

Ecological Foundations of Biodiversity: Lessons from Natural and Managed Forests of the Pacific Northwest

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Abstract

Fifteen years of research on old-growth and managed coniferous forests have provided sufficient understanding of biodiversity to suggest a basis for ecosystem management. First, natural old forests have a metaphysics—values associated with their existence and function can never be addressed fully with the scientific method alone: we cannot recreate old growth. Second, five processes underlie forest development: crown-class differentiation, decadence, canopy stratification, understory development, and development of habitat breadth. Habitat breadth results from fine-scale spatial heterogeneity that produces structural and compositional diversity—tree species diversity, foliage-height diversity, and variety of recurring vegetation site-types. Third, the processes shape trophic pathways, lead to niche diversification, and help to structure fungal, invertebrate, and vertebrate communities. The contribution of each process to niche diversification differs in strength from its contribution to variance in forest structure and composition. Decadence seems the most fundamental, unpredictable, and intractable of the processes. Theoretically, ecosystem management based on these processes can produce landscapes that provide habitat for wildlife associated with late-seral forests, sustainable production of timber and alternative forest products, ecological services such as carbon assimilation and sequestration, economic activity that sustains rural communities, and win-win solutions with good cultural fit to conflicts over land use. Fourth, substantial uncertainty exists in every aspect of ecosystem management. Thus, achieving diverse benefits from forests requires active, intentional, adaptive ecosystem management.

Introduction

Concern about loss of biological diversity in the Pacific Northwest with continued harvest of old-growth forests was widespread by 1981 (Juday 1976, Forsman et al. 1977, Franklin et al. 1981, Meslow et al. 1981). In response to this concern, the Pacific Northwest Research Station implemented accelerated research programs in 1982 for old-growth forest wildlife (Ruggiero et al. 1991), in 1987 for spotted owls, *Strix occidentalis* (ISC 1990), and finally in 1994, for forest ecosystems. Initial old-growth research was to: (1) identify species of vertebrates and plants that depend on or find optimum habitat in old growth; (2) define, classify, and inventory old growth; (3) determine the biological requirements and ecological relationships of species associated with old growth; and (4) evaluate management alternatives for old growth. Studies of plant and vertebrate communities were replicated within and among physiographic provinces in western Oregon and Washington and reported (Carey 1989, Carey and Spies 1991, Ruggiero et al. 1991). These studies measured not only abundance, but also variously space use, foraging behavior, food habits, reproductive activity, nest and den sites, seasonality in habitat associations, and geographic varia-

tion in behavior and habitat associations. With increased attention on the spotted owl, studies of owl habitat use, demography, and prey base were replicated by physiographic province (ISC 1990, Carey et al. 1992, Carey 1995, Carey and Johnson 1995, Forsman et al. 1996). Accumulated research was compiled to produce reserve-based species conservation plans (ISC 1990, Ralph et al. 1996) and regional management alternatives (FEMAT 1993, SAT 1993) that had marked social and economic impacts. Finally, cross-ownership landscape management strategies were formulated that might be more successful at meeting diverse human wants and needs from forests than apportionment of forest land into agricultural-production timber management and conservation-biology-based systems of reserves and matrix lands (Carey and Curtis 1996, Carey et al. 1996a). Experiments were implemented to test hypotheses generated by this last approach (Carey et al. 1996b, in press b). In this paper, I will discuss some lessons I learned from various accelerated research efforts, research compilations, and simulations of alternative management scenarios. Most of my discussion is based on the reports cited above; hereafter I cite only a few key references.

Old-Growth and Managed Forests as Habitat

Beginning with the earliest scientific investigations, it was apparent that old-growth (>250 years) forests in the Pacific Northwest were special—trees were large, vegetation structure was complex, and coarse woody debris loads were high compared to most forests in North America. But were the forests unique as ecosystems? In other words, did they differ significantly from second-growth forests? Once lost, could they be replaced? Did they exhibit properties that emerged only after centuries of synergistic development? Were there species of [vascular] plants or wildlife that were found only in old growth? If so, what kinds, amounts, and arrangement of old growth would be necessary to ensure viable populations? This latter question was extended to bryophytes, lichens, fungi, molluscs, spiders, mites, and insects; and, in the future, it could be extended to even more life forms (e.g., bacteria or nematodes).

Some of these questions could have been answered without research. Old-growth forests were unique: they developed (1) on specific sites with specific topographic and biogeographic positions, (2) over a specific period of time (250-750 years ago), (3) under particular climatic regimes, and (4) under highly variable and location-specific disturbance regimes. Once lost, it would be unlikely they could be reproduced through natural succession or through intentional management, simply because the physical conditions of their development are not subject to unvaried natural repetition or to human control.

Research demonstrated that there were a few species of plants and vertebrates that were unique to forests >250 years old (Carey 1989, Ruggiero et al. 1991). The spotted owl, among all the species studied, seemed most dependent on old growth given the composition of the landscapes existing in the 1980s and 1990s (Forsman et al. 1984; Carey et al. 1990, 1992; Carey and Peeler 1995). Other species such as salamanders in specific physiographic provinces were associated with particular elements of old growth (large, decaying logs) or habitats most likely to be found in old-growth environments (headwater streams with cold water, detritus-driven food webs, gravel and cobble beds, and high pool:riffle ratios). Numerous species of birds and mammals were most abundant in old growth but could be found elsewhere, too.

Abundances of many could be associated with particular elements of old growth: large, live trees; large standing dead trees; large, decaying fallen trees on land or in streams; diverse foliage-height profiles; and diverse fungal communities (e.g., Carey et al. 1991, Carey and Johnson 1995).

Thus, it appears that old-growth forests and their structural elements function differently from younger forests in providing for biological diversity. Second-growth forests without legacies and in the competitive-exclusion stage of forest development seemed the least diverse in plant and vertebrate communities; some were depauperate in species. It became apparent, however, that biological legacies (large live trees, snags, logs, soil food webs, etc.) from old growth enhanced the value of both naturally young and second-growth managed forests as habitat for various species of wildlife (see various papers in Ruggiero et al. 1991, Carey 1995, Carey and Johnson 1995, Carey et al. 1996a). These reports suggest that old-growth characteristics could be developed in some young managed stands through legacy retention and intentional management. When competitive-exclusion stages without legacies dominated a landscape, even with patches of old growth, the landscape was inhospitable to late-seral wildlife such as the spotted owl (Carey et al. 1990, 1992; Carey and Peeler 1995).

In-depth studies were conducted on species and communities particularly amenable to study and sensitive to differences in forest structure and composition: spotted owls, arboreal rodents, and forest-floor small mammals. These in-depth studies provided specific, quantitative data on elements of forest structure and composition important in supporting food webs and organisms at various trophic levels (Carey 1995; Carey and Johnson 1995; Carey and Peeler 1995; Carey et al. 1996b, *in press a*, *in press b*). Whereas abundance is an essential measure of response of organisms to environmental variables, to the structure and composition of particular biotic communities, and to biotic communities as landscape elements (Whittaker et al. 1973; Carey 1981, 1984), it is not the only pertinent measure; other demographic variables such as age structure, sex ratio, reproductive attainment, and survivorship are important (Maguire 1973). In my in-depth studies, abundance measures were reinforced by these demographic variables and by measures of space

use, temporal variation in abundance, and biotic integrity of narrowly defined biotic communities (Carey et al. 1991, 1992, 1996b, in press *a*; Carey 1995; Carey and Johnson 1995; Carey in press). Relationships among demographic measures and between demographic measures and habitat quality are complex, but abundance was never misleading in my studies.

Ecological Scale and Processes in Old-Growth and Managed Forests

Using structure and arrangement of plant communities and patterns of abundance and activity of arboreal rodents, Carey et al. (in press *a*) found five processes of forest development that resulted in emergent properties at the stand-ecosystem level in old growth: crown-class differentiation, decadence, canopy stratification, understory development, and development of habitat breadth. These processes seem to be amenable to management within limits set by climatic factors. Ecological scale was important to development of ecosystem functions and emergent properties, including niche diversification. Of all the processes, decadence poses the most challenge to managers. Decadence also seems to differ functionally across physiographic provinces (Carey 1995, Carey and Johnson 1995). Carey et al. (1996a) developed a suite of management activities based on the five processes.

Simulation of Biodiversity Pathways for Forest Management

Carey et al. (1996a) modeled landscape development and function under three markedly different terrestrial ecosystem management strategies and three riparian management alternatives. Ecosystem management strategies included (1) protection with no manipulation, (2) management to maximize net present value of wood products, (3) active management with the intention of meeting diverse demands for economic goods and ecological services from forests over the long term (management to conserve biodiversity while maximizing social, economic, and environmental sustainability). The biodiversity pathways were based on research results accumulated from various retrospective studies that compared old-growth, naturally young, and managed second-growth forests.

Simulations revealed that management to conserve biodiversity resulted in faster recovery of ecosystem and landscape function than preservation, greater social benefits than both preservation and maximizing net present value, and greater sustainable economic benefits than maximizing net present value. The various outcomes of simulated alternative management pathways constitute hypotheses that are testable in prospective experiments and adaptive management experiments.

Hypothesis Testing with Prospective Experiments

A number of field trials of alternative stand management regimes are underway in the Pacific Northwest. One in particular, the Forest Ecosystem Study (Carey et al. 1996b, in press *b*), was designed to specifically test hypotheses implied by the biodiversity pathways for forest management (Carey et al. 1996a). Another, an adaptive management experiment on the Olympic National Forest (Olympic Habitat Development Study), has been planned and treatments are being implemented in 1997-1999. Preliminary results from the Forest Ecosystem Study demonstrate that (1) the approach is practical and implementable and (2) that hypotheses about the short-term impacts of ecosystem management derived from the overall model of forest development under active management were correct. It is too early (almost five years post-treatment) to test hypotheses about long-term effects of active management. But, overall, results are encouraging (Carey et al. 1996b, in press *b*).

Uncertainty About Active Ecosystem Management

Numerous species, especially the uncommon, wide-ranging species, could not be studied effectively in the retrospective studies of old and young forests. These species are commonly suggested as associated with old-growth forests: northern goshawk (*Accipiter gentilis*), marbled murrelet (*Brachyramphus marmoratus*), Vaux's swift (*Chaetura vauxi*), red tree vole (*Arborimus longicaudus*), fisher (*Martes pennanti*), marten (*M. americana*), and bats as a group (Carey 1989). Factors limiting these species are unknown; ecosystem properties promulgating these species are also unknown.

After regional management guides were developed (by the Pacific Northwest Region of the USDA Forest Service and various ad hoc inter-agency groups) to meet the needs of vertebrates dependent on old growth, conservation groups and scientific communities demanded consideration for other life forms. As the range of life forms under consideration expanded, not only were sampling methodologies lacking, but taxonomies were also undeveloped or unclear (or unavailable except to rare, highly trained specialists). Hundreds of species were nonexclusively linked to old growth. The number of species in lower life forms is staggering. For example, Carey et al. (in press *b*) found 260 taxa (when identified to the lowest possible level, genus or species) of fungi on sample plots totaling 4 ha in size (drawn from a total area of 128 ha in the Forest Ecosystem Study); if all fungi could have been identified to species, the total taxa may have exceeded 360 species. It may not be possible to ever identify all species of fungi or invertebrates; it certainly will not be possible to elucidate their ecologies.

Even without sampling and taxonomic problems, serious theoretical problems exist. What constitutes dependency on a habitat type (Carey 1984)? What constitutes a viable population? This question may not be answerable beyond the general National Forest Management Act definition of "breeding pairs well-distributed across the planning area." Even determining populations trends of species such as the spotted owl is difficult (Forsman et al. 1996). Determining population trends and limiting factors of "anadromous" species, such as the marbled murrelet, are much more difficult (Ralph et al. 1996). What constitutes forest fragmentation? The answer is clear in island biogeography (terrestrial islands separated by open ocean) and in parts of the eastern United States (farm woodlots and small forests separated by agricultural, suburban, and urban areas), but not in forested landscapes in the Pacific Northwest (but see Carey et al. 1992, Carey and Peeler 1995, Ryan and Carey 1995).

Sampling, systematic, and theoretical questions and the unique conditions under which the old growth of today developed produce what I call the 'metaphysics of old growth'. There are many values attributed to old growth that cannot be addressed through scientific observation, analysis, or experimentation. Thus, science and technology cannot produce a substitute for, or new, old growth. Old growth is a nonrenewable, but

perishable, resource with a highly variable and uncertain 'shelf life'.

Questions of Diversity

Some conflict around management of natural resources is derived from various world views of diversity and its importance. These world views are philosophical, psychological, and cultural, and not theoretical in a scientific sense. I distinguish among three schools: production forestry (agroforestry), conservation biology, and systems ecology. Agroforestry suggests diversity per se is unimportant to the production of wood: trees require physical support (substrate of biologically active soil), nutrients, water, and light (energy) and occasional assistance in resisting attacks by pests and pathogens. Agroforestry is economically and technologically based; management is often 'cookbook' (standardized methods). Cost:benefit ratios, net present value, capital investments in land, mills, and manufacturing, and cash flow drive decision making. Monitoring focuses on timber growth and yield and market prices.

Evolutionary biology provided roots for conservation biology. Questions about why there are so many species (e.g., Hutchinson 1959) provoked an era of research on biological diversity. Crises of extinction, loss of biological (genetic) diversity, and a rending of the 'biological fabric' produced conservation biology's "call to arms" (Soulé and Wilcox 1990:7). Much of conservation biology's focus is on reserves for biological diversity; some adherents assert every taxonomic unit (genus, species, subspecies, and genetic variation within local populations) is important to long-term survival and adaptability of species and systems to which species belong. Emphasis is on conservative use of natural resources and conservation of taxonomic-genetic diversity. Management is dogmatic and noninterventionist, focusing on landscape design—numbers, sizes, and distribution of reserves and connecting corridors—or preservation of rare or unique ecosystems. Management of reserves is contrascientific and biocentric—let nature take its course, maintain the range of natural conditions, keep people out. Monitoring focuses on diversity measures, species of low abundance, and rare species. Taxa that are suggested as in need of survey and monitoring before management actions are implemented number in the hundreds in the Pacific Northwest.

Modern systems thinking (Wilbur 1995, Ray 1996) is epistemological, philosophical, scientific, psychological, and sociological. It recognizes that people are not only parts of higher systems but also that everything people do serves some human purpose (e.g., from mining minerals to establishing reserves). With regard to natural resources, systems approaches focus on intergenerational equity, sustainability, and conservation of biodiversity. Biodiversity is defined as building blocks (genes, populations, species, ecosystems), evolutionary and ecological processes that shape the blocks, and the interactions among the blocks that produces ecological and economic goods and services (Reid and Miller 1989). A true systems approach recognizes that (1) systems can be studied, described, categorized, analyzed, and modeled; (2) systems are hierarchical with emergent properties at each level; (3) humans are limited cognitively and perceptually; (4) the "truth" will never be known, there are different ways of knowing (including science and culture), and adaptive management lends itself well to learning; and (5) learning is integral to managing systems. I call the application of a systems approach to natural resources active, intentional ecosystem management: (1) active because desired future conditions are defined and interventions are planned and implemented to achieve the condition, and (2) intentional because the full range of human wants and needs and all available scientific information are used to (a) formulate very specific, hierarchical objectives, (b) to prescribe a system of interventions, and (c) to design a system of monitoring and feedback, all within the constraints of general sustainability (Goodland 1995). Monitoring focuses on matching multiple projected outputs to realized outputs, including economic, social, and ecological measures. Ecological measures focus on biotic integrity and measures of ecosystem function (Carey and Curtis 1996, Carey et al. 1996a) at multiple trophic levels (levels of hierarchy) (Carey et al. in press a, in press b). Management policies, systems, and methods must have a good cultural fit. Because of scientific uncertainties, the adequacy of a management plan is judged initially upon its intentionality and subsequently on (1) degree of validation of the underlying system model through monitoring of outputs, (2) feedback to objectives and actions, and (3) demonstration of changes in the plan and actions through adaptive management.

Conclusions

- Old growth is a unique, irreplaceable, perishable resource.
- Management of existing landscapes, future landscapes, and second-growth forests offers many opportunities to conserve biodiversity in its broadest sense.
- Active management holds more promise than apportioning the region into biodiversity reserves, matrix lands managed under new forestry principles, and timber production lands managed by agroforestry.
- Substantial scientific uncertainty (predictability under systems management) exists and will continue to exist throughout the lifetimes of those now alive.
- Monitoring and adaptive management will be necessary to achieve human goals for forest ecosystems.
- There are too many taxa potentially sensitive to forest management for species-based monitoring.
- Measures of biotic integrity, ecosystem function, and public acceptability will have to be developed.
- No single silvicultural system is appropriate for all lands; equifinality suggests there are various pathways to achieving any set of objectives; cultural fit should be used as one criterion for selecting the pathway to be implemented.
- Organizations and management are a social phenomena with implied and defined expectations on the part of participants in a social contract. Failure to communicate clearly about expectations can only result in conflict no matter whether the managing organization is private, state or provincial, or federal.
- Emerging cultural streams in the USA (Ray 1996) suggests sustainability is becoming a pre-eminent cultural value; sustainability, then, is an essential component of management plans and must be demonstrated with high intentionality.
- History has shown that organizations are not independent of their larger social environment; antisocial behavior is eventually rewarded with increased regulation.

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