Part 8

Wildlife and Forest Management in the Pacific Northwest

This page was intentionally left blank

Landscape-Scale Patterns of Forest Fragmentation and Wildlife Richness and Abundance in the Southern Washington Cascade Range

John F. Lehmkuhl, Leonard F. Ruggiero, and Patricia A. Hall

Authors

JOHN F. LEHMKUHL, is a research wildlife biologist, LEONARD F. RUGGIERO,' is a supervisory wildlife biologist and PATRICIA A. HALL[2] is a wildlife biologist, USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington 98502.

Abstract

The richness and abundance of birds, small mammals, and amphibians in the community-study stands of Douglas-fir in southern Washington were examined in relation to their surrounding landscapes. We also compared landscape patterns with the Franklin and Forman (1987) model of forest-landscape dynamics. Forest and nonforest habitats in 2025-ha landscapes were mapped around the center of old-growth study stands from current forest-type maps and aerial photographs. Map data were analyzed with geographic information systems. Vertebrate richness and abundance in study stands and their relation to landscape variables were analyzed at four scales: stand area and configuration, the habitat composition of the stand's neighborhood, the habitat composition of the entire 2025-ha landscape, and relative to indices of landscape pattern. Correlations indicated that landscape variables were weakly ($R^2 \leq 0.15$) associated with richness and abundance in young to old stands. Regression models suggested that bird richness increased from conventional edge effects associated with clearcut logging in the surrounding landscape. Bird abundance was highest in large old stands in clearcut landscapes, suggesting that logging displaced birds, which were then packed into remaining old stands. Packing also was implicated as one explanation for amphibian abundance, but elevation proved the strongest influence. Mammal richness and abundance showed little relation to landscape variables. A source-sink phenomenon between young and old forest was suggested by the higher abundance of cavity-nesting birds and the greater mammal richness in young stands surrounded by old growth. We concluded that fragmentation probably has not yet reached the critical threshold that would initiate a decline in biotic diversity, and the opportunity remains for pro-active management.

[1] Now supervisory wildlife biologist, Rocky Mountain Forest and Range Experiment Station, Laramie, Wyoming 82070.

[2] Now research assistant, School of Forestry, Northern Arizona University, Flagstaff, Arizona 86011.

Introduction

Forest fragmentation is the loss of late-successional forest habitats to timber harvest or other disturbances, and the isolation of remaining forest patches and wildlife populations. Legal mandates for public land-management agencies, and popular sentiment favoring the protection of threatened or endangered species and maintaining populations of other species has generated interest in the effects of forest fragmentation on biotic diversity (Lehmkuhl and Ruggiero, this volume; Nelson and Salwasser 1983; Nelson and others 1983; Salwasser and others 1984). Management and research on forest fragmentation have been guided by studies that describe the effects of habitat isolation in the context of island biogeographic theories of vertebrate extinction and colonization on oceanic and land-bridge islands (Diamond 1972, 1984, Faaborg 1979, MacArthur and Wilson 1967, Simberloff 1974, Terborgh 1974, Wilcox 1978) and on habitat islands in terrestrial landscapes (Brown 1971,1978, Forman and others 1976, Freemark and Merriam 1986, Galli and others 1976, Soule and others 1988, Van Dorp and Opdam 1987, Whitcomb and others 1977, Whitcomb and others 1981; also see Biological Journal of the *Linnean Society* 1986, volume 28). Extinction and colonization on habitat islands, however, may be only one of many biotic or environmental processes that determine biotic diversity in fragmented forest landscapes (Haila 1986, Haila and Jarvinen 1981, Simberloff and Abele 1982, Williamson 1981). Population viability theory (see Soule 1986 and papers in Soule and Wilcox 1980) and landscape ecology, with its emphasis on patch structure, context, and edge or boundary effects (Forman and Godron 1986, Urban and others 1987) have expanded the theoretical basis for studying the effects of fragmentation on biotic diversity (Lehmkuhl and Ruggiero, this volume).

The loss and fragmentation of old-growth Douglas-fir forest in the Pacific Northwest that results from clearcut logging exemplifies forest fragmentation. During the last 40 years, logging in Oregon and Washington has converted 80 to 90 percent of the original mature and old-growth forest into a mosaic of early and late-successional forest (Harris 1984, Meslow and others 1981, Spies and Franklin 1988). Similar cutting in coastal northern California has accomplished the same transformation in about 50 percent of the original forest there (Rosenberg and Raphael 1986). The situation varies within the region, however. Fragmentation of industrial forest is a minor issue because high harvest rates have resulted in the near-complete conversion of old forests to plantations (Spies and Franklin 1988), and the practice of cutting square-mile blocks leaves few forest fragments. Fragmentation, however, is a critical issue on public forest lands where much of the remaining pristine forest in the region is located because the more conservative harvest rates and the prevailing practice of staggered-set clearcutting of small patches have

resulted in a high degree of fragmentation in the remaining forest habitats and wildlife populations (Franklin and Forman 1987; Harris 1984; Lehmkuhl and Ruggiero, this volume).

Research on wildlife in fragmented landscapes has been conducted largely in areas of relatively simple patch dynamics such as woodlots in agricultural landscapes and mountaintop habitat islands. Managed forests differ from woodlots or mountaintop islands in several respects, however. Pattern in a managed forest is spatially dynamic. Undisturbed forest initially forms the matrix (rather than the patch, as with woodlots) until a threshold is reached where disturbed area exceeds forest area (Franklin and Forman 1987, Verner 1986). Pattern in a managed forest is also temporally dynamic. Boundaries between the forest and clearcuts initially are distinct, but with secondary succession, boundaries later become increasingly ambiguous (Rosenberg and Raphael 1986). Only a few studies in northern California (Raphael 1984, Rosenberg and Raphael 1986) have examined the effects of fragmentation in such dynamic managed-forest landscapes. The need for more research is critical.

Our research has analyzed the effects that forest fragmentation and spatial patterns of habitat availability have on wildlife diversity and abundance in western Oregon and Washington. The goals of our research were to extend the interpretation of data on the old-growth vertebrate community (this volume) beyond the stand to include the context of the landscape, to examine pattern in managed-forest landscapes and advance the theory of forest landscape dynamics, and to assess the impact of current forest management practices. Our analysis was guided by four basic questions about the richness and abundance of birds, small mammals, and amphibians. Each question addressed a succeeding, higher, landscape-scale of analysis:

- Do species richness and abundance decline with decreasing area of community-study stands as predicted by insular ecology theory? How does the length of stand edge affect richness and abundance?

- How do the proportions of habitats immediately adjacent to the community-study stands (the neighborhood context) affect species richness and abundance?

- How does the habitat composition of the entire landscape (the landscape context) affect species richness and abundance in the community-study stands?

- Can variations in species richness and abundance in the community-study stands be associated with indices of landscape pattern that convey properties of dominance, point diversity, and patch shape (fractal dimension)?

Table 1-Cross-tabulation of sample stands by age-classes assigned by Spies and Franklin (SF) (this volume) and the types assigned for this study through aerial photograph interpretation and ground-truthing

	Photo interpreted types[a]		
Ages	Young	Mature	Old-growth
Young	90 (9)	10(1)	-
Mature	20 (2)	80 (8)	
Old-growth	--	7 (2)	93 (26)

[a] SF values are percentages of types correctly typed by photo interpretation.
Number Number of stands are in parenthesis.

Table 2-Habitat types mapped in the southern Washington Cascade Range for landscape-scale studies of old-growth communities

Nonforest types	Forest types
(1) Nonvegetated	(10) Clearcut
(2) Human habitation	(11) Clearcut-forb
(3) Agriculture	(12) Clearcut-shrub
(4) Water	(13) Sapling-pole, d.b.h. 0-25 cm trees
(5) Rock	(13.1) Clearcut-sapling
(6) Wetland	(13.2) Clearcut-pole
(7) Grassland	(13.3) Natural pole
(8) Subalpine meadow	(14) Young, d.b.h. 26-51 cm trees
(9) Brush	(15) Mature, d.b.h. 52-81 cm trees
	(16) Old growth, d.b.h. (>81 cm and multistory canopy)
	(17) Hardwood-conifer
	(18) Hardwood
	(19) Riparian
	(20) Special feature

Our paper is more of a progress report than a presentation of final results. We present results for the southern Washington Cascades province; similar studies in the Oregon Cascade and Coast Range provinces are still in progress.

Methods

Mapping Procedures

Study landscapes were circular 2025-ha areas around the 45 community-study stands of old growth in the southern Washington Cascade Range. We defined landscapes by drawing a circle of radius 2.54 km from the center of the stand. Forest stands 24 ha and nonforest stands >0.4 ha initially were mapped and typed, from Forest Service Total Resource Inventory (TRI) maps, as homogeneous forest patches with similar crown diameters and canopy closure. We then updated and corrected the maps by examining color aerial photographs taken during 1982, by consulting with field personnel, and by conducting field reconnaissance. We digitized, managed, and analyzed map data with vector and raster geographic information systems (GIS) for personal computers.

Random samples of 14 percent (N = 171) of the mapped forest polygons and 6 percent (N = 76) of the nonforest polygons were ground-truthed to assess the accuracy of types determined from the TRI maps and photo-interpretation. Field crews visually truthed nonforest sites and examined forested stands with plotless sampling techniques to estimate tree frequencies, densities, and basal areas in five diameter-classes (sapling ≤ 13 cm d.b.h, pole 14-25 cm d.b.h, small sawtimber 26-51 cm d.b.h, large sawtimber 52-81 cm d.b.h, and old-growth >81 cm d.b.h with a multistory canopy). They also estimated the extent of multistory canopy, number of snags, and canopy closure. Ground-truthing determined that nonforest types concurred with 95 percent of the mapped types. Misclassification was much greater with the forested types, however. An initial comparison of mapped and ground-truthed forest types (on the basis of measured basal areas in

the five diameter-classes that were used to map the stands) showed only 68 percent concurrence between mapped types and ground-truthed types. This percentage was unacceptable, so we first reclassified mapped stands by grouping the ground-truth plots with k-means clustering (Wilkinson 1988). Cluster groups and types were initially assigned to truthed stands from photo interpretation, and then cross-tabulated to determine which mapped types characterized each cluster. This procedure formed the basis for reassigning all of the original mapped types to one of four new forest types that were defined (through cluster anlaysis) by the dominant tree diameter-classes. The new forest types were sapling-pole, young, mature, and old-growth types. The forest types assigned to the community-study stands by this method corresponded very well (90 percent) to the age-classes assigned by Spies and Franklin (this volume) on the basis of increment coring (table 1). These were the only stands in the landscapes for which age data were available. Old-growth stands showed the highest consistency with Spies and Franklin's classification, followed by young stands, and mature stands.

Map Variables

Community-Study Stand Variables

We determined the elevation, age, area, perimeter, and shoreline edge index (Patton 1975) for each community-study stand. The proportion of clearcut area, old-growth forest area, and late-successional forest (types 14, 15, 16, 17, and 19 in table 2) area were calculated for a 400-m buffer zone around the periphery of the stand. Four-hundred meters was chosen as a likely limit of edge effects (Wilcove and others 1986). Habitat patches within the study stand, such as clearcuts, were included in the buffer zone.

Landscape Variables

We characterized the composition of each 2025ha landscape by the area of clearcuts, old-growth forest, and late-successional forest. Landscape pattern was measured with several indices proposed by O'Neill and others (1988) as standard measures of landscape pattern. We measured **dominance** of habitat types as the deviation from maximum evenness according to the equation,

$$D = \log_e (n) + E \,(Pi\ \log_e\ Pi)$$

where *Pi* equals the proportion of the ith habitat type and n is the total number of types in a particular landscape. The highest possible value was slightly less than $\log_e(20) = 3$.

We measured **point diversity** not as contagion per O'Neill and others (1988), but with a raster GIS algorithm for measuring map diversity. The GIS scanned the map and determined for each 0.25-ha grid cell the total number of cells of different habitat types within a 150-m radius or "window." The mean of this frequency distribution was used as an index of point diversity, an inverse measure of contagion. High point diversity indicated a complex landscape pattern.

We calculated **the fractal dimension as two times the slope** of log(perimeter) over log(area) of all the habitat polygons in a landscape (Lovejoy 1982, O'Neill and others 1988). This index measured the complexity of polygon shapes within a range of **1** to 2. An index of 1 indicated very regular polygon shapes, such as a circle or square, whereas an index of 2 indicated highly complex polygon boundaries. A **disturbance index** was calculated as the ratio of clearcut area to late-successional forest area (O'Neill and others 1988). Indices less than one indicated relatively more forest than clearcut.

Vertebrate Data

We analyzed the common data set used for the cross-province analyses of bird (Huff and Raley, this volume), small mammal (Aubry and others, this volume), and amphibian (Bury and others, this volume a) communities. Bird occurrence was based on those individuals observed within a 50-m variable-circular-plot radius and observed on 2 or more of an average 6 sample-days per stand. Only small mammal and amphibian pitfall-data taken during autumn were analyzed. Average daily detections rather than density estimates were used to measure wildlife use. Sampling effort was the same for each stand, regardless of area, and between years.

Richness and abundance were analyzed separately for each taxon. We calculated species richness as the total number of species detected in the community-study sample-stand at each landscape's center. Total abundance in a taxon or functional group was calculated as the sum of average daily detections for all species in that group. Species richness and

abundance from 1984 and 1985 were averaged for the analysis. Associations of individual species' abundance with landscape variables were examined for those species occurring in $\geq$ 10 percent of the stands in either year.

Analytical Procedure

We visually screened the dependent variables of vertebrate species richness and total abundance for normality by examining the frequency distributions with fitted normal curves and testing with the Kolmogorov-Smimov test (Wilkinson 1988). The log of total abundance was used to approximate a normal frequency distribution. We examined the linearity of dependent-variable responses to independent map variables by fitting smoothed curves to scatterplots (Wilkinson 1988). We did not observe nonlinear responses requiring data transformations.

The univariate associations of species richness and abundance with stand, stand-buffer, landscape-composition, and landscape-pattern variables were analyzed by partial correlation holding stand elevation and age constant to separate natural from human-caused fragmentation effects as was done by Rosenberg and Raphael (1986). We used stepwise regression with an enter and removal P-value of 0.15 (Wilkinson 1988) as a multivariate exploratory technique to select a subset of variables that explained the most variation (highest R^2) in species richness or abundance. Stepwise regression is often criticized as too dependent on the correlation structure of the independent variables, but we found few strong correlations between dissimilar variables that would complicate the interpretation of stepwise regressions. Moreover, selected variables were not later removed from any of the models, so little ambiguity existed in the selection of the "best" set of variables.

The significance of stepwise regression models was tested with probabilities adjusted for stepwise regression (Wilkinson 1979 in Tabachnick and Fidel1 1983). Assumptions for regression were valid for all models: we found residuals to be normally distributed and homoscedastic from an examination of the probability plots of residuals and by plotting residuals against expected values (Wilkinson 1988). No outliers for regression models were detected from an examination of leverage statistics and standardized residuals (Sokal and Rohlf 1981). We were liberal in noting the significance of statistical relationships at $P \leq 0.10$ in tables, but generally were conservative in interpreting and discussing relationships that were significant only at $P \leq 0.05$.

Lines were fitted to data in scatterplot figures by the Lowess algorithm. Lowess smoothing is useful for examining relations between variables because it does not presuppose the shape of the function, but calculates predicted Y values from a weighted average of nearby Y values (Wilkinson 1988).

Table 3-Summary statistics for sample stand and landscape variables used in landscape-scale analysis of vertebrate community patterns in the southern Washington Cascade Range

	summary statistics			
Variable	Min	Max	Mean	Std error
Sample stand				
Area (ha)	51.0	1,689.0	488.0	49.6
Perimeter (km)	3.0	65.6	25.0	1.9
Edge index	121.0	550.0	322.0	11.8
Elevation (m)	404.0	1,218.0	762.0	31.4
Age	55.0	730.0	297.0	30.0
Stand buffer proportions				
Clearcut	**0**	0.61	0.15	0.026
Old-growth	.006	.55	.19	.020
Late-successional				
forest	.16	.94	.47	.025
Landscape composition (ha)				
Clearcut	0	.48	.13	.018
Old-growth	.03	.86	.31	.025
Late-successional				
forest	.39	.99	.77	.017
Landscape pattern indices				
Fractal	1.09	1.27	1.20	.0056
Dominance	.33	1.66	.93	.036
Point diversity	1.14	2.06	1.72	.026
Disturbance	0	1.22	.20	,035

Species-area curves, however, were fitted with straight lines to conform to the theoretical distribution (MacArthur and Wilson 1967, Wilcox 1980).

Results

Landscape Characteristics

Community-study stands-Community-study stand-areas ranged from 51 ha to 1690 ha, with a mean of 488 ha (table 3). Old-growth stands were generally larger (mean of 546 ha) than young (mean of 486 ha) or mature (mean of 352 ha) stands (table 3), but the differences were not significant by analysis of variance ($P \leq 0.05$). The mean proportion of clearcut in stand buffers was 15 percent, ranging from 0 to 60 percent. Young and mature sample stands averaged no more than 9 percent clearcut area in their buffers, but old-growth stands averaged 20 percent clearcut.

Composition of Landscapes

Clearcut area ranged from 0 to 48 percent of the total landscape area (table 3), but most landscapes had relatively small amounts of clcarcut area (<15 percent) (fig, 1A). Old-growth area was more normally distributed (fig. lB), with an aver-

age of 31 percent old-growth (table 3). Late-successional forest area was generally less variable (fig. 1C) than old-growth with most landscapes comprised of 70 to 90 percent late-successional forest. Late-successional forest and clearcut areas showed a strong reciprocal relationship (fig. 2), which conforms to Franklin and Forman's (1987) checkerboard model of forest-landscape dynamics under a clearcutting regime. The relation indicated a 50-percent cutover threshold where dominance of the landscape matrix switches from forest to clearcut habitats. Most landscapes remained well under this 50 percent threshold, where forest-clearcut edge reaches an apex. The relation was much different with respect to old growth. The regression of old-growth area against the clearcut proportion was not significantly different than zero (fig. 2). Residual variation around the regression line was consistently high, within the observed range of 0 to 50 percent clearcut.

Patch Sizes

Over 90 percent of the clearcut patches were <30 ha, with a few very large cuts on private lands of up to 150 ha. Old-growth patch size was extremely skewed toward small stands (fig. 3). Despite their greater number, the cumulative area of patches $\leq$ 10 ha accounted for only 4 percent of the summed old-growth area for all landscapes, and patches $\leq$ 20 ha totaled about 10 percent of the old-growth area. Most old-growth patches were $\leq$ 50 ha, but the maximum patch-size was 1741 ha. Late-successional forest generally occurred as larger patches (fig. 3). Late-successional patches $\leq$ 10 ha accounted for only 0.5 percent of the summed area for all landscapes, and patches $\leq$ 20 ha totaled 0.8 percent.

As the proportion of clearcut area in a landscape increased, clearcut patch-size initially increased slightly, but then remained nearly constant (fig. 4A). Old-growth patch-size increased rapidly up to about 10 percent cutover, then decreased steadily to the 50 percent clearcut point, the maximum observed in our landscapes (fig. 4B). The linear trend was not significant by regression ($P = 0.33$). Late-successional forest patch-sizes showed a small initial increase up to about 8 percent cutover, then a steady decline in patch size as with old growth (fig. 4C). The linear trend was significant by regression ($P = 0.009$), but with low explained variation ($R^2 = 0.14$).

Pattern Indices

Patch shapes were not complex as measured by the fractal index (table 3). Within the possible range of 1 to 2, our maximum index value was 1.27. Fractal dimension showed a strong negative correlation ($r = -0.72$) with clearcut area: the complexity of patch boundaries decreased as the number of regular-shaped clearcuts increased. Dominance indices suggested low habitat dominance in most landscapes, with a mean of 0.93 and a maximum value little more than half the
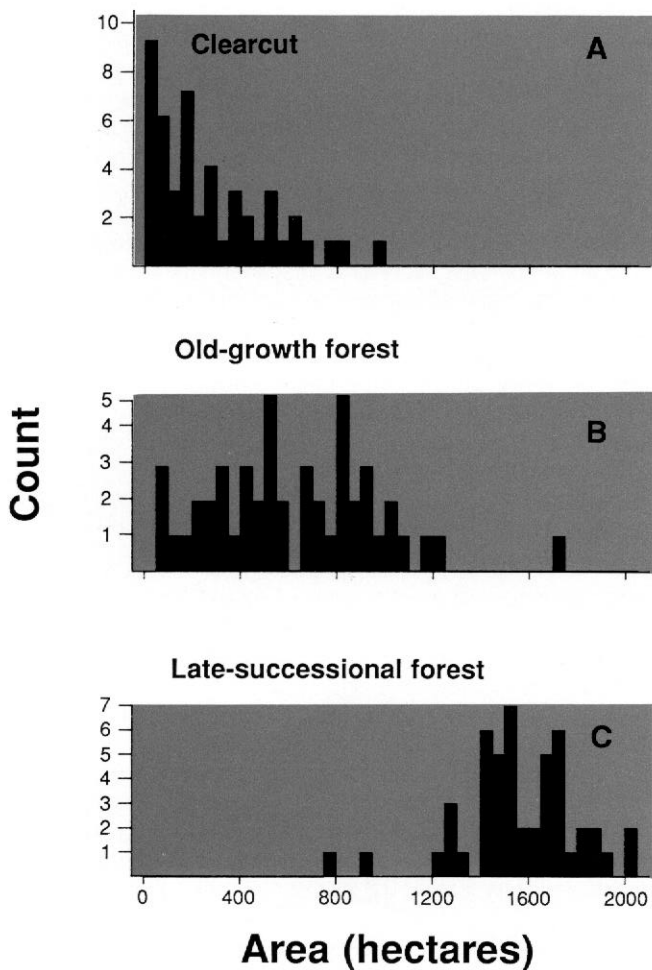
Figure 1—Frequency distributions of mean landscape clearcut, old-growth forest, and late-successional forest area in 48 landscapes around sample stands in the southern Washington Cascade Range.
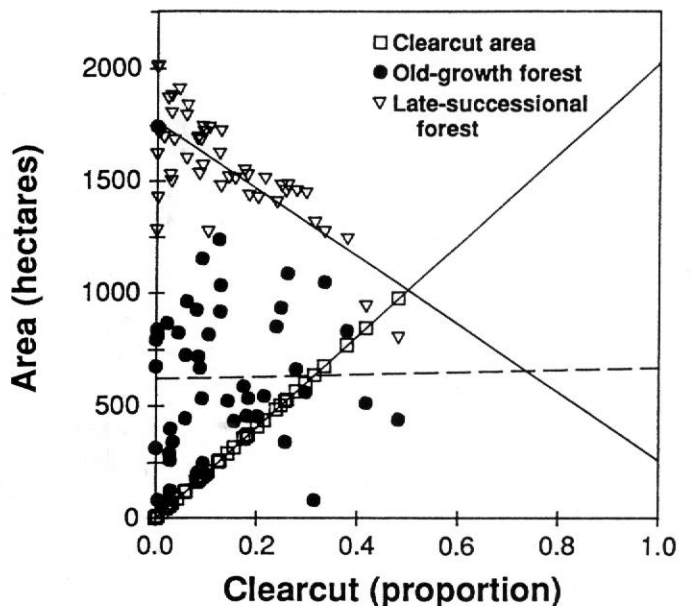

Figure 2—Relation of clearcut, old-growth forest, and late-successional forest area to the proportion of the landscape clearcut. Solid lines are linear regression lines for clearcut and late-successional forest data; dotted line is linear regression line for old-growth data.

theoretical maximum of 3 (table 3). Landscapes showed little habitat point diversity at the scale of 12 ha patches: the maximum possible index was 20 habitat-type transitions, whereas our landscapes had a maximum of 2.1 transitions and an average of 1.7 transitions in a 12-ha area. The disturbance index, the ratio of clearcut to late-successional forest, showed a relatively low amount of disturbance (table 3). Clearcuts in the majority of the landscapes were less than 40 percent the area of late-successional forest, with a mean of 20 percent.

Landscape-Vertebrate Relationships

Species Richness

All sample stands—Partial correlations, holding stand elevation and age constant, revealed few significant or strong relations between species richness and landscape variables

(table 4). Correlations were mostly weak ($R^2 \leq 0.37$), indicating ≤ 14 percent shared variation. The strongest relations were with bird and amphibian species richness. Bird richness was positively associated with the proportion of clearcut area within the buffer, and negatively correlated with the amount of late-successional forest in the buffer. Amphibian richness was most strongly correlated with the dominance index, indicating association with relatively homogeneous landscapes. Small mammal richness was not even weakly associated with any landscape variable.

We graphically examined four questions about the relation of species richness to landscape variables:

- Does richness increase with the size of the sample stand?

- Is richness in young stands greater when surrounded by old growth (may richness in young stands be "subsidized" by adjacent old forest)?

- Does richness increase from local edge effects in stands that have a clearcut buffer area?

- Does richness increase from landscape edge effects in stands located in clearcut landscapes?

Island biogeographic theory predicts a positive relation between species richness and stand area, but species-area curves revealed no significant relation between stand area and richness (fig. 5). Richness in young stands increased, as hypothesized, with the area of old growth in the neighbor-
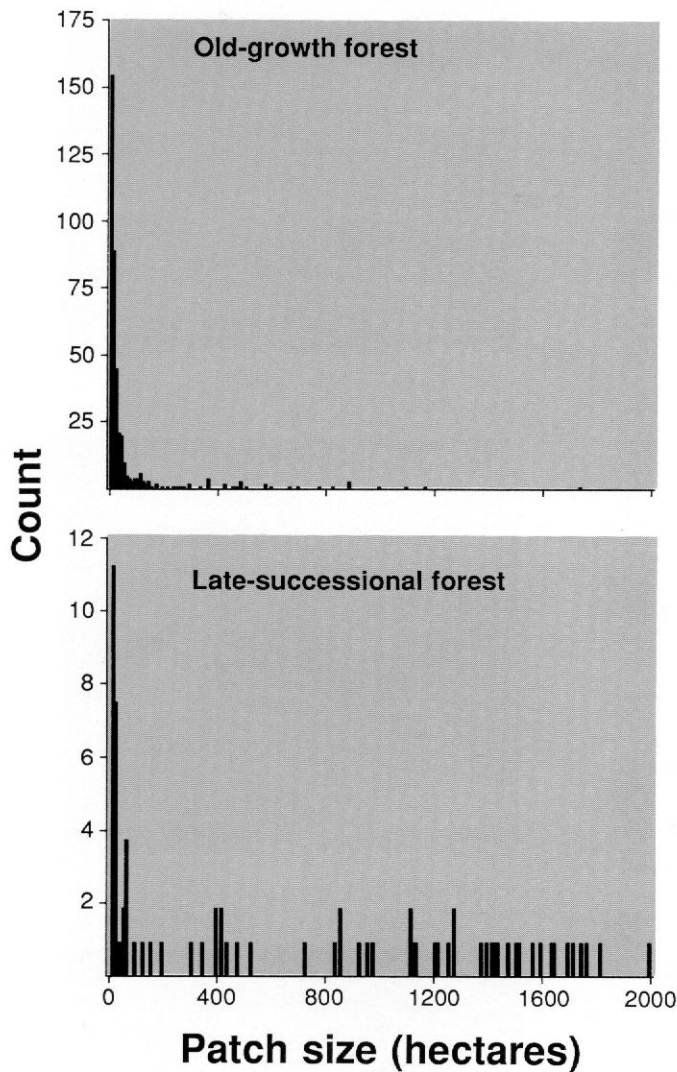
Figure 3—Patch-size distributions for old-growth and late-successional forest. Bars represent 10-ha classes.

hood, in a significant linear relation ($P = 0.085$; $R^2 = 0.36$) only for small mammals (fig. 6B). An opposite relation was evident for birds and amphibians (fig. 6A, 6C). A linear regression model for birds was significant ($P = 0.006$), but weak ($R^2 = 0.16$). The line fitted to the amphibian data indicated a slight negative relation up to a threshold of 30 percent old growth, beyond which richness declined rapidly. A linear model was not significant.

Clearcut area in the buffer of sample stands of all ages was positively but weakly associated with bird richness (fig. 7A). The linear regression model was significant ($P = 0.006$), but with low explained variation ($R^2 = 0.162$). A similar relation was indicated for bird richness and the total area of
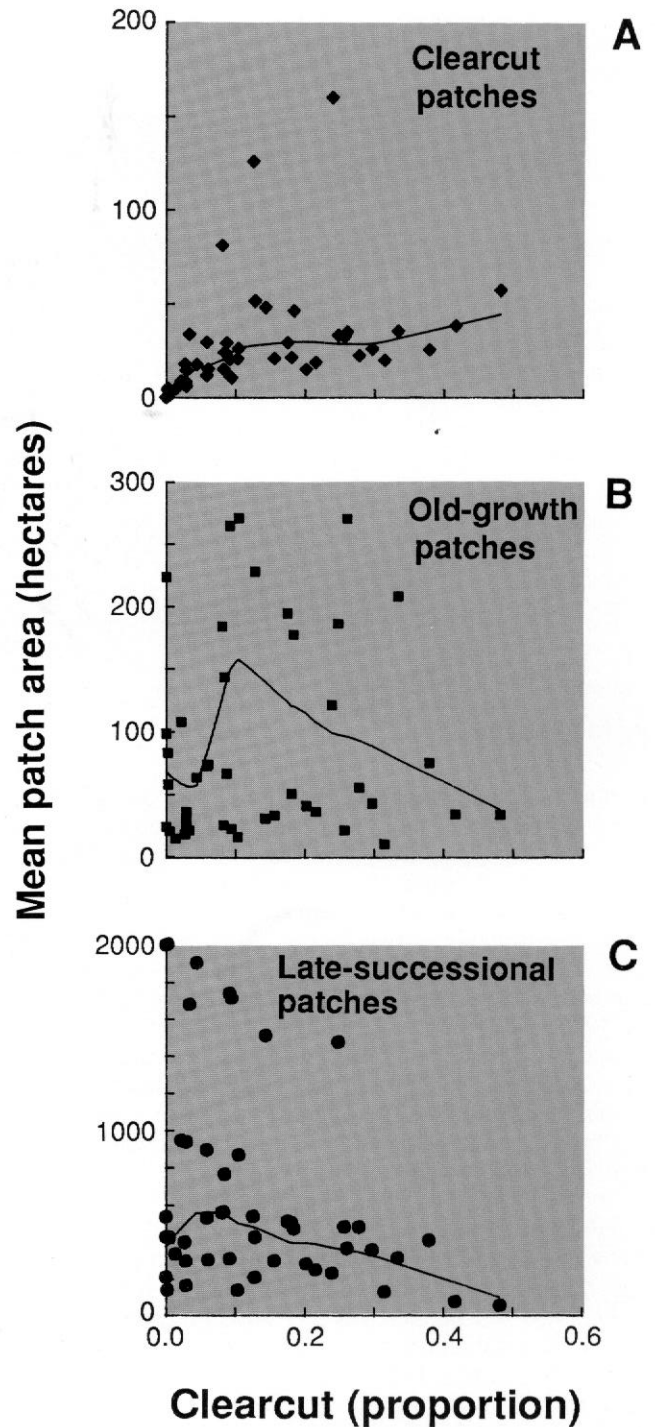

Figure 4—Relation of mean area of clearcut, old-growth, and late-successional forest patches to proportion of the landscape clearcut. Old-growth patch size was truncated at 300 ha, eliminating one outlying patch of 600 ha.

Table 4—Partial correlations (stand age and elevation constant) of bird, small mammal, and amphibian species richness and abundance with landscape variables

	Species richness			Abundance		
	Birds	Small mammals	Amphibians	Birds	Small mammals	Amphibians
Sample stand						
Area	0.05	−0.05	0.22*	0.07	0.04	0.07
Perimeter	.12	.00	.27*	.18	.01	.08
Edge index	.19	.08	.29*	.15	−.01	.00
Stand buffer composition						
Clearcut	.37**	−.17	.11	.13	.07	.24
Old-growth	−.11	.00	−.09	−.16	.11	−.29*
Late-successional forest	−.36**	.24	−.10	−.09	−.02	.05
Landscape composition						
Clearcut	.21	−.23	−.22	.15	−.24	.06
Old-growth	−.16	−.07	.13	−.31**	.04	−.14
Late-successional forest	−.14	.20	.23	−.11	.24	.02
Landscape pattern indices						
Fractal	−.12	.23	.05	−.01	−.06	−.28*
Dominance	.01	.02	.47***	−.07	.32**	.28*
Point diversity	.08	.00	−.23	.15	−.18	−.02
Disturbance	.17	−.22	−.16	.08	−.18	.06

* $P \leq 0.10$; ** $P \leq 0.05$; *** $P \leq 0.01$; **** $P \leq 0.001$.

clearcut in the landscape (fig. 8A), but it was not significant ($P = 0.107$). Both relations showed little change in bird richness up to about 18 percent clearcut, then a rising trend in richness with increasing clearcut area. The similarity of responses to clearcut area at both scales may be due to the moderate correlation between clearcut in the buffer and landscape ($R^2 = 0.78$). No associations between small mammal richness and clearcuts in the buffer (fig. 7B) or landscape (fig. 8B) were observed. Amphibian richness initially decreased as clearcut area in the buffer (fig. 7C) and landscape (fig. 8C) approached 15 percent, but beyond that percentage, richness increased steadily. The relations were weak, however, as suggested by the large residual variation. Linear regression models were not significant.

Stepwise regression models including stand age and elevation were consistent with the results of partial correlation and were significant for birds and amphibians (table 5). Bird richness was best predicted as a positive function of stand area and clearcut area in the buffer zone, and a negative function of elevation and old-growth area in the landscape. These variables accounted for 37 percent (R^2) of the variation in bird richness. The model for amphibian richness was most-strongly influenced by a negative elevation gradient, but positively influenced by habitat dominance (table 5). The amphibian model was the strongest of the three taxa ($R^2 = 0.56$).
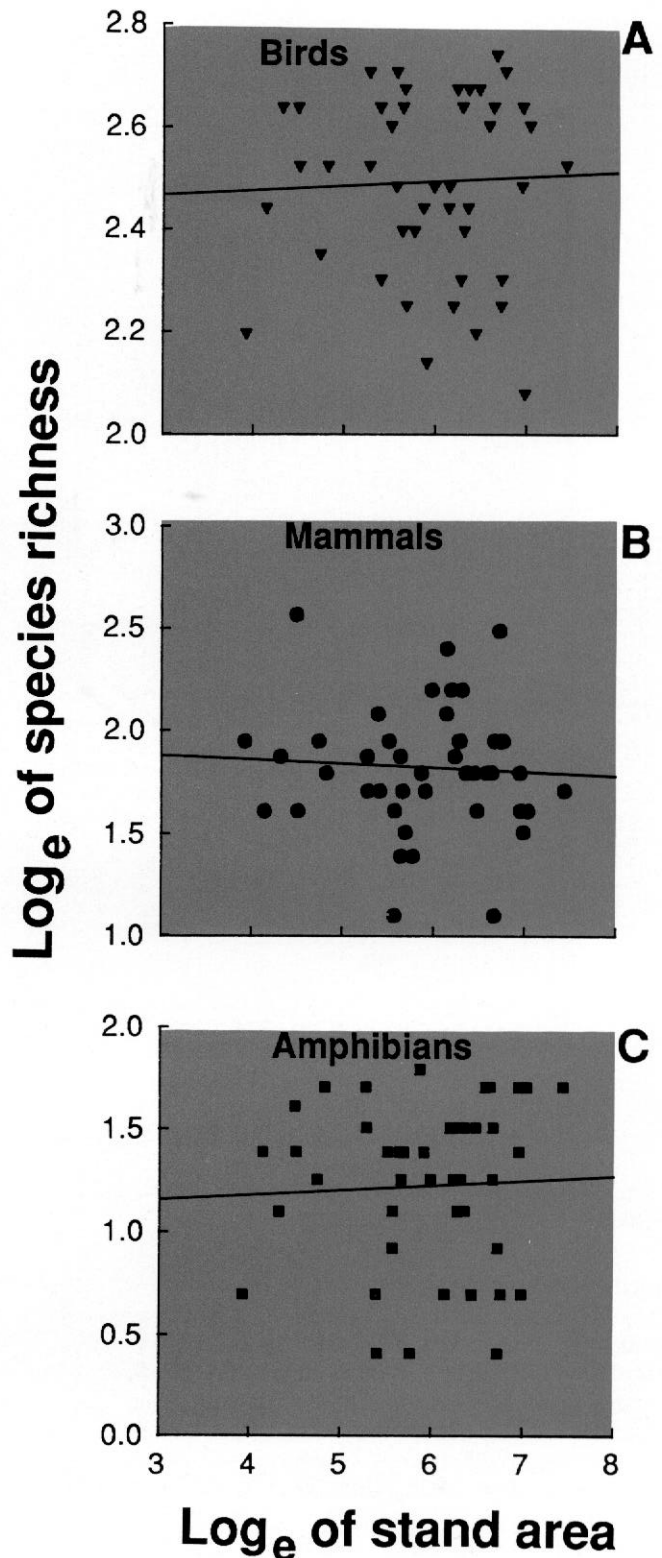

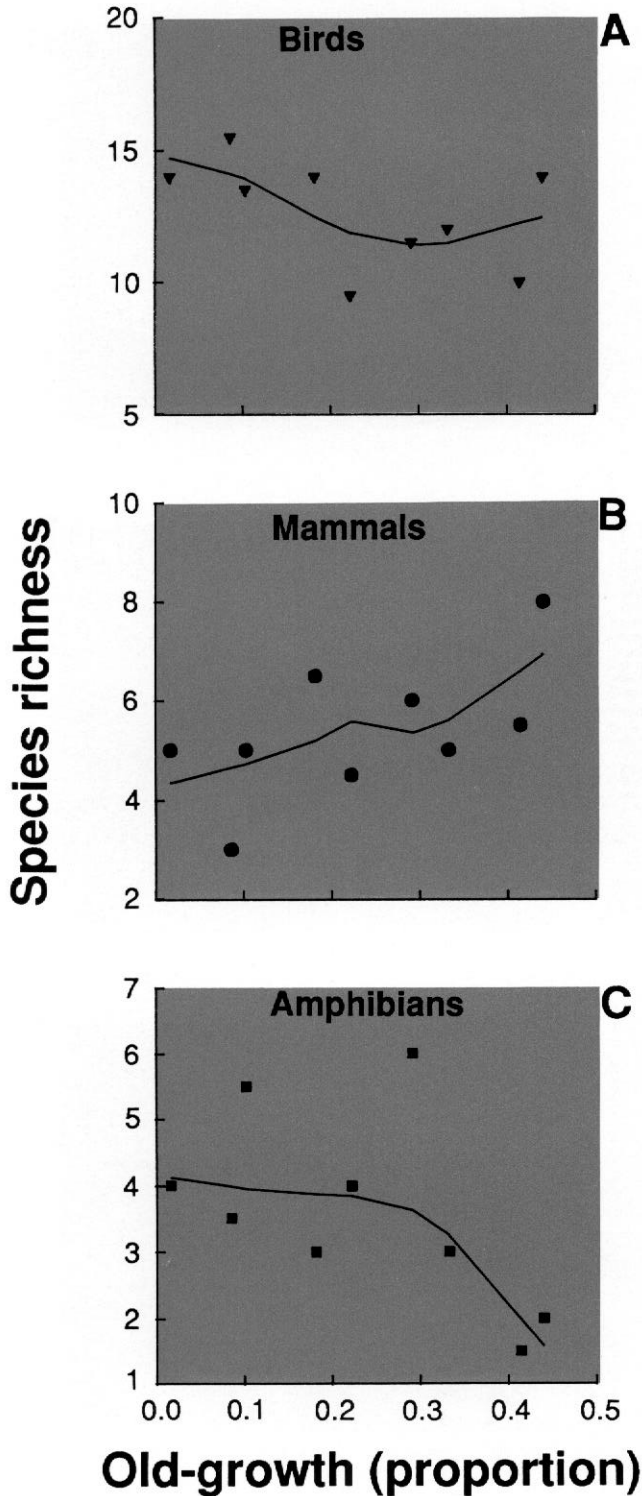Figure 5—Species-area curves for birds, small mammals, and amphibians.

Figure 6—Relation of species richness of birds, small mammals, and amphibians sampled in young stands only to the proportion of old-growth forest in a 400-m buffer zone around the sampled stand.

Old-growth sample stands—The associations between landscape variables and bird richness in the sample stands classified as old growth were consistent with stepwise regression models for all stands (table 6). Bird richness increased with landscape disturbance at neighborhood and landscape scales as indicated by a positive correlation with clearcut area in buffer zones and landscapes, and a negative correlation with fractal dimension. Bird richness in old-growth stands also showed a negative relation to elevation. In contrast to previous analyses with data from all stands, small mammal richness in old-growth stands was associated with complex patch shapes (fractal dimension). As with the regression model for all stands, amphibian richness in old-growth stands had a strong negative correlation with elevation.

Species Abundance

All sample stands—Vertebrate abundance was weakly associated through partial correlation with few landscape variables (table 4). As with bird richness in the regression model, bird abundance was negatively associated with old growth in the landscape. Small mammal abundance was correlated with habitat dominance. Amphibian abundance was not significantly correlated with any variable.

Stepwise regression suggested a model of bird abundance increasing with age and size of stands, with old growth in the immediate buffer, and with increasing clearcut area and decreasing old-growth area in the landscape (table 5). Stepwise regression was not able to select a statistically significant model of small mammal abundance. The amphibian-abundance model indicated a strong positive influence of habitat dominance, and negative influences of complex patch shape (fractal index), old-growth area in the landscape, and elevation.

Old-growth sample stands—Spearman correlations of bird abundance in old-growth sample stands contradicted the regression model for all stand ages by suggesting a negative relation with stand area (table 6). The negative associations of bird abundance with old-growth area in the landscape and with habitat dominance, however, were consistent with the regression model. Small mammal abundance in old-growth stands surprisingly showed some relatively strong correlations not evident in previous statistics: abundance was negatively associated with clearcut area in the landscape (and its related disturbance index), and was positively associated with habitat dominance. Amphibian abundance in old stands declined with elevation as in the regression model, but also with complex patch shapes in the landscape (fractal index); abundance also increased with clearcut area in the stand buffer.
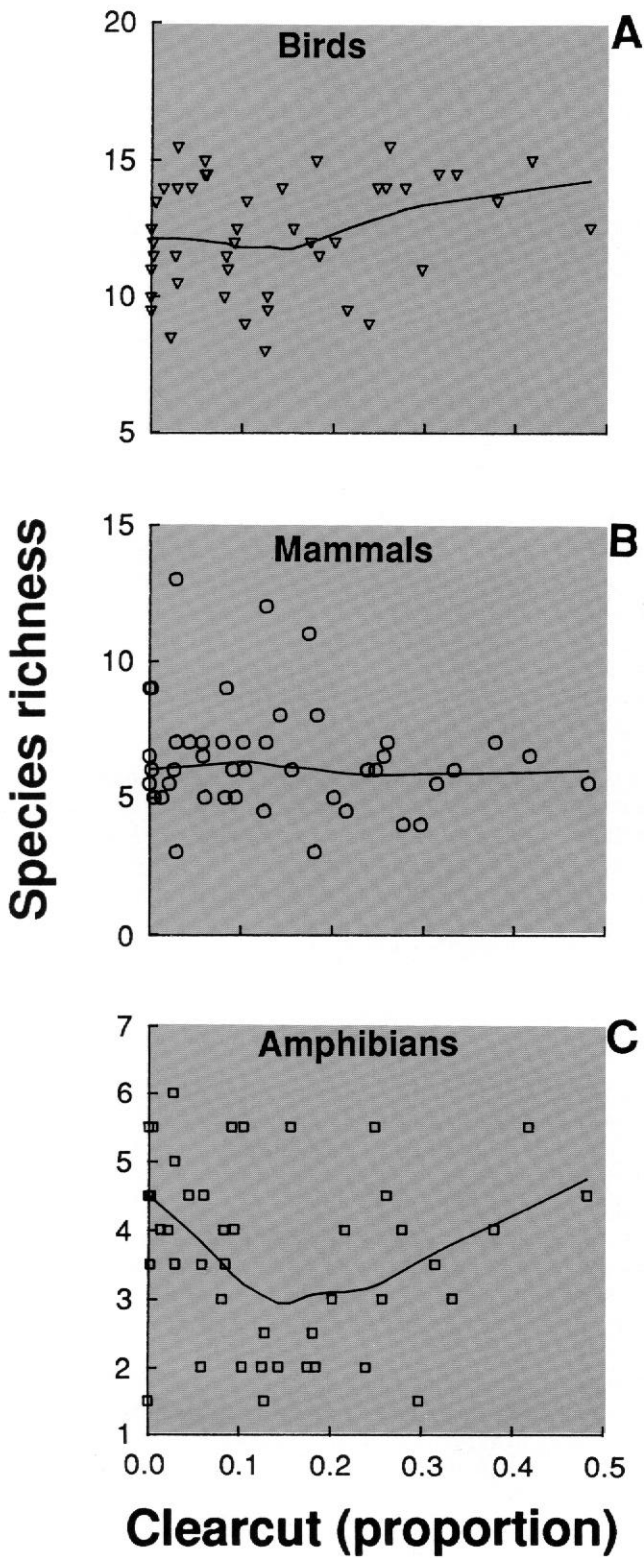
Figure 7—Relation of species richness of birds, small mammals, and amphibians to the proportion of clearcut in a 400-m buffer zone around the sampled stand.
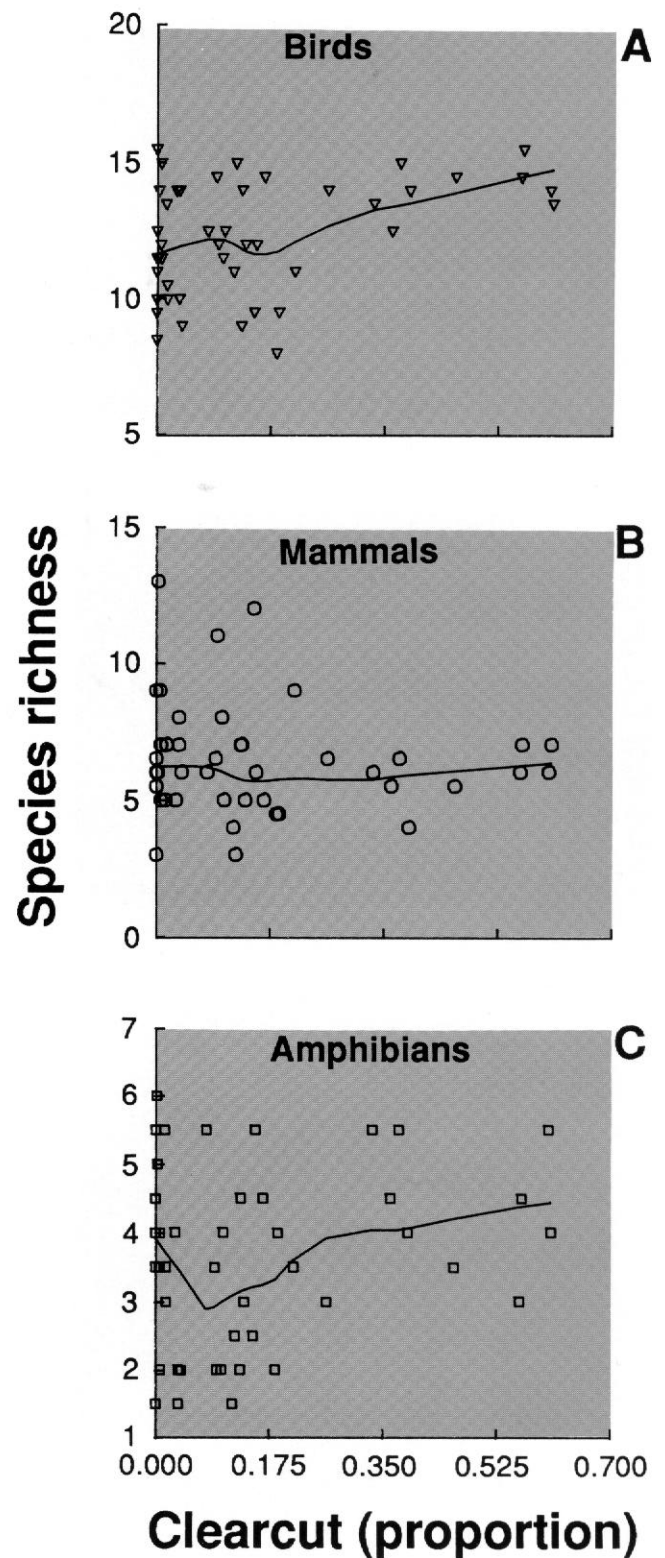
Figure 8—Relation of species richness of birds, small mammals, and amphibians to the proportion of clearcut in the entire 2025-ha landscape.