Chapter 14

Managing For Wildlife: A Key Component for Social Acceptance of Compatible Forest Management

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1. Introduction

Why manage for wildlife in U.S. forests? American society demands it. Which species should be favored? The social and cultural value of individual species continue to evolve. Large changes have taken place in less than 40 years; Kimmins (2002) states that changes in societal values have produced "future shock" in the forestry profession, with foresters and their institutions unable to adapt. Public demand for wildlife conservation has resulted in a long chain of legislation governing federal lands and supporting state and private wildlife conservation efforts (Hunter 1990). Nevertheless, controversies over forest management continue, and have led to a shift from active management for wildlife to establishment of large reserves off limits to active management (Hunter 1999). Now attention is shifting to second-growth forests where the public is concerned about biodiversity and ecosystem health (Hunter 1999, Lindenmayer and Franklin 2002, Shields et al. 2002).

Public scrutiny is no longer limited to federal lands. State agencies have recognized the need to address public concerns (Belcher 2001). Efforts to conserve wildlife on privately held forests are on the rise (Best and Wayburn 2001). Wood products companies find it necessary to develop compatible management approaches, including habitat conservation plans (Loehle et al. 2002). Public focus on wildlife conservation extends worldwide, even to coffee plantations (http://www.starbucks.com/aboutus/csr.asp). As public interest expands, it is prudent to ask what trends in values are relative to forest wildlife.

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Surveys of American cultures (e.g., Ray 1996) found that sustainability environmental, economic, and social—and other community-oriented values were on the rise. Sustainability in this sense is a broader concept than that outlined in the Montreal Process. It is more akin to the concept of compatibility Haynes et al. (2003) define as "...managing forests to produce wood and other uses in a socially acceptable manor without decreasing any other value," but with less emphasis on wood and more on human and ecological well-being (Lackey 2001). For example, in a survey of American forest values (Shields et al. 2002), the highest scoring values were (1) conserving and protecting watersheds (mean = 4.7on a scale of 1 to 5); (2) protecting ecosystems and wildlife habitat (mean = 4.6); (3) placing as much importance on future generations as on the current in land use decisions (mean = 4.5); (5) acknowledging wildlife, plants, and humans have equal rights (mean = 4.3); and (6) preserving natural resources, even if some people must do without (mean = 4.1). Utilitarian scores averaged less than 3 (indicating disagreement). Still, the public believes in allowing for diverse uses (mean = 4.1).

In this chapter, I focus on forest management for wildlife outside reserves, and how such management pertains to compatible forest management. A core aspect-of compatibility is social sustainability, or maintaining a civil society (Goodland 1995). Moving from adversarial to collaborative interactions is important to the public (Shields et al. 2002) and will help promote a civil society. Thus, I develop approaches to compatibility that are amenable to collaborative management (Wondolleck and Yaffee 2000, Behan 2001, Kemmis 2001). I use examples from Oregon and Washington where people are interested in conserving wildlife (from game to endangered species) and overall biological diversity, maintaining local communities, and obtaining useful goods and services from forests (e.g., open space, clean air and water, edible fungi and berries, floral greens, and wood products). These values are not limited to Oregon and Washington but are emerging throughout developed countries (e.g., Folke et al. 1996, Entwistle and Dunstone 2000, Holling 2001, Larson 2001).

I examine how wildlife management can address compatibility by formulating objectives for wildlife that can be (1) surrogates for diverse values related to wildlife and biodiversity in general, (2) modeled in planning exercises with a fair degree of confidence, (3) readily understood and evaluated by diverse groups of people, and (4) expressed in terms of measurable outputs. Managing forests requires managing multiple ecological processes over the long term. I summarize key processes, present a new classification of forest development based on processes, and provide an example of process-based management in simulation modeling. Finally, I discuss how well my predictions are holding up under experimental conditions.

2. Objectives for Wildlife Management

If compatibility is a goal of forest management, then it is necessary to develop mutually compatible objectives for the various components of forest ecosystems and the goods and services that forests provide. If economic objectives are paramount, then it may be useful to evaluate how environmental values are affected, to determine what some environmental opportunity costs are, and to answer the question: Is it likely that single focus management will be compatible with conservation of wildlife?

It is possible to formulate objectives for wildlife that can serve as surrogates for diverse values and that can be expressed in terms of measurable outputs. Maximizing one species of wildlife is rarely an environmental objective, and rarely will focus on just a few species meet broad objectives. In few situations will it be possible to achieve wildlife objectives in the short term. Instead, progress relative to initial conditions, management alternatives, and natural benchmarks is a realistic short-term objective. Common themes in the conservation literature can help formulate wildlife objectives, e.g., (1) keystone complexes, (2) flagship or charismatic species, (3) links among populations, communities, biodiversity, and biocomplexity, (4) ecological processes of development of forest biotic communities, and (5) forest development in dynamic landscapes.

2.1. Keystone Complexes

A keystone complex is relevant because it relates directly to ecosystem function by embodying trophic relationships at a hierarchy of spatial scales. In Oregon and Washington, the northern spotted owl (Strix occidentalis caurina) rests atop a complex, central, food web in natural, old forests (Figure 1). The primary prey of the spotted owl is the northern flying squirrel (Glaucomys sabrinus), which is also prey for American marten (Martes americana), longtailed weasels (Mustela frenata), and other mammalian predators. The flying squirrel carries lichens and mosses to its nest, sometimes over long distances, and may be important in dissemination of those plants. The flying squirrel consumes sporocarps (truffles and mushrooms) and disseminates spores of fungi that are essential symbionts to the dominant tree species in lower elevation forests-Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco)-and many other species of trees, both hardwoods and conifers. Fungi help trees take up water and nutrients and receive carbohydrates in return. The fungi use some of the carbohydrates; others are delivered to the soil and support a vast soil food web. This keystone complex can be expanded to a broader food web of predators-major prey species-primary production food bases even more representative of wildlife diversity and various ecosystem functions (Carey et al. 1999a,b; 2002).

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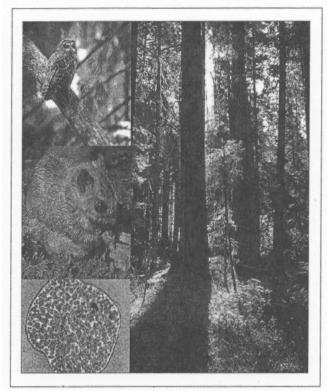


Figure 1. A keystone complex: spotted owl Eying Squirrel-truffle-Douglas-fir.

2.2. Flagship Species

Incorporating symbolic (flagship) species into forest management is essential because, by definition, people see these species as representative of highly valued ecosystems or as highly valued in their own right. People demand that these species be accounted for in management of natural resources. Some such species in the Pacific Northwest (western Oregon and Washington, coastal British Columbia, and southeastern Alaska) are the spotted owl, Roosevelt elk (a subspecies of Cervus elaphus), and Pacific salmon (seven species of Oncorhynchus). The spotted owl is symbolic of natural, old forests. The Roosevelt elk is valued by wildlife viewers because its impressive stature is easily seen from roads; it is also a prized game animal and a focus of subsistence hunting by Native Americans. Salmon are symbolic of historical Pacific Northwest culture, prized gastronomically, economically valuable in commercial and sport fisheries, and are a keystone species in many riparian ecosystems. Other groups of species are held in similar high esteem. Neotropical migratory birds and other forest birds are important to the American public. As Rachel Carson (1962) asked. What would a silent spring be like? What would a visit to a forest be without the songs of forest birds? In spring, bird songs are a major part of a forest experience (Wilson et al. in press).

2.3. Ecological Links

It is unlikely that scientists will determine the ecologies of most organisms in forests by the end of the 21st century. Forests, however, will be faced with increasing challenges from burgeoning human populations, globalization, introduction of exotic pests and diseases, and unavoidable natural catastrophes (Scheffer et al. 2001). Thus, many people want forest management to consider ecological links among species,-biotic communities, overall biological diversity, biocomplexity and ecosystem function, resistance to disturbance, and resiliency in the face of disturbance (Holling 2001, Kinzig et al. 2002). Wildlife can be used to address these concerns, at least in part (Box 1). The occurrence of numerous wildlife species can be a measure of biological diversity because wildlife occupy such diverse niches, have complex trophic relationships with other organisms, and interact with the environment at different spatial scales (Loreau et al. 2001). For example, at the landscape scale, diverse wide-ranging species such as the spotted owl, Roosevelt elk, and salmon are indicative of total landscape function and the values that landscapes provide beyond those of local ecosystems. Recovery of the spotted owl is tied to recovery of naturalistic forest ecosystems with high prey biomass within landscapes; abundance of elk is tied to the biomass of low vegetation within landscapes (e.g., Carey et al. 1999a,b). Within ecosystems, complex above-ground food webs provide abundant and diverse prey and plant biomass, promote biodiversity, reflect ecosystem function, and contribute to the biocomplexity that underlies ecosystem health (resistance to disturbance and resilience in the face of disturbance) (Lawton 1994; Carey 2003a,b). Above-ground food webs are linked to below-ground food webs by wildlife that forage on and in the forest floor. For example, forest-floor mammals feed on arthropods, fungi, and seeds in the soil and litter; thus, the structure of the forest-floor mammal community is determined by the structure of the forest floor (Carey et al. 1999b, 2002, 2003a; Carey and Harrington 2001). The structure of the biotic communities in the soil depends on and influences multiple soil processes (e.g., Liand Strzelczyk 2000), and the biodiversity of soil organisms is an indicator of soil health (Pankhurst 1997). Thus, complete forest-floor small mammal communities suggest maintenance of the multiple forest-floor trophic pathways critical to ecosystem function and productivity.

2.4. Forest Ecosystem Development

Research has created a large database on wildlife in Oregon and Washington (e.g., Ruggiero et al. 1991). Wildlife populations have been measured, key habitat elements have been identified, biotic communities and their stages of development have been described, and relationships among species, communities, stages of development, and habitat elements have been summarized in regional volumes and wildlife-habitat relationships tables (e.g., Johnson and O'Neil 2001). These summaries provide valuable guidance to managers and the public and can be adapted to simulation models to compare

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management alternatives (e.g., Carey et al. 1999b). Additionally, narrowly defined wildlife communities (≤ 10 species) have been linked to stages of forest development, and the integrity of these communities, in turn, has been linked to plant species diversity and complexity in plant community structure (Carey et al. 1999a, Carey and Harrington 2001). Thus, biocomplexity—species diversity, variety in structure, and heterogeneity in spatial arrangements—seems to produce robust ecosystems.

The ecological succession of biotic communities, development of forest biocomplexity, and natural disturbances interact with forest management to produce dynamic landscapes composed of dynamic forest ecosystems. Understanding the dynamics of disturbance and change seems essential to managing for wildlife, wood, and other values. Indeed small-, intermediate-, and large-scale disturbances that produce spatial and temporal heterogeneity are the basis for both biological diversity and biocomplexity (Whittaker 1975, Connell and Slatyer 1977, Bormann and Likens 1979, Oliver 1981, Canham et al. 1990, Carey et al. 1999a, Franklin et al. 2002). In conservation, too much emphasis has been placed on static future desired conditions. In timber management, too little emphasis has been placed on the consequences of shortening the duration and truncating the extent of dynamic processes on various values, including wood production (Curtis and Carey 1996, Carey 2003b). More emphasis is needed on managing ecological processes as opposed to focusing on static elements of structure, structural stages, or an end product. Improved classifications of forest development based on dynamic processes rather than static structures are necessary for managing processes. Key processes warrant clarification, especially those relevant to ecological stage setting, assembly of biotic communities, and maintenance of biodiversity. Wildlife can help identify those processes and evaluate the efficacy of management. A set of objectives and measures (Box 1) can be used to model:

- (1) Existing conditions (baseline) and how the landscape is likely to change without management (no-management alternative)
- (2) The landscape as composed of (a) old, natural forests (benchmark of potential) and (b) as representative of pre-settlement disturbance regimes (historical benchmark) (3) The future landscape as it changes in response to management for compatibility
- (4) The landscape as a shifting, steady-state mosaic of planned seral stages under continuous management for compatibility
- (5) The landscape under alternative management regimes

Box 1. Wildlife Objectives for Achieving Compatibility in Managed Forests in the Pacific Northwest and Ways to Measure Management Outcomes (Adapted from Carey et al. 1999b, 2003a)

Objective: Maintain capacity to support biological diversity

Method

- (1) Use published wildlife-habitat relationship (WHR) models to evaluate the capacity of the landscape to support the full complement of forest wildlife indigenous to the area, or a diverse subset of indigenous wildlife (e.g., more than 125 species of markedly different life histories). Measure this capacity as a percentage of the capacity of the landscape if it were composed of natural old-growth forests.
- (2) It is not practical to survey all wildlife; interested publics, however, can be involved in comparative and periodic surveys of some biotic communities. For example, standard landscape-level diversity of Neotropical migratory birds or forest bats can be compared to WHR model predictions for various alternative management scenarios.

Objective: Aid recovery of threatened forest species by providing habitat for them

Method

- (1) The threatened spotted owl is the flagship species for natural forest ecosystems in the Pacific Northwest. Documented habitat requirements can be used to determine the management necessary to produce habitat (particularly foraging habitat), model that management, and track habitat development in alternative landscapes. Sufficient information exists to calculate the average area of habitat used by spotted owls within an average home range; thus, current and future landscapes can be evaluated for their capacity to support spotted owls.
- (2) Spotted owls are easy to study; success in developing habitat can be determined by the actual use of managed, complex forest.

Objective: Provide for ecosystem productivity that supports complex food webs

Method

(1) A key trophic level can be used to evaluate food web complexity. For example, published WHR equations can be used to model changes in overall and individual biomass of northern flying squirrels, Douglas' squirrels, and Townsend's chipmunks (kg squirrels/ha). The biomass of these squirrels is a measure of the amount of primary productivity diverted to their foods, the reproductive outputs of fungi (truffles and mushrooms) and woody plant (fruits, seeds, nuts). Squirrel biomass measures the capacity of the ecosystem to support medium-size predators such as goshawks, spotted owls, long-tailed weasels, and American martens.

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(2) Squirrels are expensive to study. Thus, over time, random sampling and periodic evaluation of a sample of stands could be used to evaluate models and compare capacities of different stand conditions.

Objective: Maintain long-term site productivity through forestfloor biocomplexity

Method

- (1) Pacific Northwest old-growth forests have diverse forest-floor mammal communities that rely on diverse food webs based on invertebrates, fungi, lichens, and vascular plants. Forest-floor complexity also promotes diverse amphibian communities. Published WHR equations allow assessment of mammal community structure and comparison of the structure in future ecosystems to present conditions and to conditions in old-growth forests. Small mammals are prey for a variety of mammalian and avian predators. The integrity of the mammal community is an index to the diversity of food webs supported by forest-floor fauna and flora and, thus, the long-term outlook for continued ecological productivity.
- (2) Forest-floor mammals are expensive to study; evaluation of management success is best done on a sampling basis.

Objective: Provide landscape productivity for wide-ranging wildlife

Method

(1) Roosevelt elk and black-tailed deer abundance is determined by amounts of forage (lichens and foliage of herbs, woody plants, and understory trees) in combination with shelter from weather and hiding cover. Existing models can predict their abundance in a forested landscape by forage production. Thus, alternative landscape conditions, current status, and projected future conditions can be compared. Cervid abundance determines landscape carrying capacity for (a) large wide-ranging predators such as mountain lions and gray wolves, (b) subsistence hunting by Native Americans, and (c) sport hunters.

3. Processes Underlying Forest Community Development

After a catastrophe destroys much or all of a forest canopy, the ecosystem reorganizes and begins to develop anew. The degree of retention of biological legacies from the preceding forest has profound influence on the site and the organisms available to the new ecosystem (Franklin et al. 2000, 2002). Legacy retention can range from a few live trees to a mixture of trees, shrubs, and coarse woody debris, and from intact forest floor to patches of intact forest. The more legacies retained, the more a forest-influenced environment is maintained and the greater the mycorrhizal networks, species and sizes of trees, degree of spatial heterogeneity, and available species pools. Some important legacies include seeds or seedlings of multiple species of conifers and hardwoods, ectomycorrhizal fungi, large coarse woody debris, and large live trees with

epiphytic mosses and lichens. Legacies and the size and shape of the forest that was destroyed determine how distant any particular point in the reorganizing ecosystem is from sources of organisms that might colonize or recolonize a newly developing forest. The landscape context (biotic communities and seral stages) of the reorganizing ecosystem determines which species are available to recolonize a new forest. If a full complement of species is available, four basic processes determine how forests develop structurally in the Pacific Northwest and elsewhere (Carey et al. 1999a): crown-class differentiation, decadence, understory development, and canopy stratification. Each of these processes can be jumpstarted by legacies and hastened by active management and intermediate-scale disturbances. As basic structuring processes interact, two subsequent (higher order) processes determine the diversity, composition, and species structure of the biotic community: development of habitat breadth (Carey 1999a) and preinteractive niche diversification (Hutchinson 1978).

3.1. Crown-Class Differentiation

After trees have fully occupied the site, a tree canopy forms. Initially, the canopy may be dense and uniform, but over time some trees must become dominant, others codominant, subordinate, or suppressed for development to proceed. Crown-class differentiation is important for producing large trees, small dead and dying trees, and various other crown and canopy characteristics that develop habitat for a variety of forest wildlife. Differentiation occurs through natural and artificial disturbances that create gaps in the existing canopy.

Dense stocking, reliance on self-thinning, and tardy, light, evenly spaced thinning, however, can forestall differentiation, decrease biocomplexity, and lead to instability (Wilson and Oliver 2000). Structures and events that produce spatial heterogeneity can hasten the development of a complex community. Although crown-class differentiation can take place at small scales (one to a few trees), it affects the entire stand at larger scales (40 to 400 ha or more). Intermediate scale heterogeneity (0.1 to 0.5 ha), however, is necessary for development of biocomplexity. In addition to crown class differentiation, intermediate-scale legacy retention, natural disturbances, and management promote development of habitat breadth and niche diversification.

3.2. Decadence

Decadence is a complex process essential to biodiversity. Decadent trees (live trees with heart rot, standing dead trees, and fallen, decaying trees) can be retained during harvest operations. They can develop naturally through self-thinning, suppression, disease, insect attack, damage by falling trees, and weather-related events (lightning, windstorms, ice storms, and snowstorms). Or they can be created by intentional wounding, infecting, or killing. Decadent trees provide substrate for (1) a large variety of cavity-, hollow-, and crevice-nesting wildlife, (2) pecking and tearing foraging by insectivorous birds, (3) physical

partitioning of the forest floor, which reduces competition between deer and elk and among small mammals, (4) cover for small mammals and salamanders, (5) support of invertebrate communities that are prey for insectivorous small mammals and amphibians, (6) foraging sites for mycophagous small mammals, (7) travel ways, and (8) entryways to subnive an environments (see Harmon et al. 1986, Bunnell et al. 1999, and Johnson and O'Neil 2001 for reviews). Typically, forest management for wildlife emphasizes two elements of decadence: large, dead, moderately decayed conifers and large, fallen, moderately decayed conifers. The former are the trees most commonly used by cavity-excavating birds and the latter provide important shelter for terrestrial amphibians and certain small mammals. However, to focus on these structures without considering the entire process of decadence and how the process varies with seral stage is a mistake. For example, a conifer with a broken top may continue to grow, develop a new top or "basket" top, develop top rot and provide perch, roost, and nest sites for hawks, owls, eagles, ospreys, woodpeckers, squirrels, bats, and a variety of other wildlife over a long period before and after the tree dies. In younger conifer forests, deciduous trees such as red alder (Alnus rubra Bong.), willow (Salix L.), and, aspen (Populus tremuloides Michx.), provide valuable cavity trees despite their relatively small size (Carey et al. 1997, Bunnell et al. 1999). For example, red-breasted sapsuckers (Sphyrapicus ruber) will nest in small decadent willows (20 cm diameter at breast height (dbh)) in second-growth forests but use only large snags averaging more than 1 m dbh in old-growth forests. Sapsuckers (and other woodpeckers (Picidae)) are often double keystone species in keystone species complexes. For example, in Rocky Mountain forests, red-naped sapsuckers (S. nuchalis) excavate cavities in fungus-infected aspens that are required as nest sites by two species of swallows (Tachycineta spp.) and drill sap wells into willows that provide nourishment hummingbirds (Trochilidae), orange-crowned warblers for themselves. (Vermivora celata), chipmunks (Tamias spp.), and an array of other sap feeders (Daily et al. 1993). Thus, additional emphasis is warranted for providing numerous live deciduous trees subject to eventual suppression or infection with top rot early in forest development, and both conifers and hardwoods with cavities or other evidence oftop rot late in forest development to provide various sizes of cavity trees. Pileated woodpeckers (*Dryocopus pileatus*) play a cavity-creation keystone role in Pacific Northwest forests (Aubry and Raley 2002) and throughout many forests in North America. These large birds are capable of excavating nest cavities, entrances to hollow trees, and entrances to insect galleries in the interior of large, moderately decayed trees that later are used by a wide variety of birds and mammals.

3.3. Understory Development

Seeds and plants retained on site germinate, regrow if damaged, or continue to grow as light, water, and nutrients become available through canopy gaps.

Canopy closure can extirpate many of the retained species and, if long enough, even eliminate seeds from the soil seed bank. If instead of full canopy closure (limited stocking or management action such as precommercial thinning) there is crown-class differentiation, gap formation, or commercial thinning, the understory develops in stature and composition. With sufficient light, the understory increases in foliage volume and fruit production, providing wildlife with a variety of food and cover. For example, foliage of deciduous shrubs provides forage for larval moths (*Lepidoptera*) that are important food to insectivorous birds and mammals (Muir et al. 2002). Maple seeds (*Acer circinatum* Pursh and *A. macrophyllum* Pursh) and hazelnuts (*Corylus cornuta* Marsh) are especially valuable to squirrels in coniferous forest where their staple foods are produced sporadically (conifer seed) or are of low nutritive value (truffles) (Carey et al. 1999a, 2002).

3.4. Canopy Stratification

With retention or recruitment of shade-tolerant conifers and hardwoods and continued gap formation through natural mortality or silvicultural thinning, the forest begins to develop various strata of vegetation-low herbs, short shrubs, tall shrubs, and a midstory of deciduous and coniferous trees. Increased botanical diversity may be accompanied by horizontal and vertical heterogeneity in composition and foliage volume. Thus, a large variety of trophic relationships develop, and the overall habitat space begins to differentiate into diverse niches that support an enhanced variety of plants and wildlife.

3.5. Development of Habitat Breadth

With legacy retention and following a long period of gap development or management such as variable-density thinning, the forest develops patchy overstory, midstory, shrub, and herb layers. The result is a fine-scale mosaic of 0.1- to 0.5-ha patches of 10 to 30 types with each type composed of a different mix of species with different growth habits. For example, one patch may have an understory of moss with a dense midstory of a shade-tolerant conifer under a relatively open overstory; another patch may exhibit a continuous column of foliage from different plants from the forest floor to the overstory. Note that the resulting structure is quite different than the development of ladder fuels in interior ponderosa pine (Pinus ponderosa Dougl. ex Laws.) forests where flammable Douglas-fir provides ladders for ground fires to reach canopies. The patchy structure resulting from development of habitat breadth includes less flammable species in the understory than in the overstory and provides biological and physical gaps in both understory and overstory that impede the spread of potentially catastrophic disturbances such as fire and disease. Thus, intermediatescale heterogeneity has been recommended for wet to moist coastal forests (Carey et al. 1999a) and moist to dry interior forests (Reynolds et al. 1992, Graham et al. 1999, Harrod et al. 1999). The process of developing habitat

breadth (the full range of small-scale vegetation site types or patches characteristic of old, natural forests in the region) seems essential to maintenance of biodiversity in two ways. First there is an overall increase in habitat space-the volume of space the forest occupies, the overall surface area of plants within that volume, and the architectural niches formed by various life forms. Second, the diversity of life forms provides a variety of substrates and foods (foliage, seeds, fruits, nuts, and carbohydrates in root exudates) for use by other plants, fungi, invertebrate animals, and wildlife at a scale suitable for exploitation by organisms of low to moderate mobility, resulting in niche diversification.

3.6. Preinteractive Niche Diversification

When legacies have been retained or large structures (large live trees, dead trees, and fallen trees) have developed and the four basic stage-setting processes have gone on to produce habitat breath, the phenomenon of preinteractive niche diversification (Hutchinson 1978) may take place. Simply put, the forest has sufficient variation in structure, plant composition, and patchiness so many species that typically compete in simpler environments can coexist, even in large numbers. For example, resident cavity-using birds overlap in space and resource use in young, simple forests, and occupancy of these forests by some of these species may be variable or sporadic. In old, complex forests there are more cavity-using birds than in young forests; each species tends to forage on different substrates (e.g., bole and branch sizes). Similarly, decaying plants (wood and foliage) host various sizes of saprophytic invertebrates, each primarily consumed by a different insectivorous mammal (e.g., shrew (Soricidae)). Diversity in foliage cover provides hunting perches for spotted owls and protective cover for their prey. A simple forest may provide the owl with one species of prey but a complex forest provides several species (Carey et al. 1992). Thus, a complex forest provides a more stable resource for the owl and less predator pressure on any single prey species. Niche diversification operates at various trophic levels, providing for diverse forest-floor invertebrate fauna, fungi, and vascular plants; diverse insectivorous, mycophagous, granivorous, and herbivorous mammals; and diverse predators at the top of food webs (Carey 2003 a).

4. Stages of Development of Managed Forest Ecosystems

Considerable effort has gone into compiling wildlife-habitat relationships (WHR) databases across the United States. The weakest link in WHR databases may be their forest development models, which are for even-aged stands. These models were derived from timber type classifications that serve their intended purpose well. But they were not developed to account for the diverse elements of wildlife habitat; therefore they serve WHR purposes poorly unless they are augmented by numerous other habitat variables. For example, the most current WHR database for Oregon and Washington (Johnson and O'Neill

2001) cross-tabulates forest-dwelling species by 20 forest structural conditions, 9 habitat types, and almost 100 habitat elements and subcategories (see Box 2). The cross-tabulated WHR models are data-rich and useful, but cumbersome (see Appendix 1, Chapter 1 for a comparison with other classifications). Their complexity exceeds the cognitive limits of people engaging in discussions of field conditions or in collaborative management. Less complex, but still holistic models of forest development are more useful for heuristic modeling exercises and designing silvicultural prescriptions.

The simplest tree-focused model has four stages that follow large-scale disturbance: stand initiation, stem exclusion, understory development, and old growth (Oliver 1981; Appendix 1, Chapter 1). This model has proven too reductionistic for modeling WHR in simulations of Oregon and Washington landscapes (Carey et al. 1999b). Carey and Curtis (1996), building on Bormann and Likens (1979), went beyond structural classes to a set of eight developmental stages based on the processes taking place within the forest that influence development of the greater biotic (plant, fungal, and animal) community. Franklin et al. (2002) followed with an expanded classification of natural stand development. Naturally developing forests may go through as many as eight major sequential stand conditions, differing in duration from less than 10 years to more than 500 years (see Appendix 1, Chapter 1). However, management can truncate forest development, eliminate entire stages, speed up or slow down transition between stages, and produce stand conditions not found in natural forests (Carey et al. 1999b). Development may be limited to as little as 40 years in Douglas-fir forests, yet complex forests may require 70 years or more to develop, and forests producing a full array of values may require rotations of 125 to 250 years or longer (Carey and Curtis 1996). Thus, modeling active management and its effects on forest development requires a different type of classification—a non-sequential classification that can be subdivided into decadal periods. Furthermore, management for compatibility requires that models incorporate more than just the development of the tree community. Carey et al. (1999b), for example, modeled the Carey-Curtis 8 stages of biotic community development with 25 total substages. Field tests of the Carey-Curtis classification in formal experiments, retrospective comparisons of forests managed for various objectives, and in retrospective comparisons of managed and nature forest, suggested it was necessary to revise and expand the classification to account for the great diversity of conditions being produced in managed forests in Oregon and Washington (Box 2). This new classification incorporates seven stages, five of which are cross-classified as simple or complex in structure and composition. The stages differ in how resources (light, water, nutrients, and space) are allocated to plants, degree of decadence, spatial complexity, niche divergence, and resistance to change (Table1). The latter is an important consideration in management because it indicates stages in which a relatively stable state alternative to late seral forest is likely to develop in the absence of external disturbance. If such a state does develop and persists for a relatively

long time, it may be resistant to management efforts aimed at developing a complex, biologically diverse forest (Carey 2003a). In timber management, development often is limited to simple subsets of two stages, ecosystem reorganization and either competitive exclusion or biomass accumulation, with cycles (rotations) of 40 to 70 years, with few or with a variety of silvicultural manipulations (Table 2). In management for biodiversity, emphasis is on the complex subsets of ecosystem reorganization, understory reinitiation, understory development, and niche diversification with rotations of 130 years or more or, with the addition of gap dynamics, on very long rotations (350 years or more). A variety of silvicultural manipulations are used, as well as direct wildlife habitat improvements (Table 2). Despite the complexity of this classification, it, like any classification, is an artificial construct and is best applied when augmented with site-specific knowledge of environmental conditions (climate, weather, microclimate, and natural disturbance regimes), site fertility productivity, plant community development, and special landscape elements (e.g., wetlands, riparian zones, talus slopes, and cliffs).

5. Modeling Two Approaches to Forest Management

In western Washington, one favored approach to managing industrial forests was maximizing net present value of wood (NPV management) by clearcutting on 40-year rotations (following forest practices rules for greentree retention and riparian area management prior to 1995), preparing the site, and allowing natural regeneration of western hemlock (Tsuga heterophylla (Raf.) Sarg). In a modeling exercise to develop practical, but holistic, management systems, an alternative emerged: manage for biodiversity, including wildlife, wood, water, and clean air benefits by (1) clearcutting with legacy retention, (2) planting Douglas-fir with natural regeneration of other conifers and hardwoods, (3) doing precommercial thinning to promote growth and maintain biodiversity, and (4) doing up to three variable-density thinnings to remove wood products, add decadence (cavity trees), and accelerate the development of habitat breadth and niche diversification on rotations that alternated between 70 years and 130 years (Carey et al. 1999b). Biodiversity management included expanded protection of riparian and mass-wasting areas. Remarkably, the modeled loss of net present value between the two alternatives was slight—18% under old forest practices rules, 4% using comparable riparian protection developed for the biodiversity pathway, but a 13% gain with new Washington forest practices rules for riparian protection (Carey 2003b). Sustainable decadal revenues, however, various stages shifts in time while the proportions remain constant and a steady flow of wood products is produced. The differences in ecological performance of the managed landscapes were also marked (Table 3). Management for biodiversity was more than three times more effective than NPV management.

The reasons for the differences were clear. No species of wildlife were unique to the early stages in forests managed for NPV, but 14 species were unique to complex, late-seral stages and 11 to healthy riparian areas (Carey et al. 1999b). NPV management produced no habitat for spotted owls. Graphs for ecosystem productivity (Figure 2) and forest-floor productivity were similar to each other and showed that complex late seral stages supported much more diverse and abundant squirrel and forest-floor mammal communities than simple, early stages of forest development. Differences in production of deer and elk were slight. In forests managed for NPV, the large mammals find large concentrations of food in early clearcuts. In landscapes managed for biodiversity, smaller amounts of higher quality food are found throughout the landscape in all seral stages and in conjunction with shelter from the weather and hiding cover (Carey et al. 1999b). With management for biodiversity, more than 50% of the steady-state landscape was late-seral forest with less than 15% in early-seral stages, producing a landscape hospitable to late-seral wildlife and facilitative of dispersal and colonization processes. On the other hand, the NPV management landscape was universally inhospitable to lateseral wildlife.

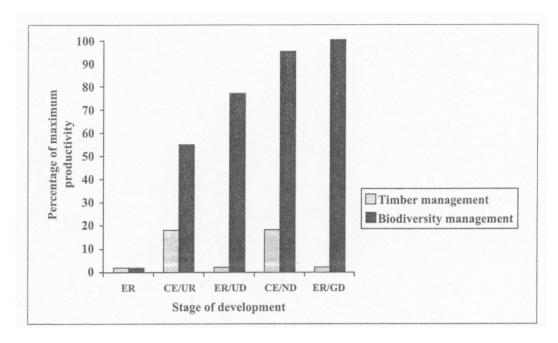


Figure 2. Effects of stage of development on ecological productivity. Ecological productivity is measured as biomass of squirrels as determined by production of truffles, mushroom, fruits, seeds, and nuts, (squirrel biomass determines carrying capacity for medium size predators). Timber management for maximum net present value alternates ecosystem reorganization and competitive exclusion on a 40 year rotation. Biodiversity management for wildlife, wood, water, and other values emphasizes five stages of development by alternating 70-year rotations with rotations of more than 130 years.

Note: $ER = ecosystem\ reorganization;\ CE = competitive\ exclusion;\ UR = understory\ reinitiation: UD = understory\ development; ND = niche\ diversification; GD = gap\ dynamics.$

Table 1. Characteristics of stages of development in managed forests without (simple) and with (complex) legacy retention, spatial heterogeneity in the canopy, and maintenance of decadence processes.

Stage	Biomass allocations	Decadence	Spatial complexity	Niche divergence ¹	Resistance to change ²
Reorganization					
Simple	trees, herbs, shrubs	none	some	some	low
Complex	trees, shrubs, herbs	much in legacies	much	much	low
Exclusion					
Simple	trees	small trees, deciduous trees	some	none	high
Complex	trees	legacy logs and snags, small trees	some	some	high
Accumulation					
Simple	trees	well-decayed small trees	some	some	high
Complex	trees	large legacy structures; small trees	some	some	high
Understory reinitiation					
Simple	trees, shrubs	possible insect/disease mortality	some	some	moderate
Complex	trees, shrubs	various ³	much	much	moderate
Understory development					
Simple	trees, shrubs, herbs	possible insect/disease mortality	some	some	moderate
Complex	various life forms4	various ³	much ⁵	much	moderate
Niche diversification	various life forms4	various ³	much ⁵	much	dynamic6
Gap dynamics	various life forms4	various ³	much ⁵	much	dynamic ⁶

Niche divergence refers to preinteractive niche diversification in which a variety of ecological niches are provided by disturbance reducing competition and promoting complexity.

Resistance to change indicates stages in which management intervention is particularly important to foster continuing development.

Large legacy live trees with decadence, snags, fallen trees, litter, and deep humus; created cavity trees and snags; felled trees, insect/disease mortality.

Conifers of different species and age cohorts, deciduous trees and shrubs, evergreen shrubs, ferns, forbs, lichens, and bryophytes arrayed in patches that differ in composition and structure.

⁵ Varying in vertical, horizontal, and temporal dimensions.

⁶ These stages have internal dynamics of change in patches over space in time; still, they are highly resistant to disturbance.

Table 2. Effects of silviculture on ecosystem complexity.

Silvicultural treatment	More complexity	Less complexity
Regeneration harvest Legacy-retention harvest Clearcutting	X	Х
Planting With natural regeneration Without natural regeneration	X	X
Weeding Retains some hardwoods & shrubs Removes hardwoods & shrubs	X	X
Precommercial thinning Clumped multi-species retention Systematic single species retention	X	X
Commercial thinning Variable density plus Systematic minus ²	X	X

I Variable-density thinning that mixes closed, moderately open, and open canopies on a 0.1- to 0.5-ha scale. It is designed to enhance woody plant diversity, maintain deciduous trees, promote recruitment of shade-tolerant trees with underplanting, and augment cavity trees and coarse woody debris when necessary.

Box 2. Stand Development in Second-Growth Douglas-fir Forests

Potential stages of development in managed, second-growth Douglas-fir forests (adapted from Carey and Curtis 1996) with approximate correspondence to stages of stand development and structural conditions. Characteristics of stages of development in managed forests are subdivided based on the lack (simple) and presence (complex) of legacy retention, spatial heterogeneity in the canopy, and maintenance of decadence processes.

Stage of development	Management and subsequent ecological processes	
Ecosystem reorganization	Management removes most overstory trees, with minor to major retention of biological components (future legacies) of the forest and planting or seeding of trees; vagile forest	
	species and native and exotic non-forest species invade	

² Light to moderate thinning with even spacing to favor one species.

Stage of development	Management and subsequent ecological processes		
Referents	and grow; plant communities establish on bare ground initially as grass-forb-herb, then shrub-tree, and finally tree dominated assemblages. Oliver (1981) Stand initiation		
Referents	Johnson and O'Neil (2001) 6 conditions, grass/forb-oper to sapling/pole-moderate		
Simple	Clearcutting variants, site preparation, planting, vegetation control, and stocking control produce an even-aged mono culture or a forest dominated by one to a few tree species.		
Complex	Variable-retention harvest systems with 5 to 30% retention o legacies, reduced and variable site preparation, and planting with natural regeneration likely establishes multiple species		
	of trees. Planting or seeding restores lost native plant diver sity if necessary; limited vegetation control ensures ful		
	stocking and vegetative diversity; and precommercial thin ning promotes multiple tree and shrub species and forestall competitive exclusion of numerous species.		
Competitive exclusion	No management occurs beyond ensuring full stocking, select ing desired species, and controlling competitors.		
Referents	Oliver (1981) Johnson and O'Neil (2001) Stem exclusion Sapling/pole-closed, small tree-single story-closed, medium tree-single story- closed, large tree-single story-closed		
Simple	Trees fully occupy the site and compete intensely for light water, nutrients, and space by growing tall quickly. Some eventually overtop and suppress shorter life forms and slower growing species. Self-thinning produces even spacing and can reduce inter-tree competition. Failure to self-thin leads to loss of crown depth and spindly trees. Competitive exclusion may extend to most vascular plants, invertebrates, and wildlife.		
Complex	Similar to simple competitive exclusion, but legacies from preceding stand (e.g., fallen trees, stumps, or patches of ir		
	forest) provide refugia within the forest for a wide variety of species. Refugia maintain some spatial heterogeneity and species diversity. Suppressed trees provide substrate for cavity-excavating wildlife and foraging for saprophytic insects and insectivorous birds and mammals.		
Biomass accumulation	Management includes conventional thinning to moderately high relative densities, selection for desirable timber species,		

Stage of development	Management and subsequent ecological processes		
Referents	Oliver (1981) Johnson and O'Neil (2001)	No equivalent Sapling/pole-moderate, small tree-single story- moderate, medium tree- single story-moderate, large tree-single story- moderate	
Simple	Trees fully occupy the site with moderate inter-tree competi- tion; even-aged codominants grow and accumulate wood biomass rapidly while providing limited resources to other life forms.		
Complex	species are maintained; grow	nd biomass of common plants th of dominant trees contributes aintain some heterogeneity and	
Understory reinitiation	Silvicultural thinning, self-thinning, and natural growth an mortality promote dominance by some trees, death of others and releases understory plants from overstory competition.		
Referents	Oliver (1981) Johnson and O'Neil (2001)	Understory reinitiation Sapling/pole-open, small tree-single story-open, medium tree-single story- open, perhaps large tree- single story-open, depend- ing on stand history	
Simple	as a shade-tolerant conifer or	paced trees leads to uniform ominance by a few species such the native clonal species salal and swordfern (<i>Polystichum</i>	
Complex	leads to variable light and moi which, with legacies, produc	uces canopy heterogeneity that isture regimes in the understory, see a heterogeneous understory, erplanting augments the underconifer species.	
Understory development	increases growth of trees, and	duces competition among trees, releases understory from com- s in stature, abundance, and	
Referents	Oliver (1981) Johnson and O'Neil (2001)	No equivalent 6 small- to medium tree- multistory conditions, depending on legacies and	

Stage of development	Management and subsequent ecological processes (continued
Simple	A homogeneous overstory with moderate to low crown closur produces an understory that is botanically diverse but still dominated by a few species and lacking a distinctive patch pattern; layers may develop, but lack of legacies preclude fully developed, complex biotic communities.
Complex	Variable-density thinning produces canopy heterogeneity with high to moderate to low crown closure by dominants and codominants. Heterogeneity produces crown differentiation, including ingrowth by hardwoods and shade-tolerand conifers. Variable understory environmental conditions produce understory patches of differing composition. Cavity-trecreation and coarse woody debris augmentation during thin ning and legacies from the preceding forest further composition.
	pound the heterogeneity. The resulting complex structure provides a diversity of niches for species within various life forms, including fungi, mosses, lichens, achlorophyllous mycotrophs, grasses, forbs, evergreen shrubs, deciduous shrubs, deciduous trees, and shade-tolerant conifers.
Niche diversification (Complex only) Referents	Additional variable-density thinning or group selection may help develop high biocomplexity, including species diversity structural diversity (live, dead, and fallen trees of various sizes; patchy understory; patchy midstory; canopy gaps; and gaps filled by shade-tolerant trees growing into the over story), and vertical and horizontal spatial heterogeneity, but the forest still has not developed the giant structures characteristic of old-growth forests. When needed, cavity-tree creation and coarse woody debris augmentation during thin ning maintain the decadence process. Oliver (1981) No equivalent Johnson and O'Neil (2001) 6 medium to large tree-multistory conditions, depending on numerous variables
Gap dynamics (Complex only)	These managed forests more than 125 years old have high niche diversification and giant trees and tree-based structures including legacies and the current dominant cohort. They are either passively managed for late-seral forest values along streams, on mass-wasting areas, in watersheds, or in reserves,
Referents	on long rotations in shifting steady-state mosaic landscapes, or with group selection for uneven-aged management. Oliver (1981) Old growth (but not natural) Johnson and O'Neil (2001) Giant tree-multistory, depending on numerous variables

Table 3. Measures of wildlife outcomes linked to compatibility in a 6828-ha landscape in western Washington, in the last 100 years of 300-year simulations maximizing net present value of timber and conserving biodiversity to produce ecological services and economic goods (adapted from Carey et al. 1999b).

Ecological measure	Timber management	Biodiversity management
Habitat for spotted owls	No	Yes
Numbers of deer and elk ¹	423/134	401/200
Vertebrate diversity (% of maximum possible) ²	64	100
Forest floor function (% of maximum possible) ³	12	100
Ecological productivity (% of maximum possible) ⁴	19	94
Landscape health (mean of the above %) ⁵	32	98

¹ Odocoileus hemionus and Cervus elaphus.

6. Conclusion

Results from prospective experimental manipulation of second-growth forests to produce biocomplexity have proven successful. The results suggest active management for joint, efficient production of a wide variety of forest values is not only possible but also desirable from a forest health view (Haveri and Carey 2000; Carey 2001, 2002, 2003a; Carey and Wilson 2001; Carey et al. 2002; Wilson et al., in press). Retrospective comparisons of managed and natural forests (e.g., Carey et al. 1992, 1999a; Bunnell et al. 1999; Carey and Harrington 2001; Muir et al. 2002; Carey 2003a) suggest the same. Widespread recognition is emerging for the need to manage for structural, compositional, and spatial complexity at multiple scales when production of multiple values in the goal(Reynolds et al. 1992, Kaufmann et al. 1994, Carey and Curtis 1996, Curtis et al. 1998, Bunnell et al. 1999, Hunter 1999, Franklin et al. 2002, Lindenmayer and Franklin 2002, Muir et al. 2002, Carey 2003a,b). Habitat elements commonly cited as important are legacies, cavity trees, deciduous trees and shrubs, coarse woody debris, and spatial heterogeneity in the overstory and understory. Management at multiple spatial scales for dynamic ecosystems and landscapes will help meet (1) goals of biological reserves; (2) human needs for wood products, clean air, clean water, open space, and naturebased experiences; and (3) worldwide demands to maintain environmental health.

² Based on 130 species of wildlife.

³ Based on the integrity of the forest-floor small-mammal community of nine species.

⁴ Based on the biomass of three squirrels (Glaucomys sabrinus, Tamias townsendii, and Tamiasciurus douglasii).

⁵ Mean of vertebrate diversity, forest floor function, and ecological productivity.

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