeneity in overstory cover and foliage-height diversity (Fig. 5), including midstory cover (Fig. 6C,D) and shrub cover, differed over the chronosequence with older stands demonstrating a finer grain.

Prevalence (% of stations) of dense shrubs was 40% in old growth and 46% in competitive exclusion, but 65% in niche diversification. Coefficients of variation for midstory cover decreased with age (r_s = -0.68); midstory occurred regularly in old stands but only occasionally in young stands. Coefficients of variation for canopy closure increased with age (r_s = 0.75); canopies became increasingly irregular with age. Vegetation structure in old growth varied on a small scale (0 ± SE m) for shrub cover >24% (47 ± 9 m), midstory cover >24% (23 ± 7 m), and canopy closure >48% (78 ± 28 m). On average, every other grid point had ≤48% canopy closure (i.e., 44 ± 8% of grid points). Canopy closure (>48% cover) was nearly continuous in competitive exclusion, but similar in old growth and niche diversification (68 ± 28 m). High midstory cover occurred at intervals of 34 ± 16 m in niche diversification; spacing was similar, but less variable, in old growth, but wider (178 ± 42 m) in competitive exclusion. Areas of high shrub cover, however, were more widely spaced in niche diversification (121 ± 69 m) than in competitive exclusion (50 ± 19 m) or old

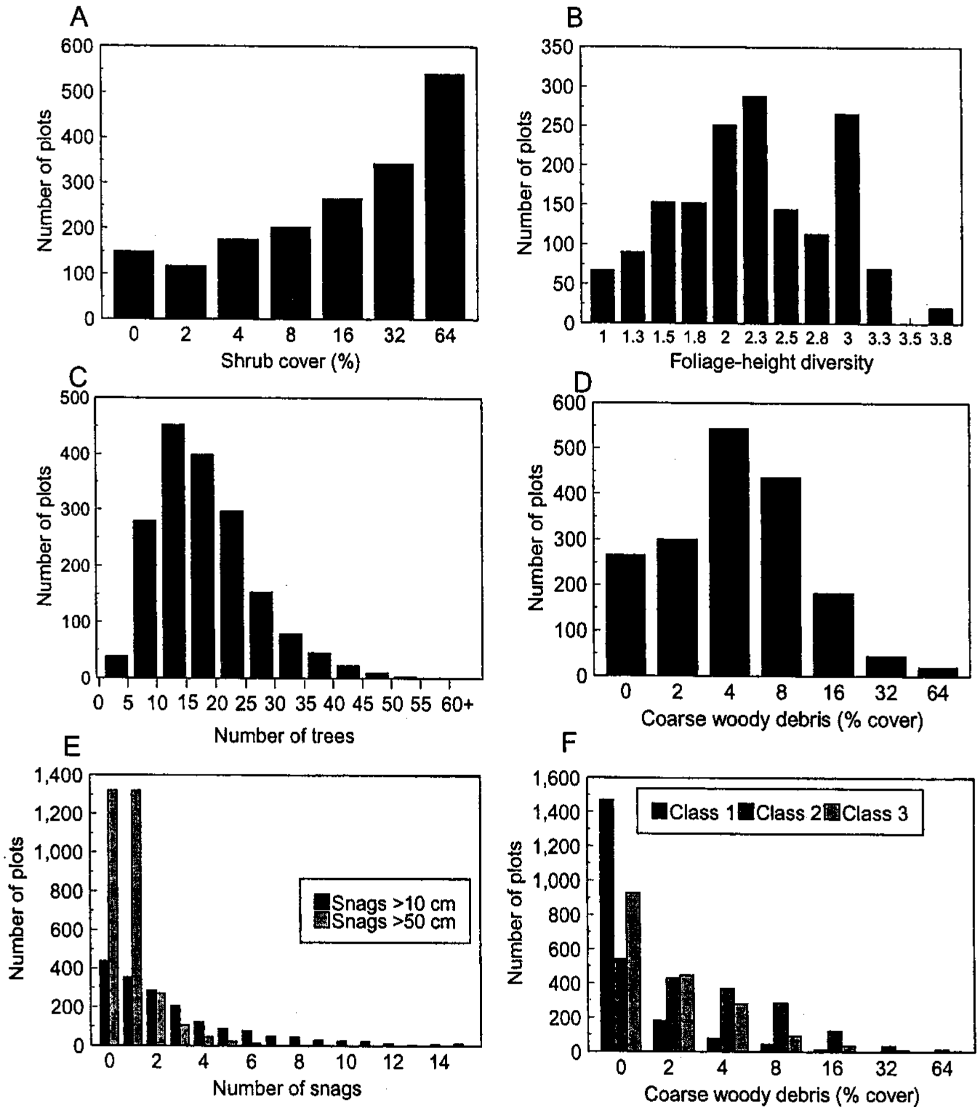


Fig. 3. Distributions of 1,789 observations on structural variables in 19 stands in southwestern Oregon, 1986-87: (A) shrub cover; (B) foliage-height diversity; (C) number of trees >10 cm dbh; (D) percent cover of coarse woody debris; (E) number of snags >10 cm dbh and >50 cm dbh; and (F) percent cover of coarse woody debris by decay class: little decay (class 1), moderately decayed (class 2), well decayed (class 3).

growth. Along the chronosequence, older stands developed increased patchiness with reallocation of foliage cover from the canopy and shrub layers to midstory and herbaceous life forms, producing full foliage profiles rather than homogeneous, discretely layered, vegetation (Fig. 7).

Structural Factors.—Four factors accounted for 63% of the variance in structure among the 1,789 plots in the 19 stands. A crown-class differentiation gradient from abundant large conifers with a herbaceous understory to medium conifers and snags (suppression mortality) accounted for 25% of the variance in structure (Table 5). Next, a decadence factor (numbers of standing dead trees >50 cm dbh and cover of fallen dead trees) accounted for 16% of the variance. A canopy-stratification gradient contrast-ed closed overstories with developed midstories. Finally,

Table 4. Structural variables (9 ± SE) for 8 old-growth (OG), 3 niche-diversification (ND), and 8 competitive-exclusion (CE) stands in southwestern Oregon, 1986-87.

Structure	OG	ND	CE	*F*	*P*
Overstory cover (%)	44.6 ± 4.1	49.1 ± 3.9	61.8 ± 0.8*	11.83	<0.01
Midstory cover (%)	43.1 ± 3.8	48.2 ± 7.0	14.4 ± 3.0*	21.18	<0.01
Foliage-height diversity (BPI)[a]	2.5 ± 0.6	2.7 ± 0.8	2.1 ± 0.7*	12.25	<0.01
Shrub cover (%)	26.5 ± 1.9	28.7 ± 11.1	34.2 ± 5.2	0.78	0.48
Shrub prevalence (% plots >24% cover)	39.5 ± 4.8	65.0 ± 8.6	46.4 ± 7.1	2.50	0.11
Herbaceous cover (%)	40.2 ± 4.1	43.6 ± 7.4	24.1 ± 7.1	2.67	0.10
Cover of fallen trees (%)[b]	8.6 ± 1.7	6.9 ± 0.9	4.4 ± 0.8	2.55	0.11
Sum of fallen-tree cover (%)[c]	9.6 ± 1.9*	7.6 ± 0.9	4.9 ± 0.9	4.93	0.02
Snags >50 cm dbh (no./plot)	0.5 ± 0.1	1.1 ± 0.8*	0.1 ± 0.0	4.20	0.03
Snags 10–50 cm dbh (no./plot)	1.1 ± 0.2	1.4 ± 0.5	4.3 ± 0.7*	12.00	<0.01
Conifers 10–50 cm dbh (no./plot)	10.6 ± 1.3	7.8 ± 1.0	12.8 ± 1.1*	2.89	0.09
Conifers >50 cm dbh (no./plot)	3.0 ± 0.3	3.1 ± 0.6	1.4 ± 0.2*	12.40	<0.01

* Indicates values significantly different from the values of the other 2 stages (Bonferroni inequality, $P \leq 0.05$).

[a] Berger–Parker Index (Magurran 1988).

[b] Cover is global (nonoverlapping) cover of coarse woody debris.

[c] Sum is sum of covers estimated for each of 3 decay classes.

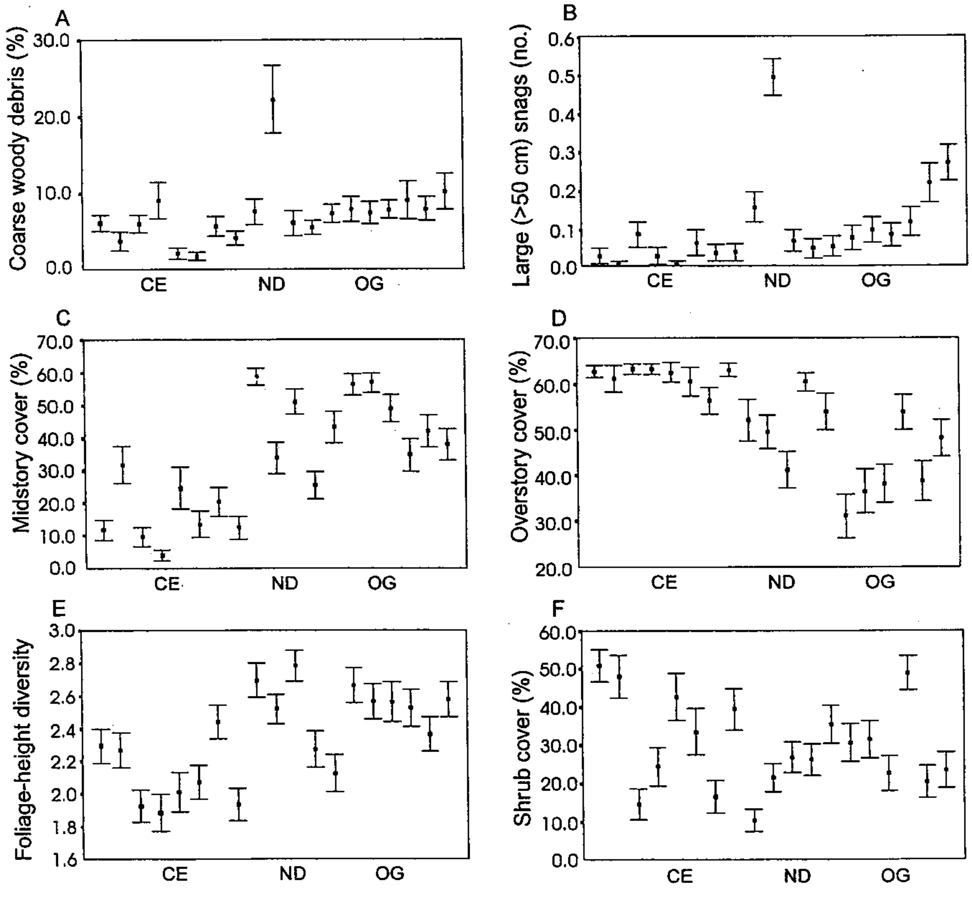


Fig. 4. Stand means (with error bars of ± 2 SE) of structural variables along a developmental sequence of competitive-exclusion (CE), niche-diversification (ND), and old-growth (OG) stages over a chronosequence of 40-350 years. The variables displayed defined the second, third, and fourth factors extracted from a data set of 1,789 observations on structural variables taken in 19 stands in southwestern Oregon, 1986-87: coarse woody debris (A) and large snags (B) defined a decadence factor; midstory cover (C) and overstory cover (D) defined a canopy differentiation gradient; and foliage-height diversity (measured by Berger Parker Index) (E) and shrub cover (F) defined an understory development gradient (*see* Table 5).

the crown-class gradient (Fig. 8) represented the chronosequence and sere of forest development well: abundance of large trees increased linearly and the abundance of 10-50-cm-dbh snags decreased linearly with both chronosequence and stage of development as would be expected with achievement of dominance and increased growth opportunities for some trees and death of others. The decadence factor encompassed variation in the degree of retention of coarse woody debris from the previous stand among niche diversification and competitive-exclusion stands and cumulative mortality of large trees in the oldest stands. Variability in retention and accumulation of coarse woody debris (Fig. 9) separate this factor from the straightforward process of forest development that would be expected if stand-replacing events produced uniform conditions (dead-wood biomass and regeneration of live trees) in thecompetitive-exclusion and niche-diversification stands. The canopy-stratification gradient encompassed slight variation in midstory development in young stands with closed canopies (mostly due to pioneering hardwoods) and marked variability in canopy closure within and among old stands, with midstory development (shade-tolerant conifers and hardwoods) inversely related to canopy closure. Thus, the third factor represents the within- and among-stand variation in canopy differentiation that is independent of age and stage of forest development. Finally, the understory factor incorporated the within- and among-stand variation in the foliage-height profile (especially shrub cover) that was independent of canopy stratification (2-layer canopy with 2 age cohorts) but includes the abundance of deciduous trees that contributes to the foliage profile in young stands. The understory factor represents transfer of cover from overstory to understory (forbs, ferns, and shrubs).

Within-stand factor analysis produced 4 factors also interpretable as crown-class differentiation (13 of 19 stands), decadence (all old growth, and 1 each in niche diversification and competitive exclusion), canopy stratification (11 of 19 stands), and understory development (17 of 19 stands). In addition, a canopy-closure factor (gradient of stem exclusion) was found in 6 of 8 competitive-exclusion, 2 of 3 niche-diversification, but only 1 of 8 old-growth stands. A few individual stands had unique factors such as deciduous versus coniferous medium-dbh trees and abundance of forbs. The first 4 factors in each stand explained 62-68% of the variance in the data sets. Thus, factors operating across stands also operated within stands; variation in decadence, however, was a larger part of variation in overall stand structure in late-seral stands than in young stands.

Table 5. Factors and variable loadings from factor analysis of 11 structural variables measured in 1,789 plots in 19 stands in southwestern Oregon, 1986-87.

Variable	Crown-class differentiation	Decadence factor	Canopy stratification	Understory development
Conifers >50 cm dbh	0.68	0.29	0.14	−0.02
Conifers 10–50 cm dbh	−0.68	0.18	0.03	−0.13
Herbaceous cover (%)	0.63	0.09	−0.27	−0.36
Snags 10–50 cm dbh	−0.55	0.02	0.46	−0.06
Fallen tree cover (%)	−0.07	0.74	−0.12	−0.07
Snags >50 cm dbh (*n*)	0.09	0.69	−0.05	−0.05
Overstory cover (%)	0.03	0	0.86	0.18
Midstory cover (%)	0.20	0.38	−0.69	0.27
Shrub cover (%)	0.04	−0.14	0.07	0.85
Foliage-height diversity	0.58	0.23	−0.18	0.59
Deciduous trees	−0.34	−0.46	−0.04	0.50
Variance explained (%)	25.4	16.1	11.4	9.8

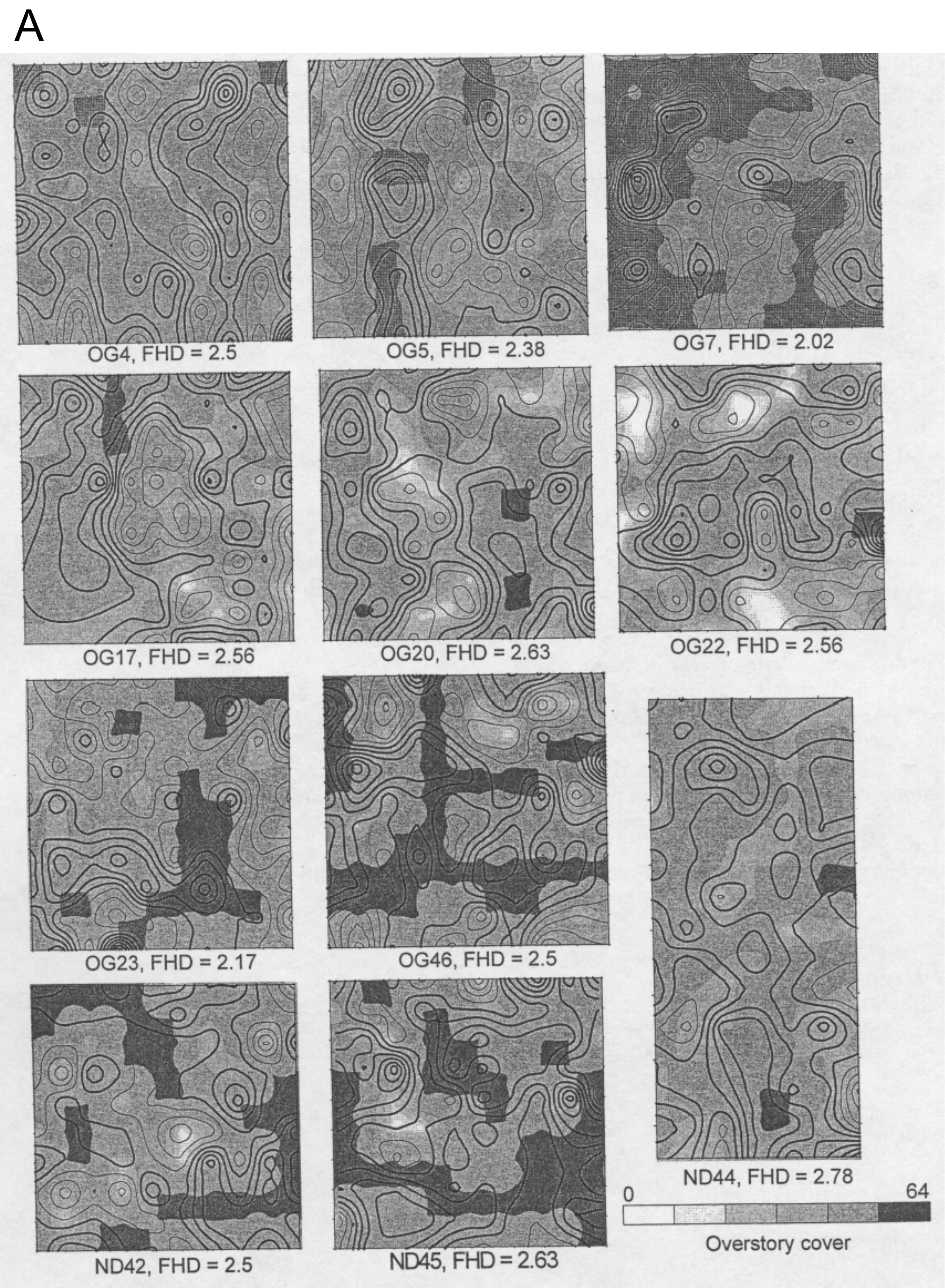
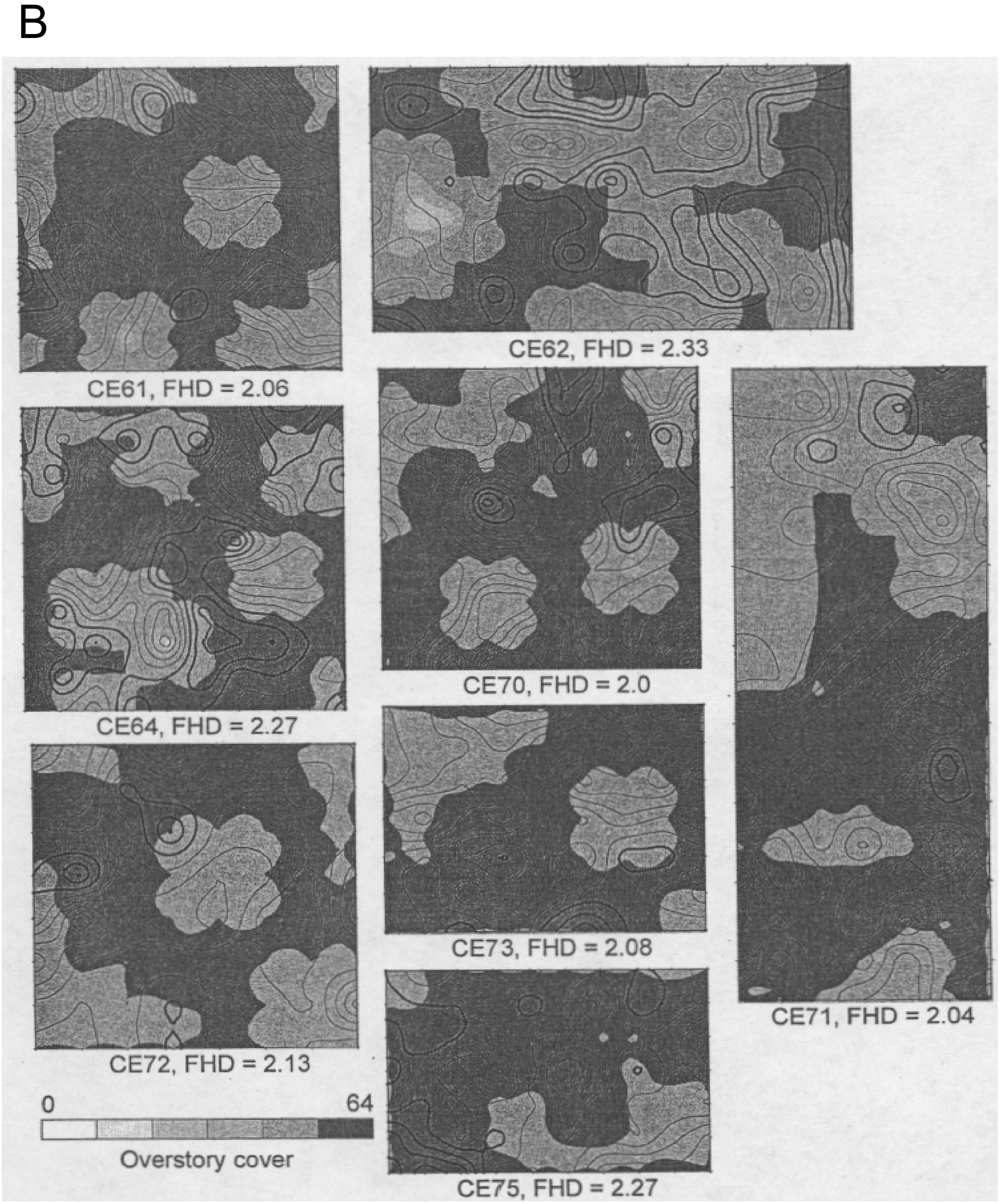


Fig. 5. Plots of overstory cover (shading) by foliage-hieght diversity (FHD) (contour lines) as measured on a 40-m scale in 19 stands of about 16 ha in southwestern Oregon, 1986-87: (A) old-growth (OG) and niche-diversification (ND) stands; (B) competitive-exclusion (CE) stands.



CE61, FHD = 2.06

CE62, FHD = 2.33

CE64, FHD = 2.27

CE70, FHD = 2.0

CE71, FHD = 2.04

CE72, FHD = 2.13

CE73, FHD = 2.08

CE75, FHD = 2.27

Fig. 5. Continued.

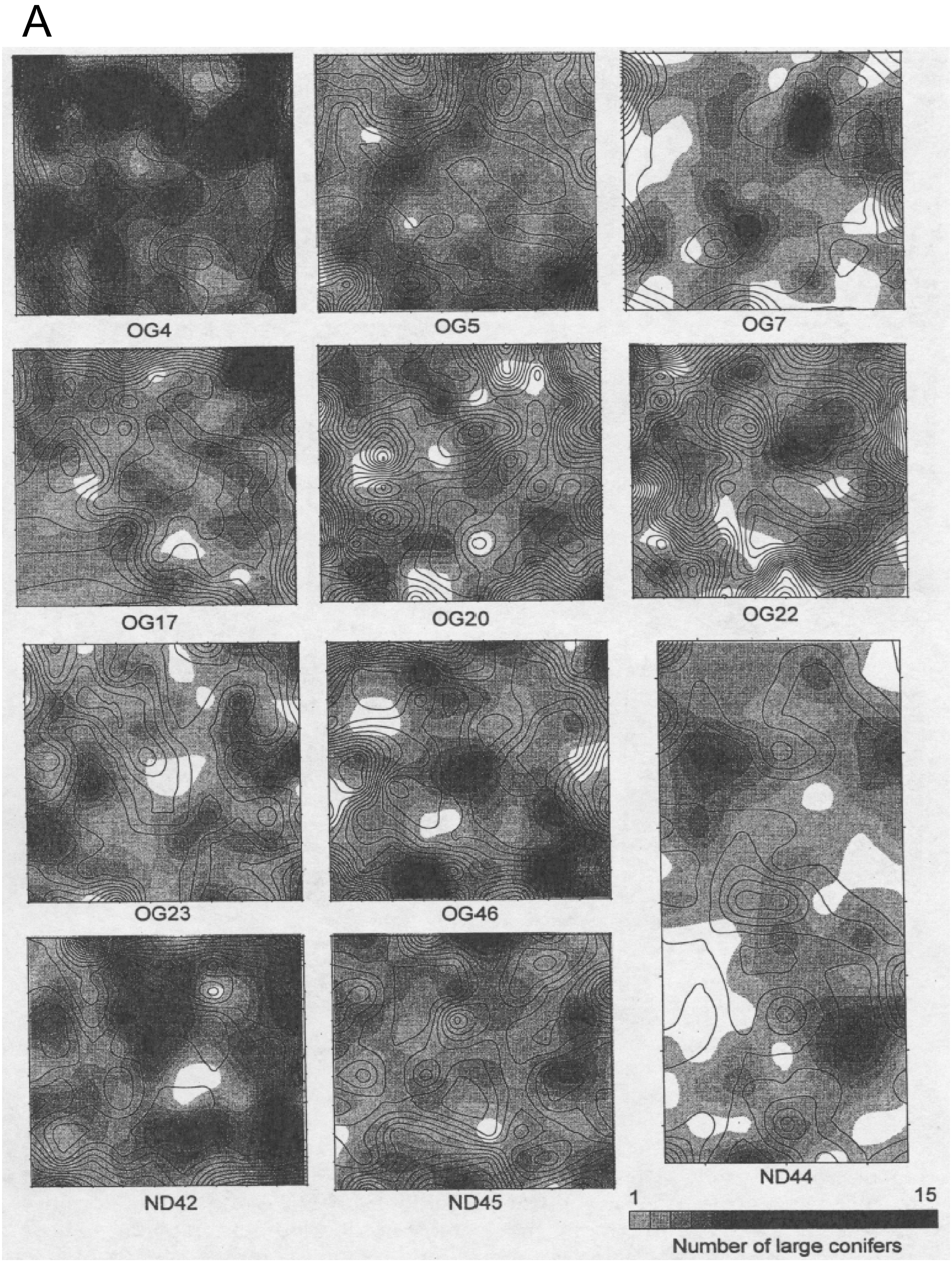


Fig. 6. Numbers of Townsend' chipmunks captured (contour lines begin at 1 and have an interval of 1 individual) plotted over number of conifers >50 cm dbh in (A) old-growth and niche-diversification stands and (B) competitive-exclusion stands; and plotted over midstory percent cover in (C) old-growth and niche-diversification stands and (D) competitive-exclusion stands in southwestern Oregon, 1985-89.

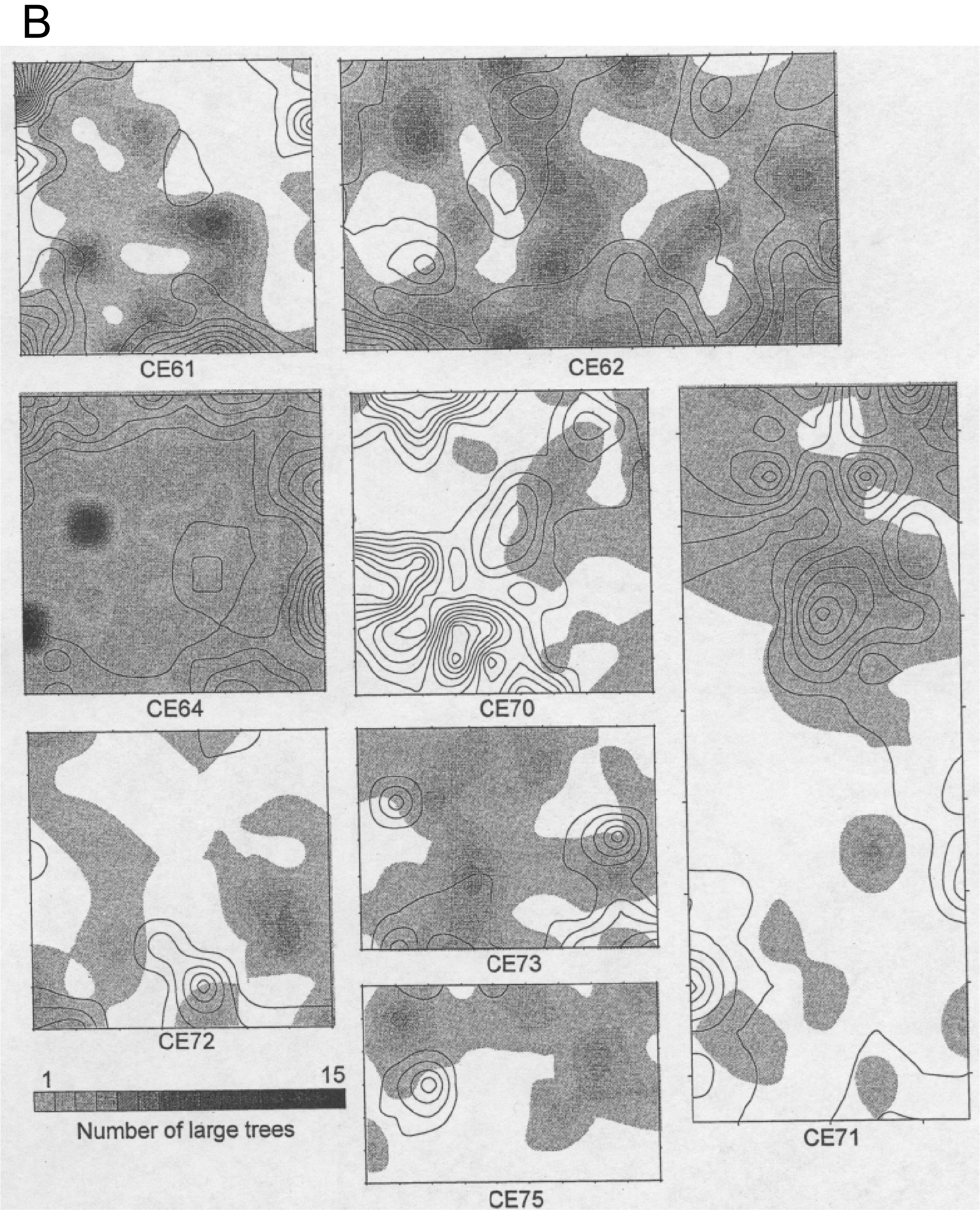


Fig. 6. Continued.

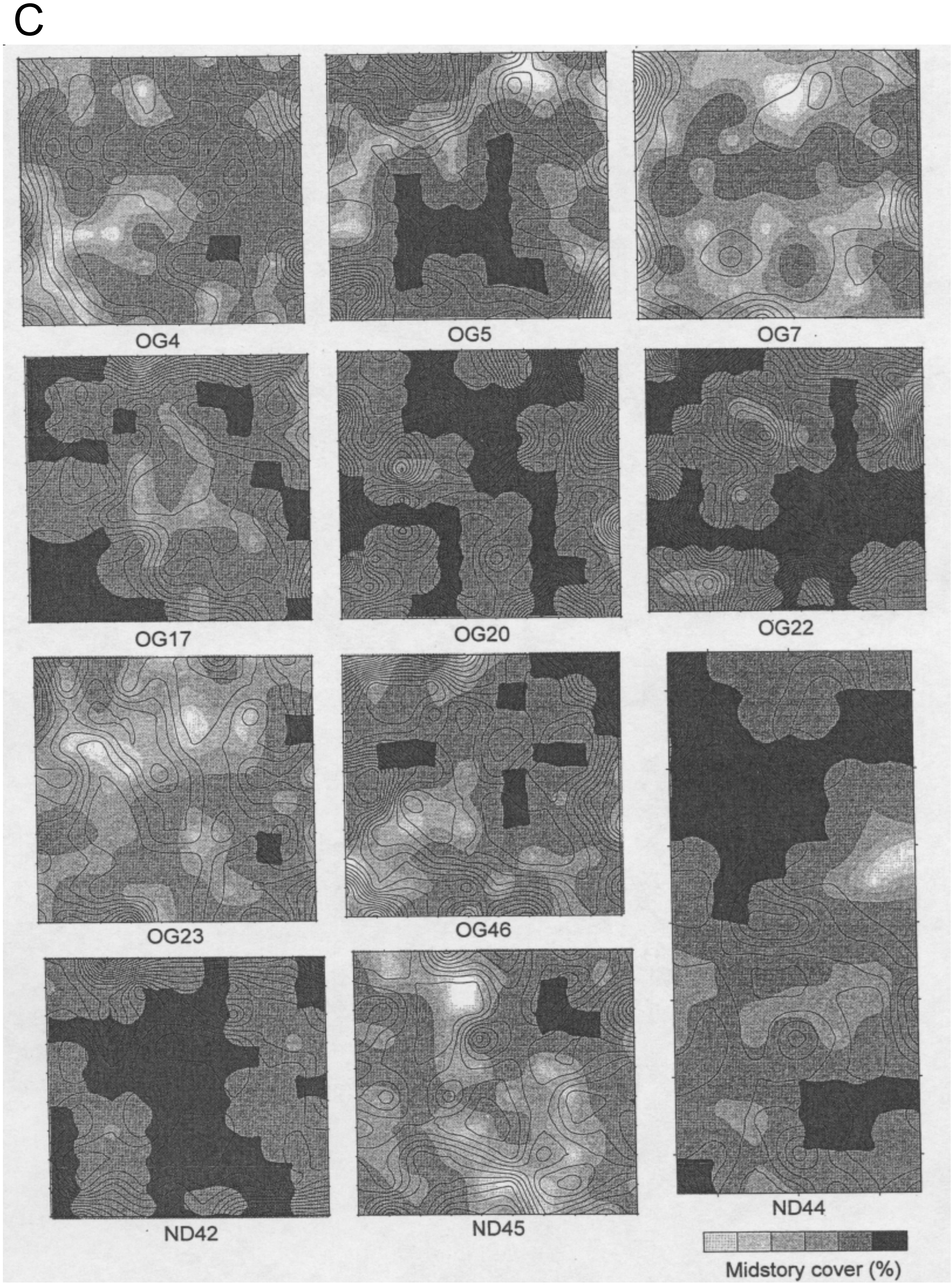


Fig. 6. Continued.

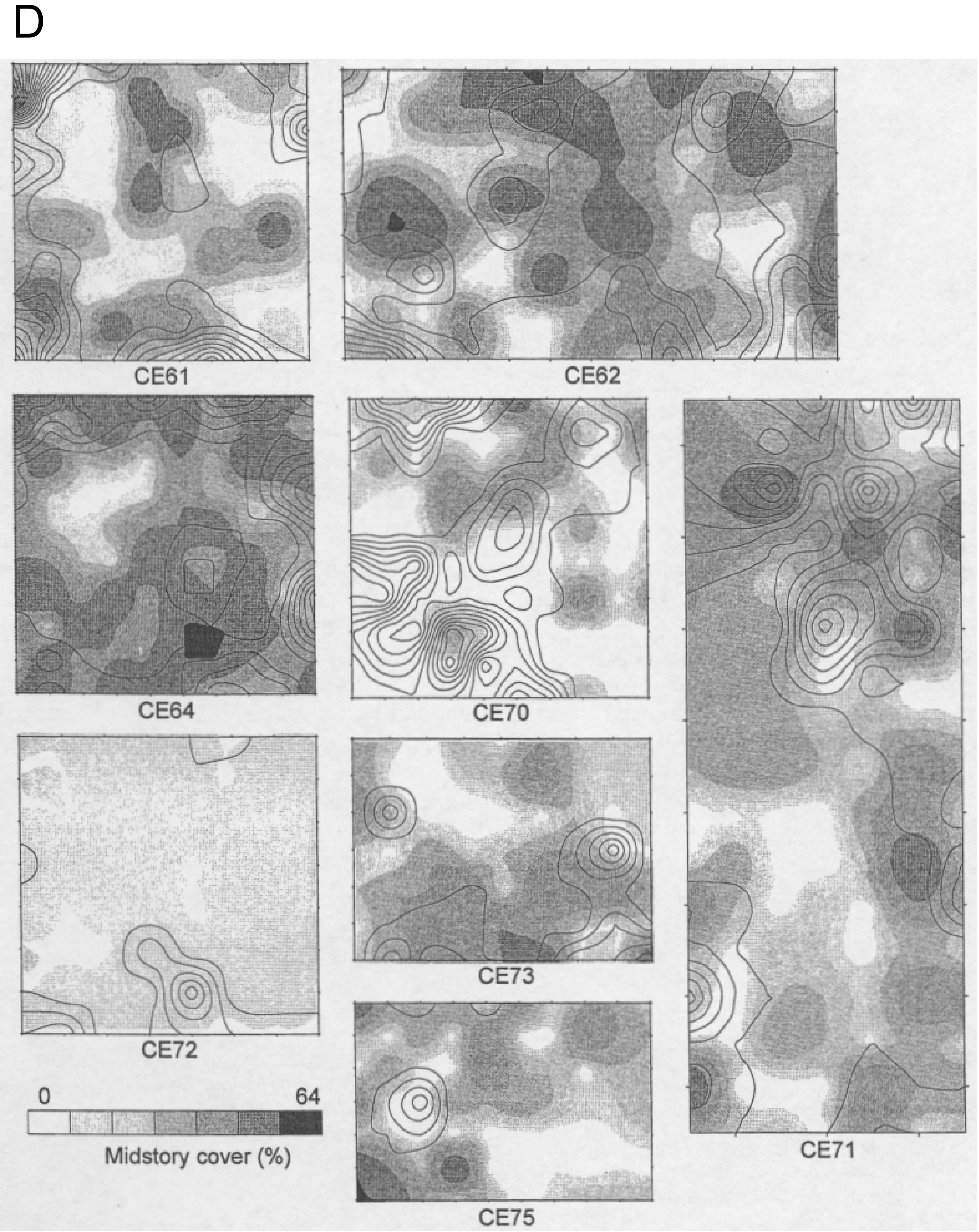


Fig. 6. Continued.

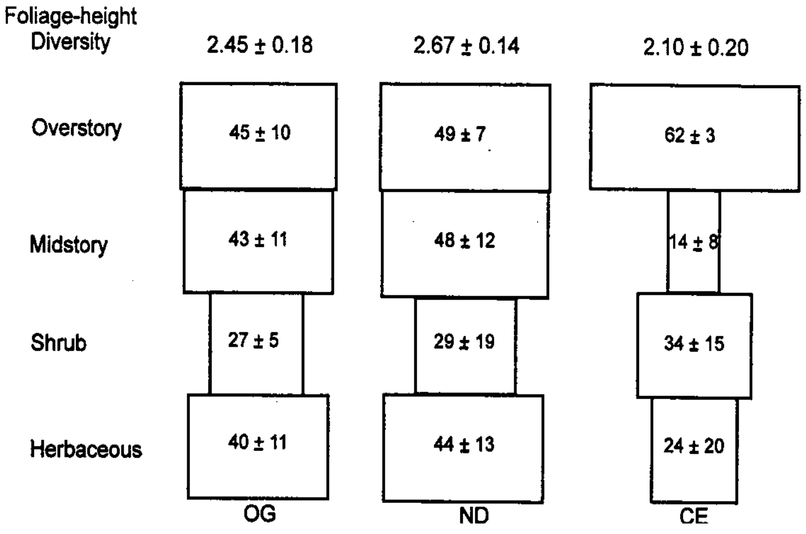


Fig. 7. Foliage-height diversity profiles showing Berger-Parker Index values and percent covers (in boxes) by vegetation layer for old-growth (OG), niche-diversification (ND), and competitive-exclusion (CE) stages in southwestern Oregon, 1986-87.

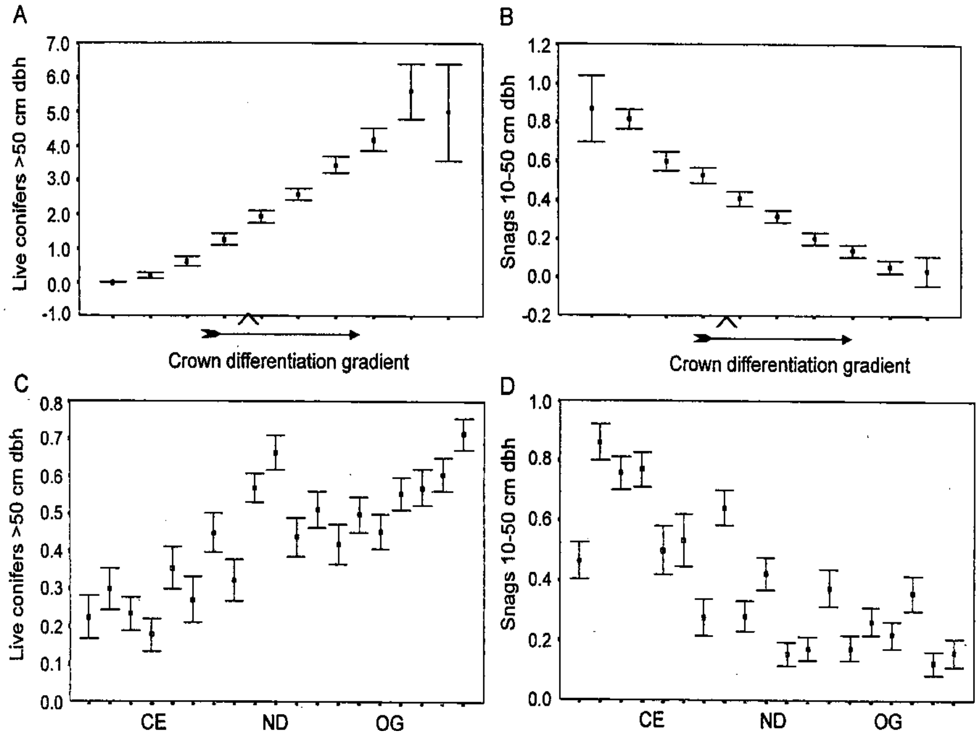


Fig. 8. Relations between large live trees, medium snags, stand age, and crown-class differentiation (the first factor of forest structure derived from data on 1,789 plots) measured in 19 stands in southwestern Oregon, 1986-87: (A) numbers of live conifers >50 cm dbh versus crown-class differentiation, (B) numbers of snags 10-50 cm dbh versus crown-class differentiation, (C) numbers of live conifers >50 cm dbh versus stands arrayed by chronosequence and seral stage, and (D) numbers of snags 10-50 cm dbh versus seral stage. Stages are competitive exclusion (CE), niche diversification (ND), and old growth (OG).

Vegetation Composition.—The 2,107 nested plots were grouped into 21 clusters, or vegetation site types (Table 6). De-trended correspondence analysis produced a vegetation zone—moisture gradient beginning with Western Hemlock Zone Douglas-fir-western hemlock wet site types through Transition Life Zone to Mixed Conifer Zone dry site types (Table 6, Fig. 10). Wet types had Douglas-fir or Douglas-fir—western hemlock—western redcedar (*Thuja plicata*) canopies with midstories of western hemlock and western redcedar with high covers of swordfern (*Polystichum munitum*) and Oregon oxalis (*Oxalis oregana*) on the ground (Table 7). Mesic Western Hemlock Zone community types had Pacific rhododendron (*Rhododendron macrophyllum*)—oregongrape (*Berberis nervosa*) and swordfern-salal (*Gaultheria shallon*) site types; dry types had creambush oceanspray (*Holodiscus discolor*) and salal. Some dry sites had salal and oregongrape in the shrub and ground layers; others had evergreen huckleberry (*Vaccinium ovatum*) and litter in the shrub and ground layers (coastal associations). Mesic Mixed Conifer Zone types had Douglas-fir, sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), and incense-cedar (*Libocedrus decurrens*) in the overstory and vine maple (*Acer circinatum*), salal, oregongrape, twin-flower (*Linnaea borealis*), and swordfern in the understory; dry types had creambush oceanspray and salal. The second gradient emphasized shrubs versus shade-tolerant conifers in the understory and, perhaps, canopy stratification from 1 to 2 layers (overstory and midstory). Overlap among clusters was evident in the canonical analysis of discriminance. The first 3 canonical discriminant functions ac counted for 49% of the variance, but provided no clear separation of clusters with pair-wise plots; 20 canonical functions were statistically significant ($P \leq 0.01$). The first discriminant canonical function mimicked the vegetation-zone gradient of the first detrended correspondence analysis gradient. The second discriminant function appeared to separate wet and dry microsites. Thus, we interpreted the clusters to represent (1) plant community types belonging to 1 of 3 different vegetation zones (Western Hemlock Zone, Transition Life Zone, Mixed Conifer Zone), (2) local, within-stand, variability in light and moisture conditions, and (3) degree of canopy differentiation into overstory and midstory layers (Figs. 7, 10).

Ten species composed 90% of the total cover in each of the 21 final vegetation site types (Tables 2, 6). Most site types included plots from all 3 seral stages; 6 were dominated by plots from competitive-exclusion and 6 by plots from late-seral stands. Six of 7 site types with well-developed midstories of shade-tolerant trees were dominated by old-growth plots; overstories generally had multiple conifer species. This group of site types spanned the array of moisture conditions. Heavy shrub layers were associated with dry sites and southern vegetation zones (Table 6). Site types with a dense overstory, but light midstory, were composed of mixtures of plots from young and old stands. Site types dominated by plots from young stands had simple Douglas-fir canopies with relatively light midstories; usually either the midstory or overstory contained some hardwood species such as golden chinkapin (*Castanopsis chrysophylla*), bigleaf maple (*Acer macrophyllum*), Pacific madrone (*Arbutus menziesii*), California-laurel (*Umbellularia californica*), or California hazel (*Corylus cornuta*). Each site type was composed of plots from several of the 19 stands (0 ± SE = 11.6 ± 0.8, ranging from 4 to 18).

All stands contained site types associated with all 3 zones. Stands contained 7-19 site types, averaging 12.7 (SD = 3.5; mean $H_B = 0.79 \pm 0.15$, $E = 0.79 \pm 0.10$), with no differences in richness, diversity, or evenness among seral stages. One stand (OG23) had especially low diversity (7 site types, $H_B = 1.03$, $E = 0.57$) and was the driest (MGV = 60 vs. mean of stand means = 172 ± 48) of the stands we studied. The range in MGV was 254. Stands differed in habitat breadth ([stand 0 + 2 SD — stand 0 — 2 SD] ÷ 254). Mean habitat breadth was higher in late-seral stands than in early-seral, managed stands: old growth (75 ± 8%, SE; with OG23 deleted, 82 ± 9%) > niche diversification (69 ± 3%) > competitive exclusion (59 ± 5%). Competitive-exclusion stands occupied a drier and narrower portion of the gradient (77 ± 109, 0

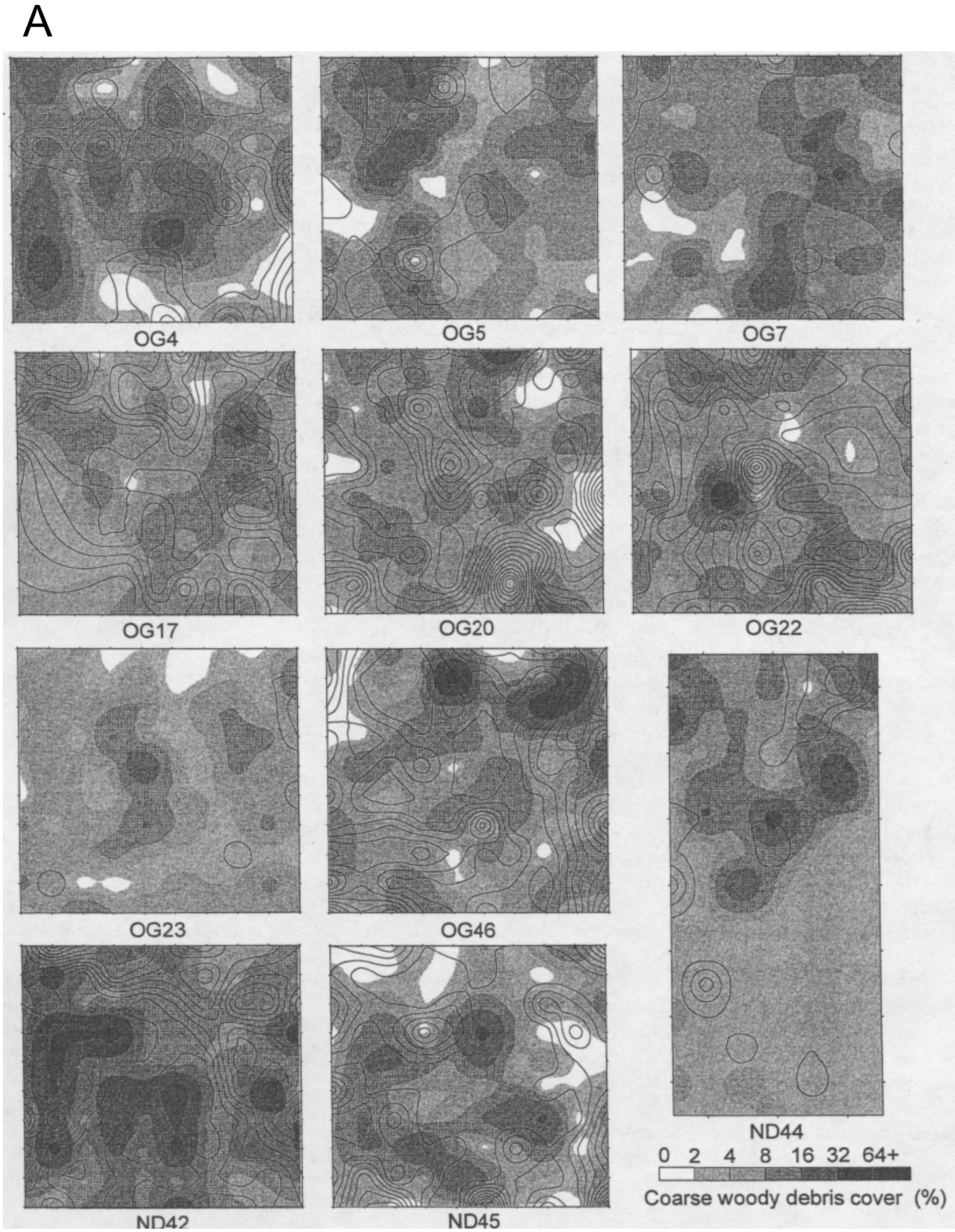


Fig. 9. Captures of northern flying squirrels (contour lines begin at 1 and have an interval of 1 capture) plotted over percent cover of coarse woody debris (shading) in (A) old-growth (OG) and niche-diversification (ND) stands and (B) competitive-exclusion (CE) stands in southwestern Oregon, 1985-89.

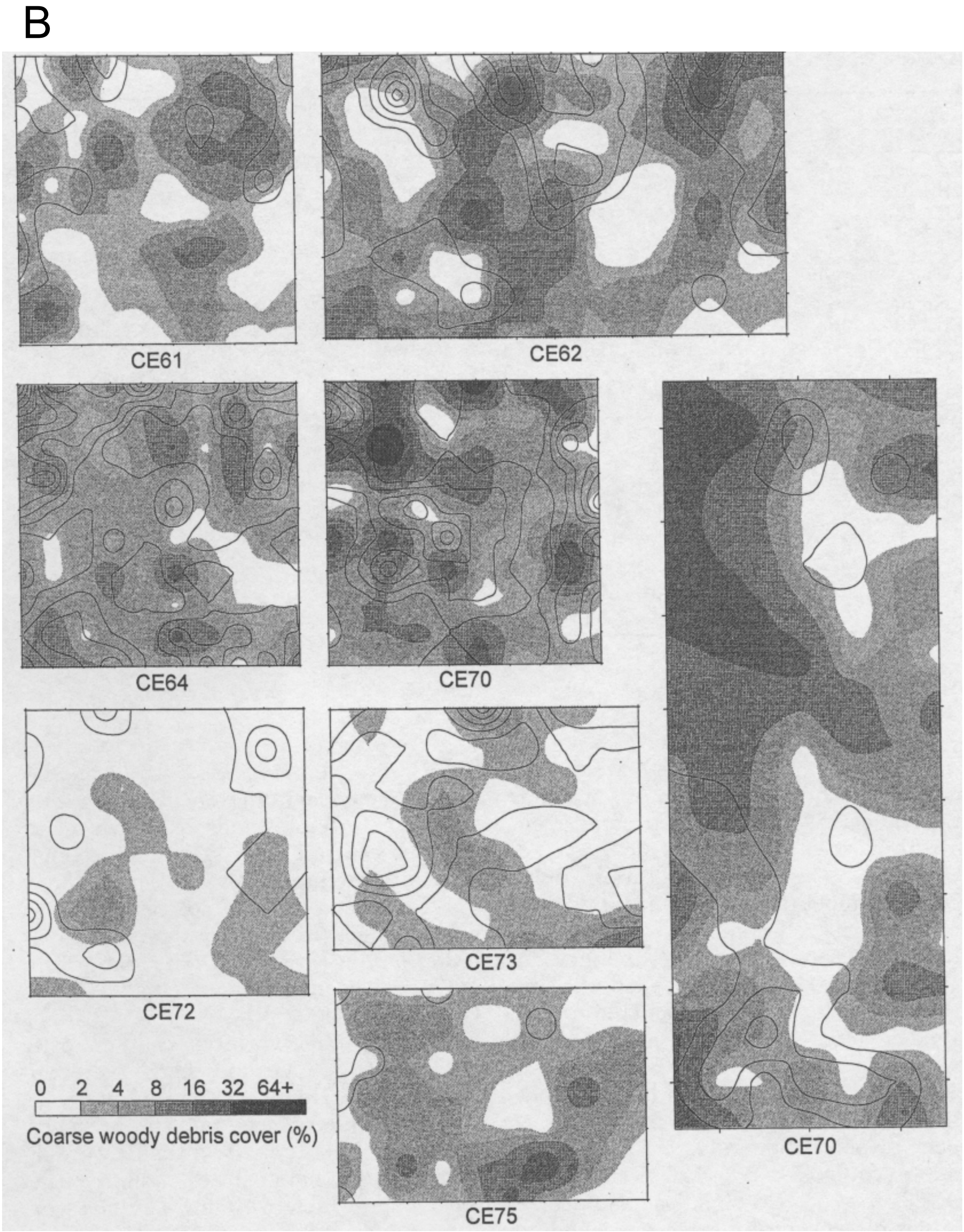


Fig. 9. Continued.

Table 6. Vegetation site types (numbered 1-22 and assigned to vegetation zones) derived from cluster analysis of 2,107 nested plots from 8 competitive-exclusion (CE), 3 niche-diversification (ND), and 8 old-growth (OG) stands in southwestern Oregon, 1986—87. Vegetation Zones are Western Hemlock (WHZ), Transition (TRZ), and Mixed Conifer (MCZ). Mean octave cover values are based on 1,789 plots used in subsequent analyses.

Site type	Site	Dominant species[a]		
		Overstory layer	Midstory layer	Shrub layer
WHZ 10	wet	PSME, TSHE, THPL	TSHE	VAOV, ACCI, GASH
WHZ 19	wet	PSME	ACCI, THPL, CACH	TSHE, VAOV, GASH
WHZ 18	wet	TSHE, PSME, THPL	TSHE, THPL	VAOV
WHZ 1	wet	PSME	TSHE	GASH, VAOV, VAPA
WHZ 8	mesic	PSME	THPL, ABGR	GASH, COCO, ACCI
WHZ 6	mesic	PSME	ACMA, ABGR, THPL	GASH, HODI
WHZ 15	dry	PSME	PSME, ABGR, TSHE	GASH, HODI, COCO
WHZ 13	dry	PSME	PSME, ACMA, THPL	GASH, ACCI, HODI
WHZ 7	dry	PSME, TSHE, LIDE	TSHE, UMCA	VAOV, TSHE
WHZ 11	dry	PSME	TSHE, THPL, UMCA	GASH, VAOV, ACCI
TRZ 20	mesic	PSME, ABGR, LIDE	ABGR, ACMA	GASH
TRZ 5	mesic	PSME	trees, UMCA	GASH, VAOV, HODI
TRZ 4	mesic	PSME	ABGR, trees	GASH, HODI
TRZ 17	mesic	PSME	UMCA, trees, CONU	ACCI, VAOV
TRZ 9	dry	PSME	trees	GASH, ACCI, HODI
TRZ 14	dry	PSME	ABGR, ACMA, PSME	HODI, COCO, GASH
TRZ 12	dry	PSME	trees, PSME, ABGR	COCO, HODI
TRZ 3	dry	PSME, ARME	CACH, PSME, ARME	GASH, VAOV, HODI
MCZ 21	dry	PSME, CACH, ARME	THPL	GASH, shrubs, COCO
MCZ 2	dry	PSME, ARME, LIDE	PSME	GASH, PSME, HODI
MCZ 16	dry	PSME, ARME	trees, ARME	VAOV, RHMA, PSME

[a] Species codes are the first 2 letters of the genus and species and are listed in Table 2.
[b] Octave scale of Gauch (1982) with category 9 = cover ≥64%.
[c] 1 = overstory of high cover; 2 = overstory + dense midstory of shade-tolerant species.

± 2 SD) than niche-diversification stands (107 ± 149) and old-growth stands (111 ± 125). Mean ecological distance (differences in MGV) between adjacent grid points increased from competitive exclusion (38.2 ± 2.8, SE; $n = 8$) to niche diversification (43.4 ± 1.2, $n = 3$) to old growth (49.2 ± 5.8; 54.3 ± 3.2 without OG23, $n = 7$). No significant auto-correlations of ecological distances were found (1—4 lags, Box—Ljung tests of significance of correlations = 0.423-2.450, $P > 0.05$). The index of dispersion (measure of contagion, I_{DCA}) showed that similar site types were clumped in distribution in all stands, ranging from 9.1 (OG23) to 60.3 (OG7) and averaging 25 ± 12 (x ± SD) with no significant differences among seral stages. Late-seral stands exhibited more site-type contrast (Fig. 11) and more fine-grained structural contrast (Figs. 5, 6, 9, 11) than young stands, and contrasts were patchy (aggregated) rather than random or uniform in distribution. The old-growth outlier in many features (Fig. 11) was OG23.

Despite the variety, the majority (>50%) of site types in 7 stands-were typical Western Hemlock Zone; in 4 stands, Mixed Conifer Zone; and in 3 stands, Transition Life Zone. Five stands were diverse, transitional mixtures of site types of all 3 zones (Table 6). Only 4 stands were classified as Western Hemlock Zone (Western Hemlock Zone site types >67% of grid points) and only 2 were classified as Mixed Conifer Zone (the outlier OG23 and CE72 with 7 site types, $H_B = 1.29$, $E = 0.73$); the majority were mixtures classified as Transition Life Zone.

In summary, cluster analysis provided 21 vegetation site types arising from the interaction of the complex regional moisture-temperature gradient, local moisture conditions (related to topographic position and edaphic effects), and degree of canopy differentiation. Poor separation of clusters suggested that environmental and developmental gradients were operating both within and among stands. Cluster analysis based on species occurrences supported combining of

Table 6. Extended.

Dominant species[a]	Octave cover (%)[b]				Canopy layers[c]	Number of plots		
Herbaceous cover	Overstory layer	Midstory layer	Shrub layer	Herbaceous cover		CE	ND	OG
POMU, OXOR	7.3	7.8	5.6	8.9	2	4	7	57
POMU, OXOR	8.4	5.6	5.6	8.8	1	18	0	23
POMU, moss, OXOR	8.5	7.1	5.4	8.5	1	1	10	38
POMU, BENE, OXOR	8.4	8.0	5.6	8.4	2	33	79	107
POMU, BENE, OXOR	8.3	6.9	6.2	8.3	1	17	10	42
POMU, BENE, forbs	8.3	6.9	6.2	8.5	1	30	23	34
POMU, forb, BENE	8.0	5.4	7.3	8.4	1	31	7	14
BENE, moss, POMU	8.0	7.3	7.6	8.1	2	18	22	21
litter, POMU, moss	8.5	7.5	6.8	6.5	2	22	7	63
litter	8.3	6.2	5.2	5.8	1	39	13	19
BENE, POMU, litter	5.9	8.8	8.1	8.5	2	0	2	34
moss, POMU	8.9	4.1	7.3	7.3	1	108	2	20
BENE, forbs, LIBO	8.6	7.3	6.6	8.6	2	29	15	58
litter, BENE, LIBO	8.9	6.3	8.8	5.8	1	30	8	10
litter, BENE, POMU	8.8	5.7	8.4	6.7	1	49	23	10
litter, moss, BENE	8.3	7.9	7.4	8.5	2	5	40	23
moss, BENE, forbs	8.9	5.1	5.1	7.2	1	49	8	11
litter	8.7	5.1	8.0	5.5	1	112	8	28
litter, moss, BENE	8.8	5.6	7.8	6.8	1	22	1	6
litter, moss, forbs	8.5	7.0	6.3	6.6	1	52	21	137
litter, forbs, RHDI	8.6	6.5	8.0	5.4	1	21	1	37

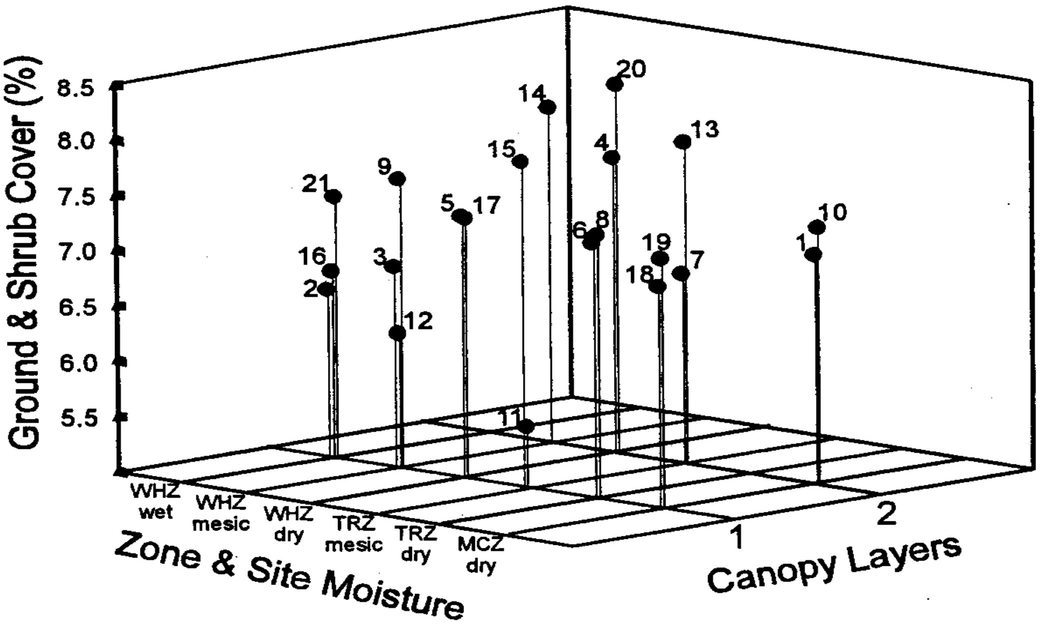


Fig. 10. The location of 21 vegetation site types in a 3-dimensional environmental space defined by zone and site moisture, number of canopy layers, and understory percent cover. Site types were derived from data measured at 2,107 points in 19 stands in southwestern Oregon, 1986–87.

Table 7. Plant species variation with site moisture in the Western Hemlock, Transition, and Mixed Conifer Zones of southwestern Oregon, 1986–87; cover categories are 0 = 0%, * = trace–5.9%, ** = 6–23.9%, *** = ≥24% cover.

	Western Hemlock Zone			Transition Zone		Mixed Conifer Zone
Species	wet	mesic	dry	mesic	dry	dry
Western swordfern	***	**	*	*	*	*
Western hemlock	***	**	**	*	*	*
Oregon oxalis	**	*	*	*	0	0
Pacific yew	*	*	*	*	0	0
Red huckleberry	*	*	*	*	0	*
Bigleaf maple	*	**	*	*	*	*
Douglas-fir	*	***	**	***	***	***
Oregongrape	*	*	**	**	*	*
Creeping snowberry	0	*	*	*	*	0
Twinflower	0	*	*	*	0	0
Tanoak	0	0	*	*	0	0
Red alder	0	0	*	*	0	0
California-laurel	0	*	*	*	0	*
Creambush oceanspray	0	*	*	*	*	*
Pacific madrone	0	*	*	*	*	*
Grand fir	0	*	*	***	*	*
Vine maple	*	*	*	**	*	*
Salal	*	*	*	*	*	**
Moss	*	*	*	*	**	*
Pacific poison oak	0	0	0	0	*	*
Fine litter	*	*	**	*	*	***

grid-point plots of different stands for multivariate analysis because the plant communities defined by our stand selection procedures were in fact homogeneously diverse; i.e., were composed of a variety of site types arrayed in fine scale.

Compositional Factors.—Five factors explained only 37% of the variance in the data set of 33 species. The factors were swordfern-Oregon oxalis gradient (a moisture gradient, 11%); abundance of Pacific madrone (with abundant litter, xeric sites; 8%); Douglas-fir versus western hemlock (overstory composition, dry to wet; 7%); midstory grand fir (*Abies grandis*) and oregongrape versus moss (dry site understory gradient, 6%); and abundance of oceanspray and California hazel in the shrub layer (a moisture gradient of increasing dryness, 6%). Cluster analysis (with 53 species) with detrended correspondence analysis provided a better overall representation of the moisture—temperature gradient than factor analysis of species abundances.

Similarly, when the species and structure data sets were combined, 6 factors explained only 42% of the variance—again with a tendency to separate out components that were discrete types versus environmental gradients. Closed-canopy Douglas-fir stands were separated from stands with well-developed midstories of grand fir. Pacific madrone and other deciduous trees with abundant forest-floor litter were separated from areas with mixed forbs (excluding oxalis) and half-shrubs (e.g., low oregongrape) on xeric sites. Swordfern-oxalis moist sites were separated from closed-canopy forest (1050 cm dbh) with little understory. Moist old growth with large snags, abundant coarse woody debris, and a midstory of western hemlock formed a unipolar gradient of western hemlock forest development. High shrub cover (vine maple and salal) formed a unipolar gradient emphasizing mesic sites. And areas of large conifers were separated from areas with

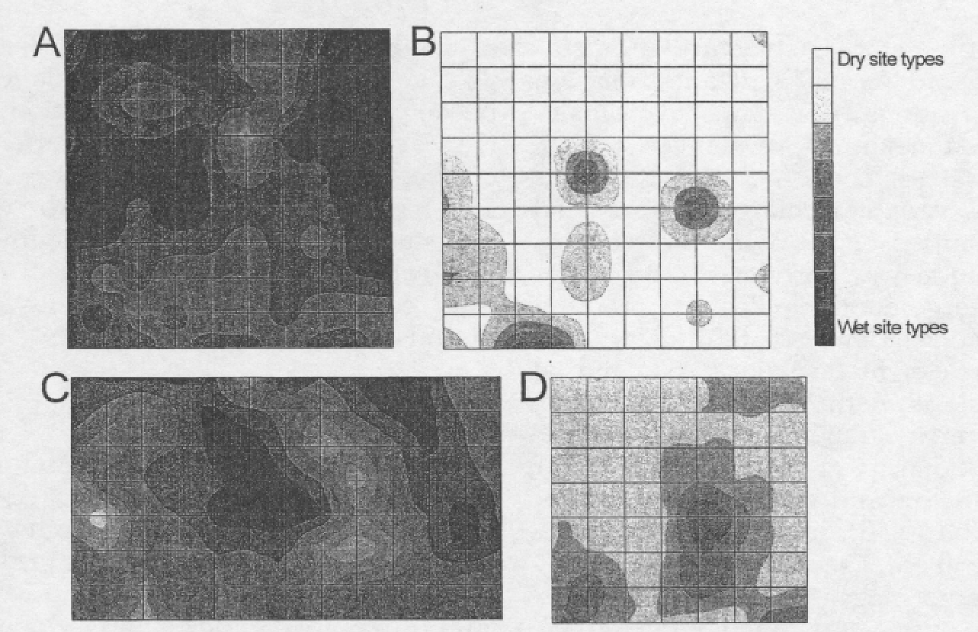


Fig. 11. Contrast among vegetation site types (shading represents plot moisture-temperature gradient values, MGV) in the moisture extremes of old-growth (OG) and competitive-exclusion (CE) stands: (A) OG5, wet, contains 100% of the range in MGV; (B) OG23, exceptionally dry, 24% in MGV; (C) CE62, mesic, 83% of MGV; (D) CE72, dry, 35% of MGV.

abundance medium snags (canopy differentiation Gradient). Most species—site relations were apparent (Table 7).

Final Variable Set.—For analysis of squirrel-habitat relations, we chose independent variables that seemed heuristic (Table 8): 9 simple, directly-measured variables, MGV, and 4 factors (crown-class differentiation, decadence, canopy stratification, and understory development) from analysis of vegetation

Variable (acronym)	Station level	Stand level
Foliage-height diversity (FHD)	index value	% prevalence
Shrub cover (SHRUB)	% cover	% prevalence
Ericaceous shrub cover (ERIC)	% cover	% prevalence
Midstory cover (MIDS)	% cover	% prevalence
Total cover of down coarse woody debris (CWD)	% cover	mean % cover
Snags >50 cm dbh (LSNAG)	no./plot	no./ha
Snags <50 cm dbh (MSNAG)	no./plot	no./ha
Live conifers >50 cm dbh (LCON)	no./plot	no./ha
Live conifers <50 cm dbh (MCON)	no./plot	no./ha
Moisture gradient value (MGV)	index value	median value
Habitat breadth	none	index value
Habitat (site type) diversity (H_{MGV})	none	index value
Habitat evenness for site type (E_{MGV})	none	index value
Crown-class differentiation factor (CROWN)	loading	mean loading
Decadence factor (DECAD)	loading	mean loading
Canopy stratification factor (STRAT)	loading	mean loading
Understory development factor (UNDER)	loading	mean loading
Stage of forest development (CE, ND, OG)	stand stage	stand stage
Vegetation zone (WHZ, TRZ, MCZ)	stand zone	stand zone
Flying squirrel total captures/100 trap nights (TCPUE)	TCPUE	mean TCPUE
Chipmunk individuals captured/100 trap nights (ICPUE)	ICPUE	mean ICPUE
Flying squirrel maximum seasonal density	none	no./ha
Chipmunk maximum seasonal density	none	no./ha

analysis of vegetation structure. For station-level and patch-level analyses, we used observations. For stand-level analyses, we used means or prevalences (e.g., % of stations with cover >24%). Relations among the variables changed with spatial scale of comparison. At points, crown-class differentiation was correlated with abundance of large conifers (Pearson product-moment correlation, r = 0.67, $P < 0.01$) and foliage-height diversity (0.57) and, at the stand level, with MGV (0.68), foliage-height diversity (0.67), coarse woody debris (0.61), density of large conifers (0.53), prevalence of midstory (0.53), canopy stratification (0.40), and understory development (-0.65). Decadence was correlated with large snags (0.70) and fallen trees (0.67) at points, but with fallen trees (0.97) and MGV (0.63) for stands. Canopy stratification was correlated with midstory cover at points (0.67) and with prevalence of patches of well-developed midstories (0.81), foliage-height diversity (0.78), and density of large snags at the stand level. Understory development was correlated with shrub cover (0.85) and foliage-height diversity (0.62) at points and prevalence of patches of dense shrubs (0.87) at the stand level. Among competitive-exclusion stands, shrub prevalence and midstory prevalence were perfectly correlated (r = 0.9999); the 2 were not significantly correlated among old-growth or niche-diversification stands. Increased numbers of significant correlations at the stand level for crown-class differentiation, canopy stratification, and directly-measured habitat variables illustrate the interdependence of the processes of individual tree growth (achieving physical dominance), demography (increasing likelihoods of damage or death of large trees with time), and canopy gap formation (stimulating midstory development in adjacent forest through increased admittance of light). Positive correlations with MGV appear to have resulted from the relative dryness of competitive-exclusion stands and lack of understory development in old growth on dry sites (e.g., OG23). Lack of significant correlation between decadence and large snags at the stand level may be explained in part by large variances (CV = 73-117%) in large snag abundance, especially among niche-diversification stands (117%, Table 4) relative to variance of coarse woody debris abundance (CV = 19%). Coarse woody debris on the ground and standing large dead trees are functionally related—as standing dead trees fall they contribute to coarse woody debris abundance.

Captures of Squirrels

We trapped for 116,305 trap nights. We caught 1,230 northern flying squirrels 3,743 times; TCPUE ranged from 0 to 100 captures/100 trap nights among grid points and from 0.6 ± 0.1 to 6.3 ± 0.5 captures/ 100 trap nights among stands. On average, over all stands, 40 ± 7% (SE) of the trap stations (grid points) had no captures of flying squirrels. Stations without captures of flying squirrels were 38 ± 12% in old growth, 39 ± 17% in niche diversification, and 45 ± 9% in competitive exclusion. We caught 1,768 Townsend's chipmunks 7,733 times; ICPUE were 0-100/100 trap nights among grid points and ranged from 3.4 ± 0.55 to 9.1 ± 1.0 captures/100 trap nights among stands; 22 ± 4% of stations had no captures of Townsend's chipmunks. Stations without captures of chipmunks were 15 ± 3% in old growth, 13 ± 4% in niche diversification, and 38 ± 3% in competitive exclusion.

Substantial parts of all stands showed no activity for each species despite 32-176 trap nights/station. Data for seral-stage categories were skewed, kurtotic, and had unequal variances (Levene's test for homogeneity of variances = 18.2 for flying squirrels and 37.4 for chipmunks; 2, 1,786 df; $P < 0.01$) necessitating nonparametric tests (Kruskal-Wallis tests). Capture rates (O ± SE, median for TCPUE) for flying squirrels were greater in niche diversification (4.0 ± 0.3, 2.2) and old growth (3.2 ± 0.1, 2.0) than in competitive exclusion (2.6 ± 0.2, 1.7) (x^2 = 13.2, 2 df, $P < 0.01$). Chipmunk captures (ICPUE) also were greater in niche diversification (7.5 ± 0.4, 5.4) and old growth (6.9 ± 0.2, 5.0) than in competitive exclusion (4.0 ± 0.3, 2.2) ($x^2 = 121.5$, 2 df, $P < 0.01$). Nested parametric ANOVA (stage, stand, points) supported the results of the Kruskal-Wallis test for flying squirrels ($F = 23.6$; 15, 1,584 df; $P < 0.01$) and chipmunks ($F = 6.9$; 15, 1,584 df; $P < 0.01$). Tukey's test ($P < 0.05$) revealed significant differences among stands within stages; some stands deviated significantly from their group mean. Heterogeneity (within and between groups) badly violated assumptions of parametric ANOVA. Maximum densities (range) for flying squirrels were 2.1/ha (1.1-3.6/ha) in old growth, 2.3/ha (1.0-3.7/ha) in niche diversification, and 1.4/ha (0.7-2.0/ha) in competitive exclusion (Kruskal-Wallis $x^2 = 1.6$, 2 df, $P = 0.46$). Maximum densities of chipmunks were higher in old growth (1.5-2.5/ha) and niche diversification (2.13.3/ha) than in competitive exclusion (0.71.8/ha; Kruskal-Wallis, $x^2 = 9.4$; 2 df; $P < 0.01$; $F = 9.2$; 2, 13 df; $P < 0.01$; Duncan test, $P < 0.05$).

Correlates of Abundance

At the point level, abundances (CPUE) of both species were positively correlated with increasing abundances of many habitat variables ($r = 0.07$-0.24, $n = 1{,}600$, $P < 0.01$). Captures of flying squirrels were not correlated with either coarse woody debris or shrub cover; highest correlations were with MGV (0.15), foliage-height diversity (0.18), and midstory cover (0.24). Captures of chipmunks were correlated most highly with crown-class differentiation (0.18) and foliage-height diversity (0.16). At the stand level, captures of flying squirrels were correlated (Pearson product-moment correlation, $n = 16$, $P < 0.05$) positively with decadence (0.59), coarse woody debris (0.56), and foliage-height diversity (0.55). Correlations, however, were higher for maximum density of flying squirrels for decadence (0.65) and coarse woody debris (0.63) but similar for midstory cover (0.51). Captures of chipmunks were correlated positively with crown-class differentiation (0.80), density of large conifers (0.72), and midstory measures—canopy stratification (0.80), foliage-height diversity (0.67), and midstory cover (0.75). Density of chipmunks was correlated with crown-class differentiation (0.74), decadence (0.76), coarse woody debris (0.70), midstory cover (0.68), and foliage-height diversity (0.56).

Thus, across spatial and temporal scales, chipmunks were associated with crown-class differentiation and canopy stratification. Flying squirrels, however, were strongly associated with decadence (particularly coarse woody debris) at the stand (population) level, with a weaker association with foliage-height diversity as a result of midstory cover at both the point and stand levels.

Realized Habitat

Four factors correctly classified 60% of points relative to use by flying squirrels (discriminant function analysis, $F = 18.9$; 4, 1,593 df; $P < 0.01$; Table 9); 74% of used stations and 44% of unused stations were correctly classified (cross-product ratio of correct to incorrect was 1.6:1). Standardized canonical discriminant function coefficients (Table 9) indicated decadence dominated the function, with canopy stratification next in importance. A good fit of a logistic regression model using directly measured variables was not obtained ($x^2 = 625$, 512 df, $P > 0.01$). Realized habitat space as characterized by discriminant function had high levels of coarse woody debris and foliage-height diversity, including high midstory cover; unused areas were characterized by high densities of medium-dbh conifers and snags (areas of stem exclusion and suppression mortality; Table 10). We were unsuccessful in obtaining a good fit of a log-linear model based on structural variables and site types (Pearson $x^2 = 503.5$, 238 df, $P = 0.00$).

Four factors correctly classified 66% of points relative to use by Townsend's chipmunks (discriminant function analysis, $F = 30.9$; 4, 1,591 df; $P < 0.01$); 88% of the used and 27% of the unused points were correctly classified (cross-product ratio = 2.7:1). Canopy stratification and crown-class

Table 9. The response of northern flying squirrels and Townsend's chipmunk populations to habitat potentially available in 16 stands in southwestern Oregon, 1985-89.

Type of response	Scale	SA[a]	Dependent variables	Type[b]	Independent variables[c]	Sum[d] (%)
Potential habitat	Point	FA	Vegetation structure	F	CROWN (25%), DECAD (16%), STRAT (11%), UNDER (10%)	63
	Point	Clus	Vegetation composition	F	MGV (24%)	24
Northern flying squirrel						60
Realized habitat	Point	DFA	Presence–absence	F	DECAD (0.8) + STRAT (0.6) + CROWN (0.3) + UNDER (0.3)	60
Habitat response surface	Stand	APR	Total captures	F	DECAD (17%) + habitat breadth (21%)	50
	Stand	APR	Total captures	D	CWD (36%) + ericaceous shrubs (14%)	39
Carrying capacity	Stand	APR	Maximum density	F	DECAD (45%) + habitat breadth (25%) – MGV (16%)	70
		APR	Maximum density	D	CWD (40%)	40
Townsend's chipmunk						66
Realized habitat	Point	DFA	Presence–absence	F	STRAT (0.7) + CROWN (0.7) + DECAD (0.3) + UNDER (0.2)	66
Habitat response surface	Stand	APR	Individuals captured	F	CROWN (36%) + STRAT (11%)	74
	Stand	APR	Individuals captured	D	MIDS (47%) + CWD (3%)	59
Carrying capacity	Stand	APR	Maximum density	F	DECAD (51%) + STRAT (14%)	72
	Stand	APR	Maximum density	D	CWD (41%) + MIDS (20%)	65

[a] Statistical analyses: factor analysis (FA); cluster analysis (Clus); discriminant function analysis (DFA); all-possible subsets regression (APR).

[b] Type of variable: F = variables derived through multivariate analyses; D = directly measured habitat elements.

[c] Variables include crown-class differentiation (CROWN), decadence (DECAD), canopy stratification (STRAT), understory development (UNDER), moisture–temperature gradient value (MGV), percent cover of coarse woody debris (CWD), percent prevalence of ericaceous shrub cover >24% (ericaceous shrubs), percent prevalence of midstory cover >24% (MIDS), and habitat breadth. Percentage of variance explained by each variable is given in parentheses except for discriminant functions, where variable coefficients are in parentheses.

[d] Total percentage of variance explained by the statistical procedure.

Table 10. Mean and SE values for habitat elements for potential, realized, and unused habitat space for northern flying squirrels and Townsend's chipmunks in 16 stands (1,600 points) in the Oregon Coast Range, 1985-89.

			Northern flying squirrel				Townsend's chipmunk			
	Potential habitat (n = 1,600)		Habitat (n = 1,050)		Nonhabitat (n = 550)		Habitat (n = 1,324)		Nonhabitat (n = 227)	
Habitat elements[a]	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Site-type value	101.2	1.7	137.6	2.4	128.2	2.9	134.6	2.1	134.1	3.9
CWD (%)	8.2	0.3	10.0	0.4	4.7	0.2	8.6	0.3	6.4	0.4
Shrub (%)	27.8	0.6	28.6	0.8	26.1	1.1	27.3	0.7	0.1	1.6
Midstory (%)	34.2	0.7	42.7	0.8	20.0	1.0	38.8	0.7	12.9	1.1
FHD	2.4	0	2.6	0	2.0	0	2.5	0	1.7	0
Large trees	2.5	0.1	2.9	0.1	1.9	0.1	2.9	0.1	0.9	0.1
Large snags	0.5	0	0.7	0	0.1	0	0.6	0	0.2	0
Medium trees	11.1	0.2	10.0	0.2	13.3	0.4	9.6	0.2	18.4	0.5
Medium snags	2.1	0.1	1.3	0.1	3.6	0.2	1.3	0.1	5.8	0.2

[a] Site type value is the detrended correspondence analysis first axis score; CWD is the sum of the covers in decay classes of fallen trees; shrub and midstory are percent cover; foliage-height diversity (FHD) is the Berger–Parker Index; and counts of coniferous trees (live and dead) are by size class (10–50 and >50 cm dbh) in 350-m^2 plots at each point.

differentiation carried the most weight in the equation (Table 9); decadence and understory development were less influential. Logistic regression had negative coefficients for suppression mortality (medium snags, -0.88) and numbers of medium-dbh conifers (-0.05) and had positive coefficients for coarse woody debris (0.55) and midstory cover (0.01); 80% of points were correctly classified (97% of used, 17% of unused) with a cross-product ratio = 6.8:1 (x^2 = 1,263, 1,264 df, P = 0.50). Realized habitat space as characterized by discriminant function analysis had large numbers of large conifers, high midstory cover, and high foliage-height diversity; areas not used were characterized by medium-dbh conifers and snags (Table 10). We were unsuccessful in obtaining a good fit of a log-linear model based on structural variables and site types (Pearson x^2 = 132.2, 48 df, P = 0.00).

On all habitat variables, the realized habitat of chipmunks was slightly less extreme, compared to the overall means, than the realized habitat of flying squirrels. Discriminant functions indicated that 66% of the potential habitat space was useful to flying squirrels (59% was used) and 83% was useful to Townsend's chipmunks (65% was used). The predictions assume equal availability of all points in the space; stand-level differences, however, apparently resulted in some points of potential habitat occurring in areas generally unsuited to the squirrels.

Use of Patches

We identified 384 patches (foraging areas used during our 8-night trapping periods) used by individual flying squirrels in 16 stands. There was no difference in patch size used by male and female (1 of 16 stands with $P < 0.05$, Mann-Whitney test) or young (<2 yr) and old flying squirrels (1 of 16 stands with $P \leq 0.05$, Mann-Whitney test). For adults, patch size was greatest in competitive exclusion (Kruskal-Wallis test, x^2 = 6.5, 2 df, P = 0.04) with patch size in niche diversification (0.79 ± 0.06 ha, n = 54) < in old growth (0.85 ± 0.05 ha, n = 192) < in competitive exclusion (0.94 ± 0.04 ha, n = 57). Overlap among patches used by individuals within a sampling period did not differ among seasons (spring and fall; t = 0.13, 204 df, P = 0.90). An individual's patch (n = 167) overlapped those of 2.3 ± 0.2 (0-9, median = 2) other individuals in late-seral forest (niche diversification and old growth) but only 1.3 ± 0.2 individuals (n = 41; 0-4, median = 1) in competitive exclusion (t = 4.10, 87.8 df, P < 0.01). Foraging patches did not differ consistently or significantly (P >

0.05) in values on structural factors from random patches of the same configuration or randomly selected points of the same number. In 3 old-growth stands with > 10 foraging patches (a total of 62 patches), foraging patches were more moist (higher MGV value for 95% of the patches) than random patches or sets of points (Wilcoxon rank sum tests, $P < 0.02$).

We identified 1,217 patches (10-day home ranges) used by Townsend's chipmunks in 16 stands. Patch size did not differ between young and old animals (Mann-Whitney tests; significant, $P < 0.05$, in only 2 of 16 stands) or among seral stages (Kruskal-Wallis tests, $\chi^2 = 0.78$, 2 df, $P = 0.69$ for males; $\chi^2 = 0.53$, 2 df, $P = 0.77$ for females). Male home ranges (1.1 ± 0.04 ha), however, were significantly (1.6 times) larger than female home ranges (0.7 ± 0.02 ha) with a difference of 0.37 ± 0.04 ha (paired t test of stand means, $t = 9.35$; 155 df; $P < 0.01$). Overlap among home ranges was greater in late-seral forest (individual ranges overlapped home ranges of 2.7 ± 0.1 other animals on average; median = 2.5; range 011) than in competitive exclusion (1.8 ± 0.1; median = 2; 0-6) ($t = 6.23$, 518 df, $P < 0.01$). Home ranges had higher values (Wilcoxon rank sum test, $P < 0.05$) for crown-class differentiation than random configurations and random sets of points for 6% of the ranges in old growth, 23% of the ranges in niche diversification, and 58% of the ranges in competitive exclusion. The trend in increasing selectivity with increasing scarcity was significant (Bartholomew's test for gradient in proportions; Fleiss 1981; $\chi^2 = 91.1$, $P < 0.01$ for random points and $\chi^2 = 25.9$, $P < 0.05$ for randomly selected configurations of points). The other evident pattern in habitat use was that 21% of home ranges in old growth and 42% of home ranges in competitive exclusion had greater understory development than randomly selected points (with the trend significant as well, $\chi^2 = 35.7$, $P < 0.05$) and configurations of points ($\chi^2 = 16.5$, $P < 0.05$) within those stand conditions ($\chi^2 = 25.9$, $P < 0.05$).

Within-stand Squirrel Responses

Analysis of flying squirrel CPUE's and directly measured structural variables in 19 stands provided 17 significant regressions ($P < 0.05$) containing a total of 47 coefficients and explaining an average of 14% of the variance in within-stand CPUE's; 13 stands had positive coefficients for understory vegetation. Analysis of Townsend's chipmunk CPUE's. produced 19 significant regressions with 71 coefficients and explained an average of 20% of the variance in CPUE's. Understory vegetation had positive coefficients in 11 stands and coarse woody debris in 12 stands; measures of stem exclusion had negative coefficients in 9 stands.

Summary of Within-stand Use

Flying squirrels (1) had higher activity by more individual squirrels (CPUE's), (2) had higher maximum densities, and (3) used more of the available habitat space (in smaller patches with more overlap among patches used by individuals) in naturally regenerated late-seral forest than in young, managed, competitive-exclusion stands (Fig. 12). Models of flying squirrel response to habitat variables within stands showed positive responses to understory development and moist sites but explained only 14%, on average, of within-stand variance in activity. Male Townsend's chipmunks used larger contiguous areas (thought to be home ranges) than flying squirrels (thought to be foraging patches) or female chipmunks. Flying squirrels, however, may use multiple foraging patches. Variance in chipmunk abundance in stands was explained by variation in understory development and coarse woody debris (positive responses) and areas of stem exclusion (avoided); but only 20% of the variation was explained by habitat variables. Neither species used exclusive areas; areas overlapped among individuals and among species. The ability of habitat variables to explain variance in abundance was greater for chipmunks than for flying squirrels as would be expected when dis-

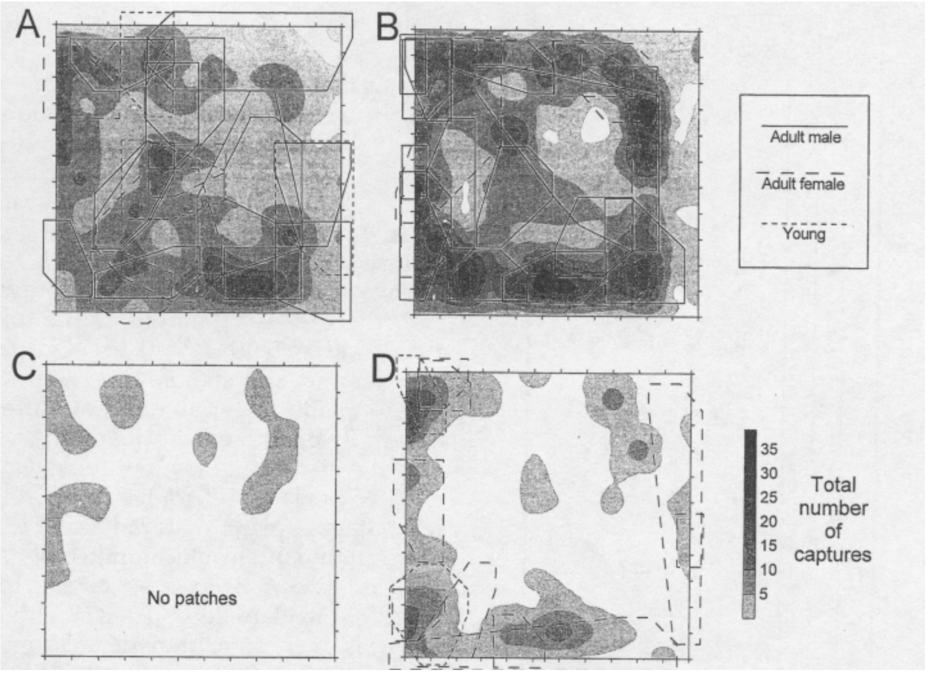


Fig. 12. Examples of good habitat (OG22) and bad habitat (CE61) in southwestern Oregon as defined by total captures (based on total trap nights across seasons, 1985-89) and patches used in 1 season by individuals: (A) northern flying squirrels in OG22, fall 1986; (B) Townsend's chipmunk in OG22, fall 1986; (C) northern flying squirrels in CE61, spring 1986; and (D) Townsend's chipmunk in CE61, spring 1986.

crete areas meeting all life requirements are described versus describing areas primarily meeting foraging requirements.

Habitat Across Stands

The best regression of flying squirrel activity against habitat factors and elements at the point level explained 11% of the variance in TCPUE (F = 18.6; 4, 590 df; $P < 0.01$; positive relations with decadence, understory development, canopy stratification, and MGV). Decadence and habitat breadth explained *50%* of the variance in mean flying squirrel activity (TCPUE) across stands (n = 16; F = 6.46; 2, 13 df; P = 0.01; Table 9). Two directly measured variables, coarse woody debris and prevalence of ericaceous shrubs, explained 39% of the variance in mean activity (F = 4.25; 2, 13 df; P = 0.04). Decadence, habitat breadth, and MGV explained 70% of the variance in maximum seasonal densities (carrying capacities) of flying squirrels (F = 9.21; 3, 12, df; $P < 0.01$; Table 9). Coarse woody debris alone explained 40% of the variance in flying squirrel carrying capacities (F = 9.16; 1, 14 df; $P < 0.01$).

The best regression of numbers of individual chipmunks against habitat factors and elements at the point level explained 14% of the variance in chipmunk TCPUE (F = 24.0; 4, 590 df; $P < 0.01$; positive relations with all 4 factors). Crown-class differentiation and canopy stratification explained 74% of the variance in stand ICPUE's (F = 18.6; 2, 13 df; $P < 0.01$). Midstory cover and cover of coarse woody debris explained 59% of the variance (F = 9.2; 2, 13 df; $P < 0.01$; Table 9). Decadence and canopy stratification were the best predictors of carrying capacity (72% of variance explained; F = 16.9; 2, 13 df; $P < 0.01$); coarse woody debris and midstory cover explained 65% of the variance in carrying capacity (F = 15.0; 2, 13 df; $P < 0.01$).

Table 11. Mean percent frequency of occurrence ($\bar{x}$, SE) of fungal taxa and percent relative density (RD) of fungal taxa groups in fecal samples of *Glaucomys sabrinus* (GLSA) and *Tamias townsendii* (TATO) in 3 seral stages in southwestern Oregon, spring 1986 and spring 1988.

Fungal taxa	Old-growth stage (n = 6)						Niche-diversification stage (n = 3)						Competitive-exclusion stage (n = 5)					
	GLSA			TATO			GLSA			TATO			GLSA			TATO		
	$\bar{x}$	SE	RD	$\bar{x}$	SE	RD	$\bar{x}$	SE	RD	$\bar{x}$	SE	RD	$\bar{x}$	SE	RD	$\bar{x}$	SE	RD
Rhizopogon	90	7	24	75	12	35	88	10	33	70	14	53	100	1	27	95	2	50
Melanogaster	61	12	14	23	16	7	48	23	13	1	1	1	70	14	15	30	20	6
Gautieria	54	13	13				43	18	10				70	13	15			
Leucophleps	63	15	18	48	6	22	36	15	10	44	10	30	41	18	9	51	21	12
Russulaceae	31	12	7	26	14	9	37	12	12	26	14	9	52	9	10	37	17	8
Hysterangium	24	5	6	17	8	8	27	22	7	2	1	1	51	18	11	41	17	12
Hymenogaster	20	6	5	9	4	4	9	4	4	10	7	6	32	16	7	39	18	8
Leucogaster	15	10	3	12	8	4	8	8	2	0			0		0	1	0	0
Elaphomyces	8	4	2				12	11	3				1	1				
Balsamia				1	1	0				0						6	3	1

Diets

Fungal spores dominated the remains of food items in fecal pellets for flying squirrels (72-82% relative density) and chipmunks (68-73% relative density) in spring (Tables 11, 12). Both squirrels had mycologically diverse diets (16-24 total taxa, 916 taxa/stand), but flying squirrels tended to have more taxa consistently present in their diets (8-10) than did chipmunks (34 taxa) (χ^2 = 5.99, P = 0.16). On average over seasons and stands, the relative density of plant material did not differ between flying squirrels (median = 33%, range = 0-82%) and chipmunks (median = 33%, range = 1-58%). Averaged within seral stages, plant material was relatively more abundant in chipmunk pellets (22-30% relative density over stages) than in flying squirrel pellets (16-27%), but differences were not statistically significant (U = 213, P = 0.86), except in old growth in 1986 (U = 0.0, P = 0.01) when relative density averaged 18 ± 11% for flying squirrels and 26 ± 9% for chipmunks. Fungal hyphae and insects, overall, were minor components of pellets (1-3% relative density). Flying squirrels consumed more fungal taxa and had more taxa consistently present in their diets in old growth than in niche diversification or competitive exclusion, but the differences in mean taxa consumed by stand were not statistically significant at $P < 0.05$ (F = 2.1; 2, 13 df; P = 0.17). Chipmunks also consumed a greater variety of fungal taxa in old growth than in niche diversification or competitive exclusion, but did not show the same trend in number of taxa consistently present and did not differ in mean taxa per stand across the seral stages (F = 0.4; 2, 11 df; P = 0.70). Dietary fungal diversity (Shannon-Wiener Index) differed between springs, with 1986 diets more diverse than 1988 diets for flying squirrels (Mann-Whitney U = 1,666, $P < 0.01$) and chipmunks (U = 3,613, $P < 0.01$); flying squirrels dietary diversity did not differ among years in niche diversification (U = 22.5, P = 0.93). In 1986, dietary diversity of flying squirrels was high-

Table 12. Diversity of fungal taxa and relative densities of major food groups in fecal samples from *Glaucomys sabrinus* (GLSA) and *Tamias townsendii* (TATO) in 3 sera) stages in southwestern Oregon, spring 1986 and spring 1988.

Diversity measures and major components	Old growth (n = 6)		Niche diversification (n = 3)		Competitive exclusion (n = 5)	
	GLSA %	TATO %	GLSA %	TATO %	GLSA %	TATO %
Taxa/stand						
$\bar{x}$	16	10	14	10	12	9
SE	1	1	0	1	1	2
Universal taxa[a]	10	3	8	3	9	4
Total number taxa[b]	24	21	21	17	17	16
Diversity[c]						
1986	1.8	1.2	1.4	0.4	1.8	1.1
1988	1.3	0.9	1.4	0.7	1.1	0.6
Relative densities						
Fungal spores (%)	75	68	82	68	72	73
Fungal hyphae (%)	2	2	1	9	0	0
Plant material[d] (%)	20	30	16	22	27	26
Insects	3	0	1	1	1	1

[a] Taxa occurring in ≥80% of the stands within a seral stage.

[b] Rare taxa (<10% mean frequency of occurrence): Agaricaceae, Chamonixia, *Cortinomyces, Destuntzia, Genea, Genebea, Glomus, Hydnotria, Hydnotryopsis, Modicella, Octaviana, Pachyphloeus, Picoa, Peziza, Scleogaster, Scleroderma, Tuber, Weraroa,* Cortinariaceae, Boletaceae, Coprinaceae, *Endogone,* and dematiaceous *Hyphomycetes.*

[c] Shannon–Wiener Index for taxa of fungal spores.

[d] Moss, lichens, fern sporangium, seeds, leaf fragments, pollen grains.

est in old growth and lowest in niche diversification (Kruskal-Wallis χ^2 = 23.0, 2 df, P < 0.01); dietary diversity of chipmunks also was lowest in niche diversification in 1986 (χ^2 = 23.1, 2 df, P < 0.01). Thus, we concluded that fungal dietary diversity did not account for differences in abundances of squirrels among seral stages.

Spring diets of flying squirrels were dominated by *Rhizopogon*, *Melanogaster*, *Gautieria*, *Leucophleps*, Russulaceae (epigeous fungi not readily identified to lower taxa), *Hysterangium*, and *Hymenogaster* in all 3 stages (Table 11). A limited collection (n = 18 fecal samples in 1 old-growth and *2* niche-diversification stands) from the fall showed similar richness (17 species) and dominance by the same taxa, with the addition of *Glomus* (OG22) and Cortinariaceae (ND42). Chipmunks consumed the same major taxa of fungi as flying squirrels, but with the noticeable absence of *Gautieria* in their diets. In old growth, chipmunks consumed 17 total taxa (9.5 ± 2.2 taxa/stand) in fall (1986) versus 22 taxa in the spring (10.5 ± 1.3 taxa/stand; t = 0.42, 8 df, P = 0.68). Fungal diversity (mean Shannon-Wiener Indexes of stands by season) differed significantly (F = 48.6; 2, 140 df; P < 0.01) among seasons (spring 1986 = 1.2 ± 0.1, fall 1986 = 0.4 ± 0.1, spring 1988 = 0.9±0.1).

Decreased dietary fungal diversity was accompanied by marked increases in percent frequency of plant materials in fecal samples. In 1986, plant material was most abundant in flying squirrel diets from niche diversification (60 ± 7% vs. 18 ± 11% in old growth and 1 ± 1% in competitive exclusion; Kruskal-Wallis χ^2 = 7.1; 2 df; P = 0.03), which had low fungal diversity (1.4 vs. 1.8 in old growth and competitive exclusion, Table 12). There were no significant differences in frequencies of plant material in 1988 (41 ± 5% in old growth, 33 ± 4% in niche diversification, and 57 ± 15% in competitive exclusion). Over all stages, plant material was more abundant in the diets of flying squirrels in 1988 (U = 25.5, P = 0.04), when fungal diversities were lower overall than in 1986. In 1988, plant material in diets sharply increased in old growth (41 ± 5% vs. 18 ± 11% in 1986, U = 0.0, P = 0.02; fungal diversity decreased from 1.8 to 1.3) and competitive exclusion (57 ± 15% vs 1.2 ± 1% in 1986, with fungal diversity dropping from 1.8 to 1.1). Chipmunks also had more plant material in their diets in 1988 than in 1986 (U = 29.0, P = 0.07), but particularly in competitive exclusion (41 ± 4% vs. 12 ± 6% in 1986, U = 0.0, P = 0.03 with fungal diversity dropping from 1.1 to 0.6). However, frequency of plant material in chipmunk diets in old growth in fall (21 ± 13%) did not increase over that in spring, even though dietary fungal diversity was low (0.4 ± 0.1). Thus, it appeared that neither squirrel was strictly mycophagous; rather, frequency of plant material in the diets differed between seasons and years but not between species of squirrel, and increased ingestion of plant material was accompanied by reduction in the variety of fungal sporocarps ingested.

Dietary fungal richness was positively correlated with increasing canopy stratification in and over both springs for flying squirrels (Spearman rank correlations and Pearson product-moment correlations gave identical results; r = 0.71, n = 21, P < 0.01) and Townsend's chipmunks (r = 0.46, n = 21, P = 0.04). Dietary fungal diversity (Shannon-Wiener Index) also was correlated positively with canopy stratification for both species, but only in the spring with low diversity (1988; Spearman rank correlation, r_s = 0.75, n = 10, P = 0.01 for flying squirrels and r_s = 0.66, n = 10, P = 0.04 for chipmunks). In 1986 (spring of high diversity), flying squirrel dietary fungal diversity also was correlated with decadence (r_s = 0.63, n = 11, P = 0.04) and mean MGV (r_s = 0.67, n = 11, P = 0.02). The experiment-wise error rate for a = 0.05 suggests that significance would be achieved at P < 0.01; thus, the latter 2 correlations may be due to chance.

DISCUSSION

Scope and Limitation

We conducted an exploratory, cross-sectional survey of squirrels and habitat characteristics in postcanopy-closure stands in southwestern Oregon. Our data are correlational and cannot be used to determine cause and effect. Our results can suggest nonexclusive hypotheses that can be tested in experiments and applied in adaptive management situations; they also contribute to the body of knowledge of Pacific Northwest forests and add to our understanding of the ecology of these forests.

Scope.—Our sample is not representative of a broader area. Even stands in the same age classes to the north in the Oregon Coast Range may differ from ours in various ways: stage of forest development, degree of riparian influence, composition of the hardwood component (e.g., red alder, *Alnus rubra*, vs. golden chinkapin), and disturbance history. Extreme variability in stand-replacing processes (windstorms, fire, clearcutting, volcanoes), climate, degree to which legacies such as coarse woody debris and live vegetation are retained, and subsequent small-scale disturbances can affect the trajectory of development for a considerable time after catastrophic disturbance.

Our competitive-exclusion stands (1) originated after clearcutting, (2) happened to have limited (but differing) retention of biological legacies, (3) were old enough to have passed through the most severe period of competition among canopy Douglas-fir, and (4) had developed relatively stable understories of salal or other shrubs. In other parts of the Pacific Northwest, similarly aged stands could be developing shade-tolerant understories or could be dominated by shade-tolerant species in the overstory (e.g., Carey 1995). Our niche-diversification stands were of mixed age with legacies of large live trees, standing dead trees, fallen trees, and understory vegetation. Other 90-200-year-old stands may be markedly different, with simple vegetation structure (*see* Spies and Franklin 1991). Due to fire history, our old growth was younger, with fewer shade-tolerant trees in the understory and midstory, than old growth to the north. Thus, our samples differed to various degrees from samples of similar ages previously described in the Pacific Northwest by Long and Turner (1974), Stewart (1986), Spies et al. (1990). Carey et al. (1991*b*, 1996*b*), Spies (1991), Spies and Franklin (1991), Rosenberg and Anthony (1992, 1993), Carey (1995), Carey and Johnson (1995), Halpern and Spies

(1995), and Huff (1995). Given the variability in Pacific Northwest forests due to differences in topography, climate, and disturbance history, caution must be used in extrapolating findings beyond study areas. The scope of our sample, even though limited, is also its strength; i.e., sufficient variation in development to allow us to clearly identify some key processes that might operate widely in the Pacific Northwest.

Limitations.—Multiscale studies pose numerous difficulties in sampling. Unpredictable events can abrogate elements of experimental design. Preferential stand selection, limited sample sizes, uniqueness of individual stands (and thus the sample), and inability to control levels of multiple variables (or mixtures of levels of variables) may produce confounded and misleading results. Because trapping to describe populations necessitates grids of traps, some lack of independence among trap stations is inevitable. All the vagaries of mark-and-recapture processes (e.g., trap-happiness and -shyness and seasonal and annual variation in probability of capture) add noise to data. Care must be used in interpreting trapping results-some assumptions must be made.

What kinds of activity do capture indices represent? Flying squirrels generally rest in dens in trees and travel arboreally to foraging patches, where they forage on the ground (Carey 1991, 1996; A. B. Carey, coauthor, unpubl. telemetry data). Flying squirrels select multiple foraging patches that may be distant from their den (A. B. Carey, coauthor, unpubl. data). Mean-maximum distances between subsequent recaptures suggest these patches may be ≤115 m across (Carey et al. 1991*a*). Thus, we assumed that TCPUE's for flying squirrels represented foraging activity indicative of habitat quality and that habitat variables meaningfully described foraging. patches defined captures. Townsend's chipmunks apparently den and travel primarily on the ground; foraging is on the ground and in shrubs and trees (Bailey 1936; Carey 1991, 1996; Sutton 1993). These chipmunks use overhead cover while traveling to foraging sites, adding significantly to travel distance between den and foraging sites in patchy environments (Harestad 1991). Home ranges based on recapture data were ≤120 m across (Carey et al. 1991*a*). Thus, we assumed chipmunk ICPUE's represented the combined locations of dens, travelways, and foraging areas used by different chipmunks. We assumed the number of individuals caught at a trap station indicated habitat quality at that trap station.

Squirrel responses to among – stand gradients may be confounded by differences in population densities, density-dependent space and resource use, and differences in predation that may affect densities of prey (Fretwell 1972). Among-stand comparisons also are confounded because stands differ in (1) the proportion of variation in habitat elements that they contain relative to the variation across the landscape and (2) within-stand relative abundance of various habitat elements. Each stand comprises a unique subset of vegetation site types and structural variation; factors limiting populations may differ from stand to stand and among seasons (Fretwell 1972). Thus, examining populations in contexta multifactorial landscape, stage of forest development, and temporal variation in population densities—is necessary.

Forest Development

Our interests lie in factors and processes influencing development of biotic communities in the Western Hemlock Zone, particularly those processes relating to maintenance of biodiversity in managed forests. We are not so much interested in absolute species diversity as we are in processes leading to an expansion of multidimensional niche space and how niche space might contribute to ecosystem resiliency and to trophic pathways supporting vertebrate communities, including (but not limited to) prey and predator populations characteristic of old-growth Douglas-fir forests.

General theories of biodiversity are lacking. Much of the literature on biodiversity focuses on the diversity of sessile species and the respective roles of disturbance, equilibrium, and competition (Connell and Slatyer 1977, Connell 1978, Pickett 1980, Connell et al. 1987, Roberts and Gilliam 1995). Literature on vertebrate diversity focuses on island biogeographic theory (MacArthur and Wilson 1967, Brown 1971, May 1975, Simberloff and Abele 1976, Whitcomb et al. 1976) and, in terrestial systems, on mountain tops and forest fragmentation. Although these theories provide useful insights about the processes of plant community development in forest ecosystem and the ramifications of large-scale anthropogenic and natural disturbances for landscape function, they are too narrowly focused to provide adequate guidance for conservation of biodiversity in managed-forest landscapes in the Pacific Northwest. Narrow focus can result in paradigm shifts emphasizing reductionism at the expense of holism (Barbour 1996) with unnecessary polarization of world views and false dichotomies of management through preservation versus intensive management for commodities. Such dichotomies cloud the view of the bigger, long-term picture of conservation of biodiversity.

The old-growth forests that have been set aside today are not in static equilibrium; they are undergoing gradual change. Without major disturbance, Douglas-fir will be replaced by shade-tolerant western hemlock, Sitka spruce (*Picea sitchensis*), Pacific silver fir (*Abies amabilis*), or other species. The Quinault Research Natural Area, >500 years old and dominated by western hemlock and Sitka spruce, supported neither flying squirrels nor spotted owls (Carey 1995). It is likely that the old growth of today will be affected by catastrophic disturbance. The eruption of Mount St. Helens destroyed habitat set aside for spotted owls (Ruediger 1985). Windstorms in 1921 and 1962 destroyed large areas of forest in western Washington and Oregon (Henderson et al. 1989). Most old growth in the Pacific Northwest developed after catastrophic fires 250-500 years ago. The present distribution of old growth is uneven, with large areas devoid of old growth and dominated by competitive-exclusion ecosystems. Dominance of landscapes by competitive-exclusion stands may prove more detrimental to conservation of biodiversity than dispersed clearcuts in landscapes of forests actively managed on long rotations in which late-seral stages of forest development predominate (Carey et al. 1996*a*). Conservation of biodiversity, sustainable forest ecosystems, and intergenerational equity in the Pacific Northwest will require a continuum of passive to active intentional management (Carey 1998).

Odum (1969) described development of ecosystems as an interacting complex of processes (some of which counteract one another) that lead to characteristic trophic structure and material cycles. He postulated that development (1) is an orderly process that is reasonably directional and therefore predictable, (2) results from modification of the physical environment by the community, and (3) culminates in a stabilized ecosystem in which biomass and symbiotic function constitute a strategy of homeostasis. This strategy consists of gradual change that results in diversity, complexity of structure and processes, and production of large structures, some of which persist through catastrophic disturbance and assist in recovery of the ecosystem. The net result of community action is symbiosis, nutrient conservation, stability (not necessarily equilibrium), and decreased entropy. Bormann and Likens (1979) also emphasized aggradation of biomass as a primary process in forest ecosystem development and introduced the concept of shifting steady-state mosaics, similar to the patch dynamics concept of Pickett (1980).

Our data and the literature (summarized below) suggest that forest development in the Western Hemlock Zone incorporates multiple, general processes that are variously dynamic and stochastic, but also many that are predictable and probable as suggested by Odum (1969) and Bormann and Likens (1979). The most deterministic is aggradation of biomass; the least deterministic might be the entry of decay into living trees. The time scale (return interval for the most frequent natural catastrophe-fire) is 250-500 years-the life expectancy of adult Douglas-fir, but many generations of chipmunks, flying squirrels, weasels, and spotted owls.

The ecosystem strategy of homeostasis

through maximum support of complex biomass structure conflicts with human goals of maximizing production or yield of wood products (Odum 1969). Silviculture, however, can be used either as a means of maximizing production of wood or as a mechanism of gradual change through small-scale and intermediate disturbances on a time scale of about 150 years. Thus, silviculture can contribute to simplification or to diversification of the ecosystem. With human intervention, the development of a complex biomass structure is not inexorable; management with low intentionality can impede or preclude development of diverse ecosystems (Carey 1995, Carey et al. 1996*b*, Carey 1998, this study). However, we hypothesize that human intervention in forest ecosystems can accelerate forest development (Carey et al. 1996*a*).

It is our contention that aggradation and redistribution of biomass, living and dead, results in niche diversification, an expansion of the niche hyperspace of the ecosystem and the community it contains the preinteractive Hutchisonian niche (Hutchinson 1958, 1978). It is this expansion that may result in emergent properties through symbiosis and synergy. Endogenous disturbance, such as top rot in living trees, is an integral part of the autogenic development of ecosystems and may need to be promoted in young forests. Thus, we hypothesize that conservation of biodiversity could be achieved in managed forests through planned human-caused disturbances and gradual change that create a multidimensional space of particular dimensions; it is those dimensions we seek to describe here. Management could strive to maintain dynamic equilibria (shifting steady-state mosaics), at both the level of the ecosystem and the level of the landscape within narrower bounds than produced over time by natural disturbance regimes. Over time, then, conservation of biodiversity would be achieved intentionally even despite (possibly aided by) frequent uncontrollable intermediate disturbances (e.g., disease outbreaks, small-scale fires, and windstorms) and rare catastrophes (large-scale windstorms, fires, and volcanic eruptions). We illustrate the processes involved through discussion of each of the structural factors derived from our data, the compositional factor, and finally spatial heterogeneity.

Crown-class Differentiation.—Forest development can differ markedly after catastrophic disturbance. The catastrophic event sets the stage for the ecological play (Hutchinson 1965) that follows. In natural forests, a continuum of conditions of legacy retention and intensity of regeneration can be found. The ecosystem initiation stage may be long (>50 yrs, Huff 1995) with substantial coarse woody debris left on site as standing dead trees, decayed fallen trees, and recently fallen dead trees (Spies and Franklin 1991); numerous live trees may be left after disturbance and understory vegetation may persist or quickly recoup. Heterogeneity produced by biological legacies, variation in natural regeneration, and intermediate disturbances during a long initiation stage may result in rapid crown-class differentiation with the competitive-exclusion stage being rare in the landscape; stands *may* move quickly into understory-reinitiation and niche-diversification stages. Thus, legacies may facilitate biodiversity and inhibit competitive exclusion. Such a scenario produced our niche-diversification stands.

With limited legacies and quick, dense natural regeneration, plant species diversity (Long 1977) and diversity of other life forms (Carey et al. 1996*b*) decrease from year 5 to 22, competitive exclusion lasts ≥70 years (Carey et al. 1991*b*), recovery of plant species diversity may be slow even at 75 years (Long 1977), and diversity peaks in, old growth (Halpern and Spies 1995). Natural thinning of young Douglas-firs produces small, ephemeral gaps as in dividual trees die. These small gaps do not contribute much to crown-class differentiation or to recovery of plant species diversity (Spies and Franklin 1989), but small gaps, the relatively thin crowns of Douglas-fir, and random variation in spacing often allow an understory of salal or swordfern to develop. This course of development is typical of stands regenerated after clearcutting and burning (Long and Turner 1974, Long 1977, Halpern and Spies 1995); e.g., the competitive-exclusion stands in our study. Intermediate disturbances such as root-rot (*Phellinus weirii*) infestations often produce heterogeneity (pockets of understory reinitiation) in second-growth stands (Holah et al. 1993, Carey et al. 1996*b*). In mesic areas where shade-tolerant species are abundant, even denser canopies may form, facilitated by legacies of well-decayed nurse trees. These competitive-exclusion stands may last longer and produce a more intense “crunch” on the biodiversity as trees strive to compete for a height advantage and exclude smaller life forms (Carey 1995, Carey and Johnson 1995, Carey et al. 1996*a*). Thus, severe disturbance followed by dense regeneration results in a stage of development that inhibits biodiversity.

Historically, clearcutting left substantially less coarse woody debris than did natural catastrophes, removed most or all live trees, and was followed by fast, dense, and monospecific regeneration of trees that quickly moved the stand into the competitive-exclusion stage. Early (ca. 1910) logging of old growth left 52-56% of preharvest biomass, contemporary logging of old growth leaves 33-41%, and contemporary harvest of second growth leaves only 31-35%—a reduction from 500-540 Mg/ha to 100-115 Mg/ha (Harmon et al. 1996). Thus, the trend has been for intensive management for timber to result in marked loss of biodiversity due to reductions in coarse woody debris and increases in homogeneity and simplicity of the resulting forest. In natural forests, coarse woody debris might decline in abundance until the old-growth stage is reached at about 190-250 years (Spies and Franklin 1991). But when trees are killed or weakened by fire, coarse woody debris recruitment may continue for >100 years (as in our niche-diversification stands) until death of older trees begins to maintain recruitment of coarse woody debris (Franklin et al. 1987). Managed stands are usually harvested while still in competitive exclusion, generally at 40-70 years (Carey et al. 1996*a*), with high utilization and rapid regeneration through planting; thus, recovery of biodiversity by the ecosystem may be restricted severely.

The most obvious features of competitive exclusion are the even-aged, dense trees and mortality due to suppression. Pioneering hardwood species, notably golden chinkapin, Pacific madrone, and bigleaf maple, produced some heterogeneity in our competitive-exclusion stands and allowed a degree of crown-class differentiation. Only 1 competitive-exclusion stand had a significant component of shade-tolerant conifers. Most appeared to be emerging from competitive exclusion. Our competitive-exclusion stands averaged 384 live conifers/ha and 123 medium snags/ha, about 50% more than the 85 snags/ha reported by Carey et al. (1991*b*) for a mixture of natural and managed competitive-exclusion stands in the Coast Range but similar to second-growth competitive exclusion on the Olympic Peninsula (121 snags/ha) (Carey 1995). For Douglas-fir of this age and size (quadratic mean diameters of 30-40 cm), excessive restriction of crown development (and concomitant mortality due to suppression) occurs at densities of 350-540 trees/ha (McArdle et al. 1961, Curtis 1982). Natural variation in stocking, advance regeneration, and occasional retention of trees from the previous stands also contributed to crown-class differentiation in our competitive-exclusion stands with maximum dbh of trees reaching 50-120 cm.

The most salient feature of niche-diversification and old-growth stands is large-dbh, tall Douglas-fir with deep crowns and large, platform branches (Franklin et al. 1981, Carey et al. 1991b, Spies and Franklin 1991). Our old stands also had shade-tolerant conifers including grand fir, western hemlock, western redcedar, and incense-cedar and some bigleaf maple and Pacific madrone. Presumably, crown-class differentiation in niche diversification and old growth was not only a result of the stage-setting catastrophe that destroyed the previous stand, but also one of disease, injury, and mortality of the aging cohort of trees that produced gaps followed by establishment and growth of shade-tolerant conifers.

Crown-class differentiation accounted for more variance in our data set than any other factor. Similarly, Carey et al. (1991*b*) reported that dbh alone could separate age classes in their sample, and Spies and Franklin (1991) reported that most variance among age classes across the Pacific Northwest could be reduced to a single canonical variate related to the standard deviation of dbh and the density of large trees. As trees become dominant they increase in dbh, height, crown depth (and often width), limb size, bark rugosity, and root networks. These architectural changes magnify individual tree dimensions and multidimensionally increase niche space. Enhanced characteristics include (1) greater, , more consistent production of seed for seed-eating birds and mammals (Manuwal and Huff 1987, Buchanan et al. 1990, Carey 1991), (2) increased surface area for mycorrhizae, epiphytic plants, and endophytic parasites (Enseen et al. 1996, Parks and Shaw 1996, Sillet and Neitlich 1996, Stone et al. 1996), (3) bark crevices, foliage, and arboreal soil for invertebrates (Denison 1973, Marian 1987, Schowalter 1989), (4) crevices for bat roosts and materials and platforms for nests of mammals and birds (Forsman et al. 1984, Gillesberg and Carey 1991, Hamer and Nelson 1995, Carey 1996, Wunder and Carey 1996, Carey et al. 1997), and (5) an increased variety of foraging substrates and prey (and niche separation) for bark-gleaning and wood-pecking birds (Carey et al. 1991*b*, Sharpe 1996). At the stand level, crownclass differentiation results in a rugose canopy that provide unique foraging spaces for bats (Wunder and Carey 1996) and birds (e.g., the olive-sided flycatcher [*Contopus borealis*] [Carey et al. 1991*b*]).

In our study, crown-class differentiation accounted for 25% of variance in vegetation structure, but proved to be a major dimension of the realized habitat of chipmunks and the most important predictor of chipmunk abundance. Mean tree dbh also was a good predictor of the abundance of Townsend's chipmunks on the Olympic Peninsula, explaining 61% of the variance (Carey 1995). Two alternative explanations of the strong correlations of abundance of chipmunks with crown-class differentiation appear reasonable: (1) crown-class differentiation was a surrogate for the entire process of forest development or (2) chipmunks were responding to heavy seed production by large, dominant trees. Conifer seed is a major dietary component for Townsend's chipmunks, who harvest and store the seed for the winter (Sutton 1993). Townsend's chipmunks seem to be food limited, and their abundance can be increased by adding seed (Sullivan et al. 1983). The same seems true for the third squirrel in Pacific Northwest forests-the Douglas' squirrel (*Tamiasciurus douglasii*), whose behavioral repertoire is geared at safekeeping sources and stores of conifer seed (Smith 1970). Chipmunks have a strategy of capitalizing on seasonally available seeds, fruits, and fungal fruiting bodies; storing food for winter; and facultatively hibernating to reduce energy needs during winter. Crown-class differentiation was a minor dimension of flying squirrel realized habitat.

Crown-class differentiation is perhaps the factor of forest development most amenable to management: (1) species composition can be determined managerially at initiation of a new stand by legacy retention, planting, and precommercial thinning, (2) management of stem density and growth rates is well founded (Curtis and Carey 1996), and (3) spacing can be varied tree to tree or patch to patch within stands (Carey 1995, Carey et al. 1996*a*,*b*). Growth of large trees and time lead to disease, injury, decay, and death of trees and consequent expansion of multidimensional niche space. Decay processes seem less deterministic; management of decadence is more problematic.

Decadence.—Abundance of fallen trees and large, standing dead trees formed a unipolar gradient that explained 16% of variance in vegetation structure. Coarse woody debris (standing and fallen) was a result of 3 separate phenomena: (1) retention of legacies through catastrophic disturbance, (2) recruitment of fallen trees through suppression- mortality, and (3) development of decadence in live trees over time. Small wildfires played roles in our niche-diversification stands and, perhaps, in our old-growth stands (*see* Juday 1977 for a history of fire in Transition Life Zone). In other areas, root-rot infestations (e.g., Holah et al. 1993, Carey et al. 1996*b*), other diseases such as white pine blister rust, *Cronartium ribicola* (Lundquist and Marian 1991), and windstorms (Carey and Johnson 1995) add to coarse woody debris. Pacific Northwest natural forests have the highest coarse woody debris loads of all forests, and coarse woody debris is of central importance in promoting ecosystem stability, habitat diversity, and long-term productivity (Marra and Edmonds 1994). For example, coarse woody debris facilitates or provides the following:

1. Nutrient cycling by adding organic matter to soil (Sollins 1982, Harmon et al. 1994).
2. Microhabitats for a rich diversity of microorganisms, arthropods, lichens, and bryophytes and seedbeds for shade-tolerant conifers and ericaceous shrubs (Harmon et al. 1986, Peck et al. 1995).
3. Refugia for mycorrhizal fungi and reservoirs of moisture during and after catastrophic disturbance, particularly on dry sites and during droughts (Amaranthus et al. 1989).
4. Ectomycorrhizal links among trees and truffle production in late-seral forests (Amaranthus et al. 1994, Amaranthus and Perry 1994, Clarkson and Mills 1994).
5. Niche diversification in small-mammal communities by enhancing forest-floor structure, soil organic matter, fungi, and invertebrate communities (Carey and Johnson 1995).
6. Habitat for salamanders (*Aneides ferreus*, *Batrachoseps wrighti*, and *Ensatina eschscholtzii*) (Corn and Bury 1991, Gilbert and Allwine 1991).
7. Foraging sites for pileated woodpeckers (*Dryocopus pileatus*) (C. Raley, Pacific Northwest Research Station, U.S. For. Serv., Olympia, Wash., pers. commun.) and their prey-ants (*Camponotus*, *Formica*, *Lasius*) (Torgerson and Bull 1995).
8. Habitat element of primary importance to the western red-backed vole (*Clethrionomys californicus*) (Hayes and Cross 1987, Tallmon and Mills 1994).
9. Physical mediation of competition between black-tailed deer (*Odocoileus hemionus*) and Roosevelt elk (*Cervus elaphus*) (Leslie et al. 1984).
10. Elevated seed beds that protect vascular plants from herbivory by ungulates.
11. Maternal den sites for arboreal rodents (Carey et al. 1997).

Of all the habitat elements we measured, coarse woody debris proved to be the best predictor of the realized habitat space, activity, and carrying capacity of northern flying squirrels and carrying capacity for Townsend's chipmunk. In our study, fallen trees were almost twice as abundant in old growth as in managed forests. High utilization of wood (near complete removal of tree boles) and intensive site preparation can result in <2% cover of coarse woody debris in second growth (Carey et al. 1996b). Managed forests in general have less coarse woody debris than late-seral forests (Spies and Cline 1988, Carey and Johnson 1995, this study). Rebuilding a store of coarse woody debris through retention of tree boles during thinning is possible and expensive (Carey et al. 1996*a*). Thus, legacy retention is especially important in setting the stage for conserving biodiversity in managed forests.

If catastrophic disturbance sets the stage, it is small-scale disturbances in the canopy that determines the pace of the ecosystem development. Whitmore (1989) claimed that gaps drive the forest cycle in all forests; but the ecological process of tree death (Franklin et al. 1987) is particularly important in expansion of niche space (e.g., Carey et al. 1991*b*, Carey 1996, Parks and Shaw 1996, Stone et al. 1996). Only 10% of the cells of living conifers are actually alive (Franklin et al. 1987). Heart rots account for 20-31% of the volume of standing trees in Pacific Northwest forests (Hennon 1995, Parks and Shaw 1996). Snapping of boles (often at the site of decay) and standing death constitute 76% of gapmakers; uprooting is the least common (21%; Lertzman et al. 1996). In the Oregon Cascades, >70% of canopy Douglas-fir die standing or from stem breakage and die without disrupting the forest (73-88% of deaths in late-seral forest); only 12-27% of the trees in late-seral forest uproot (Spies and Franklin 1989, Spies et al. 1990). Competition is the major cause of death of trees up to 100-150 years old (Franklin et al. 1987). Mechanical damage from falling trees accounts for 15% of mortality in late-seral forests (Franklin et al. 1987). Decaying and dead standing trees (1) increase structural diversity, (2) alter the canopy microenvironment, (3) promote biological diversity, (4) store nutrients and decomposers, and (5) provide critical habitat elements for wildlife (Parks and Shaw 1996).

In southwest Oregon forests, an abundance (>7/ha) of large (>50 cm dbh) snags was the primary determinant of a diverse bird community

(Carey et al. 1991*b*). In old growth, large snags were 10 times more abundant, woodpeckers 4 times more abundant, and cavity-using birds as a group >2 times more abundant than in competitive-exclusion-stage forests. These cavity-nesting birds constitute a majority of resident, overwintering small-bird species. In this study, large snags were 5 (old-growth) to 10 (niche diversification) times more abundant in late-seral, natural forests than in managed forests. Flying squirrels nested primarily in large, live old trees (presumably with heart-rot and cavities) in old growth, but in residual old-growth snags in managed forests (Carey et al. 1997). Cavities in large deciduous trees with top-rot (e.g., bigleaf maple and Pacific madrone) also were used. Small-diameter conifer snags were rarely used for nesting by birds or mammals. In the Puget Trough, however, small-diameter deciduous snags (e.g., red alder) with cavities excavated by woodpeckers were important den sites in intensively managed 65-yearold understory-reinitiation stands with few large snags; in 55-year-old competitive-exclusion stands with numerous well-decayed large snags and minimally decayed suppression mortality, flying squirrels used stick nests in tightly closed canopies-but in both environments flying squirrel populations were low (Carey et al. 1997). On the Olympic Peninsula, flying squirrels denned in residual large snags and in cavities in live conifers with top-rot (formed after tops were killed by severe, unseasonable frost 30 yr previously), but not in abundant suppressed trees. It seems that suppression mortality in conifers does not contribute significantly to the function of standing decadent trees in either provision of cavities or gap formation. Small snags usually do not have top-rot (or cavities) and do not stand very long; they do contribute to coarse woody debris on the forest floor for a relatively short time before decaying *(see* Carey and Sanderson 1981 for a review of decay processes and cavity formation). The evolution of hole-nesting in birds (and arboreal rodents) is an adaptation that allows year-round residence in temperate forests by providing bioenergetic advantages and protection from predation (Collias 1964, Short 1979). Flying squirrels have evolutionary adaptations of gliding, nocturnality, cavity-nesting (Holmes and Austad 1994), and communal denning (Carey et al. 1997). Nocturnal arboreal travel and gliding have energetic costs that are offset (37% reduction in heat loss) by denning in groups in cavities lined with plant material (Stapp et al. 1991, Carey et al. 1997). Thus, den sites large enough to hold >3 squirrels are important, and decay in the tops of large trees is important. In addition, flying squirrels change dens about every 2 weeks (perhaps as a strategy to avoid predators) and large numbers of group dens are needed (Carey et al. 1997).

Carey (1995) reported a broad correspondence between large snag abundance and population sizes of flying squirrels across the Pacific Northwest. Carey et al. (1997) suggested this correspondence is more likely to be due to large snags as indicators of overall decadence than to provision of den sites. Trees display a continuum of roles from living, sound organisms to dead, prostrate structures on the forest floor (Franklin et al. 1987). Many of these roles depend on decay forming in living trees of large size; e.g., hollow trunks of fallen trees used as dens by American marten, *Martes americana* (L. C. Jones, U.S. For. Serv., Olympia, Wash., pers. commun.). Thus, decadence in Pacific Northwest forests cannot be partitioned functionally into snags and fallen trees without losing sight of the significance of the entire process of tree decay and death and its diverse functions.

Diets and Decadence.—What accounts for the ability of decadence to explain variation inspace use, activity, and abundance of flying squirrels? It is plausible that the role of decadence in providing den sites is important for an abundance of flying squirrels (Carey 1995, Carey et al. 1997), but we were measuring space use and activity at foraging sites, not den sites. Cover of fallen trees predicted flying squirrel abundance almost as well as did decadence (which included snags as well as fallen trees). Although dietary fungal diversity was positively correlated with abundance of coarse woody debris among stands only in the year of greatest diversity, a strong connection has been made between sporocarp abundance and coarse woody debris in southwestern Oregon. Amaranthus et al. (1994) found truffle abundance is 20-30 times greater in 180-year-old forest with 27% cover of coarse woody debris than in 4-27-year-old plantations with 11-14% cover of coarse woody debris. Within late-seral forest, truffle abundance is 10 times greater in well-decayed fallen trees as in plots on mineral soil. Of the 8 genera that were most frequent in our flying squirrel diets, 5 (*Rhizopogon*, *Melanogaster*, *Leucophleps*, *Hysterangium*, and *Leucogaster*) were associated with well-decayed coarse woody debris and 2 (*Hymenogaster* and *Gautieria*) were not found by Amaranthus et al. (1994). Only *Elaphomyces* (the eight ranked genus in diets of flying squirrels) was associated primarily with mineral soil. *Balsamia*, the eight ranked genus in chipmunk diets (and not present with >5% frequency in flying squirrel pellets), also was associated with mineral soil. Clarkson and Mills (1994) also found sampling plots with fallen trees are more likely to contain sporocarps (twice as likely) and on average to have more biomass (4 times more) of sporocarps than sampling plots without fallen trees in late-seral forest in southwestern Oregon. They found that activity of mycophagous western red-backed voles is associated with truffle abundance and coarse woody debris. Of the 5 most abundant genera (*Melanogaster*, *Hysterangium*, *Gautieria*, *Genebea,* and *Rhizopogon*) found by Clarkson and Mills (1994), 4 were among the 5 most abundant in diets of flying squirrels and 3 were among the 5 most abundant in diets of Townsend's chipmunk in our study areas.

Flying squirrels in our study areas consumed fungal sporocarps year round (Maser et al. 1986). Maser et al. (1986) found 20 genera in multiseason sampling (vs. the 24 genera and families we found in our spring samples); *Rhizopogon*, *Gautieria*, *Hymenogaster*, *Melanogaster*, *Hysterangium*, *Leucophleps*, *Elaphomyces*, and *Geopora* were the dominant items in spring diets, results differing from ours only in the addition of *Geopora*. Seasonal differences in diets were high frequencies of *Elaphomyces* in January-February, decreased frequencies of *Hymenogaster* in summer-fall, and increased frequencies of *Leucogaster* in summer-fall; lichens were important dietary components in January.

Diets of northern flying squirrels in the Pacific Northwest differ geographically, but fungal sporocarps still compose the bulk of diets. In the relatively dry forests east of the High Cascades physiographic province (northeast. Oreg. [Maser et al. 1985] and northeast. Calif. [Waters and Zabel 1995]), flying squirrels consume less fungi and more lichens, plant material, and staminate cones than flying squirrels in western Oregon (Maser et al. 1985, 1986; this study). Fungi (e.g., *Rhizopogon*) still dominated the diets. Waters and Zabel (1995) found fungal sporocarps in white fir (*Abies concolor*) forest are twice as abundant in old growth as in competitive exclusion 75-95 years old with little coarse woody debris, with flying squirrel densities positively correlated with sporocarp abundance (r = 0.86). In the Puget Trough of western Washington, flying squirrels consume (in spring and fall) 16 of 21 genera and 40 of 50 species of mycorrhizal fungi found throughout the year with intensive sampling in an array of second-growth Douglas-fir stands (Carey et al. 1996*b*). *Rhizopogon*, *Melanogaster*, *Hysterangium*, *Endogone*, and *Leucogaster* were the most frequently encountered truffle genera in sampling plots, and *Rhizopogon*, *Gautieria*, *Leucogaster*, and *Melanogaster* were the most common spores in diets. *Gautieria* was most abundant in stands with high coarse woody debris loads, and *Melanogaster* was most common in stands with little coarse woody debris. Mushroom spores (*Russula*, *Peziza*, *Agaricaceae*, and *Boletaceae*) were common in diets; plant material and lichens were relatively infrequent in fecal pellets. Spring diets of flying squirrels in Douglas-fir-western hemlock forests on the Olympic Peninsula of western Washington are dominated *by Rhizopogon*, *Hysterangium*, and *Leucogaster*. Olympic Peninsula squirrels also consume spores of *Boletaceae*, *Octaviana*, *Thaxterogaster*, and *Chamomixia* (Carey 1995). Species richness in Olympic Peninsula diets is half that in the Coast Range (Carey 1995, this study) and differs between competitive-exclusion and old-growth forest, but coarse woody debris is not a good predictor of flying squirrel abundance on the Olympic Peninsula. Several differences between the Oregon Coast Range and the Olympic Peninsula can explain the differences in dietary diversities and predictive ability of coarse woody debris:

1. The Olympic Peninsula has more precipitation, cooler temperatures, and less severe summer drought than the Coast Range; coarse woody debris may not be important as moisture reservoirs and refugia for ectomycorrhizal fungi.
2. Coarse woody debris loads on the Olympic Peninsula are higher (8% in competitive exclusion, 13% in old growth) than in the Coast Range (4% in competitive exclusion, 9% in old growth), forest-floor organic matter accumulations are greater, and forest floors are moister (Carey and Johnson 1995).
3. Forests on the Olympic Peninsula are dominated by western hemlock, which does not have as many ectomycorrhizal associates as Douglas-fir. Few species are specific to western hemlock, which may have evolved to capitalize on the mycorrhizal associations of pioneering species (e.g., Douglas-fir) that establish quickly after catastrophic disturbance (Molina et al. 1992). Thus, mycorrhizal diversity (and possibly sporocarp abundance) may be relatively low in pure western hemlock competitive-exclusion stands. About 50 species associate with western hemlock in the laboratory, >100 species in the field (Kropp and Trappe 1982, Molina and Trappe 1982, Molina et al. 1992). There are 250 species that are specific to, and 2,000 species associated with, Douglas-fir (Molina et al. 1992).

In our study area, golden chinkapin, Pacific madrone, tanoak (*Lithocarpus densiflorus*), and salal are broadly receptive to numerous ectomycorrhizal fungi, form ectomycorrhizal associations that facilitate establishment of Pinaceae after catastrophic disturbance, and create spatial and temporal ectomycorrhizal links among tree species (Amaranthus and Perry 1989, 1994; Molina et al. 1992; Molina and Trappe 1982; Smith et al. 1995). Thus, it is not surprising that we did not observe differences in dietary diversity between squirrels from competitive exclusion and squirrels from old growth in the Coast Range. In summary, dietary diversity was associated with coarse woody debris sometimes, but activity of mycophagous mammals and truffle abundance in southwestern Oregon seem to be strongly associated with coarse woody debris.

Both diversity and abundance of sporocarps are important to squirrels. Although 20-50 species of hypogeous fungi may be present in any 1 stand at any 1 time, usually <5 species account for the bulk (ca. 75%) of the biomass of sporocarps (Fogel 1976, Fogel and Hunt 1979, Hunt and Trappe 1987, Luoma 1991, Amaranthus et al. 1994). These abundant fungi, however, are the ones most frequently tallied in squirrel diets and seem to be narrow (tree genus) to intermediate (tree family) in host range (Molina and Trappe 1982, Molina et al. 1992). Total seasonal production differs markedly among years; e.g., 330-1,852 g/ha (Luoma 1991) and species production differs even more markedly (often > 10-fold). Thus, taxonomic diversity is important in providing a consistent food supply to mycophagous mammals.

Laboratory analysis of truffles and mushrooms show potentially high value as foods (Fogel and Trappe 1978), but digestibility is low, near the minimum for maintenance of squirrels (Cork and Kenagy 1989). Truffle genera differ in digestibility, different taxa provide different nutrients to squirrels, and squirrels differ in ability to extract nutritive value from truffles (Townsend's chipmunk is less capable than the northern flying squirrel; A. W. Claridge, Aust. Natl. Univ., Canberra, pers. commun.). Thus, dietary diversity may be important for dietary nutritional adequacy.

Cork and Kenagy (1989) hypothesized that great abundance, high detectability (through odors that attract squirrels), and low handlingtime for fungi maximized net yield of energy and nutrients, but that a high-quality diet required more than just fungi-conifer seeds, for example. They based their hypothesis on the nutritive value of *Elaphomyces*, but the squirrel they studied (*Spermophilus saturatus*) consumed primarily *Rhizopogon* (a major constituent of flying squirrel and chipmunk diets) under natural conditions. Indeed, *Rhizopogon* is the most frequent fungal taxa found in rodent digestive tracts except in Zapodidae (Maser et al. 1978). Both the squirrels we studied made use of a wide variety of truffles and mushrooms and, in 1 year, had high frequencies of vascular plant material in their fecal pellets. Townsend's chipmunk and Douglas' squirrel aggressively consume conifer seed as well as seeds and fruits of other plants and fungi (Smith 1970, Maser et al. 1978, Sutton 1993). Across their range, northern flying squirrels consume a wide variety of nuts, seeds, fruits, staminate cones, and catkins (Wells-Gosling and Heaney 1984), but we have found no evidence of extensive conifer seed consumption in the Pacific Northwest. Based on year-round sampling of stomachs, Maser et al. (1985, 1986) concluded that flying squirrels in western Oregon primarily are mycophagous. Contrary to Maser et al. (1985, 1986), the flying squirrels in our study did not appear to be strictly mycophagous, although fungi appeared to dominate their diets. Our flying squirrels seemed to take advantage of abundant nonfungal food in spring, probably staminate cones and possibly stored seeds (unidentified in the fecal samples). In the field in western Washington, we observed flying squirrels and chipmunks availing themselves of truffles, mushrooms, pollen (e.g., *Populus trichocarpa*), seeds (e.g bigleaf maple; conifer seeds by chipmunks), and fruits (e.g., salal) (A. B. Carey, coauthor, unpubl. data). Because fecal analysis identifies indigestible components of food items (e.g., spores, cuteinized epithelial structures), we cannot estimate the relative nutritional contributions of the various food groups. Flying squirrels may consume 15 g of truffle in a single meal; stomachs and contents(mostly spores) may weigh 24-71 g for squirrels with a live mass of 152-165 g (A. B. Carey, coauthor, unpubl. data). But even relatively small amounts of high-quality food, such as maple seeds, would be nutritionally significant (Cork and Kenagy 1989).

Fungal diversity does more than provide diverse diets for squirrels. Fungi are essential in many food webs; e.g., their exudates and hyphae link above-ground and below-ground processes by providing photosynthetically fixed carbon to rhizosphere consumers such as bacteria, protozoa, arthropods, and microfungi (M. P. Amaranthus, U.S. For. Serv., Grants Pass, Oreg., pers. commun.). Roots and mycorrhizal symbionts account for 70-80% of net primary productivity; 10-40% of total photosynthates pass from roots to rhizosphere adding organic material to the soil and enhancing soil structure. Diversity in mycorrhizae provides resilience to environmental stresses and may extend the range of environments within which plants can prosper (Perry et al. 1989). Each fungal species has its own set of physiological characteristics; thus, their activity varies with temperature and moisture, and they differ in the nutrients they extract from mineral soil and organic matter (Molina and Trappe 1982, Perry et al. 1989, Molina et al. 1992). Diversity in the plant community can be quite important in stabilizing below-ground mutualists after catastrophic disturbance (Perry et al. 1989). Although much of the composition of plant communities in Pacific Northwest forests is a result of the processes of canopy stratification and understory development, ectomycorrhizal linkages among plants can reduce competition for resources, promote forest recovery after disturbance, and influence the pattern of plant succession (Molina and Amaranthus 1991, Amaranthus and Perry 1994). Thus, forest-floor structure, plant-community composition, fungal-community composition, and animals interact in mutually reinforcing ways to produce ecosystem resilience and development. Overall, biodiversity stabilizescommunity and ecosystem processes, if not population processes (Tilman 1996).

Canopy Stratification.—Processes leading to transfer of vegetation growing space from overstory to midstory and occurrence of midstory vegetation differed among seral stages. In competitive exclusion, a sparse midstory developed when conifers grew taller than their deciduous contemporaries. This midstory contributed little to foliage-height diversity and seemed coincidental with understory development. Carey et al. (1991*b*) reported similar conditions in naturally regenerated stands in the Coast Range. However, portions of some

40-70-year-old stands in the Coast Range had high foliage-height diversity; these were used for roosting by the northern spotted owl (Carey et al. 1992). In niche diversification, stratification occurred as a result of (1) retention of live old trees and possibly advance regeneration from previous stands, (2) development of a predominant even-aged cohort of conifers of mixed species following catastrophic wildfire (ca. 100 yr before), (3) establishment of deciduous trees following catastrophic wildlife, and (4) subsequent establishment of a third cohort of conifers (including Douglas-fir) after noncatastrophic wildfires. Foliage-height diversity was great with multiple components; midstory, overstory, and herbaceous cover had almost identical mean values (44 49%; shrub cover was 29%). Mean midstory cover (48%) was much greater than in competitive exclusion (14%) and similar to old growth (45%). Early histories of oldgrowth stands were unknown; but at the time of our study, the 210-350-year-old overstories were a mix of species, and midstories were primarily shade-tolerant conifers, bigleaf maple, and Pacific madrone. In the Coast Range, bigleaf maple is most abundant in old growth (Spies 1991, this study). Shade-tolerant conifers in the overstory (western hemlock, western redcedar, incense-cedar, grand fir) probably were contemporaries of the dominant Douglas-fir and a result of midstory trees gradually entering the canopy. Midstories tended to merge with overstories and understories in old growth; foliage-height diversity was high. Recently developed vegetation structure in old growth appeared to have resulted from small-scale, gap-forming processes. The higher prevalence of patches of high shrub cover in niche diversification may have been the result of intermediate scale disturbances (small wildfires). The deep, multiple layers of vegetation in old growth and niche diversification resulted in cool and humid conditions in the understory because of protection from radiation and drying winds; forest floors also were moist because of decomposing wood (Spies 1991). Thus, our niche-diversification and old-growth stands had greater covers of herbaceous plants and more diverse shrubs than our competitive-exclusion stands. Regionally, complexity of structure and resulting variety in microclimates results in late-seral forests having greater numbers of plant species and greater percent cover per species than "young" (Carey and Curtis [1996] competitive-exclusion) and "mature" (Carey and Curtis [1996] understory-reinitiation) stands (Spies 1991). In our analyses, this greater complexity and diversity, along with differences in canopy species composition, translated into greater habitat breadth. Habitat breadth accounted for slightly more variation in flying squirrel activity than decadence and, with MGV, explained about as much variation in carrying capacity as decadence explained.

Canopy stratification was the single best descriptor of the realized habitat of chipmunks. Midstory cover had the most predictive power for chipmunk activity. Decadence and canopy stratification seemed of nearly equal importance in explaining variance in chipmunk carrying capacity. Although canopy stratification explained only 11% of the variance in vegetation structure among points, its process seemed to have profound influences on the plant community and squirrels.

Gaps and Stratification.—Almost 50% of our plots in old growth fell in areas with <50% canopy closure, thereby indicating a gap. Gaps can result from the death of a single branch or tree, but normally gaps result from death of one to several canopy trees and are <0.1 ha (Spies and Franklin 1989, Spies et al. 1990). Stewart (1986) reported that gaps in old-growth Douglas-fir along the west slope of the Cascades in Oregon are generally small openings (<25 m^2) between crowns. Spies et al. (1990) reported median sizes of gaps of 19 m^2 in "mature" forest and 85 m^2 in old growth; canopy gaps in old growth were a result of the death of > 1 tree, and many were a consequence of multiple events and were >50 years old. The percentage of canopy area occupied by gaps ranged from 18% in mature (understory-reinitiation and niche-diversification stages) to 13% in old growth, with expanded gaps occupying 42 and 26% of the area, respectively. Lertzman et al. (1996) reported that 56% of forest area in coastal temperate rain forest in British Columbia is influenced by canopy openings, with 30% of the area in gaps. In our study, 48% canopy closure represented 182 m^2 of open sky in a 350-m plot; this much open sky would result from the death of 2 or 3 dominant trees and some branches of live trees. Death of 5-10 large, adjacent trees, though rare, would cause gaps of 1,100 m^2 (Spies et al. 1990). In our study, patches without significant gaps averaged 68 and 78 m apart in niche diversification and old growth, respectively. In both our study and in the Oregon Cascades (Spies et al. 1990), gaps were rare in competitive exclusion.

Tree-crown overlap in old growth in the Oregon Cascades averages only 15-30%. Much of this overlap is due to subdominant western hemlock (Spies et al. 1990). Development of midstory vegetation can maintain the connectivity among tree crowns that facilitates travel by arboreal rodents (Carey 1996). Full foliage-height profiles, found in niche diversification and old growth in our study, facilitate exit from and entry to the canopy by providing protection from predation associated with gliding over open areas and with tall expanses of clear tree boles characteristic of competitive-exclusion forests (Holmes and Austad1994, Stapp 1994). For chipmunks, the value of midstory might be in variety and abundance of seed production by conifers, hardwoods, and understory shrubs. To the benefit of both squirrels, gaps may result in increased fungal production through extended root networks of the dominant Douglas-fir, ameliorated microclimate, increased habitat breadth, niche diversification in the forest floor, and ectomycorrhizal linkages among Douglas-fir, western hemlock, grand fir, and coarse woody debris (Perry et al. 1989, Molina and Amaranthus 1991).

Understory Development.—Understory development contributed relatively little (10%) to the variance in vegetation structure among sampling points. Much of differences among stands and seral stages in understory development seemed related to relative abundance of ferns and shrubs and to composition of the shrub community All competitive-exclusion stands had salal as a major component of the shrub layer, with 1-3 other species, particularly oceanspray, California hazel, or evergreen huckleberry, present in small quantities. The herbaceous layer was dominated by moss, oregongrape (as a low, prostrate shrub), and swordfern. In niche diversification and old growth, however, Pacific rhododendron, vine maple, and conifer seedlings and saplings were added to salal, oceanspray, and huckleberries. A diversity of species and life forms occurred in the herbaceous layer: low shrubs, half-shrubs, ferns, forbs, grasses, and mosses. Nonetheless, few plant species in Pacific Northwest coniferous forests are confined to a particular seral stage (Franklin and Dyrness 1973, Spies 1991, this study).

Abundances of vascular plants and community diversity increase with stage of forest development (Stewart 1986, Spies 1991, Halpern and Spies 1995). As we also found, Spies (1991) reported that 4 processes influence understory development: (1) resource availability, (2) horizontal spatial heterogeneity, (3) vertical diversity of vegetation, and (4) fire. Aggressive shrubs of low to moderate shade tolerance (e.g., salal) form dense patches under uniform, open canopies. In tall old-growth and niche-diversification forests, shade-tolerant species are favored. Old-growth understories tend to be relatively cool and humid during dry seasons because they are protected from radiation and drying winds by deep, multiple, canopy layers. Accumulated coarse woody debris and litter on the forest floor act as moisture reservoirs. Gaps in canopies provide marked horizontal heterogeneity in the spatial distribution of light and moisture. Sunflecks of brief duration contribute 37-68% of total photosynthetically active radiation (Canham et al. 1990). Penetration of light into the understory adjacent to gaps is significant at high latitudes because of sun angle. Even though the mean and range of light levels increase with size of gaps, potential duration of light is still <4 hours and varies inversely with canopy height (≤70 m in old growth Douglas-fir). Development of shade-tolerant midstories can have significant impacts on the amount of light reaching the understory. Light penetration also varies with gap orientation; north-south gaps admit more light than east west gaps (Poulson and Platt 1989). Topographic position and edaphic gaps can increase heterogeneity in light conditions, and, with 30% of the forest area in gaps, 56% of the forest area is influenced by canopy openings (Lertzman et al. 1996). Thus, the complex of light, temperature, and moisture conditions in our study area produced the following:

1. Twenty-one site types, in part indicative of landscape-level climatic gradients.
2. Among-stand variation in environmental conditions due to slope, aspect, elevation, edaphic conditions, and stage of forest development.
3. Within-stand variation due to site moisture, edaphic gaps, regeneration gaps, canopy gaps caused by tree death, and development of shade-tolerant midstories.

All site types were found across multiple stands (most across the majority of stands), suggesting types were more a product of ecosystem development conditioned by temperature and moisture rather than a result of unique local conditions. Relative degree of within-stand heterogeneity arising from disturbance and forest development was measured by habitat breadth. Thus, habitat breadth was a measure of spatial, structural, and compositional diversity. Ultimately, habitat breadth may have influenced populations of squirrels through abundance and diversity of food and cover and ameliorated microclimates. This measure of complexity along with decadence explained 50% of the variance in flying squirrel activity and 70% of the variance in carrying capacity (with MGV). Habitat breadth was a better predictor than any measure of understory including ericaceous shrubs.

The understory factor was a minor but significant predictor of the realized habitat of both flying squirrels and chipmunks. Chipmunks increasingly selected home ranges with heavy understory as midstory decreased (i.e., from old growth to niche diversification to competitive exclusion). Carey (1995) reported that prevalence of ericaceous shrubs was correlated with abundances of both flying squirrels and Townsend's chipmunks on the Olympic Peninsula; he hypothesized that ericaceous shrubs have important value as food (fruits and ectomycorrhizal linkages promoting production of truffles) and as protection from predators. Ericaceous shrubs, snags, and the nature of the catastrophic disturbance originating the stand explained 83-85% of the variance in flying squirrel activity. Cover of ericaceous shrubs was >24% on <39% of the stand areas. Hayes et al. (1995) examined the abundance of chipmunks across a chronosequence of 12 stands (10-140+ yr-old) in the Coast Range and found high correlations with the abundance of salal (1-34% cover, median = 13%) but no other habitat variables. They proposed 3 nonexclusive hypotheses about the correlation: (1) salal fruits provide food; (2) salal provides cover from predation; and (3) salal is correlated with some other determinant of chipmunk abundance. Harestad (1991) experimentally demonstrated the importance of overhead cover to chipmunks. Differences in ability of shrub abundance to explain variance in squirrel activity among studies may be due to differences among study areas in the degree to which shrubs were lacking, variances in shrub cover relative to variances in abundance of other habitat elements, and complementarity between midstory and understory. In our study, the realized habitat space of both flying squirrels and chipmunks had >39% cover of shrubs. Mean shrub cover averaged 26-34% among seral stages, and prevalence of ericaceous shrub cover averaged 40-65%. Thus, our stands had greater cover of salal than areas studied by Carey (1995) or Hayes et al. (1995). In our study, shrub cover was less predictive than coarse woody debris for flying squirrels and midstory for chipmunks. Coarse woody debris was much less abundant in our study areas than on the Olympic Peninsula (Carey 1995) and, apparently, in the areas studied by Hayes et al. (1995). Most of Hayes' sample was too young to have developed midstories; thus midstory cover could not account for much variance (or provide overhead cover in the field). Midstories were less prevalent on the Olympic Peninsula (28 ± 6% in old growth, 11 ± 6% in competitive exclusion) than in our Coast Range study areas (73 ± 6% in old growth, 80 ± 12% in niche diversification, and 28 ± 6% in competitive exclusion). Large differences in coarse woody debris (5-24% cover) and shrub abundance (0-95% prevalence) among stands on the Olympic Peninsula also appeared to influence the structure of forest-floor small-mammal communities and the abundances of various species of shrews, mice, and voles (Carey and Johnson 1995). Dimensions of potential habitat spaces (expressed herein as statistical distributions of habitat elements) determined not only shapes of response surfaces of species (realized habitats) within a given space but also which factors would explain the most variance in animal activity in that space. Fretwell (1972) provides additional examples of how factors that limit populations can differ among locations and seasons.

Spatial Scale.—In our review of the ecology of fungi, vascular plants, and squirrels, we found that many ecosystem processes take place at the level of individual organisms (e.g., death and decay of single trees) and structural features (e.g., fruiting of mycorrhizal fungi in a decayed log). Our analysis of vegetation structure and composition generated 4 orthogonal factors and a set of vegetation site types. The factors (1) accounted for 63% of variance in vegetation structure, (2) separated realized habitat from potential habitat with an accuracy of 60-66%, but (3) explained only 14-20% of variance in within-stand activity and 11-14% of, variance in activity among points across stands. Squirrels did not appear to select any small subset of site types for their activities. Point values differed markedly within stands for many variables, but foraging patches and home ranges differed little from the stands within which they occurred.

Across stands, mean values for habitat factors and habitat elements exhibited numerous high correlations (*r* = 0.53-0.97). Stand-level differences in horizontal heterogeneity and vertical heterogeneity were apparent; heterogeneity, habitat space, and habitat breadth generally increased with time-since-catastrophic disturbance-but with niche-diversification stands having some extreme values for some elements (e.g., snags and coarse woody debris). Habitat factors and habitat breadth explained more among-stand variance in squirrel activity than individual habitat elements and provided better models of squirrel activity than classification of stands into seral stages. Factors explained 50-74% of squirrel activity and 70-72% of squirrel carrying capacity. Managed competitive exclusion, in general, had less developed niche space and coarser grain than niche diversification and old growth. Grain in old growth was less than the height of an old-growth tree (ca. 70 m); i.e., 47 m for shrub patches, 23 m for midstory development, and 78 m for areas of closed canopy. Clumped deaths of 1-3 dominant trees at high prevalences across old-growth stands and low sun angles resulted in fine-scale heterogeneity with close juxtaposition of habitat elements (snags, fallen trees, patches of shrubs, patches of midstory, patches of herbaceous cover, patches of open forest floor) and different species and life forms. In response to increased heterogeneity on a fine scale, foraging patches and home ranges overlapped more and total activity increased. Thus, accumulation of processes in late-seral, natural stands resulted in an emergent property of niche diversification that provided more stable habitat for squirrels; carrying capacities for both squirrels had maximum values in old growth. Nevertheless, individual stands deviated significantly from average conditions within nominal seral stages in their capacity to support squirrels and in various measures of habitat space. Three habitat factors, habitat breadth, and position on the moisture gradient were not correlated with the primary factor (crown-class differentiation) that explained the most variance in structure among stands and among stages. As Carey (1995) reported for the Olympic Peninsula, nominal seral stage may not always be a good predictor of habitat quality. The 4 factors representing developmental processes, habitat breadth, and MGV provided better descriptions of ecosystem development and niche diversification than nominal seral stage. Thus, we concluded that intentional stand-level management has the potential to accelerate niche diversification.

At the landscape level in our study area, Carey and Peeler (1995) found that fragmentation of late-seral forest by ecosystem-initiation and competitive-exclusion stages had negative effects on spotted owls. These managed forests were avoided (Carey et al. 1992) or used rarely. But managed and natural forests that were more advanced in development (understory reinitiation and niche diversification) were 23% of the areas regularly used by spotted owls. They also hypothesized that active, intentional management could reduce impacts of forest management on spotted owls.

Squirrel Niches.—The biomass of squirrels (Douglas' squirrel, northern flying squirrel, andTownsend's chipmunk) in creases with forest development (Carey 1995). The size of all 3 squirrels makes them especially attractive to predators common in Pacific Northwest forests; i.e., raptors, owls, and mustelids. The squirrels are near the maximum size limit for many of these predators. Abundances of chipmunks, flying squirrels, and possibly Douglas' squirrels increase with forest development despite overlap in diets, den site use, and space use (Carey 1991, 1995; Carey et al. 1997; this study). Thus, squirrels seem to be limited by variability in food abundance and predation (and territoriality for the Douglas' squirrel), not interspecific competition. Late stages of forest development provide habitat structure that mediates predation and variety in fruit production that offsets high variability in availability of individual food items. The resulting increased prey biomass attracts and supports predators.

MANAGEMENT IMPLICATIONS

Our multidisciplinary, multiscale study of vascular plants, fungi, and squirrels allowed us to move beyond. empirical descriptions of organism-environment relations to hypotheses about ecosystem processes, the functions of habitat elements, and the scale of emergent properties. We were able to identify a framework of ecological processes within which we integrated a large and fragmented literature. Several hypotheses emerged from our analysis of forest development:

1. The range in natural conditions in historical landscapes expressed as proportions of landscapes in ≤4 nominal seral stages (e.g., Oliver 1981) does not provide adequate guidance for managing forests to conserve biodiversity; biodiversity is suppressed in competitive exclusion (which historically was rare in many landscapes; Tappeiner et al. 1997*a*) and there is expansion of niche space and increased biodiversity in understory-reinitiation and niche-diversication stands.
2. Ecosystem dynamics (especially rate of forest development, uncertainty in decadence processes, and longevity of competitive-exclusion stages) suggest active ecosystem management would be more effective than passive management (withdrawals or reserves) for conservation of biodiversity in second-growth forests.
3. Important processes in forest development are crown-class differentiation, decadence, canopy stratification, and understory development; these processes provide guidance for management to conserve biodiversity.
4. Thinnings, active promotion of decadence, and legacy retention hold potential in managing forests for biodiversity, but spatial scale of management is important.
5. Effective ecosystem management requires conscious consideration of hot only the goals of various members of society and cultural fit (Carey 1998), but also the various components, processes, and interactions within and among ecosystems; we call this active, intentional, ecosystem management.

Thinning

In the Pacific Northwest, the best opportunities for conservation of biodiversity through ecosystem management lie in the millions of hectares of second-growth forest <50 years old (DeBell et al. 1997, Hayes et al. 1997). Crown-class differentiation, canopy stratification, understory development, and habitat breadth can be enhanced through thinning, but spatial patterning is important. Our spatial data provide guidance. Traditional, light commercial thinning will not preclude or move a stand out of competitive exclusion and will not increase habitat breadth. Heavy thinning with even spacing can cause stands to become drier through increased wind and sunlight, could result in salal brushfields (simple structure with low habitat breadth), and (if applied to a dense stand) could disrupt mycorrhizal links and increase probability of massive windthrow (Carey et al. 1996*b*). Recent practices in the Pacific Northwest include wide systematic spacing (125 trees/ha) at first thinning (A. B. Carey, coauthor, pers. observation; Tappeiner et al. 1997*b*); this wide spacing would undoubtedly retard forest development through drying effects, growth of a brushfield, disruption of ectomycorrhizal links, and widely separated tree crowns (Carey et al. 1996*b*). Thinnings can be used as intermediate disturbances to eliminate competitive-exclusion stages and move gradually to niche diversification. Variable-density thinning on a 0.1-0.5-ha scale that removes subordinate or codominant trees appears to have potential for increasing crown-class differentiation, canopy stratification, understory development, and habitat breadth (Carey 1995, Carey and Johnson 1995, this study). Determining the number of trees to remove can be based on relative densities derived from yield tables (Curtis 1982); we suggest that maintaining relative densities of 0.5 and 0.35 in a ratio of 2:1 over the stand could result in accelerating the development of stand structure and heterogeneity characteristic of late-seral, natural forests. Hagar et al. (1996) recommended variable-density thinning with relative densities of 0.2-0.7. Actual choice of relative densities should entail consideration of risk of windthrow, potential for creation of salal or salmonberry (*Rubus spectabilis*) brushfields, the silvics of the species being managed, and site conditions. Multiple thinnings would be necessary to (1) keep the disturbance intermediate to small scale, (2) avoid disrupting connectivity among tree crowns, (3) prevent excessive drying of the forest floor, (4) avoid development of a sparse overstory with a dense salal brushfield underneath, and (5) keep the canopy from closing into a stage of competitive exclusion.

Using 300-year simulations, Carey et al. (1996*a*) compared no-active management, management to maximize net present value of wood products, and management for biodiversity that included variable-density thinnings after precommercial thinning to 740 trees/ha (and alternating 70- and 130yr rotations). Traditional commercial thin-ping with systematic spacing allowed quick (ca. 10 yr) canopy closure and return to competitive exclusion; biodiversity targets were not met and revenues were less than with 40-year rotations and no commercial thinning. Variable-density thinnings at 30, 50, and 70 years (or 30, 60, 90 yr) and retaining stand-level densities of 247, 123, and 90 trees/ha, respectively, produced more wood and enhanced biodiversity. Biodiversity targets were met in <50% of the time required with no management. Even with active management, a long time (70-100 yr) seemed necessary to achieve niche diversification; >30% of the land base would have to be managed on 110-130-year rotations to conserve biodiversity (Carey et al. 1996*a*). In forests being restored for late-seral wildlife, biodiversity thinnings appeared to have substantial value in creating late-seral forest relatively quickly. In forest managed for economic values, biodiversity pathways produced higher levels of sustainable income and regional employment at a cost of about 15% of net present value. Thus, managing for biodiversity on industrial and multiple-use lands appears practical.

Biodiversity pathways (Carey et al. 1996*a*) include more than thinning. Maintenance of species diversity begins at final harvest and continues throughout the management cycle through planned silvicultural interventions including planting, precommercial thinning, and variable-density commercial thinnings that create a condition of gradual change. Legacy retention is an important part of biodiversity pathways.

Legacy Retention

Retention of surface humus layers, coarse woody debris, ericaceous shrubs, hardwoods, and green trees at final harvest by minimizing site preparation and burning can enhance ectomycorrhizal links and spatial patterning beginning in the ecosystem initiation stage (Carey and Johnson 1995, Franklin et al. 1997). Management of forests to conserve biodiversity or to restore late-seral conditions should incorporate conservation of coarse woody debris, prompt regeneration of conifers, control of tree spacing and species composition, and consideration of the processes of tree death and decay. Conservation of coarse woody debris and other biological legacies could begin at the harvest of a stand and continue through site preparation, precommercial, and commercial thinnings (Carey and Johnson 1995). Our study suggests that ≥10% cover of large coarse woody debris is necessary for full functioning of Coast Range coniferous ecosystems. Carey and Johnson (1995) recommended 15% cover of coarse woody debris in various sizes and stages of decay for the wet western hemlock forests on the Olympic Peninsula. Because coarse woody debris decays and is incorporated into the soil over time, retention at harvest will not be adequate to maintain recommended levels of coarse woody debris over long rotations; active management of decadence will be necessary.

Management for Decadence

Managing decadence is the most challenging aspect of intentional ecosystem management. Our research shows that decadence is more than snags and logs; it is a process that is influential in multiple aspects of ecosystem development from providing cavities for wildlife, to creating gaps in the canopy, to altering forest floor microclimate and structure. Active management may be necessary to maintain decadence in the first 150 years of ecosystem development. Thinnings without active management for decadence could result in dimunition of decadence, decline in coarse woody debris, and a change in trajectory of forest development away from complexity and resiliency. Coarse woody debris could be augmented during thinnings by leaving some (or some parts of) felled trees (Carey 1995, Carey and Johnson 1995, Carey et al. 1996*a*). Thinning operations would cause damage to living trees as naturally falling trees do, thereby providing opportunities for infection with top-rot. Additionally, managers could actively wound trees (e.g., through cavity creation) or inoculate trees with top-rot fungi (Carey 1995, Carey and Johnson 1995). Multiple thinnings can provide regular inputs of coarse woody debris to maintain a 10% cover of coarse woody debris in various stages of decay in dry Douglas-fir forests and a 15% cover in moist western hemlock forests, when natural mortality does not do so. Other specific management practices are discussed by Carey (1995), Carey and Johnson (1995), and Carey et al. (1996*a*).

Landscape Management

In managed forest landscapes, arrangement and composition of landscape units are a function of management pathway (i.e., biodiversity vs. maximization of net present value of timber) and rotation age. Long rotations (e.g., alternating 70-yr and >120-yr rotations) produce a landscape with 50% late-seral forests and <15% ecosystem-initiation stages; short rotations (e.g., 40 yr) produce a landscape devoid of late-seral forest outside of reserves and high proportions of ecosystem-initiation stages. Given a choice of a constraint of 30-40% of the forest in reserves (e.g., riparian reserves) versus 30-40% in late-seral forest, the former produces a highly fragmented landscape and the latter a landscape dominated by forests in understory-reinitiation, niche-diversification, and later stages. Active management can do much to help restore degraded riparian areas; passive management (reserves) can delay recovery of riparian areas (Carey et al. 1996*a*).

Adaptive Management

Results of retrospective studies are correlational and cannot demonstrate cause and effect. Simulation studies only test the logic of assumptions. Relations uncovered by such studies are hypotheses that can be strengthened (tested and modified) by controlled experimentation. Two complete randomized block experiments using active, intentional, ecosystem management based on biodiversity pathways are in progress. One incorporates variable-density thinning, legacy retention, and introduction of top-rot in trees through cavity creation and inoculation of decay fungi; results from 3 years posttreatment are encouraging (Carey et al. 1996b). Another (C. A. Harrington, U.S. For. Serv., Olympia, Wash. and A. B. Carey, coauthor, unpubl. data) incorporates variable-density thinning and creation of coarse woody debris structures from small-dbh trees felled during thinning; this experiment is in the treatment phase. These experiments will test some of the specific hypotheses proposed by Carey (1995), Carey and Johnson (1995), and this study.

LITERATURE CITED

AMARANTHUS, M. P., D. S. PARRISH, AND D. A. PERRY. 1989. Decaying logs as moisture reservoirs after drought and wildfire. Pages 191-194 *in* E. Alexander, ed. Stewardship of soil, air, and water resources: proceedings of Watershed 89. U.S. For. Serv., Reg. 10, Juneau, Alas.

AND D. A. PERRY. 1989. Interaction effects of vegetation type and Pacific madrone soil inocula on survival, growth, and mycorrhiza formation of Douglas-fir. Can. J. For. Res. 19:550556.

______, AND ______. 1994. The functioning of ectomycorrhizal fungi in the field: linkages in space and time. Plant and Soil 159:133-140.

______, J. M. TRAPPE, L. BEDNAR, AND D. ARTHUR. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding' plantations and its relation to coarse woody debris and animal mycophagy. Can. J. For. Res. 24: 2157-2165.

BAILEY, V. 1936. The mammals and life zones of Oregon. North Am. Fauna 55:1-416.

BARBOUR, M. G. 1996. American ecology and American culture in the 1950s: who led whom? Bull. Ecol. Soc. Am. 77:44-51.

BONHAM, C. D. 1989. Measurements for terrestrial vegetation. John Wiley & Sons, New York, N.Y. 338pp.

BORMANN, F. H., AND G. E. LIKENS. 1979. Pattern and process in a forested ecosystem. Springer Verlag, New York, N.Y. 253pp.

BROWN, J. H. 1971. Mammals on mountaintops: non-equilibrium insular biogeography. Am. Nat. 105: 467-478.

BUCHANAN, J. B., R. W. LUNDQUIST, AND K. B. AUBRY. 1990. Winter populations of Douglas' squirrels in different-aged Douglas-fir forests. J. Wild. Manage. 54:577-581.

CANHAM, C. D., J. S. DENSLOW, W J. PLATT, J.R. RUNKLE, T. A. SPIES, AND P. S. WHITE. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20:620-631.

CAREY, A. B. 1991. The biology of arboreal rodents in Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-276. 46pp.

______.1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecol. Appl. 5:648-661.

______.1996. Interactions of canopies and Pacific Northwest mammals. Northwest Sci. 69 (spec. issue):72-78.

______. 1998. Dimensions of ecosystem management. Pages 261-274 *in* J. M. Calhoun, ed. Forest policy: ready for renaissance. Inst. For. Resour. Contrib. No. 78, Coll. of For. Res., Univ. Washington, Seattle.

______, B. L. BISWELL, AND J. W. WITT. 1991*a*. Methods for measuring populations of arboreal rodents. U.S. For. Serv. Gen. Tech. Rep. PNW-273. 24pp.

______, C. ELLIOT, B. R. LLPPKE, J. SESSIONS, C. J. CHAMBERS, C. D. OLIVER, J. F. FRANKLIN, AND M. J. RAPHAEL. 1996*a*. A pragmatic, ecological approach to small-landscape management. Wash. For. Landscape Manage. Proj. Rep. No. 2, Wash. State Dep. Nat. Resour., Olympia. 98pp.

______, AND R. O. CURTIS. 1996. Conservation of biodiversity: a useful paradigm for forest ecosystem management. Wild. Soc. Bull. 24:610-620.

______, M . M. HARDT, S. P. HORTON, AND B. L. BISWELL. 1991b. Spring bird communities in the Oregon Coast Ranges. Pages 123-144 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-285.

______, S. P. HORTON, AND B. L. BISWELL. 1992. Northern spotted owls: influence of prey base and landscape character. Ecol. Monogr. 62:223-250.

______, AND M. L. JOHNSON. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecol. Appl. 5:336-352.

______, A. J. MAIN, JR., AND M. G. CAREY. 1981. Sampling populations of small mammals in Connecticut forests. Trans. Northeast Sect. Wildl. Soc. 38:90-104.

______, AND K. C. PEELER. 1995. Spotted owls: resource and space use in mosaic landscapes. J. Raptor Res. 29:223-239.

______, AND H. R. SANDERSON. 1981. Routing to accelerate tree-cavity formation. Wildl. Soc. Bull. 9:14-21.

______,D. R. THYSELL, L. VILLA, T. WILSON, S. WILSON, J. TRAPPE, E. INGHAM, M. HOLMES, AND W. COLGAN. 1996*b*. Foundations of biodiversity in managed Douglas-fir forests. Pages 6882 *in* D. L. Pearson and C. V Klimas, eds. The role of restoration in ecosystem management. Soc. Ecol. Restor., Madison, Wis.

______,T . WILSON, C. C. MAGUIRE, AND B. L. BISWELL. 1997. Dens of northern flying squirrels in the Pacific Northwest. J. Wildl. Manage. 61:684-699.

CASTELLANO, M. A., J. M. TRAPPE, Z. MASER, AND C. MASER. 1989. Key to spores of the genera of hypogeous fungi of north temperate forests. Mad River Press, Inc., Eureka, Calif. 186pp.

CLARKSON, D. A., AND L. S. MILLS. 1994. Hypogeous sporocarps in forest remnants and clearcuts in southwest Oregon. Northwest Sci. 68:259-265.

COLLIAS, N. E. 1964. The evolution of nests: and nest building in birds. Am. Zool. 4:175-190.

CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1320.

______, I. R. NOBLE, AND R. O. SLATYER. 1987. On the mechanisms producing successional change. Oikos 50:136-137.

______, AND R. O. SLATYER. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111:1119-1144.

CORK, S. J., AND G. J. KENAGY. 1989. Nutritional value of hypogeous fungi for a forest-dwelling ground squirrel. Ecology 70:577-586.

CORN, P. S., AND R. B. BURY. 1991. Terrestrial amphibian communities in the Oregon Coast Range. Pages 305-318 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coord. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-285.

CURTIS, R. O. 1982. A simple index of standard density for Douglas-fir. For. Sci. 28:92-94.

______, AND A. B. CAREY. 1996. Timber supply in the Pacific Northwest: managing for economic and ecological values. J. For. 94(9):4-7, 35-37.

DEBELL, D. S., R. O. CURTIS, C. A. HARRINGTON, AND J. C. TAPPEINER. 1997. Shaping stand development through silvicultural practices. Pages 141-164 *in* K. A. Kohm and J. F. Franklin, eds. Creating a forestry for the 21st century. Island Press, Washington, D.C.

DENISON, W C. 1973. Life in tall trees. Sci. i. Am. 228(6):74-80.

DRAPER, N., AND H. SMITH. 1981. Applied regression analysis. Second ed. John Wiley & Sons, New York, N.Y. 709pp.

ENSEEN, P.-A., K.-E. RENHOM, AND R. B. PETTERSON. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. Ecol. Appl. 6:228-238.

FLEISS, J. L. 1981. Statistical methods for rates and proportions. John Wiley & Sons, New York, N.Y. 321pp.

FOGEL, R. M. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas-fir stand. Can. J. Bot. 54:1152-1162.

______, AND G. HUNT. 1979. Fungal and arboreal biomass in a western Oregon Douglas-fir ecosystem: distribution patterns and turnover. Can. J. For. Res. 9:245-256.

______, AND J. M. TRAPPE. 1978. Fungus consumption (mycophagy) by small animals. Northwest Sci. 52:1-31.

FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the spotted owl in Oregon. Wildl. Monogr. 87. 64pp.

FRANKLIN, J. F., D. R. BERG, D. A. THOMBURGH, AND J. C. TAPPEINER. 1997. Alternative silvicultural approaches to timber harvesting: variable retention systems. Pages 111-139 *in* K. A. Kohm and J. F. Franklin, eds. Creating a forestry for the 21st century. Island Press, Washington, D.C.

______, K. CROMACK, JR., W DENISON, A. MCKEE, C. MASER, J. SEDELL, F. SWANSON, AND G. JUDAY. 1981. Ecological characteristics of oldgrowth Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-118. 48pp.

______, AND C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S. For. Serv. Gen. Tech. Rep. PNW-8. 417pp.

______, H. H. SHUGART, AND M. E. HARMON. 1987. Tree death as an ecological process. BioScience 37:550-556.

FRETWELL, S. D. 1972. Populations in a seasonal environment. Monogr. Popul. Biol. 5:3-217.

GAUCH, H. G. 1979. COMPCLUS—a Fortran program for rapid initial clustering of large data sets. Ecology and Systematics, Cornell University, Ithaca, N.Y. 59pp.

______. 1980. Rapid initial clustering of large data sets. Vegetation 42:103-111.

______. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, New York, N.Y. 298pp.

GILBERT, F. F., AND R. ALLWINE. 1991. Terrestial amphibian communities in the Oregon Cascade Range. Pages 305-318 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coord. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-285.

GILLESBERG, A.-M., AND A. B. CAREY. 1991. Arboreal nests of *Phenacomys longicaudus* in Oregon. J. Mammal. 72:784-787.

HAGAR, J. C., W. C. MCCOMB, AND W H. EMMINGHAM. 1996. Bird communities in commercially thinned and unthinned Douglas-fir stands of western Oregon. Wildl. Soc. Bull. 24:353-366.

HALPERN, C. B., AND T. A. SPIES. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol. Appl. 5:913-934.

HAMER, T. E., AND S. K. NELSON. 1995. Characteristics of marbled murrelet nest trees and nesting stands. Pages 69-82 in C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Platt, eds. Ecology and conservation of the marbled murrelet. U.S. For. Serv. Gen. Tech. Rep. PSW-GTR-152.

HARESTAD, A. S. 1991. Spatial behavior of Townsend's chipmunks and habitat structure. Acta Theriol. 36:247-254.

HARMON, M. E., J. F. FRANKLIN, F. J. SWANSON, P. SOLLINS, S. V GREGORY, J. D. LATTIN, N. H. ANDERSON, S. P. CLINE, N. G. ADMEN, J. R. SEDELL, G. W. LIENKAEMPER, K. CROMACK, JR., AND K. W. CUMMINS. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15:133-302.

______, S. L. GARMON, AND W K. FERRELL. 1996. Modeling historical patterns of tree utilization in the Pacific Northwest: carbon sequestration implications. Ecol. Appl. 6:641-652.

______, J. SEXTON, B. A. CALDWELL, AND S. E. CARPENTER. 1994. Fungal sporocarp mediated losses of Ca, Fe, Mg, Mn, and Zn from conifer logs in the early stages of decomposition. Can. J. For. Res. 24:1883-1893.

HAYES, J. P., S. S. CHAN, W. H. EMMINGHAM, J. C. TAPPEINER, L. D. KELLOGG, AND J. D. BAILEY. 1997. Wildlife response to thinning young forests in the Pacific Northwest. J. For. 95(8):28-33.

______, AND S. P. CROSS. 1987. Characteristics of logs used by western red-backed voles *Clethrionomys californicus* and deer mice *Peromyscus maniculatus.* Can. Field-Nat. 101:543-546.

______, E. G. HORVATH, AND P HOUNIHAN. 1995. Townsend's chipmunk populations in Douglas-fir plantations and mature forests in the Oregon Coast Range. Can. J. Zool. 73:67-73.

HENDERSON, J. A., D. H. PETER, R. D. LESHER, AND D. C. SHAW. 1989. Forested plant associations of the Olympic National Forest. U.S. For. Serv., Portland, Oreg. R6 ECOL Tech. Pap. 001-88. 502pp.

HENNON, P. E. 1995. Are heart rot fungi major factors of disturbance in gap-dynamic forests? Northwest Sci. 69:284-293.

HOLAH, J. C., M. V. WILSON, AND E. M.. HANSEN. 1993. Effects of a native forest pathogen, *Phellinus weirii,* on Douglas-fir forest composition in western Oregon. Can. J. For. Res. 23:2473-2480.

HOLMES, D. J., AND S. N. AUSTAD. 1994. Fly now, die later: life history correlates of gliding and flying mammals. J. Mammal. 75:224-226.

HUFF, M. H. 1995. Forest age structure and development following wildfires in the western Olympic Mountains, Washington. Ecol. Appl. 5:471-483.

HUNT, G. A., AND J. M. TRAPPE. 1987. Seasonal hypogeneous sporocarp production in a western Oregon Douglas-fir stand. Can. J. Bot. 65:438-445.

HUTCHINSON, G. E. 1958. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22:415-427.

_____. 1965. The ecological theatre and the evolutionary play. Yale Univ. Press, New Haven, Conn. 139pp.

______. 1978. An introduction to population ecology. Yale Univ. Press, New Haven, Conn. 260pp.

JUDAY, G. P. 1977. The location, composition, and structure of old-growth forests of the Oregon Coast Range. Ph.D. Thesis, Oregon State Univ., Corvallis. 206pp.

KIM, J., AND C. W MUELLER. 1978. Factor analysis: Statistical methods and practical issues. Sage Publ., Beverly Hills, Calif., Sage Univ. Pap. Ser. on Quant. Appl. in the Social Sci. 07-014. 88pp.

KROPP, B. R., AND J. M. TRAPPE. 1982. Ectomycor-rhizal fungi of *Tsuga heterophylla.* Mycologia 74: 479-488.

LERTZMAN, K. P, G. D. SUTHERLAND, A. INSELBERG, AND S. C. SAUNDERS. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology 77:1254-1270.

LESLIE, D. M., E. E. STARKEY, AND M. VAVRA. 1984. Elk and deer in old growth forests in western Washington. J. Wild. Manage. 48:762-765.

LONG, J. N. 1977. Trends in plant species diversity associated with development in a sere of *Pseudotsuga menziesii/Gaultheria shallon* stands. Northwest Sci. 51:119-130.

______, AND J. TURNER. 1974. Aboveground biomass of understory and overstory in an age sequence of four Douglas-fir stands. J. Appl. Ecol. 12:179-188.

LUNDQUIST, R. W, AND J. M. MARIANI. 1991. Nesting habitat and abundance of snag-dependent birds in the southern Washington Cascade Range. Pages 221-240 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coord. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-285.

LUOMA, D. L. 1991. Annual changes in seasonal production of hypogenous sporocarps in Oregon Douglas-fir forests. Pages 91-112 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coord. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-285.

MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J. 203pp.

MAGUIRE, B., JR. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. Am. Nat. 107:213-246.

MAGURRAN, A. E. 1988. Ecological diversity and its measurement. Princeton Univ. Press, Princeton, N.J. 179pp.

MANUWAL, D. A., AND M. L. HUFF. 1987. Spring and winter bird populations in a Douglas-fir forest sere. J. Wild. Manage. 51:586-595.

MARIANI, J. M. 1987. Brown creeper (*Certhia americana*) abundance patterns and habitat use in the southern Washington Cascades. M.S. Thesis, Univ. Washington, Seattle. 72pp.

MARRA, J. L., AND R. L. EDMONDS. 1994. Coarse woody debris and forest floor respiration in an old-growth coniferous forest on the Olympic Peninsula, Washington, USA. Can. J. For. Res. 24:1811-1817.

MASER, C., Z. MASER, J. W. WITT, AND G. HUNT. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. Can. J. Zool. 64:2086-2089.

______, J. M. TRAPPE, AND R. A. NUSSBAUM. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799-809.

MASER, Z., C. MASER, AND J. M. TRAPPE. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. Can. J. Zool. 63:1084-1088.

MAY, R. M. 1975. Island biogeography and the design of wildlife preserves. Nature 254:177-178.

MCARDLE, R. E., W H. MEYER, AND D. BRUCE. 1961. The yield of Douglas-fir in the Pacific Northwest. U.S. Dep. Agric. Tech. Bull. 201. 72pp.

MCINTIRE, P. W, AND A. B. CAREY. 1989. A microhistological technique for analysis of food habits of mycophagous rodents. U.S. For. Serv. Res. Pap. PNW-RP-404. 16pp.

MOHLER, C. L. 1987. COMPOSE—a program for formatting and editing data matrices. Microcomputer Power, Ithaca, N.Y. 57pp.

MOLINA, R., AND M. AMARANTHUS. 1991. Rhizosphere biology: ecological linkages between soil processes, plant growth, and community dynamics. Pages 51-85 in A. E. Harvey and L. F. Neuenschwander, compilers. Proc.: management and productivity of western montane forest soils. U.S. For. Serv. Gen. Tech. Rep. INT-280.

______, H. MASSICOTTE, AND J. M. TRAPPE. 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. Pages 357-423 in M. F. Allen, ed. Mycorrhizal functioning: an integrative plant-fungal process. Chapman-Hall, New York, N.Y.

______, AND J. M. TRAPPE. 1982. Patterns of ectomycorrhizal host specificity and potential among Northwest conifers and fungi. For. Sci. 28:423458.

NELSON, L., JR., AND F. W CLARKE. 1973. Corrections for sprung traps in catch/effort calculations of trapping results. J. Mammal. 54:295-298.

NICHOLS, S. 1977. On the interpretation of principal components analysis in ecological contexts. Vegetatio 34:191-197.

NORUSIS, M. J. 1990. SPSS/PC+ manuals. SPSS, Inc., Chicago, 111. [irregular pagination].

ODUM, E. P. 1969. The strategy of ecosystem development. Science 164:262-270.

OLIVER, C. D. 1981. Forest development in North America following major disturbances. For. Ecol. Manage. 3:153-168.

OTIS, D. L., K. P. BURNHAM, G. C. WHITE, AND D. R. ANDERSON. 1978. Statistical inference from capture data on closed animal populations. Wildl. Monogr. 62. 135pp.

PARKS, C. G., AND D. C. SHAW. 1996. Death and decay: a vital part of living canopies. Northwest Sci. 69 (spec. issue):46-53.

PECK, J. E., S. A. ACKER, AND W A. MCKEE. 1995. Autecology of mosses in coniferous forests in the central western Cascades of Oregon. Northwest Sci. 69:184-190.

PERRY, D. A., M. P. AMARANTHUS, J. G. BORCHERS, S. L. BORCHERS, AND R. E. BRAINERD. 1989. Bootstrapping in ecosystems. BioScience 39: 230-237.

PICKETT, S. T. A. 1980. Non-equilibrium coexistence of plants. Bull. Torrey Bot. Club 107:238-248.

PIELOU, E. C. 1977. Mathematical ecology. John Wiley & Sons, New York, N.Y. 385pp.

______. 1984. The interpretation of ecological data. John Wiley & Sons, New York, N.Y. 263pp.

POULSON, T. L., AND W J. PLATT. 1989. Gap light regimes influence canopy tree diversity. Ecology 70:553-555.

PRESTON, F. W 1981. Pseudo-lognormal distributions. Ecology 62:355-364.

RAPHAEL, M. G. 1991. Vertebrate species richness within and among seral stages of Douglas-fir/hardwood forest in northwestern California. Pages 415-423 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coord. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-285.

ROBERTS, M. R., AND F. S. GILLIAM. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. Ecol. Appl. 5:969-977.

ROSENBERG, D. K., AND R. G. ANTHONY. 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. Can. J. Zool. 70:161-166.

______, AND ______. 1993. Differences in Townsend's chipmunk populations between secondand old-growth forests in western Oregon. J. Wildl. Manage. 57:365-373.

RUEDIGER, W. C. 1985. Implementing a spotted owl management plan: the Gifford Pinchot National Forest. Pages 10-13 *in* R. J. Gutierrez and A. B. Carey, eds. Ecology and management of the spotted owl in the Pacific Northwest. U.S. For. Serv. Gen. Tech. Rep. PNW-185.

RUGGIERO, L. F., K. B. AUBRY, A. B. CAREY, AND M. H. HUFF, technical coordinators. 1991. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW 285. 533pp.

SCHOWALTER, T. D. 1989. Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon. Can. J. For. Res. 19:318-322.

SHARPE, F. 1996. The biologically significant attributes of forest canopies to small birds. Northwest Sci. 69 (spec. issue):86-93.

SHORT, L. L. 1979. Burdens of the Picid hole excavating habit. Wilson Bull. 91:16-28.

SILLET, S. C., AND P. N. NEITLICH. 1996. Emerging themes in epiphyte research in westside forests with special reference to cyanolichens. Northwest Sci. 69 (spec. issue):54-60.

SIMBERLOFF, D. S., AND L. G. ABELE. 1976. Island biogeographic theory and conservation practice. Science 191:285-286.

SKALSKI, J. R., AND D. S. ROBSON. 1992. Techniques for wildlife investigations: design and analysis of capture data. Academic Press, San Diego, Calif. 237pp.

SMITH, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecol. Monogr. 40: 349-374.

SMITH, J. E., R. MOLINA, AND D. A. PERRY. 1995. Occurrence of ectomycorrhizas on ericaceous and coniferous seedlings grown in soils from the Oregon Coast Range. New Phytol. 129:73-81.

SOLLINS, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Can. J. For. Res. 12:18-28.

SPIES, T. A. 1991. Plant species diversity and occurrence in young, mature, and old-growth Douglas-fir stands in western Oregon and Washington. Pages 111-122 in L. F. Ruggiero, K. B. Aubry A. B. Carey, and M. H. Huff, tech. coord. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-285.

______, AND S. P. CLINE. 1988. Coarse woody debris in forests and plantations of coastal Oregon. Pages 5-24 *in C.* Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin, tech. eds. From the forest to the sea: a story of fallen trees. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-229.

______, AND J. F. FRANKLIN. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology 70:543-545.

______ AND ______. 1991. The structure and function of young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91109 *in* L. F. Ruggiero, K. B. Aubry A. B. Carey, and M. H. Huff, tech. coord. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-285.

______, AND M. KLOPSCH. 1990. Canopy gaps in Douglas-fir forests of the Cascade mountains. Can. J. For. Res. 20:649-658.

STAPP, P 1994. Can predation explain life history strategies in mammalian gliders? J. Mammal. 75: 227-228.

______, P. J. PEKINS, AND W. W. MAUTZ. 1991. Winter energy expenditure and the distribution of southern flying squirrels. Can. J. Zool. 69:2548-2555.

STEWART, G. H. 1986. Forest development in canopy openings in old-growth *Pseudotsuga* forest of the western Cascade Range. Can. J. For. Res. 16: 558-568.

STICKEL, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. J. Mammal. 35:1-15.

STONE, J. K., M. A. SHERWOOD, AND G. C. CARROLL. 1996. Canopy microfungi: function and diversity. Northwest Sci. 69 (spec. issue):37-45.

SULLIVAN, T. P., D. S. SULLIVAN, AND C. J. KREBS. 1983. Demographic responses of a chipmunk (*Eutamias townsendii*) population with supplemental food. J. Anim. Ecol. 2:743-755.

SUTTON, D. A. 1993. *Tamias townsendii.* Mamm. Species 435. 6pp.

TABACHNIK, B. G., AND L. S. FIDELL. 1989. Using multivariate statistics. Harper Collins Publ., Inc., New York, N.Y. 746pp.

TALLMON, D., AND L. S. MILLS. 1994. Use of logs with home ranges of California redbacked voles. J. Mammal. 75:97-101.

TAPPEINER, J. A., D. HUFFMAN, D. MARSHAL, T. A. SPIES, AND J. D. BAILEY. 1997*a*. Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon. Can. J. For. Res. 27:638-648.

TAPPEINER, J. C., D. LAVENDAR, J. WALSTAD, R. O. CURTIS, AND D. S. DEBELL. 1997b. Silvicultural systems and regeneration methods: current practices and new alternatives. Pages 151-154 in K. A. Kohm and J F Franklin, eds. Creating a forestry for the 21st century. Island Press, Washington, D. C.

TERRY, R. D., AND G. V. CHILINGAR. 1955. Summary of "Concerning some additional aids in studying sedimentary formations," by M. S. Shvetsov. J. Sediment. Petrol. 25(3):229-234.

TILMAN, D. 1996. Biodiversity: population versus ecosystem stability. Ecology 77:350-363.

TORCERSON, T. R., AND E. L. BULL. 1995. Down logs as habitat for forest-dwelling ants-the primary prey of the pileated woodpecker in northeastern Oregon. Northwest Sci. 69:294-303.

WATERS, J. R., AND C. J. ZABEL. 1995. Northern flying squirrel densities in fir forests of northeastern California. J. WildI. Manage. 59:848-866.

WELLS-GOSLING, N., AND L. R. HEANEY. 1984. *Glaucomys sabrinus.* Mamm. Species 229. 8pp.

WHITCOMB, R. F., J. F. LYNCH, P. A. OPLER, AND C. S. ROBBINS. 1976. Island biogeography and conservation: strategy and limitations. Science 193: 1027-1032.

WHITE, G. C., D. R. ANDERSON, K. P. BURNHAM, AND D. L. OTIS. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Los Alamos, N.M. 235pp.

WHITMORE, T. C. 1989. Canopy gaps and two major groups of forest trees. Ecology 70:536-538.

WHITTAKER, R. H. 1975. Communities and ecosystems. Seconded. MacMillan Publ. Co., New York, N.Y. 385pp.

______, S. A. LEVIN, AND R. B. ROOT. 1973. Niche, habitat, and ecotope. Am. Nat. 109:479-482.

WILSON, T. M., AND A. B. CAREY. 1996. Observations of weasels in second-growth Douglas-fir forest in the Puget Trough, Washington. Northwest. Nat. 77:35-39.

WUNDER, L., AND A. B. CAREY. 1996. Use of forest canopies by bats. Northwest Sci. 69 (spec. issue): 79-85.

ZABEL, C. J., K. MCKELVEY, AND J. P. WARD, JR. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (Strix *occidentalis caurina*). Can. J. Zool. 73: 433-439.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J. 718pp.

Received 23 December 1996.
Accepted 3 July 1998.