

29

An Approach for Managing Vertebrate Diversity Across Multiple-Use Landscapes

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Introduction

There is widespread agreement that biological diversity is valuable and that it is rapidly being lost (Myers 1979, Wilson 1988, Soulé 1991). Consequently, the conservation of biodiversity has emerged as a major international issue, and numerous laws, research initiatives, and management strategies have been enacted. Yet, biological diversity continues to decline even in wealthy and technologically advanced countries (Ehrlich and Wilson 1991). The "endangered species" approach of protecting species after they are at risk is insufficient for several reasons (Rohlf 1991, Mann and Plummer 1992). Nature preservation is also failing because reserves are often too few, too small, and too isolated to maintain natural processes and species (Pickett and Thompson 1978, Noss and Harris 1986, Newmark 1987, Hunter 1991).

Many ecologists now recommend complementing these traditional approaches with rigorous efforts to maintain biodiversity in human-dominated landscapes (Noss and Harris 1986, Brussard 1991, Hansen et al. 1991). In the United States the expanse of public lands in a "semi-natural" condition provides an opportunity to use ecological principles to manage for both commodity production and biodiversity (Wilcove 1989, Westman 1990). Land stewards

are increasingly embracing this approach (Gillis 1990), and many management plans now call for resource production and for the maintenance of biological diversity at several organizational levels.

Unfortunately, no one knows how to protect "genetic, species, ecosystem, and landscape diversity" (Salwasser 1991) on lands intensively managed for wood, forage, and other products. Land managers are now wrestling with such difficult questions as: How can we manage effectively without adequate knowledge of the distribution and ecology of biodiversity? What elements of biodiversity can realistically be maintained and over what spatial and temporal scales in a managed ecosystem? What predictive approaches can best identify the likely impacts of alternative management scenarios on biodiversity and other resources? How can biological diversity be monitored to ensure that management strategies are successful?

We present here an approach for managing vertebrate species diversity in multiple-use lands at the landscape scale (e.g., 1000–20 000 ha). Vertebrates were selected because they are better known than most other organisms. Our underlying conceptual model is that animal community response to landscape change can be explained by (1) the suite of life histories represented in the local community and (2) the local trajectory of landscape change (Urban et

al. 1988, Hansen and Urban 1992, Hansen et al. 1992, Urban et al. 1992). The essence of the approach is to use data on the life history and habitat use of each species in a community to classify habitat suitability across the planning area. Computer models are then used to project habitat abundance for each species under different management regimes. With such information, land managers can choose the regime that best meets their objectives.

The approach is described in five steps and illustrated with an analysis of a watershed in western Oregon. Local objectives, data bases, and expertise will dictate how the approach can best be implemented in other settings.

Step 1: Set Clear Objectives

Objectives that clearly state the desired resource and conservation priorities are critical for successful management. Well-focused objectives facilitate the development of precise landscape designs for achieving the objectives. They also provide a basis for evaluating the success of the strategies that are implemented. Factors that should be considered when establishing objectives include the level of specification required and the regional context of the planning unit.

Minimum Specifications

Setting clear objectives relative to biodiversity is especially difficult because the term is so all encompassing. Management plans often list nebulous objectives such as maintaining "biodiversity," "ecosystem health," or "ecosystem sustainability." These broad goals are too general for building specific management prescriptions or for assessing whether the prescriptions are successful.

A biodiversity management plan should specify at a minimum: response variables, target levels, and spatial/temporal domains. *Response variables* are the entities being managed. Both the organizational levels(s) of interest (e.g., deme, species, community, landscape) and the specific entities within each level need be clearly elucidated (e.g., species level: all vertebrate species, species requiring late-seral habitats, or sensitive species). *Target level* spec-

ifies the relative or absolute abundance of the response variables that is considered sufficient (e.g., minimizing the number of species that fall below minimum viable population sizes or maintaining a specific ratio of seral stages). *Spatial/temporal domain* indicates the area and time period over which the target levels of the response variables are to be maintained (e.g., over at least 80% of the planning area for at least 100 yr). Objective criteria should be used for defining these variables, levels, and domains to facilitate evaluation of whether the objectives are met.

Hierarchical Planning

Resource patterns within a planning area both influence and are influenced by factors at broader spatial scales (Noss and Harris 1986). This necessitates a hierarchical planning framework where objectives for a particular spatial scale are set with respect to broader-scale constraints and finer-scale mechanisms (Allen and Starr 1982). The importance of a planning area for a particular species, for example, can best be determined with knowledge of the regional or continental distribution of the species. The planning area may play an important role in the larger system by providing key habitats for regionally rare species or offering strategic dispersal routes under climate change. At the same time, fine-scale patterns and processes in the planning area need be considered inasmuch as they influence local animal populations. For example, the patterning of microhabitats such as canopy layering or coarse woody debris may strongly affect the demography of local populations.

Hierarchical planning is difficult because organisms and processes differ in the characteristic scales over which they operate (O'Neill et al. 1986). Thus, it is challenging to identify one set of levels in the hierarchy (planning levels) that are meaningful for all the resources of interest. It is also difficult to obtain and integrate data across a range of scales. Coarse-scale data bases such as those being generated by the U.S. Fish and Wildlife Service's Breeding Bird Survey (Droege 1990) and Gap Analysis Project (Scott et al. 1987, 1991) are useful for establishing the regional context. Data at increas-

ingly fine spatial scales are helpful for setting local objectives. The Interagency Scientific Committee on the Northern Spotted Owl (Thomas et al. 1990) provided an excellent example of integrating data across scales and carrying out hierarchical planning for a single species.

Our example deals primarily with one level in the planning hierarchy, the landscape or watershed level. However, the principles can, and ultimately should be applied at several spatial scales.

Example

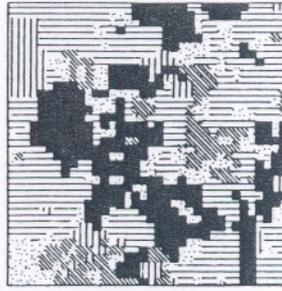
The approach was applied to a 3318-ha section of the Cook-Quentin watershed in the Willamette National Forest of the western Cascades of Oregon. This area was selected because sufficient data were readily available and land-use patterns there are typical of multiple-use federal forest lands in the region. Only vegetation and bird habitat patterns are considered. Topography, geomorphology, hydrology, and roads are ignored in this example. These factors can exert strong influence over forest productivity and/or vertebrate habitat suitability and should be considered where local data allow. The watershed is within the western hemlock (*Tsuga heterophylla*) and the Pacific silver fir (*Abies amabilis*) vegetation zones (Franklin and Dyrness 1973). Approximately 22% of the area has been clear-cut under a staggered-setting design (i.e., dispersed harvest units) and reforested. The remaining area supports natural young, mature, and old-growth stands (Fig. 1).

A regional analysis was not performed. We assumed for the example that the basin is rather unusual in the area in having large patches of mature and old-growth forests that provide habitat for late-seral bird species. We also assumed that habitats for bird species requiring large trees, snags, and/or fallen trees in open-canopy stands are rare in the watershed and in the region due to the suppression of natural disturbance and past clear-cutting (Hansen et al. 1991).

Objectives were set as follows:

1) Maximize across the planning area, in perpetuity, habitat diversity for bird species

COOK-QUENTIN WATERSHED
Present Vegetation Patterns



□	OC-N (0-20 yr)	▤	OC-M (0-20 yr)
▨	Y-N (30-70 yr)	▩	Y-M (30-70 yr)
▧	M-N (80-190 yr)	▪	M-M (80-190 yr)
■	OG (200+ yr)		

FIGURE 1. Map of current seral stage distribution in the Cook-Quentin watershed (Oregon, USA). Abbreviations are as follows and definitions of the age-classes are listed in Table 2. OC-N = open-canopy natural; Y-N = young natural; M-N = mature natural; OG = old growth; OC-M = open canopy managed; Y-M = young managed; M-M = mature managed.

requiring late-seral (mature and old-growth) habitats.

2) Maximize across the planning area, in perpetuity, habitat diversity for bird species requiring structurally rich, open-canopy habitats.

3) Produce saw timber (trees > 30 cm diameter at breast height) at levels compatible with objectives 1 and 2.

Step 2: Associate Target Species with Specific Habitat Configurations

Management goals often direct maintaining viable populations of all native vertebrates. Where this is the case, we recommend an approach intermediate between the "coarse-filter" and "fine-filter" approaches described by Noss (1987) and Hunter (1991). The coarse

filter approach of maintaining communities or ecosystems in hopes of maintaining the species within them is appropriate where knowledge is lacking on the ecologies of species of interest (as is usually the case with taxonomic groups other than vascular plants, butterflies, and vertebrates). Without explicit reference to the habitat requirements of individual species, however, it is difficult to establish landscape design criteria to maintain these species and to evaluate how well an implemented design conserves species. On the other hand, intensive management of individual species (fine-filter approach) is usually not possible for many species in a community because of limitations in detailed demographic data and in financial resources needed to acquire such data.

We suggest an intermediate approach when the goal is to maintain most or all members of a vertebrate community. We recommend that habitat suitability and life-history attributes be used as surrogates for detailed demographic data for the vertebrate species in the planning area. Objective analysis of the patterning of suitable habitats across the planning area and the life-history attributes of individual species can then be used to select the subset of species that are likely to be sensitive to landscape change and merit additional demographic research (see *Step 3*).

There is a strong theoretical basis (James et al. 1984, Pulliam 1988, Urban and Smith 1989) and empirical evidence (Capen 1981, Cody 1985, Verner et al. 1986) for using habitat as an indicator of demography. It is important that the appropriate habitat attributes and scales of habitat be considered. Most studies have focused on vegetation and documented the importance of vegetation structure and spatial patterning in explaining animal distributions (see Hunter 1990 and Rodiek and Bolen 1991). Habitat characteristics involving primary productivity, geomorphology, hydrology, soils, and disturbance history are less often considered in vertebrate studies. It is likely, however, that such factors are also extremely important and should be included in habitat analyses.

Animal habitat relationships should be measured over a range of spatial and temporal scales (Urban et al. 1992). Individual species probably operate over a characteristic range of

scales, and the habitat elements explaining most of the variation in species abundance may differ among scales (Harris 1984, Wiens et al. 1986, Neilson et al. 1992) (Fig. 2). Differences in scales of habitat use among species are probably a function of differences in life-history attributes such as body size, metabolic rates, home range size, and vagility (Hansen and Urban 1992). Thus it is desirable to measure animal habitat relations at multiple scales and to perform objective analyses of the type and strength of habitat association at each scale. These data can then be used to evaluate the response of each species to changes in habitat patterning involving one or more scales.

Several analytical methods exist for quantifying animal habitat relationships and for classifying habitat suitability in independent field plots. Common methods include simple seral-stage associations (e.g., Thomas 1979, Verner and Boss 1980, and Brown 1985), multivariate statistical methods (Capen 1981, Verner et al. 1986), and Habitat Suitability Models (HSI) (USFWS 1981, Schamberger and O'Neil 1986).

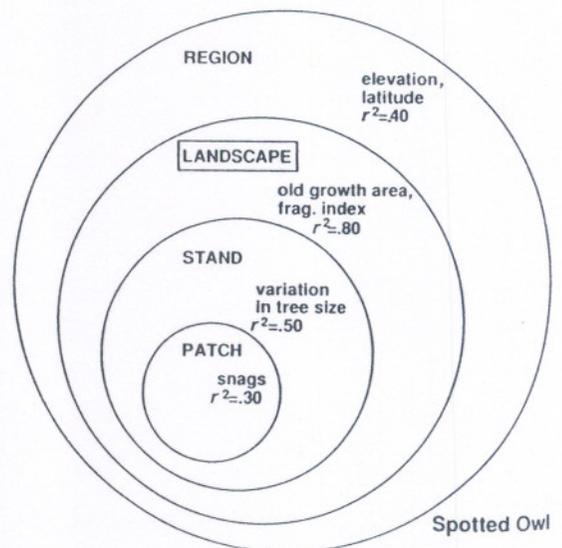


FIGURE 2. Hypothetical example illustrating that the types and strengths of animal habitat relationships may differ among spatial scales. Listed for each scale are the habitat features explaining most of the variation in Spotted Owl abundance and the strength of the association. Note in this example that the strongest correlation occurs at the landscape level.

These methods differ in the resolution of data needed for calibration and in accuracy in classifying habitat suitability. Approaches based on seral-stage association or discriminant function analysis typically identify habitats simply as suitable or unsuitable. Logistic regression generates a probability that a plot is suitable. HSI models produce output of a relative ranking from 0 (least suitable) to 1 (most suitable). And regression analyses can rate habitat quality in terms of population abundance. Which methods are most appropriate for a given application depends upon local expertise, data availability, and desired predictive capability.

While habitat may serve as a useful indicator of animal demography, it is important to point out that the relationship is seldom perfect. Biotic interactions (e.g., predation, competition, etc.), disturbances, chance demographic events, and other factors may all complicate the species-habitat associations. For this reason it is very important to validate animal-habitat models to determine if the error level is acceptable for the application at hand. Well-designed monitoring programs are useful for providing data for validation (see *Step 5*).

Land managers will typically find that information is insufficient to produce rigorous habitat models for local species. Given that management activities will proceed anyway, we recommend in the short term that managers use the best available data to good advantage. As little as we know about animal habitat associations in most regions, much more information is generally available than is currently being used for management. Over the longer term, managers should implement field studies to provide data to develop and validate habitat models.

Example

For the Cook-Quentin application we required a means of assessing bird habitat relationships that could be derived from existing studies, that considered habitat factors at two or three spatial scales, and that could interface with the habitat simulation model chosen for the application.

We settled on a simple habitat-classification scheme that considers just four variables: seral-

stage association, microhabitat association, response to edge, and minimum territory size (Table 1). The initial species list included those birds identified by Brown (1985) as having primary habitats in low- and mid-elevation conifer and conifer-hardwood forests in Oregon and Washington west of the Cascade Mountain crest. We supplemented Brown's habitat evaluation with data from the other sources listed in Table 1. Included in the analysis were the 51 species for which sufficient data were available.

Step 3: Assess the Potential Viability of Species

Objectively ranking species in terms of sensitivity to landscape change can determine which species most merit additional research or special management consideration. One approach is to map the abundance of suitable habitats across the planning area. A second approach is to examine the life-history attributes of the species.

Population viability is strongly related to area of suitable habitat (Laurance 1991) and to population size (Pimm et al. 1988), which is often a function of habitat area. Mapping habitat suitability across the planning area can identify species that may be at risk because of habitat shortages. This mapping can be done by cross-tabulating the distribution of habitat attributes over the planning area with the habitat classification functions developed in Step 2. Geographical information systems (GIS) are especially useful for managing, analyzing, and displaying these data.

Knowledge of species life histories is also useful for evaluating the potential viability of a population in a given habitat configuration. Several studies have found that certain life-history traits are strongly correlated with proneness to extinction, including short longevity, low reproductive rate, constrained dispersal, specialization on particular foods or habitats, and large home-range size (Whitcomb et al. 1981, Pimm et al. 1988, Laurance 1991). A systematic evaluation of key life-history traits of each species can identify those species

TABLE 1. Bird species, life-history traits, projected sensitivity to landscape change, and habitat suitability in the planning areas.*

Species	Reproductive effort	Nest type†	Nest height (m)†	Minimum territory size (ha)	Seral-stage assoc.‡	Micro-habitat assoc.	Response to edge§	Response to patch size§	Sensitivity score	Area suitable (%)
Neotropical migrants										
Hermit Warbler										
<i>Dendroica occidentalis</i>	4	O	17.7	0.0	M, OG	G	G	...	15	36
Solitary Vireo										
<i>Vireo solitarius</i>	4	O	11.3	1.7	M, OG	G	G	...	16	36
Hammond's Flycatcher										
<i>Empidonax hammondii</i>	4	O	7.6	0.0	M, OG	G	G	G	16	36
Western Wood-Pewee										
<i>Contopus sordidulus</i>	3	O	7.6	1.2	M, OG	G	G	...	17	36
Western Flycatcher										
<i>Empidonax difficilis</i>	6	O	4.6	0.0	M, OG	G	G	G	15	36
Olive-sided Flycatcher										
<i>Contopus borealis</i>	4	O	12.2	0.0	OC	G	E	G	17	16
Townsend's Warbler										
<i>Dendroica townsendi</i>	4	O	3.7	0.0	M, OG	G	G	...	15	36
Orange-crowned Warbler										
<i>Vermivora celata</i>	5	O	0.6	0.0	OC	G	I	...	19	10
Vaux's Swift										
<i>Chaetura vauxi</i>	5	H	1.2	0.0	OG	N	G	...	15	26
Wilson's Warbler										
<i>Wilsonia pusilla</i>	5	O	0.	0.2	G	G	G	...	17	100
Black-throated Gray Warbler										
<i>Dendroica nigrescens</i>	4	O	7.0	0.0	G	G	G	...	15	100
Western Tanager										
<i>Piranga ludoviciana</i>	4	O	11.0	0.0	OC	G	E	...	16	29
Tree Swallow										
<i>Tachycineta bicolor</i>	5	H	3.1	0.0	OC, M, OG	N	G	...	13	16
Swainson's Thrush										
<i>Catharus ustulatus</i>	8	O	3.7	0.0	Y, M, OG	G	I	...	16	48
Short-distance migrants										
American Goldfinch										
<i>Carduelis tristis</i>	5	O	4.6	0.0	OC	G	I	...	16	10
American Robin										
<i>Turdus migratorius</i>	8	O	4.6	0.0	OC	G	G	P	16	22
Western Bluebird										
<i>Sialia mexicana</i>	5	H	7.6	0.3	OC	N	G	...	13	0
Hermit Thrush										
<i>Catharus guttatus</i>	5	O	1.2	0.6	Y, M, OG	G	G	G	15	78
Rufous Hummingbird										
<i>Selasphorus rufus</i>	4	O	2.4	0.0	OC, OG	G	G	...	14	58

*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. Sensitivity score is a relative index of sensitivity to landscape change based on life-history traits. Area suitable is the percentage of the Cook-Quentin planning area that was rated as suitable habitat by the LSPA model. Migration strategy is from Ehrlich et al. 1988 and Love 1990. All other data are from Brown 1985 unless otherwise noted. ... denotes missing data.

Character variables are coded; for all variables: G = Generalist; for Nest type: O = Open, H = Hole, P = Parasite; for Seral-stage association: OC = Open Canopy (<30 yr), Y = Young (30-70 yr), M = Mature (80-190 yr), OG = Old Growth (>190 yr); for Microhabitat association: N = Natural (large trees, snags, fallen trees); for Response to edge: E = Edge specialist, I = Interior specialist; for Response to patch size: P = Positive.

†From Ehrlich et al. 1988.

‡Serving as primary habitat as defined by Brown 1985.

§From Rosenburg and Raphael 1986.

||A. J. Hansen, J. Peterson, and E. Howarth, unpublished data.

TABLE 1. (continued)

Species	Reproductive effort	Nest type†	Nest height (m)†	Minimum territory size (ha)	Seral-stage assoc.‡	Micro-habitat assoc.	Response to edge§	Response to patch size§	Sensitivity score	Area suitable (%)
Residents										
Brown Creeper <i>Certhia americana</i>	6	H	8.0	1.7	M, OG	N	G	G	13	36
Northern Goshawk <i>Accipiter gentilis</i>	3	O	12.2	100.0	M, OG	G	G	...	15	36
Winter Wren <i>Troglodytes troglodytes</i>	6	H	0.8	0.3	M, OG	N	I	P	17	19
Hairy Woodpecker <i>Picoides villosus</i>	4	H	9.8	0.0	G	N	G	G	11	78
Cooper's Hawk <i>Accipiter cooperi</i>	4	O	12.2	100.0	Y, M, OG	G	G	...	18	78
Blue Grouse <i>Dendragapus obscurus</i>	9	O	0.0	0.0	G	g	G	G	18	100
Chestnut-backed Chickadee <i>Parus rufescens</i>	7	H	2.1	1.3	M, OG	N	G	P	14	36
Sharp-shinned Hawk <i>Accipiter straitus</i>	6	O	10.7	100.0	Y, M, OG	G	G	P	18	78
Varied Thrush <i>Ixoreus naevius</i>	4	O	8.3	20.0	M, OG	G	I	...	17	19
Golden-crowned Kinglet <i>Regulus satrapa</i>	16	O	9.8	0.3	Y, M, OG	G	G	G	11	78
Pileated Woodpecker <i>Dryocopus pileatus</i>	4	H	13.8	128.0	M, OG	N	G	P	15	36
Red Crossbill <i>Loxia curvirosta</i>	4	O	7.0	0.0	M, OG	G	G	...	13	36
Red-breasted Nuthatch <i>Sitta canadensis</i>	8	H	6.7	0.9	M, OG	N	G	G	11	36
Gray Jay <i>Perisoreus canadensis</i>	4	O	5.2	64.0	Y, M, OG	G	G	...	18	77
Barred Owl <i>Strix varia</i>	3	H	10.7	0.0	M, OG	N	G	...	13	36
North Pygmy Owl <i>Glaucidium gnoma</i>	5	H	4.3	0.0	M, OG	N	G	G	12	36
American Kestrel <i>Falco sparverius</i>	5	H	14.1	100.0	OC	N	G	...	15	0
White-crowned Sparrow <i>Zonotrichia leucophrys</i>	8	O	0.8	0.0	OC	G	I	...	18	10
Rufous-sided Towhee <i>Pipilo erythrophthalmus</i>	8	O	0.8	0.0	OC	N	I	...	16	100
Song Sparrow <i>Melospiza melodia</i>	8	O	0.6	0.3	OC	G	I	...	16	10
Mountain Quail <i>Oreortyx pictus</i>	10	O	0.0	2.0	OC	G	G	G	18	22
Spotted Owl <i>Strix occidentalis</i>	2	O	6.1	100.0	M, OG	N	I	P	20	0
Northern Saw-whet Owl <i>Aegolius acadicus</i>	5	H	11.3	0.0	G	N	G	...	13	100
Northern Flicker <i>Colaptes auratus</i>	9	H	3.4	16.0	OC, M, OG	N	G	...	10	36
American Crow <i>Corvus brachyrhynchos</i>	6	O	10.7	0.0	G	G	G	...	13	100
Great Horned Owl <i>Bubo virginianus</i>	4	O	12.2	25.0	OC, M, OG	G	E	...	16	29
Red-tailed Hawk <i>Buteo jamaicensis</i>	3	O	13.1	100.0	OC, M, OG	G	G	...	14	51

(continued)

TABLE 1. (continued)

Species	Reproductive effort	Nest type†	Nest height (m)†	Minimum territory size (ha)	Seral-stage assoc.‡	Micro-habitat assoc.	Response to edge§	Response to patch size§	Sensitivity score	Area suitable (%)
Steller's Jay <i>Cyanocitta stelleri</i>	4	O	5.2	0.0	G	G	G	G	13	100
Pine Siskin <i>Carduelis pinus</i>	8	O	8.6	0.0	G	G	G	...	12	100
Purple Finch <i>Carpodacus purpureus</i>	8	O	7.0	0.0	G	G	G	...	13	100
Common Raven <i>Corvus corax</i>	8	O	6.1	0.0	G	G	G	...	13	100
Dark-eyed Junco <i>Junco hyemalis</i>	10	O	3.1	0.0	G	G	G	...	11	100

most likely to be at risk. Life-history data for vertebrates can be derived from field guides and primary ecological literature.

By assessing both habitat availability and life-history attributes, managers can identify the species that are especially sensitive to management. Such species may merit special management approaches and/or more detailed demographic studies.

Example

Habitat mapping.—Current vegetation patterns in the Cook-Quentin watershed were described using two USDA Forest Service data bases. The Mature and Over-Mature (MOM's) inventory used aerial photographs to classify stands (≥ 2 ha in size) according to tree diameter and height. These data were not validated for the Cook-Quentin landscape. Field surveys in the Fall Creek watershed on the nearby Lowell Ranger District, Willamette National Forest, indicated that the MOM's survey classified overstory size class correctly in 78% of the stands sampled (G. Marsh, unpublished report to the Willamette National Forest).

We reclassified the MOM's data for Cook-Quentin by seral stage and stand age (Table 2) for compatibility with the habitat classification functions and our landscape model. A second data set, derived from aerial photographs, delineated the location and the harvest date of all stands that were clear-cut in the past. These stands were labeled as managed, and were assumed to be devoid of the large trees, snags, and fallen trees that are known to be important

microhabitat elements for several vertebrate species, are typical in natural forests, and are generally absent in traditionally managed plantations in the region (Hansen et al. 1991). Hence, the vegetation map included three seral stages of managed forest (open canopy, young, and mature) and four seral stages of natural forest (open canopy, young, mature, and old growth). Nonvegetational features such as streams and rock outcroppings were not considered.

Habitat suitability across the basin was determined using a computer program that cross-tabulated the habitat requirements for each species with the vegetation characteristics of each 2.5-ha cell. 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 two or more neighboring patches was not considered.

Relatively little of the planning area was rated as suitable for several of the bird species (Table 1). No habitat was available for Western Bluebird, American Kestrel, and Spotted Owl (scientific names of all bird species are listed in Table 1). The open-canopy patches with natural microhabitats required by Western Bluebird and American Kestrel were not present. Also unavailable were patches of mature and old-growth forest large enough for Spotted Owl. (In reality, this species does exist in the Cook-Quentin watershed. Individual breeding pairs likely make use of several neighboring patches of older forest, a strategy not considered in our model.) Only 10% of the landscape was suit

TABLE 2. Convention used to convert USDA Forest Service vegetation data for the Cook-Quentin watershed to seral stages used in the landscape modeling application. dbh = diameter at breast height.

MOMS* vegetation classes	Landscape model	
	Seral stage	Stand age (yr)
Seedling (≤ 1.4 m height)	Open canopy	10
Sapling (1.4–6.0 m height)	Open canopy	20
Pole (> 6.0 m height, < 20 cm dbh)	Open canopy	30
Small (20–53 cm dbh)†	Young	55
Large (> 53 cm dbh)†	Mature	140
Old growth†	Old growth	250

*Mature and Over-Mature inventory (see *Step 3: Assess . . . Example: Habitat mapping*).

†Criteria for old growth described in Old Growth Definition Task Group (1986).

able for four species that require the interiors of open-canopy stands: Orange-crowned Warbler, Song Sparrow, White-crowned Sparrow, and American Goldfinch. The Olive-sided Flycatcher, an edge species, found only 16% of the landscape suitable. Nineteen percent of the area was available to Varied Thrush and Winter Wren, birds found primarily in the interiors of mature and old-growth forest. In addition to being relatively rare, habitat for many of these species was fragmented (Fig. 3), a fact that could further jeopardize local populations.

Field data were not available to validate the habitat suitability maps. As mentioned above, this is an important step in real-world applications.

Life-history traits. We also used information

on several life-history characteristics to derive a "sensitivity" index (Hansen and Urban 1992) of the potential responsiveness of each species to landscape change. Species were rated from 1 (least sensitive) to 3 (most sensitive) for each of the eight life-history traits (Table 1). A total score for a species was derived by summing the scores across traits. The rationales for the criteria generally follow the findings of Whitcomb et al. (1981). The validity of this approach was supported by a significant correlation between the sensitivity scores of Pacific Northwest bird species and their regional population trends over the past 20 yr (Hansen and Urban 1992).

Scores ranged from 11 (least sensitive) to 20 (most sensitive) (Table 1). Among those with the highest scores were Spotted Owl (20), Orange-crowned Warbler (19), Olive-sided Flycatcher (17), Winter Wren (17), and Varied Thrush (17). All of these also have limited habitat in the planning area (see above), hence they are among the species that may be most vulnerable under some management activities.

The mapping of habitats within the planning area and the life-history analyses identified several bird species potentially sensitive to landscape change that had not previously been recognized by conservationists (e.g., some early-successional species: Orange-crowned Warbler, White-crowned Sparrow). This fact emphasizes the value of objective approaches for rating species viability. Such species may merit additional research and management attention.

We emphasize that attention to spatial scale is important in assessing species sensitivity. The data we used in the life-history analysis repre-

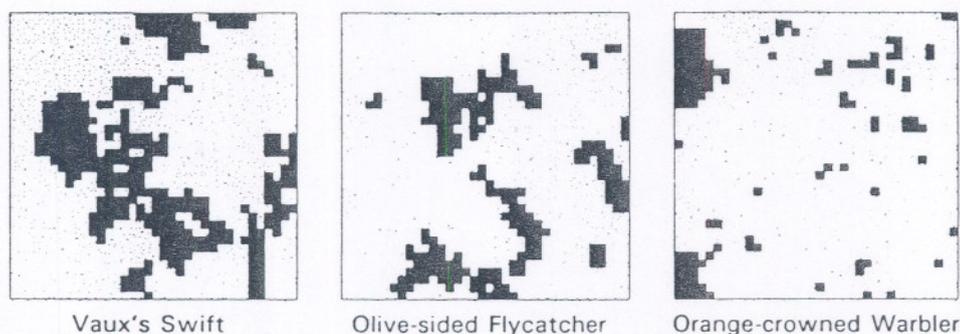


FIGURE 3. Maps of suitable habitat (■) in the Cook-Quentin planning area for bird species associated respectively (left to right) with old-growth, edge, and open-canopy interior habitats.

sent approximations across the range of each species, making this analysis more or less regional in scale. The habitat mapping, in contrast, only considered the Cook-Quentin landscape. A similar mapping effort at larger spatial scales (regional or continental) is required to place the local results in a context for evaluation. If, for example, the Orange-crowned Warbler has abundant habitats or large populations elsewhere in the region, managers of the Cook-Quentin landscape may choose not to be concerned about the shortage of habitat for this species in the planning area. As mentioned under *Step 1*, local objectives need to be derived based on information at several spatial scales.

We are now attempting to expand our approach for habitat mapping to the subregional scale. Species range maps generated by the Gap Analysis Project (Scott et al. 1987, 1991) and various continental surveys of bird population trends (e.g., Droege 1990) are also useful in establishing a broader-scale context for evaluating the sensitivity of local species.

Step 4: Project Future Habitat Patterns Under Alternative Management Prescriptions Using Simulation Models

Land managers have a long history of trying to assess the likely future consequences of differing management strategies. Key challenges for landscape management are to develop a comprehensive set of alternative landscape designs and to perform objective trade-off analyses of resource response under each design.

Designing landscapes for biodiversity is a topic currently attracting much attention, but there are few good examples or comprehensive guidelines. General principles are presented in Harris (1984) and Hunter (1991). Thomas et al. (1990) and K. N. Johnson, J. R. Franklin, J. W. Thomas, and J. Gordon (*unpublished report* [1991] to the Committee on Agriculture, U.S. House of Representatives, Washington, D.C.: available from Forest Research Laboratory Publications, College of Forestry, Oregon State University, Corvallis, Oregon, USA) offer case studies of regional-scale designs for

late-seral and riparian species in the Pacific Northwest (PNW) of the United States.

Knowledge of landscape dynamics in presettlement times may sometimes offer guidance for modern landscape design. Information on the relationships among disturbance regimes, habitat patterns, and vertebrates in natural landscapes can provide a context for understanding and managing current landscapes (e.g., Romme and Despain 1989, Hansen et al. 1991). However, we caution against using a snapshot of spatial patterns from the past as a literal guide for a desired future condition. The high level of spatial and temporal variation in many presettlement landscapes may be unacceptable today. Also, modern landscapes are often rescaled and bounded in such a way that the movements of disturbance and organisms typical in the past are not now possible (Urban et al. 1987).

Presettlement fire regimes in the PNW, for example, were extremely variable spatially and temporally (Morrison and Swanson 1990). During periods when wildfire was intense over large areas, forest-dwelling species probably persisted in small refugial areas. Some of these species likely recolonized burned habitats slowly during the decades to centuries following the disturbance. Unless such relaxation periods and suitable dispersal corridors are provided, modern populations would likely be lost under these patterns.

We conclude that there is no alternative but to use ecological principles to design landscape patterns deliberately to meet management objectives. Much work is needed on how this can best be done.

Once a set of management alternatives has been designated, trade-off analyses of resource responses can help to determine which alternatives best meet the management objectives. Computer simulation models can be extremely useful for projecting the responses of several resource variables over long time periods and large areas. A variety of models have been developed to simulate vegetation dynamics and vertebrate habitats. These models differ in the degree of biological realism in their formulations, the spatial scale at which vegetation is considered, and extent of spatial interaction among neighboring cells. Reviews can be found in Shugart (1984), Verner et al. (1986), and

Huston et al. (1988). The choice of which type of model to use for vertebrate habitat applications depends upon the questions being addressed, the data sets available, the prediction accuracy required, and the programming expertise available. Unfortunately, "easy to use" packages are not generally available. A substantial investment is usually required to adapt a general model to a particular location.

Example

Models. We used the landscape model LSPA (Li 1989, Hansen et al. 1992) and the gap model ZELIG.PNW (Urban 1990) to simulate four disturbance-management regimes in the Cook-Quentin watershed. LSPA is a geometric model that simulates change in a gridded landscape according to a user-specified timber harvest regime involving cutting-unit size, spatial distribution of cutting units, and harvest rate. Vegetation dynamics are not modeled directly; stands are assigned to seral stages based on the time elapsed since disturbance. The model calculates several landscape metrics at each time-step and classifies habitat suitability for each bird species according to the criteria described under *Step 2*.

ZELIG is a generic version of the gap model FORET (Shugart 1984) that was designed to be adapted to diverse forest types. These models simulate the establishment, growth, and death of individual trees on small plots equivalent to the area shaded by a canopy tree. Tree demography is stochastically constrained by tree life-history traits and local environmental conditions. Output from several simulated gaps is aggregated for a statistical description of stand dynamics. ZELIG.PNW is a version developed for forests in the western Oregon Cascades. It incorporates several updates to ZELIG since the model was introduced (Urban 1990), involving tree height-diameter relationships, leaf area, tree growth, and soil moisture (D. L. Urban and S. L. Garman, *unpublished manuscript*). ZELIG.PNW additionally includes sub-routines to simulate diverse silvicultural prescriptions and snag and fallen-log dynamics (Garman et al. 1992). The model has performed well in validations for chronosequences of natural and managed forests at elevations of about 1000 m in the western Oregon Cascades (Garman et al. 1992. D. L. Urban and S. L. Garman, *unpublished manuscript*) (Fig. 4).

For this demonstration ZELIG.PNW was run using environmental conditions and tree

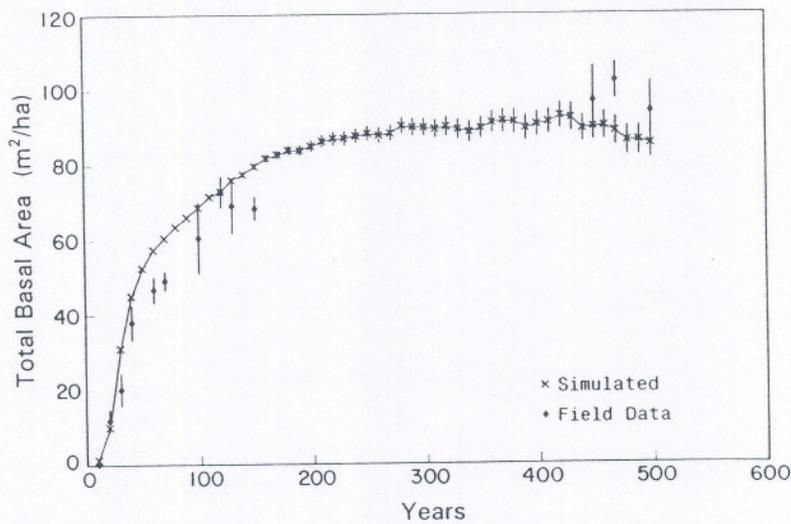


FIGURE 4. Trends in total basal area under natural succession at 1000 m elevation, western slope of the Oregon Cascades mountains as described by field data and as simulated with the gap model ZELIG.PNW (see *Step 4 . . . Example: Models*). Simulated data are based on 30 model plots. Sample sizes of field data varied from 5 to 42 reference stands. Data shown are means \pm 1 SE.

species for the 1000-m elevation in the west-central Oregon Cascades. Thirty 0.1-ha plots were modeled for each simulation and the results averaged to represent the stand. ZELIG.PNW was initialized with a 250-yr-old simulated stand for all four prescriptions. The response variables derived from ZELIG were standing basal area of saw timber (trees > 30 cm in diameter at breast height) and basal area of saw timber harvested.

Wood production across the Cook-Quentin landscape under each disturbance-management scenario was determined by first calculating the area occupied by each seral stage at each time-step. The amounts of standing saw timber and saw timber harvested for each seral stage were derived from the ZELIG runs for the time-steps equivalent to the median ages of the seral stages. These values were then summed across seral stages to obtain totals for the landscape at that time step. In the wood production run, no trees were retained during harvest, and the harvest level for each seral stage was assumed to be equal to the simulated basal area of saw timber for the mean age class within the seral stage. The same procedure was used for the multiple-use run except that basal area of saw timber harvested was reduced by 9.3% for each seral stage. This level is equivalent to the amount retained (9.8 trees/ha) at the start of the ZELIG simulation of multiple use.

The variable reported here as total wood

production was calculated as the cumulative basal area of saw timber harvested up until a time-step plus the basal area of saw timber standing at that time-step.

Management alternatives. The four disturbance-management regimes simulated are described in Table 3. A presettlement fire regime was modeled to offer a point of reference for the management prescriptions. We previously simulated the regime of high-severity fires documented for the Cook-Quentin watershed using a model similar to LSPA (Hansen et al. 1992). We generated a starting landscape for the present application by initializing the fire model with 200-yr-old forest and simulating 220 yr of forest succession to reduce the effects of initial vegetation conditions. A run for an additional 140 yr is reported here.

The other three prescriptions were initialized with present vegetation patterns in the Cook-Quentin planning area. The wood production run is typical of that used on private forest lands in the PNW today. Cutting units were maximally dispersed under a staggered-setting design. One 70-yr rotation was simulated, and the results at year 70 were considered steady state for an additional rotation. The multiple-use prescription, based on principles advanced as ecological forestry (Franklin 1992), had larger harvest units, a longer rotation, and a higher level of tree, snag, and log retention than the wood-production run. Also, the units were

TABLE 3. Natural disturbance and management alternatives simulated for the Cook-Quentin watershed (Oregon).

Model*	Variable	Prescription			
		Natural fire	Wood production	Multi-use forestry	No action
LSPA	Disturbance patch size (ha)	8.6†	22.5	40.0	NA‡
	Disturbance pattern	Random	Maximum dispersal	Maximum aggregation	NA
	Rotation length (yr)	114§	70	140	NA
	Minimum harvest or burn age (yr)	20	55	55	NA
ZELIG	Retention level (no. of trees/ha)	9.8 PSME/ha	none	9.8 PSME/ha	NA
	Inseeding rate (seeds/ha)	Natural	988 PSME	988 PSME	988 PSME
	Thinning yr 15 and 30 (stems/ha)	None	543 PSME	380 PSME	None
				163 TSHE¶	

*The landscape simulation model LSPA and the gap model ZELIG.PNW are described in *Step 4: Project future habitat patterns . . . : Example: Models*. † Patch size is modeled as an exponential function with a mean of 8.6 ha.

‡NA = not applicable.

§ Fire rotation interval is an exponential function with a mean of 8.8% of the landscape per decade.

¶PSME = *Pseudotsuga menziesii*.

¶TSHE = *Tsuga heterophylla*.

maximally aggregated using a quarter-strip cutting design (Li 1989). The final (no action) prescription had no management activities over the 140-yr simulation period.

We assumed for the purposes of bird habitat classification that all stands in the natural fire and multiple-use runs contained sufficient levels of live trees, snags, and fallen trees to support the bird species requiring these features. These features are removed under traditional clear-cutting, and thus we assumed that all harvest units in the wood-production run and harvest units under age 110 in the no-action run were unsuitable habitat for species requiring such microhabitat features.

Results. Landscape geometry and the distribution of seral stages differed substantially among the four scenarios (Fig. 5). The wood-production run lost all natural microhabitats and late seral stages by year 70 (Fig. 6a and 6b), while early seral stages remained abundant (Fig. 6c). Results of the no-action run were somewhat the inverse of those under wood production. The multiple-use run maintained high levels of natural microhabitats and moderate levels of early and late seral stages, patterns also generated by the natural-fire run. Total density of edges between patches of different seral stage, a measure of landscape fragmentation, was highest under the natural-fire regime, intermediate under no action and wood production, and lowest under multiple use over much of the simulation (Fig. 7). We did not differentiate between the habitat suitability of forest edges created by wildfire and those created by timber harvest. In reality, fire-generated edges likely differ from the edges of harvest units in structure and likely result in less extreme changes in forest interior microclimate and vertebrate habitat suitability. Even so, the fire run suggests that patch shape and seral-stage distribution were complex under the presettlement fire regime in this basin (see also Morrison and Swanson 1990). This finding counters the notion that presettlement landscapes in this portion of the Cascades were continuous expanses of old growth.

Habitat diversity for all bird species was substantially lower under wood production than under the other three scenarios (Fig. 8a), due mostly to the loss of natural microhabitats

and late seral stages. None of the 18 species primarily associated with late seral stages had habitat after year 70 under wood production (Fig. 8b); all but one of these species (Spotted Owl) had some suitable habitat in the other three runs. Habitat richness for early seral species was highest under natural fire and multiple use, slightly lower under wood production, and went to 0 under no action (Fig. 8c).

Production of saw timber was substantially greater under wood production than under multiple use. By year 140, total wood production under the wood production run was 49% greater than that under multiple use (Fig. 9). This difference was due to: (1) modeled tree-growth rates being reduced in the multiple-use prescription by overstory retention and by thinning for mixed species, and (2) more rapid conversion of older, slower-growing natural stands to younger, faster-growing plantations under the wood-production run.

This exercise is, to our knowledge, the first attempt to quantify the consequences for wildlife habitat and wood production of alternative management scenarios that considers both stand- and landscape-level factors. The simulations predict that the multiple-use prescription would maintain bird habitat diversity for all species, late-seral species, and early-seral species at levels similar to the natural fire regime. Wood production, however, is substantially reduced under the multiple-use run compared with the wood-production run. Land managers, after weighing the assumptions and limitations of the methodology, can use this information in choosing the alternative that is most likely to promote management objectives. The multiple-use run would be the obvious choice based on the stated objectives of this demonstration and the spatial and temporal scale at which the analysis was conducted.

Step 5: Implement Preferred or Experimental Strategies and Monitor the Responses of Habitats and Species

Implementation of a preferred strategy (or strategies) is an experiment in itself that can

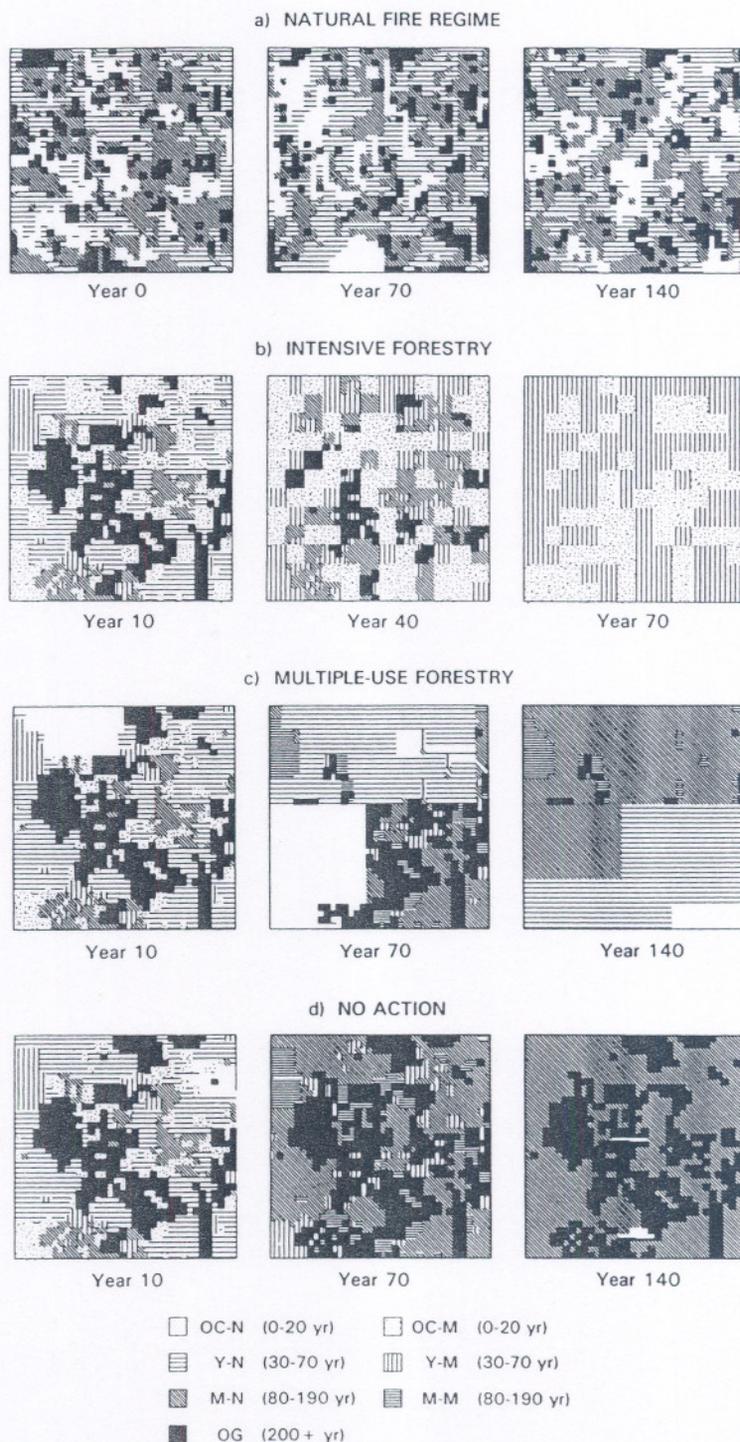


FIGURE 5. Maps of vegetation pattern in the Cook-Quentin (Oregon, USA) planning area for selected time-steps as simulated by the landscape model LSPA for four disturbance-management scenarios: (a) natural fire; (b) wood production; (c) multiple use; and (d) no additional management intervention. OC-N = open-canopy natural; Y-N = young natural; M-N = mature natural; OG = old growth; OC-M = open-canopy managed; Y-M = young managed; M-M = mature managed.

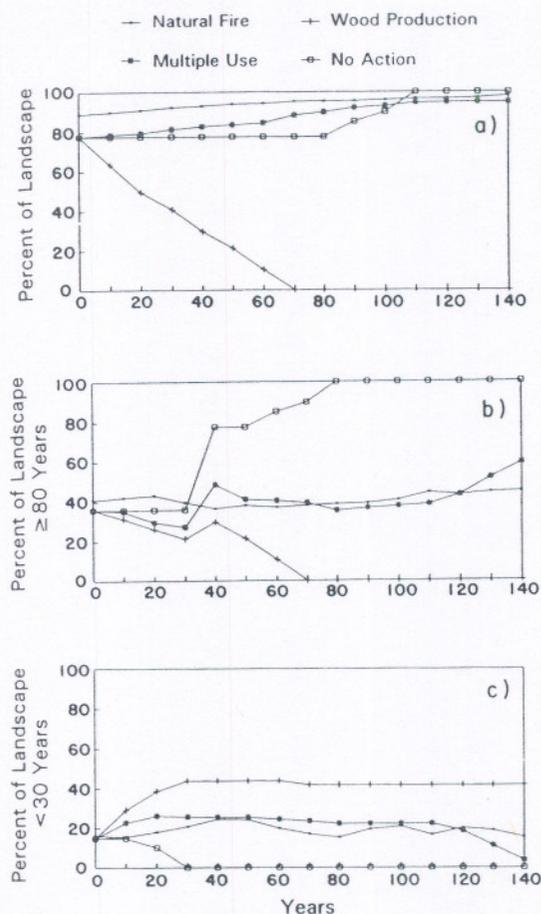


FIGURE 6. Proportion of the simulated landscape under each of four management scenarios containing: (a) levels of canopy trees, snags, and coarse woody debris sufficient for bird species requiring these features; (b) mature and old-growth forest (≥ 80 yr); and (c) early seral stands (< 30 yr).

reveal a great deal about resource response to manipulation (see Walters [1986] and Walters and Holling [1990] for reviews). In fact, land managers may sometimes wish to subdivide the planning area and implement two or more management alternatives, in a replicated fashion if possible, and compare results.

A well-designed monitoring program is critical for learning from any management experiment. This view is widely held among federal forest managers. Most forest plans in our region call for some level of monitoring, but designing and implementing effective monitoring programs is neither simple nor inexpen-

sive. This fact is in evidence in the Pacific Northwest where even the most basic information on habitat distributions in management units (e.g., snag levels in harvest units) has not been successfully assembled, let alone the more comprehensive information needed to manage vertebrate habitat diversity.

We suggest that managers of vertebrate habitats monitor the effectiveness of implementing a prescription, the responses of habitat to the management action, and the population responses of select species. Monitoring programs should consider multiple temporal and spatial scales. See Noss (1990) for a thoughtful approach to monitoring biodiversity.

Creative approaches are needed to collect these data in an efficient and cost-effective fashion. Remote sensing offers promise for sampling habitats from microsite to landscape and regional levels (e.g., Cohen and Spies 1992). Monitoring wildlife species abundance still requires field sampling. Ultimately, inter-agency cooperation may offer the best hope of designing and implementing appropriate monitoring protocols. Expanded funding levels will also be essential. The payoffs of rigorous monitoring are apt to be considerable. These data are needed both for evaluating the extent to which management objectives are met and for testing and updating wildlife habitat and computer simulation models.

Completion of Step 5 leads back to Step 1. An iterative process of reevaluating management objectives, performing trade-off analyses, and conducting management experiments of-

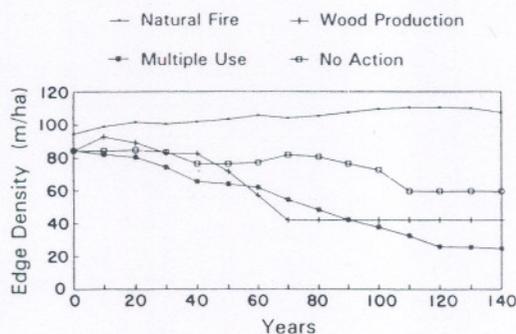


FIGURE 7. Density of edges among seven seral stages in the planning area under the four management scenarios.

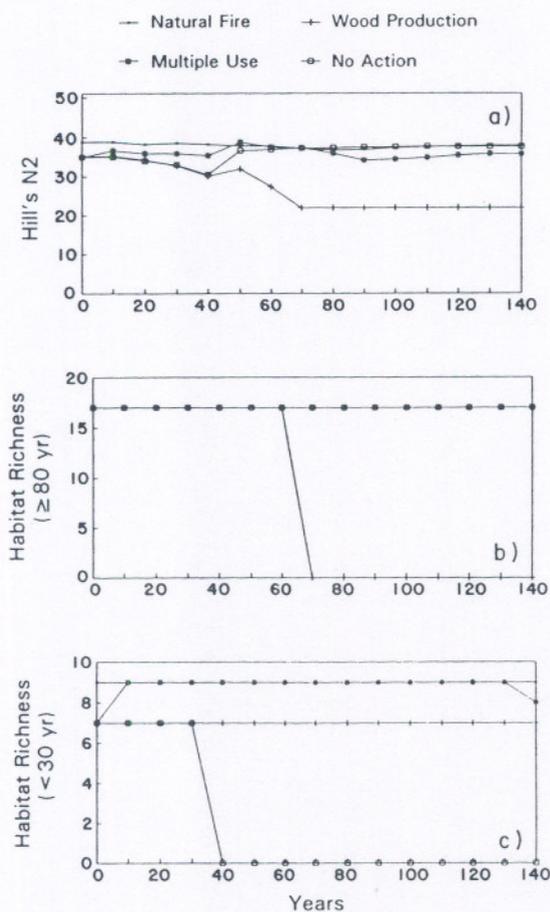


FIGURE 8. Bird habitat diversity in the planning area under the four management scenarios. (a) Diversity (Hill's N_2) for all bird species. (b) Number of species primarily associated with mature and old-growth stands with some suitable habitat (habitat richness) (total $n = 18$). (c) Habitat richness for species primarily associated with early seral habitats (total $n = 9$).

fers hope for successfully managing vertebrate diversity on multiple-use lands.

Conclusion

Society and the courts are increasingly demanding objective and effective management strategies that balance complex resource demands. The approach we describe for managing vertebrates on multiple-use lands is a logical step towards more effective management of biological diversity.

One limitation of the approach is that it is restricted to organisms for which taxonomy, habitat requirements, and life-history attributes are described. This is the case for vertebrates and vascular plants in many areas, but not for most invertebrates and nonvascular plants (which represent the great majority of species). The coarse-filter approach (Noss 1987, Hunter 1991) may be the best alternative for such groups until more information becomes available. Efforts such as this one on the better known taxa are useful for delineating the types of information that are needed on groups yet to be studied in any detail.

Another limitation of the approach is that habitat suitability is evaluated rather than vertebrate demography. As mentioned earlier, habitat is known to be an imperfect indicator of demography. Consequently, other approaches have been developed that simulate reproduction, dispersal, and survival of individual animals across complex landscapes (e.g., Pulliam et al. 1992). Unfortunately, data for parameterizing these models is available for relatively few vertebrate species and these species may not necessarily be the ones most sensitive to human activities. For this reason we advocate using the habitat-based approach as a way to consider most vertebrates in a community. The demographic approaches should additionally be used for those species that are sufficiently well known.

The demonstration for the Cook-Quentin

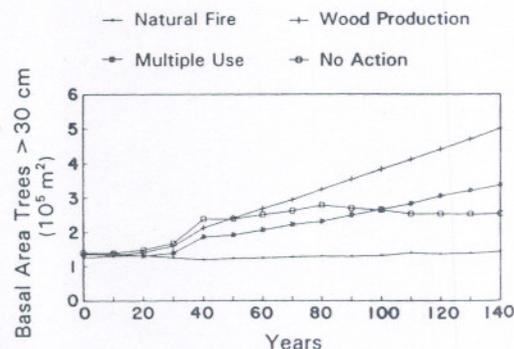


FIGURE 9. Total wood production (cumulative basal area harvested up to each time-step plus basal area of live trees) of saw timber (trees > 30 cm in diameter at breast height) in the planning area under the four management scenarios.

landscape also has various limitations. The vertebrate habitat models used have not been validated, and thus we were unable to assess the accuracy of the predictions. In reality, current data are insufficient to validate the habitat functions. We believe it is better to base management decisions on objectively derived habitat functions, even if unvalidated, than not to consider vertebrates at all. In the longer term, obtaining data for validation should be a high priority among those charged with managing vertebrate diversity.

Also, our simulations did not consider landscape attributes such as topography, stream courses, and road networks. These factors are likely important to forest productivity, logging feasibility, and animal habitat suitability in many landscapes (e.g., Li 1989). Some important ecological processes were also not considered, including propagation of natural disturbance, long-term site productivity, seed dispersal, and the role of animals in altering habitats. Knowledge of such processes is important for predicting habitat response to management. For example, traditional timber management in the region may reduce long-term site productivity and result in declining timber yields in successive rotations (Franklin 1992), an outcome not considered under our wood-production run. Some of these factors are now being incorporated into our models (topography, streams, site index, and nutrient cycling) to increase the realism of the simulations.

A final limitation is that this demonstration did not consider the regional context of the planning area. Applying the approach across neighboring landscapes would be useful for setting objectives, evaluating vertebrate species sensitivity to landscape change, and interpreting the trade-off analyses.

On the other hand, the approach is attractive in offering a logical set of steps that, when implemented iteratively, should improve both our knowledge base and the effectiveness of management. The approach allows for most vertebrates in a planning area to be considered and for their potential sensitivity to land use to be evaluated objectively. Such assessment of species sensitivity is important because species that are abundant in a location can become rare in relatively short time periods in changing

landscapes (Hansen et al. 1992). Another strength of the approach is the tandem use of simulation models and management experiments. Given that stand- and landscape-scale experiments on forest dynamics will require decades to complete, computer modeling can be used now to perform trade-off analyses of resource response under differing management strategies. Modeling also is useful for identifying information gaps. Management experiments complement modeling by providing data for parameterizing the models and for assessing the effectiveness of various landscape designs. A final strength of the approach is that it encourages use of the best information currently available. Rather than ignoring ecological data because they are incomplete, it encourages that management decisions be based on the best information that is available at the time and advocates implementation of mechanisms to improve the knowledge base.

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References

- Allen, T. F. H., and T. B. Starr. 1982. *Hierarchy: perspectives for ecological complexity*. University of Chicago Press. Chicago, Illinois, USA.
- Brown, E. R., technical editor. 1985. *Management of wildlife and fish habitats in forests of western Oregon and Washington*. USDA Forest Service Report RG-F&WL-192-1985. USDA Forest Service, Portland, Oregon, USA.
- Brussard, P. F. 1991. The role of ecology in biological conservation. *Ecological Applications* 1:6-12.
- Capen, D. E., editor. *The use of multivariate statistics in studies of wildlife habitat*. USDA Forest

- Service General Technical Report RM-87. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Cody, M. L. 1985. An introduction to habitat selection in birds. Pages 4-46 in M. L. Cody, editor. *Habitat selection in birds*. Academic Press, Orlando, Florida, USA.
- Cohen, W. B., and T. A. Spies. 1992. Estimating structural attributes of Douglas-Fir/Western Hemlock forest stands from landsat and SPOT imagery. *Remote Sensing on the Environment* 41:1-17.
- Droege, S. 1990. The North American breeding bird survey. In J. R. Sauer and S. Droege, editors. *Survey designs and statistical methods for the estimation of avian population trends*. U.S. Fish and Wildlife Service, Biological Report 90:1-4.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. *The birder's handbook*. Simon & Schuster, New York, New York, USA.
- Ehrlich, P. R., and E. O. Wilson. 1991. Biodiversity studies: science and policy. *Science* 253:758-762.
- Franklin, J. F. 1992. Scientific basis for new perspectives in forests and streams. Pages 25-72 in R. Naiman, editor. *Watershed management: balancing sustainability and environmental change*. Springer-Verlag, New York, New York, USA.
- Franklin, J. F., and C. T. Dyrness. 1973. *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, Oregon, USA.
- Garman, S. L., A. J. Hansen, D. L. Urban, and P. F. Lee. 1992. Alternative silvicultural practices and diversity of animal habitat in western Oregon: a computer simulation approach. Pages 777-781 in P. Luker, editor. *Proceedings of the 1992 Summer Simulation Conference*. The Society for Computer Simulation, Reno, Nevada, USA.
- Gillis, A. M. 1990. The new forestry: an ecosystem approach to land management. *BioScience* 40:558-562.
- Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Lessons from natural forests: implications for conserving biodiversity in natural forests. *BioScience* 41:382-392.
- Hansen, A. J. and D. L. Urban. 1992. Avian response to landscape pattern: the role of species life histories. *Landscape Ecology* 7:163-180.
- Hansen, A. J., D. L. Urban, and B. Marks. 1992. Avian community dynamics: the interplay of human landscape trajectories and species life histories. Pages 170-195 in A. J. Hansen and F. di Castri, editors. *Landscape boundaries: consequences for biological diversity and ecological flows*. Ecological Studies Series. Springer-Verlag, New York, New York, USA.
- Harris, L. D. 1984. *The fragmented forest*. University of Chicago Press, Chicago, Illinois, USA.
- Hunter, M. L., Jr. 1990. *Wildlife, forests, and forestry*. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- _____. 1991. Coping with ignorance: the coarse-filter strategy for maintaining biodiversity. Pages 266-281 in K. A. Kohm, editor. *Balancing on the brink of extinction*. Island Press, Washington, D.C., USA.
- Huston, M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological theory. *BioScience* 38:682-691.
- James, F. C., R. F. Johnston, G. J. Niemi, and W. J. Boecklen. 1984. The Grinnellian niche of the Wood Thrush. *American Naturalist* 124:17-47.
- Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology* 5:1-11.
- Li, H. 1989. *Spatio-temporal pattern analysis of managed forest landscapes: a simulation approach*. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Love, T. 1990. Distribution maps of Pacific Northwest birds using neotropical habitats. *Oregon Birds* 16:56-85.
- Mann, C. C., and M. L. Plummer. 1992. The butterfly problem. *The Atlantic* 269(1):47-70.
- Morrison, P. H., and F. J. Swanson. 1990. *Fire history and pattern in a Cascade Range landscape*. USDA Forest Service General Technical Report PNW-GTR-254, USDA Forest Service, Portland, Oregon, USA.
- Myers, N. 1979. *The sinking ark. A new look at the problem of disappearing species*. Pergamon, Elmsford, United Kingdom.
- Neilson, R. P., G. A. King, R. L. De Velice, and J. M. Lenihan. 1992. Regional and local vegetation patterns: the responses of vegetation diversity to subcontinental air masses. Pages 129-149 in A. J. Hansen and F. di Castri, editors. *Landscape boundaries: consequences for biological diversity and ecological flows*. Ecological Studies Series. Springer-Verlag, New York, New York, USA.
- Newmark, W. D. 1987. A land-bridge island perspective on mammalian extinctions in western North American parks. *Nature* 325:430-432.
- Noss, R. F. 1987. From plant communities to landscapes in conservation inventories: a look at the Nature Conservancy (USA). *Biological Conservation* 41:11-37.
- _____. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4:355-364.
- Noss, R. F., and L. D. Harris. 1986. Nodes, networks, and MUMs: preserving diversity at all scales. *Environmental Management* 10:299-309.

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- Old-Growth Definition Task Group. 1986. Interim definitions for old-growth Douglas-fir and mixed-conifer forests in the Pacific Northwest and California. Forest Service Research Note PNW-447. USDA Forest Service, Portland, Oregon, USA.
- O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A hierarchical concept of the ecosystem. Princeton University Press, Princeton, New Jersey, USA.
- Pickett, S. T. A., and J. N. Thompson. 1978. Patch dynamics and the size of nature reserves. *Biological Conservation* 13:27-37.
- Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. *American Naturalist* 132:757-785.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- Pulliam, H. R., J. B. Dunning, Jr., and J. Liu. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* 2:165-177.
- Rodiak, J. E., and E. G. Bolen. 1991. Wildlife and habitats in managed landscapes. Island Press, Washington, D.C., USA.
- Rohlf, D. J. 1991. Six biological reasons why the endangered species act doesn't work—and what to do about it. *Conservation Biology* 5:273-282.
- Romme, W. H., and D. G. Despain. 1989. Historical perspective on the Yellowstone fires of 1988. *BioScience* 39:695-699.
- Rosenberg, K. V., and M. G. Raphael. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. Pages 263-272 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Salwasser, Hal. 1991. In search of an ecosystem approach to endangered species conservation. Pages 247-265 in K. A. Kohm, editor. *Balancing on the brink of extinction*. Island Press, Washington, D.C., USA.
- Schamberger, M. L., and L. J. O'Neil. 1986. Concepts and constraints of habitat-model testing. Pages 5-10 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Scott, J. M., B. Csuti, J. D. Jacobi, and J. E. Estes. 1987. Species richness: a geographic approach to protecting future biological diversity. *BioScience* 37:782-788.
- Scott, J. M., B. Csuti, K. Smith, J. E. Estes, and S. Caicco. 1991. Gap analysis of species richness and vegetation cover: an integrated biodiversity conservation strategy. Pages 282-297 in K. A. Kohm, editor. *Balancing on the brink of extinction*. Island Press, Washington, D.C., USA.
- Shugart, H. H. 1984. *A theory of forest dynamics*. Springer-Verlag, New York, New York, USA.
- Soulé, M. E. 1991. Conservation: tactics for a constant crisis. *Science* 253:744-750.
- Thomas, J. W., editor. 1979. *Wildlife habitats in managed forests of the Blue Mountains of Oregon and Washington*. Agriculture Handbook 553. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.
- Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. *A conservation strategy for the Northern Spotted Owl*. Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl (USDA: Forest Service, USDI: Bureau of Land Management, Fish and Wildlife Service, and National Park Service). 1990-791-171/20026. United States Government Printing Office, Washington, D.C., USA.
- Urban, D. L. 1990. A versatile model to simulate forest pattern. A user's guide to ZELIG version 1.0. University of Virginia, Charlottesville, Virginia, USA.
- Urban, D. L., A. J. Hansen, D. O. Wallin and P. J. Halpin. 1992. Life-history attributes and biodiversity: scaling implications for global change. Pages 173-195 in O. T. Solbrig, H. M. van Emdem, and P. G. van Oordt, editors. *Biological diversity and global change*. Monograph 8. International Union of Biological Sciences. Paris, France.
- Urban, D. L., R. V. O'Neill, and H. H. Shugart. 1987. Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. *BioScience* 37:119-127.
- Urban, D. L., H. H. Shugart, Jr., D. L. DeAngelis, and R. V. O'Neill. 1988. *Forest bird demography in a landscape mosaic*. Publication Number 2853. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Urban, D. L., and T. M. Smith. 1989. Microhabitat pattern and the structure of forest bird communities. *American Naturalist* 133:811-829.
- USFWS [U.S. Fish and Wildlife Service]. 1981. *Standards for the development of suitability index models*. Ecological Services Manual 103. USDI Fish and Wildlife Service, Division of Ecological Services. U.S. Government Printing Office, Washington, D.C., USA.
- Verner, J., and A. S. Boss, technical coordinators. 1980. *California wildlife and their habitats: western Sierra Nevada*. USDA Forest Service, General Technical Report PSW-37. Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.

- Verner, J., M. L. Morrison, and C. J. Ralph, editors. 1986. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Walters, C. J. 1986. *Adaptive management of renewable resources*. McGraw-Hill, New York, New York, USA.
- Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. *Ecology* **71**:2060-2068.
- Westman, W. E. 1990. Managing for biodiversity. *BioScience* **40**:26-33.
- Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-205 in R. L. Burgess and D. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1986. A lesson in the limitations of field experiments: Shrub-steppe birds and habitat alteration. *Ecology* **67**:365-376.
- Wilcove, D. S. 1989. Protecting biodiversity in multiple-use lands: lessons from the U.S. Forest Service. *Trends in Ecology and Evolution* **4**:385-388.
- Wilson, E. O., editor. 1988. *Biodiversity*. National Academy Press, Washington, D.C., USA.

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