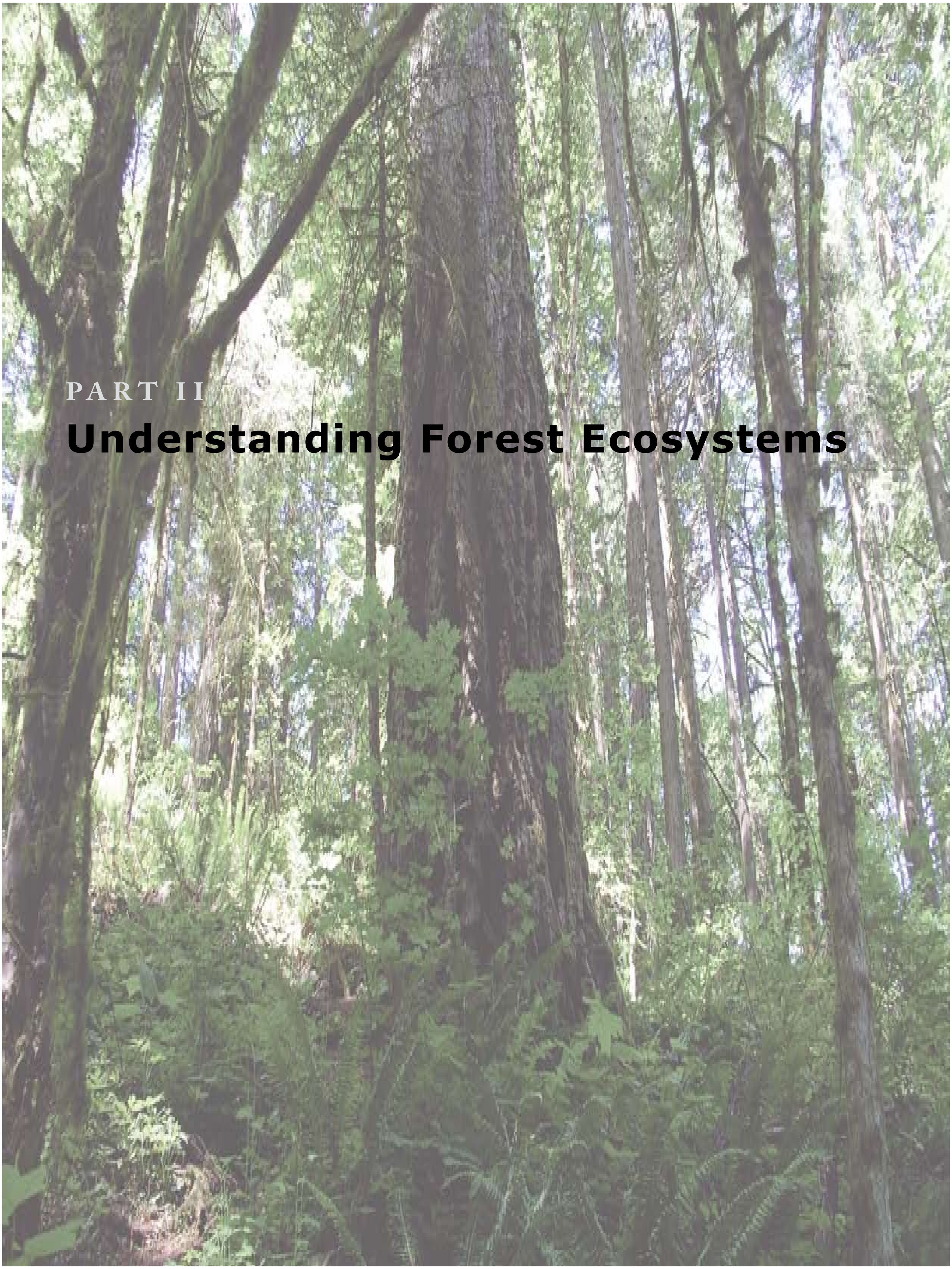


PART II

Understanding Forest Ecosystems

PART II **Key Points**

- Biodiversity is a salient feature of forests and depends upon disturbances at a variety of temporal and spatial scales.
- Temperate forests exhibit common patterns in structure, composition, and development at multiple spatial and temporal scales.
- Resilient forests develop complexity through envelopment of simpler biotic communities by more complex biotic communities over time, not replacement of one community by another.
- Key processes contributing to biocomplexity in forests include disturbances, legacy retention, crown-class differentiation, decadence, canopy stratification, understory development, development of habitat breadth, and niche diversification.
- Management is a human activity designed to meet human goals, including preservation of a natural system, recovery of a threatened species, maintenance of biodiversity, or wood production.
- Management based on ecological processes is more likely to be successful than management based on simply-defined structural conditions.
- Process-based management requires reference conditions, benchmarks, and measurable indicators of change.
- Effective management necessitates considerations of multiple spatial scales and long periods, including consideration of global climate change and human population growth.
- Active, intentional management (AIM) for conservation of nature and sustainable production of economic goods and ecological services is necessary because forests are complex and people desire diverse values from forests. AIM is hard to achieve without collaborative learning.
- Resilient forests are high in species diversity and functional groups, contain diverse ecological interrelationships, have complex physical and biotic structure, have high biomass (living and dead), are spatially heterogeneous, and are internally dynamic.
- Many characteristics of resilient forests depend on regular small disturbances, occasional intermediate disturbances, and rare severe disturbances.
- AIMing for resilient forests rests on using planned disturbances to help achieve resiliency by promoting diversity, spatial heterogeneity, biocomplexity, and accumulation of biomass.

CHAPTER 5

Terms, Concepts, and Theories

Part II of *AIMing for Healthy Forests: Active, Intentional Management for Multiple Values* provides definitions of ecological terms that can facilitate understanding and a discussion of how the science of ecology and the art of conservation are inseparable from philosophy, especially ethics. Chapter 6 examines the ecological foundations of biodiversity that underlie any conservation effort and provides examples of how these work at the landscape scale and at the scale of small forest ecosystems. Chapter 7 begins with a theoretical underpinning for active, intentional management (AIM) based on stochasticity, disturbance, and change. Building on this, the second part of the chapter focuses on structure, pattern, and process of forest ecosystems and how management of ecological processes is essential to AIM. Chapter 8 describes some of the practical and operational aspects of AIM. What then might seem missing is a cookbook of AIM recipes. But a quick review of this publication in its entirety reveals why such a cookbook for a limited region, like the Pacific Northwest, is likely to be misleading and result in unintended consequences.

- The region is ecologically diverse, and understanding local ecosystems is key to successful conservation.

- Active, intentional management must be process based with emphasis on (1) diagnosis of current conditions, (2) prognosis with and without intervention, (3) an accepted-reference condition and establishment of baseline conditions by which to judge progress, (4) use of benchmarks (alternative-management approaches) by which to judge success, and (5) choice of metrics by which to evaluate any current state of the management system.
- Active, intentional management is itself a social process that depends on good faith in collaborative learning and collaborative management. The AIM approach must be fully justified in the eyes of all stakeholders and culturally appropriate. A cookbook by its nature is pedantic, top-down instructions, or, in holarchical terms, a pathological dominator. In any event, no one I know has the knowledge to write a comprehensive cookbook for all occasions.

Terminology

Careful use of technical terms is essential to effective communication and developing common understanding. Misuse, abuse, and loose use of terms underlie much dissension in ecology and misunderstanding among various people interested in forest management and other environmental issues. For example, *habitat* is a badly abused term. It is used here according to its general definition (the place where a member, social group, population, or regional population of a species lives) and more technical definition (the range of biotic communities a species inhabits in a landscape or region).

Thus, a northern spotted owl has its habitat; a pair of spotted owls has certain habitat requirements; the elements of the habitats of spotted owls on the Olympic Peninsula include nest trees, nest groves, roost sites, foraging areas, and so on; and the habitat of northern spotted owls in lowland forests of Oregon and Washington is commonly old-growth forest. Habitat quality is best evaluated by various demographic measures of the owl—tenure of occupancy, longevity of occupants, number of young produced, owl densities, proportion of pairs breeding, and so on (fig. 12). Wildlife-habitat relationship books document the relationships between each vertebrate species in a region and its associations with plant community types, special landscape features, and specific elements of its habitat (Johnson and O'Neil 2001). However, there is no spotted owl dispersal habitat (a place where young owls often die), foraging habitat (foraging areas are but one element of owl habitat), old-growth habitat (it is old-growth forest), wildlife habitat (What is not habitat for some species of wildlife?), or snag habitat (a snag is simply a dead tree); "habitat types" are vague—more precise descriptions of vegetation are warranted for clear communication.

Figure 12—Two juvenile spotted owls. Photo courtesy of USDA Forest Service.

Vegetation can be described in terms of vegetation zones defined by environmental conditions such as temperature, moisture, distance from the ocean, elevation, side of major mountain range, and location within or among physiographic (landform) provinces. For example, the Western Hemlock Zone (Franklin and Dyrness 1973) is a broad lowland climatic zone of western Oregon and Washington that includes a variety of forest types characterized by Douglas-fir, western hemlock, western redcedar, and a variety of other trees. When referring to widespread, broad types of vegetation, zones are useful: Sitka Spruce Zone (along the coasts of Washington and Oregon), Western Hemlock Zone (widespread in the lowlands of western Washington and Oregon), Mixed Conifer-Mixed Evergreen Zone (southwestern Oregon and northern California), and so on.

There are lists of the numerous forest types for North America that are named after dominant trees, but such lists are cumbersome, not available to many people, and increasingly obsolete. Common tree species, however, can be used to identify common types of forest, as they exist in the present; for example, Douglas-fir forest (mostly Douglas-fir with other trees scarce), Douglas-fir/western hemlock forest, silver fir forest, Sitka spruce/western hemlock forest, and so on.

Many forest classifications, however, are based on the notion of climax types—the type of vegetation community that would develop under idealized stable conditions over the long-term; these are often referred to as potential natural vegetation (PNV) types and are expressed in terms of dominant overstory trees and key indicator plant species that would occur (and do occur in old growth) in the understory. They are derived from extensive sampling within vegetation zones and emphasize elevational, topographic, and edaphic (soil) relationships. They have been mapped for large areas (for example, Henderson et al. 1989 for the Olympic Peninsula of Washington and Moir 1989 for Mount Rainier). Potential natural vegetation types are only occasionally referred to here, but they do provide considerable information on the potential biodiversity of a landscape and the quality of growing conditions on a site—often more accurately than the extant vegetation. Easily confused with PNV types are plant community types. Plant communities may be grasslands, shrub lands, savannahs, forests, and other types and are often named after the dominant and key indicator species. They differ from PNV types in that, like forest types, they describe extant conditions. In this book, descriptors such as Douglas-fir/salal/Oregongrape refer to a plant community type, not a PNV, unless otherwise stated.

Forest or community type is not sufficient to describe a forest in a meaningful ecological way. It is important to include a descriptor of seral stage—where along a continuum of development of biocomplexity the forest lies. A set of seral stages that are useful in describing both natural and managed forests is provided later. However, in referring to natural forests broadly, complex forests more than 225 years or so old are called old growth (fig. 13). Old-growth and complexly structured 80- to 225-year-old forests with legacies from old growth simply are called old, natural forest (Carey et al. 1992). Any natural forest younger than 80 years old is called young forest (Carey and Johnson 1995). When talking about simply structured natural forests, the classification provides specific terms. Any forest resulting from clearcutting or logging of the majority of overstory trees is second growth, whether or not it has been logged once, twice, or more than twice, in keeping with the dictionary definition. However, it is wise to avoid using classifications of stands of trees—the typical forestry classification based on size of tree and wood product quality. Thus, talking about a second-growth Douglas-fir forest in the biomass accumulation stage with implications for forest ecosystem function and biodiversity is more informative than what a forester might call a large-sawlog Douglas-fir stand ready for harvest. For conservation purposes, a stand of trees is only a part of a forest ecosystem and forest ecosystems are elements of landscapes and landscapes are elements of regions.

Theories, Frameworks, and Points of View

The basic and applied sciences of ecology have had a popular impact unlike that of any other science (Worster 1990). Underlying this impact is the hope that this science can offer a great deal more than mere data—that it can serve as a pathway to a kind of moral enlightenment. Ecology provides understanding (what is), and ethics provides relatedness and relationships (what ought to be)—thus there are links between the cognitive-scientific and practical-ethical spheres (Rozzi 1999). Garrett Hardin, in his very influential paper in *Science* magazine (Hardin 1968), stated that lack of technical-scientific solutions to problems of human behavior resulted in the arms race, unrestrained human population growth, and the tragedy of the commons—that individuals will overuse some common resource to

Figure 13—Large fallen trees are a common sight in complex forests of the Pacific Northwest; such large coarse woody debris will provide protection and foraging sites for amphibians, small mammals, and birds for many years to come. Photo by A. Carey.

their own gain and to the destruction of that resource at the expense of the greater community. E.O. Wilson (1999a) reiterated that environmental problems are innately ethical. Paul Ehrlich (2002) recapitulated these ideas—the cutting edge of environmental science has switched from ecological and physical to behavioral with the need to alter the course of cultural evolution. The belief of Adam Smith (about 1776) that some "invisible hand" redirects individuals motivated solely by personal gain to promote the public interest is the underlying basis for our present social adoption of laissez-faire capitalism. But, the tragedy of the commons has belied the concept of the invisible hand for more than a century, as has the history of European and Euro-American exploitation of North, Central, and South America (Wright 1992). The tragedy of the commons is an ecological concept based on the idea that natural selection favors forces of psychological denial—that is, the individual benefits from his ability to deny the truth that society as a whole will suffer

(Hardin 1968, Ornstein and Ehrlich 1989). Thus, observations of unrestrained resource use (mining, overgrazing, pollution, and many other examples) and analogous phenomena in nature suggested to Hardin that there needs to be a normative concept of mutual coercion mutually agreed upon to produce social arrangements, which in turn produce responsibility. In other words, people have to agree on what is right and ethical and develop norms of behavior (and regulations and laws) that positively reinforce (provide rewards), negatively reinforce (provide punishment or threat of punishment), and remove obstacles to people acting and cooperating in ways that are socially responsible.

Many ecological concepts become normative when applied to conservation (Callicott et al. 1999). An example is the tenet that morally gross inequities throughout the world are biophysically unsustainable—perpetuating poverty has deleterious, irreversible impacts on the biosphere and hinders cooperation among parties of different socioeconomic status (Daily and Ehrlich 1996). E.O. Wilson (1998) calls for a new unity of knowledge, incorporating biology, social science, ethics, and environmental policy. Yet, he sees the greatest challenge to ecology as the cracking apart and resynthesis of the assemblages of organisms that occupy ecosystems:

- Accurately and completely describing complex systems.
- Reassembling the descriptions into models that capture the key properties of the entire ensemble.
- Measuring success by the power to predict emergent phenomena when passing from general to more specific levels of organization.

The important question is, Are there general organizing principles that allow an ecosystem to be reconstituted in full without full knowledge of all its component parts (for example, species, genes, molecules, and atoms)? Some of this synthesis will be attempted here and left to the reader to judge its success.

The ways people (including scientists) dwell in the natural world influences the ways they understand, explain, and look at nature. Franklin (1998) says naturalness is the great icon of the environmental community. Angermeier (2000) agrees "most conservationists value naturally evolved biotic elements such as genomes and communities over artificial elements," but states that this judgment is not shared by society at large and is based on intrinsic and instrumental values, including respect for nature; furthermore, naturalness is a continuum. Still, Angermeier posits, naturalness is a more reasonable guide for conservation than ecosystem features such as diversity, productivity, and evolution—the foundations for concepts such as ecological integrity and ecological restoration. All these concepts are explored here.

Barry Commoner formulated four laws of ecology that proved culturally influential but scientifically vague (Partridge 2000) (see Part 1, sidenote 5). Sagoff's antithesis is Nature does not know and Nature does not care (Partridge 2000). Thus, the ways people represent nature (e.g., in science models) constitute scenarios that inspire attitudes, behaviors, and ways of inhabiting nature. The Darwinian metaphor of the tree of life suggests common biological nature and origins that people share with all living species—a kinship, an extension of cultural respect beyond our own species, a biocentrism that values all life. A metaphor of a web of life suggests the instrumental value of biodiversity for human survival requiring an environmental ethic of environmental, economic, and utilitarian interdependence (Rozzi 1999). Thus, in any ecological paradigm or model there are values, assumptions, and worldviews that are often preconscious to the modeler and unexplained to the reader. Look and you will find some here.

Ecology has pursued an irregular course driven by seemingly diametric views of nature based on 2000 years of science, from the use of natural unknowable forces (magic) to biologically based mechanisms (Graham and Dayton 2002, Paine 2002). This course has led to debate that forces ecologists to explore how nature works and then to generate a synthesis—this cycle of thesis, antithesis, synthesis, and new thesis. Ecologists, however, are divided into subdisciplines that tend to focus on contemporary and emerging questions with the concomitant loss of previous synthesis; thus, ecology is a science of déjà vu—revisiting major conflicts (Naeem 2002) (sidenote 28). This process has taken place within the lifespan of contemporary ecologists and produced a cacophony that has postmodern philosophers denying the objectivity of science (Rykiel 2001). Thus, ecology is a mix of theory, empirical observation, worldviews, and ethical beliefs.

Naeem (2002) suggests that no single feature of the Earth's biota is more captivating than its extraordinary taxonomic diversity. He presents an emerging paradigm that is a synthesis of community and ecosystem ecology which, while concentrating on functional versus taxonomic diversity, promises to refocus attention on the broader significance of the Earth's biota. This emerging paradigm is that biodiversity governs ecosystem function versus the old paradigm and central tenet of ecology that biodiversity is primarily an

Sidenote 28—Naeem's (2002) *Déjà vu* conflicts in ecology:

- Does ecosystem or community ecology provide better insights into the working of nature?
- The relative importance of abiotic and biotic factors in governing biotic community composition
- The virtues of phenomenological vs. mechanistic research
- The relationship between biodiversity and stability
- The relative importance of taxonomic vs. functional diversity
- The relative strength of observational vs. experimental approaches

epiphenomenon of ecosystem function and secondarily structured by community processes. Neither is correct in an absolute sense—there are feedbacks between the two and these are explored here as well.

Paine (2002) is a little more circumspect about paradigms than is Naeem (2002). He says ecology has had few paradigm shifts because it is a pluralistic, multiple-causation discipline. Rather, ecology has fads, bandwagons, favored themes, and transient foci of interest that wax, wane, and recover. Bandwagons attract adherents by timeliness, vigor, showmanship, and novelty—no one doubts their reality or importance, but interests wane as limits to advancement increase. Paine says these themes have a common biological heritage—the enormous complexity of natural systems—and share a common trait—multiple causation is commonplace and unavoidable. Still, the faddish nature of ecology results in much recycling of ideas and concepts under new labels. Often progress is made, for example, the evolution of the concept of niches from the Grinnellian (niche as habitat) to the Eltonian (niche as role or occupation) to the Hutchinsonian (niche is the multidimensional space occupied

This decaying snag, which looks like an artist's sculpture, adds not only wildlife value but also aesthetic value to an old-growth forest. Photo by T. Wilson.

by a species in a biotic community as a result of interactions with other species and environmental conditions) (Graham and Dayton 2002). However, progress is hindered by ecological subspecialization that leads to parallel evolution of concepts, erasure of history as contemporary ecologists lose touch with their historical roots, and expansion of the scientific literature beyond the cognitive limits of individuals. Despite the evolution of niche concepts and the utility of the Hutchinsonian niche, the term niche has little agreed-upon meaning across subdisciplines in ecology. There are many areas in the applied ecological sciences where overreductionism, narrow specialization, and emphasis on single causes and linear relationships may be misleading.

This evolution of paradigms in ecology has followed similar upheavals in society and the physical sciences (Barabási 2003, Gleick 1987, Prigogine and Stengers 1984, Worster 1990). Thus, 18th-century beliefs in stability, order, uniformity, closed systems, and predictability have been dispelled. The 19th-century thermodynamic concept that the universe is running down with energy leaking out (entropy) has been replaced with a Darwinian concept of biological systems running up—becoming more organized. And the mid-20th-century emphasis on nonequilibrium in natural systems and the primacy of stochasticity or randomness is being replaced by an appreciation of self-organizing systems that bring order out of chaos. Prigogine won the Noble Prize for his work on nonequilibrium systems and dissipative structures. He said Man's new dialogue with nature should focus on two questions: the relationship between disorder and order (e.g., evolution) and the reversibility versus irreversibility of entropy (the roles of complex, dissipative structures, self-organization, determinism, and chance). Prigogine concludes that the universe is pluralistic and complex; structure disappears and appears; some processes are stochastic, others are probabilistic; basic processes are deterministic and reversible, but natural processes contain essential elements of randomness and irreversibility. Key concepts are complexity, nonlinearity, instability, fluctuation, surprises, and self-organization. These will be themes of management approaches developed here. Thus, we must abandon the hubris of Newton, as described by John T. Desaguliers in 1728 (Prigogine and Stengers 1984):

> Nature compelled, his piercing Mind obeys,
> and gladly shows him all her secret ways;
> 'Gainst Mathematicks she has no defense,
> and yields t' experimental Consequence.

We must learn to live with ambiguity and uncertainty; we will never have perfect predictability; we must let go of simple linear models (e.g., 2 + 2 = 4); and we cannot expect nature to reproduce her riches after we have extensively disturbed a mix of environmental variables, even if we place an area off limits to future human activity.

> Any science that conceives of the world as being governed according to a *universal theoretical plan* reduces its various riches to the drab applications of general laws thereby becomes an instrument of domination. And man … sets himself up as its master (Prigogine and Stengers 1984) [italics added].

We must rely on some natural processes of self-organization to produce adaptive complex systems. Some such natural processes include the tendency to form small tightly bound *hubs* or subsystems loosely connected to one another in networks (Barabási 2003), a theme embedded in Panarchy theory. Simply stated, "The disorderly behavior of simple systems provides a creative process that produces complexity or richly organized patterns that are sometimes stable and sometimes unstable" (Gleick 1987). We can use science and learning in understanding processes and heightening the intentionality of our decisions and actions. Like myths and cosmologies, science's endeavor is to understand the nature of the world, the way it is organized, and humankind's place in it, … the relation of being to becoming … appearance of order out of undifferentiated order (Prigogine and Stengers 1984).

Panarchy Theory

Panarchy theory (Gunderson and Holling 2002) is a decentered view (divorced from any narrow theory or discipline) that rests on the following principles: (1) the universe is composed of systems (interacting groups of things) within larger systems (interacting groups of subsystems), ranging from a microscopic soil microcosm to the global social-economic-biospheric system; (2) change, indeed surprises, are inevitable; and (3) reorganization after catastrophes resulting from change allows adaptation to the new conditions of life. Why is this important? Simon Levin (1999) describes ecosystems as dynamic assemblages of interacting components self-organized into evanescent patterns of interaction on multiple scales of space and time. Their only essential constant is change. Even the balance of nature describes a system far from equilibrium alternating between periods of relative stability and periods of dramatic change.

If this were true, then our challenge would be to avoid oversimplifying our definitions of forest ecosystems, to avoid assuming that a forest will grow into a particular seral stage no matter what has happened or might happen in the future, and to avoid trying to manage for or preserve a particular forest condition as if it were static and unchanging. It would mean ensuring our forests have all the elements that help them to be resilient after minor surprises (acute, or short-term, small to intermediate disturbances), allowing them to adapt to changing environmental conditions (slow change or chronic minor disturbances) without suffering catastrophic destruction, and when they do suffer catastrophic destruction, to recover quickly in a way that maintains the ecological services that we, and all other forms of life, need. Levin (1999) offers the "Eight Commandments of Environmental Management" (sidenote 29). Part II will explain the application of Levin's suggestions in forest conservation.

Sidenote 29—The eight commandments of environmental management (Levin 1999):

- Reduce uncertainty.
- Expect surprises.
- Maintain heterogeneity.
- Sustain modularity.
- Preserve redundancy.
- Tighten feedback loops.
- Build trust.
- Do unto others as you would have them do unto you.

CHAPTER 6

Ecological Foundations of Biodiversity

Forest ecology is about the interactions of organisms with each other and their environment. It follows, then, that forest structure, composition, function, productivity, resilience, and adaptability depend on some minimum amount of diversity of organisms available to the self-organizing system (Bazzaz 2001, Cardinale and Palmer 2002, Holling 1992, Ives et al. 2000, Lindenmayer and Franklin 2002, Loreau et al. 2001, Naeem 2002, Naeem and Li 1997, Tilman 1999, Tilman et al. 1997, Wardle et al. 2000). Diversity accumulates from site-type diversity among small plots within biotic communities to the species diversity that describes a biotic community (α-diversity), differences between communities (β-diversity), total species diversity in landscapes (γ-diversity), and the floras and faunas of regions (Whittaker 1975). Diversity influences ecological processes through a variety of mechanisms and different degrees of organization. Genetic diversity operates at the level of local species populations and metapopulations. Species diversity strongly influences processes at the level of biotic communities and ecosystems. And the diversity of biotic communities strongly influences ecological processes that operate across ecosystems within landscapes. Different processes affect diversity at different scales, thus, a top-down approach also is necessary to fully understand patterns of diversity (Whittaker et al. 2001).

It is sometimes useful to think of diversity as the number and distribution of species in Earth's biosphere, patterns of diversity as the varying forms of biotic communities in space and time, and processes of diversity as the dynamic aspects of communities driven by both endogenous (internal) and exogenous (external) influences (Bridgewater 1988). To make sense of diversity, one must first consider biogeography and what determines the pool of species in a region. The selection of species from the regional pool that are found in any particular landscape depends on the characteristics of that landscape and landscape-level processes. Within landscapes, biotic communities arise with their composition determined by the local environment as well as the character of the landscape and its dynamics. Thus, within regions, biological diversity (genes, species, and communities) differs in space and over time. Patterns measured at small scales, such as within communities, do not necessarily hold at larger scales (among communities within landscapes); nor do processes prevailing at small scales necessarily prevail at larger scales and vice versa. Consequently, understanding patterns of diversity cannot be automatically addressed by scaling locally measured variables to larger areas and longer times or by applying broad patterns or general concepts to specific locations. Furthermore, strong components of stochasticity (randomness) and historical events may be operating at each spatial scale. Nevertheless, before examining what determines the diversity of species and forest communities in forested landscapes and forest-dominated regions, it is pertinent to ask why there are so many species?—a question underlying much of ecology and evolution (Hutchinson 1959).

Why Are There So Many Species?

Early theories related diversity to competition (table 9). The more alike individuals are, the more likely they compete for limiting resources, and the more likely natural selection promotes traits that maximize efficiency of resource exploitation to the extent that individual fitness (reproductive success) benefits. The most intense competition occurs between members of the same species and leads to specializations for a limited set of resources, and, under conditions of isolation, to speciation. The next most intense competition exists between closely related species; such species evolve differences in morphological or other characters to more efficiently exploit different resources; for example, bill size differs within and among species of Darwin's finches, and the different finches specialize on different

Table 9—**Theories of biodiversity**

Theory	Contention
Area	Number of species is a result of sampling effort and environmental heterogeneity.
History	Diversity is a consequence of geologic events, dispersal events, and isolation leading to speciation.
Energy	Resource-rich environments promote diversity; partitioning of energy among species limits richness.
Stress	Benign environments support more species than harsh environments; fewer species can adapt to harsh environments.
Stability	Stable environments support more species; few species are able to adapt to varying environments.
Disturbance	Disturbance promotes diversity by disrupting competitive interaction.
Interactions	Competition, predation, parasitism, and mutualism affect niche partitioning.

Source: Adapted from Whittaker et al. 2001.

sizes of food. Within small homogeneous areas, environmental stability leads to competitive exclusion and reduced numbers of species. As environmental heterogeneity increases within a community, niche differentiation, coadaptations, predation, and mutualisms promote increased complexity and diversity (Cohen and Stephens 1978, Fretwell 1972, Gilpin 1975, Levins 1968, May 1973). If one defines the spaces available for habitation and for interactions among species by using a large variety of environmental variables (including area and timing of use) that have some importance to one or more species, it becomes apparent that a large multivariate space exists within which numerous species can exploit various parts (i.e., define their habitat by adaptation to critical environmental variables) and within which potentially competing species can partition resources through niche differentiation (Carey 1981, Hutchinson 1957, Whittaker et al. 1973). Similarities among coexisting species are least limiting where productivity is high and seasons are uniform, for example, the Tropics (MacArthur 1965). In most environments, disturbances serve to disrupt dynamics of interactions, reduce severity of competition, reduce abundances of dominant species, and promote diversity. Small- and intermediate-scale disturbances produce heterogeneity within communities that produces preinteractive niche differentiation, wherein different niches are available to similar species even before they interact and undergo behavioral or evolutionary change as a response to interactions, such as competition, with other species. Catastrophes

Sidenote 30—The cause-and-effect explanation of population regulation:

- Population regulation does entail demographic density dependence.
- Density dependence is necessary, but not sufficient for population regulation.
- Competition and predation are possible sources of density dependence.
- Environmental heterogeneity is important in predator-prey, host-parasitoid, and host-parasite systems.
- Niche differentiation is important in competition.
- The spatial dynamics of succession and development are important in maintaining mosaics (environmental heterogeneity).
- Finite dispersal, neighborhood interactions, and effects of endogenous pattern formation are also important.

destroy communities and lead to rapidly changing conditions as new communities develop. Proliferation of disturbance-dependent species results in species-rich regional flora and fauna (Bridgewater 1988). Management that homogenizes communities and spreads exotic species can lead to globalization and reduced diversity of native flora. Management that includes introductions of exotic domesticated species and marked changes in landscapes (e.g., planting trees in the Great Plains) can lead to hybridization of species with an overall loss of species diversity (Levin 2002).

Closely related, then, to the questions of why there are so many species and how they coexist are questions about what regulates population densities. A population is regulated if it persists for generations with fluctuations above zero (Hixon et al. 2002). A fundamental tenet of ecology is that population regulation is density dependent with negative feedback; in other words, the propensity to increase in size is high when population size is small and decreases as the population grows large. Extinction occurs when regulatory mechanisms that promote population growth are weaker than disruptive events (disturbances) or stochastic variation. As with diversity, ecologists examining regulation first focused on competition, then moved on to disturbances such as predation, and then to the concept of metapopulations that are demographically open to immigration and emigration and that can persist without density dependence. As in all debates in ecology, the discussion spiraled from alternative simple explanations of population regulation to a greater understanding of the complexity of cause and effect (sidenote 30). The bottom line is that population regulation is a truly community-level phenomenon (Connell and Orias 1964, Hixon et al. 2002, Hutchinson 1978) and, thus, necessarily intertwined with species diversity.

Frank Preston (1969) noted that "every naturalist from Darwin downwards has felt aggravated that a few species are very common and most are rare." The number of species and number of individuals per species in a functional group or biotic community appear to follow a log-series distribution (Fisher et al. 1943). Indeed, the lognormal distribution has emerged as the distribution underlying commonness and rarity (Preston 1948, 1960, 1962a, 1962b, 1969, 1980, 1981) and many other biological phenomena (Limpert et al. 2001). Sugihara (1980) concluded there is a minimum form of community structure involving hierarchically related niches; that niche apportionment is multidimensional, produces evolutionary ecological considerations, and results in species diversity; and that the end result is lognormal species abundance patterns. The practical import of the lognormal distribution is that with any sample of a large number of species, only a few species can be expected to be abundant; many will be rare (fig. 14). Thus, rarity is not necessarily indicative of poor or degraded environmental conditions, rather it is the rule. However, species do not necessarily retain the same relative abundances through time—environmental change (slow, fast, acute, or chronic) and stochastic (random) events affect different species differently. For example, in an experiment in increasing spatial heterogeneity in the canopy of second-growth forests (Carey et al. 1999d), native plant species diversity increased by 150 percent with concomitant changes in relative abundance (Thysell and Carey 2001a), species of litter invertebrates changed in relative abundance within functional groups at fine scales in response to treatment (Schowalter et al. 2003), the overall diversity and relative abundances of hypogeous and epigeous fungi on the forest floor increased (Carey et al. 2002), the diversity and abundance of winter birds increased (Haveri and Carey 2000), and rarer mammals increased in abundance (Carey 2000b, Carey and Wilson 2001). Many of these changes probably were due to changes in relative abundances and increased abundance of rare species in response to changes in environmental variables, but perhaps with some changes owing to germination of dormant seeds and to immigration (e.g., by ruderal plants and birds from surrounding areas). These changes illustrate that the simple number of species (often referred to as species richness) is inadequate to describe

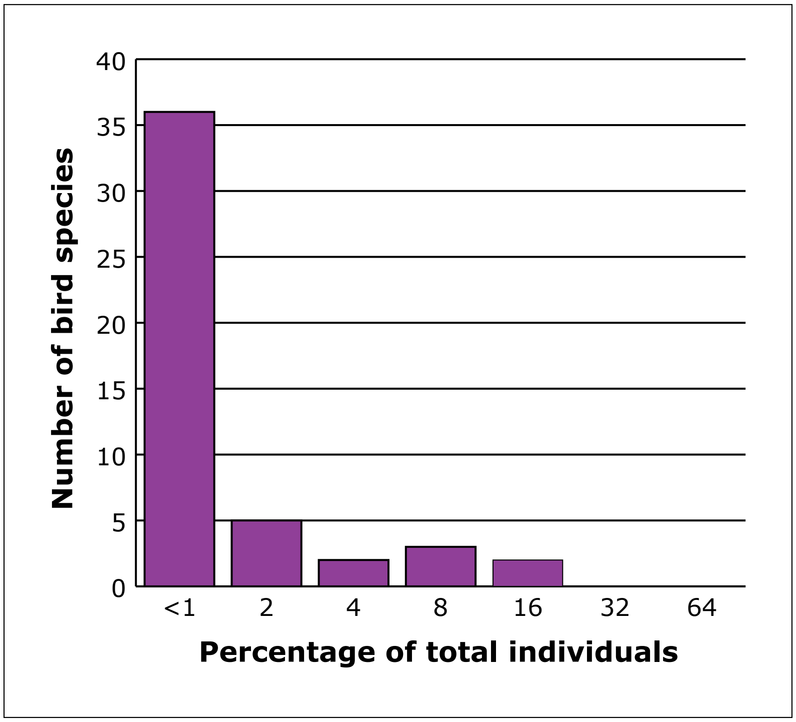


Figure 14—The distribution of occurrence in diurnal forest birds in the Oregon Coast Range (adapted from Carey et al. 1991) approximates a lognormal distribution; lognormal distributions characterize commonness and rarity in many biological phenomena.

the diversity of a community. Other useful measures include the numbers of species each accounting for, say, more than 5 percent of individuals, changes in the rank order of species, and changes in the ranks of individual species on a lognormal scale (Carey et al. 1991, Carey and Johnson 1995). The degree to which individuals are equally apportioned among species is called evenness. Increasing richness and evenness are not necessarily indicative of improving conditions for native diversity—these changes could reflect decreased overall abundance, invasion by exotic species, or replacement of rare or specialized species by common or generalist species. Comparing the structure of a biotic community in a relatively undisturbed natural environment to that in an environment under marked human influence provides a measure of the biotic integrity of the human-dominated environment (Karr 1991, 1993) and may indicate the relative sustainability of alternative management regimes in forests (Carey and Harrington 2001, Carey and Johnson 1995).

Relative rarity also increases with levels in food webs. Species at the tops of food chains—predators (fig. 15A)—are rarer than those they prey upon (fig. 15B) and nonpredators in general, including macroinvertebrate predators in Mollusca (fig. 15C), Annelida, and Arthropoda (Ahlering and Carrel 2001). For example, limited sampling in the Missouri Ozark Mountains found all 3 phyla, 8 classes, 19 orders, and 62 morphospecies with 28 percent of detected species being predatory but only 9 percent of individuals belonging to those species. Rare species are less likely to be detected during sampling

Figure 15—(A) An adult northern spotted owl and (B) a bushy-tailed woodrat. Photos courtesy of USDA Forest Service. (C) Two Burrington jumping slugs. Photo by J. Ziegltrum.

for diversity than common species, and it is difficult to establish the absence of a species. This problem of sampling is confounded when rare species are cryptic, very small, evasive, or inhabiting environments inimical to people—difficult to find even when present. Few scientists have studied stygofauna—inhabitants of caves and ground water—yet these species are numerous: 1,000 protozoa, 3,000 crustacea, 590 arachnids, 106 vertebrates (92 frogs), perhaps a total of 7,000 species (Gibert and Deharveng 2002). Nevertheless, rare species are more subject to local extinction than abundant species. Thus, expectations should be low that any particular rare species would be found in any limited sample of individuals or areas. Care must be taken to ensure the curve of species accumulation with increasing sampling effort has reached an asymptote before estimating total diversity for any particular group of species or narrowly defined community (group of species); it is much easier to detect differences in the distribution of individuals among species, the number of species per a large sample of individuals, the number of species for a specific area sampled, or the structure of the narrowly defined community. This profound characteristic of commonness and rarity of species has obvious important implications for reserve strategies, conservation goals, effectiveness monitoring, and choice of indicators.

Most of the estimated 4 to 112 million extant species have yet to be described and given a name (Wilson 1999a). Perhaps 98 percent of birds are known, 1.5 percent of algae, and less than 1 percent of bacteria. Questions about the effects of human activities on little-studied groups are literally endless. Little is known about the Grylloblattids (cockroach-crickets). These primitive insects, without wings or eyes, were discovered in Canada in 1911 and are known as ice bugs, ice crawlers, and rock crawlers (*Grylloblatta* spp.). They are found almost exclusively on mountains higher than 500 meters in Russia, China, Korea, Japan, and North America; endemism (species found only in one biogeographic area) is high in North America (fig. 16). Their preference for low temperatures (ca 4° c) slows their development—3 years may be required for eggs to hatch and 7 years to reach maturity. There are fewer species (25) in this order-suborder than

Figure 16—A rock crawler on Carpenter Ridge in the Sierra Nevada mountains, California. Photo by A. Wild © 2003.

any other order of insects. They live in environments where arthropod diversity is low. Many live on snowfields and glaciers and feed on other insects frozen on the surface of the snow or ice. One species has been found on glaciers on Mount Rainier, the tallest (about 4,400 meters) volcanic peak in the continental United States, sitting astride the Cascade Range in Washington and another species on the relatively low Mary's Peak, devoid of snowfields and glaciers, just west of Corvallis, Oregon. Studies in British Columbia, however, showed them to be widespread, with an affinity for edges between forests and clearcuts (Huggard and Klenner 2003).

Corliss (2001) asked "Have the Protozoa been overlooked?" in biodiversity calculations. He relates that more than 213,000 protists, including 92,000 protozoa, are important pathogens (causing diseases including malaria, sleeping sickness, leishmaniasis, and many others), help control bacteria, and contribute to nutrient turnover. *Eimeria* spp. are common protozoan intestinal parasites of small mammals in North America. Studies of small mammals easily uncover new species of endoparasites such as *Eimeria* (Fuller and Duszynski 1997, Torbett et al. 1982); new range records of ectoparasites, such as fleas (Main et al. 1979); new species and geographical occurrences of the smallest forms of life-like viruses (Main and Carey 1979, 1980); even new range records of the small mammals themselves (Carey 1978a); and incidentally, new records of rarer organisms such as achlorophyllous mycotrophs (Thysell et al. 1997a). A team of scientists (Memmott et al. 2000) examined the food web of one common plant species in England—scotchbroom—now an introduced pest species of growing importance in Washington (Carey 2002a). They identified 154 taxa in a food web with 370 trophic links: 19 herbivores, 66 parasitoids, 60 predators, 5 omnivores, and 3 pathogens with a total 82 functional groups, 9 orders of insects, plus vertebrates, arachnids, bacteria, and fungi. There is no end to biodiversity. Forest ecologists have just scratched the surface of biological diversity; they rarely consider parasites and pathogens, even though forests play important roles in maintenance of diseases of people, such as Lyme Disease and its tick vectors (Carey et al. 1980a, 1981).

Sidenote 31—Biodiversity according to Blondel (1987):

- Biological systems are temporal as well as spatial; they always reflect a history from glaciation to human land use changes.
- Geologic time and processes (plate tectonics, climate change, and glaciation) join and separate faunas and floras.
- Evolutionary time produces genetic changes in populations through natural selection.
- Ecological time produces changes in communities with ecological succession and community development.
- Evolutionary convergence at the level of communities is hard to distinguish from phylogeny.
- Mechanisms of community organization differ between primeval and human-dominated landscapes because of reduced diversity:
  - Size of any local population not at equilibrium is determined by local resource conditions.
  - Species distributions are broken into a mosaic of local populations which exchange propagules in accordance with local demographic conditions.
  - The prime factor affecting transfer between local populations in the same neighborhood is the specific disturbance regime and the mosaic it produces.
  - Evolutionarily, a metapopulation (the local populations of a mosaic of biotic communities) promotes genetic diversity and polymorphisms in response to disturbance regimes, predation, and competition.

Biogeography

Biogeography refers to the diversity of organisms and the regulation of diversity in heterogeneous and changing environments. It is now well understood that patterns and processes in diversity must be considered in reference to space, time, and *change*—and that these three dimensions are inextricably linked. Neither deterministic (cause-and-effect) nor stochastic (random effects) paradigms are sufficient for understanding biogeography; ecologists need biological realism and multifaceted, interactive approaches to comprehend ecological systems; thus, hierarchy theory is essential to understanding biogeography and biodiversity because it bridges biogeography, ecology, and evolution (Blondel 1987) (sidenote 31).

- Humans have played important and diverse roles in determining biogeography.
- A complicated network of interacting factors has determined the present distribution and abundance of species.

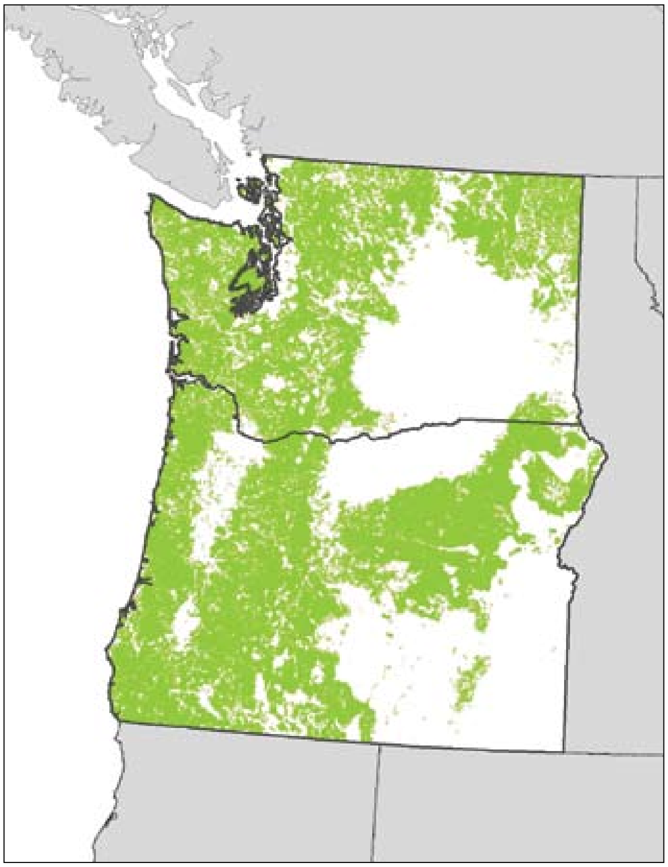
Regional diversity (regional species pool, biotic communities, and life zones) is determined by long-term global processes and the resulting biogeography. Historically, theories of diversity have not addressed clearly components of general diversity or dealt adequately with geographical scale (Whittaker et al. 2001). Thus, α-, β-, and γ diversities are used ambiguously—the terms local, landscape, and regional diversity are more intuitive. Moreover, inventorying all species is difficult, if not impossible, and knowing how heterogeneity of environmental factors differs with scale is prerequisite to evaluating differences in diversity at local, landscape, and regional scales (Endler 1977). Thus, a top-down approach is important to understanding patterns of diversity (O'Neill et al. 1986). For example, there is a grand cline globally, with low diversity at the poles and high diversity in the Tropics. Plate tectonics, continental uplift, volcanism, glaciation, global climate change, mass extinctions, replacement of higher taxa (e.g., placental mammals by marsupials), and wind and river erosion and deposition have profoundly affected patterns of species occurrences. Historical contingencies operate at every scale. Tausch et al. (1993) refer to the "Legacy of the Quaternary" (0 to 2 million years ago), with its 24 glacial events and interglacials producing spatially and temporally variable climates and instability in plant communities with species composition constantly changing. Others have drawn similar conclusions after examining paleoecological or biochronological sequences (Gagosian 2003, Hallett et al. 2003, Johnson and Mayeux 1992, Millar and Woolfenden 1999, Pielou 1991). They warn against trying to recreate presettlement vegetation—it may not be feasible. Pielou (1991) stated "At no time has there been a return to 'things as they were.'" Furthermore, the future will be different from the past.

Humans have been an overriding influence on biogeography, from exterminating the largest North American mammals 11,000 years ago to using fire to manage the natural environment; bringing about large-scale vegetation change with grazing and agriculture; purposefully and accidentally introducing novel plants, diseases, insect pests, and vertebrates into vulnerable ecosystems; using persistent toxic chemicals in agriculture, forestry, and manufacturing;

polluting air, water, and soil; and changing the global climate (Blondel 1987, Bonnicksen et al. 1999, Diamond 1998, Krech 1999, Palumbi 2001, Pyne 1997, Wright 1992).

The amount of forested area in the United States increased from 1952 to 1963, peaking at 309 million hectares, and then declined to 303 million hectares by 1997—a loss of 6 million hectares, or 2 percent (roughly the size of West Virginia); current projections suggest another 3 percent loss (9 million hectares) in total area, including a 4-percent loss of privately owned forests by 2050 (Alig et al. 2003). Along the Pacific coast, the 92 million hectares of forest existing in 1953 is expected to decline to 84 million hectares in 2050—a 9-percent decline (almost half the size of Washington state); however, private forests will decline from 34 million to 28 million hectares—a decline of 17 percent owing to land use changes (fig. 17). The climate change hypothesis predicts that the geographic range of forests will shrink owing to catastrophes or dieback and will be replaced by grasslands (Loehle 2000). Mote (2003) reports that temperatures and precipitation in the Pacific Northwest in the 20th century increased at rates higher than the global average, with effects on flora and fauna. Global climate change, changes in regional climates, and changes in land use by people have strong effects on species, biotic communities, and even biomes (Hansen et al. 2001). Climate has a strong influence on PNV and natural disturbance regimes.

Figure 17—Forty-eight percent of Oregon and Washington is covered by forest—approximately 20 million hectares or 78,000 square miles. Graphic by D. Olson.



Biogeographic diversity includes endemism and taxonomic distinctiveness, whereas local diversity focuses on numbers of species and distribution of individuals among species. The two are not necessarily positively correlated. For example, the Olympic Peninsula of Washington joined the mainland of North America because of plate tectonics but remained ecologically relatively isolated; thus, the peninsula has both numerous examples of endemism (at high elevations) and high diversity locally (at low elevations) and regionally across the peninsula, owing in part to a dramatic precipitation gradient. For example, tree crowns on the western peninsula may harbor 77 species of epiphytic plants, and tree boles may support 70 epiphytes. The endemic Roosevelt elk influences both forest structure and succession, reducing shrubs and promoting grasses (fig. 18). The magnificence of the elk and the forest caused President Grover Cleveland to set aside 891,000 hectares as the Olympic Forest Reserve in 1897; in 1907, President Teddy Roosevelt created the Mount Olympus National Monument; and in 1938, President Franklin Roosevelt created the Olympic National Park (Sharpe 1956). Islands, on the other hand, may have high endemism but few species (MacArthur and Wilson 1967, Whittaker et al. 2001). The mammalian fauna of the archipelago of southeastern Alaska provides a Pacific Northwest example of high endemism and few species.

Residual historical patterns from geologic history, climate, and physiography (e.g., biogeographic barriers such as mountain ranges, deserts, large rivers, and oceans) explain much of *regional diversity*. Western North America has 95 floristic associations each characterized by a flora, biogeographic range, and bioclimatic conditions. Washington and Oregon comprise 15 physiographic (landform) provinces, each containing multiple vegetation zones (Franklin and Dyrness 1973). Successional and developmental patterns differ significantly among the zones. Multiple types of biotic communities occur within each zone, with a total of almost 400 types. Johnson and O'Neil (2001) linked 541 species of indigenous vertebrates to 85 types of vegetation cross-classified by 26 *forest structural conditions* and 20 shrub- and grassland-structural conditions in Washington and Oregon (table 10).

The area west of the Cascade crest in Washington and Oregon contains nine major physiographic provinces, a dozen vegetation zones, and four major biogeographic barriers (the alpine of the Cascade Mountains on the east, Puget Sound in north-central western Washington, the Pacific Ocean on the west, and the Columbia River separating Washington (north) from Oregon (south). Soils range from serpentine inclusions in the south to uplifted marine sediments, volcanic ash, volcanic basalts, outflows of material from the bursting of glacial dams on Lake Missoula in distant Montana, glacial moraines, glacial outwash plains, colluviums, and alluviums with organic matter practically absent to deep layers of humus, litter, and coarse woody

Figure 18—A bull Roosevelt elk. Photo by A. Carey.

debris (standing dead trees, fallen trees, stumps, and large tree parts), depending on locale and management history.

The area is characterized by wet, mild winters, cool, dry summers, and a long frost-free season. During all seasons, prevailing westerly winds are moist. Climatic diagrams show typical Mediterranean curves, but summer fog provides about 200 millimeters of additional water and extended periods of cloudiness that reduce evaporation. During the 20th century, the region became significantly warmer (by 0.9 °C) and wetter (14 percent wetter), warming at a rate faster than the global average (Mote 2003). The vegetation spans the gamut from Mediterranean types in the Mixed-Conifer/Mixed

Table 10—Examples of wildlife habitat relationships in Oregon and Washington forests

East-side species occurrences and forest types:

Taxon	Mixed conifer	Lodgepole pine	Ponderosa pine	Upland aspen
Amphibians	12	9	13	4
Reptiles	11	12	21	5
Birds	116	83	131	77
Small mammals	43	26	31	24
Bats	11	9	15	5
Carnivores	18	13	14	10
Ungulates	9	8	7	5
All species	220	160	232	130

Source: Sallabanks et al. 2001.

West-side species occurrences and structural stages:

Taxon	Grass/forb	Shrub/seedling	Sapling/pole	Giant trees
Amphibians	19	19	20	28
Reptiles	19	16	16	17
Birds	61	92	98	140
Mammals	66	65	64	78

Source: Olson et al. 2001.

West-side species occurrences and habitat elements:

	Amphibians	Reptiles	Birds	Mammals
Rock/talus	3	10	27	35
Fallen trees	12	5	18	50
Duff/litter	10	4	5	19
Moss	1	0	5	4
Snags	4	0	57	22
Shrubs	1	0	21	11
Live trees	3	0	72	37

Source: Shield et al. 2002.

Evergreen Zone in the south (fig. 19A) to Idaho fescue grasslands and oak woodlands along the Rogue, Umpqua, and Willamette River valleys and the Puget Trough (fig. 19B) to subalpine fir, alpine meadow, and 27 glacial systems on Mount Rainier up 4,400 meters above sea level (fig. 19C) to sand dunes and shore pine at the ocean edge (fig. 19D) to conifer rain forests near sea level on the Olympic Peninsula (fig. 19E) (Daubenmire 1978, Franklin and Dyrness 1973, Peinado et al. 1997).

Figure 19—Vegetation variations of the Pacific Northwest: (A) redwoods of northern California; (B) oak grasslands near Corvallis, Oregon; (C) Mount Rainier, Washington; (D) coastal conifers along the western edge of the Olympic Peninsula; and (E) towering Sitka spruce and western redcedar in the Hoh Rainforest. Photos by A. Carey.

In Pacific North America, there are four major physiognomic groups of forests plants:

- Sclerophylls—367 taxa in oak forests and chaparrals.
- Acicular—187 taxa in upland interior forests of true fir, pine, sequoia, juniper, and some oak groups.
- Temperate—315 taxa in forests of redwood, western redcedar, western hemlock, subalpine fir, and Douglas-fir.
- Boreal—237 taxa.

Not only is the Olympic Peninsula a hotspot of endemism, the entire Pacific Northwest has a number of well-known vertebrate endemics, including Keen's mouse, Douglas' squirrel, Townsend's chipmunk, mountain beaver, red tree vole, and shrew-mole—the latter three genera are unique to the Pacific Northwest. Among birds, the northern spotted owl is a well-known subspecies unique to the Pacific Northwest. There are also more than 62 species of reptiles and amphibians, with more added as their taxonomy is revised and expanded (Leonard et al. 1993, Nussbaum et al. 1983); endemics include Cope's giant salamander, the Oregon slender salamander, Larch mountain salamander and others, including some endemic to the greater Northwest, such as the tailed frog. The transition from the Western Hemlock Zone to the Mixed-Conifer Zone is a zone of speciation for chipmunks and red tree voles.

The first sawmill in Oregon was established in 1829, and there were 173 mills by 1870. Large catastrophic disturbances occurred during the 20th century (e.g., the 1933 Tillamook Burn consumed over 97,000 hectares, and the 1962 Columbus Day Storm blew down 6 billion board feet of timber). Despite widespread logging, natural catastrophes, human-caused fires, and human settlement, western Washington and Oregon are still dominated by forests. Western Oregon is 80 percent forested with 52 percent federal, 41 percent private, and 7 percent state forest. However, of this forested area, 78 percent is less than 120 years old. Western Oregon does have 3.7 million hectares of wilderness (Campbell et al. 2002). Historically, the primary catastrophic disturbance in western Washington and Oregon has been fire. In Douglas-fir/western hemlock, Pacific silver fir, and subalpine forest types, fires have been of high severity but low frequency, and in mixed evergreen, dry Douglas-fir, and red fir forest types, fires have been of moderate severity and frequency (Agee 1998). Additional large-scale-disturbance windstorms (e.g., the 1921 blow in Washington) and smaller scale-disturbance ice storms have been relatively uncommon, and forest grew to ages of 250-, 500-, or 1,000 years or more.

Figure 20—Basalt cliffs line the edge of the Salmon River, Idaho, and provide a stunning backdrop for recreational activities, such as kayaking. Photo by A. Carey.

On the east side of the Cascade Range of Oregon and Washington, massive basalt flows covered with volcanic ash extend to the Salmon River in Idaho where they abut uplifted marine sediments (fig. 20). Mountains to the east and west form a large basin with borders of strong moisture gradients and dissected by long rivers, with the Columbia River predominant. Vegetation is diverse owing to the variety in climate, geology, landforms, hydrology, flora, fauna, and disturbances by fire, insects, pathogens, and water (Hessburg et al. 2000). Differences in physiography, lithology, topography, geomorphic processes, and climate produce broad-scale patterns; environmental gradients, successional and developmental dynamics, and patch-scale disturbances produce meso-scale patterns. Forests dominate to the north and on the slopes and foothills surrounding the basin and have increased in the Blue Mountains, Columbia Plateau, and Upper Snake River with fire suppression. Precipitation has increased markedly (by 38 percent) in the north-central area in the 20th century (Mote 2003).

Hemstrom (2001) emphasized that not only are vegetation patterns a result of such environmental variation and disturbances at multiple scales, but also that vegetative patterns influence the amount, severity, and distribution of disturbances by insects, pathogens, and fire. Numerous bark beetles (Hayes and Daterman 2001) and insect defoliators (Torgersen 2001) have major impacts on the forests. Root diseases are common (Thies 2001) as are dwarf mistletoes (fig. 21), rusts, and stem decays (Parks and Flanagan 2001). Historically, fire tended to occur at higher frequencies and lower severities (but still at scales of more than 10,000 hectares) compared to west-side forests (Agee 1998). Well before the arrival of settlers from the east, less than 3 percent of east-side forest was old growth, and it was in isolated patches (Youngblood 2001) (fig. 22). Thus, it appears that east-side forests exhibited a relatively fine-scale mosaic of different communities and developmental stages (intercommunity mosaic) compared to a relatively fine-scale developmental (intracommunity) mosaic in west-side forests.

Figure 21—Dwarf mistletoe. Photo by A. Carey.

Today, advanced forest succession and associated accumulations of biomass are increasing vulnerability of forests to catastrophic disturbances by insects, diseases, and fires (Tiedemann et al. 2000) (fig. 23). This region has high floristic diversity, with many endemics adapted to disturbance, owing to its complex biophysical environment (Croft 2001). Similarly, many of the indigenous vertebrates are disturbance adapted, benefiting from mosaics, including lynx, wolverine, and fisher (Bull et al. 2001) and a number of birds, especially those dependent on dead trees, including seven species of woodpeckers and nuthatches (Bull and Wales 2001b); seven amphibian species are of conservation concern and sensitive to disturbance (Bull and Wales 2001a).

Current vegetation patterns are a result of the interactions of grazing, timber harvest, tree planting, fire suppression, and lack of active management after planting, and topographic position. Ridge, slope, footslope, plains, and toeslopes all historically supported different communities (late-seral single-layer forest, early-seral-

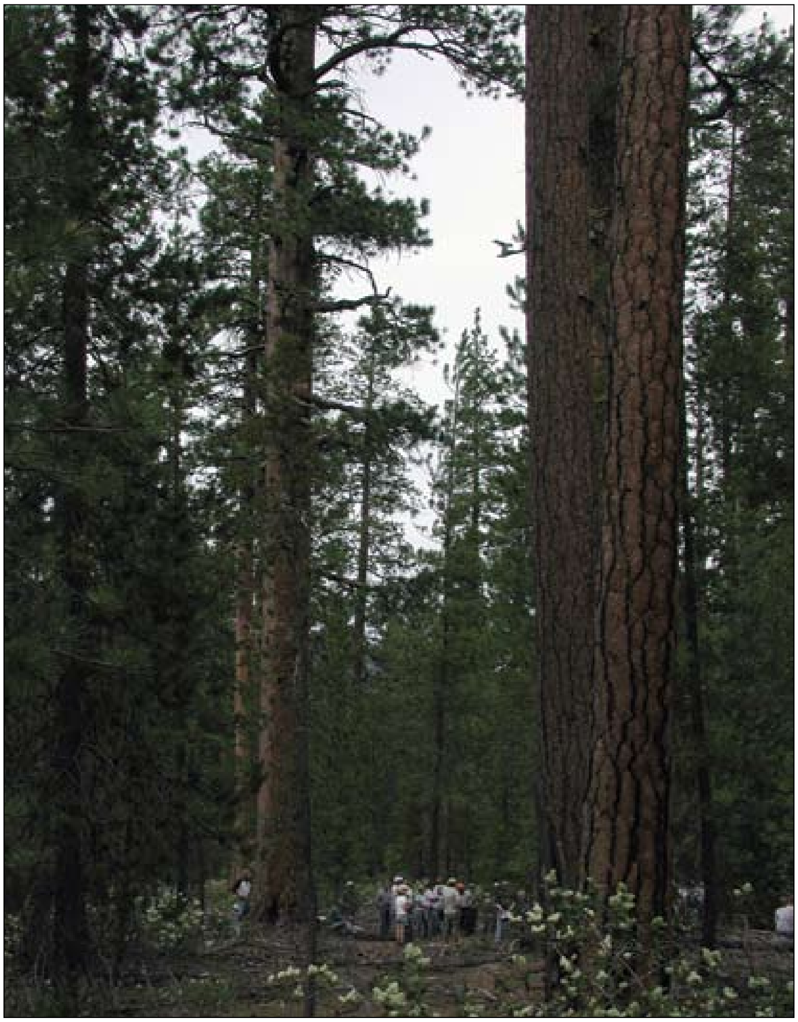


Figure 22—East-side forests: an isolated old-growth patch near Sisters, Oregon. Photo by A. Carey.

midseral forest mosaic, late-seral multilayer forest, late-seral single-layer forest, and midseral broadleaf-tall shrub mosaic, respectively) (Hemstrom 2001). Resource management has produced late-seral multilayer and early-seral mosaics on most sites with increased intertree competition, competition stress, increased susceptibility to insect attack, pathogens, and fire, and a switch from local to broad-scale disturbance patterns that changed not only patterns of plant species but vertebrates as well.

Human and natural disturbances may well have changed some ecosystem processes; for example, loss of a successional mosaic with actinorhizal shrubs (snow brush and bitter-brush) that normally replenish soil nitrogen lost by fire through nitrogen fixation could lead to long-term nitrogen depletion and reduced productivity (Busse 2000). Anthropogenic disturbances have also displaced native biotic community types and reduced productive potential for 17 or more PNV types, especially salt desert shrub, Wyoming big sagebrush/warm basin big sagebrush, mountain big sagebrush/mesic-wet, mountain big sagebrush/mesic-wet with juniper, and wheatgrass grasslands, making it difficult or impossible to restore these ecosystems to historical conditions. Major sources of change include livestock grazing, invasive species, changes in fire regimes, and climate change (Bunting et al. 2002). Hessburg et al. (2000) summarized the salient changes: decline in shrub land, loss of herb land, shift from early- to late-seral species, decline in western white pine in Idaho and Montana, dominance by shade-tolerant conifers in the Great Basin, and loss of patches with old-forest character.

Figure 23—An example of a low-intensity fire in a west-side second-growth forest. Photo courtesy of the USDA Forest Service.

These kinds of changes are common in interior western North America (fig. 24). For example, in the Targhee National Forest in Idaho, logging, grazing, and fire suppression prompted a transition from a fire-driven mosaic of grass, shrub, broadleaf, and mixed-forest community types to a conifer-dominated landscape—aspen declined from 37 percent to 8 percent, and conifer forests increased from 15 percent to 50 percent of the landscape. The problems here are not ones of fragmentation but increasing patch sizes and reduced disturbance frequencies reducing the diversity of communities in the landscape (Gallant et al. 2003).

Thus, at the *landscape scale*, topography, soils, disturbance regimes, tidal dynamics (in coastline landscapes), linked series of

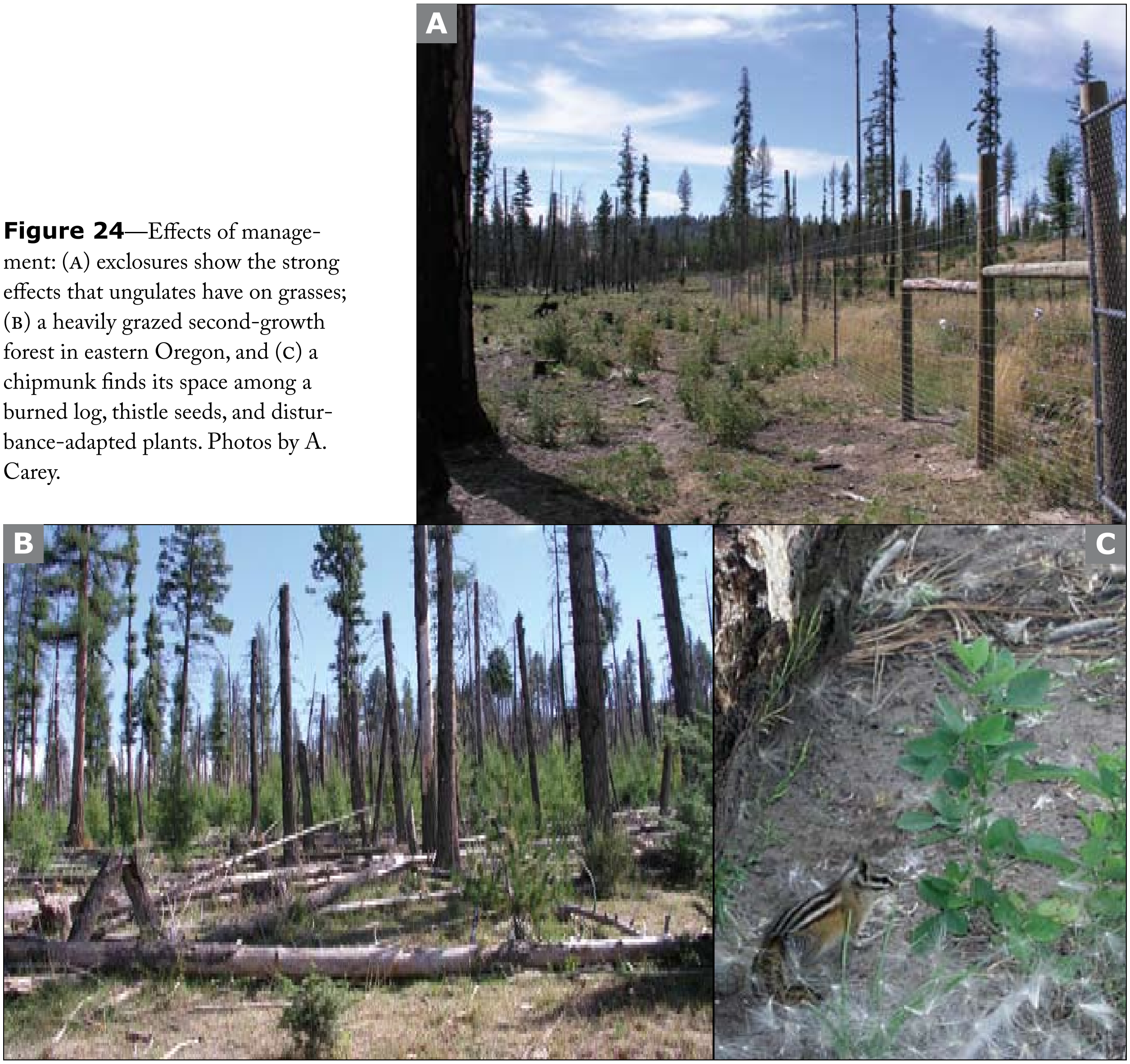


Figure 24—Effects of management: (A) exclosures show the strong effects that ungulates have on grasses; (B) a heavily grazed second-growth forest in eastern Oregon, and (C) a chipmunk finds its space among a burned log, thistle seeds, and disturbance-adapted plants. Photos by A. Carey.

events, management regimes (the nature of the shifting steady-state mosaic of a regulated forest), and cumulative effects of management activities are important. At *local scales*, microenvironmental variation, intermediate disturbances, community dynamics, patch dynamics, and management activities are important. However, Blondel states that "Since processes which produce biological diversities operate differently, and at different rates …along the scales of space, time, and change, many theories … are … more complementary than conflicting" (Whittaker et al. 2001).

Disturbance has long been recognized as a primary underpinning of biological diversity in landscapes.

Landscape Ecology

Diversity in a landscape will result from (1) natural random sampling of the regional species pool (Hubbell 2001) and (2) a variety of deterministic factors and processes operating at various scales including topographic, climatic, and edaphic diversity, history of disturbances (frequency, intensity, spatial extent, duration, and variance in times since disturbance), structural and biological legacies retained after disturbances, distances from sources of colonizers for various species, the vagility (dispersal ability) of those species, and the dynamics of biotic communities (reorganization, succession, development, creative destruction). Disturbance has long been recognized as a primary underpinning of biological diversity in landscapes because it is a major determinant of spatial heterogeneity at multiple scales (Bormann and Likens 1979, Canham et al. 1990, Carey et al. 1999c, Connell and Slatyer 1977, Foster et al. 1998, Franklin et al. 2002, Levin and Paine 1974, Oliver 1981, Petraitis et al. 1989, Pickett 1976, White 1979, Whittaker 1975). Examples of large, infrequent disturbances include the 1938 Northeast hurricane, 1980 eruption of Mount St. Helens, 1993 Tionesta tornado, 1998 Yellowstone fire, and the 1993 Mississippi floods (Foster et al. 1998). The resulting landscape patterns were controlled by interactions among the specific disturbance, the abiotic environment (especially topography), the vegetation at the time of disturbance, and the enduring legacies left by the disturbance. Northern coniferous forests are characterized by infrequent stand-replacing fires driven primarily by climate, strongly influential of plant population structure, genetics, and evolution, and inducing spatial heterogeneity (Turner et al. 2003). Spatial heterogeneity was more important than any other single environmental variable in explaining the abundance of mule deer in California—fine-grained mosaics with abundant edges, irregularly shaped patches, and high fractal dimensions allowed deer to exist within small home ranges

Figure 25—A patchy landscape dominated by clearcuts. Photo courtesy of USDA Forest Service.

(Kie et al. 2002). Heterogeneity among communities in the landscape generally increases the number of species in the landscape. For example, canopy cover gradients promote diversity of larval amphibians and coexistence of spring peepers and wood frogs in forests (Skelly et al. 2002).

Not all disturbances create complexity and heterogeneity, and not all heterogeneity promotes diversity. Traditional clearcutting, for example, produces regeneration sites that are as uniform as possible (fig. 25). When followed by planting (and often herbicide application), a simple monoculture with reduced diversity may result. In Pacific Northwest forests, most forest species are found in old-growth forests, but both managed and natural forests in closed-canopy stages from 30 to 200 years old may have markedly reduced diversity. Landscapes managed under short-rotation timber management may have increased abundances of exotic and ruderal species and markedly decreased diversity of native species (plants, fungi, and animals) (Carey 2003a, 2003b, 2003c; Carey et al. 1999c, 1999d). With short rotations and intentionally simplified stands of timber, whatever complex forest is left in the landscape is highly isolated from other complex forests and will remain so for quite some time (a century or more) even if management for timber stops. Such a landscape suffers from both loss in area of complex forests and fragmentation. For example, clearcuts less than 12 years old in British Columbia are significant barriers to dispersal of red-legged frogs, depending on weather and body mass of the frog. The warmer and drier the clearcut, the less permeable the clearcuts become because of physiological constraints on frog respiration (Chan-McLeod 2003).

Clearcuts may also be hostile environments for California red-backed voles because of lack of moisture, food, and cover (Clarkson and Mills 1994, Hooven and Black 1976, Mills 1995, Tallmon and Mills 1994), and for Douglas' squirrels and northern flying squirrels because of lack of trees. Closed-canopy competitive-exclusion forest communities with their sparse understories are inimical to Townsend's chipmunk, Keen's mouse, Oregon creeping voles, and a variety of other mammals. When rotations are short (say under 40 years), more than 25 percent of the landscape would be maintained in inhospitable conditions for animals of various life histories (Carey et al. 1999d). Thus, the life history of a species, the nature of the ecotones (a transitional zone between two communities containing the characteristic species of each), and the contrasts between juxtaposed communities determines the ecotone's degree of permeability and function as a boundary between communities—in other words, whether a hospitable mosaic is being maintained or whether the habitat of some species is being fragmented (Cadenasso et al. 2003a, 2003b).

Ecotones—loosely referred to as edges or boundaries—influence the flow not only of organisms but also materials and energy through mosaics. It is important to note that this is often a two-way flow—not only can a clearcut or field influence the microclimatic environment (light, temperature, and moisture) of a forest (Chen et al. 1995), but the reverse can happen also (Cadenasso et al. 1997). These edge effects (alteration of environmental conditions by the presence of a boundary or ecotone between two relatively homogeneous and usually contrasting environments) arise whenever areas are partitioned into patches, naturally or anthropogenically. Care must be taken, however, not to treat them as static; they are often rapidly changing in forested landscapes. Edge effects differ with disturbance regimes, time since creation, development of a sidewall of vegetation, successional or developmental state, and topographic position. Ecotones are complex three-dimensonal (at least) zones characterized by both above- and belowground gradients. These gradients exist even in the fine-scale mosaics with openings of 0.0 to 1.0 hectares (York et al. 2003). A tenfold increase in area of opening can produce a 34-percent increase in height growth of seedlings in gaps. Linear discontinuities such as narrow roads may not drastically alter the ecotone between two communities (Cadenasso et al. 1997). Understanding of how ecotonal boundaries influence the functioning of ecological systems is poorly developed (Cadenasso et al. 2003a, 2003b, 1997).

Natural catastrophic disturbances and intentional-management catastrophic disturbances, such as variable-retention timber harvesting, leave and maintain substantial biological legacies for the newly reorganizing forest. In Pacific Northwest landscapes under natural disturbance regimes or managed on long rotations with an emphasis on intracommunity biocomplexity, occasional patches of early-successional communities may add substantial species diversity to the landscape. Variation in species diversity among communities in landscapes is due to the structure, composition, and productivity of the various biotic communities, unless a community type is rare and patches are very small or small and isolated from similar communities—then it might have reduced diversity (Aars and Rolf 1999; Bayne and Hobson 1998; Bender et al. 1998; Boulinier et al. 2001; Brothers and Spingarn 1992; Debinski and Holt 2000; Lindenmayer et al. 1999, 2002; MacArthur 1965; MacArthur and Wilson 1967; McIntyre and Hobbs 1999; Opdam 1991; Robbins 1982; Whitcomb 1977; Whitcomb et al. 1976; Yahner 1985, 1988; and many others).

The effects of island size and distance from the mainland and agricultural-urban woodlot size and distance from other woodlots have been shown to reduce diversity and abundance of numerous species of various life forms. Island biogeography gave rise to conservation biology, which focuses on reserve design (single large versus several small reserves), degree of isolation of forest fragments, and the need for connecting corridors between fragments of isolated forest. However, one size never fits all; even within the narrow group of mammalian predators within a small region, measurement and mitigation of fragmentation must be scaled to species mobility (Gehring and Swihart 2003).

Fragmentation

In recent years, fragmentation has been viewed as the primary threat to diversity. Fragmentation routinely is conflated with (1) destruction of forests; (2) deliberate change in forest type (e.g., conversion of deciduous forest to conifer monocultures); (3) change in seral-stage structure of forested landscapes; (4) change in disturbance regimes of particular landscapes and regions; (5) direct human disturbance of wildlife (such as noise and mechanical impacts of forest management activities), recreational activities (hunting, fishing, birdwatching, hiking, and sightseeing), nature study, and ecological research; (6) effects of roads, which range from habitat loss to barriers to movement, pollution, and killing of wildlife by vehicles; (7) spread of exotic species; and (8) negative effects on soils, hydrology, and aquatic systems. It can be useful to distinguish between the effects of loss of forests to other uses of the land (loss of total area available for habitation by various species and loss of particular types of biotic communities) and fragmentation (isolation) of the remaining forest suitable for habitation by a species or group of species. Fragmentation refers to those effects of long-term (multiple decades to centuries) isolation of a plant community type or seral stage by markedly unlike types; short-term isolation may have no long-lasting effects. Long-term isolation includes effects on dispersal processes; small population sizes (which result in increased probability of genetic inbreeding, reduced fitness, and extirpation by various causes); effects on microclimatic and other physical modifications of isolated patch by its matrix; competition, parasitism, and predation by species well adapted to the matrix and matrix-patch interface; and aggregations of habitat elements of various wide-ranging species at scales mismatched to the species' life histories.

Fragmentation can affect forests in several different ways. For example, old-growth remnants can contribute to much of the species diversity in young forests. The amount of old-growth forest in an agricultural landscape can account for more than 65 percent of the variation in late-seral herb diversity within recently established forests (although, it may still take centuries for all herbs to recolonize and come to some equilibrium in species diversity) (Vellend 2003). In contrast, small remnant patches well separated from one another may reduce the ability of a forest to support local vertebrate populations. For example, the Oregon white oak communities of the Puget Trough of Washington are embedded in a prairie, wetland, and second-growth Douglas-fir matrix. Oak patches are dwindling in size owing to invasion by Douglas-fir and fire exclusion, and in number owing to agricultural, suburban, and urban development. The result is the near and perhaps imminent extirpation of the western gray squirrel in western Washington (Bayrakci et al. 2001, Ryan and Carey 1995). Fragmentation can also lead to scale mismatch. For example, when second-growth Douglas-fir in the competitive exclusion stage fragments old-growth Douglas-fir forest, it may result in an increase in the total area traversed by spotted owls to meet their minimum habitat area requirements at costs substantial enough to produce instability in owl pair membership (Carey et al. 1992).

Logging of old-growth forests in the Pacific Northwest has reduced markedly the total amount of old growth and produced a distribution of old growth characterized by large blocks, donuts (large blocks at mid elevations but with centers at high elevations without forest), and scattered small patches embedded in a landscape of second-growth forest. Although some scattered patches are small enough to suffer climatic influences of adjacent nonforest (shrub-sapling stages), the nonforest usually develops quickly into closed-canopy forests, and the remnant patches of old growth retain their associated flora and fauna (e.g., Neotropical migratory birds, Carey et al. 1991; aquatic amphibians, Bury et al. 1991b; vascular plants, fungi, and small mammals, Carey 1995, Carey and Johnson 1995, Carey et al. 1999b, Corn and Bury 1991a; and invertebrates, Marcot 2004). For these organisms, logging old growth led to habitat loss and habitat degradation but did not lead to effects of fragmentation, although recolonization of logged-over streams by aquatic amphibians did not take place after four to five decades (Bury and Corn 1991, Corn and Bury 1989), and questions remain about the ability of red tree voles to colonize developing second-growth forests (Carey 1999; Corn and Bury 1986, 1988; Gillesberg and Carey 1991).

A recent survey revealed little experimental evidence to support the contention of fragmentation effects (Debinski and Holt 2000). Only 20 experiments were uncovered, 6 in forests and 14 in old fields. Arthropods showed the best fit to the theory. Birds, mammals, early-successional plants, long-lived species, and general predators did not respond as expected. The reasons for lack of fit to theory were edge effects, competitive release, and the spatial scale of the experiment.

Whereas fragmentation is often stated as deleterious to biological diversity, mosaics are thought to increase diversity. Thus, it is important to distinguish between mosaics and fragmentation. Mosaic phenomena belong to two broad subgroups (Whittaker and Levin 1977):

- Intracommunity patterns related to microsite differentiation and species responses to it, such as development of habitat breadth or diversity in vegetation site types—microsites are the places where plants are rooted, and variation in microsite and the species occupying them produces a mosaic differentiated both physically and biologically.
- Intercommunity successional and developmental mosaics for which disturbance is a major determining force.

There is almost universal occurrence of mosaics in natural biotic communities. The diversity of these internal mosaics is a consequence of the evolution in natural communities toward diversity of both species and interspecies relationships. Disturbance disrupts patterns in vegetation communities owing to environmental gradients, producing a mosaic of communities. The disturbance mosaic and the mosaic owing to variation in biotopes (physical landscape elements, or *places of life*; larger physical sites that support biotic communities) result in a variety of more or less stable states in the landscape in the absence of further disturbance.

The pervasive notion that the *matrix* in which forest *fragments* are embedded is hostile to organisms within those fragments is often, even usually, not the case. A landscape considered structurally fragmented may still be functionally *variegated* (diversified) to some species (McIntyre and Hobbs 1999). Several factors are often overlooked when applying principles of island biogeography to old-growth forests in forested landscapes:

- Within such landscapes, the majority of old-growth-associated species are found in most seral stages of forest development (Ruggiero et al. 1991).
- Almost all old-growth-associated species will be found in

younger forests if those forests have significant biological legacies and intracommunity complexity (Carey 1989; Carey et al. 1992, 1999b, 1999c).

- Connectivity in a forested landscape can be achieved by several mechanisms besides corridors (including riparian areas) dedicated to spatial connectivity:

    - Permeable edges—edges between seral stages that do not present barriers to dispersal—also provide spatial connectivity.
    - Maintenance of shifting steady-state mosaics in forests managed under long rotations provides temporal connectivity among patches of old-growth/old-complex forests.
    - The earlier the seral stage—the shorter its duration and the lower its proportion of the landscape under intentional management for biodiversity (Carey et al. 1999c) and the greater the likelihood of maintaining old-growth species, such as the spotted owl (Carey et al. 1992, Carey and Peeler 1995) and northern goshawks (Finn et al. 2002) in the landscape.
    - Various landscape elements, such as areas with potential for deep-seated or rapid-shallow landslides, wetlands, and rock outcrops, maintained in intact forest contribute to a finer scale mosaic than most operational landscape units, providing refugia for organisms of limited vagility and foraging opportunities for organisms of high mobility.
    - Roads provide dispersal corridors, facilitate movement, and increase accessibility of different patch types for many native species.
    - High nest parasitism and predation are often associated with forest edges in agricultural-urban landscapes. However, in forested landscapes, parasitism may be rare in ecotones, and predation may be more prevalent in interiors of biotic communities than in ecotones (Tewksbury et al. 1998).

Allen and Hoekstra (1990) suggested the useful analogy of biotic communities in a landscape as wave interference patterns between processes and organisms interfering with and accommodating each other—a more useful, dynamic, concept than specific black-and-white communities (either habitat or nonhabitat for various species) etched into a map of places in the landscape. The main evidence for fragmentation effects has been from studies of birds in generally nonforested landscapes. In managed forest landscapes, however, a proliferation of songbird fragmentation studies has produced a growing awareness that avian diversity and abundance reflects the quantity of the different biotic communities available rather than the spatial arrangement or *fragmentation* of any one of them (Cushman and McGarigal 2003, Lee et al. 2002, Lichstein et al. 2002, Lindenmayer et al. 2002). Furthermore, the accumulated research does not support the concepts of consolidating clearcutting to reduce edge and landscape heterogeneity. Haila (2002) described the concept of island biogeography as an "intellectual attractor" that is too ambiguous to be useful in terrestrial environments—all natural environments are *fragmented* and that different organisms and ecological systems experience *fragmentation* in variable and even contradictory ways. Thus, any analysis of fragmentation must be context specific given the variety of organisms and multiplicities of temporal and spatial scales. In terrestrial systems, it is impossible to distinguish between disturbance and fragmentation as conventionally defined; distinguishing between fragmentation and a mosaic is a matter of degree and permanence of change in capacity to support a complete biotic community.

Isolation, Connectivity, and Viability

Ecologists have focused on number and overall connectivity of patches of habitat of particular species or of biotic communities supporting assemblages of species as landscape features. Landscape details include the size, shape, and edge permeability of the patches (Buechner 1989). Much discussion relates to the viability of a species metapopulation in a patchy environment in which local populations are subject to periodic extinction. Viability, under these premises, depends on successful dispersal and colonization of vacated or underpopulated patches. Some patches may be dispersal sinks that absorb more dispersers than they produce, effectively removing individuals from the metapopulation.

Four factors influence the movement of animals into sinks: (1) the perimeter-area ratio of the source patch, (2) the size of the sink relative to the size of the source, (3) the distance that dispersers can travel through a sink, and (4) the ease with which individuals move across the edges of the source patch. Sinks are only important to the degree to which they absorb individuals that may have gone on to colonize vacated habitats or individuals that emigrate as a matter of life history from an underpopulated patch and subsequently are unable to return. A sink can be a valuable source of colonists when it is near a source patch, yet does not suffer from the same forces that occasionally bring about extinction of the population in the source patch. Sources that routinely produce surplus animals that immigrate may occasionally suffer abrupt extinctions of their own population (or in the case of overdispersed species, such as the spotted owl, the death of a member of a breeding pair). Defining landscapes simply in terms of sources and sinks is as problematic as defining them in terms of habitat and nonhabitat. Few documented cases exist of strict sinks, but many exist of varying quality of habitat.

Emphasis on patchiness in relation to dispersal and colonization stems from island biogeography (MacArthur and Wilson 1967). A crucial difference between islands and continental systems is the ability of species to move between areas. Island biogeography sought an understanding of the species-area relationship and factors influencing the relationship (e.g., isolation and island elevation) in the context of islands in an inhospitable sea (MacArthur and Wilson 1967). Confusion often results from application of island concepts to forested landscapes (Carey and Harrington 2001). Misapplication of island concepts has contributed to failure to identify factors relevant to diversity at particular scales in continental environments, especially because scale of isolation differs with species life histories (Whittaker et al. 2001). Insularization of terrestrial communities occurs when climate change produces isolated mountaintop communities (Brown 1971) or when land use within a landscape changes dramatically, for example, returning Neotropical migratory birds encounter increasing fragmented forests as agriculture isolates woodlots in the Midwest (Whitcomb et al. 1977).

In western Washington, the western gray squirrel once found habitat in the Oregon white oak-dominated ecotones between prairies, Douglas-fir forest, and wetlands in landscape mosaics maintained by judicious prescribed burning by indigenous peoples to maintain an important source of medicinal plants and carbohydrates such as camas root. Gray squirrels require more than 5 hectares of juxtaposed oak woodland, Douglas-fir forest, and wetlands for habitation (Ryan and Carey 1995); a minimum effective population size in this environment would certainly require more than 50 occupied sites within a small landscape for genetic reasons alone (Soulé and Wilcox 1980). In the last century, fire suppression and fire exclusion have led to invasion and dominance of the oak woodland-prairie-wetland mosaic by Douglas-fir (Thysell and Carey 2001b). Reduced frequency of occurrence, size, and vigor of oak woodlands and motor vehicle traffic along roads near the remaining woodlands now threatens the continued existence of populations of western gray squirrels in western Washington (Ryan and Carey 1995). Even though a substantial area of oak woodlands and oak-fir ecotones remain, they are widely scattered across a landscape dominated by Douglas-fir forest, prairies, and human development. Western gray squirrel populations have crashed (Bayrakci et al. 2001). Although underconnected landscape elements can produce problems in dispersal, colonization, and maintenance of viable populations, excessive connectivity between individual organisms and homogeneity of communities can lead to increased susceptibility to density-dependent catastrophic disturbances, such as disease.

Temporary Isolation

In the western Washington lowlands, isolation by glaciation, postglacial hydrologic events, maintenance of landscape mosaics by indigenes, agriculture, forestry, development of transportation networks, and urbanization resulted in genetically distinct populations of northern flying squirrels in the Black Hills and the Puget Trough lowlands (Wilson 1999b). Timber harvest within the lowlands reduced genetic variability in local populations in the short term, but genetic diversity recovered rapidly because of outbreeding with nearby local populations. The flying squirrel is remarkably well adapted to avoiding inbreeding with its promiscuous mating system and long (relative to body size and population density)-distance movements (1 to 5 kilometers) by males to find mates. Multiple paternities of single litters have been documented (Wilson 1999b). Similarly, in Finland, the Siberian flying squirrel is threatened by past land use changes but now benefits from improved landscape permeability afforded by second-growth forest of low-quality habitat (Reunanen et al. 2000).

Conclusions on fragmentation in other studies of small mammals in the Pacific Northwest are debatable (Carey and Harrington 2001). Studies of Keen's mouse isolated in old-growth forests separated by clearcuts raised concern about effects of fragmentation (Lomolino and Perault 2000). Other studies found California red-backed voles isolated in old growth by clearcuts (Mills 1995). Both concluded there were negative effects of forest fragmentation and called for systems of reserves and corridors. Keen's mouse, however, is common in forests 40 to 90 years old with a western hemlock component (Carey and Harrington 2001, Carey and Johnson 1995, West 1991) and California red-backed voles also are common in young forests (Corn and Bury 1991a, Gilbert and Allwine 1991) (table 11). If isolated by clearcuts, isolation would be relatively short lived. Thus, temporal landscape dynamics, such as shifting steady-state mosaics maintained by regulated forests, are important considerations but rarely considered in landscape-scale studies of the effects of forest management on vertebrates.

Dispersal and Colonization

"Opportunities for movement and habitat diversification provided by the spatial aspect of the environment make possible in a variety of ways coexistence of species that could not otherwise survive together" (Levin 1976). Furthermore, if a landscape is heterogeneous, different combinations of species are likely to be favored in various locations and maintained elsewhere principally by dispersal from more favored regions, and this will act to increase the overall species richness. Dispersal in heterogeneous environments serves to lessen fluctuations in species populations and may increase population persistence by several orders of magnitude (Roff 1974a, 1974b). Dispersal is also important in colonization of newly developed regeneration niches. For example, Schwarz et al. (2003) found that, for seven species of trees at Hubbard Brook Forest in New Hampshire, environmental factors, disturbance, and competition operated within the local patch, but spatial autocorrelation suggested that neighboring patches were important as sources of colonizers consistent with seed-dispersal distance. Elevation was the primary environmental factor, followed by slope angle, and soil chemistry. In Amazonian forests, spatial heterogeneity plays an important role in the coexistence of Neotropical ant species that feed on the same species of plant. Where the food plants are found in high densities, the more fecund species dominate. Where the food plants are well distributed, the species that is the better long-distance flier dominates. A dispersal-fecundity tradeoff allows two genera to treat spatial heterogeneity in patch density as

Table 11—Relative abundances (percentage of value in old growth) of the western red-backed vole in young, mature, and old-growth forests in the Oregon western Cascades and Coast Range

	Seral stage		
Province	**Young**	**Mature**	**Old growth**
West Cascades	85	71	100
Coast Range	67	111	100

Source: Adapted from Corn and Bury 1991a and Gilbert and Allwine 1991.

a niche axis, and heterogeneity allows coexistence of the ants in the landscape (Yu et al. 2001).

Movement of organisms through landscapes depends on how they move and their capacity for movement. The wind-dispersed seeds of some plants and the spores of some fungi move long distances through and above the vegetation. The seeds of other plants, the spores of hypogeous fungi, and propagules of lichen move little or depend on dispersal by animals. Invertebrates exhibit huge variety in mechanisms and range in movement, moving from centimeters to kilometers. Migrating birds, waterfowl, many raptors, and bats move across the landscape in the air, well above the vegetation, little influenced by the nature of the biotic communities below, other than the contribution of the communities to the quality of the landscape as migratory corridor or as a habitat (an arrangement of patches suitable for foraging, roosting, nesting, and other essential behaviors). Other birds, in their daily activity, may confine their movements to particular strata of vegetation or show various degrees of willingness to move between landscape elements of markedly different natures. Terrestrial amphibians, reptiles, and some small mammals move through litter on the ground for relatively short distances of less than 5 to 50 meters on a daily basis (e.g., shrews and some salamanders) but farther when dispersing. Other mammals move on the surface of the forest floor from 50 to 500 meters daily (e.g., mice and chipmunks) to more than 1 kilometer (deer and elk). Squirrels (from the family Sciuridae) move daily from 100 meters to more than 1 kilometer through forest canopies (Carey 1991, 2000a).

Characteristics of the landscape that influence animal movement include environmental grain (the size of the patches within biotic communities and landscapes), sharpness of edges, nature of boundaries, connectivity, and interface permeability. Success of transit among landscape elements depends on the relative habitat quality of the various landscape elements (Basquill and Bondrup-Nielsen 1999). Adjacent elements each with high quality as habitat present few barriers to movement; the boundaries, edges, and ecotones between them have high permeability. Permeability can be measured by a species' willingness to cross the boundary. Permeability is also influenced by (1) motive to move, (2) the characteristics of the habitat of origin, (3) the characteristics of the patch of destination, and (4) the characteristics of the ecotone. A dispersing animal may be more willing to cross an unfamiliar or inhospitable environment than a foraging animal. An animal leaving a saturated or poor-quality habitat may move more willingly into a less populated or higher quality habitat.

Habitat selection itself is density dependent (Greene and Stamps 2001). Animals generally adapted to exploiting forests, for example, Neotropical migratory birds (fig. 26), may show minor effects on abundance but not distribution, in landscapes dominated by forests over 40 years old, even if the oldest forests are isolated by younger forests in the landscape. In other words, young forests are slightly poorer quality habitat for Neotropical migrants and markedly poorer for year-round resident birds, but both groups persist in the young growth, and their abundances are unaffected in the old forest (Carey et al. 1991, Haveri and Carey 2000). In Quebec landscapes where forests were fragmented by agriculture and urbanization, nonmigratory movements of breeding Neotropical migratory birds were affected by landscape composition and configuration. Other effects of fragmentation beyond habitat loss and limitation of movements among patches of habitat may include nest parasitism and predation (Belisle et al. 2001), especially in nonforested landscapes.

Linear features of the landscape, such as trails, roads, roadsides, fencerows, streams, and poorly vegetated ridgetops may variously facilitate or impede movement depending on the species. Roads and roadsides provide corridors for dispersal and enable gene flow in small mammals in fragmented forests in Australia (Bennett 1990). However, it can be difficult to distinguish a travel corridor from a linear habitat. For example, white-footed mice in the United States prefer structurally complex fencerows over their *natural* habitats of intermediate to simple structure (Merriam and Lanoue 1990).

Figure 26—A western tanager is a common spring and summer visitor to the Pacific Northwest. Photo courtesy of USDA Forest Service.

Passerine birds in Poland used shrub corridors to make greater use of a pine-meadow-lake mosaic than a mosaic without shrub corridors (Dmowski and Kozakiewicz 1990). Simulation models suggest that any corridor is better than none, high-quality corridors can increase metapopulation size, and populations in isolated patches of habitat, even if connected by low-quality corridors, are most vulnerable to extinction (Henein and Merriam 1990). In Great Britain, the European red squirrel has an effective dispersal distance of less than 1.5 kilometers between patches of forest separated by fields. Deforestation resulted in genetic isolation. Corridors that linked patches of forest and patches that were less than 1.5 kilometers apart allowed the squirrels to disperse by using patches as stepping stones. Limited reforestation allowed northern genes to leapfrog through hundreds of forest fragments and hundreds of kilometers in 20 years (Hale et al. 2001). This increased connectivity in the landscape, however, is raising fears of epidemic spread of the parapox virus that is deadly to squirrels. In Italy, extensive forest and forested corridors are allowing the spread of introduced eastern gray squirrels, which are threatening the continued existence of the native European red squirrel; the fear is that forested corridors will lead the eastern gray squirrel to France (Lurz et al. 2001).

Landscape Epidemiology

Concerns about settlers contracting zoonotic diseases (diseases of wild animals transmissible to people) in the former Soviet Union led to the development of landscape epidemiology (Pavlovsky 1966), a long-forgotten precursor to today's landscape ecology that evolved primarily from island biogeography (MacArthur and Wilson 1967). Pavlovsky died at the age of 81 in 1965. He developed his theory of the natural nidality (sensu site, nest, or niche) of pathogen persistence in 1939. Pavlovsky showed that the presence of organisms pathogenic to humans or their domestic animals could be predicted from the characteristics of the landscape. Investigation of the landscape-biotic community-pathogen complex relationship could be used to identify modifications of the landscape to break the transmission of pathogens among wild animals or changes in human use of the landscape that would reduce the risk of exposure of people and domestic animals to the pathogens. Pavlovsky implemented successful landscape management programs by using a hierarchical approach starting with biogeographic regions and scaling down to landscapes and biotic communities within landscapes. Efficacy entailed understanding the community ecology of the pathogen as well as the autecologies of the hosts and vectors of the pathogen. In the United States, landscape epidemiology has been used in research on rabies ecology and control in the Mid-Atlantic States (Carey 1982, 1985a; Carey et al. 1978), the ecology of Colorado tick fever in Rocky Mountain National Park in Colorado (Carey 1978c, Carey et al. 1980b, McLean et al. 1993), and Lyme disease in New England (Carey et al. 1980a, 1981). Studies of host-parasite systems, more than perhaps any other systems, mandate a consideration of variety in spatial scale—from landscapes of tissues within an organism (Carey and McLean 1978) to landscapes of biotic communities that support the parasite, vector, and hosts (Carey 1979; Carey et al. 1978, 1980b) and to regional (Carey 1982) and global (Carey and McLean 1983) variations in the ecology of a pathogenic organism. Epidemiology also reinforces the idea of being careful about what one wishes for—Hunter (1999) stated the goal of conservation biology was to preserve all species down to the lowest microbe; many would disagree with the values (and outcomes) implicit in that goal.

Landscape-epidemiological approaches incorporating spatial analysis in nested hierarchies of scale are now providing better understanding of diseases and parasites of wild plants, including trees. In Arizona, mistletoes that infect mesquite trees are spread by the Phainopepla, a bird that consumes its fruits and defecates its seeds. The pattern of infections and spread, however, is influenced by different factors at different scales (within tree, within the neighborhood of the tree, and across the landscape) that reflect interactions of the three species and the external environment (Aukema 2003b). Many diseases of trees are influenced by the structure and composition of biotic communities and landscapes. Basic epidemiology predicts that large numbers of susceptible hosts in contact with one another invite an epidemic—the larger the numbers, the greater the spatial extent of dense populations of susceptible individuals, and the greater the adjacencies of similar populations, the greater the epidemic catastrophe. For example, root diseases are important natural disturbance agents affecting all tree species in all forest ecosystems in eastern Oregon and Washington (Thies 2001). Shifts in tree species composition following fire exclusion (to species vulnerable to root rot), partial cutting, and management that retained high densities of trees have led to increased root disease. In fact, fire exclusion, introduced diseases, and management that produced high tree densities have led to a widespread decline in forest health (Tiedemann et al. 2000). Dense monocultures of variants ill-adapted to environmental conditions (offsite plantings) are well-known for their low vigor and susceptibility to needle diseases (Kavanagh et al. 2000) and root diseases (Filip 1999). The emergence of Swiss needle cast as a serious problem in coastal Douglas-fir illustrates these basic principles of epidemiology (Filip et al. 2000). Defoliating insects can produce major disturbances; these include spruce budworm, Douglas-fir tussock moth, Pandora moth, and larch casebearer, and others, maybe two dozen species overall (Torgersen 2001). Risks of outbreaks of these insects increase with low tree species diversity and high densities of susceptible trees.

It is also well known that introduction of novel diseases and insect pests can produce catastrophes; for example, chestnut blight, white pine blister rust, and numerous others. These introduced diseases may have surprisingly widespread effects even in the absence of dense, spatially extensive populations of susceptible individuals. For example, a disease complex is causing a decline in Pacific madrone. The primary pathogen is *Nattrassia mangiferae*, which causes cankers and shoot blight. Infected trees are stressed and become vulnerable to *Fusicoccum aesculi*, the secondary pathogen that causes branch dieback. All ages and all sizes of madrone are affected (interestingly, the complex can also cause skin disease in people and other animals). The primary pathogen was probably introduced into California with Persian walnut trees in the 1960s. The low resistance of madrone, severe weather stressing madrones, and fire suppression (fire destroys the disease inoculum) have allowed the disease to spread rapidly despite the scattered, patchy nature of madrone distribution (Elliott et al. 2002). Houston (1992) explicated a simple model for dieback and decline diseases:

Healthy trees + Stress = Altered tree tissues → Dieback

Altered tree tissues + More stress = Further alteration of tree tissues → Continued dieback.

A more complex theory emphasizes S, E, P, and B:

- S—simplified forest structure creates a predisposition to dieback;
- E—edaphically extensive sites to which the species is not well-adapted, including shallow soils poorly buffered from climatic extremes, increases probability of stress;
- P—periodically recurring perturbations owing to weather and climate instability produce stress; and
- B—biotic agents provide the coup de grace (Mueller-Dombois 1992).

Interactions between diseases, insect outbreaks, and other disturbances are widely recognized (Bebi et al. 2003, Hayes and Daterman 2001). For example, the White River National Forest had widespread fires in 1879 and a spruce beetle outbreak in the 1940s. Forests that burned in 1879 were less affected by the beetle outbreak in the 1940s. However, neighboring stands dominated by Engelmann spruce and elevation influenced the susceptibility of forests to insect infestation. Forests affected by the beetles showed no higher susceptibility to subsequent fire. The authors concluded that large, infrequent disturbances (fire, beetles) are often the dominant factors structuring an ecosystem and produce lasting ecological legacies. Subsequent ecological processes are strongly influenced by climatic and topographic factors and the contingencies of spatial arrangement of survivors, timing of availability of propagules, and barriers to spread of disturbance.

Landscape Mosaics

Mosaics can be variously hostile to biodiversity, supportive of biodiversity, inimical to particular species, or scaled such that they are supportive of all the indigenous flora and fauna. When landscapes are degraded by disturbances or lack of disturbances (natural or anthropogenic), effects of insularization owing to habitat loss are rarely distinguishable from direct effects of habitat loss or degradation without consideration of a variety of life-history characteristics of the organisms of interest. Spotted owls in the Western Hemlock Zone of southwestern Oregon occupied increasingly large areas as old-growth forests were harvested and replaced by early-seral stages (Carey et al. 1990). Eventually, owls were no longer able to track their prey base and their social structure began to break down (Carey et al. 1992). Although owls foraged in forests other than old growth, these foraging areas were either widely scattered or only intermittently suitable for foraging (Carey and Peeler 1995). In the Mixed Conifer Zone, more varied prey with a greater total biomass allowed owls to occupy smaller ranges and to use less old forest than in the Western Hemlock Zone just to the North. Isolation of blocks of old forest by intervening large clearcuts, however, was equivalent to the loss of an entire prey species in terms of energy expended to access sufficient amounts of old forest (Carey and Peeler 1995). Nevertheless, the grain (scale of patches) in the landscapes was small enough that dispersal and recolonization processes remained successful. Thus, the effects of timber harvesting on spotted owls were habitat loss and degradation of the landscape as a whole as a context for spotted owl habitat. It is not clear if there were negative effects owing to insularization. Spotted owls foraged in isolated patches. There was no evidence of either impediments to recolonization of vacated habitat or genetic isolation, either by barriers to movement or isolation by distance. Long-term genetic effects would be unlikely, given current population sizes and landscapes gradually improving in habitat quality. Markedly reduced metapopulation size and reduced reproductive attainment owing to pair instability, however, increases the probability of local extinctions that, theoretically, could cascade into regional extinctions.

As with spotted owls, landscape use greatly affects Tengmalm's owl in Finland, a small woodland owl that preys on voles whose abundance varies over 3- to 4-year cycles (Korpimaki 1988). Agricultural lands are its preferred foraging areas when voles are numerous. Spruce forest is preferred when voles are low in abundance on agricultural lands. Pine plantations are avoided. Of 104 territories studied for 10 years, more were occupied in only 1 year or in 5 or more years than would be expected by chance. Twenty-nine areas of the landscape were never occupied. Owls in good territories benefited from vole peaks by foraging over farmlands and shifting to alternate prey in woodlands during the low phase of the vole cycle. These more structurally complex portions of the landscape provided opportunities for prey switching. Poor territories supported breeding pairs only in peak vole years. Nearly all females shifted territories between successive breeding attempts, moving to more experienced males who could track local prey populations, rather than just moving to territories in better structured portions of the landscape. Males did not change territories.

Because predators are especially challenged by variable landscapes, theoretical ecologists have begun to model the dynamics of predators in patchy environments. They have developed models of predator distribution based on relative prey abundance (Bernstein et al. 1991). These models assume intake rate maximization, predator learning, nonnegligible prey handling time, and mutual interference between predators. Independent variables include travel costs between patches and the structure of the environment. When travel costs are small, prey depletion is slow, interference is moderate, predators conform to an ideal free distribution, and prey mortality is density dependent. As travel costs increase, the rate-maximization predator becomes more sedentary, and the population settles out at distributions far from the ideal free distribution. Prey mortality approaches density independence and later negative density dependence. In semicontinuous environments, with prey density correlated between neighboring patches, the slower the rate of spatial variation in prey (i.e., the coarser the environmental grain), the poorer the adjustment to the ideal free distribution, on account of the predator's need for learning. When the sample of the landscape within the reach of the individual predator is unrepresentative of the average prey density in the landscape (grain is coarse relative to the range of the predator), predators cannot learn the global distribution of foraging opportunities and fail to optimize intake. Predators shift ranges whenever the gain rate in the current patch is lower than the expected mean gain rate for the landscape as a whole. Well-informed predators should treat the world as though it were discontinuous (patchy) by aggregating only in patches with prey density above a certain threshold. As the cost of shifting foraging areas goes up, it still pays predators in very poor patches to move. Nevertheless, for patches above a certain threshold, cost of migration offsets potential gains of moving and predators do not migrate. Above that threshold, predators are distributed at random across patches with inverse density dependence between intermediate and good patches. If the cost of migration is very high, predators do not move even from poor patches, and predator mortality becomes inversely density-dependent across patches. These model simulations do not address, but do illustrate, that patch quality defined in terms of absolute prey abundance is of paramount importance in maintaining healthy predator populations even though relative differences between patch types may remain high (Carey and Peeler 1995).

Southwestern Oregon has suffered some of the most severe effects of timber harvesting on landscape composition in the Pacific Northwest (Carey et al. 1992, Carey and Peeler 1995). Patches of old-growth forest often were isolated from one another, with intervening expanses of early seral stages. However, studies of terrestrial amphibians (Corn and Bury 1991b), forest birds (Carey et al. 1991), and small mammal communities (Corn and Bury 1991a) revealed no fragmentation effects. Similarly, salamanders occupied even small patches of old growth in coastal British Columbia, suggesting such patches retain value as habitat (Dupuis and Bunnell 1999). Species of terrestrial salamanders in southwestern Washington respond differently to timber harvests but generally remain present in stands after thinning (Grialou et al. 2000). The reasons for lack of fragmentation effects are two: few species have distributions confined to old growth (Carey 1989), and forests develop rapidly after timber harvests, thus the duration of absolute isolation is too short for untoward genetic effects or stochastic demographic processes that

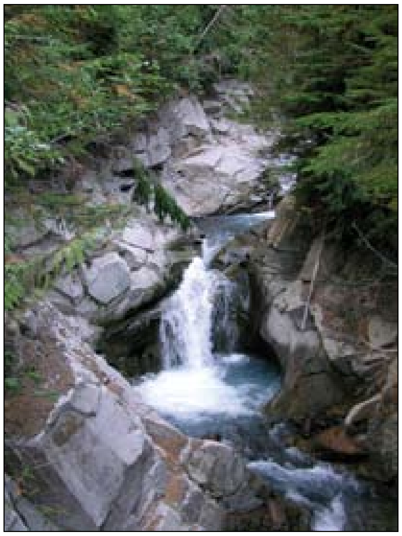


Figure 27—A cascading watercourse through a basalt streambed. Photo by A. Carey.

may lead to extinction. The effects of continued isolation of old-growth fragments by clearcuts and competitive exclusion stages are unknown but would be expected to have negative impacts on a number of species, especially some of those that are poor dispersers and that have low reproductive potential (Carey 1989). Aquatic amphibians do show effects of isolation. Timber harvesting across small water courses in southwestern Oregon evidently led to extinction of local populations; these sites remained uncolonized decades later (Bury et al. 1991b, Corn and Bury 1989). The reasons for lack of colonization, however, are unclear—Did the streams remain unsuitable for habitation? Were there no nearby (relative to ability) sources of colonizers? Was the forest surrounding the streams inhospitable to dispersers (of low permeability)? Were the streams below the reaches studied even less hospitable (less permeable to dispersers) than the reaches themselves?

Landform Variability

Landform sets the stage for the ecological theatre—the diversity of biotic communities in a landscape—and the evolutionary play (Hutchinson 1965). Variability in landform includes differences in elevation, aspect, slope, and lithology, for example, basalt versus marine sediments. These factors influence many other environmental variables, such as solar radiation (including photosynthetically active radiation), temperature regime, wind, precipitation, soil moisture, substrate texture, mass soil movements, and erosion, on a finer scale than the influence of overall climate. Topography and geology locally, as well as regionally, determine degree of dissection by watercourses, presence of wetlands, cliffs, rock outcrops, and talus, soil-site characteristics, and abundance of fine sediments in streams. Together, these determine the types of, and variation in, potential natural vegetation and availability of niches of highly specialized animals. For example, a substrate of marine sediments is more easily eroded than one of basalt (fig. 27). Streams running through marine sediments or glacial outwash are more likely to have large woody debris incorporated in their structure, and pools formed by large woody debris are likely to accumulate sediments (figs. 28A, C) following large upstream disturbances, reducing interstices between rocks that are important to larval giant salamanders; these streams are also less likely to have the smooth rocks needed by tailed frogs (Wilkins and Peterson 2000). Still, these streams may provide reaches suitable for spawning by Pacific salmon (fig. 28B).

Natural disturbance history, anthropogenic disturbances such as accidental fire, purposeful fire, grazing, timber management, and zoning (transportation corridors, cities, towns, suburbs, agricultural lands, rangelands, managed forests, parks, natural areas, and wilderness) determine the actual diversity within, and particular nature of, biotic communities in the landscape. The interplay between landscape character and biodiversity has led to the conclusion that environmental variation would be a good surrogate for directly measuring organismal diversity (Faith and Walker 1996). For example, in western Washington, Bosakowski (1997) found more bird species (78 species) in a landscape managed as an industrial forest than Manuwal and Huff (1987) found in natural forests more than 40 to 500 years old (46 species). This, however, is a comparison of apples and oranges—a sample of a landscape with all its inherent variability compared with a sample of narrowly defined forest conditions. The landscape still lacked species dependent on old growth, the seral stage that was in shortest supply. This example does illustrate problems inherent in reducing measurement of biodiversity to a single

Figure 28—(A) and (B) coarse woody debris creates pools along a stream; (C) sediment deposition along a stream favored by chum salmon (note the dead chum salmon). Photos by A. Carey.

(or a few) indexes—too much information is lost; effects of variability at different scales and effects of variability within types are lumped into coarse categories of landscape units (either physical or biotic, usually not both); information on entire ecosystems and species groups is lost, including effects of isolation on particular types of landscape units.

Landform Analysis, Communities, Habitats, and Niches

The ecosystem concept and ecosystem management have been challenged on the basis that ecosystems cannot be precisely defined and that ecosystem size differs with the size of the organism, life form, or process of interest. This challenge is only defensible for strict, narrow views of the world. Definition of ecosystems and scales of ecosystem management must include, of course, an appreciation of the various spatial scales at which various organisms operate—from viruses to spotted owls (Carey and Curtis 1996; Carey et al. 1978, 1980a, 1980b, 1992, 1999b). A hierarchy of scales is also necessary. Landscape analysis allows scaling of variation in geomorphic features and of the biotic communities that result from the interaction of landform and historical and contemporary disturbance regimes. Scaling is commonly used in watershed analyses, supported by systems ecologists (Odum 1971), community ecologists (Whittaker et al. 1973), population biologists (Hutchinson 1978), landscape ecologists (O'Neill et al. 1986), and empirical data from the Pacific Northwest (Carey and Peeler 1995). Scaling is essential to ecosystem and landscape analysis and management. Scaling can be related to various life forms and life histories.

A useful hierarchy begins with units homogeneous in aspect, slope, slope position, elevation, soil, geomorphology, rainfall zone, and other characteristics that make up landscapes and are the *places* where plants and animals settle. These are biotopes—*places of life* (Hutchinson 1978) and can be described in terms of their potential natural vegetation. For example, Henderson et al. (1989) mapped the 64 forested plant associations of the Olympic National Forest on this basis. Note that Hutchinson (1978) describes biotopes as being homogeneously diverse—in other words, they can be broken down into successively more homogeneous subparts and scaled up into larger units that may also be homogeneously diverse such as a shifting, steady-state, mosaic landscape. Yet, in the rugged topography of the Pacific Northwest, a natural ecological scaling, which is also operationally appropriate, presents itself with the variation in

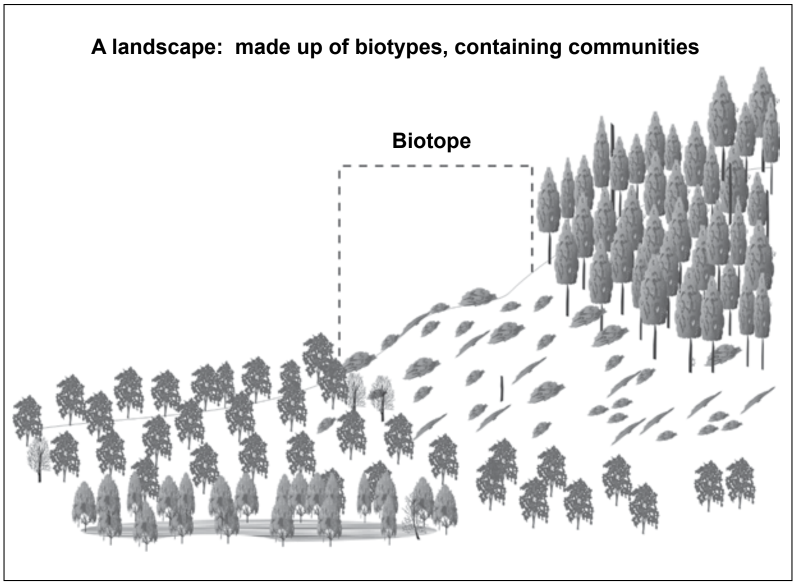


Figure 29—A schema for precise terminology—a landscape is made up of relatively homogeneous units of landform. These units are biotopes, or "places of life." Biotopes illustrated here are a wetland, a lowland, a toe of a slope, and a mid-slope. Biotopes are occupied by biotic communities, which are often characterized by their dominant vegetation and seral stage. This landscape is composed of forest communities that differ in species composition and seral stage. The range of biotic communities a species can inhabit is called its habitat. Quality of habitat can be inferred by plotting the density of the species across the array of biotic communities. Thus, habitat is defined by each species' use. Only part of each biotic community may be suitable to a species because of specific environmental requirements or because of interactions with other species. The part of the community used by species is called a niche. The niche is determined by both the ability of a species to exploit the resources in the community and other species that might compete for those resources, prey upon the species, or parasitize the species. Both habitats and niches can be described by multiple environmental variables. These variables describe potential habitat and niches (the complete multivariate space available) and realized habitats and niches (the space actually used) (adapted from Carey 1981, Whittaker et al. 1973). These concepts are of paramount importance in modeling landscapes and in landscape management. Few species are confined to a single biotic community, and species interactions may be influenced by the overall character of the landscape or just by adjacent communities that differ in species composition.

landform (Carey and Peeler 1995); the task may be more difficult in a Midwestern prairie or a lowland tropical rain forest. The species occupying and invading the biotope interact to form biotic communities that together with the physical aspects of the biotope are ecosystems (fig. 29). Because *biotope* has received poor acceptance in the lexicon of North American ecology, hereafter, *landscape unit* is used interchangeably with biotope, depending on context.

The ecosystem is the basic functional unit of ecology (Begon et al. 1986; Hutchinson 1978; Odum 1963, 1971; O'Neill et al. 1986; Whittaker et al. 1973) and is defined as "an ecological community together with its environment, functioning as a unit" (Pickett 2000). Odum (1971) used small forests (e.g., on a hillside) as examples of ecosystems; Bormann and Likens (1979) defined them as small, "watertight" watersheds of 10 to 50 hectares. This scale seems appropriate for Pacific Northwest terrestrial biotic communities as well (Carey and Peeler 1995, Carey et al. 1999d). However, Odum (1971) pointed out that aquatic systems must be defined at a larger scale, such as a drainage basin. A tenfold larger scale (100 to 500 hectares) seems appropriate for smaller streams and rivers. Watersheds in the Pacific Northwest run in the thousands of hectares (say 5,000 to 20,000 hectares for state of Washington designated Watershed Administrative Units). In reality, three attributes are important in defining landscape units: structure (the spatial relationships among the distinctive ecosystems composing the landscape), function (interactions among the ecosystems), and change (the alteration of the structure and function of the ecological mosaic through time) (Turner 1989). Landscapes are aggregations of ecosystems. Each successive level of aggregation can be considered a building block for serving larger ecological functions and larger conservation goals. The ecosystem is the fundamental building block but cannot be understood or effectively managed without considering intracommunity heterogeneity and landscape and regional contexts. Landscapes sum into physiographic provinces that have characteristic vegetation zones or life zones and eventually into biomes and, finally, the biosphere.

The basic operational unit in forestry is the stand—a more or less homogeneous group of trees. Stand identification rests on the age and species composition of the dominant trees and, as a result, can vary markedly from less than 5 hectares to thousands of hectares. Thus, stands may be perceived as having greater homogeneity than their associated biotic communities. Thus, using traditional forestry criteria may result in an excessively coarse scale for identification and delineation of ecosystems. Traditionally, botany has focused on a very small scale—much less than 0.5 hectare. Miller et al. (2002) examined spatial patterning of ground-layer species in old-growth northern hardwood forests by using 0.25-square-meter plots in grids of 1,860-square-meter grids. Ground-layer species were autocorrelated (clumped) at less than 2.5 to 21 meters depending on tree sapling density—randomly distributed at high sapling densities but clumped at low densities. The smallest scale autocorrelations resulted from vegetative reproduction and larger scale patterns from dispersal within a patchy environment. Microtopography and coarse woody debris were important to the maintenance of plant diversity within the biotic community, and the authors emphasized the need for within-community microhabitats or patchiness, suggesting a much larger scale would be relevant to plant communities. Busing and White (1993) looked at the effects of area on old-growth eastern hemlock-hardwood forest attributes by using 0.1-hectare subplots within 1.0-hectare plots. They found canopy gaps were generally less than 0.05 hectares, but that tree density, basal area, mass, leaf mass, and large tree density suggested a grain or patch size of about 0.2 hectare (one tree occupying 0.05 hectare). Canopy openings covered 13 percent of the area with most less than 200 square meters, but a multiple tree fall gap was more than 1000 square meters. Beckage and Clark (2003) also found that spatial heterogeneity in deciduous forests was important in providing unique regeneration niches that maintained a diversity of trees; York et al. (2003) found the same in Sierra Nevada conifer forests with experimental gaps of 0.1 to 1.0 hectare. However, the size, intensity, and spatial distribution of compositional patches were not affected solely by gap size but also by microtopography, seed dispersal distances, vegetative reproduction, and species interactions. Their results suggest a scale much larger than 1 hectare would be appropriate, especially because within-community heterogeneity is so important. As Kint et al. (2003) concluded, tree distribution and patterning ("positioning") determines different light regimes and regeneration patterns; the mixture of tree species also helps to determine light regimes and litter composition as well; and vertical and horizontal differentiation resulting from positioning, mixtures of tree species, age distributions, and competition determines spatial variation in microclimate, food supply, and structural complexity that provides for a variety of animals and plants. So, studies of forest plants suggest that communities range in size from tens to hundreds of hectares or more but have substantial heterogeneity at the scale of 0.2 to 0.5 hectare or less. This is very similar to the scale of variation in tree canopies, understory vascular plants, fungi, and use of patches by arboreal rodents in old-growth conifer forests in southwestern Oregon (Carey et al. 1999b).

Well, what about animals? Morris (1987) examined the question of scale in relationship to individual animals and populations. He suggested that both individuals and populations respond in one of two general ways. "Fine-grained species" [actually species responsive to fine environmental grain] use subsets of the mosaics within biotic communities in direct proportion to the abundance of the subsets; coarse-grained species select some communities over others. The possible scales that could be considered include the species' geographic range, the spatial scale at which population density varies, temporal scales of generation time, migration and dispersal distances, territory or home-range sizes, and the space and time of daily activities. He suggests distinguishing between two aspects of habitat. Macrohabitat would be the minimum area corresponding to that within which an average individual performs all of its biological functions during typical activity cycle (essentially the original definition of home range). Microhabitat would be defined by the physiochemical variables that influence allocation of time and energy within the macrohabitat/home range. This approach, however, is excessively individual-of-species specific; considering the responses of species populations is much more informative (Maguire 1973). Describing habitat in terms of the range of biotic communities used, the relative value of those communities as measured by some population response, the necessity for specific habitat elements, and the role of within-community heterogeneity in promoting coexistence of species, is much more informative for species adapted to fine-grained mosaics (biotic communities) and species responsive to coarse-grained landscapes. Using a population approach will help converge on a common scale related to the natural scale of biotic communities and will result in much smaller units than forestry criteria, say covering 10 to 200 hectares. This is also the mappable scale of aspect (the direction a hillside faces) in topographically well-dissected, mountainous landscapes (Carey and Peeler 1995). Biotic communities of this size are just large enough to support populations of vertebrates of low mobility: terrestrial and aquatic salamanders (Bury and Corn 1988a, 1988b; Bury et al. 1991a, 1991b); passerine birds (Carey et al. 1991, Huff et al. 1989, Huff and Raley 1991); forest-floor small mammals (Carey and Johnson 1995); and arboreal rodents (Carey 1991, 1995). This scale is amenable to examining niche complementarity and its effect on ecosystem function and source-sink dynamics for many species (Bond and Chase 2002). However, a small area (less than 10 hectares) may not withstand the climatic and biologic influences of an adjacent ecological community of markedly different character (Chen et al. 1992). Indeed, no ecosystem stands alone—all are influenced by, and receive organisms from, the other ecosystems in the landscape. A 10-hectare area is too small to support even an individual spotted owl; a spotted owl might forage over 140 hectares in a night (Carey 1993; Carey et al. 1990, 1992). Much larger areas may be too small to contain an aquatic ecosystem large enough to support a fish community (Odum 1971). Thus, 10- to 200-hectare biotopes along with the plant, fungal, and animal communities they support and the water and energy they receive are good fundamental terrestrial building blocks. This scale is appropriate for examination of biodiversity and ecosystem function. At this scale, management can be used to set back, maintain, or accelerate the process of forest development, promote simplicity or complexity in the forest community, and provide for either paucity or diversity of ecologic services, recreational experiences, and economic goods. Thus, the lay of the land and the condition of the ecosystem provides the actual size of the ecosystem management unit. Natural drainage patterns, operational restrictions imposed for streamside zones and other fragile-soil areas, and the economics of tracking and managing small isolated parcels of land also influence management unit boundaries and the resultant character of the landscape.

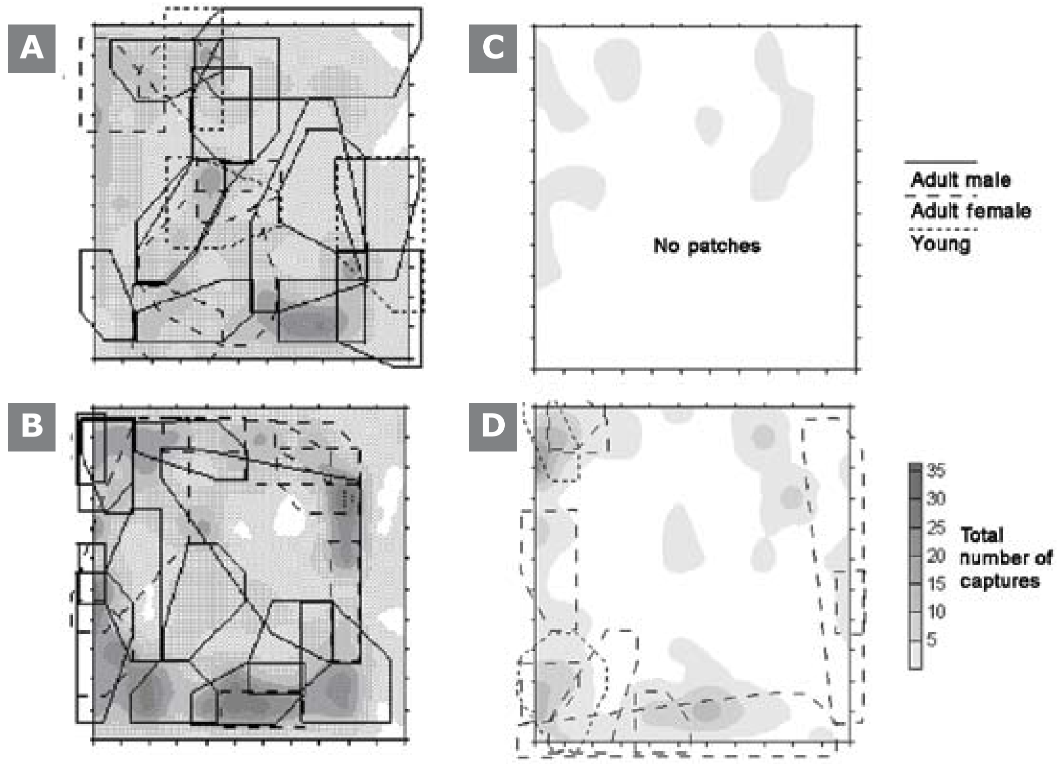
Streams are divided into classes (orders) based on their size and position in the watershed. The contributions of streams and streamsides to biodiversity differ markedly (Hawkins et al. 1983). Small streams and wetlands usually contain detritus-based communities supporting amphibians as top predators; many of these amphibians occupy upland communities as adults (Leonard et al. 1993). Larger streams usually contain photosynthesis- and detritus-based communities supporting fish as top predators. Additionally, streamside biotic communities include species unique to the riparian zone, including some amphibians (Olympic torrent salamander), birds (American dipper), and small mammals (water shrew). Other species, such as Roosevelt elk, prefer riparian communities over upland communities (Raedeke 1988, Woodward et al. 1994). Riparian forests also provide corridors that direct, facilitate, and impede movements of both small and large vertebrates. A minimum landscape unit for aquatic communities is the small watershed.

For the second-level operational building block, the life histories of animals of medium mobility in a terrestrial landscape provide guidance; for example, a pair or two or three of spotted owls, a resident fish stock, populations of screech owls, blacktail deer, and Roosevelt elk, or multiple populations of northern flying squirrels. Managerially, the scale includes the ability to manage for water quality, maintain ecological services in the face of small catastrophic disturbances (wildfires, windstorms, and timber harvests), produce a sustained yield of wood products, and support a small timber mill (only a part of a timber-dependent human community). This is the scale of watersheds; watersheds are naturally discrete landform units (Bormann and Likens 1979, Odum 1971). One or more watersheds constitute a landscape. Small watersheds in the state of Washington are 6,000 to 20,000 hectares. Small landscapes aggregate into larger units that can provide for a population of spotted owls, several populations of the largest mammal—Roosevelt elk, multiple fish stocks, metapopulations of amphibians, small mammals, and small birds, and a base for local economies. At larger scales, focus is on connectivity and permeability: river systems, ecological corridors (for gene flow through dispersal and for migration), and even highway systems. Large landscapes are 200,000 to 400,000 hectares.

Ecological theory explains simply patterns of abundances of a wide variety of plants, arthropods, and vertebrates by three factors (Brown 1984): (1) each species is limited by a combination of physical and biotic variables that define multidimensional habitats and niches; (2) spatial variation is somewhat stochastic but usually autocorrelated; and (3) closely related, ecologically similar species differ in no more than a few niche dimensions. The factors that regulate the distribution and abundance of a species, however, may vary with season (Fretwell 1972). Populations living in seasonal environments are exposed to regular changes in resource quality and abundance. Within a given space and time, individual animals are faced with choices about which areas or biotic community to inhabit. This habitat selection is part of the foundation on which the structure of small mammal communities lies (Rosenzweig 1989). Even resource partitioning is mainly achieved by habitat selection. At the large scale, the selection is among biotic communities and is called habitat. At a fine scale (*microhabitat*), selection occurs within a biotic community. Habitat preferences change more readily than resource preferences and are highly density dependent (resource preferences are only weakly density dependent). Thus, habitat preferences are most easily measured when a species is rare and are likely to decay at high densities (overall high resource levels). Habitat selection assumes (Fagen 1988) (1) animals move freely to preferred habitats, (2) animals prefer the available habitat offering the highest per capita resource availability, (3) resource availability is highly predictable, (4) moving between habitats costs little, (5) moving within each habitat costs the same as moving between habitats, and (6) individual reproductive success within each habitat decreases as population density increases. The fundamental niche of species is the set of environmental conditions and resources that permit a population to persist when not limited by competition or predation; this niche can be described evolutionarily as the environment in which mean fitness is 1 or more and outside of which mean fitness is less than 1. Natural selection operates principally as a conservative force to improve fitness within the fundamental niche (Holt and Gaines 1992).

In summary, landscapes are composed of biotopes occupied by biotic communities. The array of communities a species inhabits defines its habitat in that landscape. Within a biotic community, a species makes use of only a part of the available space; this use is dependent on interactions with other species and the space actually occupied is the niche (Carey 1981, Hutchinson 1978, Whittaker et al. 1973). For example, in the Montane Zone of the Rocky Mountains, Richardson's ground squirrel is confined by its colonial social behavior and habit of denning in burrows to areas of deep, friable soil such as meadows and aspen groves; thus deep soil determines its habitat. The golden-mantled ground squirrel has a much broader habitat; it is capable of inhabiting most of the biotic communities in the montane landscape. However, the golden-mantled ground squirrel can be excluded from communities on deep soils by the aggressive Richardson ground squirrel. In those areas, rock outcrops and the Richardson ground squirrel defines the niche of the golden-mantled ground squirrel. The least chipmunk has even a broader habitat spanning several zones; but its occurrence in any particular area depends on physical aspects of the habitat that allow it to avoid confrontation with other more aggressive chipmunks and ground squirrels (Carey 1978b, 1981; Heller 1971). In the Pacific Northwest, the northern flying squirrel occupies a wide range of biotic communities. Its abundance, however, varies markedly across those communities in response to various habitat elements that provide food, cover, and shelter. The squirrel can be extirpated from communities that are low-quality habitat by predation by long-tailed weasels. Even in high-quality habitat, its population density can be reduced sharply by predation by spotted owls (Carey et al. 1992). Within communities that provide poor-quality and those that provide high-quality habitat, the flying squirrel still only uses a fraction of the available space (fig. 30). In southwestern Oregon, use seems to be conditioned by coarse woody debris and interactions with truffles at the fine scale (microhabitat) and diversity of vegetation site types at a slightly large scale (habitat breadth) (Carey et al. 1999b) (table 12). In western Washington, factors determining the niche of the flying squirrel seem more related to the presence of mast-producing hardwoods in addition to vegetation complexity, abundance of cavity trees, competition primarily with chipmunks, and predation by owls and weasels (Carey 1995, 2000a, 2000b; Carey and Harrington 2001).

Figure 30—Habitat is defined by the use of a species. Use is often measured as density (number of animals per hectare), and density is often determined by the use of space. Good habitat for both (A) northern flying squirrels and (B) Townsend's chipmunks was provided by old growth, and bad habitat for both (C) flying squirrels and (D) chipmunks was provided by second growth (adapted from Carey et al. 1999b). Shading reflects the numbers of captures of the squirrels and the lines represent short-duration foraging patches (flying squirrels) and home ranges (chipmunks). Note there are unused portions for each species in both stands.



Communities and Ecosystems

Biotic communities comprise the species occupying a particular biotope (site in a landscape) that, together with that site, form a local ecosystem that supports those local species populations. Much debate has taken place over whether or not biotic communities are real assemblages of interacting species or haphazard assemblages of species whose composition reflects historical contingencies and random sampling from a regional species pool. The latter reductionist view reflects narrow focus and lack of consideration of interactions taking place at various levels of biological, spatial, and temporal

Table 12—**Population response of northern flying squirrels to environmental variables in Oregon**[a]

Response measure	Scale	Dependent variable(s)	Independent variable(s)[b]	Variance explained[c]
Potential habitat (Total habitat space sampled)	Points in a landscape	▪ Variance in vegetation structure	▪ Crown-class differentiation (25%), decadence (16%), canopy stratification (11%), understory development (10%)	63%
		▪ Composition	▪ Position on a moisture gradient (24%)	24%
Realized habitat	Points in a landscape	▪ Presence-absence of squirrels	▪ Decadence (0.8) + canopy stratification (0.6) + crown-class differentiation (0.3) + understory development (0.3)	60%
Habitat quality	Among communities	▪ Abundance	▪ Decadence (17%) + habitat breadth (21%)	50%
Carrying capacity	Among communities	▪ Maximum abundance over time	▪ Decadence (45%) + habitat breadth (25%) – position on the moisture gradient (16%)	70%

[a] The entire area sampled was described by the structure and composition of the vegetation; structure could be reduced to four independent variables, and composition to one independent variable. Flying squirrels occupied only a part of the available space, and this part was described well by the four structural variables. Variance in abundance across the biotic communities, however, was best explained by decadence (fallen trees and snags) and by complexity of the vegetation community (habitat breadth). The maximum attainable densities of squirrels were best predicted by decadence, habitat breadth, and position on a moisture gradient indicating that rich mesic communities supported higher populations than communities on dry sites or very wet sites.

[b] Different types of statistical analysis were used depending on the nature of the dependent variable. The values in parentheses represent the relative contribution (or importance, which could be negative or positive) of each independent variable in explaining the variance in the dependent variable. These values may or may not sum to the values in the variance explained column or to 100 percent because the exact statistical meanings of these values varies with the analytical method.

[c] The total percentage of variance explained by the statistical procedure.

Source: Adapted from Carey et al. 1999b.

organization. Such a view is most likely to be held by one who focuses on large, immobile organisms, such as tropical trees, that are species rich, diverse in dispersal ability, and adapted to environmental homogeneity (Hubbell 2001). The former view is more likely to be held by ecologists who must consider competitive, mutualistic, host-parasite, predator-prey, and complex food web relationships of species of markedly varying mobility and dispersal capability coexisting in spatially and temporally heterogeneous landscapes and biotopes (Tilman and Kareiva 1997).

Many of the contentious issues in ecology carry over into the applied ecology of forest ecosystem management and conservation of biodiversity. The concept of biodiversity, at its basic level, is a community concept. The same can be said of functional groups, guilds, niche, ecosystem, ecological succession, forest development, biotic integrity, resilience, stability, and forest health. The contemporary question boils down to: Are assemblages of species in place and time (1) simply an accident of history built upon by random immigrations and extinctions versus (2) a result of a self-organizing adaptive system, conditioned by history and drawing from regional species pools, but forming assemblages consisting of tightly connected nodes of species loosely connected into a larger system of tightly connected nodes (Barabási and Bonabeau 2003, Dunne et al. 2002), all within an evolving holarchic system that develops in biocomplexity until some major external force causes catastrophic collapse, followed by reorganization? In other words, is the basic unit of ecology, the ecosystem, a site inhabited by a chaotic or random assemblage of species or an organized, ecological, system? To many ecological modelers, statistical ecologists, and mathematicians, arrangements in space and time do seem poorly predictable, unstable, and chaotic. To naturalists, often imbued with a tolerance of ambiguity born of experiential appreciation of natural wonder, the patterns and organization in nature are manifest—familiar and predictable but often accompanied by delightful or fearful surprises. In the stochastic view, there is no logical need for conservation. In the systems view, conservation is required to maintain keystone species, keystone complexes, and a species pool that provides for redundancy in functional groups, which facilitates system adaptability and change through time.

Another major ambiguity in defining, discussing, and studying biotic communities is that limiting consideration to a subset of species on a site (or among sites) requires decisions that are somewhat arbitrary. Examples of arbitrarily defined biotic communities include mosses, lichens, herbs, achlorophyllous mycotrophic plants, shrubs, trees, hypogeous ectomycorrhizal fungi, epigeous mycorrhizal fungi,

In the stochastic view, there is no logical need for conservation.

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In the systems view, conservation is required to maintain keystone species, keystone complexes, and a species pool that provides for redundancy in functional groups, which facilitates system adaptability and change through time.

Sidenote 32—Growth form (also referred to as growth habit or life form)—how plant species are put together and shaped, such as forbs, grasses, lichens, shrubs, trees, vines, etc. (Grime 1977).

litter arthropods, forest-floor mollusks, forest-floor salamanders, Neotropical migratory birds, forest-floor small mammals, arboreal rodents, and bats. Certainly, these groups of species that are more-or-less similar in some aspects of their phylogenies, physiognomies, physiologies, and ecologies are more comprehensible than the totality of species, more likely to exhibit apparent niche differences (resource partitioning, differences in trophic relationships) that allow explication of system function, and more likely to be keyed to a recognizable subset of elements of forest ecosystem structure or composition—but they are not independent of interactions with other species or groups of species, even species at different trophic levels, of markedly different sizes, and with various life histories.

Certain aspects of community-level diversity are axiomatic. Species diversity within biotic communities generally increases with the spatial extent (area) of the community, history of intermediate disturbances, time since last major disturbance up to some asymptote, and heterogeneity. Diversity within a specific community can vary markedly with time since catastrophic disturbance, with high diversity as the disturbed site is colonized by exploiters and low diversity when a few species dominate the system (as in the competitive exclusion stage of forest development). Diversity increases with differentiation (e.g., crown-class differentiation, or development of dominance, codominance, subordinance, and suppression among trees and species of trees, and differentiation among microsites owing to effects of dominant plants on light, moisture, microclimate, and soil chemistry) arising from interactions (competition, predation, mutualism) that modulate species fluctuation in species abundances. Diversity also increases with development of spatial complexity arising from accumulation of biomass and small-scale disturbances but decreases (at least for vertebrates and vascular plants) in the absence of disturbance as the ecosystem maintains a relatively stable quasi-climax state. With succession (replacement of one relatively discrete biotic community by another) and development (envelopment) of communities over time in forest-dominated systems, the trend is toward increased biomass, a system shift from production to maintenance of biomass, vertical stratification by increasing diversity of growth forms (sidenote 32), complexity in arrangement of physical and biological structures in space, diversity in species composition, increases in niche complementarity, selection for competitive ability, and tightening and slowing of nutrient cycling, as products of community self-organization and self-regulation (Carey et al. 1999b, Franklin et al. 2002, Margalef 1968, Odum 1969, Pickett 1976, Whittaker 1972).

Note, the difference between *succession*—replacement of a grass community by a shrub community by a tree community or replacement of a deciduous tree community by a conifer-dominated community—and *development*. Development is a process by which ecosystems (the abiotic and biotic circumstances of a site) expand in multivariate dimensions with each expansion *enveloping*, not displacing, the preceding condition. A young second-growth Douglas-fir forest can develop from the competitive exclusion stage, in which the firs each attempt to capture as much of the multidimensional growing space as possible to the exclusion of weaker firs and other members of the community, to diverse communities undergoing development of habitat breadth (vegetation-microsite type diversity) and preinteractive niche diversification (these concepts will be discussed in detail later). Although, many of the firs maintain their positions of dominance for centuries, most of the originally scarce species increase in abundance, and new species are recruited. Thus, species diversity is not an unchanging property of a community. Species extinctions, speciation, and invasions occur at multiple scales simultaneously.

Biological diversity decreases in systems exploited by humans. In exploited ecosystems, community succession and development are often truncated, the maturity and complexity of ecosystems are reduced, and fewer species and life forms produce the bulk of the biomass. Management often deliberately simplifies biotic communities and sometimes even the physical variability of the ecosystem. Even the structure of the soil may be simplified with a concomitant decrease in the diversity of soil organisms. Weeds and pests increase rapidly and disperse easily. Strong exploitation of very mature ecosystems may produce a total collapse of a rich organization (Margalef 1968). The root causes of loss of biodiversity are often stated to be destruction and fragmentation of natural plant communities, although pollution, invasion by exotic species, overharvesting of resources, and disease can be important (Wilson 1999a). Conversion of forest, wetlands, and grasslands to farmland, suburban, urban, and industrialized areas in eastern North America resulted in some extinctions, multiple widespread extirpations, and reduced vertebrate populations and led to the Federal Aid to Restoration of Wildlife and Fish Acts in 1937 and 1950 (Allen 1954). Nevertheless, the same patterns of exploitation and loss of biological diversity continued in western North America (Lee 1993).

Diseases, such as chestnut blight, Dutch elm disease, white-pine blister rust, and many others have had profound effects on composition and structure of forest communities. The effects of epidemic disease and reduced biodiversity may be acute in the short term but still produce chronic results. For example, chestnut blight, fire exclusion, agricultural clearing, clearcutting for timber harvest, and purposeful increases in deer populations disrupted a dynamic equilibrium among upland oaks to the extent that white oak, once supreme among oaks prior to the arrival of Europeans in eastern North America, is in dramatic decline (Abrams 2003). The most dramatic example is a drop from composing 33 percent of all oaks to 9 percent in eastern West Virginia. Such compounded perturbations have produced similar ecological surprises in a variety of systems (Paine et al. 1998). Shifts to some alternative relatively stable state of lowered diversity in response to slow change or chronic stress may occur dramatically and rapidly (Holling 1986, Scheffer et al. 2001).

Self-Organizing Systems

What is this idea of self-organizing systems? R.H. Whittaker (1969) described organization as the means by which functioning complexity is maintained through time. Salient organizing principles include competitive interplay (leading to niche structure) and adaptive diversification (leading to complex food webs). Thus, diversity increases during development, and overall diversity in tree-species-rich broadleaf forest tends to be higher than in evergreen conifer forests dominated by a few tree species. Diversity of vascular plants tends to decrease with decreasing environmental stability and increasingly extreme conditions that might interfere with development of greater organization and complexity. The diversity of a community, then, is a form of complexity, of organized differentiation, and expresses the kind of organization—competitive interplay, role differentiation, and diverse interactions—tending to modulate community fluctuation. Microsite variation alone is insufficient to provide for even the diversity of tree species; interactions among dominants and subordinates and among species are key (Fox 1977). Positive interactions (mutualisms and facilitation) play a critical role in ecological communities by reducing physical and biotic stresses and by contributing to development (or even creating new biotic communities) on which many species depend (Mulder et al. 2001, Stachowicz 2001). Simply by growing, many species alter their local environment by shading, blocking the wind, intercepting precipitation, and altering soil chemistry by their litter and exudates. Mutualists, such as ectomycorrhizal fungi on the roots of conifers and rumen bacteria and protozoa in the four-chambered stomachs of deer and elk, are essential to nutrient transfer and trophic facilitation. Some species are ecosystem engineers, and modify the environment by their activities (e.g., American beaver and the big-time excavator of trees, the pileated woodpecker). Less obvious engineers are wood-boring insects and decay-causing fungi. These species provide critical habitat elements for numerous species including refuge (protective cover and protected nest sites) from physical stress, predation, and competition. Diversity within functional groups like ectomycorrhizal fungi and bryophytes is thought to help maintain an ecosystem through environmental change and under environmental stress.

When self-organizing forces for evolution of diversity interact with the technological capacity of postindustrial socioeconomic-environmental systems, a predicament arises. A system of accelerating growth and increasing complexity stretches ever tighter the means of organization while producing social and environmental problems ever more difficult and beyond realistic prospects of solution, increasing tensions and frustrations of people who must maintain the organization and try to deal with problems, and producing increasing numbers of people who scorn the system and its complexities without a rational sense of the limitations on alternatives (Whittaker 1969). Thus, Holling (2001) incorporates social, economic, and environmental levels in the hierarchies of Panarchy theory to examine how we might move toward sustainability, which he defines as the capacity to create, test, and maintain adaptive complexity while maintaining development—the process of creating, testing, and maintaining opportunity. He defines self-organization as the development of complex adaptive systems in which multiple outcomes are possible and dependent on accidents of history. Diversity and the individuality of components, localized interactions among components, and an autonomous process that uses the outcomes of those local interactions to select a subset of those components for enhancement are characteristic of complex, adaptive systems. Thus, he states, if sustainability means anything, it has to do with the small set of critical self-organized variables and the transformations that can occur in them during the evolutionary process of societal development. Thus, Holling (2001) suggested a dozen truisms (sidenote 33). Panarchy theory describes how a healthy sociological system can invent and experiment, benefiting from inventions that create opportunity while it is kept safe from those that destabilize. Panarchy theory is discussed more in depth later, but now let's return to some fundamentals of biological diversity.

Sidenote 33—Current understanding of Panarchy theory (Holling 2001):

- Multiple stable states are common.
- An adaptive cycle is the fundamental unit of dynamic change.
- Not all adaptive cycles are the same; some are maladaptive.
- Sustainability requires both change and persistence.
- Self-organization shapes long-term changes.
- There are three types of learning—incremental, lurching, and transforming.
- The world is lumpy.
- Functional diversity builds resilience.
- Tractability comes from the rule of hand (x>3).
- Emergent behavior emerges from an integrated system.
- Management must take surprise and unpredictability into consideration.
- Adaptive management outperforms optimization for stable targets.

Formation of Biotic Communities

Various theories provide different perspectives on how species populations assemble into biotic communities (Belyea and Lancaster

1999, Gotelli 1999). Trait-environment theory posits that certain traits of individual species allow those species to occur together in specific biotic communities. Island biogeography theory asserts that assembly incorporates competition and stochastic colonization processes. Contingent ecology relates that assembly is conditioned by the specifics of the locality and its history. Deterministic ecology claims that community assembly conforms to some general principles. Fundamental principles that apply widely in community formation are called assembly rules. These rules constrain the behavior of the assembly process and arise from various processes occurring within the community. The same rule may apply to communities that differ historically and may lead to similar or to divergent trajectories, depending on a number of variables, including regional species pool, specifics of the locality, and specifics of history. As far as we can tell, dispersal constraints, environmental constraints, and internal dynamics of populations within communities interact to select species that not only can coexist but also interact to increase biomass and to produce nonrandom spatial distributions of species. Dispersal constraints determine the pool of potential colonists and result from species-specific traits, storage effects, landscape ecology, and history. Environmental constraints restrict species establishment and mediate interactions among residents and successful colonists. Environmental changes can lead to changes in communities. Assembly rules are general and mechanistic and operate within the situation-specific constraints imposed by colonization sequence and environment. An example of a rule is the proportion of total resources consumed increases as each additional species invades. Internally, species compete for the same resources within, but not between, functional groups. This rule suggests that a common pattern should be that invading species are likely drawn from different functional groups until each group is represented, before the pattern repeats itself. As resource use increases within a functional group, interspecific competition increases, and species overdisperse to minimize niche overlap. Rules operate within and across trophic levels and whole systems through resource dynamics and spatial dynamics to select sets of coexisting species. The interaction of an assembly rule operating at one level of community organization (e.g., within a functional group) with a rule operating at another level of organization (e.g., across trophic levels) may lead to patterns of community structure that could not be predicted from either rule working independently. This phenomenon can be viewed as an emergent property of self-organization as well as evidence of a chaotic system.

A.S. Watt (1947), in his presidential address to the British Ecological Society, emphasized a patchwork mechanism of community assembly. Aggregates of individuals and species form different kinds of patches—these patches form a mosaic that constitutes the community; thus, recognition of patchiness is fundamental. Patches (or phases) are dynamically related to each other, and when this dynamic produces orderly change, there is persistence in the community pattern. Much later, Ives et al. (2000) argued that complex communities composed of modular subcommunities lead to community stability and species richness. Departures from the inherent tendency to orderliness may be caused by fortuitous (stochastic) obstacles to the normal sequence of events, with the final community structure resulting from causes of order and causes of disorder (Watt 1947; note the similarity to the self-organizing system that produces order out of chaos). Watt emphasized relationships among components of ecosystems in space and time, saying these relationships constituted the primary means of maintaining the integrity of the community. Thereby, he argued for communities defined as homogeneously diverse dynamic assemblages with a recognizable pattern just as Hutchinson (1978) did 30 years later. Watt described the community as a space-time mosaic, wherein each patch is dependent on its neighbors and develops under conditions partly imposed by them. Watt (1947) provided examples from diverse biotic communities—bogs, bracken-grass heaths, beech-birch woods, tropical forests, and others. He emphasized process over structure—the thing that persists is the process and its manifestation in space-time patterns. Emphasis on process over structure is essential for effective management and conservation of naturalistic ecosystems (Carey 2003a, 2003c; Carey et al. 1999b) and is a theme of this book. Like Holling (1969) 20 years later in his adaptive cycle and Bormann and Likens (1979) 30 years later in their studies of the dynamics of northeastern forests, Watt (1947) talked about a cycle of change with an upgrade phase that accumulates biomass and develops habitat potential and downgrades that can come about through insects, diseases, and physical disturbances. Time and again, throughout the brief history of ecology, the same phenomena become repeatedly recognized for their importance and are renamed and reincorporated into ecological theories that provide us with a broader and deeper understanding of how nature works. Patchiness provides a diversified (spatially heterogeneous) environment providing diverse regeneration niches for plants and fundamental niches of animals among the various patches. Dynamic processes and environmental heterogeneity within the community are important determinants of biological diversity (Huston 1979).

Chesson (2000) provided yet another, different, perspective on community organization by asking what mechanisms maintain species diversity. How do species coexist? Coexistence mechanisms function in two ways: (1) equalizing—minimizing the average difference in fitness among species and (2) stabilizing—increasing negative *intraspecific* interactions over negative *interspecific* interactions. Stabilizing mechanisms are essential for coexistence and include resource partitioning, frequency-dependent predation, and mechanisms that depend on fluctuations (variability) in population densities and in environmental factors in space and time. Complementarity in resource use leads to higher net primary production, a broader base for diversity (Hooper 1998). Complementarity or partitioning of resources by plants comes about through difference in rooting that affects access to water and nutrients, difference in architecture that helps fill aboveground space more efficiently, differences in phenology that allow different species to harness the same resources, but at different times of the year, and differences in physiology that lead to differences in type of nitrogen used or sources for phosphorous. Some species aid the growth of other species through provision of resources or amelioration of harsh environments in a process of facilitation. For example, some species fix nitrogen in a form available to other species, whereas some shade the soil and conserve moisture and alter the microclimate, providing niches for other species. Finally, the interplay of behavioral, biological, chemical, physical, and social interactions that affect, sustain, or are modified by living organisms in the community brings about biocomplexity.

Biocomplexity arises as temporal, conceptual, and spatial boundaries are breached and the system exhibits emergent, or unexpected, properties—in other words, the whole of system behavior is greater than the sum of the parts (Michener et al. 2001). For example, in Arizona, with large crown fires in the absence of elk, there is a positive relationship between severity of fire and regeneration of aspen via asexual reproduction; sprouting is 10 times greater at high fire intensities than intermediate intensities; there is virtually no regeneration without fire. Elk selectively browsed aspen ramets after high-severity fires, two times more than after intermediate-severity fires, thus largely negating the increased regeneration.

Fire and elk had different effects on arthropods (53 taxa in 11 orders and 21 families). Fire alone had no effect, but fires of intermediate severity, followed by elk browsing, increased arthropod diversity by 30 percent and abundance by 40 percent. Severe fire followed by browsing reduced diversity by 69 percent and abundance by 72 percent. The interaction of fire and elk produced four types of arthropod assemblage within the community mosaic, overall a marked increase in diversity. Thus, scaling up from populations to community-level interactions revealed unexpected outcomes; greater complexity (in time, space, and multiple factors) produced reversal of effects, unexpected outcomes, or emergent properties (Bailey and Whitham 2002).

Ecosystem Structure

Structure is another term frequently used in forest ecology and conservation that means different things to different people. According to the dictionary, a structure is something made up of a number of parts put together in a particular way. Chad Oliver (Oliver and Larson 1990) uses structure to refer to his stages of stand development (stand initiation, savanna, stem exclusion, understory reinitiation, and old growth) and talks about structure-based management in which landscapes are intentionally managed to contain a variety of structures (stages of stand development). Structure is also defined as the way parts are put together; for example, forest ecologists will select a number of variables to measure to describe the structure of a particular forest or to compare the structures of forests of different histories. With this meaning, Spies (1998) suggested that forest structure is both a product and a driver of ecosystem processes and biological diversity. Franklin et al. (2002) described the structural development of natural forest ecosystems and its implications for forest management and conservation.

Important components of structure include live trees of various sizes, vertical foliage distribution, horizontal variation in canopy density, and coarse woody debris. Note that limiting structure to these types of variables is just seeing trees for the forest—trees do provide physical structure but not all structure (table 13) (figs. 31A–E). The structure of narrowly defined biotic communities can be described in terms of species richness, evenness, and ranking of species (Carey 1991, 1995; Carey and Harrington 2001; Carey and Johnson 1995; Carey and Wilson 2001). Populations of a species are often described in terms of age structure and its implications for future growth of that population. Closely related to the concepts of structure are architecture and growth form.

Architecture is sometimes used to refer to how tree growth (how the bole, branches, bark, and foliage are put together) differs among species. Tree architecture can influence environmental conditions such as light and precipitation penetration through the tree crown, and it may provide diverse sites for occupancy by a variety

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Table 13—Key structural attributes of Pacific Northwest old-growth forests identified before and after systematic study in western Washington and Oregon

Before study	After study
▪ Large live trees	▪ Diverse tree sizes
	▪ Diverse tree species
▪ Large standing dead trees	▪ Abundant live and dead trees with cavities
▪ Large fallen dead trees	▪ Dead organic biomass is high, but composition and abundance differ among forest types
▪ Horizontal heterogeneity	▪ Horizontal patchiness
	▪ Diverse patch types
▪ Multilayered canopy	▪ Canopy gaps
	▪ Variable foliage height diversity
	▪ Biocomplexity

Source: Adapted from Carey et al. 1999a and Franklin et al. 1981.

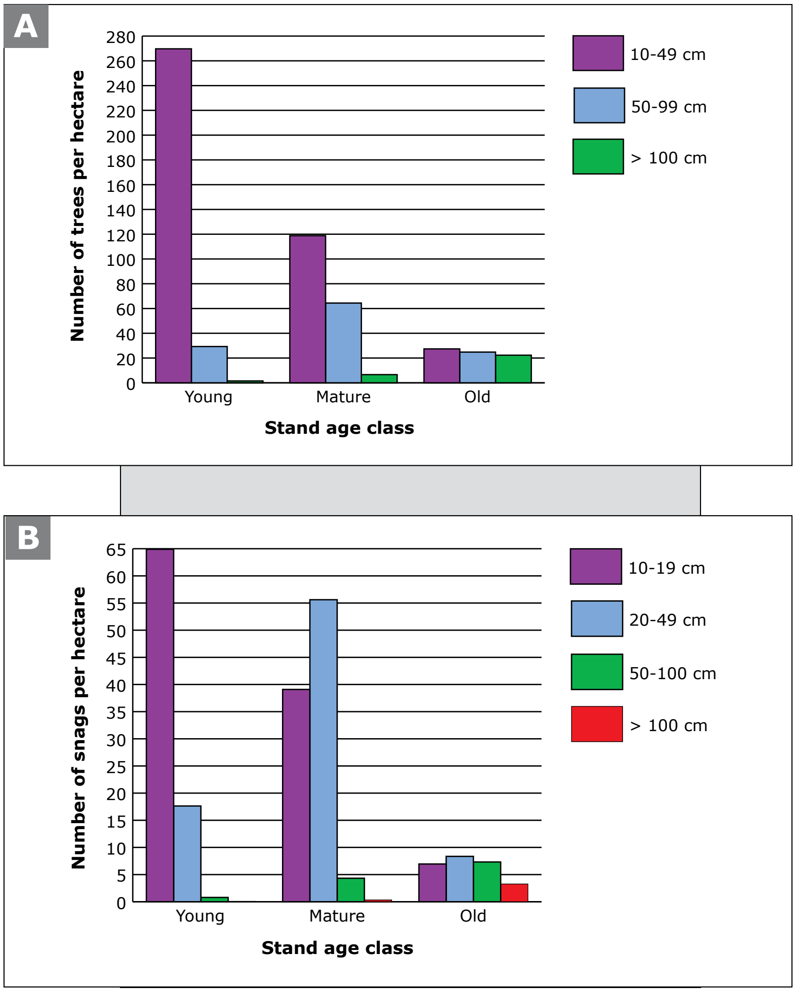
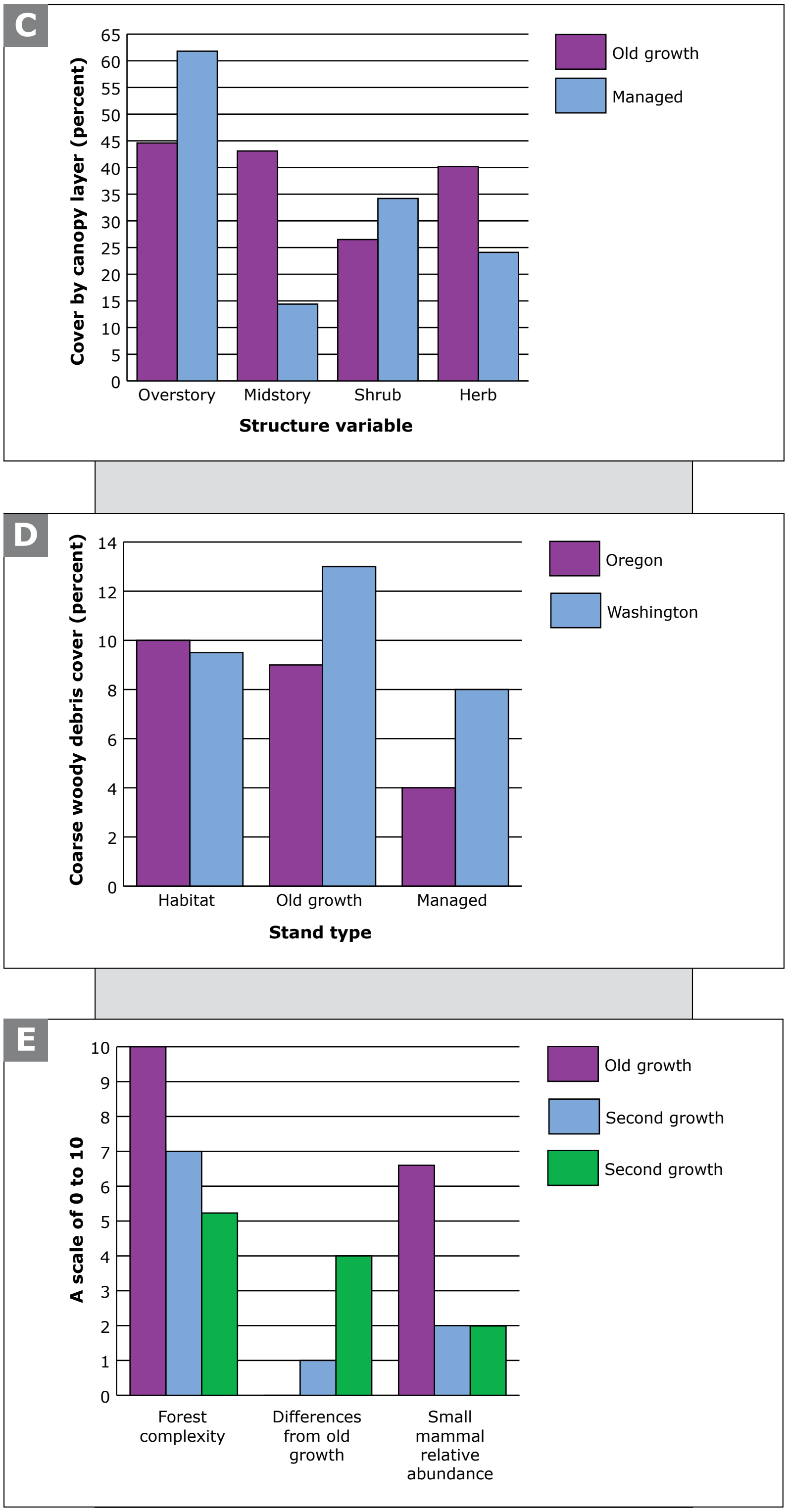


Figure 31—(A) Number of trees per hectare by diameter at breast height (DBH) in young, mature, and old stands of the southern Oregon Coast Range. (B) Number of snags per hectare by DBH in young, mature, and old stands of southern Oregon Coast Range (adapted from Carey et al. 1991). (C) Foliage-height profiles (percentage of cover by canopy layer) in managed and old-growth forests. (D) Coarse woody debris cover in northern flying squirrel habitat and in Oregon and Washington old growth and managed forests (adapted from Carey et al. 1999b). (E) Biocomplexity in old-growth and two samples of second-growth forests on the Olympic Peninsula (standardized to 10 for old growth); the degree to which complexity of small mammal communities differs from those in old growth and overall relative abundance of small mammals (adapted from Carey and Harrington 2001).


C
Cover by canopy layer (percent)
0
5
10
15
20
25
30
35
40
45
50
55
60
65
Overstory
Midstory
Shrub
Herb
Structure variable
Old growth
Managed
D
Coarse woody debris cover (percent)
0
2
4
6
8
10
12
14
Habitat
Old growth
Managed
Stand type
Oregon
Washington
E
A scale of 0 to 10
0
1
2
3
4
5
6
7
8
9
10
Forest complexity
Differences from old growth
Small mammal relative abundance
Old growth
Second growth
Second growth

(continued from page 185)

organisms from spiders in furrows in rugose bark to lichens, mosses, and liverworts on branches. Architecture is also used to refer to how forest canopies are put together and how variation in canopy architecture might influence ecosystem processes and biological diversity (Carey 1994).

Growth form is a more general concept about how plant species are put together and differ from other species, for example, forbs, grasses, lichens, shrubs, and trees (USDA National Resources Conservation Service 2004) (table 14). Growth form has obvious implications for ecosystem structure. Small-scale architecture—e.g., how twigs and leaves or needles are put together—influences plant physiology and tolerance for a range of environmental conditions, such as light, temperature, and moisture. Growth form also affects a plant's competition strategy (Grime 1977) (table 15). However, architecture and growth-form concepts illustrate that structure and especially function are often not independent of species composition. Species composition affects various ecosystem functions in multiple ways in and beyond contribution to structure, for example, production of chemical leachates, nitrogen fixation, support of mycorrhizal activity, phenology of fruit and seed production (food for animals),

Table 14—Growth forms and definitions

Growth form	Definition
Forb/herb	▪ Vascular plant without significant woody tissue above or at the ground; forbs and herbs may be annual, biennial, or perennial, but always lack significant thickening by secondary woody growth and have perennating buds borne at or below the ground surface
Graminoid	▪ Grass or grasslike plant, including grasses (Poaceae), sedges (Cyperaceae), rushes (Juncaceae), arrow-grasses (Juncaginaceae), and quillworts (*Isoetes*)
Lichenous	▪ Organism generally recognized as a single "plant" that consists of a fungus and an alga or cyanobacterium living in symbiotic association; often attached to solid objects such as rocks or living or dead wood rather than soil
Nonvascular	▪ Non-vascular, terrestrial green plant, including mosses, hornworts, and liverworts; always herbaceous, often attached to solid objects such as rocks or living or dead wood rather than soil
Shrub	▪ Perennial, multistemmed woody plant that is usually less than 4 to 5 meters in height; shrubs typically have several stems arising from or near the ground, but may be taller than 5 meters or single-stemmed under certain environmental conditions
Subshrub	▪ Low-growing shrub usually under 0.5 meter tall, never exceeding 1 meter tall at maturity
Tree	▪ Perennial, woody plant with a single stem (trunk), normally more than 4 to 5 meters in height; under certain environmental conditions, some tree species may develop a multistemmed or short growth form (less than 4 meters in height)
Vine	▪ Twining/climbing plant with relatively long stems, which can be woody or herbaceous

Source: USDA National Resources Conservation Service 2004.

digestibility of foliage, production of toxins (e.g., phenols) in foliage, resistance or propensity to disease, insect attack, and decay, and many other phenomena that markedly influence species interactions. For example, Douglas-fir is relatively decay resistant after injury and provides decayed wood for excavation by woodpeckers usually only after death of a major part of the tree; long-lasting fallen Douglas-fir provide regeneration niches for various plants and an important habitat element for numerous animals. Grand fir commonly experiences heart rot while alive and provides dens for American marten after the tree falls. Ponderosa pine and western redcedar may undergo substantial heart rot to the extent of producing a hollow, live tree useful for denning by American black bears and squirrels and roosting by Vaux's swifts and pileated woodpeckers. Unfortunately, many forest ecologists and wildlife biologists bend the third meaning of *structure* (an organ or part of an organism; something constructed)

Table 15—**Plant characteristics of the three primary competition strategies**

Plant characteristic	Competitive	Stress tolerant	Ruderal
Shoot morphology	▪ High dense canopy; extensive lateral spread above- and below-ground	▪ Extremely wide range of growth patterns	▪ Small stature; limited lateral spread
Leaf form	▪ Robust, often mesomorphic	▪ Small, leathery, or needle	▪ Various, often mesomorphic
Litter	▪ Copious, often persistent	▪ Sparse, sometimes persistent	▪ Sparse, not usually persistent
Maximum potential growth rate	▪ Rapid	▪ Slow	▪ Rapid
Growth form	▪ Perennial herbs, shrubs, and trees	▪ Lichens, perennial herbs, shrubs, and trees (often very long lived)	▪ Annual herbs
Leaf longevity	▪ Relatively short	▪ Long	▪ Short
Leaf phenology	▪ Well-defined peaks of leaf production coinciding with period(s) of maximum potential productivity	▪ Evergreens with various patterns of leaf production	▪ Short periods of leaf production in period of high potential productivity
Flowering phenology	▪ Flowers produced after (or, more rarely, before) periods of maximum potential productivity	▪ No general relationship between time of flowering and season	▪ Flowers produced at the end of temporarily favorable period
Proportion of annual production to seeds	▪ Small	▪ Small	▪ Large

Source: Grime 1977.

to refer to individual elements of the ecosystem, for example, referring to a snag (standing dead tree) as a structure or providing the various structures (in the sense of the elements of the habitat) that a species needs. Thus, one forest ecologist may discuss structure-based management and mean the management for a limited number of stages of stand development in a landscape, another may be referring to managing tree species composition and tree growth to replicate some idealized stage of structural development of forest ecosystems, and a third may be discussing how to provide the individual components of a forest thought to be important to either individual species or a variety of species of wildlife. Again, such emphasis on structure without careful consideration of processes may not at all produce the desired outcomes. Stand structural stages based on tree size class and diameter at breast height (d.b.h.) do not address most aspects of biocomplexity. Idealized stages of structural development based on tree sizes do not necessarily correlate well with ecosystem function because they do not address composition and internal dynamics, or if they do, they do so superficially. Ecological correlates of ecosystem function in natural old-growth forests with all its biocomplexity do not have the same correlation with function in a simplified, managed forest. For example, d.b.h. and variance in d.b.h. can discriminate among managed young, naturally young, naturally mature, and naturally old forests, and thus would be correlated with the functions of old forest, such as providing habitat for spotted owls. Yet, these old, natural forests are complex—spatially heterogeneous, structurally diverse, biologically diverse, and dynamic. Plantations can be managed to produce large trees and even trees of two age classes and thus, trees of large d.b.h. and high variance in d.b.h. Yet these forests are often simple in structure despite having two canopy layers—dominated by a few species and reasonably static—continuing to accumulate biomass in trees, but failing to partition biomass among growth forms, produce structure through decadence, and maintain a dynamic, spatially heterogeneous environment. There is a great and inexorable tendency to reduce ecosystem management to the provision of a limited set of static elements—trees of large d.b.h., snags of large d.b.h., logs of large d.b.h.—without understanding that processes *are* functions. These elements set as goals are actually intermediate products of complex processes; the dynamics of the system are more important than a few simple elements. An example of the latter is the importance of intermediate disturbances to the maintenance of biological diversity in forest ecosystems (the Intermediate Disturbance Hypothesis).

Ecological correlates of ecosystem function in natural old-growth forests with all its biocomplexity do not have the same correlation with function in a simplified, managed forest.

Forest Structuring Processes

Once a forest has been established, there are four basic internal processes that develop structure over time: crown-class differentiation, decadence, canopy stratification, and understory development (Carey et al. 1999b). Nevertheless, conditions immediately prior to and during establishment (type of catastrophic disturbance, extent of disturbance, duration and repetition of disturbance, degree of legacy retention, landscape context) influence how the forest develops. As complexity of structure develops, overall habitat space increases—a process of development of habitat breadth. The increase in dimensions of the community allows for *preinteractive* niche diversification. In the 500- to 1,000-year continuum of development of natural, old-growth forests, numerous structural stages may occur (Franklin et al. 2002). In managed forests, however, some processes may be eliminated, others truncated, and some accelerated; complexity may be restricted or enhanced; thus, a variety of *states* of development can be identified but these do not constitute a continuum—that is, they are not necessarily inevitable, inexorable, sequential, or even conducive to continuing development of complexity (tables 16, 17, and 18).

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The dynamics of the system are more important than a few simple elements.

Table 16—**Stages of forest development based on ecological processes**[a]

Generic model	Timber/wildlife (duration in years)	Natural development	Active management	Simple	Complex
Stand initiation	▪ Grass-forb (2 to 5) ▪ Shrub (3 to 10) ▪ Open sapling-pole (8 to 20)	▪ Disturbance and legacy creation ▪ Cohort establishment	▪ Ecosystem reorganization	✓	✓
Stem exclusion	▪ Closed sapling-pole-sawtimber (40 to 100)	▪ Canopy closure ▪ Competitive exclusion ▪ Biomass accumulation	▪ Canopy closure ▪ Competitive exclusion ▪ Biomass accumulation	✓ ✓ ✓	✓
Understory reinitiation	▪ Large sawtimber (10 to 100)	▪ Maturation ▪ Vertical diversification	▪ Understory reinitiation ▪ Canopy stratification ▪ Niche diversification	✓ ✓	✓ ✓ ✓
Old growth	▪ Old growth (200 to 700) ▪ Climax (700+)	▪ Horizontal diversification ▪ Pioneer cohort loss	▪ Natural old growth ▪ Natural climax		✓ ✓

[a] Stages used in a generic model of forest development contrasted with structure-based timber classes used in a wildlife habitat relationship model, a model of Douglas-fir forest development under natural conditions, and a model for active ecosystem management.

Source: Adapted from Carey and others 1999b, Brown 1985, Franklin and others 2001, Oliver 1981, Oliver and Larson 1996.

Table 17—**Potential stages of development in managed, second-growth Douglas-fir forests with approximate correspondence to stages of stand development and structural conditions**

Stage of development	Management and subsequent ecological processes
Ecosystem reorganization:	▪ Removal of a majority of overstory trees with minor to major retention of biological components (future legacies) is followed by planting or seeding of trees, colonization by vagile forest species and by native and exotic invasive nonforest species, and succession from bare ground to grass-forb-herb communities to shrub-tree communities to a tree-dominated community. ▪ Referents: Stand initiation; 6 conditions (as identified by Johnson and O'Neil 2001)—grass/forb-open to sapling/pole-moderate
Simple	▪ Clearcutting variants, site preparation, planting, vegetation control, and stocking control produce an even-aged monoculture or a forest dominated by a few tree species with one species dominant.
Complex	▪ Variable-retention harvest systems with 5 to 30 percent retention of legacies, depending on area size and context; reduced and variable site preparation; planting with natural regeneration expected to establish multiple species of trees; planting or seeding to restore lost native plant diversity if necessary; limited vegetation control to ensure full stocking and vegetative diversity; precommercial thinning to promote multiple tree and shrub species and forestall competitive exclusion of numerous species.
Competitive exclusion:	▪ No management beyond ensuring full stocking, selecting desired species, and controlling competitors. ▪ Referents: 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 with one another and other plants for light, water, nutrients, and space by growing tall quickly, eventually overtopping and suppressing shorter life forms, and slower growing species and conspecifics. ▪ Self-thinning produces even spacing and, sometimes, reduced intertree competition; failure to self-thin leads to loss of crown depth and spindly trees; competitive exclusion may extend to a majority of vascular plants, invertebrates, and wildlife.
Complex	▪ As above, except legacies from the preceding stand (from fallen trees to stumps to patches of intact forest) provide refugia within the forest for a wide variety of species; refugia maintain some spatial heterogeneity and species diversity; suppressed trees may 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, and removal of decadent, defective, and competing trees. ▪ Referents: None; 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 intertree competition; even-aged codominants grow and accumulate wood biomass rapidly while providing limited resources to other life forms.
Complex	▪ Low to moderate diversity and biomass of common plant species are maintained; growth of dominant trees contributes to maintenance of homogeneity; legacies maintain some heterogeneity and diversity.

Stage of development	**Management and subsequent ecological processes**
Understory reinitiation:	▪ Silvicultural thinning, self-thinning, and natural growth and mortality promote dominance by some trees, death of other trees, and release of plants in the understory from overstory competition. ▪ Referents: Understory reinitiation; sapling/pole-open, small tree-single story-open, medium tree-single story-open, perhaps large tree-single story-open, depending on stand history.
Simple	▪ A uniform canopy of evenly spaced trees leads to uniform understory conditions with dominance by a few species such as a shade-tolerant conifer or native clonal species such as salal and swordfern.
Complex	▪ Variable-density thinning produces canopy heterogeneity that leads to variable light and moisture regimes in the understory, which, together with legacies, produce an understory of patches of diverse composition, but generally low in stature. ▪ When necessary, due to previous management or competitive exclusion, underplanting augments the understory with key deciduous and conifer species.
Understory development:	▪ Thinning or other mortality reduces competition among trees, increases growth of trees, and releases understory from competition; understory develops in stature, abundance, and species diversity. ▪ Referents: None; six small to medium tree-multistory conditions, depending on legacies and decadence.
Simple	▪ A homogeneous overstory with moderate to low crown closure produces an understory that is botanically diverse but still dominated by a few species and lacking a distinctive patchy pattern; layers may develop, but lack of legacies precludes a fully developed, complex biotic community.
Complex	▪ Variable-density thinning produces canopy heterogeneity with high to moderate to low crown closure by dominants and codominants; heterogeneity produces crown class differentiation, including ingrowth by hardwoods and shade-tolerant conifers. Variable understory environmental conditions produce understory patches of differing composition. ▪ Cavity-tree creation and coarse woody debris augmentation during thinning and legacies from the preceding forest further compound 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	▪ Additional variable-density thinning or group selection may further contribute to developing 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 overstory), 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 thinning maintain the decadence process. ▪ Referents: None; six medium to large tree-multistory conditions, depending on numerous variables.

Stage of development	Management and subsequent ecological processes
Gap dynamics	▪ Managed forests more than 125 years old with high niche diversification and trees and tree-based structures of giant size, including legacies and the current dominant cohort. ▪ Either passively managed for late-seral forest values along streams, on mass-wasting areas, in watersheds, or in reserves, on long rotations in shifting steady-state mosaic landscapes, or with group selection for uneven-age management. ▪ Referents: Old growth (but not natural); giant tree-multistory, depending on numerous variables

Source: Adapted from Carey and Curtis 1996, Johnson and O'Neil 2001, and Oliver 1981.

(continued from page 191)

Legacy retention—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. 2002, 2000). Legacy retention can range from a few live trees to a mixture of trees, shrubs, coarse woody debris, and intact forest floor to entire 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, large live trees with epiphytic mosses and lichens, and large dead trees. Legacies can provide fuel for future or ongoing disturbance—e.g., from the falling of damaged and dead trees owing to decay or wind or fires in the accumulated fuel. 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 other species are available to recolonize a new forest. If a full complement of species is available, four basic processes—crown-class differentiation, decadence, understory development, and canopy stratification—determine how forests initially develop structurally in the Pacific Northwest and many forests elsewhere (Carey et al. 1999b). 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—development of habitat breadth (Carey et al. 1999b) and preinteractive niche diversification (Hutchinson 1978)—increase the diversity, composition, and structural complexity of the biotic community.

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 and others codominant, subordinate, or suppressed for development to proceed. Crown-class differentiation is important to producing large trees, trees with large branches and deep crowns, canopy heterogeneity and rugosity, small dead and dying trees, and a variety of other crown and canopy characteristics that develop habitat space for a variety of forest organisms. Differentiation can come about through (1) retention of coarse woody debris and other elements that cause patchy regeneration such as advance regeneration and larger trees of different sizes, (2) establishment of multiple species of trees (each with different growth rates), (3) self-thinning, (4) small- and intermediate-scale natural disturbances (including lightning, fire, windstorms, ice storms, insect infestations, and infections by pathogens), and (5) management (e.g., precommercial thinning, commercial thinning, and fertilization). 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). Elements 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 (say 40 to 400 hectares or more). Intermediate-scale heterogeneity (0.1 to 0.5 hectare), however, is necessary for development of biocomplexity. Intermediate-scale legacy retention, natural disturbances, and management promote not only crown-class differentiation but also the higher level processes leading to habitat breadth and niche diversification.

Decadence—Decadence is a complex process essential to biodiversity. Decadent trees (live trees with wounds or active decay, standing dead trees, and fallen, decaying trees) can be retained during harvest operations. They can develop naturally as a result of 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, topping, infecting, or killing. Decadent trees have essential roles in providing substrate for (1) a large variety of cavity-, hollow-, and

Table 18—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[a]	Resistance to change[b]
Ecosystem reorganization:					
Simple	Trees, herbs, shrubs	None	Some	Some	Low
Complex	Trees, shrubs, herbs	Much in legacies	Much	Much	Low
Competitive exclusion:					
Simple	Trees	Small trees, deciduous trees	Some	None	High
Complex	Trees	Legacy logs and snags, small trees	Some	Some	High
Biomass 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[d]	Much	Much	Moderate
Understory development:					
Simple	Trees, shrubs, herbs	Possible insect or disease mortality	Some	Some	Moderate
Complex	Various[c]	Various[d]	Much[e]	Much	Moderate
Niche Diversification					
	Various[c]	Various[d]	Much[e]	Much	Dynamic[f]
Gap dynamics					
	Various[c]	Various[d]	Much[e]	Much	Dynamic[f]

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

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

[c] 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.

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

[e] Varying in vertical, horizontal, and temporal dimensions.

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

Source: Adapted from Carey and Curtis 1996, Johnson and O'Neil 2001, and Oliver 1981.

crevice-nesting wildlife; (2) pecking and tearing foraging by insectivorous birds; (3) physical partitioning of the forest floor that 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 arthropods, birds, small mammals, and amphibians; (6) foraging sites for mycophagous small mammals; (7) travel ways; (8) entryways to subnivean environments; and (9) rooting and nutrient sources for a variety of plants and fungi (see Bunnell et al. 1999, Harmon et al. 1986, and Johnson and O'Neil 2001 for reviews). Typically, forest management for wildlife emphasizes only one or 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 differs 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 various of other wildlife over a long period before it dies and thence long after. In younger conifer forests, deciduous trees such as red alder, willow, and aspen provide valuable cavity trees despite their relatively small size (Bunnell et al. 1999, Carey et al. 1997). For example, red-breasted sapsuckers will nest in small decadent willows (20 centimeter d.b.h.) in second-growth forests but use only large snags averaging 113 centimeter d.b.h. in old-growth forests. Sapsuckers (and other woodpeckers of the family Picidae) are often double keystone species in keystone species complexes. For example, in Rocky Mountain forests, red-naped sapsuckers excavate cavities in fungus-infected aspens that are required as nest sites by two species of swallows and drill sap wells into willows that provide nourishment for themselves, hummingbirds, orange-crowned warblers, chipmunks, and an array of other sap feeders (Daily et al. 1993). Thus, additional emphasis is warranted on 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 of top rot, late in forest development, to provide various sizes of cavity trees (relatively small deciduous trees and relatively large conifers). Pileated woodpeckers play a cavity-creation keystone role in Pacific Northwest forests (Aubry and Raley 2002) and, actually, 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.

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. In the absence of full canopy closure (limited stocking, disturbance, or management action such as precommercial thinning) and with 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 invertebrate and vertebrate animals with a variety of food and cover. For example, foliage of deciduous shrubs, such as oceanspray provides forage for larval moths (Lepidoptera) that are important food to insectivorous birds and mammals (Muir et al. 2002). Vine and bigleaf maple seeds and hazelnuts are especially valuable to squirrels in coniferous forests, where their staple foods are produced sporadically (conifer seed) or are of low nutritive value (truffles) (Carey et al. 1999b, 2002).

Canopy stratification—As canopy dominants attain full stature, subordinates die, and disturbances cause gaps through the death of canopy dominants and codominants, and canopy dominants lose control of the light regime. Increased light to the understory, along with retention or recruitment of shade-tolerant conifers and hardwoods, and continued gap formation through natural mortality or silvicultural thinning, allows various strata of vegetation—low herbs, short shrubs, tall shrubs, and a midstory of deciduous and coniferous trees—to develop. Control of the internal light regime now rests with the midstory and tall-shrub shade tolerants, and diversity in the interior environment of the forest increases. 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.

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-hectare patches of 10 to 30 vegetation site types with each type composed of a different mix of species that differ in growth form. For example, one patch may have an understory of moss with a dense midstory of shade-tolerant conifers 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 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, intermediate-scale heterogeneity has proven beneficial for wet to moist coastal forests (Carey et al. 1999b) and moist to dry interior forests (Graham et al. 1999, Harrod et al. 1999, Reynolds et al. 1992). 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 the maintenance of biodiversity in two obvious 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 the variety of growth forms. Second, the diversity of plant life and growth 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.

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 breadth, the phenomenon of preinteractive niche diversification (Hutchinson 1978) may take place. Simply put, the forest has developed sufficient variety in structure, diversity in plant composition, and patchiness (and patch types) such that many species that typically would 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, all are present and in greater abundance than in young forest; each tends to forage on different substrates (e.g., bole and branch sizes) and, thus, more separately in fine-scale space. Similarly, a variety of decaying plants (wood and foliage) produces various sizes of saprophytic invertebrates, each primarily consumed by a different insectivorous mammal (e.g., shrew, Soricidae) with appropriate-size mouth parts. 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 of prey (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 2003a).

Ecosystem Development and Community Succession

Diversity begets diversity. However, if the diverse communities are all simply structured, have high contrast, or are arrayed in too coarse or too fine a grain, species diversity could decrease. Change begets diversity. However, if change is too frequent, too severe, or too simplifying, diversity could decrease. Static conditions are thought to reduce diversity, but a dynamic equilibrium such as a shifting, steady-state mosaic (at either the ecosystem or landscape scales or both) may maintain high diversity. Diversity within communities generally increases as the ecosystem increases in biocomplexity but can decrease over time in stages where stability is high and dynamics are low (Whittaker 1965). Diversity in landscapes generally increases with the number of disparate community types in the landscape but can decrease in landscapes where disparate community types have been deliberately simplified by management for commodity production. Few communities, however, are fixed in space and time. Most undergo development and many undergo succession. Most are eventually affected by some kind or some suite of disturbances, natural, anthropogenic, or both. How can one go about sorting out all these diverse influences at the larger scales on diversity? Modeling provides the most tractable approach. Of course models are only as good as their underlying concepts are sufficient to the purpose of the model and the degree to which the incorporated databases reflect reality.

Wildlife-Habitat-Relationships Models

Considerable effort has gone into compiling databases that relate species occurrences to community types, stages of community development, and various elements of landscapes (e.g., caves, cliffs, and talus slopes) and elements of biotic communities (e.g., snags, coarse woody debris, and deciduous tress). For vertebrates, these databases are known as Wildlife Habitat Relationship (WHR) models. Similarly, considerable effort has gone into plant community and forest type classifications. The WHR databases have several weaknesses; for example, (1) they assume static conditions, (2) they do not incorporate measures of resistance to change or susceptibility or probability of disturbance, (3) they generally do not project future trends, even in the absence of disturbance, and (4) their models of forest development are derived from models of timber growth and yield in even-aged stands of trees that serve their intended purpose well but are too tree-focused for modeling diversity (e.g., they lack information on biocomplexity). Timber models were not developed to account for the diverse elements of wildlife habitat; therefore, they serve WHR purposes poorly, unless augmented by numerous other habitat variables. Thus, the most current WHR database for Oregon and Washington (Johnson and O'Neil 2001) cross-tabulates forest–dwelling species by 20 *forest structural conditions*, 9 *habitat types*, and almost 100 *habitat elements* and subcategories. Structural conditions include grass/forb—open, grass/forb—closed, shrub/seedling—open, shrub/seedling—closed, sapling/pole—open, sapling/pole—moderate, sapling/pole—closed, small tree—single story—open, and so on, up to large tree—multistory—closed and giant tree—multistory. Habitat types range from west-side lowland conifer-hardwood forest to upland aspen forest. Categories of forest habitat elements include down wood, litter, duff, shrub layer, moss, flowers, lichens, forbs, fungi, underground plant parts, ferns, herbaceous layer, snags, tree size, mistletoe brooms, dead parts of live trees, hollow trees, tree cavities (fig. 32), bark, legacy trees, large branches, fruits, seeds, nuts, and edges. Numerous other habitat elements, ecological and abiotic, are tabulated. The cross-tabulated WHR models are data-rich and useful but cumbersome. Their complexity exceeds the cognitive limits of people engaging in discussions of field conditions or in collaborative management. Still, with careful incorporation into simulation models, they allow exploration of the consequences of alternative conservation scenarios and estimations of vertebrate diversity at multiple scales, at least (Carey et al. 1999d). However, they generally do not incorporate spatial interactions among communities. Analysis of spatial relationships in landscapes as it relates to species persistence and maintenance of biodiversity is in its infancy. Less complex, but still holistic models of forest development are more tractable and can be quite useful for heuristic modeling exercises and designing silvicultural prescriptions. Of course, the more reductionist the model, the less predictive ability it may have in the real world.

Forest Development Models

The simplest tree-focused model of forest development has four stages that follow either a natural or human-created large-scale disturbance: stand initiation, stem exclusion, understory development, and old growth (Oliver 1981). This model has proven too reductionist for modeling WHR in simulations of Pacific Northwest landscapes (Carey et al. 1999d). Carey and Curtis (1996), building on Bormann and Likens (1979), went beyond stand-structure classes to a set of eight developmental stages based on the processes taking place within the forest ecosystem that influence the development of the

Figure 32—(A) A northern flying squirrel and (B) a deer mouse peer out of natural tree cavities. Photo A by W. Colgan III; Photo B by A. Carey.

greater biotic (plant, fungal, and animal) community. Franklin et al. (2002) followed with an expanded classification of natural stand development (still focused on trees), nominally based on structure, but in actuality incorporating processes (e.g., canopy closure and biomass accumulation) and a large body of literature, including work on how stand development differs in managed and natural forests. Naturally developing forests may go through as many as eight major sequential stand conditions, differing in duration from less than 10 to more than 500 years. However, management can truncate the sere of 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. 1999c, 1999d). 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 nonsequential classification that can be subdivided into decadal periods. Furthermore, management for biocomplexity and emergent properties requires that models incorporate more than just the development of the tree community. Carey et al. (1999c), 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 natural forests, suggested it was necessary to revise and expand the classification to account for the great diversity of conditions being produced in managed forests in the Pacific Northwest (see table 17). 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 being allocated to plants, degree of decadence, spatial complexity, niche divergence, and resistance to change (see table 18). 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 persist for a relatively long time, it may prove very difficult to alter its trajectory to development of 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 (see tables 17, 19). 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 (say 350 years or more). A variety of silvicultural manipulations are used, as well as direct wildlife habitat improvements (see tables 17, 19). 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 and productivity, plant community development, and special landscape elements (e.g., wetlands, riparian zones, talus slopes, and cliffs).

Reserve Design

Conservation biologists have taken a markedly different approach than wildlife biologists using WHR models to compare alternative landscape management scenarios. Conservation biologists have focused on reserve design—how to protect as many of the desired communities in the landscape as possible and setting aside areas in hope that managed forests might develop into forests similar to naturally old forests, despite differences in type of catastrophic disturbance, legacy retention, and probable future natural disturbance regimes. They hope future natural disturbance regimes will provide the change necessary to maintain high diversity. Which approach is better: designating reserves or managing change? Is maintaining biodiversity compatible with production of commodities and active management of the land? Is a concept of general sustainability, incorporating environmental, social, and economic sustainability practical? Are reserves necessary? A case study, the Washington Forest Landscape Management Project examined the question and provides some insight.

Washington Forest Landscape Management Project

Exploitation of forests in the Pacific Northwest over the last 150 years repeated the history of eastern North America. Small areas of natural forest were reserved, and the remaining forests were freely exploited. Commercially valuable forests were harvested and replaced with naturally regenerated second-growth forests in degraded watersheds. Mounting degradation led to regulatory emphasis on reforestation, efficient production of wood, and economic stability (sustained yield), without thorough consideration of cumulative impacts at watershed and higher spatial scales. As harvests of old growth proceeded and landscapes became increasingly dominated by early-seral stages, first the spotted owl, then the marbled murrelet, and later, numerous salmonids were designated as threatened with extinction. Public concerns led to restrictions on forest management. Conservation focus switched from stands of timber to landscapes and from wood production to conservation of fish, water, and wildlife and to general sustainability. A presidential initiative to resolve the social conflict produced the 1993 Northwest Forest Plan for management of federal lands. The plan was an effort by disciplinarily diverse academicians, scientists, and managers to address environmental, economic, and social concerns. The plan emphasized late-successional reserves, an aquatic conservation strategy,

Table 19—**Effects of silviculture on ecosystem complexity**

Silvicultural treatment	More complexity	Less complexity
Regeneration harvest:		
▪ Legacy-retention harvest	✓	
▪ Clearcutting		✓
Planting:		
▪ With natural regeneration	✓	
▪ Without natural regeneration		✓
Weeding:		
▪ Retains some hardwoods and shrubs	✓	
▪ Removes hardwoods and shrubs		✓
Precommercial thinning:		
▪ Clumped multispecies retention	✓	
▪ Systematic single species retention		✓
Commercial thinning:		
▪ Variable density plus[a]	✓	
▪ Systematic minus[b]		✓

[a] Variable-density thinning with mixed-closed, moderately open, and open canopies on a 0.1- to 0.5-hectare scale designed to enhance woody plant diversity, maintain deciduous trees, promote recruitment of shade-tolerant trees with underplanting and augmentation of cavity trees and coarse woody debris when necessary.

[b] Light to moderate thinning with even spacing to favor one species.

Source: Adapted from Carey 2003a and Carey et al. 1999b.

monitoring threatened species, and identification, inventory, and management of numerous rare and cryptic species (Staebler 1994). In 2002, the plan was judged a failure in need of overhaul by Chief Bosworth of the USDA Forest Service because timber production projected under the plan was reduced by 75 percent in practice (to 5 percent of the preplan harvests) because of litigation over species sensitive to timber harvest (Dodge 2002, Milstein 2002). Almost 50 percent of the planned timber harvests were to have come from unreserved old growth, and those harvests met especially strong public opposition.

What went wrong with the Northwest Forest Plan? The plan failed to address the debate about what constitutes sustainability—a debate arising from cultural differences among the three major cultural streams in perceptions, values, and beliefs (see Part I) (Ray 1996). However, there are lessons learned from implementation of the Northwest Forest Plan and recent research that suggest better ways of managing landscapes. Indeed, the plan stressed adaptive management. Recapitulation of the federal research response to the forest management crisis in the 1980s and the application of new knowledge in a congressionally mandated modeling study of cross-ownership landscape management provide some insights.

Research Response to the Old-Growth Crisis

By 1980, much of the public was dismayed at the continuing harvest of old-growth forests. Old-growth forests are 250 to 1,000 years old; many are described as cathedral-like, with boles meters in diameter sweeping upwards to canopies almost 100 meters tall. People find these forests awe-inspiring and spiritual. Scientists postulated that old-growth forests were ecologically unique (Franklin et al. 1981) and that numerous species of wildlife depended on old-growth forests (Meslow et al. 1981), particularly the spotted owl (Forsman et al. 1984). Others perceived these forests as warehouses of highly valuable timber that would decay if not harvested and that were essential to the economic and social stability of timber-dependent communities. The onus was placed on Forest Service Research to determine quantitatively the uniqueness of old-growth forest, how much remained, the extent to which wildlife was dependent on it, the species that were dependent on it, the elements of old growth those species were dependent upon, the amounts and distribution of old growth that should be retained to meet conservation objectives, and the degree to which old-growth values could be achieved in managed forests. The USDA Forest Service implemented a coordinated program of research that included replicated, geographically stratified studies of plant, reptile, amphibian, bird, and mammal communities in old-growth (over 250 years), mature (100 to 200 years), and young (40 to 80 years) natural forests, and the research findings have been published (Carey and Spies 1991, Ruggiero et al. 1991). Later, it implemented a separate program of research on the northern spotted owl that included geographically stratified studies of its prey base, habitat use, and demography (Carey et al. 1992, 1999b). Finally, additional studies compared naturally old forests to managed forests (Carey 1995, 2000b; Carey and Harrington 2001; Carey and Johnson 1995; Carey et al. 1999b). The results were used to design treatments to restore lost biodiversity to managed stands (Carey et al. 1999d) and management systems (biodiversity pathways) for small landscapes (Carey et al. 1999c).

Natural Forests

Compared to forests around the world, Pacific Northwest old-growth forests are special—the trees are large and long lived, the vegetation structure is complex, decaying organic biomass is high, and fungal and small mammal communities are especially diverse (Carey 1998b). Old-growth forests are heterogeneous as a set, however; members of this set developed on specific sites that differed in topographic and biogeographic positions, period of development (250 to 750 years), climatic regime, and disturbance regime. Once lost, it is unlikely the old growth could be reproduced either through natural succession or through intentional management simply because the physical conditions of its development are not subject to unvaried natural repetition or to human control. Furthermore, the complete species composition of old growth has not been, and currently cannot be, fully determined; thus, indisputable demonstration of successful re-creation is impossible. Nevertheless, few species of plants and vertebrates are unique to old growth (Carey 1989, Ruggiero et al. 1991).

The spotted owl, among all vertebrates studied, seemed most dependent on old growth given the composition of the landscapes of the 1980s (Carey et al. 1992, Carey and Peeler 1995, Forsman et al. 1984). Other species were associated with particular elements of old growth (see table 13) or undisturbed headwater streams most likely to be found in old growth. Numerous species were most abundant in old growth but were found in other seral stages as well.

Often, abundances were associated with one or more attributes of old growth that were less abundant in younger or managed forests (Carey 1989). Thus, old growth functions differently than many younger forests in that its biocomplexity allows greater biomass and diversity in a number of narrowly defined biotic communities (Carey et al. 1999b, Ruggiero et al. 1991). Many younger natural forests with biological legacies from preceding old-growth forests, however, support vertebrate communities with greater biomass than those in many old-growth forests (Carey 1995, Carey and Johnson 1995, Carey et al. 1999b, Ruggiero et al. 1991), despite smaller average tree sizes. Other young forests support complete biotic communities and even provide habitat for spotted owls (Carey and Peeler 1995). Thus, it became apparent that management cannot indisputably re-create old growth, that any such re-created old growth could be regarded as anthropogenic and not wild or natural in any case, and that attempts to harvest old growth would be contentious and lead to litigation. But, it is not at all clear that forests equivalent to old growth will develop from second growth on those same sites if simply left alone to organize and grow themselves—they lack legacies, equivalent landscape and regional contexts, and similar climate regimes. Improved knowledge of old growth and its importance to people suggested that old growth might best be reserved for its ecological, scientific, and spiritual values (Carey 1998a, 1998b).

Old-Growth Versus Managed Forests

Whereas as many naturally young forests support biotic communities similar to those found in old growth (Ruggiero et al. 1991), many managed forests are depauperate in structure, species, and ecological function (Carey 1995, 1998b, 2000b; Carey and Harrington 2001; Carey et al. 1996b, 1999b). First, many (but not all) managed forests developed without legacies from the preceding forest; these legacies include coarse woody debris, live trees with their mycorrhizal and epiphytic associates, and soil seed banks holding numerous native species of plants and animals. Second, most managed forests were regenerated as dense monocultures that further reduced native diversity through competitive exclusion but allowed exotic species to persist, at least in soil seed banks (Carey et al. 1999b, Halpern et al. 1999, Thysell and Carey 2001a). In intensively managed forests, brush control, precommercial thinning, herbicides, and commercial thinning all are used as tools to reduce diversity. Indeed, stands maintained in the competitive exclusion stage may be more deleterious in terms of biodiversity and landscape function than the small areas of clearcutting that would occur with long rotations (Carey et al. 1999c). Legacies and often spatially variable, multispecies regeneration in natural stands allow key ecosystem structuring processes to proceed at accelerated rates compared to second-growth forests. These processes include crown-class differentiation, decadence, canopy stratification, and understory development and set the stage for higher level processes that lead to biocomplexity: development of habitat breadth and preinteractive niche diversification (Carey et al. 1999b). Understanding processes underlying forest ecosystem development and the structure of trophic hierarchies allows formulation of management systems to develop or restore biocomplexity to second-growth forests (Carey et al. 1999b, 1999c, 1999d). Both comparative ecological studies (e.g., Carey 1995, 1998b, 2000b; Carey and Harrington 2001; Carey and Johnson 1995; Carey et al. 1999b; Carey and Peeler 1995) and formal experiments (Carey 2001, Carey et al. 1996b, Carey and Wilson 2001, Thysell and Carey 2001a) demonstrate that it is erroneous to assume that forested landscapes are dichotomous (diverse old natural forests versus depauperate young forests), that landscape elements (e.g., early seral stages) are unchanging through time, and that second-growth forests will develop essential characteristics of old-growth forests without management intervention.

Modeling Landscape Alternatives

Increasing restrictions on forest management with continuing controversy after the Northwest Forest Plan had negative economic impacts on rural communities and impeded watershed restoration efforts. As lists of species likely affected by timber harvests and other management activities grew, and complexity of management for multiple individual species increased, public officials in the state of Washington wondered if there was not a better way of pursuing economic, social, and environmental sustainability. They requested a study to determine if holistic, cross-ownership, management could lead to better solutions than landscape zoning and single-species conservation plans; an interdisciplinary team of scientists and technical specialists was assembled from the Washington Department of Natural Resources, Washington Department of Wildlife, University of Washington, Oregon State University, and the Pacific Northwest Research Station of the USDA Forest Service (Carey et al. 1999c).

Pragmatic evaluation of management alternatives requires that computer simulations be grounded in reality; thus, the team chose a real landscape in western Washington for which detailed data on stand conditions, tree growth and yield, streams, wildlife-habitat relationships, transportation networks, unstable slopes, operational costs, distance to timber markets, and market values were available. Because alternatives were to be pertinent to diverse landowners, from industrial forests to state-managed school trust lands to tribal lands, they calculated net present value of extracted wood products and sustainable decadal revenues over the long term (300 years). Tradeoffs between economic and environmental values would be manifest; however, many values produced would accrue to society in general, not to the individual landowner or trust. Thus, public subsidies or other benefits might be required as incentives to private landowners. Total landscape management would include non-reserved federal lands and would have to be acceptable to the public at large. Thus, these five ecological indices were used to evaluate alternative silvicultural systems and landscape management scenarios (Carey et al. 1999c):

- Ability of the landscape to support wide-ranging old-growth species, based on estimates of the area of late-seral forest required to support one pair of spotted owls, the only threatened species with documented habitat requirements.
- Capacity to support vertebrate diversity based on published accounts of the habitat requirements of 130 species, evaluated as percentage of maximum possible capacity.
- Forest-floor function, defined as the biotic integrity of the forest-floor small mammal community (the top of the forest-floor food web), based on published equations predicting species abundances, and providing part of the prey base for generalist vertebrate predators (weasels, coyotes, bobcats, owls, and hawks).
- Ecological productivity, defined as the biomass (kilograms per hectare) of three species of squirrels and as representing the system's production of fungal sporocarps, fleshy fruits, and seeds of trees (consumed by squirrels) and capacity to support medium-sized predators (weasels, owls, and hawks that consume squirrels).
- Production of deer and elk, based on published models, and taken to represent the system's capacity to support large predators (wolves and mountain lions), subsistence hunting by indigenous peoples, and sport hunting.

Given metrics for comparing results, the next choices were on constraints on management. The team decided that all alternatives should produce a *regulated* forest that produced a relatively even flow of outputs on a decadal basis. Because the existing landscape had imbalanced age classes (primarily 50-year-old stands) as a result of rapid harvesting of old growth, achieving regulation required up to 100 years. Minimal protection of streams was required by state regulations at the time of the simulations, and this protection was commonly deemed unsatisfactory; new regulations would be forthcoming. Federal land managers had adopted requirements of watershed analyses and wide interim buffers around streams, from which management was excluded; this exclusion, however, became more or less institutionalized. Thus, the state and federal approaches provided two extremes, with the state regulations deemed marginal at the outset. Applying the new federal approach to the landscape produced surprising results—34 percent of the landscape was withdrawn from management, and significant parts of the remaining landscape, especially in headwater areas, were so isolated and overdispersed as to become economically infeasible to manage. Similar results were obtained as federal managers began implementing the new guidelines. The team reviewed federal riparian constraints and found, to its surprise, that they were based as much on an upland wildlife and dispersal corridor strategy as on an aquatic conservation strategy. Furthermore, there were few empirical data to support the corridor strategy, the interim guidelines precluded restoration efforts in riparian areas (riparian areas in the landscape to be modeled were highly degraded and devoid of conifers, essential sources of coarse woody debris for instream structure), and the constraints provided relatively little protection to headwater streams, seeps, and mass-wasting areas. The team sought alternatives. First, they shifted emphasis from large streams and rivers to small streams; the impacts on the entire landscape remained large, and the same suite of problems persisted. Finally, they adopted as a third alternative (to the state and federal alternatives), precluding mechanical operations on streambanks and adjacent to headwater seeps and streams; allowing thinning and other restoration efforts in narrow riparian buffers, but not clearcutting; and allowing thinning, but not clearcutting, on mass-wasting areas. The total area in the landscape constrained by this approach was less than 15 percent and did not isolate patches of upland forest.

Next, the team chose three classes of alternative landscape management scenarios: (1) protection, but no manipulation; (2) maximizing net present value of timber commensurate with existing state of Washington forest practices rules; and (3) management for biodiversity, defined as species, biotic communities, and ecosystems, and the ecological services and economic goods they provide. For maximizing timber production, the team used input from industrial forest managers about the feasibility and reasonableness of silvicultural practices and empirical growth-and-yield models. Numerous simulations were done, but the final alternative was clearcutting, site preparation, natural regeneration, precommercial thinning at 15 years, clearcutting at 40 years, and existing minimum state riparian management guidelines. Alternative silvicultural regimes for conserving biodiversity were developed, too. The final alternative included clearcutting with legacy retention, no site preparation, planting of Douglas-fir and natural regeneration of other conifers and hardwoods, regulation of spacing and maintenance of tree species diversity with precommercial thinning at 15 years, and variable-density thinning to induce spatial heterogeneity, maintain tree species diversity, recruit coarse woody debris, and remove wood products at 30-, 50-, and 70 years with final harvest by clearcutting with legacy retention alternating between 70 and 130 years. Rotation ages were deliberately calculated to balance timber revenues with ecological outputs. The new riparian/mass-wasting area management was superior to other riparian management alternatives.

Results of the final simulations were surprising to the team and forest managers. Simply protecting second-growth forest caused the landscape to go through waves of forest development. Initially a substantial ecological crunch occurred because of degraded watersheds and oversimplified stands; a long time (200 years) was required for these stands to achieve an old-growth-like condition (under a possibly unwarranted assumption that time alone would indeed produce naturally complex, old forests). Timber management with minimum constraints produced a landscape inhospitable to over 20 vertebrate species and allowed no recovery of degraded streams; its sustainability was uncertain, but net present value was maximal. Timber management with riparian reserves drawn from federal guidelines, produced relatively narrow, well-separated strips of late-seral forest in the long term, unlikely to function fully as late-seral forest because of their continued adjacency to clearcut and young forests; clearcutting was intensified in the available uplands owing to removal of streamside and adjacent small patches from forest management. Biodiversity management, as it was designed to do, produced significant ecological benefits (see Part 1, table 5), including supporting a pair of spotted owls and producing numbers of deer and elk comparable to the timber management regime.

But, surprisingly, costs were relatively low—only a 15-percent loss in net present value compared to maximizing net present value of timber extraction. Assuming (as occurred) increased riparian protection would be mandatory and eliminating costs of improved riparian/mass-wasting management from comparisons, biodiversity management resulted in only a 6-percent decrease in net present value. Other economic values increased: decadal revenues increased by 150 percent, forest-based employment quadrupled, and the wood products manufacturing sector diversified and relied more heavily on high-quality wood products and value-added manufacturing (Lippke et al. 1996). Initially, the team included a constraint of 30 percent of the landscape in late-seral forest to support one pair of spotted owls; the final shifting steady-state mosaic maintained more than 50 percent of the landscape in late-seral stages, and less than 15 percent of the landscape was in clearcuts in any decade, resulting in a landscape fully permeable to dispersing late-seral species.

Implications

Conservation biologists once argued the relative merits of single, large reserves versus multiple small reserves, the need for conserving genetic diversity, and the need to restrict active management. Forest managers focused on plantation management, transportation networks, and watershed restoration. Now it is becoming recognized by both that active management for biodiversity is needed to restore degraded ecosystems and to produce fully-functional forests outside of reserves. Reserves play important social and ecological roles, but they alone cannot conserve biodiversity. Research and experience have shown that reserve systems can become self-fulfilling prophecies of highly isolated diverse forests separated by depauperate second-growth forests and developed areas and that conventional timber management can oversimplify forest stands to the detriment of stand and landscape function. As human populations grow and increasing demands are placed on our environment, highly intentional systems management (Carey et al. 1999c) and total landscape management will be necessary to conserve the biodiversity of natural-cultural mosaics and the ecological services and economic goods it provides. Shifting, steady-state mosaics of complex forest ecosystems should promote system resilience (Holling 2001). But, the question remains, what kind of management can promote biocomplexity and what evidence for such management exists. A second case study illustrates some of the possibilities—The Forest Ecosystem Study.

The Forest Ecosystem Study

In the latter part of the 20th century, it was time to move beyond biodiversity reserves into *actively* managing forests to conserve biodiversity, including communities and ecosystems and the economic goods and ecologic services they provide (di Castri and Younes 1990, Entwistle and Dunstone 2000). People were demanding both environmental and economic sustainability (Folke et al. 1996, Goodland 1995, Reid and Miller 1989). In the Pacific Northwestern United States, for example, forests are expected to perpetually provide commodities; revenues for landowners, schools, and roads; economic support to local communities; habitat for all forest wildlife and plants; recreational and spiritual experiences; and clean air and water (Carey et al. 1999c, Carey and Wilson 2001). Timber management, however, had simplified forests (Carey et al. 1999b, 1999c; Franklin 1993a, 1993b) and contributed to invasion by exotic species (Halpern et al. 1999, Hobbs and Humphries 1995, Thysell and Carey 2001a), imbalanced biotic communities (Carey 2000b, Carey and Harrington 2001, Haveri and Carey 2000, Wilson and Carey 2000), low prey biomass for vertebrate predators (Carey et al. 1992), and poorly functioning food webs (Carey et al. 1996b, 2002; Colgan et al. 1999). High-quality timber was becoming scarce and low-quality timber overabundant. Environmental degradation and nonsustainable harvests had led to restrictions on harvesting natural forests and disruption of local, regional, and even global timber markets.

In the Pacific Northwest, natural forests and contemporary managed forests differed in structure, composition, and function (Carey 1995, Carey and Harrington 2001, Carey and Johnson 1995, Carey et al. 1999b). Juxtaposed diverse ecosystem elements in natural forests contributed to emergent properties associated with biocomplexity. The scale of variation in arrangement that contributed to synergy was on the order of 0.1 to 0.5 hectare, or 80 to 100 meters (Canham et al. 1990, Carey et al. 1999b). Biotic legacies from preceding forest, propagules from adjacent stands, forest developmental processes, and development of spatial heterogeneity all contributed to compositional diversity and habitat breadth (diversity of vegetation site types). Stand tending for timber, however, purposefully reduced complexity and diversity at the local, landscape, and even regional scales (Carey 2000b, Carey and Harrington 2001). Consequently, population densities of a vertebrate species in managed forests varied in complex ways that reflected not only the abundance of its habitat elements, but also abundances of other ecosystem elements that determined the overall mix of vertebrate species and the degree of species interactions with one another. Biotic integrity (the structure of a narrowly defined community as measured by species relative abundances within the community compared to that in old growth), nevertheless, varied more or less predictably in response to complexity of vegetation structure and absence of various compositional elements because biocomplexity is prerequisite to preinteractive niche diversification, community diversity, and ecosystem resilience (Carey et al. 1999b, Hutchinson 1978, Tilman 1996). Intentional management, nevertheless, should be able to promote biocomplexity (Carey et al. 1999b, 1999c). Retention of legacies of individual live trees, dead trees, coarse woody debris, or even patches of forest can be used with even-age management systems to jump-start ecosystem development processes. Such variable-retention harvest systems transcend traditional silvicultural conventions such as clearcutting (Franklin et al. 1997). Thinning inevitably influences all forest developmental processes, including decadence and development of habitat breadth. Variable-density thinning with underplanting offers to restore tree species diversity and accelerate understory development and canopy stratification. Retaining decadent trees, wounding trees, inoculating trees with top-rot fungi, and creating cavities in trees should promote decadence essential to ecosystem development (Carey et al. 1999b, Franklin et al. 1987). Variable-density thinning creates canopy mosaics in second-growth stands and could promote vegetative heterogeneity similar to that in old growth (Carey and Johnson 1995, Carey et al. 1999b). By removing subordinate and codominant trees, variable-density thinning produces small patches such that light, water, nutrients, and space become available spatially in various amounts to other vegetation. Effects, however, extend beyond the borders of the altered patches of canopy because of low sun angles in the Pacific Northwest. Thus, fine-scale heterogeneity creates an even more diverse mosaic of environmental conditions and potentially numerous patch types in the understory (Canham et al. 1990). Maps of canopy cover and understory plant associations revealed natural mosaics of 0.1- to 0.5-hectare patches with a 2:1 ratio of closed to open canopy promote biocomplexity (Carey et al. 1999b) (fig. 33). Yet, no one had intentionally created such a mosaic experimentally or even managerially.

Experimental Design

In 1991, the Forest Ecosystem Study was established as an experiment to test the efficacy of various techniques for active management of forest to promote biocomplexity (Carey et al. 1999d). The study was located southeast of Olympia, Washington, in the Puget Trough, a low-lying (120 to 165 meters), flat to rolling plain (Carey et al. 1999d). Forests in the Puget Trough had been harvested by extensive clearcutting that provided relatively homogeneous forest without confounding effects of adjacency of natural forest. As with many soils in western Washington, the soils were coarse-textured gravelly-sandy loams formed as a result of glacial recession and glacial outwash. Annual precipitation was 800 to 900 millimeters with only 10 to 15 percent during summer. Vegetation was temperate coniferous forest—the Douglas-fir-oceanspray association of the Western Hemlock Zone.

The study incorporated four approximately 100-hectare *blocks* of forest; four 13-hectare *plots* were delineated in each block (a total of 16 plots). Each plot was subdivided into 64 (0.16-hectare) *cells* by an 8 × 8 grid with 40 meters between grid points and a 40-meter buffer around the grid. This grid provided a template for treatments and sampling (figs. 33, 34). Two blocks had been clearcut around 1927 and later—more than 10 years prior to the study—conventionally thinned twice to a final residual density of 225 trees per hectare

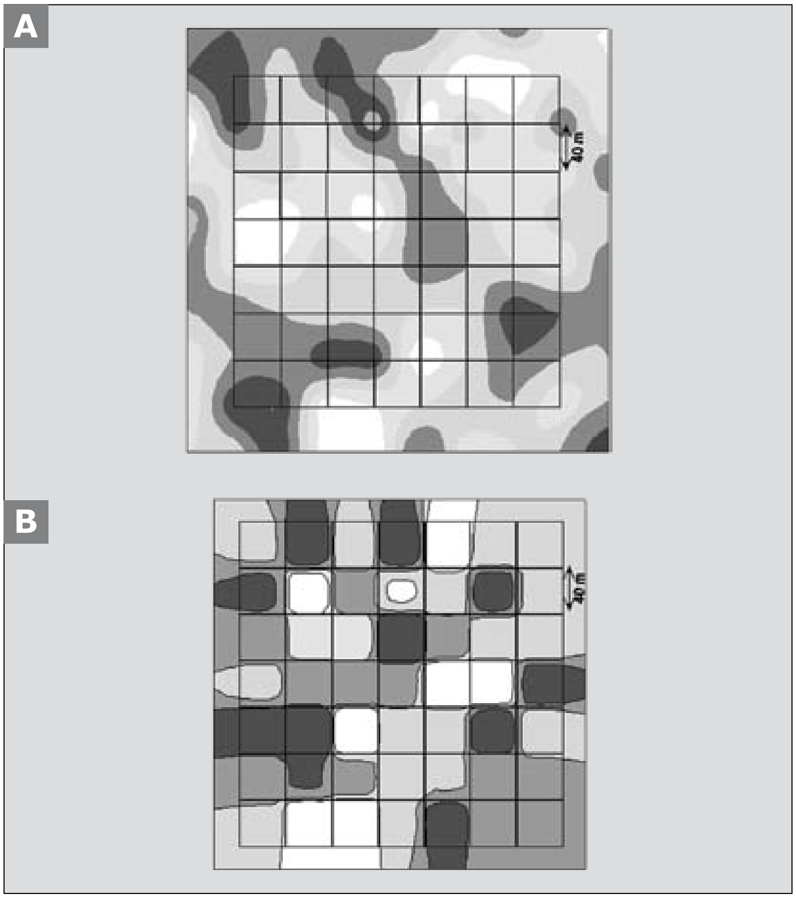

Figure 33—Recreating spatial heterogeneity characteristic of old forests in second-growth forest canopies with variable-density thinning: (A) densities of trees more than 50 centimeters in diameter at 1.5 meters aboveground in a 280-year-old Douglas-fir forest—shading (light to dark) represents densities from 3 to 45 trees per hectare, based on 225 sampling points (from Carey et al. 1999b); (B) relative densities of Douglas-fir more than 20 centimeters in diameter at 1.5 meters following variable-density thinning of a 56-year-old second-growth stand; shading (light to dark) represents relative density classes of less than 3.25, 3.25 to 4.75, 4.75 to 6.75, and greater than 6.75 (adapted from Carey et al. 1999c).

(approximately 7 meters between trees). Few trees (less than one per hectare) were retained from the preceding old-growth forest, and dead trees were removed. Canopy trees were 51 to 54 centimeters in diameter at 1.5 meters aboveground; cover of coarse woody debris was 2 to 3 percent; cover of understory vascular plants was 88 percent, dominated by the evergreen shrub, salal, the evergreen swordfern, and brackenfern. Shade-tolerant conifers were rare. These plots were called as *timber plots*. Two other blocks had been clearcut around 1937, with 2.7 live trees per hectare and 3.5 dead trees per hectare retained from the preceding old growth. Woody debris included old decaying fallen trees (7 to 8 percent cover), stumps of old trees (48 per hectare), and abundant (3 percent cover) small trees killed by suppression or root rot. Understory cover was patchy and 34 percent, dominated by salal. Canopy trees were 600 per hectare and 34 centimeters in diameter at 1.5 meter. Few shade-tolerant conifers were present. These plots were called *legacy plots*.

Experimental treatments included variable-density thinning to induce heterogeneity into tree canopies, underplanting with red alder, western white pine, grand fir, and western redcedar to restore lost tree species diversity, and decadence management for cavity

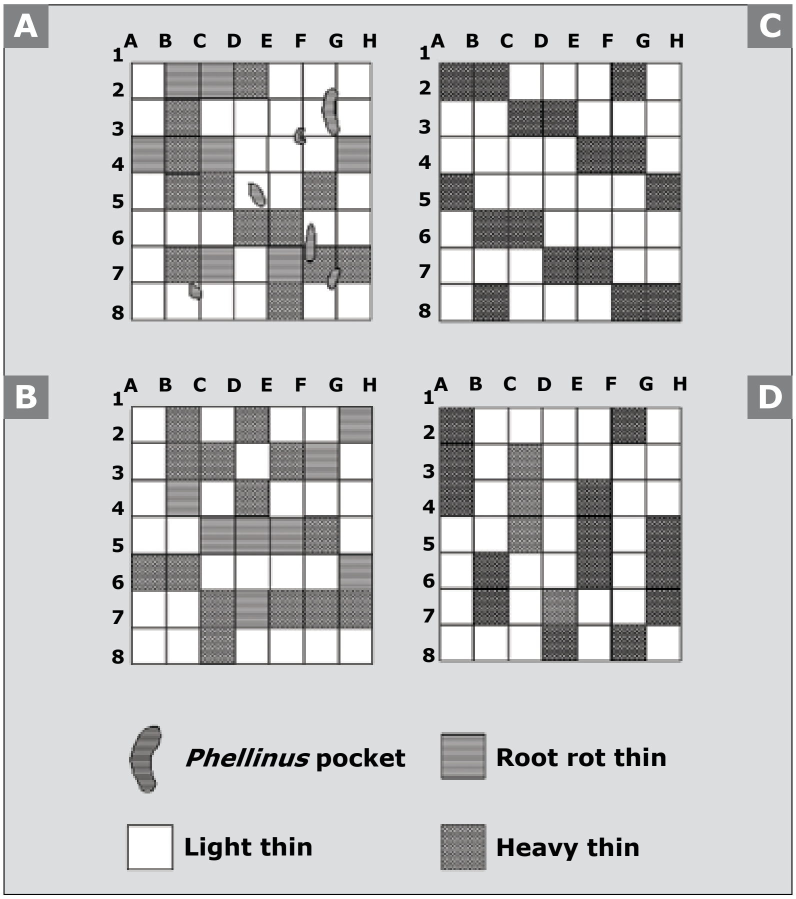

Figure 34—Actual and potential applications of variable-density thinning: (A) Star 101—shows random assignment of subtreatments with actual root rot pockets, (B) Farley 302—shows random assignments of subtreatments with simulated root rot pockets, and (C & D) systematic assignment of light (LT) and heavy thins (HT) (as possible operational applications) in a 2:1 ratio of LT to HT (Carey et al. 1999c).

trees to accelerate ecosystem development. Sampling grids were surveyed, and baseline data were collected in 1991 and 1992. Then, plots were treated by the landowner (Fort Lewis Military Reservation) and contractors with one of four randomly assigned treatments in spring, 1993: control; variable-density thinning with underplanting; dens for squirrels; and variable-density thinning combined with dens. In the first 5 years, supplementary dens had minor effects on flying squirrels (Carey 2002b). Relative density (RD) was used to determine how much to thin; RD is an index to intertree competition in even-aged evenly spaced stands of trees (Curtis 1982). For Douglas-fir, RD ranges from 0 to a biological maximum of 14; excessive crown restriction occurs with RD >7. Conventionally thinned timber plots had RD = 6.5 (biomass accumulation stage) and unthinned legacy plots had RD = 7.2 (emerging from competitive exclusion to biomass accumulation). An implementation team of research and management foresters randomly assigned RDs of 2, 4, and 6 to the cells and RD = 6 to the buffer of each variable-density thinning plot to achieve a 2:1 ratio of light (residual RD >4.75) to heavy thinning (RD <4.75) and a mean residual RD of 4.7 to 4.8. Plots treated with variable-density thinning were called *mosaic plots*.

Response variables were chosen from two perspectives. The first set of variables was drawn from the keystone complex symbolic of Pacific Northwest old growth (forests over 250 years old): northern spotted owl-northern flying squirrel-ectomycorrhizal fungi-Douglas-fir (Carey 2000a). The spotted owl is the flagship species for old growth and has been designated a threatened species by both federal and state governments. The flying squirrel is the primary prey of the owl. Hypogeous ectomycorrhizal fungal sporocarps are the primary food of the squirrel; the squirrels disperse the spores and associated micro-organisms (Li et al. 1986) throughout the forest. Mycorrhizal fungi enhance the ability of Douglas-fir to absorb water and nutrients from the soil and receive carbohydrates in return. The fungi move photosynthetic carbohydrates from trees to the mycorrhizosphere, providing support for a vast array of microbes, insects, nematodes, bacteria, and other soil organisms (Ingham and Molina 1991). Aboveground, the food web expands laterally to include other raptors and mustelids; three species of squirrels; forest-floor small mammals; seeds, fruits, and fungal sporocarps; and various trees and shrubs. Thus, the complex provides a framework that is both functional and heuristic in evaluating forest ecosystem development in response to heterogeneity induced into canopies and to forest management generally (Carey et al. 1999c). The spotted owl and other predators, however, respond to ecosystems at the landscape scale (Carey et al. 1992) and cannot be used to evaluate management at small scales. Thus, research focused on the abundances of three squirrels—the northern flying squirrel (fig. 35A), the Douglas' squirrel (fig. 35B), and Townsend's chipmunk—and compared their abundances to the simultaneously high abundances of all three species in complex old forest. The diets of the three species overlap, but the flying squirrel is a truffle specialist, the Douglas' squirrel a conifer seed specialist, and Townsend's chipmunk is a fruit generalist, feeding on seeds of conifers, seeds and nuts of deciduous trees, berries of shrubs, and truffles, but relegated to areas of high shrub cover in summer and hibernating belowground in winter. Thus, the combined biomass of these three species is a measure of ecological productivity—the reproductive fruits of the forest ecosystem and the capacity of the ecosystem to support diverse vertebrate predator assemblages (Carey et al. 1999c).

The second set of variables focused on forest-floor function, because it is the foundation for sustainability of forest ecosystems (Carey et al. 1996b). Mechanical operations, killing trees, and altering microclimate affect forest-floor function. A basic feature of most forest soils is dominance of biological activity by fungi, particularly ectomycorrhizal fungi. Variables included degree of dominance by fungi as measured by biomass ratios for total fungi to total bacteria, active fungi to active bacteria, and fungal-feeding nematodes to bacteria-feeding nematodes; biomass of predatory nematodes; and biomass and diversity of sporocarps of ectomycorrhizal Ascomycetes, Basidiomycetes, and Zygomycetes (hereafter referred to as truffles); diversity of epigeous fungi; and the coverage of fungal mats (*Piloderma* sp., *Hysterangium* sp., *Gautieria* sp.) (Carey et al. 1996b, Ingham and Molina 1991). Consideration of forest-floor function

Figure 35—(A) A northern flying squirrel consumes a truffle. Photo by W. Colgan III. (B) A Douglas' squirrel postures to defend its food source. Photo courtesy of American Mammal Society.

was extended hierarchically to litter invertebrates, abundance and diversity of vascular plants, and the integrity of the forest-floor small mammal community. This community, dominated by shrews, is particularly diverse in Pacific Northwest forests compared to the rest of the world (Carey and Harrington 2001, Carey and Johnson 1995). Because disruption of soil by mechanical operations and simplification of forest ecosystems by timber management can promote invasion by exotics (Halpern et al. 1999), exotic species were recorded and their tenure in the system tracted. Finally, resident birds play important roles in Pacific Northwest forests in regulating insect populations by insectivory and in decadence processes by excavating cavities in trees (Manuwal and Huff 1987). These birds are particularly sensitive to the simplifying effects of timber management on decadence and seed diversity. Thus, the diversity and abundance of birds in winter was measured (Carey 2003a).

Soil Food Webs and Forest-Floor Character

Both timber and legacy plots had fungal-dominated soils in terms of total-biomass and active-biomass ratios. Total fungal biomass in legacy plots, however, was almost three times greater than in timber plots. Fungal mats covered 66 percent of legacy plots compared to 25 percent of timber plots. Abundances of fungal-feeding nematodes were similar. Bacteria-feeding nematodes in timber plots were 1.5 times more abundant than in legacy plots. Predatory nematodes were most abundant in timber pots. Variable-density thinning had no effect on total biomass ratios but *increased* the dominance of fungi over bacteria in both timber mosaics and legacy mosaics. Total fungal biomass remained unchanged in timber mosaics but decreased in legacy mosaics. Fungal feeding nematodes decreased in timber mosaics but increased in legacy mosaics. Bacterial feeding nematodes and predatory nematodes increased with degree of disturbance within both types of mosaics. Truffle standing crop biomass averaged 0.5 kilogram per hectare but varied markedly (0 to 1.8 kilograms per hectare) seasonally in both timber and legacy plots. Of 28 species of truffles found in untreated forest, 19 species were in timber plots, with 7 of those species only in timber plots, and 21 species were in legacy plots, with 9 of them only in legacy plots. *Rhizopogon* was the dominant genus, with a relative frequency of 40 to 47 percent. *Gautieria* and *Leucogaster* were more frequent in legacy plots than in timber plots, and *Melanogaster* and *Hysterangium* were more frequent in timber plots. Truffle production was reduced in mosaics (from a frequency of 18 percent in control plots to 13 percent in variable-density thinning plots) in the short term with heavily thinned cells most reduced (to 10 percent). Truffle diversity increased to 48 species (versus 28 species in controls) and productivity quickly recovered. *Gautieria* and *Hysterangium* decreased in abundance in mosaics, but *Melanogaster* increased in species diversity and biomass. A total of 64 mushroom species were found prior to treatment, 37 (19 mycorrhizal) in legacy plots and 44 (15 mycorrhizal) in timber plots. Richness of ectomycorrhizal mushrooms was consistently highest in the legacy plots. After variable-density thinning, 108 mushroom species were found in legacy mosaics (versus 89 species in controls), and 78 species were found in timber mosaics (versus 65 in controls). Contrary to expectations, variable-density thinning did not significantly reduce the amounts of large coarse woody debris through mechanical destruction but did add small coarse woody debris in the form of logging slash and unmerchantable stems. Additional large coarse woody debris has been recruited in the form of diffuse root-rot mortality. The forest floor microclimate (temperature and moisture) increased in heterogeneity—mosaics maintained the array of moisture and temperature regimes that controls had but also developed some warm, some moist and warm, and some dry patches. Variable-density thinning produced increased patterning in litter invertebrate communities; all functional groups were maintained, but species dominating the functional groups now differ spatially in response to the induced heterogeneity that includes differences in new litter, added coarse woody debris, increased vascular plant cover, and soil disturbance as well as changes in light and moisture (Schowalter et al. 2003).

Understory Plants

Legacy plots had 27 to 40 species of understory plants compared to 49 to 87 species in the timber plots. Of 91 species found in timber plots, 51 species were not found in legacy stands, and 18 were nonnative species (1 tall shrub, 2 low shrubs, 13 herbs, and 2 grasses). Of 47 species in legacy stands, four were not found in thinned stands, including the old-growth associate Pacific yew, and one was nonnative. Community structure differed with management history, with timber plots dominated by aggressive clonal native shrubs and ferns. Timber plots had greater cover for total understory (88 percent versus 34 percent), tall shrubs (12 percent versus 5 percent), salal (25 percent versus 13 percent), swordfern (16 percent versus 3 percent), and brackenfern (9 percent versus 2 percent). Mosaics initially had reduced understory cover and increased importance of 20 native and 11 exotic species. Two native species decreased in importance. Three years later, understory recovered, species richness increased by 150 percent, only four exotic species persisted in importance, and eight natives increased and seven natives decreased in importance. Underplanting has established root-rot-resistant trees in root-rot pockets that will restore canopy cover and increase the resilience of the forest and, in other heavily thinned areas, increase resistance to spread of root rot. Shade-tolerant trees are now established in patches throughout the plots and have the potential, with continued growth, to begin influencing understory patterning.

Small Mammals

Timber plots had 1.5 times the numbers and 1.7 times the biomass of small mammals of legacy plots, presumably because of their greater abundance and diversity of vascular plants. Keen's mouse, a dominant species in natural forests, was rare in both forests. The Oregon creeping vole was inordinately abundant in timber (3rd ranked) compared to legacy plots (7th ranked) and natural stands. The montane shrew was also inordinately abundant in timber plots (2nd ranked). Neither management produced communities typical of natural forests. After variable-density thinning, deer mice, Oregon creeping voles, and vagrant shrews increased in abundance in mosaics. No species decreased in abundance.

Squirrels

Northern flying squirrels were twice as abundant in legacy as in timber plots (1.0 per hectare versus 0.5 per hectare). Townsend's chipmunks were the opposite (0.2 per hectare versus 0.8 per hectare). Douglas' squirrels were low in abundance in both (0.1 per hectare). Flying squirrels decreased in abundance in legacy mosaics immediately following variable-density thinning (concomitantly with a decline in truffle production) but recovered within 5 years (along with truffle production). Chipmunks increased sharply in legacy mosaics following variable-density thinning and remained high. Douglas' squirrels did not respond to variable-density thinning in the short term. It remains to be seen if flying squirrels and Douglas' squirrels will increase over time as tree diversity increases and as trees increase photosynthetic activity and allocate additional carbon to seeds and ectomycorrhizal associates. California hazel and bigleaf maple are present and may begin producing high-quality nuts and seeds for the squirrels in response to the more open canopy and available light.

Wintering Birds

Species richness was higher in timber (16 species) than in legacy plots (12 species). Richness was unchanged in timber mosaics, ranging from 14 to 22 species 3 to 5 years after variable-density thinning. Richness varied annually but was consistently higher in legacy mosaics than in legacy controls in post variable-density thinning years 3 to 5 (12 to 16 species versus 10 to 16 species in controls). The proportion of stand area used increased in mosaics for two of eight abundant species (winter wren and song sparrow). No species used legacy controls more than thinned or mosaic stands. Cavity-excavating birds (Picidae) were present but low in abundance in all stands.

Implications

All stands maintained fungal-dominated soils, despite continued disturbance in the timber mosaics—three significant removals of subordinate and codominant trees over 20 years by commercial thinning. Mechanical disturbance associated with thinning, however, appeared to destroy near-surface fungal mats and promote *Melanogaster* over *Hysterangium* and *Gautieria*; the latter are more important foods to mycophagists. Induced heterogeneity nevertheless increased total sporocarp diversity. Sporocarp diversity rivaled that in old-growth forests around the region. Impacts of variable-density thinning on truffle production were brief. There is no clear, general effect of management on production of the sporocarps of hypogeous ectomycorrhizal fungi across the region other than effects on fungal mats (Carey et al. 2002). Retaining unthinned patches in mosaics might help conserve fungal mats.

Conventional thinning had produced rich understories dominated by clonal native species with numerous exotic species present in the timber plots. Legacy management had produced depauperate understories. Canopy mosaics markedly increased diversity and abundance of native species in both but only ephemerally increased exotics. With underplanting, variable-density thinning is leading to increased spatial heterogeneity. Achlorophyllous mycotrophic plants were reduced in abundance in areas of dense understory; retaining small unthinned patches in mosaics would help conserve these species.

Both conventional thinning and legacy management had produced imbalanced small mammal communities, with some species common in natural forests low in abundance. Inducing heterogeneity had immediate positive impacts on forest-floor mammals, but restoration of shade-tolerant midstories and development of midstory deciduous trees (e.g., bigleaf maple) will be required to restore biotic integrity. Chipmunks increased markedly in legacy mosaics with only brief declines in flying squirrels. Flying squirrels remained rare in previously thinned stands, perhaps owing to dense homogeneous understories that promoted excessively high and uniform chipmunk abundance. Similarly, variable-density thinning had positive effects on the winter birds and increased the overall habitat quality in mosaics. Bird communities, however, continued to have low abundances of cavity-excavating birds. Promoting deciduous trees (e.g., red alder) early in stand development provides

A variety of trees—both living and dead—along with steep terrain and fog creates dramatic scenery in Olympic National Forest, near Forks, Washington. Photo by T. Wilson.

short-lived trees for cavity excavation in the short term; decadence management may prove essential to maintaining cavity-excavating birds in managed forest.

In summary, this experiment has demonstrated that active, intentional management has potential in restoring and maintaining biological diversity in second-growth forests and in increasing the resilience of such forests to such disturbance agents as wind (larger more wind-firm trees), disease (resistance to spread of root rot), and insects (increased diversity and abundance of overwintering birds) without increasing potential for wildfire (forest floors remained moist; indeed, increased plant cover in the understory should generally produce moister and cooler conditions in the future). Increased diversity in the squirrel community and increased cover on the forest floor should reduce the potential for repetition of past severe predation by long-tailed weasels that decimated flying squirrel populations from time to time. Increased diversity of trees and shrubs bearing hard mast and increased production of hard mast should result in increased numbers and lower fluctuations in squirrel populations (all three species) as well. Inducing heterogeneity into homogeneous, closed canopies has positive effects on diverse biotic communities and ecosystem function as habitat even in the short term (5 years) in forests managed with conventional thinning for timber production and with legacy retention only. The rapidity of the growth of shade-tolerant trees in the understory will determine the rate at which heterogeneity continues to increase, and only time will tell if reduced elements of diversity (e.g., cavity trees, certain small mammals, and certain birds) will be restored; deciduous trees and shrubs are now well establish in the understory.

Stochasticity, Disturbance, and Change

Resolving fear of environmental stochasticity (randomness), uncertainty, unpredictability, and change is aided by systems theory and an understanding of chaos theory and self-organizing systems. Bertalanffy proposed a self-integration (self-organization) model of hierarchical order with four related concepts of change (Regier 1993): (1) progressive integration, or complexity, with parts dependent on the whole; (2) progressive differentiation, or parts becoming more specialized; (3) progressive mechanization, or limiting parts to a single function; and (4) progressive centralization, or certain parts dominate the system. This theory applies to organisms, societies, and ecosystems. Natural historians take self-organization as self-evident—their practical insights flow from comparative empiricism that is a synthesis of both perception and analytical understanding. Academic ecology, however, often consists of abstractions that are mobilized as "band-wagon" paradigms that may not be very pragmatic but may provide fruitful avenues of research to develop fundamental principles.

Empirical observation asserts that biotic communities develop and succeed one another on stages set by environmental variables–geographic location, landform, site characteristics, precipitation, and temperature (Clements 1936). Colonization by pioneers that grow rapidly and withstand physical extremes resets the stage for species replacement through competition. Biomass accumulates, internal regulation of biochemical and physical processes increases, variability is reduced, and a more-or-less stable climax condition results: equilibrium centered, with major disturbance exogenous. It is clear that there are communities that do this, for example, old-growth forests in the Pacific Northwest (Holling 1986). However, many biotic communities, including those in the Pacific Northwest, are subject to regular and irregular, minor and major, endogenous and exogenous disturbances at frequencies often in some way related to the lifespan of their longest lived or most persistent species, such that these species are adapted to the disturbance. For example, the foliage of fire-adapted species is significantly more combustible than related species in communities not subject to frequent fires.

Theoretically, most species can be described on a continuum from *r*-strategists (opportunists selected for maximizing returns in unpredictable-unstable environments) to *K*-strategists (equilibrium species selected for efficiency of foraging in predictable-somewhat stable environments) (MacArthur and Wilson 1967). *K* is the symbol for equilibrium carrying capacity in population models, and *r* is the intrinsic rate of increase in populations. *K*-strategists tend to be larger in size and have lower reproductive potential, longer lifespans, less dispersal ability, and more competitive ability than *r*-selected species. Ecosystems also have strategies for development; in other words, they are self-organizing but regulated by physical, chemical, and biological processes (Odum 1969). The *r* and *K* concepts can be used to describe ecosystem functions, for example, exploitation and conservation (Holling 1986) (table 20). Early-seral stages emphasize exploitive processes (binding nutrients, rapid accumulation of biomass, and modification of the environment). Later-seral stages emphasize increased organization through trophic and competitive interactions (cooperation and coadaptation) that reduce variability and, if uninterrupted long enough, reduce diversity.

Table 20—Pianka's (1970) correlates of *r*- and *K*-selection[a]

Feature	*r*-selection	*K*-selection
Climate	Variable and/or unpredictable	Fairly constant and/or predictable
Mortality	Often catastrophic, nondirected, density-independent	More directed, density dependent
Survivorship	Often Type III Deevey survivorship curves	Usually Type I or II Deevey survivorship curves
Population size	Variable in time, nonequilibrium	Fairly constant, equilibrium
Intra- and inter-specific competition	Variable, often lax	Usually keen
Relative abundance	Often does not fit broken stick model	Usually fits broken stick model
Favored by selection	▪ Rapid developement ▪ High r_{max} ▪ Early reproduction ▪ Small body size ▪ Semelparity	▪ Slow development, greater competitive ability ▪ Lower resource thresholds ▪ Delayed reproduction ▪ Small body size ▪ Iteroparity
Length of life	Short	Long
Leads to…	Productivity	Efficiency

[a] The theory of r- and K-selection for life history evolution dominated demographic thinking in the 1960s and 1970s, became archaic in the 1980s, and now has arisen anew to incorporate density-dependent population regulation, resource availability, environmental fluctuation, and predation risk.

Source: Reznick et al. 2002

Hierarchy Theory

Forces of change operate at different scales. Within a given multivariate space, regions of stability expand, contract, and disappear over time in response to changes in slow variables (such as tree growth, fuel accumulation, and increasing herbivore populations). Abrupt change occurs because multiple stable states emerge as slow variables change. Jumps between stability domains may be triggered by exogenous disturbances. External events may lead to highly repetitive consequences by reinitiating ecosystem development. Variability, then, produces diversity as a consequence of cyclic shifting of competitive advantages among species within and among different scales. Thus, change is an internal property of each system, gradual for long periods followed by inevitable jump events.

Hierarchy theory provides useful stability and resilience concepts:

- There can be more than one stability region; multiple equilibria are possible.

- Behavior is discontinuous when elements of a system move from one stability domain to another because they become attracted.
- Precise kind of equilibrium (steady state or stable oscillation) is less important than the fact of equilibrium.
- Parameters of the system that define the existence, shape, and size of stability domains depend on a balance of forces that may shift in patterns of variability in space and time; managerially reduced variability is likely to lead to smaller stability regions whose contraction can lead to sharp changes.

Stability emphasizes equilibrium, low variability, and resistance to and absorption of change. Resilience emphasizes the boundaries of stability domains and events far from equilibrium, high variability, and adaptation to change (the school of linear interactions, however, treats resilience in an opposite fashion—how fast the variables return toward their equilibrium following a perturbation). Holling (2001) developed this theory further into Panarachy.

Panarchy Theory

Ecology has always been concerned with stability—whether natural systems have developed sufficient resilience or stability to absorb increasing human populations and demands for food, fiber, and aesthetic needs (Holling 1969). The concept of a global biochemical homeostasis—that life keeps the atmosphere optimal for the contemporary biosphere—provides a global rationale for rehabilitation, protection of ecosystems, and land-use management (Holling 1986). Global homeostasis prompts questions: How do ecosystems absorb, buffer, or generate change? Why are we surprised when causes, behaviors, and results sharply differ from what we expected? In answer to the latter, our expectations develop from interactions of the metaphors we use to provide understanding and our perceptions of memorable events, both of which are incomplete. Three influential metaphors are (1) nature as equilibrium, (2) nature engineered with multiple equilibria, and (3) nature evolving.

Equilibrium emphasizes constancy in time, spatial homogeneity, linear causation, and images of a benign nature wherein management mistakes can be made, but recovery is assured, for example, the traditional production forestry paradigm (Barrett 1962, Smith 1962). Multiple equilibria suggest a more dynamic system, with spatial heterogeneity and nonlinear causation. Two different beliefs arise from multiple equilibria: (1) landscapes are fixed or we have sufficient knowledge to keep them fixed, and (2) key features are maintained by variability itself and by maintaining the configuration (structure) of a system. In other words, structure-based management can maintain multiple equilibria. This is the unspoken underlying paradigm for conservation biology with its reserves and management for the range in natural variation (e.g., Hunter 1999).

Evolutionary change suggests generative, competitive, and behavioral processes maintain the characteristics of the system. When variability changes, parameter values shift, landscapes change, stability domains shift, key variables become more homogeneous, and perturbation can no longer be absorbed. When control is internal and self-regulated, organizational change may occur. When control is external *and* continuing control requires ever-increasing vigilance, pathologies may develop. Thus, progressive evolution requires not only function but also organization (food webs and trophic relations). The complexity of systems emerges not from random assemblage of numerous controlling processes but from self-organizing systems and a small set of critical processes that create and maintain the self-organization (Holling 2001). Diversity and individuality of components, localized interactions among components, and an independent process that uses the outcomes of local interactions to select components for enhancement are characteristics of complex, adaptive systems. Pragmatic sustainability has to do with the set of critical self-organized variables and their transformation during system development. There is simplicity behind complexity that can be understood and communicated lucidly. This is known as adequate integrative theory—as simple as possible, but not simple; dynamic and prescriptive, but not static and descriptive; embracing uncertainty and unpredictability (Holling 2001). This paradigm underlies intentional systems management for conservation of biodiversity, where biodiversity includes the variety of taxa (genes, species, populations), organization (communities, ecosystems, life zones, biomes), processes (evolutionary, ecological, managerial), and products (goods, services, experiences) (Carey et al. 1999c).

Hierarchies and adaptive cycles comprise the basis of socioecological systems across scales (Holling 2001). Panarchy is the hierarchical structure in which socioecological systems are interlinked in never-ending adaptive cycles of growth, accumulation, restructuring, and renewal. Panarchy theory is a model of complex system behavior that describes how a healthy system can invent and experiment, benefiting from invention that produces opportunities, while being safeguarded from those that destabilize because of their nature or excessive exuberance. Space-time hierarchies are semiautonomous rather than top-down authoritative structures. Their levels are formed from the interaction of elements with shared speed and spatial attributes. Each level operates at its own pace, and each communicates a small set of information to the next higher, slower, and coarser level. Slower and larger levels set the conditions within which faster and smaller ones function. Thus, the forest moderates the climate for individual trees. The levels of a dynamic hierarchy serve two functions: (1) conserve and stabilize conditions for the faster and smaller levels and (2) generate and test innovations by experiments occurring within a level. Examples of hierarchies in space and time are (1) breeze, thunderstorm, front, long wave, El Niño, and climate change; and (2) needle, crown, patch, stand, forest, and landscape. A time-population size hierarchy is individual, small group, contract, policy, law, constitution, and culture. Another is fad, values, and traditions.

The adaptive cycle (fig. 36) transforms hierarchies from fixed, static structures to dynamic, adaptive entities whose levels are sensitive to small disturbances at the transition from reorganization to rapid growth. Three properties shape the adaptive cycle and the future state of a system: (1) inherent potential that is available for change; this potential determines the possible range of future options and can be considered the wealth of the system; (2) internal controllability or the degree of connectedness between internal variables and processes; the degree of flexibility of the system; and the degree to which it can control its own destiny; and (3) adaptive capacity or resilience, a measure of vulnerability to unexpected, unpredictable shocks. Wealth, connectedness, and adaptive capacity are general properties from the scale of a cell to the biosphere. In the adaptive cycle, the trajectory alternates between long periods of slow accumulation and transformation of resources (from exploitation to conservation, r to K) with shorter periods that create opportunities for innovation (from release to reorganization, Ω to α) (fig. 36).

Ecosystem dynamics consist of not only the two functions (exploitation and conservation) that determine succession and development but also creative destruction functions that result from increasing strength of connections in maturing ecosystems that can result in abrupt change. Conservation leads to wealth and becomes an accident waiting to happen—a buildup of stored energy that either is dissipated by local internal disturbance leading to increased complexity or released by wind, fire, disease, or insect outbreaks. When timing is set by the slowest variable (e.g., growth of a dominant Douglas-fir cohort), forces of change can lead to intense, widespread mortality (e.g., catastrophic fire or epidemic disease).

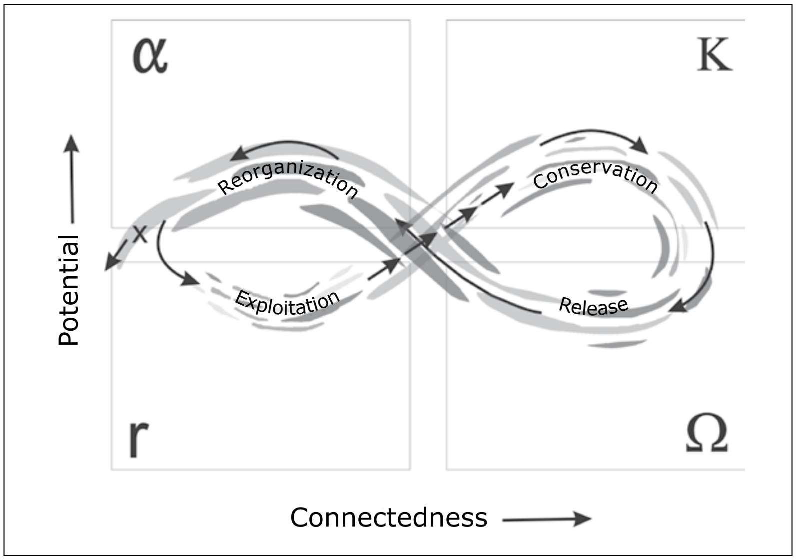

Figure 36—The adaptive cycle of self-organizing systems (adapted from Holling 1986, 2001). Ecosystems may have four primary functions (*r*, exploitation; *K*, conservation; Ω, release; α, reorganization), here arrayed in a two-dimensional space of stored resources potentially available (e.g., accumulated biomass, Y-axis) and connectedness (sensitivity to perturbation, X-axis). As plants exploit a newly cleared forest, the ecosystem moves rapidly to accumulation of biomass (conservation), and the stored potential of the system becomes great and connectedness is high. High connectedness increases susceptibility to perturbation. Minor perturbations release some of the stored potential for niche diversification and reorganization of the system into a more complex, less connected structure with high potential. Catastrophes can release most or all of the potential and return the system to exploitation. With legacies, exploitation (*r*) can move rapidly to conservation (*K*); without legacies, exploitation may last longer with low connectedness and low potential.

Individuals constituting slow variables eventually senesce and die, but their impacts are local and not synchronous. When timing is set by the fastest variable, changes are less intense, and spatial impacts, although synchronous over large areas, are patchier. These functions are called creative destruction even though organisms are destroyed, because their success in competition, appropriation of resources, and accumulation of biomass results in a release of tightly held resources promulgating the fourth function, creative renewal (e.g., ecosystem reorganization). Rapid cycling produces patchy ecosystems; slow cycling can produce waves across space (e.g., spruce budworm outbreaks). Things can go awry, however, during renewal. Savannahs can become dominated by woody shrubs because of loss of capacity for water retention. Burning can shift forest vegetation to bogs and eventually peat lands. Clearing tropical forests can produce scrub savannahs. The degree of resilience of a system is determined by the balance between the processes of mobilization (freeing resources for other uses) and retention (e.g., of biological legacies, including coarse woody debris and living plants).

It has long been argued that more species and more interactions confer more stability to biotic communities. The argument is that the more pathways available for movement of energy and nutrients, the less the effect of removing one pathway. Although May (1973) showed that increasing the diversity of randomly connected networks actually decreased stability, ecosystems are not randomly connected (Holling 1986, May 1973). Ecosystems have a hierarchical structure in space, time, and speed of variables. Thus, the relevant measures of species diversity, which is one measure of complexity, should not involve all species but only those contributing to physical structure and dynamics. The most significant measure of complexity concerns the degree of connectedness within ecosystems. Extensive land clearing to produce monocultures produces high connectedness through pest loads and little resistance. In other words, the pattern of connectedness and the resultant balance between stability and resilience are a consequence of the pattern of external variability the system has experienced. In the Tropics, consistent temperature and precipitation produce highly stable forests of low resilience, sensitive to disturbance by humans, and characterized by high species diversity. Temperate systems have high climatic variability, low stability, and high resilience, resistant to disturbance by humans. Hierarchical systems are not static in kinds or strengths of connection that determine resilience. Succession introduces connectedness. Overconnectedness produces discontinuous change, increases variability, and leads to resilience. Underconnectedness leads to collapse of resilience, especially during the destabilized part of the cycle, especially if mobilization is not balanced by retention. Forest ecosystem development disrupts overconnectedness through fine-scale patchiness and promotion of tree species diversity and balances mobilization by intermediate and fine-scale disturbances with biomass accumulation in dominant trees, retention of coarse woody debris on the forest floor, and accumulating slowly decaying organic matter into the soil (Carey et al. 1999b). Thus, adaptive cycles embrace opposites—growth and stability versus change and variety (Holling 2001). The spatial and temporal patterns generated by the four major ecosystem functions (exploitation, conservation, creative destruction, renewal) determine the qualitative structure of the ecosystem. The resultant architecture of the ecosystem provides a variety of niches occupied by different species.

General sustainability suggests a complexity that can overwhelm understanding. At best, efforts to manage ecosystems are experiments testing a general hypothesis of stability and resilience. Management to reduce variability represents an equilibrium-centered view of constant nature. It achieves short-term objectives, but eventually the system evolves into a qualitatively different system—the biophysical environment becomes more fragile and more dependent on vigilance and error-free management. Reduced variability produces reduced resiliency and spatial homogenization produces increased connectedness; the result is surprises. The implications for management are (1) ecosystems have a natural rhythm of change; restricting temporally and homogenizing spatially produces surprises (e.g., Swiss needle cast); (2) developing predictive tools should have a lower priority than designing systems that are flexible enough to undergo renewal after unexpected events. Holling (2001) summarized the current understanding of panarchies (see sidenote 33). It appears that spatial contagion and biotic legacies generate self-organized patterns over scales in space and time (Carey et al. 1999b, 1999c).