In: A.J. Hansen and F. di Castri (eds). 1992.
Landscape Boundaries: consequences for biotic diversity
and ecological Flows. Springer-Verlag. New York.

8. Avian Community Dynamics: The Interplay of Landscape Trajectories and Species Life Histories

Andrew Hansen, Dean L. Urban, and Barbara Marks

Introduction

Human activities are a primary determinant of landscape patterning over much of the globe (Forman and Godron 1986). Land-use practices alter the distribution of patch types, converting, for example, natural habitats to agricultural and urban lands during periods of human expansion and allowing natural habitats to reemerge in periods of human decline (Lepart and Debussche, chapter 4, this volume). Humans also rescale landscapes, often by homogenizing spatial patterns, by increasing the density of sharp edges and boundaries, and by altering the spatial and temporal domains of disturbances (Franklin and Forman 1987, Urban et al. 1987).

Such changes in landscape patterns sometimes have substantial effects on plant and animal communities. To the extent that some habitat types, such as late-successional forest, wetlands, or riparian habitats, are lost in anthropogenic landscapes, so are the species and guilds dependent upon them (Wilson 1988). At the same time, organisms able to capitalize on human habitats are apt to expand and may become pests (Mooney and Drake 1986, di Castri et al. 1990). The reduction of structural heterogeneity within landscape patches further reduces the abundance of native species. In the Pacific Northwest (PNW) of the United States, for example, over 150 species of vertebrates are associated with standing and fallen dead

trees (Brown 1985), microhabitat features that are generally reduced or lost in managed forest (Hansen et al. 1991).

A plethora of studies over the past two decades has revealed the consequences to species diversity of rescaling and repatterning landscapes. The application of island theory (MacArthur and Wilson 1967) to habitat islands focused attention on community response to habitat size (Forman et al. 1976, Galli et al. 1976, Ambuel and Temple 1983, Freemark and Merriam 1986, Robbins et al. 1989) and to isolation (MacClintock et al. 1977, Lynch and Whitcomb 1978, Urban et al. 1988). Several other landscape metrics have been found to explain variation in patterns of biodiversity, including boundary characteristics (Kroodsma 1982, Gates and Gysel 1978, Brittingham and Temple 1983, Wilcove 1985, Harris 1988), patch juxtapositioning (Harris 1984), and patch diversity (Roth 1976).

Forested landscapes undergoing fragmentation by nonforest lands have received particular attention. Initial forest clearing is often dispersed over a landscape, creating openings with sharp edges within the forest matrix (Ripple et al. 1991). Continued clearing reduces total forest area, decreases the size distribution of remaining forest patches, and increases the distance between forest patches (Urban et al. 1988). Such changes in forest patterning may elicit a suite of ecological responses. Microclimates may become more extreme in isolated forest patches (Franklin and Forman 1987). Vegetation structure and composition may differentiate between forest edge and interior due to differences in microclimate, disturbance rates, seed dispersal, and herbivory (Ranney et al. 1981; Forman and Moore, Chapter 11, this volume; Küppers, Chapter 14, this volume). These events can cause substantial change in ecological processes, such as decomposition (Klein 1989), nutrient cycling (Ryszkowski, Chapter 13, this volume), pollination (Jennersten 1988), and predation (Gates and Gysel 1978, Wilcove 1985, Small and Hunter 1988). Perhaps best known are the effects of forest fragmentation on forest birds and mammals: Studies primarily from the eastern deciduous forest of North America indicate that species associated with forest interiors generally decline, while those specializing on forest edges increase in abundance (Whitcomb et al. 1981; Noss 1983; Terborgh 1989; Merriam and Wegner, Chapter 7, this volume). Fragmentation is the prevalent trajectory of landscape change in several human-dominated forest regions of the world, including parts of western Europe, eastern North America, and Latin America. The negative consequences of fragmentation have been a rallying point for ecologists and conservationists for the past decade, with the concepts developed in the few regions that are well studied being exported to others where local data are often lacking.

Other than forest fragmentation, however, common trajectories of landscape change in human-dominated systems remain little recognized or studied. A subtly different form of landscape change from forest fragmentation by nonforest is the conversion of natural forests to managed plantations or tree farms. This is common in the northwestern United States, western Canada, and parts of Latin America. Patterns of species diversity in forests being converted to plantations are likely to differ from those in forests being fragmented by agricultural lands. Sharp forest–nonforest edges are a transient phenomenon in managed forest landscapes due to forest regrowth. Also, the regenerating plantations cannot be modeled as nonhabitat for many species, but rather as habitat of variable quality and permeability to movements. Managed forests also often differ from natural forests in having less variable patch sizes, fewer late-successional stands, and less structural heterogeneity within stands (Hansen et al. 1991). Consequently, species diversity is likely to be lower in managed forests than in natural forests.

Another landscape trajectory, common in regions with a long history of human settlement, is forest resurgence following the abandonment of agricultural lands. Driven by changing social and economic factors (di Castri et al. 1988), this phenomenon, termed *deprise agricole* by the French, has occurred over portions of southern Europe (Lepart and Debussche, Chapter 4, this volume) and the southeastern United States (Turner 1987). Forest expansion in such areas is substantially altering habitat type, grain size, boundary characteristics, and species diversity (Lepart and Debussche, Chapter 4, this volume).

In this chapter, we emphasize that forest fragmentation and its associated consequences are a subset of a more general phenomenon that drives patterns of biodiversity. Two key components of the phenomenon are the local trajectory of landscape change and the life-history attributes of the species in the local community. These components are apt to vary between geographical locations, and, thus, caution is needed when extrapolating the patterns observed in one system to other systems.

Here, we use a simulation model to explore animal community response to the aforementioned three landscape trajectories: (1) forest fragmentation, (2) conversion of natural forest to managed forest, and (3) *deprise agricole*. The simulated landscapes are classified in terms of suitability for a hypothetical animal community that includes all combinations of three life-history traits. Actual bird communities are apt to include only a subset of these strategies, thus, we also examine landscape suitability for the PNW avifauna. Lastly, we summarize the results of a related study (Hansen and Urban, in press), on the effects of species life histories on community response to landscape change. That study suggested that communities in distinct geographical locations are likely to have differing life-history structures and, consequently, to have different responses to a specific landscape change.

The implication of this work is that effective conservation strategies need be based on both the characteristics of the local communities and the local landscape patterns. Knowledge of local pattern and process can allow land managers to design landscapes that optimize biodiversity and other resources (Hunter 1990, Westman 1990, Hansen et al. 1991).

Modeling Approach

Simulating bird community dynamics under these landscape trajectories requires the ability to model landscape change and to predict the responses of individual bird species to these changes. We chose to model landscapes with the Landscape Spatial Pattern Analysis (LSPA) program, a simple geometric model developed by Franklin and Forman (1987) and modified substantially by Li (1989). LSPA simulates changes in a gridded landscape of variable grain size and extent. Designed to emulate the effects of timber harvest, the model modifies the state of the landscape at each time step, according to a user-specified harvest regime, which involves cutting-unit size, spatial distribution of cutting units, and harvest rate. Cells selected for harvest can be either converted permanently to nonforest or aged at each time step, to simulate forest regeneration.

This modeling approach was selected because it simulates the key patterns that distinguish the three landscape trajectories of interest. Patch-type dynamics are modeled as a Markov process. A disadvantage of this approach is that tree demography and other ecological processes are not modeled explicitly, as is the case, for example, with gap models (Shugart 1984). Thus, within-stand heterogeneity and variation in stand performance are not directly considered. The advantage of the approach, however, is that the computational simplicity allows rapid simulation of landscape-scale patch geometry. Patch size, shape, and juxtapositioning can be simulated as a function of the disturbance regime.

Various approaches have been used to associate animal species with specific landscape elements. Efforts to link the demographies of several species in a community to landscape pattern have generally been limited by lack of data (Urban et al. 1988). A popular alternative has been to model the abundance of habitats suitable for a species as a surrogate for the demography of the species (e.g., Urban and Smith 1989). Habitat suitability indices have been developed, using either nonquantitative data on habitat use or detailed multivariate characterizations of microhabitat use (see Verner et al. 1986 for a review). Neither approach, however, has commonly been used to account for landscape-scale effects. We chose to link birds with landscape elements, based on various bird life-history attributes, because (1) life-history data are generally available for bird species, so nearly all members of a community can be considered, and (2) life-history traits account for a range of spatial scales, including microhabitat, stand, and landscape levels, thus allowing us to compare bird response to different landscape dynamics.

The three landscape trajectories simulated are shown in Figure 8.1.

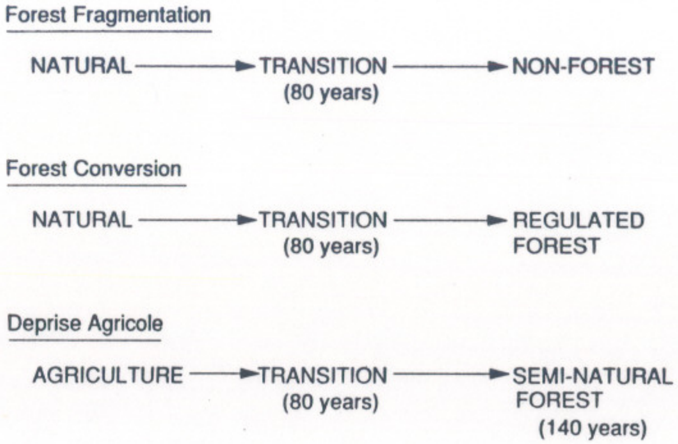


Figure 8.1. The three trajectories of landscape change simulated in the study.

Forest fragmentation was modeled as the deforestation of a "natural" landscape over an 80-year period, using a checkerboard cutting design. Cutting units underwent forest regeneration in the run simulating conversion of natural forest to managed plantations. *Deprise agricole* was simulated by allowing patches in a nonforest landscape to gradually undergo forest regeneration for an 80-year period and allowing forest development to continue for an additional 140 years.

The abundance of suitable habitats for hypothetical life-history guilds was assessed at 10-year intervals under each landscape scenario. The hypothetical guilds were delineated by taking all logical combinations of three important life-history traits (seral stage association, microhabitat association, response to edge). The idea here was to identify how a generic community would respond under each landscape trajectory. Real-world communities are not likely to include a balanced set of life history guilds, thus we also determined habitat abundance for the species represented in an avifauna from the Pacific Northwest United States.

Methods

LSPA Simulations

We used version 1x of LSPA (Li 1989) and modified it, as necessary, for our applications. The dimensions of the simulated landscapes were 27 × 27 cells, scaled such that each cell covered 2.56 hectares (ha), and total area was 1866 ha. Cutting units were placed using the checkerboard distribution option, which maximally disperses the cuts. This distribution mimics the pattern commonly used on federal forest lands in the PNW (Franklin and Forman 1987). Cutting units were 23 ha (9 cells) in area and square in shape. Harvest rate was 12.49% of the total area per time step. The *time step* was conceptualized as 10 years, and thus the rate simulates an 80-year harvest rotation. Forest patches were considered to age 10 years at each time step; output patches were classified into four age classes: open canopy (0–20 yr), young (30–70 yr), mature (80–190 yr), old growth (≥ 200 yrs). Timber harvest was assumed to remove all biomass, and thus, plantations were considered to be devoid of the structural elements (large trees, snags, fallen trees) typical of all age classes of natural forest in the PNW (Hansen et al. 1991). For this reason, patches generated by wildfire were distinguished from those created by timber harvest.

Both the forest fragmentation and the forest conversion runs were initiated by inputting a map generated under a natural fire regime (see following section). All natural patches were eligible for clearing in the forest fragmentation run; only those older than 60 years were eligible for harvest in the forest conversion run. The *deprise agricole* projection started with a nonforested map. Land abandonment was simulated as occurring in 23-ha patches with a checkerboard distribution at a rate of 12.49% per decade. Forest development was considered to occur on abandoned patches. The total simulated time period was 220 years. No disturbance was included in this run, reflecting the common practice of suppressing natural disturbance in many rural areas. Natural microhabitats were assumed to appear in stands at 110 years of age.

Fire Model

Wildfire was the major type of disturbance in many presettlement landscapes in the PNW (Franklin 1988), so we developed a model to simulate landscape pattern under a natural fire regime. Fire patterns vary across the region. We used the fire regime described for the Cook–Quentin watershed in the west slope of the Cascade Mountains in central Oregon (Morrison and Swanson 1990) because it was readily available.

The fire model was initialized with a landscape that was covered with 200-year-old forest. The proportion of landscape to be burned per time step was determined by generating a random normal deviate (Press et al. 1986) with a mean of 8.85% ($SD = 13.35$), the proportion of area burned per decade by high-severity fires in the Cook-Quentin drainage during 1700–1900. Morrison and Swanson (1990) defined high-severity burns as those killing more than 70% of canopy trees. A burn was initiated in a randomly selected cell if the cell had not been previously selected in the time step and if it was in a patch more than 20 years old. The fire was spread to neighboring cells, using the random walk algorithm of Li (1989). The maximum size of the burned patch was determined by generating a random deviate under a negative exponential distribution (Press et al.

CLASSIFICATION CRITERIA

Patch Type:	Microhabitat:	Edge:
OC - open canopy (0-20 yrs)	N - natural (uncut)	I - interior (>160 m from OC/CC edge)
CC - closed canopy (30-190 yrs)	G - generalist (all)	E - edge (OC/CC edge)
OG - old growth (>190 yrs)		G - generalist (all)
G - generalist (all)		

GUILDS

OC-N-I	OC-G-I	CC-N-I	CC-G-I	OG-N-I	OG-G-E
OC-N-E	OC-G-E	CC-N-E	CC-G-E	OG-N-E	G-N-G
OC-N-G	OC-G-G	CC-N-G	CC-G-G	OG-N-G	G-G-G

Figure 8.2. Hypothetical bird guilds and the life-history criteria used to define them.

1986), with a mean of 15.85 ha, the average size of high-severity burns in the Cook—Quentin drainage. This value was determined by digitizing Figure 14 from Morrison and Swanson (1990). The model continued to burn patches until the total allowable area was burned. The simulation was run for 220 years, in order to generate a steady-state landscape pattern. The map for year 220 was then used as input for the forest fragmentation and forest conversion runs.

Habitat Classification

A habitat subroutine was added to LSPA that determined the proportion of a landscape suitable for each guild or species and calculated various indices of community diversity. The diversity indices reported here are species richness (total number of species) and Hill's N2 (a measure of the number of abundant species) (Ludwig and Reynolds 1988).

Criteria for establishing the hypothetical life-history guilds included seral stage association, microhabitat association, and response to edge (Fig. 8.2). The 18 hypothetical guilds include all combinations of the life-history categories that make sense ecologically. Habitats were classified as suitable or unsuitable for a guild, based on whether they met the criteria defining the guild.

The habitat suitability criteria for PNW bird species included the aforementioned plus a minimum-area requirement, based on the territory or home range size of the species (Table 8.1). The PNW bird species were from among those identified by Brown (1985) as having primary habitats in

Table 8.1. Bird Species and Life-History Traits Used to Model Community Response to Landscape Dynamics[a]

Species	Seral Stage	Micro-habitat	Response to Edge[b]	Minimum Territory Size (ha)
Blue grouse *Dendragapus obscurus*	G	G	G	0
Mountain quail *Oreortyx pictus*	OC	G	G	2
Great horned owl *Bubo virginianus*	OC, M, OG	N	I	25
Northern pygmy owl *Glaucidium gnoma*	M, OG	G	G	0
Spotted owl *Strix occidentalis*	M, OG	N	I	100
Northern saw-whet owl *Aegolius acadicus*	G	G	G	0
Barred owl *Strix varia*	M, OG	N	G	0
Vaux's swift *Chaetura vaioa*	OG	N	G	0
Rufous hummingbird *Selasphorus rujus*	OC, OG	G	G	0
Hairy woodpecker *Picoides villosus*	G	N	G	0
Northern flicker *Colaptes auratus*	OC, M, OG	N	G	16
Pileated woodpecker *Dryocopus pileatus*	M, OG	N	G	128
Olive-sided flycatcher *Contopus borealis*	OC	G	E	0
Western wood-pewee *Contopus sordidulus*	M, OG	G	G	1.2
Hammond's Flycatcher *Empidonax hammondii*	M, OG	G	G	0
Western flycatcher *Empidonax difficilis*	M, OG	G	G	0
Tree swallow *Tachycineta bicolor*	OC, M, OG	N	G	0
Gray jay *Perisoreus canadensis*	Y, M, OG	G	G	64
Steller's jay *Cyanocitta stelleri*	G	G	G	0
American crow *Corvus brachyrhynchos*	G	G	G	0
Common raven *Corvus corax*	G	G	G	0
Chestnut-backed chickadee *Parus rufescens*	M, OG	G	G	1.3
Red-breasted nuthatch *Sitta canadensis*	M, OG	N	G	0.9

Table 8.1. (cont.)

Species	Seral Stage	Micro-habitat	Response to Edge[b]	Minimum Territory Size (ha)
Brown creeper *Certhia americana*	M, OG	N	G	1.7
Winter wren *Troglodytes troglodytes*	M, OG	N	I	0.25
Golden-crowned kinglet *Regulus satrapa*	Y, M, OG	G	G	0.25
Western bluebird *Sialia mexicana*	OC	N	G	0.25
Swainson's thrush *Catharus ustulatus*	Y, M, OG	G	I	0
Hermit thrush *Catharus guttatus*	Y, M, OG	G	G	0.6
American robin *Turdus migratorius*	OC	G	G	0
Varied thrush *Ixoreus naevius*	M, OG	G	I	20
Solitary vireo *Vireo solitarius*	M, OG	G	G	1.7
Orange-crowned warbler *Vermivora celata*	OC	G	I	0
Black-throated gray warbler *Dendroica nigrescens*	G	G	G	0
Townsend's warbler *Dendroica townsendi*	M, OG	G	G	0
Hermit warbler *Dendroica occidentalis*	M, OG	G	G	0
Wilson's warbler *Wilsonia pusilla*	G	G	G	0.2
Western tanager *Piranga ludoviciana*	OC	G	E	0
Rufous-sided towhee *Pipilo erythropthalmus*	OC	G	G	0
Song sparrow *Melospiza melodia*	OC	G	I	0.28
White-crowned sparrow *Zonotrichia leucophrys*	OC	G	I	0
Dark-eyed junco *Junco hyemalis*	G	G	G	0
Purple finch *Carpodacus purpureus*	G	G	G	0
Red crossbill *Loxia curvirosta*	M, OG	G	G	0

Table 8.1. (cont.)

Species	Seral Stage	Micro-habitat	Response to Edge[b]	Minimum Territory Size (ha)
Pine siskin *Carduelis pinus*	G	G	G	0
American goldfinch *Carduelis tristis*	OC	G	I	0
Sharp-shinned hawk *Accipiter striatus*	Y, M, OG	G	G	100
Cooper's hawk *Accipiter cooperi*	Y, M, OG	G	G	100
Northern goshawk *Accipiter gentilis*	M, OG	G	G	100
Red-tailed hawk *Buteo jamaicensis*	OC, M, OG	G	G	100
American kestrel *Falco sparverius*	OC	N	G	100

[a] Bird species were drawn from those listed by Brown (1985) as having primary habitats in low- to mid-elevation conifer and conifer–hardwood forests in western Oregon and Washington. Character variables are coded. Seral stage: G—generalist, OC—open canopy (<30 yr), Y—young (30–70 yr), M—mature (80–190 yr), OG—old growth (>190 yr). Microhabitat: G—generalist, N—natural (large trees, snags, fallen trees). Response to edge: G—generalist, E—edge, I—interior. Where minimum territory size is unknown, it is listed as 0.

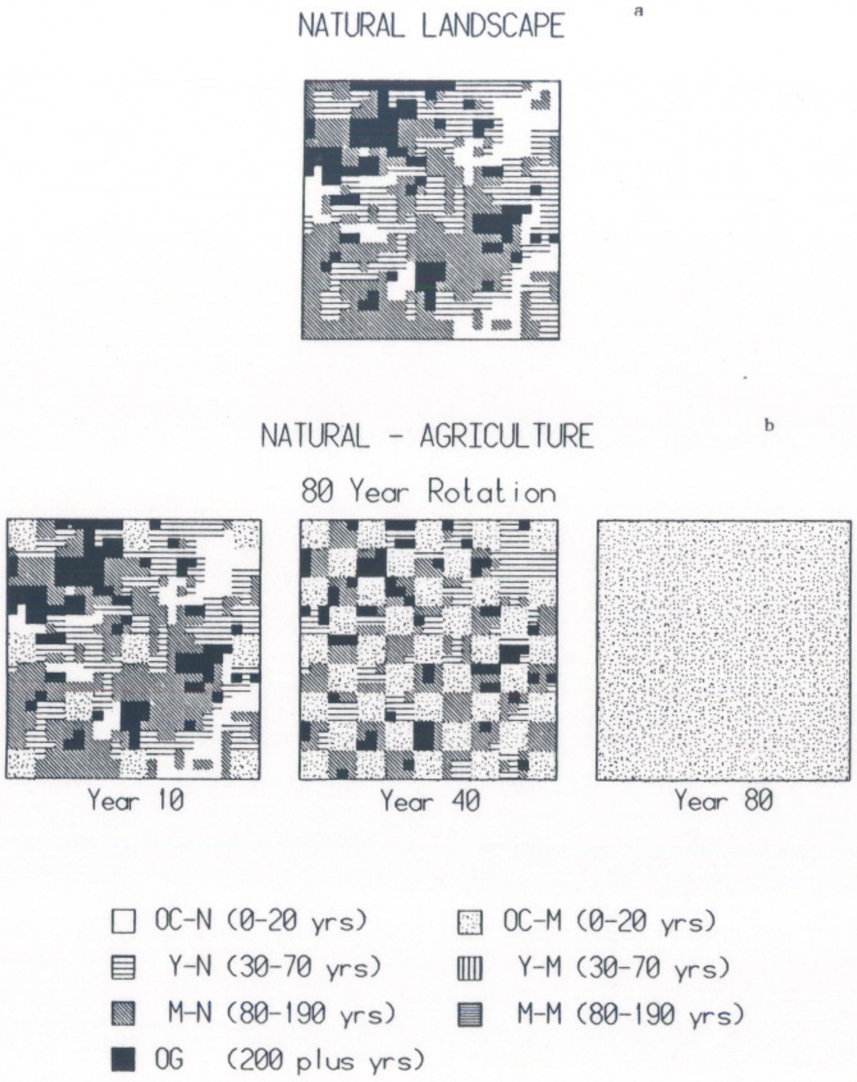
[b] From Rosenburg and Raphael (1986) and Hansen et al. (unpublished data).

low and midelevation conifer and conifer–hardwood forests in Oregon and Washington west of the Cascade Mountain crest. Brown derived life-history information from previous studies in the region. We supplemented Brown's life-history accounts with data from the other sources listed in Table 8.1. Included in the analysis were 51 species for which sufficient life-history data were available. For those species responding to edges, the zone of attraction or avoidance was assumed to be within 160 m of the edge. Also, the area requirement had to be met within a patch; use of nearby patches was not considered.

Results

Simulated Landscape Patterns

The map generated under the presettlement fire regime was complex in seral-stage distribution (Fig. 8.3A). Open-canopy patches covered 15% of the area (Fig. 8.4A). The forested area included 16% young, 53% mature, and 15% old growth stands (Fig. 8.4C). Patches were relatively

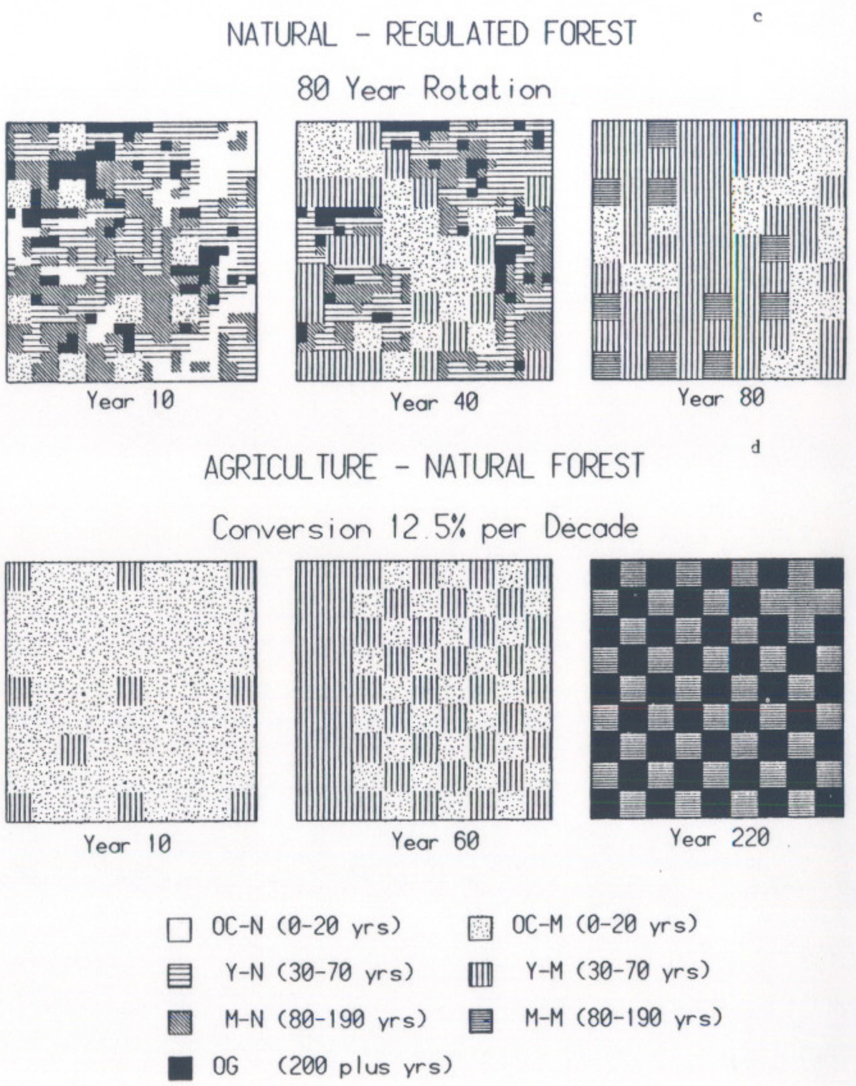


NATURAL LANDSCAPE

NATURAL - AGRICULTURE

80 Year Rotation

Figure 8.3. Maps of the simulated landscapes at various time steps. The natural landscape (a) represents year 220 under the fire regime described for a watershed in the central Oregon Cascade Mountains by Morrison and Swanson (1990). The forest fragmentation (b) and conversion to regulated forest (c) runs were initialized with map (a) and subjected to a checkerboard timber harvest regime with an 80-year rotation. The simulation of *deprise agricole* (d) started as nonforest land, underwent forest regeneration for 80 years; forest development continued for 140 years more.



NATURAL - REGULATED FOREST

80 Year Rotation

AGRICULTURE - NATURAL FOREST

Conversion 12.5% per Decade

small and variable in size. Old-growth patches, for example, averaged 10.5 ha, with a standard deviation of 15.1 ha. Consequently, the areas of forest and open-canopy interior habitats (> 160 m from edge) were substantially less than total forest and open-canopy area (Figs. 8.4A and 8.4B).

In the simulation of forest fragmentation, forest area was gradually replaced by nonforest (Figs. 8.3B and 8.4A). Old growth covered less than 3% of the landscape after year 10, and the natural open-canopy stage disappeared by year 30 (Fig. 8.4C). Density of forest–nonforest edges increased to midrotation and then decreased to 0 by year 80. Forest interior area dropped sharply during the first 4 decades to 10% of the landscape,

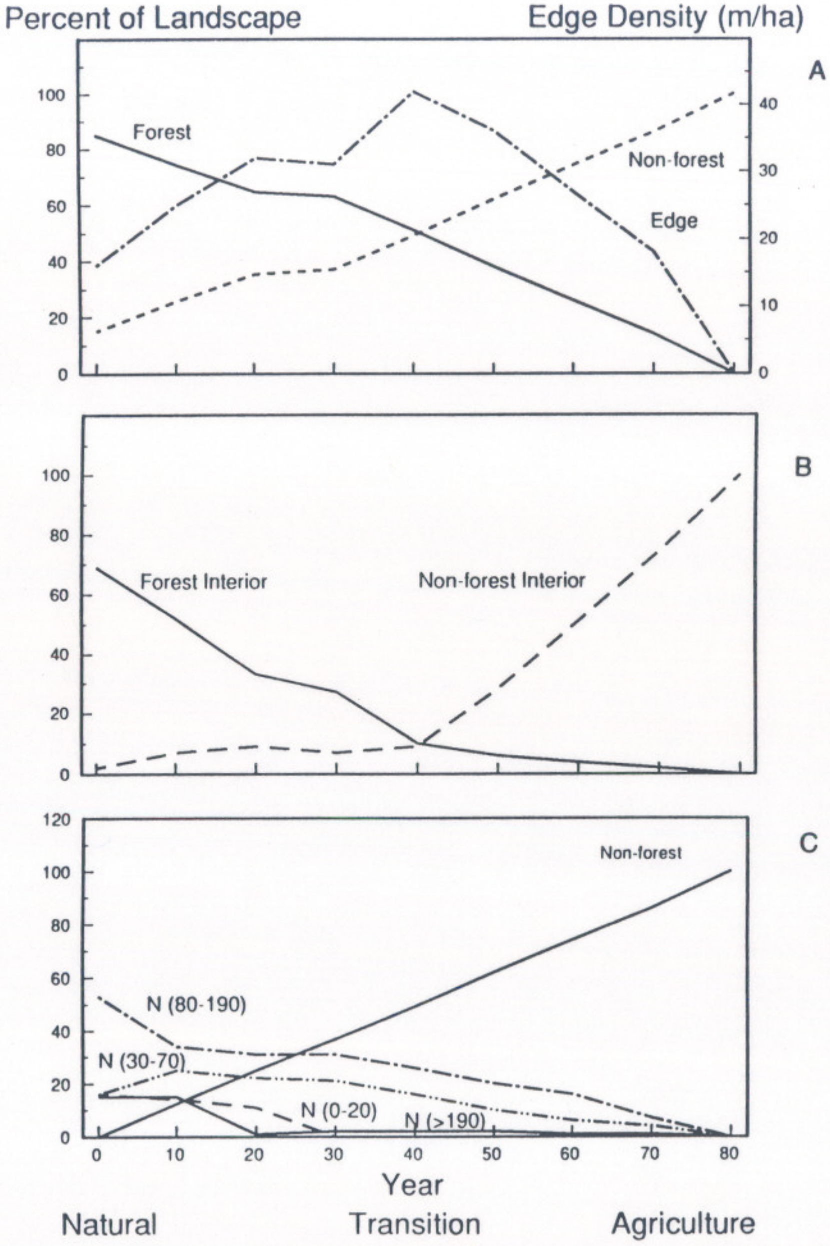


Figure 8.4. Change in abundance of (A) forest cover and forest–nonforest edge, (B) interior habitats (> 160 m from forest–nonforest edge, and (C) seral stages during the simulation of forest fragmentation. In (C), "N" refers to stands generated by wildfire, and numbers denote stand age in years.

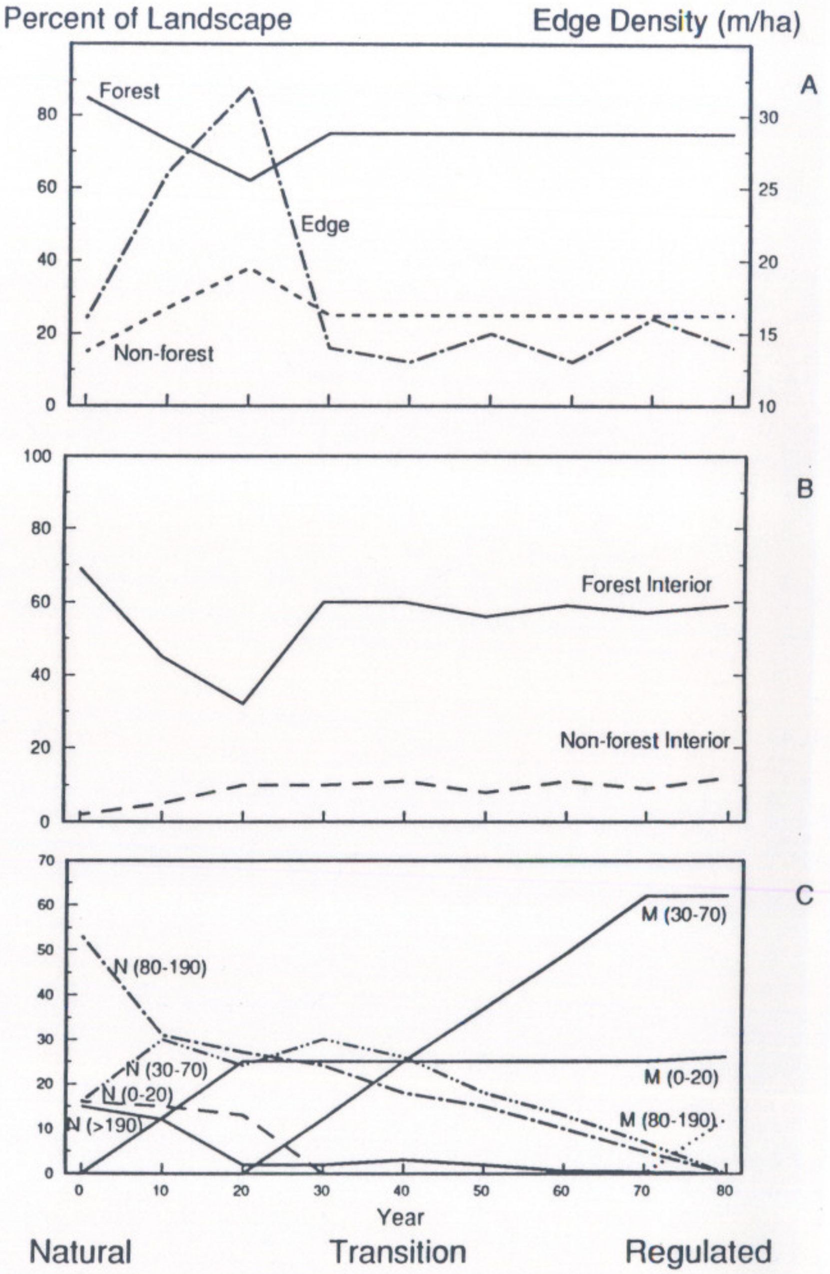


Figure 8.5. Change in abundance of (A) forest cover and forest–nonforest edge, (B) interior habitats (> 160 m from forest–nonforest edge, and (C) seral stages during the simulation of conversion of natural forest to managed plantations. In (C), "N" refers to stands generated by wildfire; "M" indicates stands generated by timber harvest; and numbers denote stand age in years.

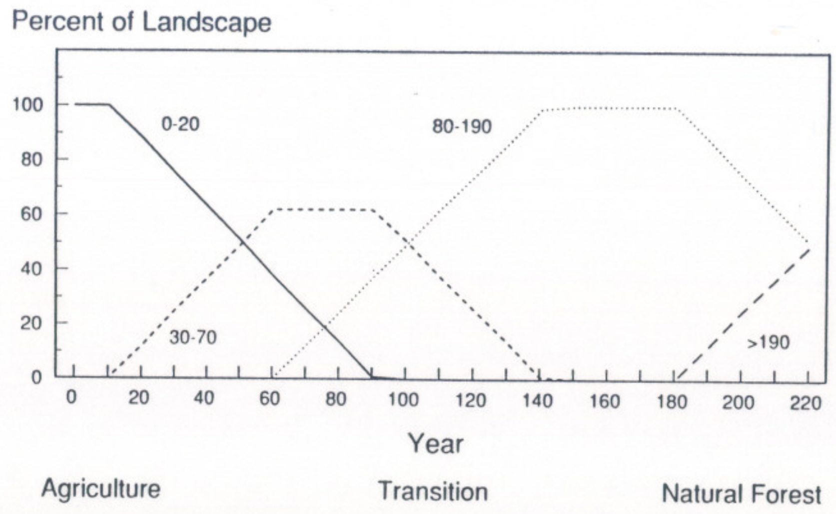


Figure 8.6. Distribution of stand age classes (years) in the simulation of *deprise agricole*.

then decreased more slowly to 0% by year 80 (Fig. 8.4B). The area of nonforest interior showed an inverse pattern.

Simulated conversion of natural forest to managed forest (Fig. 8.3C) differed substantially from the forest fragmentation scenario. Forest area dipped somewhat by year 20 due to the presence of open-canopy stands from both wildfire and logging (Fig. 8.5A). Thereafter, forested area increased to a steady-state level only slightly below that in the natural landscape, as the natural sere was replaced with a managed sere (Fig. 8.5C). Forest interior area equilibrated just below and open-canopy interior area just above levels in the natural landscape (Fig 8.5B). Edge density peaked earlier, and total edge density was substantially less than in the forest fragmentation run.

Nonforest area was lost at a rate of 12.5% per decade in the *deprise agricole* run and reached 0% at year 90 (Figs. 8.3D and 8.6). In the absence of disturbance, forest–nonforest edge density stayed at 0 for the remainder of the run, while forest interior area remained at 100%. Each seral stage dominated successively, and by year 220, mature and old-growth stands each occupied 50% of the landscape.

Life-History Guilds

Diversity of habitats for life-history guilds differed little during the first 70 years between the forest fragmentation and forest conversion runs (Fig. 8.7). Both guild richness and Hill's N2 dropped substantially between years 20 and 30 as natural open-canopy and old-growth interior habitats were lost. Hill's N2 declined gradually thereafter, in association with the dwindling natural seral stages. Richness dropped rapidly after year 70, as the last natural habitats disappeared. By the end of the simulations, richness under fragmentation and conversion was 17% and 33%, respectively, of levels in the natural landscape.

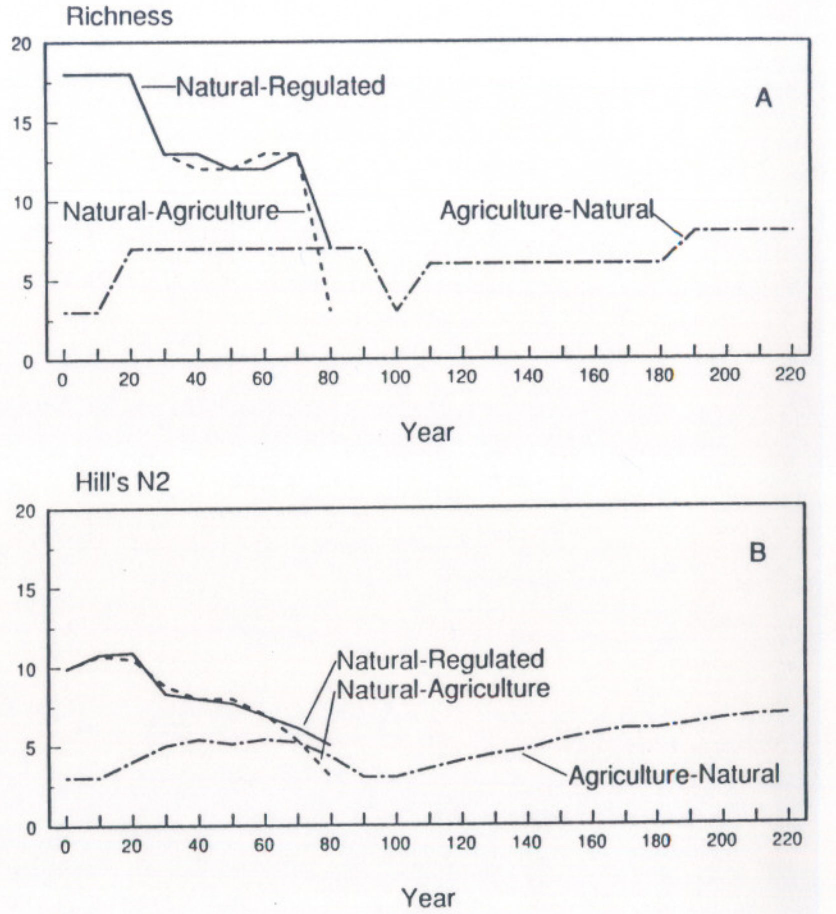


Figure 8.7. Richness (A) and diversity (B) of habitats for hypothetical life-history guilds over the three simulated landscape trajectories.

The two runs differed, in that only open-canopy, microhabitat generalists persisted under fragmentation, while closed-canopy, microhabitat generalists also persisted in the regulated forest. Habitats for closed-canopy interior specialists were nearly as abundant in the regulated forest as in the natural landscape.

Diversity was initially low under *deprise agricole*, with only open-canopy, microhabitat generalists present (Fig. 8.7). Habitat for closed-canopy, microhabitat generalists became available by year 20, and richness increased. This level was maintained until year 100, when open-canopy stands were lost and diversity fell. At year 110, natural microhabitats are assumed to develop, and habitats for three additional guilds appeared. Diversity then remained stable until year 190, when old-growth habitats became available. Even 220 years after land abandonment, richness was only 44% of that in the natural landscape because neither open-canopy nor edge habitats were available.

PNW Birds

Diversity of habitats for PNW bird species declined gradually over both the forest fragmentation and forest conversion simulations (Figure 8.8). The drop in richness was especially pronounced at year 80. Only 38% and 56% of the species present in the natural landscape persisted in the two fully converted landscapes.

No habitat was available for the spotted owl, even in the natural landscape, because large patches of mature and old-growth were not present. Habitats for species requiring open canopies with snags (American kestrel, western bluebird) dropped out of both runs by year 30. Late-successional species with large area requirements (pileated woodpecker, varied thrush, northern goshawk) were not represented either in the forest fragmentation run after year 30 or in the conversion run after year 60. Similarly, closed-canopy species with large area requirements (gray jay, sharp-shinned hawk, Cooper's hawk) found no suitable habitats in the fragmented landscape after year 40. Among the species losing habitat at year 80 were several requiring late-successional stands and/or natural microhabitats. Only open-canopy or seral-stage generalists had habitat remaining at the end of the forest fragmentation run. Nine species, most associated with closed-canopy stands, were able to persist in the managed forest landscape but not in the fragmented landscape. Among them were gray jay, golden-crowned kinglet, Swainson's thrush, Cooper's hawk, and sharp-shinned hawk.

The *deprise agricole* run started with the same open-canopy habitats that were present at the end of the fragmentation run (Fig. 8.8). Habitats for six closed-canopy, microhabitat generalists with various area requirements became available between years 30 and 70. Richness increased dramatically in year 80 when mature forest developed. Nine open-canopy species were lost at year 110, but the development of natural microhabitats provided habitat for 8 additional species. Thereafter, habitat became available for three additional late-successional species (spotted owl, pileated woodpecker, and Vaux's swift). No habitats existed at the end of the run for nine species requiring open-canopy patches, and none existed for three forest–non-forest-edge species. Thus, species richness at the end of this run was 76% of that for the natural landscape.

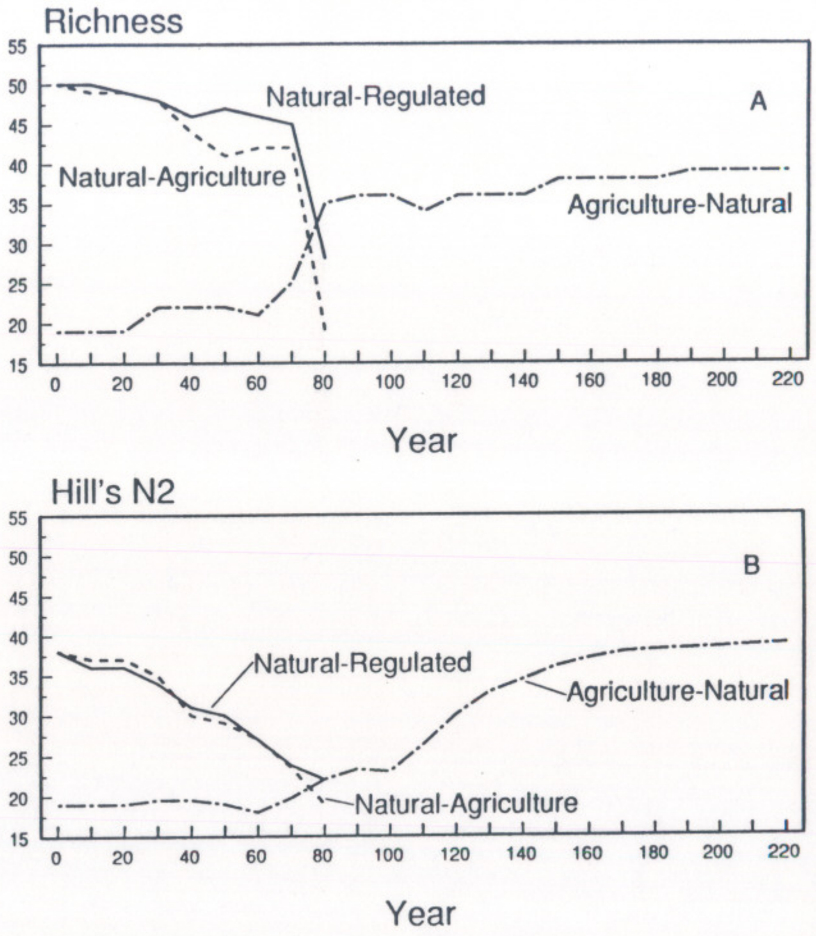


Figure 8.8. Richness (A) and diversity (B) of habitats for PNW bird species over the three simulated landscape trajectories.

Discussion

Simulated Landscapes and Bird Communities

The landscape generated under the PNW presettlement fire regime included an unexpectedly complex pattern of seral stages. Contrary to current perception in the region, old growth comprised only about 15% of the landscape, an amount equivalent to that occupied by the open-canopy stage. Moreover, the relatively small patch sizes and variable patch shapes resulted in little interior habitat in either old-growth or open-canopy patches. The spotted owl, a species well known for requiring large tracts of late-successional forest, had no suitable habitat in the simulated landscape. This result is partially due to the model assumption that the area requirements of a species had to be met within a single patch. In reality, the spotted owl is known to incorporate several patches into one home range (Thomas et al. 1990). Also, the fire regime we modeled is probably more extreme than is typical of locations further north and more coastal in the region (Morrison and Swanson 1990). A third factor is that the model did not consider topographic effects that cause some locations to be less prone to fire. Even so, the simulation illustrated the complex nature of presettlement landscapes in the region (see also Hemstrom and Franklin 1982, and Morrison and Swanson 1990). This heterogeneous landscape did provide habitat for all other species and guilds included in the model. Life-history guild and bird-species richness and diversity were as high or higher in the natural landscape than in any of the anthropogenic landscapes.

The simulations of fragmentation of forest by nonforest and conversion of natural forest to managed plantations pointed out important differences between these two trajectories. The abundance of forest cover maintained in the managed forest landscape provided habitat for four more guilds and nine more species of closed-canopy birds than under forest fragmentation. Among these were species requiring large patches of closed forest, such as sharp-shinned hawk and Cooper's hawk. Even forest interior habitats remained abundant in the regulated forest, providing habitat for the hermit thrush and the Swainson's thrush, the two PNW species known to be associated with interiors of young closed-canopy stands. Interestingly, the eight bird species in the eastern deciduous forest known to be extremely sensitive to forest fragmentation (Whitcomb et al. 1981) would appear, based on their habitat requirements, to be able to persist in a hardwood forest managed according to this regime.

The forest fragmentation and forest conversion runs were similar in depicting the loss of later seral stages and natural microhabitats. Consequently, guild and bird-species richness and diversity dropped substantially in these runs, especially in the last decade. Mature and old-growth stands will, of course, never develop in forests managed under an 80-year rotation. Silvicultural techniques for maintaining and producing large trees, snags, and fallen trees in managed forests are currently being tested in the PNW (Franklin et al. 1986). Our results are in agreement with other studies on the potential benefits to vertebrate diversity of maintaining such microhabitat features (see Hansen et al. 1991). Our simulations indicate that maintaining adequate levels of these microhabitats in plantations and retaining 12.5% of the landscape in late-successional forest would provide some suitable habitat for 100% of the guilds and 92% of the bird species considered in the model. The habitats provided for some species under this regime would undoubtedly be too small to support viable populations. Nonetheless, this result makes clear that strategies are available for dramatically increasing avian habitat diversity in managed forests over levels expected under traditional forest practices.

Habitat diversity for guilds and bird species did increase substantially in the simulation of *deprise agricole*. Even closed-forest interior species, such as hermit thrush and Swainson's thrush, had some habitat available by year 30, and habitats for several bird species were added as natural microhabitats and mature stands developed. However, habitat diversity never reached the levels of the natural landscape. Under the suppression of natural disturbance, open-canopy and edge habitats were not available after year 100.

These results make clear that bird communities can be expected to change dramatically where nonforest lands are allowed to undergo forest succession. In such landscapes, rarity can be expected to shift from late-successional and/or forest interior species to open-canopy species and/or edge species. Field studies are needed to document the sorts of changes now taking place in areas undergoing *deprise agricole*. In parts of southern France, for example, it appears that the garrigues (oak chaparral) vegetation present when the lands were cleared for agriculture centuries ago is now being replaced by a temperate hardwood forest, and the bird community is undergoing major flux (M. Debussche, personal communication, October 1987).

These results also have implications for the management of nature preserves, such as wilderness areas and national parks. To the extent that disturbance is excluded, these areas should not be viewed as representative of natural landscapes. Seral-stage distribution, grain size, boundary characteristics, and species diversity all are expected to change, following the suppression of disturbance. Our model suggests for the PNW avifauna that in the absence of disturbance sufficient to create open-canopy habitats, species richness will not exceed 76% of what would occur under a natural disturbance regime.

Modeling Approach

LSPA has some obvious limitations for modeling animal habitat dynamics. Vegetation dynamics are accounted at a level far simpler than that at which birds select habitat. Within-stand plant demography and structure, for example, are not considered directly. This necessitated the simplifying assumptions that (a) all stands generated by natural disturbance provided sufficient levels of large trees, snags, and fallen trees for guilds and species requiring them; (b) these features occurred at insufficient levels following logging; (c) and abandoned patches attained these microhabitat features at year 110. These assumptions are probably generally appropriate for some lands in the PNW, but exceptions are extremely common. The model also does not deal with bird demography or dispersal. The fact that some suitable habitat may exist in a landscape provides little indication that it will be colonized by a species or that viable populations can be supported. Finally, the life-history attributes of guilds and bird species are extremely simple in formulation and are derived from inadequate data in the case of some species. For these reasons, we would not expect these predictions to correlate very well with independent field data from specific locations.

It is the simplicity of the model, however, that makes these analyses possible in spite of the inadequate data base. Detailed vegetation models have not yet been designed to account for landscape pattern. LSPA deals with vegetation at a coarse scale in order to allow attention to be focused on landscape geometry. Also, the assumptions about microhabitat patterns in natural and managed stands depict extreme situations to illustrate the consequences of removing all stand structure during timber harvest. Assessing bird habitat requirements in terms of life-history traits has two advantages. First, such data are available for most species, so analyses of many members of a community are possible. Second, the life-history attributes code animal habitat associations at spatial scales ranging from microhabitats to landscapes. Hence, the consequences of habitat dynamics at all these levels can be analyzed. In sum, we feel that LSPA is a good tool for examining hypothetical responses of landscape patterns and animal communities to disturbance.

The Role of Species Life Histories

Just as landscape trajectories may differ among geographical locations, so may the suites of life-history strategies represented in local communities. This possibility has important implications for understanding community response to landscape change (Hansen and Urban in press). Life-history traits set limits on the types and scales of resources that can be used by a species. Because life histories are shaped by long-term environmental, demographic, and genetic factors, the suite of life histories represented in communities of organisms is likely to differ among geographic locations. Consequently, communities from distinct biomes should differ in response to a given trajectory of landscape change in ways predictable based on the life-history traits of each community.

We (Hansen and Urban in press) tested this hypothesis by comparing the representation of various life-history guilds in avifaunas from the eastern deciduous forests (EDF) and PNW forests. The communities differed relatively little in the number of species in the guild associated with microhabitat features typical of natural forests (large trees, snags, fallen trees). The EDF avifauna, however, included many more species associated either with forest edges and small habitat patches or with habitat interiors and large habitat patches than did the PNW community. Similarly, the life-history guild identified by Whitcomb et al. (1981) as being highly sensitive to forest fragmentation included eight species in the EDF and none in the PNW. Alternatively, predators requiring large forest tracts were better represented in the PNW.

We also ranked the relative sensitivity of each community, based on the life-history traits of their species. The EDF avifauna was found to have a higher index of sensitivity, both to forest fragmentation and to landscape change in general. Among the PNW species with high scores for sensitivity to forest fragmentation were several forest species that have received little attention thus far from conservationists and land managers. Similarly, several species associated with open-canopy habitats were ranked as highly sensitive to landscape change. Some of these species are declining in abundance in the PNW.

The validity of using life histories to predict community response to landscape change was supported by the fact that the sensitivity scores for PNW species correlated significantly with independent data on species population trends. We would expect that the species most sensitive to landscape change would be undergoing population increases or decreases during this period of dramatic landscape change in the PNW.

This analysis provided evidence that life-history traits are likely to differ among communities and that these differences can cause communities from distinct geographic locations to respond uniquely to a given landscape trajectory. An obvious implication is that conservation strategies should be uniquely tailored to a region, based on the types of life-history attributes represented in the community. The challenge in parts of the EDF, for example, is to expand the abundance of forest interior habitats to benefit the large groups of forest-dwelling neotropical migrants while also maintaining sufficient habitats for the large guild of edge specialists. The focus in the PNW should be on maintaining natural microhabitats, large tracts of forest for forest predators, and sufficiently large openings for open-canopy specialists.

Implications

In total, our results suggest that forest fragmentation and the loss of forest interior species, a topic of great concern among conservationists, is only an example of a more general phenomenon. At the core of the phenomenon is the suite of changes in ecological processes associated with changing landscape patterns. These changing processes fuel differential responses in plant and animal species, according to their life-history strategies, and, collectively, they define the characteristics of communities.

Effective conservation planning clearly needs to embrace this paradigm. Approaches are needed that evaluate past, present, and possible future landscape dynamics in an area and their ecological consequences. It is also important to examine the life-history characteristics of the local community and to examine the responses not just of species thought to be sensitive, ut also of a broad range of guilds and species. Landscape change is sufciently rapid in some regions that the types of species experiencing rarity s in a state of flux. It is not widely appreciated yet, for example, that ortions of the EDF reached maximum deforestation in the 1800s and that fforestation may now be jeopardizing species associated with open habiats. Similarly, conservation strategies in the PNW that advocate only the etention of old-growth habitats and late-successional species probably err n assuming that open-canopy species are weedy and will always do well n disturbed landscapes. Some of these species are presently declining in bundance, possibly because the microhabitats or patch sizes they require re not being created at sufficient levels. Attention to the paradigm that inks disturbance, landscape dynamics, and plant and animal communities an provide both a basis for regional biodiversity plans and knowledge for designing landscapes to optimize conservation of biodiversity and other natural resources.

Summary

Patterns of animal diversity in an area reflect complex interactions among disturbance, landscape dynamics, and the life-history traits within the animal community. Life-history attributes set constraints on the types and scales of habitat that are suitable for a species. Also, the suite of life histories represented in a community influences the ways in which the community will respond to landscape change. Communities from distinct geographic locations are likely to differ in life histories and, thus, in response to a given trajectory of landscape change. The life-history guild found to be most sensitive to forest fragmentation in the EDF, for example, is not represented in the PNW avifauna A comparison of life histories between the two communities suggested that the EDF avifauna is more sensitive to forest fragmentation and landscape change than the PNW avifauna (Hansen and Urban, in press).

Trajectoris of landscape change also differ among regions. Our modeling effort indicated that fragmentation to a nonforested landscape produces acute changes in landscape spatial patterns and dramatically reduces native bird diversity. Bird diversity was not as affected in the simulated conversion of natural forest to managed plantations. The loss of natural microhabitats and late-seral stages does make such landscapes unsuitable for several species. However, forest regrowth and the transient nature of forest edges allows habitat for some closed-forest species to persist. Forest development following abandonment of agriculture land is associated with a gradual increase in habitat diversity. Simulated bird diversity under all three of these landscape trajectories, however, was lower than in the natural landscape.

An important implication of these findings is that conservation strategies should be tailored to specific regions, based on local animal life histories and landscape patterns. Conservation plans based on generalities from one biome are not likely to be effective in other biomes. Clearly, the most effective conservation strategies will be holistic in considering entire plant and animal communities and will involve designing anthropogenic landscapes to optimize maintenance of biodiversity and other natural resources.

Acknowledgments. We thank J. van Sickle for advice on modeling and M. Berg for help with word processing. The chapter benefited from reviews by D. Wigham, S. Garman, P. Lee. This research was supported by the Coastal Oregon Productivity Enhancement (COPE) Program, College of Forestry, Oregon State University, Corvallis, Oregom.

References

Ambuel B, Temple SA (1983) Area-dependent changes in bird communities and vegetation of southern Wisconsin woodlots. Ecology 64:1057–1068

Brittingham M, Temple SA (1983) Have cowbirds caused forest songbirds to decline? BioScience 33:31–35

Brown ER, (tech ed) (1985) *Management of wildlife and fish habitats in forests of western Oregon and Washington.* USDA Forest Service R6-F&WL-192-1985, Portland, Oegon

di Castri F, Hansen AJ, Debussche M (eds) (1990) *Biological invasions in Europe and the Mediterranean Basin.* Kluwer Academic Publishers, Boston

di Castri F, Hansen AJ, Holland MM (eds) (1988) A new look at ecotones. Biol Intl (special issue) 17:1–163

Forman RTT, Galli AE, Leck CF (1976) Forest size and avian diversity in New Jersey woodlots with some land use implications. Oecologia 26:1–8

Forman RTT, Godron M (1986) *Landscape ecology.* Wiley, New York

Franklin JF (1988) Pacific Northwest forests. In Barbour MG, Billings WD (eds) *North American terrestrial vegetation.* Cambridge University Press, New York, pp 104–127

Franklin JF, Forman RT (1987) Creating landscape patterns by forest cutting: Ecological consequences and principles. Landscape Ecol 1(1):5–18

Franklin JF, Spies T, Perry D, Harmon M, McKee A (1986) Modifying Douglas-fir management regimes for nontimber objectives. In Oliver CD, Hanley DP, Johnson JA (eds) Proceedings of a symposium modifying Douglas-fir management regimes for nontimber objectives, Seattle, Washington, 18–20 June, 1985. USDA Forest Service, Seattle, Washington, 373–379

Freemark KE, Merriam HG (1986) Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biol Conserv 36:115–141

Galli AE, Leck CF, Forman RTT (1976) Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93:356–364

Gates JE, Gysel LW (1978) Avian nest dispersion and fledgling success in field–forest ecotones. Ecology 59:871–883

Hansen AJ, Spies TA, Swanson FJ, Ohmann JL (1991). Conserving biodiversity in managed forests. BioScience 41(6):382–392

Hansen AJ, Urban DL (in press) Avian responses to landscape pattern: the role of species life histories. Landscape Ecol

Harris LD (1984) *The fragmented forest.* University of Chicago Press, Chicago

Harris LD (1988) Edge effects and conservation of biotic diversity. Conserv Biol 2(4):330–332

Hemstrom MA, Franklin JF (1982) Fire and other disturbances of the forests in Mount Rainier National Park. Quat Research 18:32–51

Hunter ML Jr (1990) *Wildlife, forests, and forestry*. Prentice Hall, Englewood Cliffs, New Jersey

Jennersten O (1988) Pollination in dianthus–deltoides caryophyllaceae effects of habitat fragmentation on visitation and seed set. Conserv Biol 2(4):359–366

Klein BC (1989) Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia Brazil. Ecology 70(6):1715–1725

Kroodsma RL (1982) Edge effect on breeding forest birds along a power-line corridor. J Appl Ecol 19:361–370

Li H (1989) Spatio-temporal pattern analysis of managed forest landscapes: a simulation approach. PhD thesis. Oregon State University, Corvallis, Oregon

Ludwig JA, Reynolds JF (1988). *Statistical ecology*. John Wiley & Sons, New York, New York.

Lynch JF, Whitcomb RF (1978) Effects of the insularization of the eastern deciduous forest on avifaunal diversity and turnover. In Marmelstein A (ed) *Classification inventory, and analysis of fish and wildlife habitat*. USDI Fish and Wildlife Service, Washington, D.C., pp 461–489

MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey

MacClintock, L Whitcomb RF, Whitcomb BL (1977) Island biogeography and "habitat islands" of eastern forest. II. Evidence for the value of corridors and minimization of isolation in preservation of biotic diversity. Amer Birds 31:6–16

Mooney HA, Drake JA (eds) (1986) *Ecology of biological invasions of North America and Hawaii*. Springer-Verlag, New York

Morrison PH, Swanson FJ (1990) *Fire history in two forest areas of the central-western Cascade Range of Oregon*. USDA Forest Service PNW-GTR-254, Portland, Oregon

Noss RF (1983) A regional landscape approach to maintain diversity. BioScience 33:700–706

Press WH, Flannery BP, Teukolsky SA, Vetterling WT (1986) *Numerical recipes*. Cambridge University Press, New York

Ranney JW, Bruner MC, Levenson JB (1981) The importance of edge in the structure and dynamics of forest islands. In Burgess RL, Sharpe DM (eds) *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, pp 67–96

Ripple WJ, Bradshaw GA, Spies TA (1991) Measuring forest fragmentation in the Cascade Range of Oregon. Conservation Biology 57(1):73–88

Robbins CS, Dawson DK, Dowell BA (1989) Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildlife Monogr 103:1–34

Rosenberg KV, Raphael MG (1986) Effects of forest fragmentation on vertebrates in Douglas-fir forests. In Verner J, Morrison ML, Ralph CJ (eds) *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. The University of Wisconsin Press, Madison, Wisconin, 263–272

Roth RR (1976) Spatial heterogeneity and bird species diversity. Ecology 57:773–782

Sharp B (1990) Population trends of Oregon's neotropical migrants. Oregon Birds 16(1):27–42

Shugart HH (1984) *A theory of forest dynamics: the ecological implications of forest succession models*. Springer-Verlag, New York

Small MF, Hunter ML (1988) Forest fragmentation and avian nest predation in forested landscapes. Oecologia 76:62–64

Terborgh J (1989) *Where have all the birds gone?* Princeton University Press, Princeton, New Jersy

Thomas JW, Forsman ED, Lint JB, Meslow EC, Noon BR, Verner J (1990) *A Conservation strategy for the northern spotted owl*. USDA Forest Service, USDI Bureau of Land Management, USDI Fish and Wildlife Service, and USDI National Park Service, Portland, Oregon

Turner MG (1987) Land use changes and net primary production in the Georgia, USA, landscape: 1935–1982. Environ Manage 11(2):237–247

Urban DL, O'Neill RV, Shugart HH (1987) Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. BioScience 37:119–127

Urban DL, Shugart HH, Jr, DeAngelis DL, O'Neill RV (1988) *Forest bird demography in a landscape mosaic*. Oak Ridge National Laboratory Publication No. 2853, Oak Ridge, Tennessee

Urban DL, Smith T (1989) Microhabitat pattern and the structure of forest bird communities. Am Nat 133(6):811–829

Verner J, Morrison ML, Ralph CJ (eds) (1986) *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin

Westman WE (1990) Managing for biodiversity. BioScience 40(1):26–33

Whitcomb RF, Robbins CS, Lynch JF, Whitcomb BL, Klimkiewicz K, Bystrak D (1981) Effects of forest fragmentation on avifauna of the eastern deciduous forest. In Burgess RL, Sharpe DM (eds) *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York

Wilcove DS (1985) Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214

Wilson EO (ed) (1988) *Biodiversity*. National Academy Press, Washington, D.C.