

# From Ecology to Forest Management

**H**ow does one move from understanding various ecological processes underlying biological diversity and ecological resilience to pragmatic methods for managing second-growth forests for economic, ecologic, and social values? How does one actively and intentionally manage for multiple values? The problems seem enormous: forestry seems to lack an adequate scientific basis (Perry 1998), and ecology seems to lack an accepted theoretical framework derived from first principles (Belovsky et al. 2004) (sidenote 34). Furthermore, predicting system behavior is difficult because it depends on numerous variables and their interactions (20 components provide countless potential interactions) and causes and effects are difficult to demonstrate, yet emergence of new structure and function seems essential (Schneider and Kay 1994). The solution to conserving nature may be to stop managing for fixed idealized states, to begin appreciating that complex systems emerge from the interaction of biological entities with each other and the environment, and to change our focus from biodiversity to biocomplexity, the defining property of all ecosystems (Dale et al. 2000, Dybas 2001, Holling 1992, Schneider and Kay 1994) (sidenotes 35, 36). Finally, we must recognize that temperate zone forests in the Northern and Southern Hemispheres (one-fourth of the world's forests), are mosaics shaped by fire (fig. 37), wind, herbivory, other natural disturbances, and,

**Sidenote 34**—Ten fundamental problems in ecology (Belovsky et al. 2004):

- Ecology is faddish—issues come and go without resolution.
- Ecologists exhibit poor scholarship, ignoring the past literature (and literature from allied fields).
- Integration of empirical and theoretical ecology is inadequate.
- Integration of natural history and experimentation is inadequate.
- There is implicit belief in single causes despite evidence for multiple causation.
- Application of equilibrial and disequilibrial perspectives are often misguided.
- Ecological studies are inadequate in replication in space and time.
- Data collection lacks rigor, which hinders comparison of studies.
- Forces driving studies are often methods or statistics, not questions.
- Basic ecology is often conducted as distinct from applied ecology.

increasingly, human activities including fire suppression, logging, grazing, and fossil fuel consumption (Frelich 2002).

In forest ecology, three fundamental practices for managing second-growth forests for multiple values are (1) retention and protection of biological legacies during and after harvests of timber (sidenote 37); (2) long rotation times between major harvests (sidenote 38); and, in the interim, (3) active creation of biocomplexity in managed forests (Carey 2003a, Franklin et al. 2002) (sidenote 39). Legacy retention addresses problems of dispersal-limited species like lichens, and jumpstarts the development of biocomplexity during reorganization. A significant amount of time is required for forests to accumulate biomass and develop a complex structure at multiple scales. Active creation of biocomplexity with a variety of manipulations prevents competitive exclusion and a persistent state of low diversity and limited function.

In fire-adapted forests, management of fuels and diseases with mechanical treatments, grazing, and prescribed fire is also fundamental but complex (Tiedemann and Woodard 2002, Wright and Agee 2004). All AIM practices include management of disturbances of varying intensity and frequency. All species have evolved in the presence of disturbance and, in a sense, are matched to recurrent patterns of disturbance (Frelich 2002, Paine et al. 1998, Tausch et al. 1993). In this context, full intentionality must be brought to the patterns of disturbance that should be induced and that will occur spontaneously as well as to operations, including consideration of



**Figure 37**—Natural regeneration begins to show itself among the snags left by a large-scale fire in the Wallowa-Whitman National Forest in northeast Oregon. Photo by T. Wilson.

purposes, risks, experience, and engineering and geological methodology in the design and management of logging systems and transportation systems. Situations in which risks of environmental damage owing to logging and transportation systems cannot be reduced to an acceptable level (a background disturbance level) will preclude AIM with silviculture. In addition, AIM for biocomplexity may entail restoring lost diversity (planting, underplanting, and seeding) and removing exotic species. In western Washington, common exotics with potential to seriously modify forests include English ivy, English holly, and, along roads and in clearings, scotchbroom. Costs and economic returns of various AIM techniques are often cited as reasons for doing some and not doing others; but poor (partial) AIM is unlikely to hit the target (fig. 38).

Given the potential for purposeful manipulation of ecological processes and unintentional interference with other ecological processes throughout the life of a forest, understanding variability in how temperate and boreal forests develop is necessary for developing pragmatic management systems and avoiding unintended consequences (Frelich 2002). Variation is a genuine property of ecological systems that includes variation in space and in time *in processes* that generate the patterns we observe (Benedetti-Cecchi 2003). This conception of variation is much different than the range in natural variation *in patterns* that has attracted so much attention; those patterns are the result of multiple processes and stochastic events. Although there is a lack of coherent theory linking variation in processes to variation in responses of organisms and systems (patterns), one must grasp and use the processes by which biotic communities organize themselves and understand how the relative influence of each process varies from place to place and time to time with changes in the biophysical environment, including disturbance regime and regional species pool. Thus, key questions are: How much variance is found in the relative importance of basic processes? What are the adaptations in pragmatic management that must follow as one moves from one physiographic province to another or from one forest type to another within the same physiographic province? What are the relationships among the processes that produce complex forest structure and biological diversity and that lead to healthy, resilient ecosystems? To what degree can forest development be guided managerially? To what degree will unhindered and unaided self-organization of forest ecosystems, after destruction of forests by logging, grazing, agricultural clearing, and fire exclusion, produce the materials and services we value for ourselves and for other forms of life?

**Sidenote 35**—Guidelines for ecosystem management (Schneider and Kay 1994):

- Maintain a hierarchical perspective with careful attention to scale and extent.
- Examine the spatial, temporal, thermodynamic, and informational aspects (dynamics).
- Recognize that system behavior is emergent and catastrophic—dynamic with a degree of unpredictability and with phases of rapid change.
- Accept that ecosystem self-organization unfolds like a symphony—one needs to understand the rules of composition.
- Accept that living systems are self-organizing and will look after themselves—the challenge is to learn to work with these self-organizing processes to meet our needs while preserving the integrity of the system.
- Accept that one must not destroy, but rather must maintain the biodiversity needed for the regeneration processes.

**Figure 38**—A marksmanship analogy: that’s the point of intentionality—AIM carefully, or not at all. In a marksmanship analogy, it is not sufficient to chamber a cartridge and pull the trigger. Target identification, a clear field of view, a safe backdrop, knowledge of ballistics and trajectory, estimation of distance and wind, matching of rifle and cartridge to purpose, careful matching of stock to cheek and shoulder, alignment of rear sight with front sight, careful breathing, and gently squeezing the trigger, are all necessary for high marksmanship. The marksmen-practitioners will be familiar with all the details of technique. Other practitioners and observers are essential to spotting and target identification (interdisciplinary /collaborative management teams), safety (range officer/regulatory agencies), and choosing experts and sharpshooters to support and withdrawing support from the “plinkers” shooting beer cans in a quarry (all stakeholders). Graphic by A. Wilson; photo by A. Carey.



## Structure, Pattern, and Process

Much literature exists on the structure of forests, the composition of forest communities, the processes influencing their development, and the patterns of biotic communities imposed on the landscapes by natural and anthropogenic disturbance regimes, particularly for western North America (sidenote 40). A large reading list could also be constructed just on disturbance and resulting patterns in and of biotic communities (Frelich 2002, Korpilahti and Kuuluvainen 2002, Pickett and White 1985b). Much of the disturbance literature addresses landscape dynamics, fragmentation, and design of reserves and corridors. There is also extensive literature available on silvics (Burns and Honkala 1990a, 1990b) and silvicultural systems and techniques (Barrett 1962, Burns 1983, Curtis et al. 1998, Kohm and Franklin 1997, Nyland 2001, Smith 1962), especially for timber management.

## Synthesis

A major impediment to achieving synthesis and consensus on how to address the challenge of conservation of nature in managed forest ecosystems lies in deeply rooted ecological philosophies related to

concepts of equilibria, stability, succession, development, and alternative stable states. Frelich (2002) suggested many “false” arguments ensue over these concepts as a result of narrow perspectives on the part of the antagonists. He posited that questions of scale and differences in spatiotemporal perspective underlie arguments over these concepts. For example, stability is a function of the length of time of observation and size of area observed. He suggested that interactions of neighborhoods, cumulative disturbance severities, and degree of dominance by late-seral species produce four categories of landscape dynamics that affect stability in species composition and in age structure over time and space and how and whether succession or development takes place (table 21).

Neighborhoods are small groups of trees (10 to 20 meters across) that exist within larger forest communities at the scale of tree-fall gaps, spot fires, and root-rot pockets—a scale of about 50 square meters or about 100 neighborhoods per 0.5 hectare; a 0.5-hectare area, then, may have over 50 patches of significant disturbance (gaps owing to the death of more than two trees). Differentiation of patches also reflects differences in soil and substrates, climatic variation owing to elevation, patterns of invasion by tree species, and positive neighborhood effects when two species or species groups grow together. These complex effects can produce distinctive patches of understory-midstory vegetation at the scale of 0.1 to 0.5 hectare (Carey et al. 1999b). Frelich (2002) suggested that if some relative stability in age structure is to be maintained, the minimum area occupied by a forest community should be 50 times the patch size—or more than 5 to 25 hectares, sizes coincidentally and commonly dictated by complex topography (Carey and Peeler 1995). The minimum landscape required to absorb infrequent severe disturbances of less than 2,000 hectares might be 15,000 hectares or more, with no single disturbance occupying more than 20 percent of the area in a 250-year period for temperate deciduous-conifer forests. Induced disturbance regimes (say variable-retention harvesting of 25-hectare biotic communities on variable rotations averaging 100 years) also requires landscapes of 15,000 hectares or more to maintain a shifting-steady-state mosaic on a decadal basis (Carey et al. 1999c). Frelich (2002) referred to “punctuation times” for disturbances that maintain quasi-equilibria in age structure and composition in large landscapes; disturbances of 0.1 to 0.5 hectare can take place on the scale of decades, 10 to 100 hectares on the order of 0.5 to 10 centuries, and 1,000–10,000 hectares on the order of millennia (fig. 39).

Neighborhood effects are widespread and important forces operating in forests. In general, neighborhood effects are the ways in

**Sidenote 36**—Guidelines for landscape management (Dale et al. 2000):

- Examine impacts of local decisions in a regional context.
- Plan for the long term and the unexpected.
- Preserve rare landscape elements and their associated species.
- Avoid uses that deplete natural resources.
- Retain large contiguous or connected areas of complex forest.
- Minimize the introduction and spread of exotic species.
- Avoid or compensate for the effect of human development on ecological processes.
- Implement management compatible with the natural potential.



**Sidenote 37**—Biological

legacies are diverse:

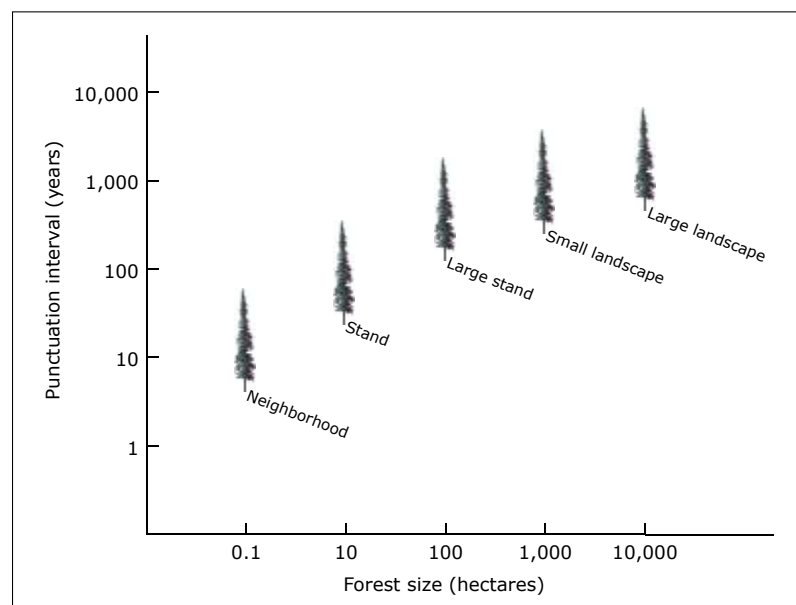
- Large, old, live conifers with their unique architecture and epiphytic plants, decay organisms, and ectomycorrhizal fungal associates
- Large, old, live deciduous trees with their unique architecture, epiphytic associates, decay organisms, and mycorrhizal symbionts
- Large, dead, standing trees and their associates and inhabitants
- Large, fallen trees on the ground and in streams with their associated biotic communities
- Intact patches of forest floor with their associated flora, fauna, seedbanks, and advance regeneration
- Intact patches of forest, including trees, epiphytes, understory, litter, humus, soil seedbanks, and soil food webs
- The biotic communities associated with intact headwater seeps, streams, and other wetlands
- The biotic communities associated with various intact physical landscape elements such as rock outcrops, talus slopes, balds, and special soil types

**Figure 39**—Frequency of disturbance events that disrupt age structure for a variety of forest sizes in Upper Michigan’s hemlock-hardwood forest (adapted from Frelich 2002).

which trees alter their immediate surroundings. A more formal definition is:

Any process mediated by canopy trees that affects the replacement probability by the same or other species at the time of canopy mortality. Neighborhood effects are defined in relation to dominant tree species or groups of species. Positive neighborhood effects (analogous to feedback effects) are processes that promote self-replacement; negative effects are processes that deter self-replacement (unless no other species are available); and neutral effects are processes that neither favor nor disfavor self-replacement (Frelich 2002).

For example, as the canopy of a Douglas-fir-dominated forest grows and closes, death of a Douglas-fir favors replacement by shade-tolerant species such as western hemlock, if seeds or seedlings are present—a negative neighborhood effect for Douglas-fir. But death of a large, dominant western hemlock also favors western hemlock—a positive neighborhood effect for hemlock. There are two types of neighborhood effects: (1) overstory-understory effects, positive or negative, that influence the species composition of seedlings and saplings by shading, litter character, stump sprouting, and seed rain; and (2) disturbance-activated effects, operating mainly in forests perpetuated by intense fire, where seedlings are killed along with canopy trees and new regeneration is due to serotinous seed rain (jack pine, lodgepole pine) or sprouting from underground



root stocks (aspen). Disturbance effects, however, will also result from species adaptations to colonization and dispersal. In the Pacific Northwest, disturbance gaps may be colonized by wind-blown western hemlock seeds (from kilometers away) and bird-transported

**Table 21—Four categories of landscape dynamics in temperate evergreen-deciduous forests with reference to correspondence in some forest types of western North America**

Category A—Positive neighborhood effects and low-severity disturbance:

- Adjacent stands differ in composition owing to species interactions.
- Low- to moderate-severity disturbances produce different-aged patches at the neighborhood, stand, and landscape scales.
- Stability of age structure is low in the neighborhood, moderate in stands, and high in landscapes.
- Composition stability is high in neighborhoods, stands, and landscapes.
- High-severity disturbance is rare and destabilizes composition.
- Landscape consists of a matrix of late-successional species, all-aged neighborhoods, and stands with a few stand-size inclusions of even-aged early-seral species.
- Examples: western hemlock-sitka spruce in Washington, British Columbia, and Alaska and hemlock-hardwoods in eastern North America

Category B—Positive neighborhood effects and high-severity disturbance:

- Patches on uniform soils owing to species interactions.
- Low- to moderate-severity disturbance plays a minor role.
- High-severity disturbance is common and stabilizes composition in the neighborhood, stand, and landscape.
- Stable age structure is rare in neighborhoods and stands but may occur on large landscapes.
- Successional episodes proceed during periods without crown fire.
- Landscape is a matrix of large complex-shaped stands of even-aged early-seral species with a few small stand-size inclusions of uneven-aged late-seral species.
- Examples: lodgepole pine in Yellowstone National Park and Alberta, Canada, and near-boreal jack pine

Category C—No or negative neighborhood effects and low-severity disturbance:

- Patches of different composition and different age caused by tree-fall gaps and other small disturbances.
- Composition stability is low among neighborhoods, moderate to high in stands and landscapes.
- Severe disturbance is rare and destabilizes composition in neighborhoods, stands, and landscapes.
- Successional episodes are initiated by moderate- to high-severity disturbance.
- Landscape matrix is a fine-grained (neighborhood-scale) mosaic of late-seral species with stand-scale inclusions of even-aged early-seral species.
- Examples: red spruce, white spruce, and paper birch in the Northeastern United States; spruce, fir, birch, and cedar in Minnesota; and Douglas-fir, western hemlock, and western redcedar in the Pacific Northwest

Category D—No or negative neighborhood effects and moderate- to high-severity disturbance:

- Patches of different composition caused by any disturbance.
- Disturbance perpetuates instability of species composition; compositional stability is low among neighborhoods and stands, but differs in landscape.
- Stability of age structure is low among neighborhoods and stands but may be high in landscapes
- Successional episodes initiated by disturbance of any severity.
- Landscape matrix of large complex even-aged stands of mixed early- and mid-seral species with stand-scale inclusions of older forests.
- Examples: white pine, red maple, and northern red oak forests in eastern North America and Oregon white oak-fir-wetlands mosaics in the Puget Trough in Washington

Source: Frelich 2002.

**Sidenote 38**—What is a long rotation?

- Certainly one that meets or exceeds the culmination of mean annual increment of tree diameter growth—say a minimum of 100 years in Douglas-fir forests.
- It differs with forest type, type of land ownership and associated goals—for example, for Douglas-fir forests, 100 years (industrial forest), 100 to 150 years (state trust lands), and 150 to 350 years (federal multiple-use lands), and a maximum that is indeterminate (late-successional reserves).
- Not a goal with uneven-age management or when no final harvest is planned.

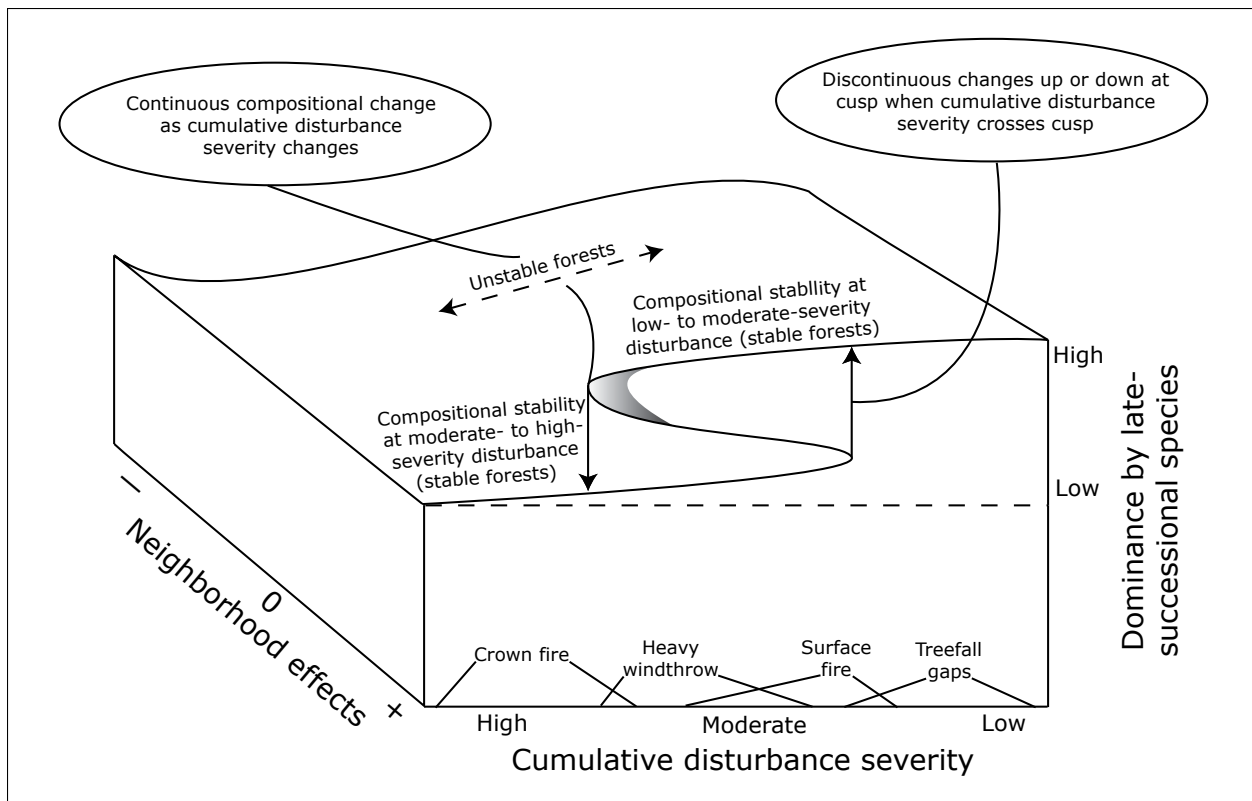
Pacific madrone seeds as well. Conifers and hardwoods often have contrasting neighborhood effects, favoring their own reproduction and reducing the success of the other. Neighborhood affects nutrient availability, light characteristics, duff and coarse woody debris characteristics, and differential biota (such as mycorrhizae) in the forest floor in conifer and hardwood forests. Combined with disturbance regimes, neighborhood effects influence stabilities at the neighborhood, stand, and landscape levels. Landscape categories A and C may produce shifting-steady mosaics. Category A produces a self-perpetuating quasi-climax similar to those described by Clements (1936). Category B produces nonclimax forests of jack pine, red pine, or lodgepole pine. Category C may produce development of complex forests with development reset by infrequent severe disturbance—Douglas-fir can persist in the canopy in significant numbers for over 750 years. This longevity is particularly striking in the context of global climate change wherein most forests in the United States developed during interglacial periods that allowed maximum periods of development of a particular forest type of only 1,000 to 5,000 years (Frelich 2002). Category D resembles the individualistic successional model with no stable endpoint. Rather than focus on succession, Frelich (2002) suggested thinking of vegetation growth stages that integrate development (structural changes) and successional (compositional) changes over time; the concept of envelopment over time, mentioned earlier, may be more appropriate. Ecosystem development stages (see table 17) incorporate concepts of alternative stable states and developmental processes that may avoid or skip particular stages, and the possibility of regression to earlier stages in the absence of disturbance. In any case, severe disturbance always initiates a new sequence of development (envelopment) but not always a new successional sequence. Frelich (2002) proposed a cusp-catastrophe model (fig. 40) that also allows alternative stable states, regression, jumps, and surprises, with possibilities for instability and hysteresis, and that predicts development as a consequence of the interaction neighborhood effects, cumulative disturbance severity, and degree of dominance by late-seral species.

To further clarify differences among succession, development, and envelopment, *succession* is defined as “a directional change in species composition over time, where one species group replaces another” (Frelich 2002). Changes in composition of lesser magnitude than complete replacement are called “fluctuations”—changes in the relative proportions of two or more species. Thus, development sometimes is accompanied by succession, but often it is not. At least five models of succession are extant (Frelich 2002). The cyclic model



is  $A \rightarrow B \rightarrow C \dots \rightarrow A$ , and has been attributed to Watt (1947). An example is an aspen forest giving way to red maple giving way to northern hardwoods-hemlock forest followed by fire resulting in a new aspen forest. If this model is true and inexorable, as some argue, then managers can let nature take its course or harvest to emulate the principal regional disturbance and let nature take its course. The convergent model is one with one endpoint from different beginnings  $A \rightarrow C$  and  $B \rightarrow C$  and has been attributed to Clements (1936). For example, Douglas-fir being replaced by western hemlock and red alder being replaced by western hemlock. If this is true—that succession proceeds to a single climax state no matter what starting conditions are—then managers can let nature take its course, and it does not matter what is done in active management, old growth develops anyway. A less common model is the divergent model in which A can go to either B or C depending on feedback mechanisms that magnify initially minor differences (e.g., differences in soil) and perpetuate the divergence. For example, postfire aspen may go to pine, oak, or maple forest. This model calls for careful consideration of initial conditions, context, site qualities, and desired future condition in formulating how to nudge the system onto the desired trajectory. The parallel model says  $A$ -disturbance  $\rightarrow A$  and  $B$ -disturbance  $\rightarrow B$  as is common in boreal forests of North America.

**Figure 40**—General form of the cusp-catastrophe model, showing how changing disturbance severity affects the composition of stands dominated by species with negative, neutral, and positive neighborhood effects (Frelich 2002).



Managers can let nature take its course or “cut and run.” Finally, a Gleasonian individualistic model recognizes multiple pathways of succession and emphasizes continuous change without necessarily a stable endpoint. Such complexity calls for careful AIM to achieve explicit, diverse goals. Our collective empirical experience in deforestation and oversimplified monocultures and near monocultures obviates the first four models even in the long term, given past and present human activities of fire exclusion, logging, grazing, introduction of exotic forest pests and diseases, and global climate change. But the larger question is really whether in most forest management situations are we more often faced with succession or are we more often faced with development (Frelich 2002)? And, again, development is as, or more, often envelopment than it is succession. Envelopment entails adding niche dimensions and species but not necessarily loss of species. Concepts of development through envelopment always recognize that disturbance regimes are complex, interactions abound, and spatial context is important, including both landscape permeability to dispersal and larger scale neighborhood effects of sources of colonizers and ameliorators of environmental conditions. Here again, good AIM is required.

## Problems

The problem we face is not so much lack of information but a means to separate the wheat from the chaff (knowledge from ideology), a universally acceptable way of synthesizing and integrating this information to produce some basic principles to guide conservation activities (sidenote 41), and institutions capable of collaborative AIM in the present and future. Traditional ecosystem science emphasizing energy and material flows and population biology emphasizing genetic and species diversity have yet to be reconciled for conservation purposes. As with many environmental problems, social and psychological factors impede progress as much as disciplinary tunnel vision within the sciences (Dietrich 1992, Harris 1996, Kesey 1982). For example, temperaments with an “internal locus of control” prefer taking action to achieve objectives (AIM for multiple values); those with an external locus of control prefer to let things happen (let nature take its course). Field trips for empirical assessments of assumptions, experiential group learning and, especially, formal feedback from experienced professionals can provide “reality checks” (Carey et al. 1999a). Professional experience and inherent biophysical variability argues against both cookbook approaches and leav-

ing things to chance and for thoughtful application of principles. Thus, in the context of conservation of nature and the goods and services it provides, the accumulated research does provide useful information—not so much on absolute species diversity as on forest dynamics and expansion of niche space as prerequisites to high relative diversity. Complexity of niche space contributes to ecosystem resiliency and to trophic pathways supporting plant, fungal, invertebrate, and vertebrate communities, including keystone species, keystone complexes, and prey and predator complexes characteristic of old-growth Douglas-fir forests (Carey et al. 1999b, 1999c). Theories about complexity and expansion of niche space provide a substantial basis for ecological forestry and the production of a variety of goods, services, and values (Carey et al. 1999b). But, niche theory and theories of community development do not necessarily answer all pertinent questions about conservation of rare species, cryptic species about whom little is known, total species diversity, or genetic diversity. The ecological sciences offer little in the way of assurances about human behavior in resource management—fidelity, trustworthiness, scholarship, and degree of intentionality.

*The accumulated research does provide useful information—not so much on absolute species diversity as on forest dynamics and expansion of niche space as prerequisites to high relative diversity.*

## Biological and Functional Diversity

Much research on biodiversity has focused on sessile species and the roles of disturbance, equilibrium, and competition (Connell 1978, Connell et al. 1987, Connell and Slatyer 1977, Pickett 1980, Pickett and White 1985a, Platt and Connell 2003, Roberts and Gilliam 1995). Concern about lichens, bryophytes, vascular plants, fungi, and invertebrates resulted in severe restrictions on forest management on federal lands in the Pacific Northwest, despite the general consensus that disturbance underlies biodiversity (Levin and Paine 1974, Paine et al. 1998, Petraitis et al. 1989, Pickett 1976, White 1979, White and Jentsch 2001) (sidenotes 42, 43). One definition of *disturbance* is “any rapid release or reallocation of community resources”—tree fall, silviculture, and hurricanes can all increase diversity (Sheil and Burslem 2003). Of course, silviculture has been used most commonly to decrease diversity, as is common in plantation monocultures where any species other than the crop tree species are discouraged by maintaining high tree densities, mechanical destruction, and chemical applications (Carey 1998b). Another definition of disturbance is “a relatively discrete event in time that disrupts the ecosystem, community, or population structure and changes the resources, substrate availability, or physical environment” (White and Pickett

**Sidenote 39**—Creating bio-complexity in Pacific Northwest forest ecosystems includes:

- Maintaining extant species diversity.
- Restoring lost species diversity.
- Ensuring a minor deciduous component in coniferous forest ecosystems.
- Maintaining deciduous forest, meadow, and grassland ecosystems historically present in predominately coniferous forest landscapes.
- Promoting spatial heterogeneity that produces a diverse array of vegetation site types (habitat breadth).
- Promoting a diversity of foliage height profiles among the site types.
- Promoting structural diversity in tree sizes and conditions (live, decadent, dead, standing, and fallen).
- When historically common, maintaining a proportion of the landscapes in forest ecosystems of the type that resulted from catastrophic disturbances such as fire or wind.
- Protecting and promoting the growth of large trees on areas prone to mass wasting or erosion, including areas of colluvium, shallow rapid landslide potential, and deep-seated landslide potential.
- Protecting wetlands.
- Promoting a shifting steady-state mosaic of various complex stages of forest development within the landscape.
- Promoting all this heterogeneity and patchiness on a scale of 0.2 to 0.5 hectare within ecosystems and 10 to 200 hectares among ecosystems within the landscape.

1985) (sidenote 44). Disturbances localized in space and time produce patterns of heterogeneity by renewing limiting resources and permitting their use by species that are not among the dominant species (Levin and Paine 1974). Disturbances comprise continua of minor to major events and changes, endogenous and exogenous to the community, from tree fall to volcanism and from succession to climate change (White 1979). Because of disturbances, forests are structurally dynamic. Dynamic structure produces dynamic environments (chemicals, temperature, moisture, airflow, radiation, and species mix) within the community. The spatial and temporal heterogeneity that results provides the setting for evolution of life history traits adapted to persistence in heterogeneous landscapes (sidenote 45). Science suggests (1) most forests are subject to small-scale local disturbance and occasional larger disturbances, (2) many other processes unrelated to disturbance also interfere with the competitive exclusion that reduces diversity, but (3) there is widespread occurrence of forests of low diversity near younger, richer forests (Sheil and Burslem 2003).

In the late 20<sup>th</sup> century, research on vertebrate diversity emphasized island biogeographic theory, metapopulations and demographic stochasticity, dispersal and colonization processes, and, in terrestrial systems, mountaintops and forest fragmentation (Brown 1971, Gotelli 1999, MacArthur and Wilson 1967, May 1975, Simberloff and Abele 1976, Whitcomb et al. 1976). These studies assumed more-or-less static ecosystems and landscapes. More recent research emphasizes stochasticity in every process, chaos theory and Panarchy theory (dynamic systems), and neutral theories, for example, random sampling of regional species pools (Hubbell 2001). Perhaps the only generally accepted principle from that time is that there is no reason to believe that every biotope-patch-ecosystem in the landscape should be populated by every species in the regional species pool capable of living in the environment of that patch. Island biogeographic theory informs conservation biology, wherein management attempts to create systems of self-maintaining islands (reserves) and connecting corridors. An emerging generalization in conservation biology is that high levels of environmental stochasticity increase the likelihood of population extinctions. Coexistence theory, however, suggests there are circumstances in which environmental stochasticity increases the chance of persistence, depending on the interactions of life history traits and environmental variability (Higgins et al. 2000). Principles from conservation biology were used to design late-successional reserves on federal lands in the Pacific Northwest in order to provide at least temporary refuge for

species not known to inhabit simplified second-growth forests. A sole focus on preserving species populations, subspecies, and species through the creation of reserves, however, is inappropriate even if the ecological qualities of reserves could be maintained in perpetuity (Franklin 1993b). Conservation, however, must move beyond reserve strategies because it is fundamentally impossible to deal with more than a small fraction of even the known species on a species-by-species basis, most species are unknown, and, in reality, biotic communities set aside in reserves will change.

Old forests that have been set aside are not in static equilibrium; they are in a more-or-less dynamic equilibrium undergoing slow change and eventually heading toward catastrophic change, according to Panarchy theory (Gunderson and Holling 2002) and history. Without major disturbance in old-growth Douglas-fir forests, Douglas-fir eventually (on the scale of centuries) will be replaced by western hemlock, Pacific silver fir, or other shade-tolerant species (fig. 41). The new biotic community, dominated by shade-tolerant species and no longer being disrupted by the death and falling of large dominants, may become more simply structured and less compositionally diverse than the immediately preceding developmental stages. The same holds true for other forest types (Bormann and Likens 1979). For example, in the absence of intermediate disturbance, a mix of subalpine fir and Engelmann spruce will be replaced by spruce (Oosting and Reed 1952, Parish et al. 1999). Mixed-oak forests may follow any one of three developmental pathways, but all end in dominance by white oak—timing may be variable, disturbances may change successional dynamics, and exact species composition may determine the occurrence of species-specific waves of mortality (Goebel and Hix 1997).

In many forests, internal dynamics and endogenous disturbances maintain diversity (and resilience) over long periods. Sugar maple replaces yellow birch and is replaced by American beech—but falling of isolated large beech allows yellow birch to reestablish and a shifting mosaic to form within the community (Forcier 1975). Gap-phase replacement, with a mosaic of patches containing varying proportions and densities of saplings and seedlings, characterized Minnesota maple-basswood forests (Bray 1956) in a process similar to

*Disturbances localized in space and time produce patterns of heterogeneity by renewing limiting resources and permitting their use by species that are not among the dominant species.*

**Figure 41**—Western hemlock saplings grow from a nurse log. Photo by T. Wilson.





**Sidenote 40**—References on forest ecology and management:

- Allen et al. 2001
- Bergeron 2000
- Bobiec 2002
- Bobiec et al. 2000
- Bormann and Likens 1979
- Busing and White 1993
- Canham et al. 1990
- Carey 2003a
- Carey et al. 1999a, 1999b
- Clements 1916, 1936
- Connell and Slatyer 1977
- Cooper 1960
- Dale et al. 1986
- Denslow 1980
- Donnegan and Rebertus 1999
- Forcier 1975
- Foster et al. 1996
- Fox 1977
- Franklin and Waring 1980
- Franklin et al. 1987
- Franklin et al. 2002
- Frelich 2002
- Goebel and Hix 1997
- Grime 1977
- Halpern 1988, 1989
- Halpern and Franklin 1990
- Harrod et al. 1999
- Holling 1992
- Huff 1988
- Jones 1945
- Kimmins 1996
- Massman 1982
- Odum 1969, 1971
- Oliver 1981
- Oliver and Larson 1996
- Oosting and Reed 1952
- Parish et al. 1999
- Peet and Christensen 1987
- Peltzer et al. 2000
- Perry 1994, 1998
- Perry et al. 1989
- Pickett 1976
- Poage and Tappeiner 2002
- Roberts and Gilliam 1995
- Ryan et al. 1997
- Shugart 1984
- Shugart and West 1980
- Stewart 1986

that observed in plant communities in England (Watt 1947). Fox (1977) compared virgin forests in Michigan, Tennessee, Pennsylvania, Florida, and Wyoming and concluded that forests maintaining a compositional equilibrium did so through a dynamic equilibrium of patch types, changing in time and space. His results did not support the hypothesis that mosaics of spatially fixed microsites that favored one species over another would provide for species coexistence in perpetuity (Freyer and Ledig 1972). Ziegler (2002) reported similar results in her study of New York Adirondack forests and review of studies in Michigan, Pennsylvania, and New York. Nevertheless, fine-scale (within biotope) environmental heterogeneity certainly has the potential to contribute to biological diversity (Frelich 2002). Fox (1977) proposed three hypotheses about how autogenic (self-organizing) biotic heterogeneity is sufficient and important to species diversity: (1) forest tree species dynamics are the result of interactions between dominant and subordinate trees at the scale of one to a few large canopy trees; for example, a dominant plant can provide a microhabitat for a younger or smaller plant; (2) processes leading to interactions, especially those regulating density and species composition, all operate on very local scales (except seed dispersal); and (3) local regulation of species composition occurs because dominant trees interact directly with smaller plants through root and mycorrhizal grafting thereby uniquely altering the mortality and growth of various species of seedlings and saplings that are nearby. Thus, the important scale of heterogeneity was one to six or so canopy trees, or about 0.2 hectare. A duality of scales of patchiness was found in old-growth hemlock-hardwood forests maintaining a dynamic compositional equilibrium in the absence of major exogenous disturbances in the Smoky Mountains of Tennessee (Busing and White 1993). Observed canopy gaps (averaging 0.01 hectare) and physical structure (biomass, basal area) varied with these gaps; but spatial variation in composition occurred at 0.5 to 1.0 hectare reflecting the interaction of canopy gaps, microhabitat, patterns of seed dispersal, vegetative regeneration, and species interactions. These authors noted that the potential for high spatial variability of compositional parameters has long been recognized and that 0.5 hectare is the minimum area for evaluating change in physical parameters, and about 1 hectare is the minimum for compositional parameters (as both relate to trees, only).

Succession to a climax community can result in lowered diversity (at least of vascular plants and vertebrates) and lowered bio-complexity as species are lost through succession (Whittaker 1975) and even the abundance of fallen trees and standing decadent trees

decreases (Bormann and Likens 1979, Carey 1983). For example, northern hardwood forests over 200 years old in West Virginia had less structural complexity (e.g., a lack of cavity trees and lack of understory) than 80- to 100-year-old second growth nearby. Similarly, Scheller and Mladenoff (2002) found understory diversity was lower in old-growth northern hardwood forests in Wisconsin and Michigan than in even-aged second growth which, in turn, had less diverse understories than uneven-aged second growth. Differences in species composition in the understory were the result of sunlight and coarse woody debris; each age class had its own characteristic combination of understory composition, diversity, and spatial patterning. Large- and small-scale disturbances, such as hurricanes and blowdowns, respectively, promoted various aspects of understory regeneration in Southeastern hardwood forests, such as seed germination, growth of seedlings and established plants, and fruit and seed production (Kwit and Platt 2003). Mid-altitude forests on Mount Rainier that have not had a major disturbance in close to a millennium have the appearance of a much younger forest in biomass accumulation stage—most of the original dominants have fallen, and even the fallen trees are well-decayed and indistinguishable from the forest floor. Not much is known about the effect of quasi-climax stages on micro-organisms, nonvascular plants (lichens, bryophytes), fungi, and invertebrates. For example, the Quinault Research Natural Area on the Olympic Peninsula of Washington, is over 500 years old (middle-aged old growth) and dominated by very large western hemlock and Sitka spruce and large, fallen trees (fig. 42). During a 3-year study, it supported neither flying squirrels nor spotted owls (Carey 1995). It did, of course, support a great diversity of other organisms, including ferns, lichens, mosses, and liverworts (and, most likely, a high diversity of organisms in the forest floor).

In any case, it is likely the old growth of today eventually will be affected by catastrophic disturbance. The eruption of Mount St. Helens in 1980 destroyed old-growth forests set aside for spotted owls (Ruediger 1985) (fig. 43), recapitulating an earlier eruption in 1480 (Agee and Krusemark 2001). Volcanism and other geologic processes (such as those associated with glaciation and glacial recession) have shaped the landscapes in Washington and Oregon not only through basaltic lava flows, creation of pumice fields, lahars, and massive eruptions, but also long-distance ash deposition and large-scale flooding. An earthquake that caused substantial tree fall may have set the stage for a massive fire in 1700 near Mount Hood, and a sunspot minima may have led to global cooling, drought, and lightning that led to a large fire event in 1493 (Agee and Krusemark

- Swedish National Board of Forestry 1990
- Tappeiner et al. 1997
- Van Pelt and Franklin 2000
- White 1985
- Whittaker 1956, 1960, 1965, 1975
- Whittaker and Levin 1977
- Winter et al. 2002a, 2002b

**Sidenote 41**—Some basic principles of forest conservation:

- Protect highly valued rare, fragile, and threatened ecosystems.
- Maintain healthy forests across landscapes and regions, and especially near where people live and work.
- Manage forest for multiple values by maintaining legacies, by using long rotations (time between major harvests), and actively managing for biocomplexity.
- Encourage people to experience the forests and to learn about their functions and values.

**Sidenote 42**—The Intermediate Disturbance Hypothesis (Connell 1978)—“the highest diversity of tropical rain forest trees should occur either at an intermediate stage in succession [development] after a large disturbance or with smaller disturbances that are neither very frequent nor infrequent; either represents an open non-equilibrium.”

**Sidenote 43**—If disturbance underlies biodiversity, why is there such an emphasis on reserves and restricting management even in second growth? Three likely explanations:

- Many see old-growth species as “*K*-selected” species, adapted to stable conditions which are increasingly rare and thus in need of protection when they exist, as defined by the presence of such a species.
- A perverse adaptation of the precautionary principle (Principle 15 of United Nations 1972) by which any uncertainty precludes human action and proponents of action must demonstrate efficacy of action.
- Deep distrust among ecological disciplines, managers, regulators, and conservation groups based on the history of exploitation of natural resources in the United States. Jack Ward Thomas (2002), former leader of the Forest Ecosystem Management Assessment Team that provided the basis for the Northwest Forest Plan and former Chief of the USDA Forest Service, provides a review.

2001). Windstorms in 1921 and 1962 destroyed large areas of forest in western Washington and Oregon (Henderson et al. 1989). At the same time, the introduced white-pine blister rust changed the nature of Cascade old-growth forests, adding numerous large snags but decimating various species of pine. Ponderosa pine now infiltrated by Douglas-fir has increasing vulnerability to catastrophic destruction (Harrod et al. 1999).

Most old growth in the Pacific Northwest developed after catastrophic fires 300 to 600 years ago. “Natural fire rotations” appeared to be 465 years for Mount Rainier and 347 years for Mount Hood (Agee and Krusemark 2001). Fires were more frequent in the Oregon Coast Ranges in the 19<sup>th</sup> and 20<sup>th</sup> centuries (Juday 1977, Wimberly and Spies 2001). In some areas, fires reduced the prevalence of western hemlock, a species poorly adapted to fire. These fires have been attributed to the end of the Little Ice Age but were concurrent with the arrival of settlers from the Eastern United States. Both settlers and Native Americans used fire to maintain grasslands, promote grazing, and clear forest. As disturbance regimes change, patterns of forest development that follow future catastrophic disturbances may differ from the patterns of the past—the climate, natural and anthropogenic disturbance regimes, regional and local species pools, and regional and landscape environmental contexts already differ from the past.

Natural disturbances, timber harvest, and land use changes have produced an uneven distribution of old growth with large intervening areas dominated by developed areas and managerially simplified competitive-exclusion stages of second-growth forest. Landscapes dominated by competitive-exclusion stages (through their negative

**Figure 42**—Regine Carey stands between large, fallen trees on the 600-hectare Quinault Research Natural Area, an undisturbed old-growth forest of the Olympic Peninsula. Photo by A. Carey.



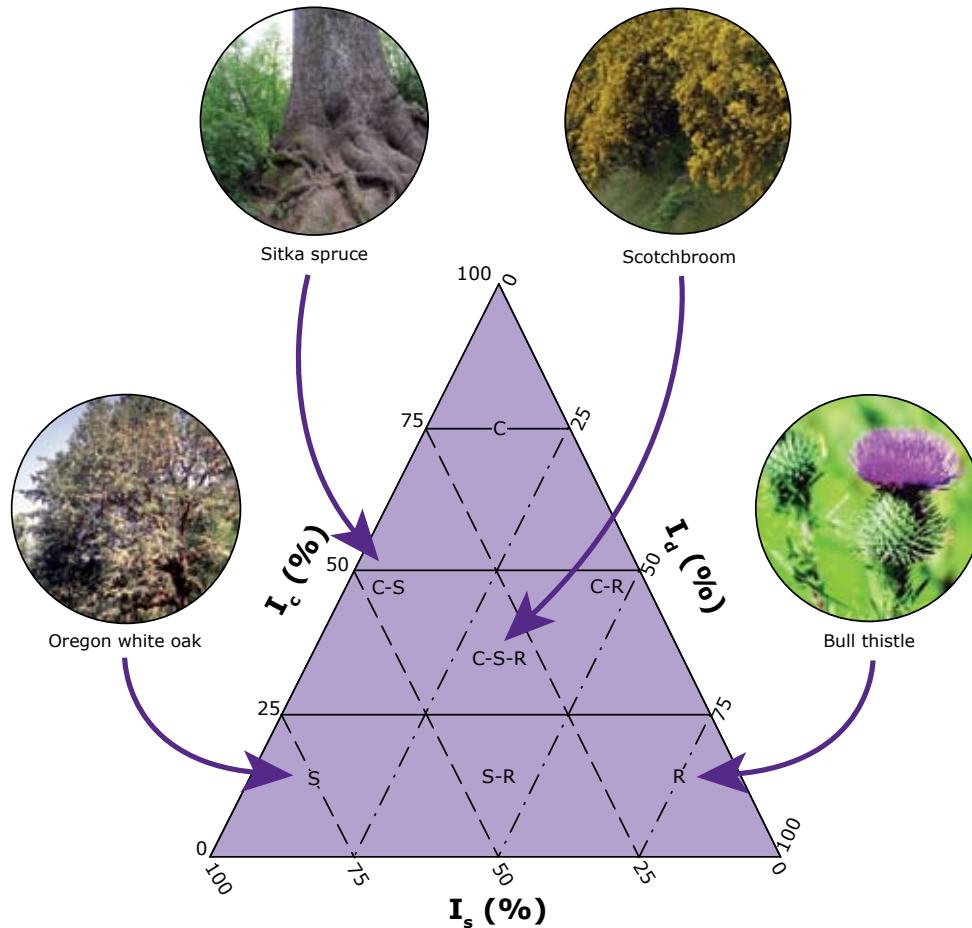
effects on dispersal and colonization processes) may prove more detrimental to nature conservation than either (1) large areas of forests destroyed by catastrophe but contain substantial embedded legacies or (2) dispersed clearcuts in landscapes of forests actively managed on long rotations in which complex stages of forest development predominate and landscape permeability is maintained (Carey et al. 1999c). Managerially simplified stands with exacerbated competitive exclusion and biomass accumulation *work against interactions* of environmental factors and the functional ecologies of species that are the foundation for maintenance of plant species diversity, not only in temperate forests but also in boreal forests (Messier et al. 1999) and diversity in plant communities in general (Grime 1977). Even productivity declines, often quickly, when biomass accumulates rapidly and a syndrome of changes leads to reduced carbon assimilation (Ryan et al. 1997).

Plants require energy, water, and mineral nutrients for growth; natural environments, however, differ in orders of magnitude in the availability of these resources. For example, light varies 100-fold from the canopy to the rain-forest floor; precipitation varies 500-fold from deserts to tropical rain forest; and nitrogen ranges almost 300-fold from the poles to the tropical rain forest (Chapin et al. 1987). The functional ecology of plants can be represented by a three-sided triangle of interaction wherein the sides represent the importance of competition, disturbance, and environmental stress in determining the strategy a plant species (or even a life history stage) takes. Grime (1977) labels these strategies as *C* (high competitive ability in stable environments), *S* (high stress tolerance with reduction in vegetative and reproductive vigor), and *R* (short lifespan and high seed production in severely disturbed environments) (fig. 44) (see table 15). In plants, *R* stands for ruderal; in animals, *r* is the symbol of a measure of reproductive ability. Animal ecologists use *K*, the symbol for carrying capacity, to represent strategies that emphasize long life, low reproduction, and survival in stable environments and *r* to represent short life, high reproduction, and adaptation to volatile environments (Hutchinson 1978, Reznick et al. 2002) (fig. 45) (see table 20). Grime's triangle, however, allows subdivision of a 3-D space to describe various life histories, and he recognizes that conditions on a biotope change through time as plants modify the environment. Species in a dynamic community exhibit a multiplicity of strategies—this multiplicity is one basis for ecosystem resilience. In forest communities, architectural adaptations allow seedlings of different species to grow under different environmental conditions (Messier et al. 1999). In other words, complex, dynamic ecosystems



**Figure 43**—Between 1980 and 1986, Mount St. Helens had several small steam and ash eruptions as a series of dome building eruptions built the 1,000-foot tall lava dome in the crater. This photo shows a dome-shattering explosive eruption that occurred in the fall of 1982. Photo by P. Frenzen.

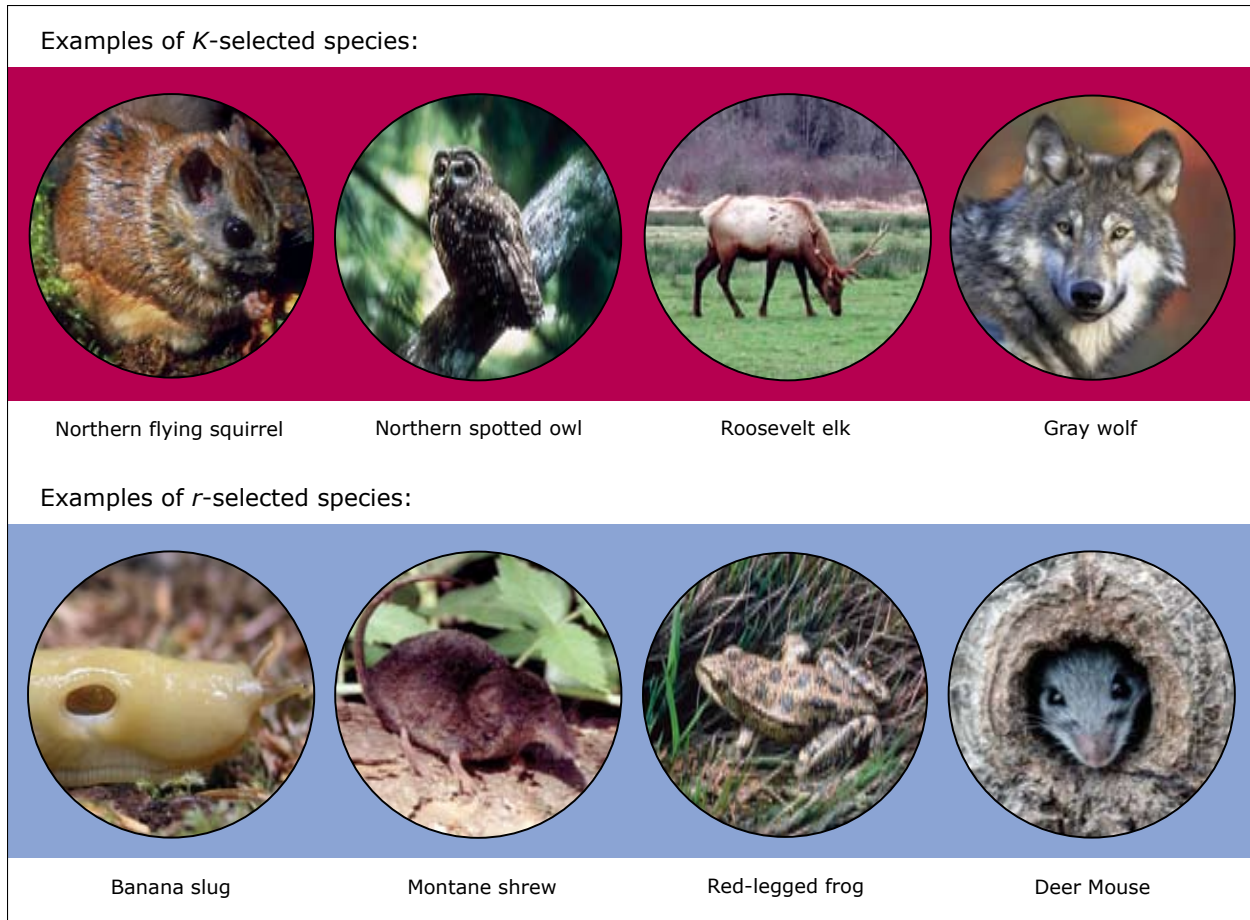




**Figure 44**—Model describing the various equilibria between competition, stress, and disturbance in vegetation and the location of primary and secondary strategies.  $I_c$ —relative importance of competition (—),  $I_s$ —relative importance of stress (-----), and  $I_d$ —relative importance of disturbance (—•—). Ruderal (*R*), competitive (*C*), and stress-tolerant (*S*) strategies along the *r*-*K* continuum (adapted from Grime 1977). Graphic by A. Wilson; oak photo courtesy of USDA Forest Service; thistle photo courtesy of USDI Bureau of Land Management; Sitka spruce photo by T. Wilson; scotchbroom photo by A. Carey.

make room for a diversity of species within the various functional groups. Adaptations include steep leaf angles (to minimize photoinhibition by allowing more light to penetrate to lower leaves), horizontal leaves (to shade competitors), and allocation of carbon to leaves versus stems and branches. Lower relative growth rates and higher allocation to roots is more characteristic of late-seral forest (species that emphasize maintenance of accumulated biomass) than early-seral forest species (species scrambling to compete for ephemeral resources). Allocating carbon to foliage and stem growth helps in competition for light; allocating carbon to fine roots enhances competitive ability for nutrients. In conifers, pines are less efficient at intercepting light (0.16 STAR [shoot silhouette to needle surface] ratio) than firs (0.28). With diminishing light and increasing shade tolerance, lateral branch growth is favored over height growth, number of whorls and interwhorl branches is decreased, live-crown ratio is decreased, and horizontal display of needles and branches is increased (fig. 46). Thus, crown architecture must achieve some balance in a complex system by performing conflicting tasks such as enhancing photosynthesis, adapting





for survival in the winter, and allowing light to penetrate to deeper layers—one result is the conical crown of many conifers (Messier et al. 1999). As trees grow, their requirements for sunlight change. The tuliptree requires 12 percent full sunlight at 1-meter tall but 25 percent full sunlight when 10 meters tall. Some conifers produce one kind of needles when growing in the shade and must produce new, different needles for growing in sunlight. Shade-tolerant trees like western hemlock and some firs and spruces can grow for extended periods in a shaded understory, awaiting release by large falling trees causing gaps, severe windstorms toppling the overstory trees, and outbreaks of defoliating insects (Messier et al. 1999). Thus, species diversity in forests is dependent upon large and small gaps and functional relationships among size of canopy opening, nature of above- and belowground environments, and the response of the seedlings and saplings of various species. Natural thinning (self-thinning) and even intentional (managerial) thinning may produce deaths of individual trees that may be relatively inconspicuous but collectively determine much of the structure, development, and dynamics of forest ecosystems (Peet and Christensen 1987, Thysell and Carey 2001a).

**Figure 45**—Examples of *K*- and *r*-selected species. Graphic by A. Wilson; flying squirrel photo by W. Colgan III; banana slug photo by T. Wilson; owl and shrew photos courtesy of USDA Forest Service; elk and mouse photos by A. Carey; red-legged frog photo by M. Jennings, U.S. Fish and Wildlife Service; wolf photo by G. Kramer, U.S. Fish and Wildlife Service.

**Sidenote 44**—Order and disorder—“To many ecologists, natural disturbances are key ecosystem processes rather than ecological disasters that require human repair” so said prominent ecologists in the public debate over removal of damaged trees after natural disturbance and subsequent attempts at restoration (Lindenmayer et al. 2004). This quotation is an especially telling statement of worldviews and a policy opinion. It is telling because these leading scientists lumped all disturbances into one group rather than distinguishing among small, intermediate, and catastrophic disturbances or between autogenic (endogenous disturbances that are normal and regular parts of ecosystem development) and exogenous forces that may be either part of a disturbance regime characterizing a region over a long term or rare geologic or weather events. The quotation, however, is prefaced to refer to “Recent large-scale natural disturbances including wildfires that burn [millions of hectares].”

What are the pertinent definitions of the key words according to the Oxford English Dictionary?

- Disturbance: an outbreak of disorder ... interference with the ... due course ... of any ... process.
- Disaster: anything that befalls of a ruinous or distressing nature ... a sudden .... calamity.
- Catastrophe: an event producing a subversion of the order or system of things ... a sudden and violent change in the physical order of things ... affecting the earth's surface and the living beings upon it....

Shugart (1984), however, emphasized that the individual attributes and population dynamics of species as they relate to competition, although important, interact with processes of facilitation and small-scale (0.1 to 0.2 hectare) gap formation, compared to even smaller gaps (0.04 to 0.08 hectare) in tropical forests. Thus, temperate forests demonstrate a regularity of pattern indicative of a multiplicity of plant-environment and plant-plant interactions; Shugart (1984) thus joined Odum (1969) in stressing self-organizing phenomena.

In summary, research has provided useful and important insights about the processes of plant community development in forest ecosystems, mechanisms leading to and maintaining biological diversity, and the ramifications of large-scale anthropogenic and natural disturbances for landscape function. As a practical matter, individual studies and individual syntheses generally are narrowly focused. This narrow focus, at times, has resulted in emphasizing reductionism at the expense of holism (Barbour 1996). Narrow, intradisciplinary foci have led to unnecessary polarization of worldviews among scientists and among conservationists, including false dichotomies of management by preservation versus intensive management for commodities and maximum economic return on investment (sidenote 46). Such dichotomies cloud the view of the bigger, long-term picture of conservation of nature. Maintaining these dichotomies, however, is a choice, not inevitability. We have the potential collectively to develop the holistic, integrated worldviews that are needed for effective conservation. It seems that an emphasis on ecological processes and system dynamics underlying forest development and maintenance of biodiversity offers more promise than a focus on specific structural elements, particular endpoints of structural development, particular patterns of a limited set of idealized “structural stages,” rare species, absolute species diversity, or leaving recovery of ecosystem and landscape function to time and chance alone.

## Processes Underlying Forest Development

Ironically, it is the history of environmental fluctuations, natural disturbance processes, and subtle, often indirect, human impacts that shape the characteristic structure, composition, and ecosystem processes of old growth (Foster et al. 1996).

Ecologists have been arguing about the nature of virgin forests since 1924 (Jones 1945). Jones's review documented common ages

of dominants around 300 years old in beech forests in Europe, 350 years in pine forests of Asia, 350 years in hemlock forests of eastern North America, and with the oldest and largest trees (750+ years for several species) in California, Oregon, and Washington. Coastal British Columbia trees, however, rival those in other parts of the Pacific Northwest. Northern coniferous forests seemed smaller in stature (of course, we now know the oldest trees may be quite small evergreens in xeric parklands and woodlands). He noted that there were many types of structure in virgin forests: even-aged, single-storied, uniformly closed-canopy forest; two or more ages in either separate stories or separate groups; all ages present, intimately intermingled, with irregular open canopies; all ages in a mosaic of even-aged groups; and all ages present with a regular, uniform canopy and a storied structure. The most common structure seemed to be dominance by old stems, but with a wide range of ages, and two to three canopy gaps per hectare. Fire seemed of supreme importance in the origination of natural forests but “tempest,” fire, root-rot, heart rot, insect attack, and disease produced various phases of senescence, or large amounts of decadence. Climatic changes brought about “re-adjustment” of dominant species. But in all cases, the forests were in dynamic equilibrium with individuals dying and being replaced by individuals of other species with compensatory changes taking place elsewhere; in other words, the shifting-steady-state mosaics later described by Fox (1977), Bormann and Likens (1979), Shugart and West (1980), Pickett (1980), Oliver (1981), and Franklin et al. (2002). Not too bad for the turn of the century. A more recent review of old growth in temperate and boreal forests of Europe (Nilsson et al. 2003) found that the older canopy trees were 200 to 300 years old even in forests without significant harvests for over 2,000 years. Large (more than 70 centimeters) d.b.h. trees numbered 10 to 20 per hectare (40 to 60 square meters basal area per hectare) depending on forest type and site, with 10 percent of all standing trees dead, and with snags composing 30 percent of dead tree volume. These deciduous and mixed deciduous-conifer old-growth forests were judged to be similar to those in the Eastern United States. But the authors found that old growth in the Pacific Northwest had older, larger trees, fewer trees per hectare, but with greater basal area and total volume of trees and with a larger proportion (30 percent) of standing trees dead (fig. 47).

Development of forest ecosystems from reorganization through old growth is an interacting complex of processes (some of which counteract one another) that lead to characteristic trophic structure (food webs) and material cycles (Beckage et al. 2000, Bergeron

Thus, there are disturbances, localized or widespread, mild or intense, acute or chronic; and there are catastrophes—acute, intense, and widespread. Some disturbances are ecosystem processes (endogenous to the ecosystem) and some are exogenous forces destructive of the established system, its processes, and its biological diversity. Human reaction to disturbances differ with the intensity, acuteness, and distance from the observer. Policies on how to deal with disturbances are by definition based on human worldviews and human values, not “objective” science; they are often formulated hastily during and immediately after major disturbances. The scientists propose “... to formulate salvage harvest policies before major disturbances ... exemption of [certain] large areas ... [and] good planning should guide the timing and intensity of salvage harvesting.”



**Figure 46**—A western hemlock’s unique lateral branching allows it to survive in the shadow of larger conifers. Photo by A. Carey.



**Sidenote 45**—Generalities from studies of disturbance (White and Jentsch 2001):

- Disturbance is a primary cause of spatial heterogeneity and influences competition, environment, and substrate and resource availability.
- Disturbance is crucial to biotic diversity and an important evolutionary force that produces both complementarity and redundancy in biota that promote ecosystem stability.
- Disturbances shape communities to be resilient in the face of disturbance through functional redundancy.
- Humans are a major source of minor and major environmental disturbances and influence the rate and intensity of natural disturbances, often to the detriment of biological diversity.
- Disturbances differ with topography, climate, and soil development.
- Disturbances differ with feedback and interactions—disturbance can promote further disturbance.
- Disturbances differ in heterogeneity, patch size, intensity and severity, and legacies.
- Disturbances differ in space and time.
- Systems respond to disturbance in three ways: threshold responses, scale-independent responses, and continuous responses.
- Species and communities differ in their responses to different disturbances.

2000, Odum 1969). Development after catastrophic destruction and reorganization usually (1) is an orderly process that is reasonably directional and therefore predictable, (2) results from modification of the physical environment by the community, and (3) culminates in a stabilized ecosystem in which biomass and symbiotic function constitute a strategy of homeostasis, but not necessarily a classic old-growth condition (see table 17). The reorganization phase itself is highly variable in nature and length—in the Pacific Northwest regeneration of trees in sufficient number to create a forest can take 30, 50, or more years after a catastrophic fire (Huff 1995, Poage and Tappeiner 2002, Winter et al. 2002a), and spatial heterogeneity can be very high owing to legacies and differences in seed sources.

In late-seral forests, shifting-steady-state mosaics (dynamic patches) (Pickett and White 1985b) provide for a degree of dynamic equilibrium through gradual changes in space and time both within forest ecosystems and across forested landscapes. Various exogenous disturbances and environmental heterogeneity within the biotope interact with a variety of ecological processes to promote biocomplexity within the ecosystem. Without disturbances (exogenous and endogenous), the development of biocomplexity will be truncated. Biocomplexity within the biotic community develops as patches begin to differ in character, rate of change, and type of change over time more than would be expected on a uniform site without successive disturbances. Thus, forest development in lowland, carefully cultured plantations is likely to be quite different than in upland heterogeneous sites subject to various minor and intermediate exogenous disturbances but little intensive culture.

It is essential to effective management to realize that the catastrophic destruction and the legacies it generates set the stage for the development to follow. Different disturbance regimes set different stages (Frelich 2002). The effects of timber harvesting and other human activities may be quite different from those of most natural disturbances in the case of clearcutting and somewhat similar in the case of partial cutting (sidenote 47). In numerous locales in North America, including the Capitol Forest of Washington (*Capital Forest: The Forest That Came Back*, Felt 1975), unregulated timber harvesting led to deforestation and erosion. In both western Oregon and Washington in the 20<sup>th</sup> century, forests destroyed by wildfire reburned; for example, the forest destroyed by the Tillamook Fire of 1933 burned again in 1939, 1945, and 1951, probably as a result of human activity (Agee 1991). Potential for reburns can be high in early succession to Douglas-fir on moist sites, but once crowns close, potential for fire decreases. Forests may then develop for another 200 to 500 years

with their character conditioned by a specific catastrophic disturbance and the legacies it left. If the forests go undisturbed for 700 to 1,000 years, Douglas-fir will be lost, and Pacific silver fir and western hemlock will be the primary seed sources of a new postfire regeneration. In more mesic sites in the Oregon Cascades, partial burns after canopy closure may occur every several decades or centuries; forest development follows a different course, with a mixed dominance of Douglas-fir and other species maintained. And in dry sites in southwestern Oregon, partial burns are common; true firs and hemlock may be rare and multiple age classes of Douglas-fir and hardwoods such as madrone or tanoak may be common. Thus, the importance of biological legacies and disturbance regimes and their contributions to reforestation has been recognized since Clements' work on forests in 1916, the Hubbard Brook forest experiments of the 1960s, and reforestation of the area around Mount St. Helens in the 1980s (Franklin and MacMahon 2000, Franklin et al. 2002).

The most important ecological insight from studies of natural boreal, montane, and temperate coniferous forests and tropical forests is that forest ecosystems are highly varied and dynamic in



**Sidenote 46**—False dichotomies—A major wildfire in southwestern Oregon ignited a firestorm of countervailing philosophies among prominent scientists that precluded intentional analysis and planning (Lindenmayer et al. 2004, Sessions et al. 2003, Thomas 2002). Should the forests have been managed to reduce fuels before the fire? Should damaged timber be salvaged for its economic value and jobs? Should damaged timber be salvaged to underwrite restoration efforts? Does salvage cause damage rather than speed recovery? Should nature be allowed to take its course? Should the reorganizing forest be managed to speed recovery of late-seral forest conditions? These questions are less about science and more about value and purpose. The most pertinent questions are why, where, when, how, how much, in what manner, for what specific purpose, at what risk, with what uncertainty, for what collective result?

**Figure 47**—Old-growth trees on the Olympic Peninsula—some living, some dead. Photo by T. Wilson.



**Sidenote 47**—Second-growth forests may differ markedly from one another, even in the same region. Influences to a forest include:

- Site characteristics—elevation, slope, aspect, homogeneity of topography, soils, site fertility, wetlands, rock outcrops, and many other physical features, including site modification by fire or erosion
- Amount of legacies retained from the previous forest
- Time since reorganization
- History of disturbance and management after reorganization
- Amount and scale of spatial heterogeneity
- Stage of forest development
- Species and life-form diversity
- Resilience and potential for development following disturbance
- Health, presence and effects of common forest diseases and pests
- Overall biocomplexity

structure and composition and in the patterns they form on landscapes (Foster et al. 1996). All ecosystems studied have exhibited some responses to past human activity. The rate of change in disturbance processes and associated ecosystem attributes was greatest in the historical (not contemporary) period, and many present-day old-growth forests comprise anomalous or unique assemblages relative to those of their historical counterparts. Another way of saying this is that those old-growth forests that survived when the majority were destroyed may have been unusual in their character, their location, or both. Old-growth forests today represent adaptations to past environments, including human activities, and are not necessarily as well-adapted to future environmental conditions—but might well be highly adaptive, owing to their biodiversity. Old-growth forests in the Pacific Northwest at best represent less than 6,000 years of existence in a time of continuing climate change (Brubaker 1991). Thus, their adaptiveness probably is not a result of tight coevolution of species over the long term in a stable environment but rather successful self-organization that allowed accumulation of biomass and biocomplexity. Across North America, human activities on regional to local scales with various direct and indirect impacts on ecosystems, altered climate and cloud and precipitation chemistry, eliminated native species (e.g., passenger pigeons, deer, elk, moose, and beaver—all of which influence some forest processes), introduced exotic species, including pathogens (e.g., chestnut blight, Dutch elm disease, beech bark disease, hemlock woolly adelgids, white pine blister rust), and changed fire regimes. Thus, to be effective, strategies for the preservation, management, and restoration of old growth or for the conservation of nature in general must be based on acceptance and anticipation of change (Foster et al. 1996). Comparisons of natural forest and second-growth forests deliberately shaped by silviculture have repeatedly illustrated that conventional silviculture does not mimic natural disturbances, promote the same developmental processes that occur naturally, or produce resilient ecosystems with high capacity for adapting to change (Bergeron et al. 1999, Carey 2003a, Price et al. 1998). Not only is a new forestry needed, but managers must look beyond stands and landscapes to the region and to the globe if planning is to be reasoned.

## Exogenous Disturbances

Earth is first and foremost a “fire planet” in which an oxygen-rich atmosphere and carbon-based living organisms

regularly conspire to create conditions that make combustion and widespread conflagration a recurrent, indeed inevitable fact of life (Cronon in Pyne 1997: ix).

When people think of forest fires, they usually think of wild (unplanned and unmanaged) fire. But, the history of human use of fire is long and astounding. Fire has been used purposefully, indiscriminately, commonly, and frequently. Much of the Earth's biological diversity has resulted from the presence of people and their use of fire. Fire also provided the means by which people claimed nature, rendered it habitable, and refashioned it into pastoral and agricultural landscapes worldwide (Pyne 1997). Human use of fire over the ages purposefully shaped the subsequent biotic communities in North America, from the southeastern pine parklands to the interior prairies of Kentucky to the prairies and oak woodlands and savannas of western Washington (Pyne 1997, Thysell and Carey 2001b, Tveten and Fonda 1999). But conversion of forest to grazing and agricultural purposes was not the only use or cause of forest fires. The interaction of geologic events, climate change, natural forest fire regimes, indigenes' purposeful use of fire, accidental and malicious use of fire by indigenes and settlers from the Eastern United States, fires resulting from careless logging practices, fires resulting from the construction and operation of railroads, forest management and fire exclusion, and arson reshaped many forested landscapes and their biotic communities, particularly in the inland Northwest, but even in the Pacific Northwest (Pyne 1997).

Long before settlers from Europe arrived, indigenous peoples managed landscapes and maintained particular biotic communities across North and Central America with deliberate use of fire (Krech 1999, Pyne 1997, Wright 1992). Settlers from the Eastern United States found the landscapes managed by indigenous peoples in the Pacific Northwest (Oregon's Willamette Valley and Washington's Puget Trough) particularly attractive. The first U.S. settlers in Washington usurped, for their own agricultural purposes, the prairie, woodland, and wetland mosaics managed with fire by the Nisqually people in the Puget Trough. The nearby Skokomish people of the eastern Olympic Peninsula maintained shrub parklands dominated by Douglas-fir for winter grazing by Roosevelt elk and perhaps for berries (fig. 48) and basket material; there is evidence (prairies up to 1,200 hectares) that people on the west side of the peninsula did likewise. Coastal indigenes also intensively managed estuaries for root and tuber production (Deur 2002, Turner and Cocksedge 2001). Yakama people (and perhaps the Cowlitz,

*To be effective, strategies for the preservation, management, and restoration of old growth or for the conservation of nature in general must be based on acceptance and anticipation of change.*



**Figure 48**—Red and blue huckleberry can be found growing side by side on the Olympic Peninsula. Photo by T. Wilson.

Nisqually, and Puyallup) burned subalpine forest on Mount Rainier to push back the forest and maintain parklands for their berries and support of deer, elk, and mountain goats. The Calapooya people of the interior valleys of western Oregon used fire to maintain prairies and oak woodlands and to shape the adjacent conifer upland forests of the Coast and Cascade Ranges, perhaps again for grazing by wild ungulates, oak woodlands, and parkland berry fields. Numerous plants that once thrived in the managed natural-cultural mosaics of the Pacific Northwest Amerindian cultures are now threatened by the subsequent introduction of exotic plants and the continuing land use changes of an ever-growing U.S. population (Carey 2002a, Thomas and Carey 1996, Thysell and Carey 2001b). Farther south in the Sierra Nevada, the Nisenan community managed the forest with fire for 2,000 years (along with lightning-ignited fires in drought years) for hunting grounds and cordage until they were decimated by introduced malaria and dislocated and persecuted by gold miners in the mid-19<sup>th</sup> century (Stephens and Collins 2004). Subsequent mining, grazing, logging, and, finally, fire suppression produced markedly different fire regimes and forest conditions. Now conservationists debate about desirable future conditions for these forests, with increasing doubt about natural variation concepts based on historical ecology.

Of all the temperate and tropical forests of North and Central America, it is likely that the low- to mid-elevation old-growth forests of the Pacific Northwest are among the least affected by indigenous peoples (Pyne 1997). Northwestern coastal forests with high annual rainfall in fall, winter, and spring are relatively fire-resistant, and the trees grow too large to be razed by stone-age people or even preindustrial iron-age people. In any case, dry summers and lack of domesticated grains and root vegetables limited opportunities for farming; indeed, it appeared carbohydrates may have been more limiting to Pacific Northwest indigenes than protein or fat, given abundant, salmon, deer, and elk and the considerable time they spent harvesting and drying berries, camas roots, and tubers of wetland plants. Much of the temperate forests of the Eastern United States and forests in Central America had been changed into croplands, woodlands, and savannas well before the arrival of European settlers. Fires, however, were rare in northern New England, where windstorms, small and large, were major stimuli of natural change (Ziegler 2002). Fire-return intervals were 1,000 years or more in the Adirondack Mountains of New York. The spruce-beech-fir-hemlock-birch forests of northeastern Maine were in a climax stage in the early 19<sup>th</sup> century with evidence of a natural fire-return interval

of 800 to 1,150 years (tree lifespans less than 300 years) (Lorimer 1977). But just to the south, fires were common in western Maryland old-growth oak forests from 1615 to 1958—42 fires with a return interval of 8 years (Shumway et al. 2001). Catastrophic fire-return intervals in the Pacific Northwest were long as well but variable. For example, fire frequency in mountain hemlock forests of southwestern British Columbia, as well as in much of the Pacific Northwest, varied continuously over the last 11,000 years, linked to climate change via large-scale atmospheric patterns (Hallett et al. 2003). There has been continuous climate change in North America since the last major ice age (Pielou 1991), even the last 2 million years (Tausch et al. 1993). Catastrophic fire-returns intervals have been as short as 150 to 300 years in wet mountain hemlock forests, and 230 to 240 years in the Oregon Coast Range and in southeastern British Columbia montane spruce forests, and as long as 1,200 to 2,400 years in coastal British Columbia mountain hemlock and western hemlock forests (Hallett et al. 2003). About 20 percent of very wet hypermaritime forests and very wet maritime forests of Vancouver Island, British Columbia, have gone more than 6,000 years (up to 12,000 years) without fire; forest on terraces have gone 4,400 years without fire, forest on hills have gone 740 years without fire, but all forest on south-facing hills all burned within the last 1,000 years (Gavin et al. 2003). These almost fire-free forests are marked by ubiquitous gaps and tree replacement rates of 35 to 390 years. Otherwise, fire is nearly universal in western North America, but marked by heterogeneity in regimes and heterogeneity internal to individual fires (Lertzman et al. 1998, Wimberly 2002) (fig. 49). There is substantial variability in fire intensity even in the absence of underlying ecological or physical patterns (Wright and Agee 2004). Even modest temporal variability in fire frequency can induce significant variation in forest age structure over time. Openings caused by fires differ from a low of 0.03 to 0.3 hectare in southwestern ponderosa pine forests to 0.8 to 2.7 hectares in red fir/Douglas-fir forests to more than 3,200 hectares in Oregon mountain hemlock and to more than 10,000 hectares in conifer forests in Idaho, Washington, Oregon, and Alaska (Agee 1998). Fire severity ranges from high in subalpine fir, Pacific silver fir, western hemlock, and Douglas-fir forests; to moderate in mixed-conifer/mixed-evergreen, dry Douglas-fir, and red fir forests, and low in mixed-conifer, ponderosa pine, and oak-woodland forests. In other words, fire severity is highest where it is wettest and coolest, fires are infrequent, and extreme weather sets the stage. And fires are lowest where it is warmest and driest and vegetation is adapted to frequent fires; but the extent and severity of

forest fires is not necessarily well correlated. Thus, fire regimes can be characterized as low-severity/nonlethal, mixed-severity/moderately lethal, and high-severity/lethal. For example, in unlogged ponderosa pine-Douglas-fir forest in the Colorado Front Range, evidence was found of light fires in 1534, 1686, 1700, 1775, 1841, and 1963 and moderate-intensity fires in 1587, 1631, 1723, and 1851. The historical landscape was less densely forested than today; forests had low densities of trees, open canopies (10 to 30 percent canopy cover), and openings over 15 to 25 percent of the landscape; some dominant trees persisted for 500 to 600 years. However, at higher elevations in Colorado (2,100 to 3,000 meters in Rocky Mountain National Park), crown fires were part of the natural disturbance regime (Ehle and Baker 2003). Of 103 historical disturbance events, 97 percent were due to fire and 7 percent of those were high-severity fires (70 percent were low-severity fires). At least one crown fire occurred within 300 years in seven of the nine plots studied. Crown fires produced dense even-aged stands that, because of subsequent surface fires, developed into less dense uneven-aged stands after 200 to 300 years. Thus, the fire ecology of high-elevation ponderosa pine forests in Colorado is somewhat different than that in the lower elevation Front Range and those in the Southwest. Historical fire produced a mosaic landscape in Colorado just as it did in the Oregon Coast

**Figure 49**—A forest fire in Montana's Bitterroot Valley during the 2000 fire season. Photo by J. McColligan, Alaska Fire Service, Bureau of Land Management.





Ranges (Wimberly and Spies 2001) despite differences in intensity and frequency. But logging, grazing of livestock, fire suppression, and urban encroachment have produced young second-growth forests that are densely stocked and that have excessive fuel loads resulting in unusually severe fires and widespread insect epidemics (Kaufmann et al. 2003) (fig. 50). In the 58-million-hectare interior Columbia River basin (46 percent forested), physiographic diversity, the interaction of three major air masses, and summer drought produces at least 22 forest types with fire-return intervals ranging from 6 to 419 years (with a mean of 51 years) (McKenzie et al. 2000b). In addition to seasonal and annual droughts, fires were correlated with multiyear climatic signals, such as the Pacific decadal oscillation, until the 20<sup>th</sup> century when wet-weather decades, logging, fire suppression, and perhaps changes in burning practices of Native Americans, reduced fire frequencies (Hessl et al. 2004, Wright and Agee 2004). Spatial patterning in ponderosa pine forests in the Columbia basin differs with site—cool, dry grass and warm mesic sites have smaller clumps and higher densities of trees than hot, dry, shrub lands that exhibit strong clumping historically with limited seedling establishment (Harrod et al. 1999, Wright and Agee 2004). Larger openings between clumps of trees may produce increased fuels for fire, which when low in intensity, may favor seedling establishment.

**Figure 50**—The effects of pine bark beetle on a forest near Fort Collins, Colorado. Photo by A. Carey.



Historically, these forests had patch sizes of 0.09 hectare (with a range of 0.005 hectare in mesic sites to 0.2 hectare in xeric sites) similar to 0.06 to 0.13 hectare in the Southwest and 0.02 to 0.29 hectare in eastern Oregon. The density of residual large trees (greater than 50 centimeters d.b.h.) was highly variable, 5 to 9 trees per 0.5-hectare plot (a maximum of 19 trees per hectare), whereas fire exclusion, grazing, and timber management have produced more homogeneous stands with 50 trees per hectare, highly vulnerable to bark beetle attack and crown fires. Presettlement forests were at low risk to crown fire and bark beetle attack, suggesting a relatively fine-scale pattern of 0.1 to 0.3 hectare would be an appropriate grain size for managed ponderosa pine mosaics. Land use changes and management practices have affected these forests as profoundly as those in Colorado (Harrod et al. 1999, Tiedemann et al. 2000). There is no such thing as a forest free of fire, and when management has excluded fire then the option of “letting nature take its course” no longer constitutes a sustainable conservation strategy (Agee 2002). Climate, environment, and people interact to produce both disturbance regimes and forests of varying character.

The lack of upland forest destruction by indigenes and long fire-return intervals do not mean that Pacific Northwest forests developed free of human influence. Significant variation in the climate of the United States was due to human activities in Europe and Asia. Eurasians had destroyed their own forests relatively rapidly 5,000 to 8,000 years before the present, beginning with slash-and-burn agriculture, then irrigation of rice fields, followed by development of iron technology, use of charcoal for fuel, harvests of timber for ship building, and urban development—even to the point of affecting climate through agricultural production and loss of forests (Ruddiman 2003). This period of Eurasian deforestation and induced climate change coincided with the establishment of “modern” forest types in the Pacific Northwest (Brubaker 1991). Germans invaded Slavic countries to get wood in 1,000–1,100 AD (Farrell et al. 2000). Great Britain denuded Ireland of trees for naval purposes; reforestation is beginning only now. Even European boreal forests were destroyed (Berglund 1991). Of course, boreal forests are fire-adapted forests, with decadal surface fires and crown fires by the century, depending on degree of drought, dry lightning, and wind, even without human use of fire (Pyne 1997). Thus, boreal forests are more easily burned than Pacific Northwest forests. The only extant temperate forest in Europe that has a natural stand structure is the Białowieża Primeval Forest (primarily a *Tilio-Carpinetum* mesic forest) in Poland (Bobiec 2002). As in most old-growth temperate forests, this

forest shows an irregular distribution of legacy (or pioneer cohort) trees; large amounts of coarse woody debris (87 to 160 cubic meters per hectare) and decadence (25 percent of total aboveground biomass); spatial heterogeneity or patchiness; complex avian and mammal communities; relictual invertebrates, fungi, and epiphytic flora; and evidence of successive disturbance by fire, storms, and insect outbreaks. The destruction of European forests had ramifications for Pacific Northwest forests by stemming glaciation (sidenote 48) and, when bubonic plague decimated European populations, it led to reduced carbon dioxide emissions, reforestation, carbon sequestration, and to the Little Ice Age (1300–1900 AD)—the climatic period in which the contemporary Pacific Northwest old growth developed. Undoubtedly there were differences in Pacific Northwest climate, disturbance regime, and the subsequent development of structure and composition of these forests from what would have occurred if deforestation followed by plague had not occurred in Europe. For example, palynological review of 5,000 years of disturbance and vegetation change revealed only two major fires, but a rise in western hemlock pollen began 1,000 years ago in the vicinity of the Queets River on the western Olympic Peninsula, in response to a cooling climate during the Little Ice Age (Greenwald and Brubaker 2001). The history of direct and indirect interactions of people, prevailing climate regimes, continuous climate change, and rare geologic and weather events suggest landscape patterns of the past are not of particular value in designing landscapes of the future. The profound impacts of land use change and forest management of the last century suggest that, even if climate was predictably cyclic and modern people could be removed from a region, it is unlikely we could re-create the biotic communities of the past (Carey 2003a, 2003c; Tiedemann et al. 2000).

What is known for certain is (1) climate will change; (2) human populations and their impacts on local, regional, and global environments will increase for the indefinite and foreseeable future; and (3) burgeoning populations and environmental degradation in developing countries (as happened in Europe historically) will have significant social, economic, and environmental impacts not only in the Pacific Northwest, but also around the globe. The Pacific Northwest is downwind of China. Already we receive substantial deposits of Gobi Desert dust. China's rapid economic development portends huge increases in burning of fossil fuels; there will be environmental ramifications in the Pacific Northwest. Furthermore, low- to mid-elevation forests of the Pacific Northwest are subject to infrequent, unpredictable catastrophic fires, major windstorms, earthquakes,

**Sidenote 48**—“We are an Ice Age creation but a fire creature” (Pyne 1997).

tsunamis (Everham and Brokaw 1996, Henderson et al. 1989, Sinton and Jones 2002, Stathers et al. 1994), and volcanoes (Franklin and MacMahon 2000). Climatically based disturbance regimes will change. Biological disturbances are becoming of increasing importance. From 1920 to 1989, spruce beetles killed most of the spruce on 850,000 hectares in south-central Alaska; in the 1990s, spruce beetles killed spruce on another 800,000 hectares (Ross et al. 2001) (fig. 51). Interior Northwest forests now seem particularly vulnerable to catastrophic loss owing to interactions of insect pests, disease, and fire as a result of complex historical contingencies including land use changes, drought, fire exclusion, grazing, introduction of exotic species, and homogenizing timber management. In other regions of North and Central America, fire, hurricanes, and tornados regularly cause catastrophic destruction of forest. Continent-wide, the threat of forest destruction (or at least substantial modification) from introduction of exotic diseases and insect pests and spread of existing ones, such as Swiss needle cast, sudden oak death fungus, Asian longhorned beetles, European pine shoot beetles, and emerald ash borers, is not only real but a major event is probable. Hemlock wooly adelgids are causing severe problems in the 11 eastern states comprising the range of eastern hemlock. The worst recorded outbreak of southern pine beetles affected 4.9 million hectares in 2001 and 5.7 million hectares in 2002 (USDA Forest Service 2003). Mountain pine beetles have shown a dramatic increase from 344,000 to 647,000 hectares affected in 2002. Spruce beetles have increased in Arizona, Colorado, Montana, Utah, and Wyoming. Unregulated logging continues in underdeveloped countries, as does conversion of native forests to plantations of exotic species and forest land to agricultural uses. Thus, in our domestic policy, it may be beneficial to emphasize conservation and general sustainability. In our foreign policy, it may be beneficial to emphasize sustainable development and social justice. But, in the least, we must manage our forests such as to maximize their capacity to adapt to an ever-changing environment and allow us to move toward a self-sustaining future.

**Figure 51**—Adult spruce beetle. Photo by D. McComb, USDA Forest Service. Spruce beetle damage. Photo by W. Ciesla, Forest Health Management International. An adult spruce beetle with eggs. Photo by E. Holsten, USDA Forest Service.



## Endogenous Disturbance

After catastrophic disturbance, the developmental endpoint in Pacific Northwest Douglas-fir forests is the “pioneer cohort loss stage” at 800 to 1300 years. Strong spatial patterning (horizontally and vertically) is characteristic of these forests (Franklin et al. 2002). This patterning occurs despite apparent marked differences in degree of stocking in the early stages of forest development (Poage and Tappeiner 2002; Winter et al. 2002a, 2002b). Some of this patterning is the result of occasional (say decadal to multidecadal) small- to intermediate-scale exogenous disturbances such as fires, thunderstorms, rainstorms, windstorms, ice storms, snowstorms, disease epidemics, and widespread insect outbreaks. But significant patterning is a result of various endogenous processes including density-dependent mortality owing to competition (suppression of subordinate trees by dominant trees), endemic disease spread, and insect attack; density-independent accidents and tree fall; symbioses and local biotic interactions; local flooding and mass-wasting (landslide) events; and other local environmental changes. Tree death from heart and root rots is common (Carey et al. 1996b, Hennon 1995, Holah et al. 1993, Huff 1995, Parks and Shaw 1996, Thies 1999, Thies and Sturrock 1995). Root rots can become epidemic in the first 50 years of forest development, reducing stem density, creating gaps, and promoting understory development (Thysell and Carey 2000). However, competition is the major cause of death in most conifer forests under 100 to 150 years old (Carey et al. 1999b, 1999d; Franklin et al. 1987). Heart rots play multiple ecological roles in forests from providing a substrate for excavation of cavities by woodpeckers (fig. 52), to hollow trees for bears and Vaux’s swifts, to weakening boles, contributing to bole breakage, tree fall, and gap formation. Bole breakage is a leading cause of death of trees in older forests. Snapping of boles and standing death constitute more than 75 percent of gapmakers in the Pacific Northwest; uprooting accounts for 21 percent (Lertzman et al. 1996). Mechanical damage by falling trees to other trees accounts for 15 percent of mortality in old forests (Franklin et al. 1987). In interior (Idaho and Montana) western hemlock forests, rots can become excessive in 100 to 120 years; in British Columbia, decadence in western hemlock prevails at 225 years. In old-growth hemlock-spruce forests, more than 30 percent of the gross volume of wood is affected by rot; 50 percent of the wood volume in old western redcedar trees is rotten; 80 percent of old-growth Douglas-firs have heart rot (Hennon 1995). Heart rot fungi infects vigorous Douglas-fir at an early age (say 50 years) through small twigs and eventually leads

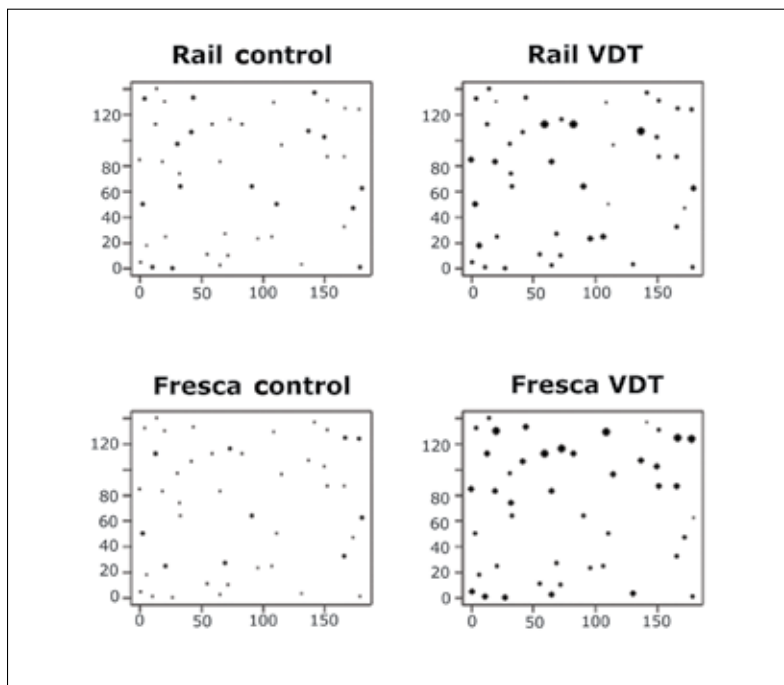


to tree death more than 150 to 170 years later contributing to loss of the pioneer cohort of Douglas-fir and their replacement by shade-tolerant species beginning at 300 to 400 years in the life of the forest. Canopy trees dying while standing, boles breaking, and uprooting are common causes in many forests of North and Central America, producing a spatial-temporal mosaic of patches in different stages of recovery following the disturbance created by the falling tree (Putz et al. 1983). As a result of this variety of noncatastrophic exogenous and small- to intermediate-scale endogenous disturbances, a variety of canopy patterns can form, ranging from continuous closed canopy punctuated at 40 to 150 meters by 1- to 2-meter-wide low-density gaps (20 percent open) to 2- to 6-meter-wide, low-density gaps (40



**Figure 52**—The importance of heart rot—a pair of pileated woodpeckers nest in an excavated tree cavity. Photo courtesy of USDA Forest Service.

percent open) in young forests to 2- to 30-meter-wide gaps (more than 60 percent open) 40 to 110 meters apart in old forest (Bradshaw and Spies 1992). In southwestern Oregon, 50 percent of old forest had less than 50 percent canopy closure, indicating a gap; these gaps were 70 to 80 meters apart (Carey et al. 1999b). In coastal British Columbia, as forests age, canopies become more open and more heterogeneous (Frazer et al. 1998, Hedberg and Blackwell 1998); 56 percent of old forest area is affected by canopy openings, with 30 percent of the area actually in gaps (Lertzman et al. 1996). Gaps are generally less than 0.1 to 0.2 hectare (Carey et al. 1999b, Spies and Franklin 1989, Spies et al. 1990). Additional patterning is caused by topoedaphic features, especially wetlands and small streams (Carey 1988). The influence of canopy changes on microclimate varies with gap size, season, and degree of understory and midstory development (Benton 1998, Gray et al. 2002). Variation can be extreme in large gaps, with hot dry conditions at the northern end (greatest exposure to sun) and cool, moist conditions at the southern end, which may remain shaded by the adjacent trees. Research has shown that experimentally induced fine-scale canopy heterogeneity can result in a patchy understory microclimate that maintains the range of conditions in untreated stands while adding to the diversity of patches available (fig. 53). This phenomenon is not only prerequisite to development of habitat breadth (Carey et al. 1999b) but also may increase the ability of second-growth forests to support year-round resident wildlife (Haveri and Carey 2000).



**Figure 53**—Distributions of maximum air temperature on June 7, 2002, (cool day), in four study plots on the Olympic Peninsula. Relative temperature value at each point is indicated by the size of the circle. Axes numbers indicate meter location on plot. Control plots are on left, and plots treated with variable-density thinning (VDT) are on right (Aukema 2003a).

**Sidenote 49**—Lessons from the 1998 Yellowstone National Park (YNP) fire (Turner et al. 2003):

- Many northern coniferous forests, like some in YNP, are characterized by natural stand-replacing fires that are infrequent (return intervals of 100 to 500 years), but severe.
- Climate is the primary driver of stand-replacing fire regimes, with variation in fuels less important.
- Catastrophic disturbance influences plant population structure, genetics, and evolution.
- Spatial heterogeneity resulting from catastrophic fire is the rule, not the exception.
- Fires and fire regimes are not all the same, thus wildfire management must be site specific.

Spatial complexity also characterizes forests in regions with chronic low- to moderate-intensity disturbance regimes incorporating wildfire, such as ponderosa pine forests, mixed-conifer forests, and southeastern longleaf pine, flooding in Neotropical riverine forests, or wind, such as the *Nothofagus* forests of Tierra del Fuego (Franklin et al. 2002) (sidenote 49). Complexity is the major factor determining mammalian diversity in South American forests, as a consequence of preinteractive niche diversification (August 1983, Grelle 2003, Mares et al. 1986). Spatial heterogeneity makes construction of models predictive of fire frequency in the interior Columbia basin difficult; large amounts of data at fine resolution are required (McKenzie et al. 2000b). In the absence of human activity, small- to intermediate-scale disturbances result from the interaction of weather, other agents of disturbance, and forest structure and composition that are consequences of past small- to large-scale disturbances: drought creating stress leading to defoliator insect outbreaks; a dry-lightning storm igniting fires (table 22); a wind event causing blowdown; weather patterns leading to periodic intense grazing by grasshoppers, microtine rodents, rabbits, hares, deer, elk, moose, and bison (Frelich 2002).

The frequent and recurring nature of small- and intermediate-scale disturbances and their interactions with the ecosystem suggests they could be considered integral to the system rather than forces exogenous to but impinging on the system. For example, the 2-year spruce budworm exhibits a 32- to 45-year periodicity in defoliating spruce and fir resulting in growth reduction and understory release in high-elevation and high-latitude spruce-fir forests (Parish and Antos 2002). Frequent low-intensity fires on the east

**Table 22**—Interactions of climate, fire frequency, and fire intensity produce different types of forests

Frequency of light surface fires (in years)	Frequency of intense (crown and severe surface) fires (in years)			
	25–100	100–500	500–1,000	>1,000
<25	<ul style="list-style-type: none"> <li>▪ Jack pine barrens</li> <li>▪ Aspen parkland</li> </ul>		<ul style="list-style-type: none"> <li>▪ Ponderosa pine</li> <li>▪ Southern pine</li> </ul>	<ul style="list-style-type: none"> <li>▪ Bur oak savanna</li> <li>▪ Giant sequoia</li> </ul>
25–100		<ul style="list-style-type: none"> <li>▪ Red/white oak</li> <li>▪ White/red pine</li> </ul>		
>100	<ul style="list-style-type: none"> <li>▪ NW boreal forest</li> <li>▪ Jack pine/spruce</li> <li>▪ Spruce/fir/birch</li> </ul>	<ul style="list-style-type: none"> <li>▪ NE boreal forest</li> <li>▪ Spruce peatlands</li> <li>▪ Lodgepole pine</li> <li>▪ Interior Douglas-fir</li> </ul>	<ul style="list-style-type: none"> <li>▪ Coastal Douglas-fir</li> <li>▪ Western hemlock</li> <li>▪ Sitka spruce</li> </ul>	<ul style="list-style-type: none"> <li>▪ Sugar maple/basswood</li> <li>▪ Sugar maple/hemlock</li> </ul>

Source: Frelich 2002.

slopes of the central Washington Cascades exhibit negative feedback through fuel reduction (Wright and Agee 2004). In the boreal forests of eastern Canada, the spruce budworm may kill balsam fir in the canopy and release seedlings in the understory, controlling canopy turnover in the absence of fire. When human activities have promoted overly dense, stressed stands of trees, buildup of fuels for forest fire, and overly simplified forests, what would have been small- to intermediate-scale more-or-less endogenous disturbance can become individually magnified or jointly cascade into catastrophic destruction of the forest. Various management techniques can be used to reduce the risk of catastrophes. Small-scale timber harvests (patch cuts, partial cuts, and thinnings) can be useful in forests subject to small- and intermediate-scale disturbances. They can also be used where moisture stress is high to promote advance regeneration under the shelter of a partial canopy while maintaining forage for wildlife and decreasing potential for frost damage and erosion (Kneeshaw et al. 2002). Prescribed fire is useful in maintaining biotic integrity and promoting resilience in fire-adapted forests. Under certain circumstances, grazing also becomes a use that can contribute to resilience.

Forests subject to frequent light to moderate disturbances form mosaics. Patches in these mosaics are often mistaken for independent stands of trees, whereas in reality, they constitute a late-seral-stage mosaic (Franklin et al. 2002). Despite variety in disturbance regimes, most forests maintain mosaics in their late-seral stages with a grain size in the range of about 0.1 to 1.0 hectare, probably with a central tendency of 0.2 to 0.5 hectare. For example, White (1985) found establishment of ponderosa pine was infrequent in Arizona, maybe requiring 40 years, with stems aggregated in groups of 3 to 44 trees, 0.02 to 0.29 hectare; ages within groups were variable, with the most homogeneous having a range of 33 years and the least with a range of 268 years. In that area, it appeared seedlings established after the death of one to two large trees in a small area of intensive fire in an otherwise low-intensity fire area. Cooper (1960) reported similar aggregations in southwestern ponderosa pine but with a narrower range of ages within them. In the markedly different old-growth Douglas-fir forests of southwestern Oregon, the grain of mosaics was still 0.2 to 0.5 hectare including in Western Hemlock Zone forests and Mixed-Conifer/Mixed Evergreen Zone forests (Carey et al. 1999b). This scale of patchiness is widespread (Canham et al. 1990).

In general, forest development following catastrophes consists of gradual change and envelopment that result in diversity, complexity

***Most forests maintain mosaics in their late-seral stages with a grain size in the range of about 0.1 to 1.0 hectare, probably with a central tendency of 0.2 to 0.5 hectare.***



**Sidenote 50**—Windthrown versus clearcut—what is the difference after 70 years (Price et al. 1998)? Wind left behind legacies that led to heterogeneity when compared to clearcutting:

- Coarse woody debris—0.09 cubic meter per square meter versus 0.04 cubic meter per square meter
- Gaps—17- by 90-meter transect versus 2- by 90-meter transect
- Veteran trees larger than 60-centimeter diameter at breast height (d.b.h.)—11 versus 4
- Snags larger than 20-centimeter d.b.h.—20 versus 5
- Range in live tree d.b.h.—127 centimeters versus 80 centimeters
- Arboreal macrolichens—15 taxa versus 10 taxa
- Percentage of fallen trees larger than 70 centimeters—20 percent versus 0 percent

of structure and processes, and production of large structures, some of which persist through subsequent intermediate and catastrophic disturbances and assist in recovery of the ecosystem (sidenote 50). For example, populations of most vascular plants quickly recover to original levels even after clearcutting and burning, although on severely burned sites, some species may experience local extinction (Halpern and Spies 1995) and grasses and annual forbs (including exotic species) may be more common, and perennial ferns and shrubs less common, than after wildfire, owing to soil disturbance (Peltzer et al. 2000). But as the tree canopy closes and light, water, and nutrients are funneled into producing wood, plant diversity may be suppressed for over 20 years (Halpern and Spies 1995, Long 1977), and abundance and diversity may remain low for 60 years or more (Thyssel and Carey 2000). Even the seeds of native plants may disappear from the soil seed bank (Halpern et al. 1999, Lezberg et al. 1999, McKenzie et al. 2000a). Biomass accumulates rapidly across a chronosequence of 3 to 9, 30 to 40, 65 to 100, and over 200 years in various forest types in coastal Pacific Northwest forests, for example, 3.5, 232, 463, and 687 megagrams per hectare (Mg/ha) (1 megagram = 1,000,000 grams) in wet western hemlock forest and 0.6, 143, 423, and 586 Mg/ha in dry Douglas-fir (Hedberg and Blackwell 1998). Tree density and biomass accumulation, however, has high local variation, even in 140-year-old coastal Oregon spruce-hemlock forests, for example 462 to 750 Mg/ha (with 144 to 155 Mg/ha in coarse woody debris) (Acker et al. 2000). Coastal Oregon forests may store up to 1,127 megagrams of carbon per hectare (Mg C/ha), coastal Washington forests, 307 Mg C/ha less. Similarly, Oregon Cascade Range forests store 75 Mg C/ha more than Washington Cascade forests. Overall, Pacific Northwest forests store 338 Mg C/ha—the highest of any forests in the world; 1 percent is in understory vegetation, 6 percent in the forest floor, 10 percent in woody debris, 15 to 32 percent in the soil, and 53 to 67 percent is in trees. Eastern Oregon forests, however, store only 195 Mg C/ha (Smithwick et al. 2002). Coarse woody debris can be especially variable in space and time (Carey and Harrington 2001, Carey and Johnson 1995, Carey et al. 1999b, Wells and Trofymow 1998). Coarse woody debris cover can vary fivefold (5 to 24 percent, averaging 13 percent) in old growth and threefold (5 to 16 percent, averaging 8 percent) in second growth on the Olympic Peninsula versus  $10 \pm 2$  percent cover in old growth and  $4 \pm 1$  percent in second growth in the Oregon Coast Ranges—a twofold difference in second growth between regions (sidenote 51). On southern Vancouver Island, coarse woody debris ranged from 17 to 38 Mg/ha (55 to 149 square meters per hectare) in Douglas-fir

forest to 65 to 199 Mg/ha (307 to 636 square meters per hectare) in western hemlock-western redcedar forest—a two- to threefold variation within forest type and fivefold variation between forest types (Wells and Trofymow 1998). After reorganization, alternative stable states are possible, especially in managerially simplified forest—for example, the competitive-exclusion and the biomass-accumulation stages; development beyond these stages may require significant exogenous disturbance. Silvicultural treatments that foster spatial and temporal diversity of resources and environments can be effective in maintaining not only plant species (Carey and Johnson 1995; Carey et al. 1999b, 1994; Halpern and Spies 1995; Thomas and Carey 1994; Thysell and Carey 2001a) but also structural elements and animal communities. Without successive exogenous disturbances, change may be slow or rapid depending on the stage that was set, the legacies that were retained, the environmental heterogeneity inherent to the biotope, and internal disturbances such as root diseases and tree fall. The net result of successful community development is symbiosis, nutrient conservation, stability (not necessarily equilibrium), and decreased entropy.

Accumulation of biomass is fundamental to forest ecosystem development (Bormann and Likens 1979)—it provides resistance to change with minor disturbance and sets the stage for reorganization conditioned by legacy retention with catastrophic disturbance. This accumulation of biomass occurs in the form of various living plants, their exudates and litter fall, and dead and decaying plants and plant parts, down to carbon in the soil food webs (table 23).

Forest development, throughout temperate forests, incorporates multiple other processes that are variously dynamic and stochastic, but also many that are predictable and probable (Bobic et al. 2000, Bormann and Likens 1979, Franklin et al. 2002, Odum 1969) (side-note 52). The most deterministic process, however, is accumulation of biomass; less deterministic are the entry of decay into living trees and development of rich epiphytic communities (especially in the absence of legacy retention during clearcutting). Forests with rare catastrophic disturbances but with chronic intermediate and small-scale disturbances are characterized by spatial heterogeneity, especially horizontal patchiness that develops over time. Note, however, that even these processes of generating structural complexity in the forest are a subset of broader ecological processes such as fundamental physical and chemical processes that contribute to soil development and govern nutrient availability and cycling, belowground microbial and fungal processes, dispersal, colonization, competition, facilitation, symbiosis, development of habitat breadth, preinteractive niche

**Sidenote 51—Coarse woody debris (CWD)**—How much is enough? How many snags and fallen trees of various sizes and decay classes are necessary to maintain full ecosystem function? The question has been of intense interest for more than 50 years (Elton 1966, Hamilton and Cook 1940). A national symposium on snags was held in 1983 (Davis et al. 1983) and one on dead wood in 1999—for which the proceedings neared 1,000 pages (Laudenslayer et al. 2002). Coarse woody debris more than 10 centimeters in diameter is difficult to measure because it is not uniformly distributed in forests; rather it tends to be complexly distributed in randomly scattered clumps as a result of gap formation and individual large fallen trees of various species. In other words, multiple processes produce CWD. Trying to measure CWD with a few small plots almost guarantees underestimates owing to many plots with 0 values—for example, Rose et al. (2001, table 1 [in Johnson and O’Neil 2001]) reported very low levels of CWD in Pacific Northwest conifer forests compared to studies that used more intensive sampling. Line intercept methods are preferred but are time consuming. There is no consensus on what measure to use: percentage cover, volume, or biomass. Even when CWD is precisely measured, it is difficult to know how to apply empirical data on the abundance of a structure element of the forest to management recommendations. The responses of keystone species or keystone complexes to CWD can be useful. For example, analyzing space use by flying squirrels suggests that a 10-percent cover of large CWD

diversification, postinteractive niche partitioning, and development of emergent properties. The natural time scale of forest development is long, perhaps 100 to 250 years in eastern deciduous forests (Bormann and Likens 1979, Carey 1983, Oliver and Larson 1996), 250 to 750 years in Pacific Northwest forests—the life expectancy of adult Douglas-fir—and longer in other forests, for example, more than 1,000 years in coastal redwood forests in California and western redcedar forests on Vancouver Island in British Columbia (Franklin et al. 2002, Oliver and Larson 1996). But hundreds or more generations of salamanders, warblers, shrews, mice, squirrels, weasels, and spotted owls occur during the life of a long-lived Douglas-fir or redwood tree.

The ecosystem strategy of homeostasis through maximum support of complex biomass structure conflicts with management goals of maximizing yield of wood products (Odum 1969) and, especially, maximization of net present value from timber production (Carey et al. 1999c). Silviculture, however, can be used either as a means of maximizing return on investment or as a means of optimizing public and private values, including product and biotic-community diversification, with gradual change managed by small- and intermediate-scale disturbances on a time scale of about 150 years. Thus, silviculture can contribute to simplification or to diversification of the ecosystem. With active management, the development of a complex biomass structure is not inexorable; management with low intentionality can impede or preclude development of diverse ecosystems (Carey 1995, 1998b; Carey et al. 1999b, 1999c). However, management of forest ecosystems can accelerate forest development (Carey et al. 1996a).

**Table 23—Accumulation of biomass is directly related to the elements of forest structure and their spatial patterning**

Individual structures	<ul style="list-style-type: none"> <li>▪ Live trees</li> <li>▪ Large-diameter trees</li> <li>▪ Large-diameter branches</li> <li>▪ Lower canopy tree community</li> <li>▪ Ground community</li> <li>▪ Standing dead trees (snags)</li> <li>▪ Large woody debris (logs)</li> <li>▪ Root wads and soil pits</li> <li>▪ Soil organic layers</li> </ul>
Spatial patterns	<ul style="list-style-type: none"> <li>▪ Vertical distribution of foliage/canopy</li> <li>▪ Horizontal distribution of various elements</li> <li>▪ Gaps and antigaps</li> </ul>

Source: Franklin et al. 2002.

Accumulation of biomass, living and dead, *and in different life forms*, contributes to niche diversification, an expansion of the niche space within the ecosystem—the preinteractive niche differentiation (Hutchinson 1957, 1978). This expansion may result in synergism through symbiosis and other mutualisms. Other endogenous processes, such as top rot in living trees, also are integral to autogenic development of ecosystems and may require managerial stimulus in managed second-growth forests. Thus, hypothetically, it is possible to conserve biodiversity in managed forests through planned management disturbances and gradual change that expands various dimensions of the ecosystem (sidenote 53). Management can maintain dynamic shifting steady-state mosaics at both the level of the ecosystem and the level of the landscape within narrower bounds than produced over time by natural disturbance regimes. Over time, then, conservation of biodiversity and adaptive ecological innovation in response to regional and global change would be achieved intentionally even despite (possibly aided by) frequent uncontrollable intermediate disturbances (e.g., disease outbreaks, small-scale fires, and windstorms) and rare catastrophes (large-scale windstorms, fires, and volcanic eruptions). Simple maintenance of a shifting steady-state mosaic, however, may not be adequate to meet all the goals of conservation. Ecological forestry must rest on processes underlying development of structure and composition in complex forests (Carey et al. 1999b, 1999c; Franklin et al. 2002; Oliver and Larson 1996). Beyond legacy retention, reorganization of biotic resources, colonization, and establishment of a new forest community after catastrophic disturbance, there are four structural processes and two compositional processes that constitute the necessary minimum subset of processes that must be considered in designing ecological forest management (Carey et al. 1999b). These are crown-class differentiation, decadence, understory development, canopy stratification, development of habitat breadth, and niche diversification.

### Crown-Class Differentiation

Crown-class differentiation is the achievement of dominance (full growing space) by some trees, codominance by others, and subordination of yet other trees (table 24). It also includes differentiation in branches within crowns that occurs as a result of the differentiation in crown class among trees. In a densely stocked plantation, trees compete with one another through rapid height growth; the one that overtops its neighbors wins, and, thus, there is a tendency toward

provides sufficient foraging area for truffles of ectomycorrhizal fungi for near complete use of an area of forest in the Pacific Northwest (Carey et al. 1999b). In moist forests in Washington, however, complex forest-floor small mammal communities seem to require about 15 percent cover of CWD (large and small) to reach their potential diversity and abundance (Carey and Johnson 1995). This suggests an additional 5 percent cover of smaller CWD would help maintain forest-floor function in moist forests. But research has shown that CWD does not operate independently of other forest elements and that dynamics are important. The full process of decadence from decay in living trees, to decaying standing dead trees, to decaying fallen trees must be kept in mind. A rule of thumb for management is to aim for 10 percent cover of large (more than 50 centimeters in diameter) fallen trees in dry to mesic Douglas-fir forests and 10 percent cover of large and 5 percent cover of small CWD in mesic western hemlock, Douglas-fir, Pacific silver fir, or Sitka spruce forests, beginning with inputs in the form of legacies and continuing with each silvicultural entry to ensure a regular stream of inputs until gap formation begins in the late-seral stage to eventually recover levels of CWD when necessary and then to maintain them thereafter.



**Sidenote 52**—Processes leading to structural complexity of forests, in general order of occurrence through time (Franklin et al. 2002):

- Disturbance and legacy creation
- Establishment of a new cohort of trees and other plants
- Canopy closure of the tree layer
- Competitive exclusion of ground flora
- Lower tree canopy loss and death and pruning of lower branch systems
- Biomass accumulation
- Density-dependent tree mortality owing to self-thinning, wind, disease, and insects
- Canopy gap formation
- Generation of standing dead and fallen trees
- Uprooting of trees
- Understory reinitiation
- Establishment of shade-tolerant trees, shade-patch or antigap development
- Maturation (achievement of maximum height and crown spread) of the dominant tree cohort
- Canopy elaboration through canopy stratification and reestablishment of lower branch systems
- Development of live-tree decadence
- Development of large branches and branch systems
- Development of rich epiphyte communities
- Loss of original dominants

even spacing among dominant trees. When regeneration is moderately dense or patchy in density, trees “forage” and avoid neighbors by growing toward areas with high resource availability (less competition from neighbors); thus, in many species, tree crowns are rarely positioned directly above the stem. Crowns are displaced toward gap centers, especially subcanopy, and crown depth is greatest toward gaps (Muth and Bazzaz 2002). As trees get large and achieve dominance, the largest branches within their crowns may approach an asymptotic maximum length (around 9 meters in old Douglas-fir) and break, or die back (Ishii et al. 2000a, 2000b). Epicormic branches may then grow to replace the dead or dying branches, especially in the lower crown. Three crown patterns can result in Douglas-fir: mature crown, old crown, and stressed crown. The mature crown has an increasingly wider range of branch diameters toward the lower crown with the diameter distribution of dead branches constant; overall, the crown shape is conical with larger branches lower. The old crown has a few large-diameter branches, with the larger branches in the upper crown, and many dead branches. The stressed crown has small-diameter branches with only a few live branches and limited crown depth owing to insect or pathogen attack. In the lower crown of live old trees, nearly 50 percent of shoots and foliage are epicormic; in the mid and lower crown, reiteration of shoot cluster units maintains the remnants of large, broken branches and helps prolong the tree’s lifespan (Ishii and Ford 2001). It is remarkable that median size mid-crown branches in a 400-year-old tree may be more than 20 centimeters in diameter, more than 8 meters long, and more than 150 years old. The effects of this crown elaboration on the ecosystem are profound (Carey 1996). Not only are nest sites for spotted owls, marbled murrelets, and northern goshawks thus produced, but variation in branch size and health allow niche partitioning by cavity-using birds in their foraging (Carey et al. 1991)

**Table 24**—Crown-class differentiation in young (40–72 years), mature (80–120 years), and old forest (200–525 years) in the Oregon Coast Ranges as measured by average densities (trees per hectare) in three diameter-at-breast-height (d.b.h.) classes

D.b.h. class (in centimeters)	Young	Mature (Trees per hectare)	Old
10–49	270	120	27
50–99	30	65	25
>100	2	7	22

Source: Adapted from Carey et al. 1991.

(table 25) and, apparently songbirds as well (Shaw and Flick 1999). Massive seed production provides a large foraging environment for Douglas' squirrels (Shaw and Flick 2002) as well as important winter habitat for a variety of resident birds (Haveri and Carey 2000, Manuwal and Huff 1987). Individual old-growth trees may support 2 to 18 kilograms of epiphytes (totaling 132 to 271 kilograms per hectare), including alectoroid lichens, cyanolichens, other lichens, and bryophytes (Clement and Shaw 1999). Not only do these epiphytes provide nest materials and nest sites for mammals and birds (Carey 1996, Carey et al. 1997, Gillesberg and Carey 1991) (table 26), but the lichens play important roles in nutrient cycling, especially adding nitrogen to the soil during lichen fall, and providing forage for squirrels and ungulates. Thus, retention of live trees with heavy epiphyte abundances provides a source of propagules in newly reorganizing ecosystems and may have profound effects (Carey et al. 1991, Peck and McCune 1997). Collectively, the differentiated crowns form a rugose canopy that in itself provides added niche dimension, for example, for foraging by bats and olive-sided flycatchers (Carey et al. 1991, Wunder and Carey 1996). Thus, differentiation of

**Sidenote 53**—“At this stage of forest ecology, we should be able to describe the conditions constituting a healthy forest more precisely than ‘presettlement’ ... science-based approach looking quantitatively at the various components, values, and functions of ecosystems may be the key to describing healthy forest ecosystems” (Tiedemann et al. 2000).

**Table 25**—Partitioning of foraging space by cavity-nesting birds in the Oregon Coast Range, 1985–1986, based on 888 observations of foraging birds

Species	Red-breasted sapsucker	Hairy woodpecker	Pileated woodpecker	Chestnut-backed chickadee	Red-breasted nuthatch	Brown creeper
Vertical location	-Midcanopy	-Midcanopy -Understory	-Upper canopy	-Midcanopy -Lower canopy -Understory	-Midcanopy -Upper canopy	-Midcanopy -Lower canopy -Understory
Horizontal location	-Mainstem	-Mainstem	-Mainstem	-Center <sup>a</sup> -Outer <sup>a</sup>	-Mainstem -Center <sup>a</sup>	Mainstem
Tree species	-Douglas-fir -Bigleaf maple	-Douglas-fir	-Douglas-fir	-Douglas-fir -Western hemlock	-Douglas-fir	-Douglas-fir -Western hemlock
Tree condition	-Live	-Live -Dead—moderately decayed	-Live -Dead	-Live	-Live	-Live
Tree size	-Medium -Large	-Large -Medium	-Large -Very large	-Very small -Small -Medium	-Large -Medium	-Medium -Large
Crown class	-Subordinate -Dominant -Suppressed	-Dominant -Subordinate -Suppressed	-Dominant	-Dominant -Suppressed -Subordinate	-Dominant	-Dominant -Subordinate

<sup>a</sup> Branches.

Source: Carey et al. 1991.

**Table 26**—Nest materials<sup>a</sup> of arboreal rodents that were taken from artificial nest boxes and tree cavities on treated (variable-density thinning) and control plots in two forests at Fort Lewis, Washington

Type of nest materials	Legacy forest <sup>b</sup>		Thinned forest <sup>c</sup>	
	VDT plots	Control plots	VDT plots	Control plots
<b>Moss species:</b>				
<i>Dicranum tauricum</i>	0.00	0.00	.26	.40
<i>Hylocomium splendens</i>	.10	.36	.08	0.00
<i>Hypnum circinale</i>	.40	.76	1.97	7.19
<i>Isoetecium stoloniferum</i>	23.20	40.72	60.03	42.29
<i>Kindbergia oregana</i>	9.60	3.36	11.05	12.24
<i>Kindbergia praelonga</i>	0.00	.08	0.00	0.00
<i>Plagiotbecium undulatum</i>	.50	.40	.79	1.31
<i>Rhizomnium glabrescens</i>	0.00	0.00	0.00	.05
Total mosses	38.00	45.68	74.18	63.48
<b>Liverwort species:</b>				
<i>Frullania nisquallensis</i>	0.00	.88	.08	0.00
<i>Porella navicularis</i>	0.00	.04	1.21	.43
<i>Radula complanata</i>	0.00	0.00	0.00	.02
<i>Scapania bolanderi</i>	0.00	0.00	.08	.02
Total liverworts	0.00	.04	1.28	.48
<b>Lichen species:</b>				
<i>Alectoria sarmentosa</i>	23.50	5.16	.03	0.00
<i>Alectoria vancouverensis</i>	0.00	0.00	0.00	0.00
<i>Bryoria pseudofuscescens</i>	0.00	4.64	0.00	.05
<i>Cetrelia cetrarioides</i>	0.00	.44	0.00	0.00
<i>Cladonia ochrochlora</i>	0.00	0.00	.03	0.00
<i>Evernia prunastri</i>	0.00	0.00	0.00	.02
<i>Hypogymnia duplicate</i>	.10	.04	0.00	0.00
<i>Hypogymnia enteromorpha</i>	0.00	.24	0.00	0.00
<i>Hypogymnia imshaugii</i>	0.00	0.00	0.00	0.00
<i>Hypogymnia physodes</i>	0.00	.16	.18	0.00
<i>Hypogymnia tubulosa</i>	0.00	0.00	0.00	0.00
<i>Lobaria pulmonaria</i>	0.00	0.00	.10	0.00
<i>Mengazzia terebrata</i>	0.00	.04	0.00	0.00
<i>Platismatia glauca</i>	.50	.28	0.00	0.00
<i>Ramalina menziesii</i>	0.00	.16	.03	0.00
<i>Usnea filipendula</i>	0.00	0.00	0.00	0.00
<i>Usnea wirthii</i>	2.00	7.24	1.54	1.38
Total lichens	26.10	19.28	1.97	1.45

<sup>a</sup> Mean percentage of nest material. All material that has a mean value of zero occurred in the nests less than 0.01 percent.

<sup>b</sup> The legacy forest had been clearcut in ~1937, but many live and dead trees had been left. The forest had regenerated naturally into even-aged Douglas fir before our treatments (see Carey et al. 1999d).

<sup>c</sup> The thinned forest had been clearcut in ~1927 and later conventionally thinned twice. Few trees were retained from the preceding old-growth forest and dead trees were removed (see Carey et al. 1999d).

Source: Gross 1999.

branches within crowns and crown-class differentiation among trees are interlinked processes fundamental to development of ecosystem complexity. The rate at which differentiation proceeds depends on degree of intertree competition, legacies (biological legacies and the conditions during reorganization, including exogenous disturbances), natural disturbances, and management activities.

**Competition**—Just as trees jockey for canopy position, various tree species may partition the forest floor for fine root concentration—for example, western hemlock and salal roots become concentrated in the upper forest floor, but western redcedar roots may be found throughout a soil profile (Bennett et al. 2002). Douglas-fir seems to specialize in extending its fine root capacity through symbiosis with numerous ectomycorrhizal fungi. That plants build and maintain themselves from energy and materials in the environment and must share limited resources is the basis for the self-thinning rule, one of the few long-lived quantitative propositions in ecology (Torres et al. 2001). At low light levels (less than 40 percent full sunlight), growth of Douglas-fir is so restricted that little difference can be seen among sites markedly different in quality (Drever and Lertzman 2001). Western redcedar, however, approaches maximum radial and height growth at 30 percent full sunlight. Still, quantification of the relationships between growth in mass, density, basal area, and death owing to suppression has proven intractable (Torres et al. 2001, Zeide 1991), despite considerable economic implications (King et al. 2002).

For Pacific Northwest Douglas-fir, optimum growth occurs at initial seedling spacing of 3.7 to 4.6 meters (470 to 740 trees per hectare), but many naturally regenerated stands and plantations are denser than that (Miller et al. 1993, 2004). Site preparation, burning, and planting Douglas-fir can result in greater dominance by Douglas-fir, more rapid attainment of height, and earlier canopy closure, leading to competitive exclusion. Natural regeneration after site preparation and burning takes place over a longer period, establishes a more even mix of species, may result in slower growth owing to competition with resprouting shrubs, and may keep a diverse plant community longer; furthermore, without burning, growth of advance regeneration and natural seeding may negate the positive effects of planting on wood production (Miller et al. 1993). Even in plantations planted to 1,060 Douglas-fir per hectare, more than 9,900 additional trees per hectare (Douglas-fir, western hemlock, and red alder) may become established naturally. Natural regeneration outside of plantations may be as dense as 3,500 to 14,000 trees



per hectare. On the eastern Olympic Peninsula, in the area of the first (1930) extensive plantings of Douglas-fir in the Pacific Northwest, natural regeneration of western redcedar and western hemlock vastly outnumbered that of Douglas-fir following clearcutting in 1917 through 1919 and wildfire in 1924 through 1925; in the Cascade Range, however, Douglas-fir regenerates well naturally (Miller and Anderson 1995). With 9,900 trees per hectare at 9 years, 78 percent of trees may die by 26 years (Miller et al. 1999). But by that time, competition among trees will have taken its toll on other life forms. Still, the process of competition and differences among species in growth rates and shade-tolerance maintains the potential for crown-class and intracrown differentiation, despite the slow growth of the surviving trees. Similar results were obtained in the first experimental planting of Douglas-fir in 1925 in the southern Washington Cascades. Seedlings were planted at 1.2-, 1.5-, 1.8-, 2.4-, 3.0-, and 3.7-meter spacings (6,723 trees per hectare to 746 trees per hectare). By age 70, the densest plantations had declined to less than 2,000 trees per hectare and the least dense retained more than 500 trees per hectare. Dense plantings suffered suppression mortality, reduced growth, and damage from snow and wind. Such stands, if resilient enough to continue to develop through time, may undergo crown-class differentiation in addition to heavy mortality (Carey et al. 1999b, Miller et al. 2004). The least dense plantations, with more than 500 trees per hectare still have sufficient trees to sustain the process of crown-class differentiation—and the trees are larger and more vigorous than in the dense plantations. Silviculturists commonly focus on the 100 largest trees per hectare—these 100 trees will form a dominant class that fully occupies the site on long rotations (say 80 years or more). Additional variability in tree size and subsequent crown condition may be caused by differences in soil type, depth, and water-holding capacity that can occur at fine scales (1 hectare or less) (Miller et al. 2004). After 70 years, the 100 largest trees averaged 28 centimeters in d.b.h. and 23 meters in height in the dense (1.2- to 1.5-meter spacing) plantations compared to 43 centimeters in d.b.h. and 35 meters in height in the plots planted to 3.0- and 3.7-meter spacing (Miller et al. 2004). There is some evidence for a positive effect of high stand density (up to around 3,000 trees per hectare) on early (first 5 years) growth of Douglas-fir (Woodruff et al. 2002). Some of this increased above-ground growth could simply be related to competitive strategies in Douglas-fir aimed at achievement of dominance; other explanations include increased animal browsing in low-density plots, increased interspecific competition in low-density plots, a higher probability

that at least some seedlings find exceptionally good microsites in dense plots, and qualitative changes (ratio of red to far-red light) in side-light, such as light reflected from adjacent trees, that influences the allometry of growing seedlings (the plant parts in which growth is concentrated). In any case, the phenomenon is short lived. Without thinning, dense stands eventually suffer high mortality (Wilson and Oliver 2000, Woodruff et al. 2002) after drastically reducing diversity of the biotic community.

Silviculturists emphasizing wood production state “Capturing the full productive potential of a site requires prompt establishment of a uniform stand of trees” (Miller et al. 1993). Of course, they are speaking strictly about rate of tree growth (wood production) and not joint ecological and economic productivity—or even long-term site productivity. Natural regeneration is usually not uniform nor of a single species. Thus, in managing for multiple values, a balance must be struck with planting to promote development of a new forest (versus a shrubland, grassland, or parkland—unless that is a desired condition, as in ponderosa pine on dry sites), managing densities of trees to promote rapid growth (470 to 740 stems per hectare provide for optimum wood production for Douglas-fir), and managing densities, species composition, and spacing of trees to allow for continued development of a diverse plant community supportive of animal life and resilient to disease, insect attack, and other disturbances. When Douglas-fir plantations were thinned experimentally to 740 trees per hectare at 9 years, the volume of Douglas-fir at 26 years was 2.5 times that without thinning, with dominants in the thinned stands twice as large as those in unthinned stands (Miller and Anderson 1995). Of course, as trees grow in size, either further reduction in density or increased crown-class differentiation is needed for continued rapid growth of dominants. Conventional thinning promotes growth but does not necessarily lead to crown-class differentiation (Carey et al. 1999d). Conventional thinning produces a stand of big trees that may develop deep and differentiated crowns; in time, such stands may recruit shade-tolerant trees that add to vertical structure. In the short term, conventional thinning may increase susceptibility to windthrow (for several years) (Huggard et al. 1999). In any case, in densely stocked forests, there seems to be universal potential for age-related declines in growth from competition-related changes in forest structure and resource-use efficiencies of individual trees that can result not only in differentiation but in reduced overall growth (Binkley et al. 2002). Thus, to promote development of complex forest ecosystems, some balance of rapid growth and crown-class differentiation must be achieved. This seems possible through legacy

retention, multispecies management, and variable-density thinning (fig. 54).

Competition among trees affects other plants also. Experimental thinning in true fir-hemlock stands in the Pacific Northwest, showed not only markedly increased tree growth (5.8 square meters of basal area versus 40.5 square meters 10 years after thinning) with reductions in tree density (1,750 trees per hectare versus 250 trees per hectare) but also increased understory productivity, including berry production (Curtis et al. 2000). Tree cover was 66 percent in thinned stands and 90 percent in unthinned stands; understory cover increased from 58 percent to 72 percent (with an addition of four species) in thinned stands and decreased from 58 percent to 37 percent (with a loss of five species) in unthinned stands as the trees grew larger and competition increased. Thus, without thinning, trees reduce one another's growth, exclude other plant life forms, and decrease the productivity of the ecosystem, especially for terrestrial herbivores and granivores. An unexpected observation in the thinning trials was colonization by epiphytes in both thinned and unthinned stands by 10 or more cryptogamic epiphytes. Thinning not only increases lights but by causing root gaps also increases the availability of water and minerals to understory plants, resulting in marked increases in understory abundance and diversity (Thomas et al. 1999; Thysell and Carey 2000, 2001a). Fertilization, however, can speed canopy closure and lead to reduced understory (Thomas et al. 1999).

Although light is often the factor most limiting understory development in coastal forests, tree root competition for moisture and nutrients becomes important in western interior forests (Riegel et al. 1995). Establishment of a new cohort of trees may occur only

**Figure 54**—(A) A forest that was thinned once conventionally shows a dense understory with no midstory species, whereas (B) a forest that was thinned once conventionally and once with variable-density thinning 6 years earlier shows much more diversity in its understory and midstory species. Photos by A. Carey.



infrequently—40 years might elapse in southwestern ponderosa pine forest, and even then, regeneration is often spatially aggregated in groups of 3 to 44 trees in patches of 0.02 to 0.29 hectares (White 1985). This kind of reproduction of ponderosa pine commonly follows the death of one to two large trees in areas intensively burned in an otherwise low-intensity fire area. Ponderosa pine reorganization does not require much crown-class differentiation in its progression to park-like conditions. At a scale slightly larger than the small regeneration patches, a mosaic may thus be maintained over time (Cooper 1960, White 1985). Cooper (1960) described the pattern of southwestern ponderosa pine as a result of community development governed by fire and shade intolerance. Shade intolerance produces even-aged groups of trees originating in small openings. The identity of the group is maintained by fire as the group matures; young groups of trees are protected by lack of fuel on the forest floor. Litter beneath mature trees provides fuel for fire that prevents establishment of young trees. Thus, fire counteracts the tendency of trees to take on a random (or in mesic sites, a uniform) distribution. Old trees die and groups break up; what took 200 years to develop might be gone in less than 20 years; fire then prepares a seedbed, allowing regeneration. There is now a general consensus on an urgent need to restore ponderosa pine forests to dynamic mosaics (Allen et al. 2002) (sidenote 54). Historically, frequent surface fires, episodic regeneration, insect infestations, and drought produced spatially heterogeneous patterns at local and landscape scales.

Differentiation in crown class among trees occurs not only as a result of intraspecific competition but also interspecific competition, differences among species in growth rates under various conditions, variety in age classes at the time of ecosystem reorganization, spatial heterogeneity in the distribution of trees during and after reorganization, and heterogeneity in the biotope itself. Crown-class differentiation results in growth rates differing among trees and differences in tree diameter, height, crown width, height to live crown, crown depth, branch size, and other elements of tree architecture (Carey et al. 1991, 1999b; Ishii et al. 2000b; Ishii and Wilson 2001) (fig. 55). In forest ecosystem development, organization of foliage in three-dimensional space is more important than total amount of foliage (van Pelt and Franklin 2000). For example, Pacific Northwest old growth has the highest leaf area index of any forest in the world (fig. 56). Even-aged forest with similarly sized trees with foliage in one layer will have dramatically different crown architecture and understory light conditions than a tall forest with high foliage-height diversity with the same amount of leaf area index. Particularly at

**Sidenote 54**—How to restore ponderosa pine forests (Allen et al. 2002):

- Reduce threat of crown fire.
- Prioritize and strategically target treatment areas.
- Develop site-specific reference conditions.
- Implement multiple conservation initiatives.
- Use existing forest structure as a template.
- Restore ecosystem composition.
- Retain trees of significant size or age.
- Consider demographic processes.
- Integrate process and structure.
- Control and avoid introducing exotics.
- Foster regional heterogeneity by using complex topography, hydrology, and soils.
- Protect sensitive communities.
- Assess cumulative effects.
- Protect from overgrazing.
- Monitor and conduct research.
- Manage adaptively.

high latitudes with low sun angles, the narrow crowns of conifers can help promote three-dimensional structure. With differentiation, stands may move quickly into understory-reinitiation and niche-diversification stages. A significant part of vertical development of old-growth Douglas-fir/western hemlock forests is due to the slow invasion of the canopy by western hemlock and western redcedar (Ishii et al. 2000b). Loss of dominants promotes recruitment of new species and stratification, with Douglas-fir dominating at 30 to 50 meters in height, western hemlock at 10 to 45 meters, Pacific silver fir at less than 45 meters, Pacific yew below 20 meters, and western redcedar throughout the canopy.

**Biological legacies and reorganization**—Biological legacies can facilitate differentiation and inhibit homogeneous intercrown competition through (1) rapid growth of trees established before reorganization and released by destruction of the overstory, (2) continued growth of surviving overstory and midstory trees, and (3) spatial



**Figure 55**—A complex forest has a variety of tree architectures. Graphic by A. Wilson; Photos courtesy of USDA Forest Service.



heterogeneity of tree regeneration during reorganization owing to spatial variation in seed and seedbed availability and owing to falling dead trees (sidenote 55). There is a strong negative nonlinear relationship between gap light and the height, d.b.h., density, and volume of legacy trees, and aggregation of retained trees provides a broad variety of structural elements and environmental conditions, especially photosynthetically active radiation (Drever and Lertzman 2003). Legacy retention produced niche-diversification stages in fewer than 100 years after ecosystem reorganization in the Oregon Coast Ranges (Carey et al. 1999b). Streams also produce discontinuities in canopies that promote crown-class differentiation and species diversity (Carey 1988, Pabst and Spies 1999). Thus, the catastrophic event sets the stage for the ecological play to follow (Hutchinson 1965). Even catastrophic disturbances differ locally in intensity and produce wide ranges in retention of legacies and regeneration of trees. Natural disturbances rarely eliminate all the structural elements of the destroyed forest, even in cases of sequential intense disturbances (Franklin et al. 2000, 2002) (table 27).

Clearcutting for timber production, on the other hand, at the height of its development in the mid-20<sup>th</sup> century, called for elimination of legacies and species not contributing to commercial value throughout the life of a stand of trees (Barrett 1962, Smith 1962). For example, clearcutting called for cutting all stems more than 5 centimeters in diameter, removal of natural and logging debris by mechanical disruption and burning, elimination of vascular plants through burning and herbicides, planting a commercially valuable tree species, and sometimes fostering growth by fertilization. Stand tending during and after reorganization included continuing removal of vegetation competing with commercially valuable crop trees (cleaning, weeding, application of herbicides, precommercial thinning, and even pruning to produce uniformity) (fig. 57) and killing trees with decadence (defect or decay) during precommercial and commercial thinnings or “improvement cuts.” This approach was generalized to areas of markedly different climates and disturbance regimes, often inappropriately so and sometimes compounded by fire exclusion and grazing of livestock (Cooper 1960, Harrod et al. 1999, Tiedemann et al. 2000).

Second growth intensively managed for timber (fig. 58) often has lost many of the elements needed for development into complex forests with high resilience and potential adaptiveness. Indeed, in the 1980s, Pacific Northwest foresters began questioning the wisdom of clearcutting followed by burning with its potential for loss of nutrients through volatilization and leaching; loss of soil through

**Figure 56**—Multiple layers of understory species contribute to the Pacific Northwest’s high leaf area index. Photo by A. Carey.



**Table 27**—Biological legacies differ with type of major disturbance in temperate and boreal forests

Legacy	Wildfire	Windstorm	Clearcutting
Large live trees	Some	Some	None
Standing dead trees	Many	Some	None
Fallen trees	Many	Many	Few
Advance regeneration	Patchy	Much	Little
Undisturbed forest floor	Patchy	Patchy	Little

Source: Adapted from Franklin et al. 2002.

erosion; soil compaction by machinery; loss of genetic diversity in trees; lack of natural legacies, such as coarse woody debris, old large trees, and deciduous trees; and negative effects on values other than timber production (Williamson and Twombly 1983). Decades later, similar concerns are still being raised (Harmon and Marks 2002, Hennon et al. 2002, Stark and Hart 1999, Thompson et al. 2003, Wikstrom and Eriksson 2000). Fear of loss of timber productivity after harvest of old growth and site preparation by burning have not materialized in controlled studies, but loss of nutrients and soil organic matter, soil compaction, stream sedimentation, and effects on tree species composition of the new forest are evident—Douglas-fir and hardwoods are favored over other conifers (Heninger et al. 2002, Miller and Bigley 1990). Retention of 20 to 30 trees per hectare in clearcuts in western Washington ameliorated changes in



**Figure 57**—Regine Carey stands in a recently pruned conifer forest on the Olympic Peninsula. Photo by A. Carey.

soil and air temperatures but not nutrient loss (Barg and Edmonds 1999). But green-tree retention can have positive effects on vegetation structure, small mammals, songbirds, woodpeckers, spotted owls, Vaux's swifts, and marbled murrelets (Hunter and Bond 2001, Mitchell and Beese 2002, Sullivan and Sullivan 2001, Sullivan et al. 2001, Tittler et al. 2001). Tillage of skid trails helps offset soil compaction by machinery. In Alaska, clearcutting had largely negative consequences on wildlife and fish with canopy closure 25 to 35 years later nearly eliminating all understory for wildlife for more than 100 years (Hennon et al. 2002). Legacies, including alder, may mitigate the impacts of clearcutting.

Substantial controversy reigns over the treatment of forests destroyed by natural catastrophes or seminatural catastrophes (e.g., a wildfire arising from anthropogenic ignition may be intensified by the ways humans shaped the environment in the past, and contributed to by their shaping the climate of the present). As usual, positions among conservationists rapidly become polarized (Lach et al. 2003) with Op Ed letters and with emphasis on all-or-none approaches (Adams and Ringer 1994, Beschta et al. 1995, Blaine 2004, Fitzgerald 2002, Lindenmayer et al. 2004, Oregon Forest Resources Institute 2002, Sessions et al. 2003, Thomas 2002). Hyperbole abounds. Jim Strittholt (Director of the "Conservation Biology Institute") is quoted (Blaine 2004) as proclaiming firmly: "There is no ecological justification for post-fire salvage logging in any post-fire environment ... Someone will get rich ... You see a replanted lush green site with the eye of a forester, and you see a returning resource ... You look with the eye of an ecologist, and you see a plantation, not a wild place. If you go in and salvage and plant, that's not a wild place. That

**Sidenote 55**—Biological legacies influence crown-class differentiation:

- Advanced regeneration responds quickly to overstory removal.
- Large live trees provide structure in themselves, sources of seed, and eventually disrupt the developing canopy by falling.
- Large snags occupy some growing space but provide an opening enhancing unequal distribution of light and water, and they eventually fall disrupting the developing canopy.
- Large fallen trees contribute to patchiness in regeneration by being unsuitable as seedbeds to some species but suitable seedbeds to other species; tall stumps do likewise; both may raise regeneration above browsing animals.
- Deciduous trees may outcompete conifer regeneration and contribute to patchiness as well as species diversity.
- Shrubs can contribute to patchiness and reduced density in tree regeneration.



**Figure 58**—This recently thinned forest lacks in the important elements necessary for the development of complexity. Photo by A. Carey.

will never be a wild place.” Strittholt’s position accurately identifies the nature of the debate. Wildness, wilderness, uncontaminated by humans, humans guilty of profaning nature, nature must be protected from humans’ corrupting influence—all are perceptions of the urban environmentalist long separated from nature (Dietrich 1992). The opposite stance being that of humans immersed in and making a living from nature—and making deliberate choices about what to destroy, what to exploit, what to intensively cultivate, what to maintain, and what to restore. One view accepts restoration ecology in a variety of forms; another would restrict it to passive management through reserves. One view would promote biological diversity by intentional actions, another would either exploit or reserve. For example, the former might plant and shape the slope with coarse woody debris to minimize erosion and sedimentation of important fish-bearing streams to save a threatened salmon strain; the latter may let nature take its course while the strain becomes extinct, and patiently wait for however long it takes for the forest to regrow, the stream to rehabilitate itself, and another strain of fish to successfully colonize the stream. I have heard serious ecologists state words to the effect “Sooner or later it will become old growth, even if it takes thousands of years” even in the face of reasonably certain climate change that might preclude forests of the past from recurring. Thus, the debate is not science-based; it is based in worldviews, culture, and sources and systems of ways of knowing. It is based on values, not ecology—Is it better to let nature take its course or is it better to attempt to facilitate system recovery to a humanly desired future state? It is in the eye of the beholding person not in the province of nature. Is nature a fine-tuned watch with a place for everything and everything in its place? Little science supports that idea. Is nature totally stochastic and directionless—nature as value-free, no natural catastrophes are possible because they are, after all, natural? Let nature take its course—even if nature has no grand plan, no cybernetic guidance system, and no supreme manager guiding the way? Given the Gaia hypothesis, the only extraterrestrial input is solar energy, everything on the planet is natural, and everything is the result of self-organization and natural selection; thus, even the human population explosion precipitating the sixth major extinction event in the history of the planet (Thomas et al. 2004) is natural. But, nature *is* and ecosystems *are*; outside of this earth-bound reality, our emotional perceptions and intellectual concepts may or may not be accurate assessments of what *is*. Ecology refers to the relationships between organisms and their environments, not to wildness or wilderness or even nature. Wildness, wilderness, and natural are

in the eye of the beholder except in the extremes. Are Douglas-firs germinating from seed collected from the cones of old-growth trees but sown from a helicopter no longer natural? What if they were one to two generations grown in a nursery? Is the resulting forest never to be wild—even if one observes a cougar killing a deer there? What about seeing a spotted owl catching a flying squirrel to feed to its young? What about being lost, spending the night, and hearing the wolves howl?

Active management following catastrophic destruction of a forest can take many forms and produce diverse results. Salvage logging can take all to no living trees, all to no large dead trees, or take trees from selected patches. Similarly, seeding or planting can be done in a variety of ways and produce a variety of results. As in every aspect of forest management, the degree of intentionality determines in major part the risks of unintended consequences. Postfire salvage logging has the potential to markedly alter subsequent bird communities, especially year-round resident species, canopy and cavity nesters, and insectivores (McIver and Starr 2001, Morissette et al. 2002). Salvage removal of large wood affects development of the plant community and may reduce species richness while increasing conifer growth in the early years (McIver and Starr 2001). Of course the effects of salvage logging differ depending on the percentage of dead and damaged trees removed, how much of each tree is removed, the degree to which homogeneity and heterogeneity are emphasized, how well retention of legacies (live and dead trees and patches of intact forest) is managed, and the other practices instituted simultaneously with tree removal, such as felling trees perpendicular to slopes to reduce surface runoff and planting appropriate tree species to accelerate forest recovery. Log retrieval systems differ considerably in their effect on soils, with ground-based systems having greater negative effects than aerial systems (Adams and Ringer 1994, Beschta et al. 1995, Sessions et al. 2003). Ground-based logging, however, under certain circumstances can disrupt water-repellent soil layers developed by severe fires and thereby increase infiltration and decrease overland flow. Salvage can mitigate erosion with the use of logging residue to impede overland flow, and thus contribute to ecosystem recovery. Salvage can also reduce the probability of damaging insect outbreaks (McIver and Starr 2001). Post-wildfire seeding, designed to control erosion, may have unintended consequences in limiting conifer establishment, promoting exotic species, limiting establishment of native herbs and shrubs, and yet have no effect on total plant cover; biological legacies and adaptations for dispersal by native plants such as wind dispersal function



**Sidenote 56**—Postfire logging (McIver and Starr 2001):

- The immediate effects of salvage will differ with severity of burn, slope, soil type, road building, and weather.
- Logging systems differ in impacts.
- Sometimes logging residue decreases erosion.
- The probability of insect population buildups that may infect adjacent intact stands can be reduced.
- Logging can kill volunteer seedlings.
- Broadcast burning can change plant succession.
- Patches of disturbed soil encourage a variety of plant species.
- Skid trails can negatively influence future tree growth.
- Logging can reduce vegetation biomass, increase abundance of exotic species, and reduce native species richness.
- Logging can have negative effects on postfire wildlife populations.
- Cavity-nesting birds are the wildlife most likely to be affected by logging.
- Some wildlife may benefit from salvage logging.

well in the absence of seeding with nonnative grasses and legumes (Schoennagel and Waller 1999). Thus, management of legacies associated with intense disturbances is complex, and a high degree of intentionality is necessary in the analysis of the need for legacy management and in formulating a restoration plan for such sites (sidenote 56). Answers to questions about salvage and restoration after natural or anthropogenic catastrophes are not simple all-or-none answers if conservation is aimed at achieving the diverse values that society needs and wants from forests. The answers can be simple only if the goal is simple—let nature proceed unhindered and unaided (no matter what the short- or long-term consequences are) versus recover economic value before it is lost (no matter what the short- or long-term consequences are). It seems obvious, however, that care must be exercised and substantial legacies must be retained if rapid ecosystem recovery is to be obtained (Franklin et al. 2000, Sessions et al. 2003).

Second-growth forests differ markedly in character depending on how and when they were established and how they were subsequently treated. Simple near-monocultures of Douglas-fir or western hemlock and Douglas-fir/red alder stands are common in the Pacific Northwest. In areas logged from railroad systems during World War II on the Olympic Peninsula, however, some complex second-growth forests have developed under the influence of heavy loads of legacy coarse woody debris; in southwestern Oregon, selective or partial harvests left many legacies that allowed reorganization to produce complex second-growth forests. In the Sierra Nevada of California, railroad logging so efficiently removed all trees that scientists had trouble reconstructing fire histories (Stephens and Collins 2004).

Ecosystem reorganization after natural catastrophic destruction of the tree canopy and reestablishment of a tree canopy may take a long time (more than 50 years, Huff 1995) with substantial coarse woody debris left on site as standing dead trees, decayed fallen trees, and recently fallen dead trees (Spies and Franklin 1991). Numerous live trees and multiple species of trees may be left, germinate, or invade after disturbance, and understory vegetation may persist or quickly recoup. Over large areas, heterogeneity produced by biological legacies, variation in natural regeneration, and intermediate disturbances during a long reorganization stage may result in rapid crown-class differentiation with the competitive-exclusion stage being rare in the landscape and rapid growth of Douglas-fir and other trees (Poage and Tappeiner 2002, Tappeiner et al. 1997). In western Oregon, low tree densities are promoted by (1) lack of seed

sources following disturbance, (2) sporadic seed production, (3) seed predation, (4) inadequate safe sites for seedling establishment, (5) climatically unfavorable periods, (6) early competition by herbs and shrubs, and (7) herbivory. On a small site in Washington following catastrophic fire, regeneration was also prolonged—40 years or more—but eventually a high density of trees was attained, followed by significant natural thinning of the original cohort of Douglas-fir (Winter et al. 2002a). Surviving Douglas-fir developed deep crowns. Although some western hemlock may have been present from origin, at least three disturbances (at 90, 250, and 430 years) promoted subsequent major recruitment and growth episodes for western hemlock with many secondary pulses of growth in between (Winter et al. 2002b). The presence of even-aged cohorts in patches is compelling evidence of disturbance (Duncan and Stewart 1991). Similarly, in an Engelmann spruce-subalpine fir-lodgepole pine forest in southern interior British Columbia, pine became established in the first 5 years, spruce increased over the first 50 years, but few fir became established in the first 50 years after catastrophic fire (Antos and Parish 2002). Spruce present in the canopy in the old-growth stages had differentiated in response to a combination of partial disturbances and endogenous autogenic processes. Releases occurred in most decades but were concentrated around 110 years and 300 years after origination; these may have been related to spruce budworm outbreaks that produced canopy thinning. Patchy budworm outbreaks led to patchy establishment of fir. Furthermore, different age categories of trees showed different patterns of aggregation. The oldest trees showed no overall deviation from a random pattern, trees originating at 100 years showed patterns that differed among plots, and trees that originated at 300 years were clumped at distances up to 20 meters. Thus, the process of crown-class differentiation and the development of crown-class differentiation in the trees collectively may recur throughout the duration of structurally and compositionally diverse forests (sidenote 57). Antos and Parish (2002) suggested that most old, fire-initiated forests are similarly structured by a combination of exogenous partial disturbance and autogenic processes and that management should incorporate similar dynamics. There was no evidence of exogenous disturbance in the first 200 years. Then episodes of disturbance were reflected by periods of release in the understory; after disturbance, firs were able to attain positions in the canopy. In boreal forests, regeneration following fire, spruce budworm infestation, windthrow, or timber harvests depends on numerous biotic parameters: (1) production of seeds and asexual regeneration of stems as a function of surviving tree densities; (2)

**Sidenote 57**—Promoting crown-class differentiation:

- Legacy retention—live trees, standing dead trees, fallen trees, and seed banks
- Promoting multiple tree species during reorganization during planting, weeding, and precommercial thinning
- Variable-density thinning
- Underplanting
- Multiple entries for tree removal
- Individual tree release
- Tree limbing or topping to foster development of reiterated trunks or complex crowns

dispersal of seed by wind; (3) germination of dormant seeds in the soil; (4) organic layer depth after disturbance as it affects germinant mortality; and (5) advance regeneration of shade-tolerant trees (Greene et al. 1999). In dry areas characterized by competition for moisture and by frequent return intervals for fires of light to moderate severity, crown-class differentiation may not be an important process—savannahs and widely spaced groves of trees may form in response to poor, infrequent, or short-lived regeneration (Cooper 1960). But, regeneration occurs in patches, and crown-class differentiation is apparent among patches, and eventually within patches early in the development of those patches.

**Timber management**—Timber management shortens reorganization and quickly moves the stand into competitive exclusion or biomass accumulation. With limited legacies and a dense cohort of naturally or artificially established trees, the diversity of plant species and many other life forms decreases with canopy closure. The resulting competitive exclusion and biomass accumulation concentrated in trees may last over 70 years (Carey et al. 1996a, 1999b; Long 1977) and recovery of plant species diversity may be slow even at 75 years (Long 1977); peak in diversity may be delayed until old growth (Halpern and Spies 1995). Similarly, small mammal abundance and diversity are reduced as the canopy closes and understory decreases and may remain low for decades (Carey and Harrington 2001, Hooven 1969, Wilson and Carey 2000). In plantations, evenly spaced seedlings may fail to differentiate, are susceptible to diameter-growth stagnation, and may become unstable (Wilson and Oliver 2000). Stagnation can increase susceptibility to windthrow if thinning occurs later. Natural thinning of young Douglas-firs produces small, ephemeral gaps as individual trees die. These small gaps do not contribute much to crown-class differentiation or to recovery of plant species diversity (Spies and Franklin 1989). Nevertheless, small gaps, the relatively thin crowns of Douglas-fir, and random variation in spacing often allow reinitiation of an understory of salal or sword-fern. The density, basal area, foliar productivity, biomass, and cover of salal is related almost exclusively to light, increasing with increasing transmission of light through the tree canopy (Vales 1986). This course of development is typical of forests reorganizing after clearcutting and burning (Carey et al. 1996b, Halpern and Spies 1995, Long 1977, Long and Turner 1975). Intermediate disturbances such as root-rot infestations often produce pockets of understory reinitiation in second-growth stands (Carey et al. 1996b, Holah et al. 1993). In mesic areas where shade-tolerant species are

abundant, even denser canopies may form, facilitated by legacies of well-decayed nurse trees. These competitive-exclusion stands may last longer and produce an intense ecological “crunch” on biodiversity as trees strive to compete for a height advantage and exclude smaller life forms (Carey 1995, 1996; Carey and Johnson 1995; Carey et al. 1996b; Stewart 1986, 1988). Overstory cover explains more than 50 percent of the variance in shrub cover, including vine maple cover; even stronger relationships exist with maximum total shrub cover, total herbaceous cover, and the cover of each of the three functional groups of herbs (Carey et al. 1999b, McKenzie et al. 2000a). Thus, severe disturbance followed by dense regeneration results in a stage of development that inhibits biodiversity.

Land use change, grazing, timber management, and fire exclusion have produced dense, relatively homogeneous, mixed-species ponderosa pine forests at risk to catastrophic destruction in areas previously characterized as ponderosa pine woodlands (Wright and Agee 2004 and many others). Not only are present forests more homogeneous, but often large trees have been removed, small trees occur in thickets, community composition has shifted to less fire-resistant species, understory grasses and forbs have decreased in abundance and have been replaced by deep mats of slowly decomposing needles that disrupt nutrient cycling, decrease biological diversity, and disrupt hydrologic cycles. Old-growth ponderosa pine forest is rare and what were meadows associated with these old-growth forests are now forests.

**Competitive exclusion stages**—If crown-class differentiation is delayed, the ecosystem may enter the competitive exclusion stage of development, wherein the system actually becomes more simplified over time instead of increasing in complexity. Salient features of competitive exclusion are even-aged, dense trees and suppression mortality. Hardwoods, notably red alder, giant chinquapin, Pacific madrone, and bigleaf maple, occasionally produce heterogeneity in competitive-exclusion stands that allows some crown-class differentiation. Shade-tolerant conifers may be rare in the understory during competitive exclusion, especially on dry to mesic sites. Second-growth competitive-exclusion stands 40 to 70 years old averaged 384 live conifers per hectare and 123 snags per hectare in the Oregon Coast Range (Carey et al. 1999b), about 50 percent more than the 85 snags per hectare reported by Carey et al. (1991) for a mixture of natural and managed competitive-exclusion stands there, but similar to second-growth competitive exclusion on the Olympic Peninsula (121 snags per hectare) (Carey 1995). In the Puget Trough

of Washington, 60-year-old competitive exclusion averaged 500 Douglas-fir per hectare (34 snags per hectare). For Douglas-fir of this age and size (quadratic mean diameters of 30 to 40 centimeters), excessive restriction of crown development (and concomitant mortality owing to suppression) occurs at densities of 350 to 540 trees per hectare (Curtis 1982, McArdle et al. 1961). In eastern deciduous forests, 490 trees per hectare would be common (Bormann and Likens 1979). In western interior Northwest forests, trees are often smaller and their densities substantially higher. In Wyoming, subalpine spruce-fir forests, both species grow slowly as seedlings and saplings and live suppressed for many years until released by some disturbance (Oosting and Reed 1952). For example, 337-year-old subalpine forest canopies in interior British Columbia may have 450 stems per hectare (with nearly 800 more stems per hectare subcanopy), even after an 80-year period of reorganization followed by 200 years of growing without disturbance followed by major mortality owing to bark beetles (which released suppressed trees also), then another, but shorter, bark beetle outbreak 30 years later, and a small outbreak 60 years after that (Parish et al. 1999). The diversity of effects that disturbance can have on forest dynamics is well recognized. Large fires can produce extensive homogeneous stands of trees, whereas insects, disease, and blowdown create patchiness and fine-scale heterogeneity (Parish et al. 1999). Natural variation in stocking, advance regeneration, and occasional retention of large trees from previous stands may contribute to crown-class differentiation in otherwise dense second growth.

**Discussion**—A salient feature of Pacific Northwest niche-diversification and old-growth stands is large Douglas-fir with deep crowns and large, platform branches, epicormic branches, and reiterated trunks (Carey et al. 1991, Franklin et al. 1981, Spies and Franklin 1991), architecture unlikely to develop in competitive-exclusion and biomass-accumulation stages. Old stands also have shade-tolerant conifers including grand fir, western hemlock, western redcedar, and incense cedar and sometimes bigleaf maple or Pacific madrone. Presumably, crown-class differentiation in niche diversification and old growth was not only a result of the stage-setting catastrophe that destroyed the previous stand, but also one of multiple species, competition, disease, injury, and mortality of the aging cohort of trees that produced gaps followed by establishment and growth of shade-tolerant conifers. Density-dependent processes (e.g., inter-tree competition and disease outbreaks such as root rot) are more likely in younger forests and density-independent processes (e.g.,



gap formation owing to individual large trees falling because of butt decay by velvet-top fungus) are more likely to occur in older forests.

Crown-class differentiation accounts for more variance in stand structure than any other factor. Diameter at breast height alone can separate age classes in broad-scale surveys (Carey et al. 1991), and most variance among age classes across the Pacific Northwest can be reduced to a single canonical variate related to the standard deviation of d.b.h. and the density of large trees (Spies and Franklin 1991). But, large-diameter trees can also be grown in plantations, and, in these simplified ecosystems, d.b.h. no longer serves as a good predictor of stage of ecosystem development; such trees may have quite homogeneous, simply structured crowns (fig. 59). In old forests, as trees became dominant they not only increased in d.b.h., but also in height, crown depth (and often width), limb size, variation in limb size, occurrence of epicormic branching and reiterated branches and trunks, bark rugosity, and root networks (fig. 60). These architectural changes magnified individual tree dimensions, and multidimensionally increased niche space for other animals and plants. Enhanced characteristics included (1) greater, more consistent production of seed for seed-eating birds and mammals (Buchanan et al. 1990, Carey 1991, Manuwal and Huff 1987); (2) increased surface area for mycorrhizae, epiphytic plants, and endophytic parasites—up to 97 species of lichen can occur in a small stand with well-differentiated crowns (Enseen et al. 1996, McCune et al. 2000, Parks and Shaw 1996, Sillet and Neitlich 1996, Stone et al. 1996); (3) bark crevices, foliage, and arboreal soil for invertebrates (Denison 1973, Mariani 1987, Schowalter 1989); (4) crevices for bat roosts and materials and platforms for nests of mammals and birds (Carey 1996, Carey et al. 1997, Forsman et al. 1984, Gillesberg and Carey 1991, Hamer and Nelson 1995, Wunder and Carey 1996); and (5) an increased variety of foraging substrates and prey (and niche separation) for bark-gleaning and wood-pecking birds (Carey et al. 1991, Sharpe 1996). At the stand level, crown-class differentiation results in a rugose canopy that provides unique foraging spaces for bats (Wunder and Carey 1996) and birds (e.g., the olive-sided flycatcher) (Carey et al. 1991).

Crown-class differentiation accounted for 25 percent of variance in vegetation structure in a mixed sample of young and old stands in Oregon and provided a major dimension of the realized habitat of Townsend's chipmunks (Carey et al. 1999b). Mean tree d.b.h. also was a good predictor of the abundance of Townsend's chipmunks on the Olympic Peninsula, explaining 61 percent of the



**Figure 59**—This conventionally thinned forest has a dense understory, no midstory, and an overstory of trees in intense competition with each other. Photo by A. Carey.

variance (Carey 1995). Two alternative explanations of the strong correlations of abundance of chipmunks with crown-class differentiation appear reasonable: (1) crown-class differentiation was a surrogate for the entire process of forest development or (2) chipmunks were responding to heavy seed production by large, dominant trees. Conifer seed is a major dietary component for Townsend's chipmunks, which harvest and store the seed for the winter (Sutton 1993). Townsend's chipmunks seem to be food limited, and their abundance can be increased by adding seed (Sullivan et al. 1983). The same seems true for the third squirrel in Pacific Northwest forests—the Douglas' squirrel, whose behavioral repertoire is geared at safekeeping sources and stores of conifer seed (Smith 1970). Chipmunks have a strategy of capitalizing on seasonally available seeds, fruits, and fungal fruiting bodies, storing food for winter, and facultatively hibernating to reduce energy needs during winter. Crown-class differentiation is a minor dimension of flying squirrel realized habitat; flying squirrels specialize on truffles, mushrooms, and fruits and seeds of shrubs and deciduous trees.

**Figure 60**—An old-growth forest on the Olympic Peninsula shows complexity in tree architecture. Photo by T. Wilson.



Crown-class differentiation is perhaps the factor of forest development most amenable to management: (1) species composition can be determined managerially at initiation of a new stand by legacy retention, planting, allowing natural regeneration, and maintaining and promoting diversity during precommercial thinning; (2) management of stem density and growth rates is well founded, and quantitative measures exist for the degree of intercrown competition in trees (Curtis and Carey 1996); and (3) spacing can be varied tree to tree or patch to patch within stands to promote both crown-class differentiation and crown development (Carey 1995, Carey et al. 1996a, 1996b). Growth of large trees and the passage of time lead to disease, injury, decay, and death of trees and consequent expansion of multidimensional niche space. Thus, the ecological influence of crown-class differentiation extends beyond tree architecture to interaction with decay processes to produce decadent structures of large biomass. Decay processes seem less deterministic than differentiation; yet, management easily can have marked impacts on decadence.

## Decadence

The Oxford English Dictionary (OED) defines *decadence* as “The process of falling away or declining (from a prior state of excellence, vitality, prosperity, etc.); decay; impaired or deteriorated condition.” Decadence has long been recognized as playing important ecological roles in forests, not only for soil organisms and plants, but for animal communities as well (Elton 1966, Hamilton and Cook 1940). In forests, decadence refers to both state of the forest (degree of decadence) and to processes by which trees (1) become infected with rots, often as a result of physical damage, insect attack, or disease; (2) balance decadence with renewal—broken tops with reiterated trunks and large dead and broken branches with epicormic branches; (3) develop decayed heart wood, cavities in their tops, and hollow boles; (4) uproot or break and fall to gradually decay to become incorporated into soil; and (5) die while standing and gradually decay to fall or break up into smaller pieces (fig. 61) (table 28).

Contrary to the OED definition, a modicum of decadence in forests contributes to “vitality and prosperity” and renewal. Of particular importance to forest conservation is maintaining long-term site productivity. For example, coarse woody debris can be important in cation cycling in base-poor systems, in maintaining surface organic layers in areas where decay is rapid or fires are frequent, in





**Figure 61**—Decadence in a second-growth forest in the Puget Trough: a recently snapped tree bole and an adjacent uprooted tree. Photo by A. Carey.

retaining moisture during dry periods and preventing erosion during wet periods, for seedling establishment in coastal Pacific Northwest forests, and as habitat for a variety of organisms (plants, fungi, and animals) in most forests (Laiho and Prescott 1999). In relation to sustaining site productivity and timber harvesting, the question is whether the total nutrient pool left on site in biological legacies (rather than simply coarse woody debris) and the rate of nutrient input through weathering and precipitation are large enough to offset loss of nutrients in harvested timber. Management of faster cycling materials, such as ground vegetation and nonwoody litter, may be as or more important than coarse woody debris. For example, on Rocky Mountain conifer forests in Alberta, Canada, coarse woody debris did not appear to make significant contributions to nitrogen and phosphorous cycling; the organisms producing woody decay may have actually competed with plants for the limiting nutrients that became available. Litter and coarse woody debris, however, do provide refugia during fires for a variety of beneficial fungi, microbes, and invertebrates that are important to nutrient cycling and decomposition in western interior forests (Niwa et al. 2001) and are thus important to forest resilience. Coarse woody debris is a major component of Rocky Mountain forests and is important to forest soils (Graham et al. 1994). The dynamics of coarse woody debris differ with forest type, seral stage, insect and disease activity, weather events, fire-return intervals, and management activities. The wood lasts 60 to 500 years depending on the ecosystem type, longer in mesic systems and shorter in xeric systems. Amounts range from 66 Mg/ha in cedar-hemlock forests to 23 Mg/ha in ponderosa pine

**Table 28**—Density of standing dead trees (snags) by diameter class and age class in young, mature, and old forests in the Oregon Coast Range<sup>a</sup>

Snag size (d.b.h. in cm)	Young	Mature	Old
>100	0.1	0.3	3.3
>50	0.8	4.3	7.3
20–49	17.6	55.6	8.4
10–19	64.9	39.0	7.0

<sup>a</sup>This illustrates the transition from density-dependent mortality to density-independent mortality and from smaller trees to larger trees with increasing forest development. In Washington, snags larger than 50 centimeters d.b.h. were more abundant in old growth—averaging 24 per hectare—than in second growth—only 1 to 15 per hectare.

Source: Carey et al. 1991.

forest (fig. 62). The abundance of ectomycorrhizal root tips is a good indicator of the health of Rocky Mountain forest soils and exhibits a strong positive relationship with soil organic matter, which is positively related to coarse woody debris inputs. Empirical data suggest that optimum soil organic matter can be maintained by 10 to 20 Mg/ha of coarse woody debris, depending on forest type (sidenote 58). Historically, wildfires left 100 to 600 Mg/ha, depending on forest type. Maintaining well-distributed 15 to 30 Mg/ha on dry sites and 30 to 50 Mg/ha on mesic sites by minimizing roller chopping, chipping, and smashing slash while using prescribed fire to remove needles and branches (hazard fuels) can maintain the ecological roles of coarse woody debris.

In the Pacific Northwest, there has long been an interest in the role of coarse woody debris in nutrient cycling and long-term site productivity; however, our understanding is still limited (Edmonds and Chappell 1994; Edmonds et al. 2000; Edmonds and Murray 2002; Marra and Edmonds 1994, 1996; Sollins 1982; Sollins et al. 1980). In Douglas-fir/western hemlock/western redcedar forests, decay of coarse woody debris over the long term does result in net nitrogen mineralization (Hart 1999). Catastrophic inputs of coarse woody debris assist forest recovery by timing of nutrient release that



**Sidenote 58**—The role of coarse woody debris in Rocky Mountain forests (Graham et al. 1994):

- Protects the forest floor and mineral soil from erosion and mechanical disturbance
- Protects new seedlings from livestock grazing
- Key habitat element for many species of wildlife
- Important in stream ecology
- Interrupts airflow, provides shade, insulates and protects new forest growth
- In mesic forests, provides seedbeds and nursery area for conifer seedlings
- With advanced decay, holds large amounts of water providing moisture for vegetation during dry periods
- Stores nutrients (sulphur, phosphorous, nitrogen) that are released through decay or burning
- Provides humus for ectomycorrhizal root tips

**Figure 62**—A fallen ponderosa pine near Sisters, Oregon. Photo by A. Carey.



matches nutrient demands and helping to prevent erosion. In many old-growth forests, more than 20 percent of the area of the forest floor is covered by coarse woody debris (fig. 63) with well-decayed boles covering more than 5 percent of the forest floor. This material can contribute to rapid recovery of the system after disturbance. Trees retained after catastrophic disturbance (natural or managed) often show signs of old age and decadence: fungal infections, large cracks, densely furrowed bark, broken tops, multiple leaders, cavities and basal hollows, large-diameter limbs defective in form, numerous epiphytes, and deep crowns suggestive of an open-grown growth form (Hunter and Bond 2001). Catastrophic fires, insect outbreaks, and epidemics of disease often leave large numbers of snags used by woodpeckers and other cavity-using birds (Imbeau and Desrochers 2002, Johnson and O'Neil 2001, Lundquist and Mariani 1991, Rose et al. 2001). Snags used by cavity excavators may differ markedly in abundance from 453 per square kilometer in Oregon to 233 per square kilometer in British Columbia to 1.3 per square kilometer in the Cariboo Parklands of Alberta (Bonar 2000, Johnson and O'Neil 2001). Reviews of snag abundance and use by wildlife have been



**Figure 63**—Coarse woody debris, both standing and fallen, provides shelter and places to forage for wildlife. Photo courtesy of USDA Forest Service.

compiled for practically all regions of North America in wildlife-habitat relationships books; Johnson and O'Neil (2001) provided a recent review for Washington and Oregon. The importance to wildlife of standing dead trees, live trees with moderate to heavy decay (fig. 64), and fallen trees cannot be overstated (Bunnell et al. 1999), and substantial effort has gone into modeling the dynamics of coarse woody debris, including models that produce advisory output for managers (Mellen and Ager 2002; Mellen et al. 2002, 2004; Wilhere 2003). Conventional timber management in Washington includes (1) clearcutting with retention of 7 to 12 wildlife trees per hectare followed by planting 1,075 Douglas-fir per hectare; (2) precommercial thinning at 15 years of the plantation to 741 trees per hectare; (3) commercial thinning at 30 years (if done) to 346 trees per hectare; and (4) clearcutting at 50 years (Wilhere 2003). Such management results in snag densities of about 20 percent of the total snags and 1 percent of the large snags in natural forests. Average predicted densities were 3.9 small snags per hectare, 6.2 medium snags per hectare, and 0.1 large (more than 64-centimeter d.b.h.) snags per hectare. In conifers, it is the moderately decayed large snags and very large (more 80-centimeter d.b.h.) snags that provide most of the cavities used by birds. Similarly, the importance of forest decadence to aquatic systems is profound (Acker et al. 2003).

Live trees with extensive decay, standing dead trees, and fallen trees are used by a tremendous diversity of plants, fungi, microorganisms, invertebrates, and vertebrates (Boddy 2001, Harmon et al. 1986, Jonsson and Kruys 2001, Kruys and Jonsson 1999, Kuuluvainen et al. 2001, Maser and Maser 1988, Maser and Trappe 1984, McComb and Lindenmayer 1999, Siitonen 2001). Coarse woody debris is characteristic of natural forests from the spruce taiga in the Ural Mountains of Russia (36 fallen trees more than 10 centimeters in d.b.h. along 10 meters of transect) to the Pacific Northwestern United States, where up to 27 percent of the forest floor may be covered with coarse woody debris (Marra and Edmonds 1994). In Scandinavian forests, 4,000 to 5,000 species (20 to 25 percent of all species) are associated with coarse woody debris, which averages 60 to 90 cubic meters per hectare in old growth but only 2 to 10 cubic meters per hectare in managed forests (fig. 65). Furthermore, the process of decadence is important in the development of spatial complexity



**Figure 64**—Western redcedar trees can compartmentalize decay and remain alive, even with such large cavities. Photo by A. Wilson.



**Figure 65**—Coarse woody debris in a managed forest in Sweden. Photo by A. Carey.



in the forest and in the soil. Trees dying lose their foliage and allow light to penetrate the canopy more fully. Falling trees may damage other trees and create larger canopy gaps. Fallen trees provide structure to the forest floor and seed beds for a variety of plant species; eventually they become incorporated into the soil and fully infiltrated by roots; various organisms, especially beetles, convert fallen trees into humus and fine organic matter in the soil. Large dead wood (standing dead trees, fallen trees, and large tree parts) resulting from decadence is often referred to as coarse woody debris.

Abundance of coarse woody debris accounted for 16 percent of the total variance in vegetation structure in managed and natural forests in southwestern Oregon (Carey et al. 1999b). Cover of fallen trees in the Oregon Coast Ranges averaged 10 percent in old growth, 7 percent in niche diversification forest, and 4 percent in competitive exclusion forests. In Washington, cover of fallen trees averaged 13 percent in old growth but ranged from 2 to 13 percent, averaging 8 percent in second growth (Carey and Harrington 2001).

Sites used by flying squirrels averaged a 10 percent cover of fallen trees in both regions. The types and abundance of coarse woody debris resulted from three separate phenomena: (1) retention of live, damaged, and dead trees through and after the catastrophe that initiated the reorganization of the ecosystem; (2) death of young trees through suppression, disease, weather damage, fire, and falling large trees; and (3) development of decadence in live trees over time. Intermediate and small-scale disturbances including wildfires (Juday 1977), diseases such as root rot (Carey et al. 1996b, Holah et al. 1993) and white pine blister rust (Lundquist and Mariani 1991), windstorms (Carey and Johnson 1995), snowstorms, and ice storms (Carey et al. 1997) promote decadence. These disturbances, however, are stochastic and differ in frequency and intensity from place to place and time to time, producing high variance in decadence within age classes of forest that may differ markedly in other elements of structure as well.

Historical clearcutting left substantially less coarse woody debris than did natural catastrophes, removed most or all live trees, and was followed by fast, dense, and monospecific regeneration of trees that quickly moved the stand into the competitive-exclusion stage. Early (about 1910) logging of old growth left 52 to 56 percent of preharvest biomass, contemporary logging of old-growth leaves 33 to 41 percent, and contemporary harvest of second-growth leaves only 31 to 35 percent—a reduction from 500 to 540 megagrams per hectare to 100 to 115 megagrams per hectare (Harmon et al. 1996). The trend has been for intensive management for timber to result in marked loss of biodiversity owing to reductions in coarse woody debris and increases in homogeneity and simplicity of the resulting forest. Management can deconstruct ecological processes and shape them to narrow ends. Maintenance of homogeneity through maintaining evenly spaced trees can promote biomass accumulation without crown-class differentiation, forestall or prevent suppression mortality, and remove trees with incipient decadence. Decoupling of basic processes has profound influences on ecological complexity, diversity, and resilience. Even in natural forests, processes can be decoupled. After especially severe catastrophes, coarse woody debris declines in abundance until old growth is reached at about 190 to 250 years (Spies and Franklin 1991). But when trees are killed or weakened by fire, coarse woody debris recruitment may continue for over 100 years (as in contemporary niche-diversification stands) until death of older trees begins to maintain recruitment of coarse woody debris (Franklin et al. 1987). Managed stands are harvested during competitive exclusion, or if precommercially or commercially

**Sidenote 59**—Considerations for managing cavity trees (Bunnell et al. 1999):

- Manage a continuum from live trees to standing dead trees to fallen trees to trees incorporated in the soil.
- Twenty to thirty percent of the vertebrate fauna [of British Columbia] use cavities—57 species in interior Douglas-fir forest; the proportion of species using cavities increases with mean fire size and frequency of fire.
- Decay states differ between deciduous trees (sound sapwood, heart rot) and conifers (moderately decayed sapwood and heartwood).
- Birds and mammals commonly prefer hardwoods over conifers, even small d.b.h. hardwoods, but 66 percent of weak excavators use only dead trees, and some of these are the most threatened by lack of decadence management.
- A number of species (e.g., Vaux's swift, black bears, American marten) use hollow trees that require heart rot and a long time of decay.
- Size matters—densities of cavity users is correlated with densities of large snags but not small snags, and cavity users respond the most to increases in snag densities primarily at low snag densities; conifers more than 80 centimeters and deciduous trees more than 40 centimeters with height more than 20 meters are sought out; 2.4 large snags per hectare supports 50 percent of the maximum density; increase in number of cavity nesters reaches a maximum [levels out] at about 5 large snags per

thinned, during biomass accumulation, generally at 40 to 70 years old, with high utilization of wood and rapid regeneration through planting (Carey et al. 1999c). With intensive management for timber, recovery of biodiversity by the ecosystem may be restricted severely because of reduced crown-class differentiation and decadence.

**Decay in live trees**—The entry of decay-causing organisms, the development of decay, and the timing of tree death varies markedly with species (Browne 1956, Eslyn and Highley 1976). Decay in live trees that enables cavity excavation by woodpeckers, allows cavities to develop for squirrels and other mammals, and leads to hollow trees is more common in deciduous trees than in conifers (sidenote 59). The processes leading to decay in deciduous trees are well understood (Carey 1981, Hansen 1966, Manion and Zabel 1979, Shigo 1979, Wagener and Davidson 1954, Wilkes 1982) as are factors underlying the distribution of live cavity trees (Carey 1983). For example, in relatively even-aged oak-hickory forests in West Virginia, the spatial pattern of the occurrence of the various species of oak, hickories, and other trees was roughly determined by slope position, aspect, and other variable site qualities in a small landscape (Carey 1983). But the species differed markedly in their propensity for forming discrete cavities useful to wildlife, for becoming hollow trees, and for longevity. White oaks, especially chestnut oak, were, perhaps, the best cavity providers, with northern red oak and scarlet oaks not as prolific. Older forests, dominated by northern hardwoods had even fewer cavities. In southwestern Oregon old-growth forests, large, old, dead, moderately decayed Douglas-fir provided the majority of cavities for birds (Carey et al. 1991). But on the Olympic Peninsula, large, live western redcedar with heart rots were important to pileated woodpeckers (Aubry and Raley 2002). In the western Washington Cascades, large, old, white pines that died from blister rust provided the greatest number of cavities (Lundquist and Mariani 1991). Grand fir is not as long-lived as Douglas-fir, but it is a good cavity tree and is somewhat unique among the firs in regularly becoming a hollow tree, that, when it falls, provides den sites for American marten and other mammals. Deciduous trees, such as red alder, willow, Pacific madrone, and bigleaf maple are apt to have cavities earlier in the life of a forest than Douglas-fir. Similarly, species differ in their susceptibilities to different diseases and in the timing when mortality might occur and contribute to coarse woody debris on the forest floor. Studies of second-growth forest in the Puget Trough of Washington, surprisingly, found increasing recruitment of large tree boles to the forest floor in stands more than



70 years old as a result of root rot. In natural forests, there is often a dearth of coarse woody debris recruitment between 40 and 150 years or so.

**Fallen trees**—Pacific Northwest forests have the greatest coarse woody debris loads of any forests, and accumulated dead biomass is thought to be of central importance in promoting ecosystem stability, habitat diversity, and long-term productivity (Carey and Harrington 2001; Edmonds et al. 2000; Graham and Cromack 1982; Marra and Edmonds 1994, 1996). Functions of coarse woody debris include (1) nutrient cycling by adding organic matter to soil (Harmon et al. 1994, Sollins 1982); (2) microhabitats for a rich diversity of microorganisms, arthropods, lichens, and bryophytes and seedbeds for shade-tolerant conifers and ericaceous shrubs (Harmon et al. 1986, Peck et al. 1995); (3) refugia for mycorrhizal fungi and reservoirs of moisture during and after catastrophic disturbance, particularly on dry sites and during droughts (Amaranthus et al. 1989); (4) ectomycorrhizal links among trees and truffle production in late-seral forests (Amaranthus and Perry 1994, Amaranthus et al. 1994, Clarkson and Mills 1994); (5) niche diversification in small mammal communities by enhancing forest-floor structure, soil organic matter, fungi, and invertebrate communities (Carey and Johnson 1995); (6) habitat for salamanders (clouded salamander, Oregon slender salamander, and *Ensatina*) (Butts and McComb 2000, Corn and Bury 1991b, Gilbert and Allwine 1991); (7) foraging sites for pileated woodpeckers and their prey: ants (e.g., *Camponotus*, *Formica*, and *Lasius* spp.) (Torgersen and Bull 1995); (8) habitat element of primary importance to the western red-backed vole (Hayes and Cross 1987, Tallmon and Mills 1994); (9) physical mediation of competition between blacktail deer and Roosevelt elk (Leslie et al. 1984); (10) elevated seedbeds that protect vascular plants from herbivory by ungulates; and (11) maternal den sites for arboreal rodents (Carey et al. 1997).

Of all the various elements of ecosystems, cover of fallen trees best described high-quality habitat for northern flying squirrels and Townsend's chipmunk in southwestern Oregon (Carey et al. 1999b); 15 percent cover might be optimal for mammals in wet to mesic forest, 10 percent cover in drier forests. Large fallen trees are almost twice as abundant in old growth as in managed forests, although the amount of coarse woody debris in second growth differs markedly with historical logging method and degree of legacy retention (Carey 1995, Carey and Harrington 2001, Carey and Johnson 1995). In the late 20<sup>th</sup> century, nearly complete removal of tree boles and

hectare in the Pacific Northwest.

- Preferences for snags for foraging are similar to the preferences for nesting.
- The most compelling evidence of declines in vertebrate abundance resulting from forest management practices is in cavity nesters owing to lack of nesting and foraging sites.
- Management that reduces snags includes short rotations and thinnings.
- Sustained provision of cavity trees may require creating cavity trees or snags, withdrawing a portion of the forest from management in the short term; incorporating aging trees into management in the long term; providing a minimum of two large snags per hectare and preferably four large snags per hectare with retention of some smaller snags for foraging. Retaining snags in patches is operationally efficient, safer, takes advantage of spatial clumping of dead trees, and seems effective in attracting cavity-excavating birds.

intensive site preparation had resulted in less than 2 percent cover of coarse woody debris in many second- and third-growth forests (Carey et al. 1996a). Managed forests in general have less coarse woody debris than late-seral forests (Carey and Johnson 1995, Carey et al. 1999d, Spies and Cline 1988), but some, particularly on the western Olympic Peninsula, may have retained substantial biomass (Carey and Harrington 2001). Rebuilding a depleted store of coarse woody debris through retention of tree boles during thinning is possible but expensive (Carey et al. 1996a). Thus, legacy retention is especially important in setting the stage for conserving biodiversity in managed forests (Franklin et al. 1997).

**Decadence as a process**—If catastrophic disturbance sets the stage, it is small-scale disturbances in the canopy that determine the pace of the ecosystem development. Gaps drive the forest cycle in all forests (Whitmore 1989). The ecological process of tree death (Franklin et al. 1987) is particularly important in expansion of niche space (Carey 1996, Carey et al. 1991, Parks and Shaw 1996, Stone et al. 1996). Only 10 percent of the cells of living conifers are actually alive (Franklin et al. 1987). In eastern Washington and Oregon, four species of mistletoes, 50 species of rusts, and several rots play an important role in decadence (Parks and Flanagan 2001). Indeed, a case can be made that mistletoes are keystone species in forests and woodlands worldwide—97 vertebrate families consume mistletoes and 50 use them as nest sites (Watson 2001). Heart rots account for 20 to 31 percent of the volume of standing trees in Pacific Northwest forests (Hennon 1995, Parks and Shaw 1996). Snapping of boles (often at the site of decay) and standing death constitute 76 percent of gapmakers; uprooting is the least common (21 percent) (Lertzman et al. 1996). In the Oregon Cascades, more than 70 percent of canopy Douglas-fir die standing or from stem breakage and die without disrupting the forest (73 to 88 percent of deaths in late-seral forest); only 12 to 27 percent of the trees in late-seral forests uproot (Spies and Franklin 1989, Spies et al. 1990). In some mature forests, for example, mixed-wood forests in Poland, windthrow is a major source of mortality for individual trees (Bobiec et al. 2000). Competition, however, is the major cause of death of conifers up to 150 years old (Franklin et al. 1987). Mechanical damage from falling trees accounts for 15 percent of mortality in late-seral forests. Decaying and dead standing trees (1) increase structural diversity, (2) alter the canopy and understory microenvironments, (3) promote biological diversity, (4) store nutrients and decomposers, and (5) provide critical habitat elements for wildlife (Parks and Shaw 1996). The role of coarse woody debris in

developing complex and productive forest floors and soils is generally accepted but poorly quantified.

**Decadence and wildlife**—The importance of standing dead trees (snags) and standing live trees with sufficient top rot to allow for formation or excavation of cavities by cavity-using birds and mammals has long been a focus of wildlife conservation, and the literature is large and diverse (Barkalow and Soots 1965, Bellrose et al. 1964, Brewer 1961, Brown and Bellrose 1943, Conner et al. 1976, Dalke 1948, Davis et al. 1983, Dennis 1971, Erskine and McLaren 1972, Fischer and McClelland 1983, Frank 1948, Gysel 1961, Ken-deigh 1961, McClelland and Frissell 1975, Panicker 1980, Scott et al. 1977). The densities of cavity-using birds have been correlated with abundances of snags, especially snags over 50 centimeters in d.b.h. in the conifer forests of Oregon (Mannan et al. 1980), Washington (Zarnowitz and Manuwal 1985), and California (Raphael and White 1984). In southwestern Oregon forests, an abundance of large snags (more than 7 per hectare with greater than 50 centimeter d.b.h.) was the primary determinant of a diverse bird community (Carey et al. 1991). Large snags were 10 times more abundant, woodpeckers 4 times more abundant, and cavity-using birds as a group 2 times more abundant in old growth than in competitive-exclusion forests. Cavity-nesting birds constitute a majority of resident overwintering small-bird species. The keystone northern flying squirrel dens primarily in large, live old trees (presumably with heart rot and cavities) in old growth, but in residual old-growth snags in managed forests in southwestern Oregon (Carey et al. 1997). Cavities in large deciduous trees with top rot (e.g., bigleaf maple and Pacific madrone) also were used. Small-diameter conifer snags were rarely used for nesting by birds or mammals. In the Puget Trough, however, small-diameter deciduous snags (e.g., red alder) with cavities excavated by woodpeckers were important cavity sites in intensively managed second-growth stands with few large snags. In second growth with numerous well-decayed large snags and minimally decayed suppression mortality, flying squirrels resorted to stick nests in tightly closed canopies—but in both environments flying squirrel populations were low (Carey et al. 1997). On the Olympic Peninsula, flying squirrels denned in residual large snags and in cavities in live conifers with top rot (formed after tops were killed by freezing 30 years previously) but not in abundant suppressed trees. It seems that suppression mortality in conifers does not contribute greatly to the function of standing decadent trees in either provision of cavities or gap formation. Small snags usually do not have top rot (or

cavities) and do not stand very long; they do contribute to coarse woody debris on the forest floor for a relatively short time before decaying (Carey and Sanderson 1981 review of decay processes and cavity formation). The evolution of hole-nesting in birds (and arboreal rodents) is an adaptation that allows year-round residence in temperate forests by providing bioenergetic advantages and protection from predation (Collias 1964, Short 1979). Flying squirrels have evolutionary adaptations of gliding, nocturnality, cavity-nesting (Holmes and Austad 1994), and communal denning (Carey et al. 1997). Nocturnal arboreal travel and gliding have energetic costs that are offset (37 percent reduction in heat loss) by denning in groups in cavities lined with plant material (Carey et al. 1997, Stapp et al. 1991). Thus, den sites large enough to hold more than three squirrels are important, and decay in the tops of large trees is important. In addition, flying squirrels change dens about every 2 weeks (perhaps as a strategy to avoid predators) and large numbers of group dens are needed (Carey et al. 1997).

There is a broad correspondence between large snag abundance and population sizes of flying squirrels across the Pacific Northwest (Carey 1995). This correspondence, however, is more likely a result of large snags as indicators of overall decadence than to provision of den sites (Carey et al. 1997). Trees display a continuum of roles from living, sound organisms to dead, prostrate structures on the forest floor (Franklin et al. 1987). Many of these roles depend on decay forming in living trees of large size; for example, hollow trunks of fallen trees used as dens by American marten. Thus, decadence in Pacific Northwest forests cannot be partitioned functionally into snags and fallen trees without losing the significance of the entire process of tree decay and death and its diverse functions. This is especially true in relation to the role of accumulated organic matter on the forest floor. Fallen trees transform into rotting logs, humus, and organic soil formed through the action (digestion of wood and mechanical mixing of the soil) of invertebrates. Forest-floor organic matter influences a variety of life forms in the forest floor, and its role relative to ectomycorrhizal fungi essential to the growth of many trees and their production of truffles (the food of many mammals that are prey for vertebrates higher on the food chain) has been the subject of much discussion and speculation.

**Fallen trees and truffles**—What accounts for the ability of decadence to explain variation in space use, activity, and abundance of flying squirrels and other small mammals? It is plausible that the role of decadence in providing den sites is important for an abundance

of flying squirrels (Carey 1995, Carey et al. 1997), but abundance of fallen trees predicted flying squirrel abundance almost as well as did decadence (which includes snags as well). Fungal sporocarps (truffles) compose the bulk of the diet of the flying squirrel, and a strong connection has been made between truffle abundance and coarse woody debris in southwestern Oregon. Truffle abundance is 20 to 30 times greater in old forest with more than 25 percent cover of coarse woody debris than in young plantations with less than 15 percent cover of coarse woody debris (Amaranthus et al. 1994). Within old forests in drier parts of the Pacific Northwest, truffles are 10 times greater in well-decayed fallen trees than in mineral soil. Of the eight genera that are common in flying squirrel diets (Carey et al. 2002, 1999b), five (*Rhizopogon*, *Melanogaster*, *Leucopheps*, *Hysterangium*, and *Leucogaster*) were associated with well-decayed coarse woody debris (Amaranthus et al. 1994). Only *Elaphomyces* (the eighth-ranked genus in diets of flying squirrels) was associated primarily with mineral soil. *Balsamia*, the eighth-ranked genus in chipmunk diets (and not present with more than 5 percent frequency in flying squirrel pellets), also was associated with mineral soil. Clarkson and Mills (1994) also found sample plots with fallen trees are more likely to contain sporocarps (twice as likely) and on average to have more biomass (four times more) of sporocarps than sampling plots without fallen trees in late-seral forest in southwestern Oregon. They found that activity of mycophagous western red-backed voles is associated with truffle abundance and coarse woody debris. Of the five most abundant genera (*Melanogaster*, *Hysterangium*, *Gautieria*, *Genebea*, and *Rhizopogon*) found by Clarkson and Mills (1994), four were among the five most abundant in diets of flying squirrels, and three were among the five most abundant in diets of Townsend's chipmunk as well.

Flying squirrels consume 20 to 24 genera of fungal sporocarps year-round (Carey et al. 2002, 1999b; Maser et al. 1986). *Rhizopogon*, *Gautieria*, *Hymenogaster*, *Melanogaster*, *Hysterangium*, *Leucopheps*, *Elaphomyces*, and *Geopora* are the dominant items in spring diets. Seasonal differences in diets include high frequencies of *Elaphomyces* in January-February, decreased frequencies of *Hymenogaster* in summer-fall, and increased frequencies of *Leucogaster* in summer-fall; lichens are important dietary components in January. Diets of northern flying squirrels in the Pacific Northwest differ geographically, but fungal sporocarps still compose the bulk of diets. In the relatively dry forests of northeastern Oregon and California, flying squirrels consume less fungus and more lichen, plant material, and staminate cones than flying squirrels in western Oregon (Carey et al.



1999b; Maser et al. 1985, 1986; Waters and Zabel 1995). *Rhizopogon* still dominates the diet, flying squirrel densities are positively correlated with sporocarp abundance, and fungal sporocarps are twice as abundant in old-growth white fir as in competitive-exclusion stands 75 to 95 years old with little coarse woody debris (Waters and Zabel 1995). In the western Washington lowlands, flying squirrels consume 16 of 21 genera and 40 of 50 species of mycorrhizal fungi found in second-growth Douglas-fir forest (Carey et al. 2002, 1996b). *Rhizopogon*, *Melanogaster*, *Hysterangium*, *Endogone*, and *Leucogaster* are the genera most frequently encountered in the soil, and *Rhizopogon*, *Gautieria*, *Leucogaster*, and *Melanogaster* are the common spores in diets. *Gautieria* was most abundant in stands with high coarse woody debris loads, and *Melanogaster* was most common in stands with little coarse woody debris. Flying squirrels were more than twice as abundant in forests with 6 to 8 percent coarse woody debris than in forests with less than 2 percent coarse woody debris. Mushroom spores (*Russula*, *Peziza*, *Agaricaceae*, and *Boletaceae*) were common in diets; plant material and lichens were relatively infrequent in fecal pellets. Spring diets of flying squirrels in Douglas-fir-western hemlock forests on the Olympic Peninsula of western Washington are dominated by *Rhizopogon*, *Hysterangium*, and *Leucogaster*. Olympic Peninsula squirrels also consume spores of *Boletaceae*, *Octaviana*, *Thaxterogaster*, and *Chamomixia* (Carey 1995). Dietary species richness on the Olympic Peninsula is half that in the Oregon Coast Range (Carey 1995, Carey et al. 1999b) and differs between competitive-exclusion and old-growth forest; but coarse woody debris is not a good predictor of flying squirrel abundance on the Olympic Peninsula. Several differences between the Oregon Coast Range and the Olympic Peninsula can explain the differences in dietary diversities and influence of coarse woody debris.

The Olympic Peninsula has more precipitation, cooler temperatures, and less severe summer drought than the Coast Range; coarse woody debris is generally abundant (Carey and Harrington 2001), and thus coarse woody debris may not be important as moisture reservoirs and refugia for ectomycorrhizal fungi. Coarse woody debris loads on the Olympic Peninsula are higher (8 percent in competitive exclusion, 13 percent in old growth) than in the Coast Range (4 percent in competitive exclusion, 9 percent in old growth), forest-floor organic matter accumulations are greater, and forest floors are moister (Carey and Johnson 1995). Forests on the Olympic Peninsula are dominated by western hemlock, which does not have as many ectomycorrhizal associates as Douglas-fir. Few species are specific to western hemlock, which may have evolved to capitalize on

the mycorrhizal associations of pioneering species (e.g., Douglas-fir) that establish quickly after catastrophic disturbance (Molina et al. 1992). Thus, mycorrhizal diversity (and possibly sporocarp abundance) may be relatively low in pure western hemlock competitive-exclusion stands. About 50 species associate with western hemlock in the laboratory, more than 100 species in the field (Kropp and Trappe 1982, Molina et al. 1992, Molina and Trappe 1982). There are 250 species that are specific to, and 2,000 species associated with, Douglas-fir (Molina et al. 1992).

In southwestern Oregon, giant chinquapin, Pacific madrone, tanoak, and salal are broadly receptive to numerous ectomycorrhizal fungi, form ectomycorrhizal associations that facilitate establishment of conifers after catastrophic disturbance, and create spatial and temporal ectomycorrhizal links among tree species (Amaranthus and Perry 1989, 1994; Molina et al. 1992; Molina and Trappe 1982; Smith et al. 1995). Thus, it is not surprising that there are not differences in dietary diversity between squirrels from competitive exclusion and squirrels from old growth in the Coast Range. In summary, dietary diversity was associated with coarse woody debris sometimes, but activity of mycophagous mammals and truffle abundance in southwestern Oregon seem to be strongly associated with coarse woody debris.

Management affects composition of truffle communities in various ways (Carey et al. 2002). More species and genera are found in soil and in feces in forests with old-growth legacies than in thinned forests managed without consideration for legacies or decadence. Second-growth forests in the Puget Trough had 48 species (Colgan et al. 1999). Broad surveys of managed and old-growth forests found 43 species in western Washington (North et al. 1997) and 47 species in Oregon (Luoma 1991). Because total truffle production differs markedly among seasons and years (e.g., 330 to 1,852 grams per hectare) and species production differs even more markedly, often more than tenfold (Luoma 1991), taxonomic diversity is important in providing a consistent food supply to mycophagous mammals. Total truffle diversity, however, differs little among the physiographic provinces of western Oregon and Washington, but the northern forests of the Olympic Peninsula and North Cascades forests seem to have greater dominance by a single species than forests in the Puget Trough or in Oregon (Carey et al. 2002). Flying squirrel diets were rich in Puget Trough legacy forests (seven commonly occurring genera) compared to similarly managed forests on the Olympic Peninsula (four genera) and similar in diversity to diets in old-growth forests on the peninsula (six genera). Diets in thinned

forests in the Puget Trough had the same number of genera (four) as diets in the legacy forests on the peninsula. Flying squirrel diets in the Puget Trough and on the Olympic Peninsula had fewer genera than flying squirrel diets from the warmer, drier, southern Oregon Coast Range (12 genera in old growth and 9 in extensively managed forests) (Carey 1995, Carey et al. 1999b).

Truffle production is important to mycophagous animals. Flying squirrel abundance varied with truffle abundance in northeastern California (Waters and Zabel 1995). In southwestern Oregon, local foraging by flying squirrels was correlated with abundance of coarse woody debris (Carey et al. 1999b), and coarse woody debris was positively correlated with truffle abundance (Amaranthus et al. 1994). Even though 20 to 50 species of hypogeous fungi may be present in any one stand, usually fewer than five species account for the bulk of the biomass of sporocarps (Amaranthus et al. 1994, Carey et al. 2002, Colgan et al. 1999, Fogel 1976, Fogel and Hunt 1979, Hunt and Trappe 1987, Luoma 1991, North et al. 1997). These abundant fungi, however, are the ones most frequently tallied in squirrel diets and seem to be narrow (tree genus) to intermediate (tree family) in host range (Molina et al. 1992, Molina and Trappe 1982). Four genera common in flying squirrel diets across the Pacific Northwest (Carey 1995, Carey et al. 1999b), *Gautieria*, *Leucogaster*, *Leucophleps*, and *Elaphomyces*, were less abundant in soil or feces in thinned forests than in forests with legacies of coarse woody debris. Production of truffles by *Gautieria* (and *Hysterangium*) is reduced by thinning in the short term (Colgan et al. 1999) and, apparently with conventional thinning, that effect is long lasting but not universal for species of *Hysterangium*. For example, *H. coriaceum* and *H. crassirhachis* were more abundant in forests with legacies and *H. setchellii* was more abundant in thinned forest—an example of the resilience of the ectomycorrhizal community resulting from species diversity (and redundancy) within a functional group. *Leucogaster citrinus* and *Elaphomyces granulatus* are listed as late-seral species (Castellano et al. 1999, USDA and USDI 1994) and are common in legacy forest but not in conventionally thinned forest, demonstrating that legacy retention can be important in maintaining functional group and species diversity through intentional management disturbances. Moreover, 71 late-seral epigeous (mushroom-producing) fungi also occurred in second-growth forests in the Puget Trough (Carey et al. 1999d). Fruiting of *Melanogaster*, like *H. setchellii*, was favored by thinning (Colgan et al. 1999); *Melanogaster* truffles were six times more frequent in soil and twice as abundant in flying squirrel feces in thinned than in legacy forest. On the other hand, three of four

*Rhizopogon* species occurred only in thinned forest. Several species of *Rhizopogon* are associated with early stages of forest development and are often abundant on tree roots following disturbance (Molina et al. 1997). Several factors may explain low truffle production by certain species in thinned forest. Species that form hyphal mats may be more susceptible to mechanical damage by logging operations. Thinning may change microclimate to the detriment of these species. *Hysterangium* and *Gautieria* were reduced in abundance in shelterwood stands 17 and 20 years after timber harvest (Waters et al. 1994). *Gautieria* mats were found only in the rooting zone of retained old-growth trees 2 years after a shelterwood harvest in the Oregon Cascades (Aguilera et al. 1993), and *Hysterangium* spores were rare in feces of Siskiyou chipmunks in shelterwood stands in southwest Oregon (McIntire 1984). Shelterwood harvests remove a greater proportion of trees than thinning, and considerable time may be required after disturbance for such taxa to recover and fruit. North and Greenberg (1998) hypothesized that reduction in biomass of *E. granulatus* in managed compared to natural old forests was a consequence of reduction of thick organic layers with high root density in managed forests. *Rhizopogon parksii*, the other species they studied, was not associated with organic layers. The areas studied by North (North and Greenberg 1998, North et al. 1997) are on the cool, moist end of the Western Hemlock Zone. At the opposite extreme (hot, dry) in southwestern Oregon, Amaranthus et al. (1994) found a close association between truffles of various species and decaying logs on the forest floor.

Truffle abundance, although important to mycophagous mammals, is but one of several important factors. On the Olympic Peninsula, flying squirrel abundance was correlated more with understory development (Carey 1995) and abundance of mast-bearing trees (vine maple and bigleaf maple)—ancillary sources of high-quality food—than with coarse woody debris (Carey and Harrington 2001). Flying squirrels were almost twice as abundant in legacy as in conventionally thinned forest, whereas chipmunks were four times more abundant in thinned forest (Carey 2000b, 2001). Food and cover well explain differences in chipmunk abundance (Carey 2000b, 2001) but not differences in flying squirrel abundance, given that (1) truffle biomass was equal in the two forest types, (2) flying squirrels consumed all species of truffles present (Carey et al. 2002, Colgan 1997, Colgan et al. 1999), (3) truffles are nutritionally poor (Claridge et al. 1999, Cork and Kenagy 1989), and (4) vascular plant parts consumed by flying squirrels (Thysell et al. 1997b) have high nutritive value (Cork and Kenagy 1989). Locally, flying squirrel abundance

may be determined by (1) availability of dens (Carey 2001, Carey et al. 1997), (2) habitat-mediated predation (Carey et al. 1992, Wilson and Carey 1996), (3) competition with chipmunks and Douglas' squirrels in environments simplified by forest management (Carey and Harrington 2001), and (4) ancillary food sources (Carey and Harrington 2001, Ransome and Sullivan 1997, Thysell et al. 1997b). Studies suggest the hypothesis that simultaneously high populations of northern flying squirrels, Townsend's chipmunks, and Douglas' squirrels in the Douglas-fir keystone complex—a characteristic of old, natural forests (Carey 1995)—results from ecological processes of development of habitat breadth and niche diversification (Carey et al. 1999b) and not a single limiting factor (Carey 2001, Carey and Harrington 2001) or single limiting process.

The chemical composition of truffles suggests high food value (Fogel and Trappe 1978), but digestibility of truffles is low, near the minimum for maintenance of squirrels (Cork and Kenagy 1989). Truffle genera differ in digestibility, different taxa provide different nutrients to squirrels, and squirrels differ in ability to extract nutritive value from truffles (Townsend's chipmunk is less capable of extracting nutrients from truffles than the northern flying squirrel). Thus, dietary diversity may be important for nutritional adequacy. Great abundance, high detectability (through odors that attract squirrels), and low handling time for truffles maximize net yield of energy and nutrients to squirrels, but a high-quality diet requires more than just truffles (Cork and Kenagy 1989). Squirrels eat a wide variety of truffles and mushrooms and, sometimes, vascular plant material (especially seeds and other reproductive parts). Townsend's chipmunk and Douglas' squirrel eagerly consume conifer seeds as well as seeds and fruits of other plants and fungi (Maser et al. 1978, Smith 1970, Sutton 1993). Across their range, northern flying squirrels consume a wide variety of lichens, nuts, seeds, fruits, staminate cones, and catkins (Wells-Gosling and Heaney 1984) but not much conifer seed. Flying squirrels in the West primarily are mycophagous year-round, although lichens are important winter foods in some areas (Carey 1995; Carey et al. 2002, 1999b; Currah et al. 2000; Maser et al. 1985, 1986; Rosentreter et al. 1997). Flying squirrels may consume 15 grams of truffle in a single meal; stomach contents (mostly spores) may weigh 24 to 71 grams for squirrels with a live mass of 152 to 165 grams. But even relatively small amounts of high-quality food are nutritionally significant to squirrels given the low food value of truffles (Cork and Kenagy 1989). Thus, flying squirrels are not strictly mycophagous, even though fungi dominate their diets. Flying squirrels and chipmunks eat lichens, mushrooms, staminate



cones, pollen (e.g., cottonwood), seed (e.g., bigleaf maple; conifer seed by chipmunks), and fruits (e.g., salal) in addition to truffles.

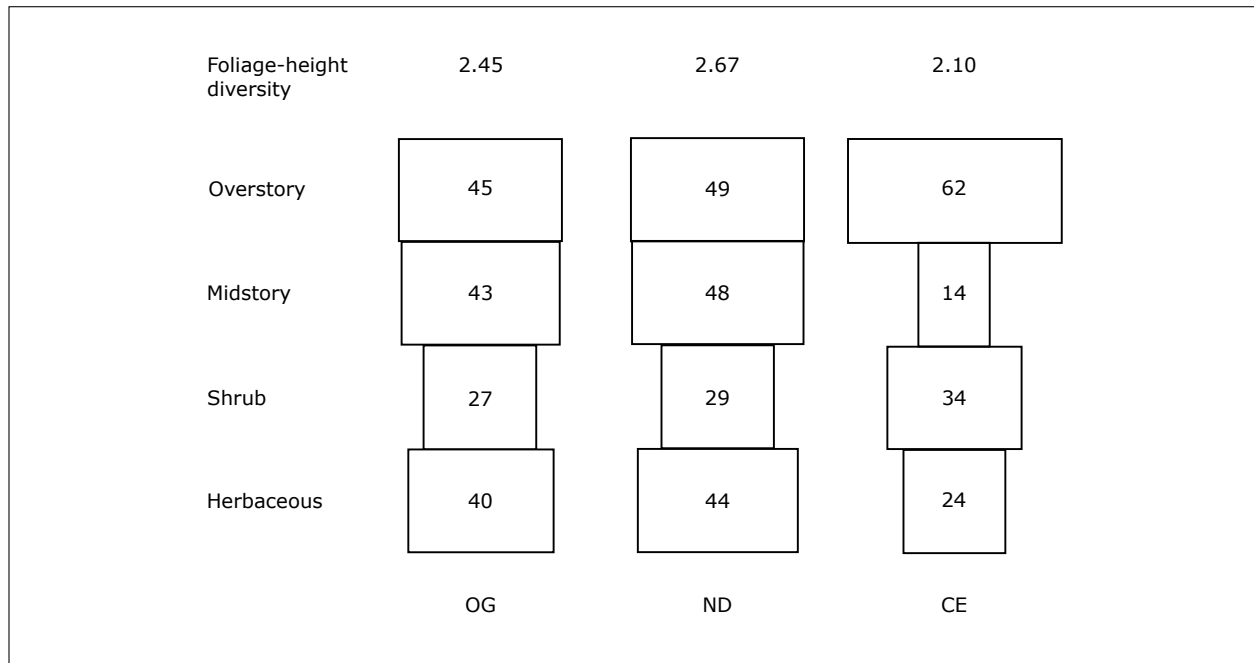
**Importance of soil organic matter and fungal diversity**—Fungal diversity does more than provide diverse diets for squirrels. Fungi are essential in many food webs; their exudates and hyphae link above- and belowground processes by providing photosynthetically fixed carbon to rhizosphere consumers such as bacteria, protozoa, and arthropods. Roots and mycorrhizal symbionts account for 70 to 80 percent of net primary productivity; 10 to 40 percent of total photosynthates pass from roots to rhizosphere adding organic material to the soil and enhancing soil structure. Diversity in mycorrhizae provides resilience to environmental stresses and may extend the range of environments within which plants can prosper (Perry et al. 1989). Each fungal species is thought to have its own set of physiological characteristics; thus, their activity differs with temperature and moisture, and they differ in the nutrients they extract from mineral soil and organic matter (Molina et al. 1992, Molina and Trappe 1982, Perry et al. 1989). Diversity in the plant community can be quite important in stabilizing belowground mutualists after catastrophic disturbance (Perry et al. 1989). Although much of the composition of plant communities in Pacific Northwest forests is a result of the processes of canopy stratification and understory development, ectomycorrhizal linkages among plants can reduce competition for resources, promote forest recovery after disturbance, and influence the pattern of plant succession (Amaranthus and Perry 1994, Molina and Amaranthus 1991). Thus, forest-floor structure, plant-community composition, fungal-community composition, and animals interact in mutually reinforcing ways to produce ecosystem resilience and development. Overall, biodiversity stabilizes community and ecosystem processes, if not population processes (Tilman 1996).

## **Canopy Stratification**

Jerry Franklin likes to say that forests mature like men do—the living biomass progressively slips downward (see also Massman 1982). Processes leading to transfer of foliage abundance from overstory to midstory and understory and even the occurrence of a midstory differ among seral stages (fig. 66). In competitive exclusion, a sparse midstory may develop when conifers grow taller than their deciduous contemporaries. This midstory contributes little to foliage-height

diversity and seems coincidental with understory development (Carey et al. 1991, 1999b). However, portions of some 40- to 70-year-old stands in the Oregon Coast Range had high foliage-height diversity; these were used for roosting by the northern spotted owl (Carey et al. 1992). In niche diversification, stratification occurs as a result of (1) retention of live old trees and possibly advance regeneration from previous stands, (2) development of a predominant even-aged cohort of conifers of mixed species following catastrophic wildfire (say 100 years before), (3) establishment of deciduous trees following catastrophic wildfire, and (4) subsequent establishment of a third cohort of conifers (including Douglas-fir) after noncatastrophic wildfires. Foliage-height diversity is great, distributed among midstory, overstory, and herbaceous cover with mean values about 45 percent with shrub cover lower, less than 30 percent. Mean midstory cover is much greater than in competitive exclusion (less than 15 percent) and similar to old growth (also 45 percent). Early histories of old-growth stands are generally unknown or only partially explainable from dendrochronology (Tappeiner et al. 1997). Nevertheless, in southwestern Oregon, 210- to 350-year-old overstories were a mix of species, and midstories were primarily shade-tolerant conifers, bigleaf maple, and Pacific madrone. In the Coast Range, bigleaf maple is most abundant in old growth (Carey et al. 1999b, Spies 1991). Shade-tolerant conifers in the overstory (western hemlock, western redcedar, incense-cedar, grand fir) often are contemporaries of the dominant Douglas-fir and a result of midstory trees gradually

**Figure 66**—Foliage-height diversity profiles showing the Berger-Parker index and percentage of covers (in boxes) by vegetation layers for old-growth (OG), niche-diversification (ND), and competitive-exclusion (CE) stages in Oregon Coast Range, 1986–87 (Carey et al. 1999b). The Berger-Parker index is a scientific measurement for foliage-height diversity—the larger the number, the larger the diversity in vegetation layers.



entering the canopy. Midstories tend to merge with overstories and understories in old growth; foliage-height diversity is high.

Development of high foliage-height diversity and spatial heterogeneity in forest plant communities depends on growth of shade-tolerant tree seedlings in the understory into the midstory. Light is usually the factor limiting seedling development on moist, fertile sites, but root competition for nutrients and moisture among various plants may occur on dry and infertile sites (Coomes and Grubb 2000). Dry woodlands allow 20 times more light to penetrate than wet forests do. Both overstory trees and understory shrubs influence seedling recruitment in ponderosa pine forests (Keyes et al. 2001). Thus, germinants, seedlings, and saplings exhibit significant spatial aggregation. A high prevalence of patches of dense shrub cover in niche-diversification west-side Douglas-fir forest may be due to intermediate-scale disturbances (tree-fall gaps, small wild-fires, windthrow, ice storms). Silvicultural thinning has the potential to promote growth of the retained dominants while encouraging growth of shade-tolerant trees in the midstory; the density of retained trees, the timing of multiple entries, and the sizes and crown classes of trees being removed can be varied as appropriate to forest type and local conditions, while also creating spatial heterogeneity and recruiting dead wood to the forest floor (Carey 1995, 2003a, 2003c; Carey and Johnson 1995; Carey et al. 1999b, 1999c; Garman et al. 2003).

Deeply layered vegetation in old growth and niche diversification results in cool and humid conditions in the understory and protection from radiation and drying winds; moistness of forest also increases with amount of decomposing wood (Spies 1991). Thus, late-seral forests have greater covers of herbaceous plants and more diverse shrubs than competitive-exclusion forest. Complexity of structure and resulting variety in microclimates results in greater numbers of plant species and greater percentage of cover per species than in homogeneous stands (Carey 2003a; Carey and Curtis 1996; Spies 1991; Thysell and Carey 2000, 2001a). Deciduous tall shrubs and trees, in particular, add substantially to biodiversity by providing foliage for consumption by insects (especially moths and butterflies, whose larvae are eaten by birds and terrestrial insectivores), an architecture hospitable to lichens, and fruits (flowers, catkins, seeds, and nuts) of high food value for insects, birds, and mammals (Bunnell et al. 1999, Carey 2000a, Muir et al. 2002). Thus, complexity and species diversity translates into habitat breadth and preinteractive niche diversification. Habitat breadth accounts for more variation in small mammal activity than does decadence (Carey and Harrington 2001,

Carey et al. 1999b). Canopy stratification, however, was the single best descriptor of the realized habitat of chipmunks. Midstory cover had the most predictive power for chipmunk activity. Decadence and canopy stratification seemed of nearly equal importance in explaining variance in chipmunk carrying capacity. Although canopy stratification explained only 11 percent of the variance in vegetation structure among points, its process seemed to have profound influences on the plant and squirrel communities.

**Gaps and stratification**—In older forests, development of diversity in vegetation structure and composition stems from small-scale, gap-forming processes (Poulson and Platt 1989). In coastal temperate rain forests, over 50 percent of the forest area is influenced by canopy openings due to the death of 1 to 10 trees (Carey et al. 1999b, Lertzman et al. 1996, Spies and Franklin 1989, Spies et al. 1990, Stewart 1986). Tree-crown overlap in old growth averages only 15 to 30 percent. The median size of gaps is less than 100 square meters in old growth but less than 20 square meters in mature forest (Spies et al. 1990). Death of 5 to 10 large, adjacent trees, although rare, would cause gaps of 1,100 square meters. Gaps more than 0.1 hectare and relative tree densities more than 3.5 promote seedling growth in the understory (Brandeis et al. 2001, Coates 2000). Gaps are rare in competitive-exclusion and biomass-accumulation stages, although diseases like root rot can form small to moderately sized gaps.

Overlap among tree crowns in old growth is due in large part to subdominant western hemlock (Spies et al. 1990). This development of midstory vegetation maintains connectivity among tree crowns that facilitates travel by arboreal rodents (Carey 1996). Full foliage-height profiles, found in niche diversification and old growth, facilitate exit from and entry to the canopy by providing protection from predation associated with gliding over open areas and with tall expanses of clear tree boles characteristic of competitive-exclusion forests (Holmes and Austad 1994, Stapp 1994). Stratified canopies provide increased niche space for summer and winter birds (Carey et al. 1991, Shaw and Flick 1999). For chipmunks, the value of midstory might be in variety and abundance of seed production by conifers, hardwoods, and understory shrubs. To the benefit of all squirrels, gaps may result in increased fungal production through extended root networks of the dominant Douglas-fir, ameliorated microclimate, increased habitat breadth, niche diversification in the forest floor, and ectomycorrhizal linkages among Douglas-fir, western hemlock, grand fir, and coarse woody debris (Molina and Amaranthus 1991, Perry et al. 1989). Furthermore, gaps create a mosaic

of open and closed canopy that promotes a mosaic of understory vegetation site types, including areas of high foliage-height diversity. This mosaic affords a modicum of protection to small mammals in areas of heavy cover and opportunities for foraging by predators in more open areas (Carey et al. 1992). Thus, gap formation and canopy stratification are prerequisite to development of complex understories.

### **Understory Development**

In the Pacific Northwest, succession of early seral communities, from the catastrophic release of ecosystem resources to tree canopy closure, depends on the biological legacies retained during disturbance, the degree of soil disturbance, and colonization by ruderals. Succession may be quite variable—a slow progression from herbs to shrubs to trees—with years, or even decades, in between stages, to quick occupancy by conifers. With invasion by grasses, the soil ecology may become dominated by bacteria instead of fungi, and a long delay may occur before trees become established. On the other hand, joint establishment of multiple life forms is common, and there are strong and predictable relationships between herbs and woody plants (McKenzie et al. 2000a). In some cases, deciduous trees may grow quickly and suppress conifers; in other cases, when both are present, conifers may eventually grow through and overtop the deciduous trees. In most cases, trees, by virtue of sustained growth, longevity, and size, quickly dominate the site (Halpern and Franklin 1990, Halpern and Spies 1995, McKenzie et al. 2000a). In Alaska, alder-conifer mixes maintain a species-rich and abundant understory, even compared to old growth. Herbs and shrubs increase after logging then virtually disappear if the tree canopy is dominated by conifers; the understory may remain depauperate for more than 100 years (Hanley, in press). Light precommercial thinning can produce a short-lived increase in shrubs with a slight increase by herbs, especially forbs; heavier thinnings offer more promise of promoting understory that is favorable to other life forms, such as deer; but if thinnings are too heavy, producing over 60 percent full sunlight, then western hemlock will regenerate. Depending on tree density, the tree canopy may quickly close or slowly close but often, without disturbance, the end result is a stage of competitive exclusion with little understory. Sooner or later, the understory will begin to develop. Thus, in areas where trees become well established, understory development contributes relatively little (10 percent) to the variance in



forest vegetation. In the relatively dry Oregon Coast Range, much of the differences among stands and seral stages in understory development seemed related to relative abundance of ferns and shrubs and to composition of the shrub community (Carey et al. 1999b). Most competitive-exclusion stands have salal as a component of the shrub layer, with 1 to 3 other species, particularly oceanspray, California hazel, or huckleberry, present in small quantities. Herbaceous layers are dominated by moss, oregongrape (as a low, prostrate shrub), and swordfern (Thysell and Carey 2000). Natural and silvicultural thinning can promote diversity and growth in understory (Muir et al. 2002; Tappeiner and Zasada 1993; Thysell and Carey 2000, 2001a) with profound effects on food webs (Carey 2003a, Hayes et al. 2003, Muir et al. 2002). In niche diversification and old growth, however, Pacific rhododendron, vine maple, and conifer seedlings and saplings were added to salal, oceanspray, and huckleberries. A diversity of species and growth forms occurred in the herbaceous layer: low shrubs, half-shrubs, ferns, forbs, grasses, and mosses. Nonetheless, few plant species in Pacific Northwest coniferous forests are confined to a particular seral stage (Carey et al. 1999b, Franklin and Dyrness 1973, Spies 1991).

Abundances of vascular plants and community diversity increase with stage of forest development (Halpern and Spies 1995, Spies 1991, Stewart 1986). Four processes influence understory development: (1) resource availability, (2) horizontal spatial heterogeneity, (3) vertical diversity of vegetation, and (4) fire (Carey et al. 1999b, Spies et al. 1990). Aggressive shrubs of low to moderate shade tolerance (e.g., salal) form dense patches under uniform, open canopies (Thysell and Carey 2000, 2001a). In tall old-growth and niche-diversification forests, shade-tolerant species are favored. Old-growth understories tend to be relatively cool and humid during dry seasons because they are protected from radiation and drying winds by deep, multiple, canopy layers. Accumulated coarse woody debris and litter on the forest floor act as moisture reservoirs. Gaps in canopies provide marked horizontal heterogeneity in the spatial distribution of light and moisture. Sunflecks of brief duration contribute 37 to 68 percent of total photosynthetically active radiation (Canham et al. 1990). Penetration of light into the understory adjacent to gaps is significant at high latitudes because of sun angle. Even though the mean and range of light levels increase with size of gaps, potential duration of light is still below 4 hours and varies inversely with canopy height (70 meters in old-growth Douglas-fir). Development of shade-tolerant midstories can have significant impacts on the amount of light reaching the understory. Light penetration also differs with

gap orientation; north-south gaps admit more light than east-west gaps (Poulson and Platt 1989). Changes in topographic position and edaphic gaps increase heterogeneity in light conditions, and, with 30 percent of the forest area in gaps, 56 percent of the forest area is influenced by canopy openings (Lertzman et al. 1996).

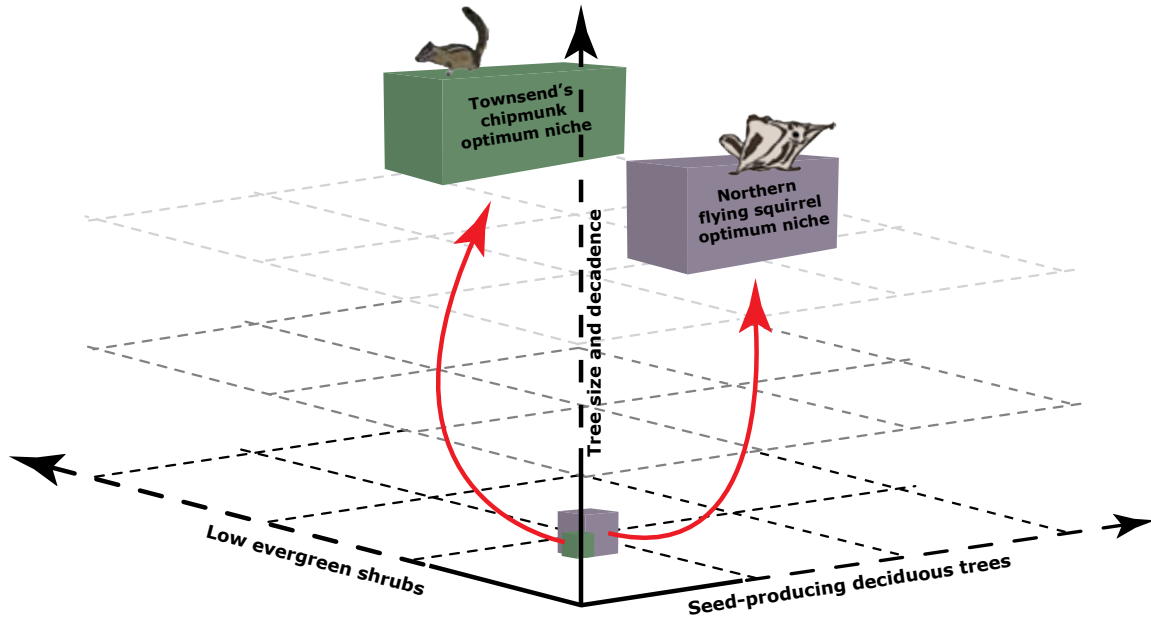
Understory development influences animal populations. For example, understory development is a minor but significant predictor of the realized habitat of flying squirrels, chipmunks, and many other small mammals (Carey 1995, Carey and Harrington 2001, Carey and Johnson 1995, Carey et al. 1999b, Carey and Wilson 2001). Chipmunks increasingly select home ranges with heavy understory as midstory decreases (that is, from old growth to niche diversification to competitive exclusion). The prevalence of patches of ericaceous shrubs also is correlated with abundances of both flying squirrels and Townsend's chipmunks on the Olympic Peninsula. Ericaceous shrubs, snags, and the nature of the catastrophic disturbance originating the stand explained 85 percent of the variance in flying squirrel activity. Patches of ericaceous shrubs covered about 40 percent of flying squirrel habitat. In the middle Oregon Coast Range, abundance of chipmunks across the early stages (ecosystem reinitiation to understory reinitiation) is highly correlated with abundance of salal but no other habitat variables (Hayes et al. 1995). Three explanations exist for correlation with ericaceous shrubs: (1) the fruits of the shrubs provide food, (2) shrubs provide cover from predation, and (3) shrub cover is correlated with some other determinant of chipmunk abundance. The importance of overhead cover to chipmunks has been experimentally demonstrated (Harestad 1991).

### **Development of Habitat Breadth**

Legacies, the four basic structuring processes of crown-class differentiation, decadence, canopy stratification, and understory development, and spatial heterogeneity combine to allow an emergent, or second-order, process to unfold. This process is development of habitat breadth and it consists of the development of a fine-scale (less than 0.2 hectare) mosaic of vegetation patches (or vegetation site types) that differ in species composition, vertical diversity in foliage abundance (foliage height profiles), and in the types and abundance of food and cover available to animals. In southwestern Oregon, spatially complex light, temperature, and moisture conditions produced 21 of these small patch types related in part to (1) landscape-level climatic gradients; (2) among-stand variation in environmental

conditions owing to slope, aspect, elevation, edaphic conditions, and stage of forest development; and (3) within-stand variation owing to site moisture, edaphic gaps, regeneration gaps, canopy gaps caused by tree death, and development of shade-tolerant midstories. All site types were found across most stands, suggesting types were more a product of ecosystem development conditioned by temperature and moisture rather than unique local phenomena. Site types can be used to measure fine-scale heterogeneity (degree of development of habitat breadth) arising from disturbance and forest development. Habitat breadth is also an index to biological diversity because diversity of fine-scale patches of vegetation influences fungal, invertebrate, and vertebrate diversity through abundance and diversity of food and cover and ameliorated microclimates (Carey et al. 1999b, Colgan et al. 1999, Schowalter et al. 2003). Fine-scale environmental heterogeneity that promotes biological diversity also is likely to foster mutualisms (Bronstein 2001) as well as mitigating competition and predation. The phenomenon of increased diversity and abundance across all major life forms following increased forest complexity (increased numbers and lengths of axes of the unrealized [unexploited] niche space) is the result of the emergent property, preinteractive niche diversification (Hutchinson 1978) (figs. 67, 68). Development of habitat breadth and niche diversification work against one or two species dominating a functional group and promote the coexistence of species—for example, green-tree retention in variable-retention harvest units in British Columbia helped prevent an irruption of Oregon creeping voles and allowed southern red-backed voles to remain moderately abundant throughout the reorganization and early development of the ecosystem (Sullivan and Sullivan 2001). In western Washington, species common during ecosystem reorganization but usually rare to missing in spatially homogeneous competitive exclusion and biomass accumulation stages are also present in experimental gaps (Gitzen and West 2002), second growth with managerially induced understory reinitiation (Wilson and Carey 2000), and old, natural forests (Carey and Johnson 1995). Thus, differences in habitat breadth along with differences in decadence can explain as much as 50 percent of the variance in flying squirrel activity and 70 percent of the variance in habitat quality.

The roles of different ecological factors differ among biotic communities and even within biotic communities that are environmentally heterogeneous. For example, vegetation heterogeneity plays a dominant role in insect population dynamics and community structure, both of which are important to insectivorous birds and mammals. Differences among species within a trophic level, differences



in species interactions in a changing environment, changes in population demography with population density, identities of individual species, and environmental variation are as important determinants of population and community dynamics as are the number of levels in a food chain, or the position of the system along a resource gradient. The effects of ecological factors can cascade up or down in the trophic system; thus flow of interactions is as important as flow of energy (Hunter and Price 1992). For example, shrubs provide food and cover to squirrels. Marked differences in ability of shrub abundance alone to explain variance in squirrel activity among studies is due to differences among studies in (1) the degree to which shrubs of various kinds are lacking, (2) variances in shrub cover relative to variances in abundance of other habitat elements, and (3) complementarity between midstory, understory, and decadence. In other words, few wildlife-habitat relationships are based on simple linear relationships involving one or two habitat elements. As Billick and Case (1994) stated, “the dynamic behavior of the full community cannot be predicted based on observations of interactions between pairs of species.” Rather, almost always a complex of elements is involved, there is redundancy in some functions of some elements, and interactions with other species are important. Large differences in coarse woody debris (5 to 25 percent cover) and shrub abundance (0 to 95 percent prevalence) among stands on the Olympic Peninsula influence the structure of forest-floor small mammal communities and the abundances of various species of shrews, mice, and voles, but even small differences in plant species composition may be as

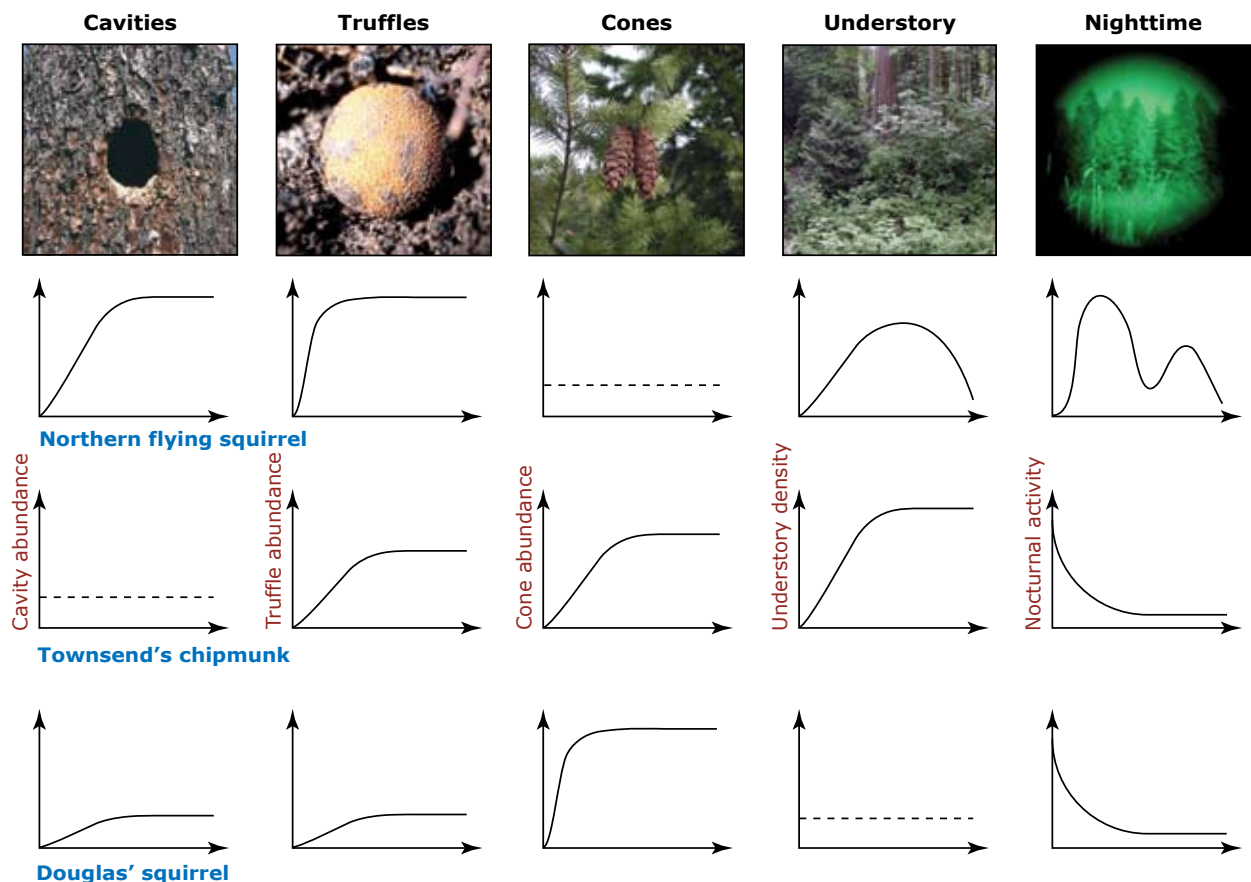
**Figure 67**—Through preinteractive niche diversification, there is an expansion of overall niche space and niche dimensions (evergreen shrubs, seed-producing deciduous trees, large conifers, decadence, etc.), providing a greater separation of species niches as well as creating more space available for a greater number of individual animals. Graphic by A. Wilson; flying squirrel illustration by J. Perkins.

important (Carey and Harrington 2001, Carey and Johnson 1995). Dimensions of potential habitat spaces (usually expressed as statistical distributions of habitat elements) determine not only habitats realized within a given space but also which factors explain the most variance in animal activity in that space. It is generally accepted that factors limiting populations differ among locales and seasons (Fretwell 1972).

### Spatial-Scale & Spatiotemporal Heterogeneity

In the ecology of fungi, vascular plants, invertebrates, and vertebrates, many ecological processes take place at a physical scale of less than 50 square meters, the level of individual organisms (the death and decay of a tree), structural features (fruiting of an ectomycorrhizal fungus in a decayed log), and the neighborhood of a dominant tree. The four structuring processes of forest biotic communities (crown-class differentiation, decadence, stratification, and understory development) take place at varying small scales—the first two at the level of individual trees and the last two at the level

**Figure 68**—Biocomplexity creates more niche dimensions, which allows different species to coexist together. Blue words represent the X-axes; Brown words represent the Y-axes. Graphic by A. Wilson; Photos courtesy of USDA Forest Service.

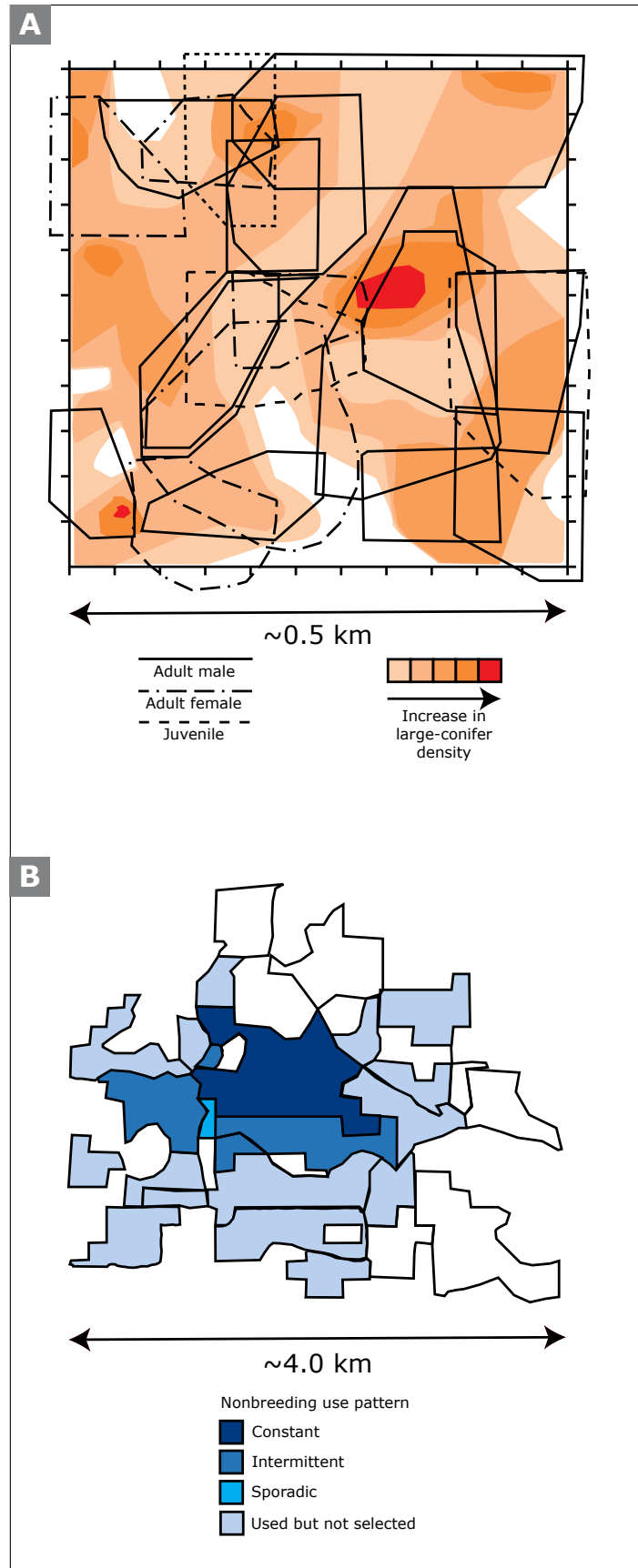




of small patches (0.01 to 1.0 hectare). The interactions among these processes that develop habitat breadth, however, are exemplified at scales of 0.1 to 0.5 hectare over areas of 10 to 100 hectares, account for two-thirds of the variance in vegetation structure across biotic communities, and can be used to differentiate realized habitat (actually occupied) from potential habitat (the total multivariate habitat space available) of organisms of intermediate mobility (small amphibians, birds, and mammals) with an accuracy of about 65 percent within biotic communities. But the four structural processes explain less than one-fifth of the variance in animal activity within biotic communities. For example, squirrels do not select any small subset of vegetation site types for their activities; their foraging patches and home ranges may differ little, on average, from the larger biotic communities in which they occur. Differences lie in the proportion of the area of the biotic community used, the size of foraging patches, the size of home ranges, and the densities of the populations (Carey et al. 1999b) (fig. 69). Amount of area used generally tends to increase with body size of mammals: red-backed voles tend to be more restricted in their movements than deer mice, and deer mice are more restricted than eastern gray squirrels (Carey 1981). Still, within a group of similar size, home ranges can differ markedly—the Douglas' squirrel is much localized in its movements (tens of meters), the flying squirrel may travel a kilometer or more in a night, over several hectares (Carey 2000a) (fig. 70). Predators, of course, tend to have larger body sizes and substantially larger home ranges than their prey. Pairs of spotted owls have home ranges spread over 500 to 3,000 square kilometers and larger depending on level of forest fragmentation, prey base, and physiographic province (Carey et al. 1992).

Processes taking place at scales of 1 to 100 hectares, the level of populations (demographic processes) and biotic communities (self-organization of the community), include, for example, competitive exclusion, development of species richness in a plant community, predator-prey interactions, and postinteractive niche separation (multivariate community spaces actually occupied by species population in the presence of other species). Habitat selection of wide-ranging vertebrates and dispersal and colonization processes of many species take place at the scale of 100 to 10,000-hectare landscapes, or even larger. Models that incorporate both demographic and environmental factors suggest that genetic diversity and divergence in populations is most affected by the proportion of biotic communities in the landscape that are occupied (as affected by disturbance frequency) and the density of individuals within the communities as

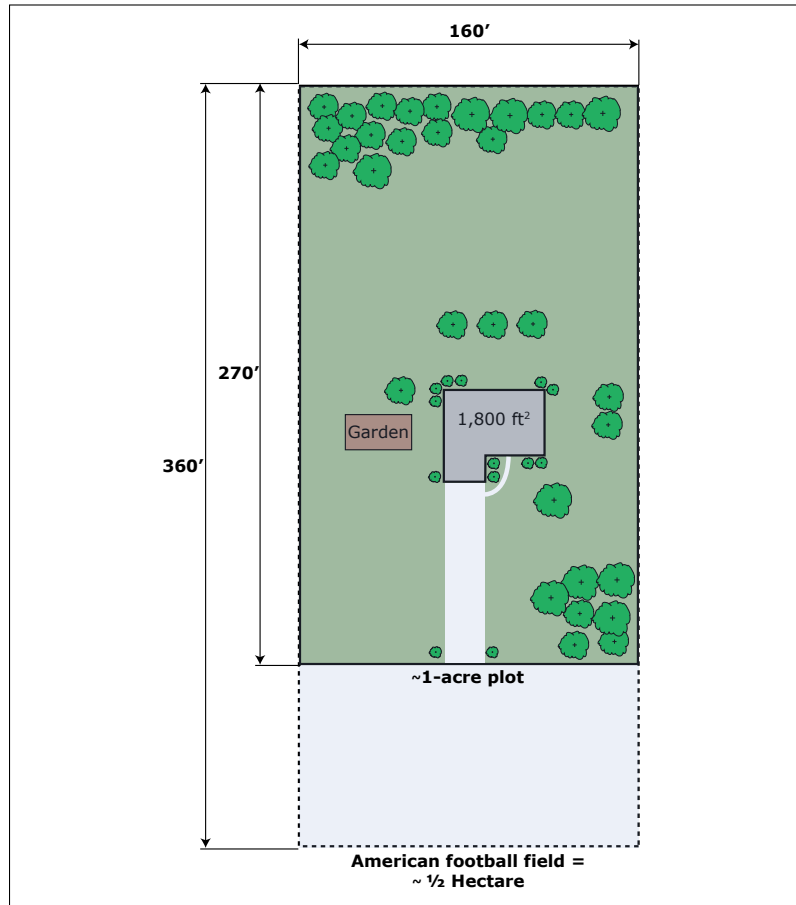
**Figure 69**—Differences in home range size: (A) Movement patterns of three northern flying squirrels on an approximately 0.5-square kilometer plot of 300-year-old trees—the darker the background color, the higher the density of large conifers; (B) areas used by a northern spotted owl across about 4.0 square kilometers of forest during the nonbreeding season (adapted from Carey et al. 1999b and Carey and Peeler 1995). Graphic by A. Wilson.



determined by habitat quality (Gibbs 2001). This is a key point in landscape design—avoidance of environmental conditions and community structure that leads to depauperate communities (low proportions of communities occupied for many species), with poor-quality habitat for many species that do inhabit them, and that also reduce permeability of the landscape to dispersal. However, highly subdivided local populations suffering frequent local extinction may retain more diversity than less subdivided populations of equivalent size (Ray 2001), suggesting that shifting-steady state mosaics, with a low-to-moderate proportion of the landscape in reorganizing and early-seral states may provide many opportunities for maintaining genetic diversity and maximizing adaptiveness. This, in essence, is part of the creative destruction hypothesis of Holling's Panarchy theory. Thus, understanding how scale interacts with habitat quality is important to AIM for conservation of genetic diversity (table 29).

Across biotic communities in the landscape, various habitat dimensions exhibit high correlations ( $r > 0.50$ ) with one another. That communities may differ in horizontal heterogeneity and vertical heterogeneity is apparent; heterogeneity, habitat space, and habitat breadth generally increase with time since catastrophic disturbance—but with niche-diversification communities having extreme values for some elements (e.g., snags and fallen trees). Structuring processes and habitat breadth explain more among-community variance in squirrel activity than individual habitat elements and provide better models of squirrel activity than even classification of communities into seral stages. Processes explain up to 75 percent of squirrel activity and squirrel carrying capacity. Managed forests in competitive exclusion, in general, have less developed niche space and coarser grain than forests in niche diversification and old-growth forests. Grain in old growth was less than the height of an old-growth tree (around 70 meters); that is, 50 meters for shrub patches, 25 meters for midstory development, and 80 meters for areas of closed canopy (Carey et al. 1999b). Small gaps (loss of one to three dominant trees) at high frequencies across old growth and low sun angles produce fine-scale heterogeneity with close juxtaposition of habitat elements (snags, fallen trees, patches of shrubs, patches of midstory, patches of herbaceous cover, patches of open forest floor) and different species and life forms. In response to increased heterogeneity on a fine scale, foraging patches and home ranges overlap more and total activity increases. Thus, accumulation of processes in late-seral, natural stands results in an emergent property of niche diversification that provides more stable habitat for squirrels; carrying capacities for squirrels have maximum values in old growth.

**Figure 70**—Visualizing acres and hectares: There are 2.5 acres in 1 hectare. An American football field is approximately a half hectare in size. A 1-acre house plot fills approximately 75 percent of a football field. Thus, a squirrel moves across a good part of a suburban neighborhood in one night. Graphic by A. Wilson.



Nevertheless, individual communities deviate significantly from average conditions within their nominal seral stages in their capacity to support squirrels and in various measures of habitat space. As Carey (1995) reported for the Olympic Peninsula, nominal seral stage may not always be a good predictor of habitat quality. Structuring processes, habitat breadth, and site moisture provide better descriptions of ecosystem development and niche diversification than nominal seral stage. Given process-based community development, AIM has the potential to accelerate niche diversification.

The role of spatial scale can be illustrated by the ecology of fishers in south-central British Columbia (Weir and Harestad 2003), goshawks in the Southwestern United States (Reynolds et al. 1992), and spotted owls in the Pacific Northwest (Carey 1985b, 1993; Carey et al. 1992, 1999b; Carey and Peeler 1995; Carey et al. 1990). Weir and Harestad (2003) described spatial scales as habitat elements within patches within biotic communities within home ranges within landscapes within the geographic range of the species. Fishers avoided areas without overhead (overstory or shrub) cover. The fishers selected areas for foraging at the biotic community and patch scales on

the basis of coarse woody debris, foliage height diversity, and shrub cover; in other words, a complex forest floor provided the primary foraging areas for fishers. However, an overly complex forest floor (more than 80 percent shrub cover), may reduce the likelihood of capturing prey, and dense canopies intercept snow, leaving the forest floor more open. Fishers selected particular habitat elements for resting and denning, such as mistletoe brooms in spruce and cavities in deciduous trees, respectively. American marten exhibited similar selectivity in Ontario (Fryxell et al. 1999).

Goshawks exhibit selectivity at multiple spatial scales in the Pacific Northwest (Finn et al. 2002), interior Northwest (Hanauska-Brown and Bechard 2003), and Southwestern United States (Drennan and Beier 2003, Reynolds et al. 1992). The northern goshawk breeds in coniferous, deciduous, and mixed forest in North America (Reynolds et al. 1992). It uses various forest types, ages, structural conditions, and seral stages. The goshawk preys on small birds and mammals including robins, grouse, squirrels, and hares. In the Southwest, it is found in ponderosa pine, mixed species, and spruce-fir forests but has been declining in response to timber harvest, fire suppression, and grazing. Reynolds et al. (1992) developed management recommendations for goshawks based on several tenets: (1) goshawks and their prey are limited by their food and habitat; (2) abundant prey reduces the probability of food limitation on goshawks; (3) a wide variety of prey is less likely to result in goshawk population fluctuations than one or two prey species; and (4) active, intentional management for goshawks can sustain goshawk habitat. They concluded that past management had produced thickets of small trees prone to fire, insects, and diseases and will require disturbance before developing further. They also recognized that forest

**Table 29—The scales and attributes of ecosystems**

	<b>Structure</b>	<b>Composition</b>	<b>Processes</b>
Regional	▪ Major landform features	▪ Regional species pool	▪ Climate, weather, and geologic events
Landscape	▪ Landscape patterns and dynamics	▪ Landscape elements	▪ Disturbance regimes
Biotic community	▪ Relative abundance of life forms, functional groups, and species	▪ Species, genotypes, and ecotypes	▪ Development, mutualism, synergy, competition, and predation
Population	▪ Age structure and sex ratio	▪ Genetic diversity	▪ Colonization, birth, death, and dispersal

Source: Adapted from Noss 1990.



reorganization, growth, and development differ with location and that no single management prescription is likely to be appropriate for all sites. Large live trees, snags, and fallen trees, however, are important elements of the habitat of a variety of plants and animals and *every hectare should contain several*. A landscape most suitable to goshawk persistence would be one of an interspersed mosaic of developmental stages.

Goshawk habitat requirements include two to four nest patches (around 12 hectares) of large old trees with dense canopy cover. A family area of 170 hectares around a nest patch consisting of a variety of forest types and conditions is necessary for fledglings to hide in (patches of dense trees) and to learn hunting techniques (patches of herbaceous and shrubby understory mixed with small openings, snags, and logs). A larger foraging area of around 2,200 hectares is needed. This latter area is best characterized by large trees, relatively open understories, with small (0.1 to 0.8 hectare) to medium (0.8 to 1.5 hectare) openings (with a maximum width of 40 to 60 meters), with dense patches of thickets scattered throughout; the majority should be mid-aged to old forest (Reynolds et al. 1992). Active, intentional management techniques include long (200- to 300-year) rotations, legacy retention with live legacy trees in groups of 3 to 6 with 2 to 5 groups per hectare, 5 to 7 snags per hectare, 7 to 12 fallen trees per hectare, and 12 to 35 megagrams of coarse woody debris per hectare; thinning from below with non-uniform spacing, minimizing road density and permanent skid trails; and prescribed burning to reduce fuels. Projected benefits beyond those to goshawks include improved landscape function, habitat for old-growth species, reduced susceptibility to catastrophic disturbance, increased forest productivity, enriched mycorrhizal communities, forest products, and forage production.

Spotted owls selectively use old forest out of proportion to its occurrence in mosaic landscapes, and concentrations of old forests result in smaller home ranges and more stable social structures (Carey et al. 1992, Carey and Peeler 1995, Carey et al. 1990). Selection for complex forests and forest floors for foraging is related to prey abundance and opportunities to catch prey for spotted owls in the Pacific Northwest (Carey et al. 1992, 1999b); but as old forests are fragmented, prey may be depleted temporarily by owl predation, and owls may switch to younger forests, especially younger complex forests, where prey may be temporarily higher than in the exploited old growth. Thus, at the landscape level, replacement of late-seral forest by ecosystem-reorganization and competitive-exclusion stages has negative effects on spotted owls (Carey and Peeler 1995). These

managed forests are avoided or used rarely, although, where dusky-footed woodrats are abundant, owls may forage along forest-clearcut edges (Diller and Thome 1999, Giusti 1999, Solis and Gutierrez 1990, Ward et al. 1998) and in early-seral stages (Carey et al. 1992). But managed and natural forests more advanced in development (understory reinitiation and niche diversification) may be around 25 percent of the areas regularly used by spotted owls for roosting and foraging. The biomass of squirrels (Douglas' squirrel, northern flying squirrel, and Townsend's chipmunk) increases with forest development (Carey 1995). The size of all three squirrels makes them especially attractive to predators common in Pacific Northwest forests, such as hawks, owls, and weasels. The squirrels are near the maximum size limit for many of these predators. Abundances of chipmunks, flying squirrels, and Douglas' squirrels increase with forest development despite overlap in their diets, den site use, and space use (Carey 1991, 1995; Carey et al. 1999b, 1997). The squirrels seem limited by variability in food abundance and dens but not interspecific competition in complex environments. Late stages of forest development provide habitat structure that mediates predation and variety in fruit production that offsets high variability in availability of individual food items. The resulting increased prey biomass attracts and supports predators.



# AIM for Resilient Forests

Active, intentional management for resilient, biologically complex forests has the purpose of maintaining forested ecosystems and landscapes that first and foremost are capable of adapting to changing environmental conditions, including global climate change. Managing for resiliency is the first obligation for intergenerational equity. Managing for biocomplexity serves the purpose of maintaining biological diversity and the diverse values contemporary society desires from its forests, including broad values of environmental sustainability, social civility and equity, and economic activity. These values are diverse: clean air and carbon sequestration; clean water with modulated flows; open, green space; aesthetic, natural places for recreation and spiritual renewal; complete biotic communities of plants, fungi, invertebrates, and vertebrates; healthy soils with minimal erosion; abundant populations of various species of wildlife and fish; provision for subsistence hunting, fishing, and gathering guaranteed to Native Americans as obligated by treaties; opportunities for hunting, fishing, and gathering by other people; opportunities for wildlife viewing and nature study; sustainable flows of wood products that allow society to meet its needs domestically from environmentally beneficial forestry without contributing to degradation of the environment in less-developed countries and that contributes to

**Sidenote 60**—The Seven Stages of Ecosystem Management (Brussard et al. 1998)—Ecosystem management is managing areas at various scales in such a way that ecosystem services and biological resources are preserved while appropriate human uses and options for livelihood are sustained. The stages of ecosystem management are:

- Delineate the system to be managed.
- Define strategic goals [degree of intentionality].
- Develop a comprehensive understanding of the ecosystem.
- Analyze the socioeconomic contexts.
- Link the socioeconomic and ecological understandings in a heuristic model.
- Implement experimental management actions.
- Monitor results, assess long-term success or failure, and apply learning to the next management action.

domestic economic activity and the support of rural communities; sustainable flows of commercial nontimber products such as mushrooms, floral greens, and other natural products; and revenues to landowners be they federal, state, trusts, corporate, or nonindustrial, small, private landowners. This is a tall order.

Management can be passive (the choice is made not to intervene in any way except to reduce or exclude human activities), reactive (responding only to threats or emergencies), or active (deliberate actions are taken). Passive management includes designation of reserves, such as research natural areas, wildernesses, national parks, late-successional reserves, and areas devoted to particular species. The Nature Conservancy has a long history of success in establishing reserves of especially valuable (aesthetically, scientifically, biologically, and rare in the landscape) ecosystems. Some actions, such as fire threat reduction and restoration activities, may be appropriate in some of these reserves. Passive and reactive management contribute to achieving some of the goals of AIM (including some that cannot be achieved with active management, such as protection of old-growth forests) but cannot fully achieve AIM for multiple values. Active management of forests occurs anytime silvicultural practices are implemented, even when the stated intent is management for one or a narrow set of particular products, species, or structures rather than management of processes. This, of course, is not the same as AIM for resilient, complex forests that are valued by people for diverse reasons. This difference between common active management and AIM is in intent. Active, intentional management can be evaluated by using the concept of intentionality—the degree to which all information (social, economic, and ecological) has been considered in determining how to manage ecological processes for sustainability of complex social, economic, and ecological systems (that is, what the manager thinks about in deciding “what to chop”). Thus, AIM, and other less-developed forms of ecosystem management (Brussard et al. 1998, Grumbine 1994) (sidenotes 60, 61), are significant in that they focus on whole systems (AIM addresses holarchies), not some few parts of a system; they include public involvement in goal setting (AIM extends that to on-the-ground collaborative management and monitoring); they integrate conservation into economic activity (AIM includes noncommodity instrumental values and aesthetic-spiritual values as well); and they shift from a paradigm of linear comprehensive management to cyclic-incremental or adaptive management (AIM extends this shift to nonlinear thinking and managing for system adaptiveness). Ecosystem management has as its overriding goal to “ensure that ecological services and biological

resources do not erode irreversibly as a result of human activities;” sustainable ecosystem management maintains or enhances current utility, future potential, containment, and resilience (Brussard et al. 1998) (sidenote 62). On the other hand, AIM seeks to integrate values for ecological services and biological diversity into the very thought processes underlying management. Active, intentional management attempts to integrate applied sciences—forestry, wildlife management, range management, recreation management, epidemiology, integrated pest management, fire threat reduction, transportation system management, and forest engineering. Also, AIM emphasizes maintaining a high diversity of species, keystone complexes, ecosystem function, and ecosystem adaptability to changing environmental conditions. There are well-documented (1) patterns of commonness and rarity of known species—most are rare (Preston 1948, 1960, 1962a, 1962b, 1969, 1980, 1981); (2) significant roles of randomness and stochasticity in influencing species occurrences (Hubbell 2001); (3) substantial ignorance of most species (most have yet to be described); and (4) inevitable change in ecosystems (sidenote 63) and the composition of their biotic communities through time and space, all of which owing to the increasing stress from increasing human populations, species invasions, global climate change, surprises, and shifts among alternative stable states (Gunderson and Holling 2002, Johnson and Mayeux 1992, Paine et al. 1998, Tausch et al. 1993). Active, intentional management does not pretend to maintain all species in every place where they once occurred or where they could potentially occur under extant conditions. It does seek to conserve biological diversity and recognizes the special values of keystone, flagship, relict, aesthetic, and charismatic species, species diversity, and functional group diversity to ecosystem stability (table 30) and productivity, conservation of nature, and to people; thus, AIM focuses on reality and empiricism when setting goals. For example, species dominance, and even membership, of functional groups might change, but the ecological function may be retained; reduction of the diversity within functional groups, then, may result in loss of system adaptiveness. Active, intentional management seeks to control the introduction of, and to remove, introduced and damaging exotic species but also recognizes species introductions will occur no matter what steps are taken and that not all introduced species will result in significant impairment of ecosystem function or loss of native diversity. And not all introductions of damaging species, from whatever source, will be reversible, even with substantial effort. Thus, AIM focuses as much as possible on (1) management of processes to maintain native diversity and maximize resilience and adaptiveness;

**Sidenote 61**—What is ecosystem management? (Grumbine 1994)—Ecosystem management is integration of scientific knowledge of ecological relationships within a complex sociopolitical and values framework toward the general goal of protecting ecosystem integrity, including the protection and maintenance of:

- Natural ecosystem types (biotic communities)
- The diversity of native species
- Ecosystem health and integrity
- Ecosystem processes
- Ecosystem services
- Human economies based on ecological principles
- Sustainable production of ecosystem products

**Sidenote 62**—“Viable” systems (Brussard et al. 1998):

- Currently provide expected goods and services with reasonable efficiency
- Have present uses that are not disrupting processes, which generate and maintain the desired composition, structure, and function of the ecosystem or its future potential
- Have a present use and current condition that does not degrade areas beyond the systems borders
- Have the capacity for self-maintenance and self-regeneration after moderate external stresses or perturbations



**Sidenote 63**—Ecosystem stability and the balance of nature according to Johnson and Mayeux (1992):

- Common assumptions about ecosystem stability and a delicate balance of nature are unwarranted paleoecologically, biochronologically, and biogeographically.
- Species have been *added* and *removed* without greatly affecting ecosystem function.
- Natural ecosystems exhibit greater stability (inertia) in physiognomic structure and functional processes than in species composition.
- Some ecosystems persist in unstable rather than stable states.

And according to Tausch et al. (1993):

- There is no natural vegetation (equilibrium condition); plant communities differ in space and time.
- No area is without some human impact.
- No management is impossible given human impacts and exotic invasions.

(2) use of developmental pathways and trajectories to predict and manage for future conditions; and (3) use of baselines, benchmarks, and monitoring of carefully selected groups of species to judge failure, progress, and success (table 31). Active, intentional management strives to integrate individual, social, economic, and environmental values into a coherent whole that is normative in determining which human demands and management practices are appropriate in managing the interactions of individuals, human communities, and biotic communities. Key fundamental values for AIM for general sustainability include intragenerational, transnational, and intergenerational equity. Intentional management requires broad participation by stakeholders and a new, sophisticated role for scientists as (1) science interpreters; (2) decentered participant-facilitators of issue formulation, debate, and issue resolution; (3) modelers and testers of resolutions; and (4) participant-facilitators in group learning (sidenote 64). Good AIM requires separating the wheat from the chaff in collaborative experimental learning processes, embracing ambiguity, uncertainty, and change, and proceeding with the highest intentions and most decentered views.

## Components

A dozen or more on-the-ground tactics are used in AIM strategies for biodiversity, biocomplexity, resilience, and general sustainability.

## Legacy Retention

Active, intentional management extends the concepts of green-tree retention, snag retention, structural retention, and variable-retention harvest systems to retention and maintenance of both biological and geological legacies during every step of active management. In managed forests, variable-retention harvesting is often the catastrophic disturbance/creative destruction event/reorganizing force that sets the stage and determines the species retained onsite to reorganize into a new community. Legacy retention should be integrated with protection of rock outcrops, talus slopes, balds, meadows, seeps, springs, wetlands, headwater streams, colluvial soil, areas of deep-seated landslides, areas of shallow-rapid landslides, streamsides, riversides, and areas of excessively poor potential for growth of trees. These geological features form a template for the retention of intact patches of forest (clumped and linear legacy retention) and form the

first basis of a landscape mosaic. The degree of retention of biological legacies outside these patches then differs inversely with rotation age of forests (time between major harvests that result in ecosystem reorganization) and size of harvest units: the shorter the rotation age, the greater the legacy retention in variable-retention harvest systems; the larger the harvest unit, the greater the retention. Both Washington and Oregon (and many other states) have minimum guidelines for retention outside of the geologic areas. The goal of AIM is to maintain a biologically-complex forest over the landscape

**Table 30—Characteristics of ecosystem stability and resilience that can be used predictively or in monitoring**

Characteristic	Definition	Example
Inertia	<ul style="list-style-type: none"> <li>Resistance to change in structure, function, or trajectory of development</li> </ul>	<ul style="list-style-type: none"> <li>A gap-phase complex-forest mosaic is unaffected by low to moderate tree mortality because trees regenerate and grow; even gaps of 5 to 7 trees can be assimilated. A conifer forest with poor height : diameter ratio has little inertia in the face of wind, ice, or snowstorms; older ponderosa pine parklands are little affected by low- to moderate-severity surface fires.</li> </ul>
Elasticity	<ul style="list-style-type: none"> <li>Rapidity or time of restoration of structure, function, and trajectory of development</li> </ul>	<ul style="list-style-type: none"> <li>Older closed-canopy Douglas-fir monocultures may have less elasticity than a multispecies multitolerance complex; a multispecies complex may require 120 years to develop from reorganization to niche diversification; fire-prone lodgepole pine forests recover rapidly from crown fires owing to serotinous cones.</li> </ul>
Amplitude	<ul style="list-style-type: none"> <li>Brittleness, or range of disturbances from which the system can recover structure, function, and trajectory</li> </ul>	<ul style="list-style-type: none"> <li>Complex forests in landscapes of complex forests may recover from minor to catastrophic disturbance; simplified forests may not recover complex structure and function from even patch-level disturbances such as root rot; with prolonged fire exclusion, many forest types may not recover after a catastrophic disturbance.</li> </ul>
Hysteresis	<ul style="list-style-type: none"> <li>Degree to which restoration is an exact reversal of the path of degradation, more relevant to chronic than acute disturbance</li> </ul>	<ul style="list-style-type: none"> <li>After disturbance, do the last species to die return first, or are they last in a succession of species? What happens when livestock are removed from a range?</li> </ul>
Malleability	<ul style="list-style-type: none"> <li>Ease of permanent alteration; degree to which the recovered system differs from the original system prior to disturbance</li> </ul>	<ul style="list-style-type: none"> <li>Depending on disturbance regime, a complex forest may return along a continuum from a complex state of high biotic integrity to a species-poor, simplified alternative stable state.</li> </ul>

Source: Adapted from Westman 1978.

**Sidenote 64**—Roles of scientists, technologists, and land managers in collaborative management:

- Scientists are often (1) historians of the development of new knowledge and new practices; (2) philosophers, relating science to different values (Ph. D. is doctor of philosophy—the study of the nature and principles of knowledge, truth, existence, and moral and aesthetic values); (3) technical or technological experts and advisors; (4) informed public citizens; and (5) critical thinkers.
- Technical specialists play different roles—they (1) help to set organizational priorities and management standards; (2) compile specific local information on environmental variables, populations, and habitat relationships; and (3) make measurement and collect data.
- Land managers often (1) know the history of specific pieces of land—its characteristics, use and utility, and response to management; (2) have conducted case history experiments; (3) serve as implementers of management decisions; (4) may offer a particular land ethic; and (5) may be knowledgeable about economic, agronomic, and ecologic productivity.

and each site, biotope, and ecosystem within the landscape. In western Washington, conservation of biodiversity seems to be possible if less than 15 percent of the landscape is in early-seral stages of forest development in any decade and about 15 percent of each variable-retention harvest unit is retained as forest. Actual retention, however, must be determined in major part by the combination of geologic influences on retention and effects of rotation age and harvest unit size on reducing forest influence at the level of site and landscape.

During intermediate treatments (precommercial and commercial thinnings), legacies should be identified, protected, and enhanced. Skips in thinnings can be used to protect ecologically important features such as cavity trees, moderately decayed snags, small wetlands, intact patches of forest floor, and legacies left during the preceding reorganizing disturbance (such as intact patches of older forest). Large fallen trees can be protected and even sometimes moved and replaced to facilitate movement of equipment. Gaps can be used to favor growth of selected trees like bigleaf maple or madrone, promote epicormic branching on legacy trees, and release advanced shade-tolerant regeneration.

## Multispecies Management

At each step of active management from variable-retention harvests to planting to precommercial and commercial thinning, care is taken to ensure multiple site-appropriate trees species are maintained. Two or more species of conifers and two or more species of deciduous trees are desirable for numerous ecological and economic reasons, but not, of course, in equal abundance. Beyond trees, in making decisions about what to manipulate, attention is paid to promoting a variety of tall shrubs as well. The relative abundances of species to be promoted differ with site, potential natural vegetation classifications, predictions about what might happen to plant communities with climate change, management of decadence (e.g., maintaining deciduous trees that might become cavity trees and conifers, like grand fir, that have high potential to form hollow trees), and opportunities for diversification of wood products in terms of species (e.g., Douglas-fir, western redcedar, and red alder all have different markets) (figs. 71, 72).

## **SAVE Trees and Shrubs**

Over 50 species of trees and shrubs in the Pacific Northwest have special attributes that are valuable ecologically (SAVE). These SAVE trees exist in almost all forest (see, e.g., Carey and Gill 1980 and Carey and Healy 1981 for Appalachian forests). Wilson and Carey (N.d.) provide a list of these for the Pacific Northwest (table 3.2) and guidance on marking for retention during precommercial and commercial thinning and variable-retention harvesting. A few of these go a long way. If absent, seeding and underplanting some of these may be appropriate.

## **Planting, Underplanting, and Seeding**

Planting is used to recover a forested condition quickly and to ensure some minimum level of tree species diversity and density. Substantial natural regeneration usually accompanies planting. When management or lack of management has resulted in closed-canopy monocultures, underplanting and seeding can be useful tools to restore lost diversity of trees and shrubs, particularly tall shrubs, deciduous trees, and shade-tolerant trees, depending on site and region.

## **Precommercial Thinning**

After legacy retention, precommercial thinning provides the next most important intervention to ensure that biological diversity is promoted instead of discouraged and to set the stage for the fine-scale mosaic that will characterize the developing ecosystem. Of course, legacy maintenance is an important factor in precommercial thinning. But the main features of precommercial thinning are (1) maintenance of tree and shrub diversity, (2) promotion of crown-class differentiation, (3) promotion of rapid growth, and (4) opportunities to develop isolated dominant trees with deep crowns that provide shelter and foraging normally found only in older trees. Although empirical guidance is lacking, precommercial thinning offers opportunities for experimenting with spatial pattern to produce bio-complexity. Clumps of deciduous trees could be maintained. Shade-intolerant trees can be alternated with shade-tolerant trees to hasten crown-class differentiation and, in time, canopy stratification. Providing growing space to individual deciduous trees like red alder and black cottonwood can lead eventually to cavity tree formation

during periods of community development in which few cavities are being formed in conifers. Providing growing space to individual bigleaf maple enhances numerous aspects of biocomplexity.

### Commercial Thinning

Heretofore, considerable discussion has been devoted to the benefits of commercial variable-density thinning, and it will not be repeated here. But it is important to recognize, that commercial thinning offers the same opportunities as precommercial thinning to ensure tree and shrub diversity, implement SAVE tree guidelines, and protect legacies. In addition, commercial entries also provide the resources for decadence management—stimulating the development of cavity trees and augmenting coarse woody debris on the forest floor—and underplanting and seeding to restore missing elements of diversity. Thus, thinning also can be used to mitigate effects of past mismanagement and to restore forest health, including increasing resistance to wind and snow damage, reducing susceptibility to crowding, moisture stress, and insect attack, mitigating the effects of dense monocultures on development and spread of root disease, and reducing risk of catastrophic fire. As in all aspects of AIM for resilience, the situations will always be complex and will require site-specific analyses as well as landscape- and regional-scale analysis and planning. In addition to decadence management, underplanting,

**Table 31—Prediction and description of stability and resilience**

Index	Inertia	Recovery
1	▪ Adaptation of indigenous species to environmental fluctuation	▪ Proximity of recolonization sources and landscape permeability
2	▪ Degree of functional redundancy	▪ Mobility of propagules and biological legacy retention
3	▪ Cleansing capacity for pollutants	▪ Physiochemical suitability of site for recolonization
4	▪ Chemical and biomass accumulation buffering	▪ Biocomplexity and niche diversification
5	▪ Proximity of key variables to change thresholds	▪ Toxicity of site, presence of ruderal, and exotic species
6	▪ Degree of management efficacy	▪ Degree of management efficacy

Source: Adapted from Cairns and Dickson 1977 and Cairns 1986.



and seeding, prescribed fire at times can be a useful adjunct in commercial thinning. In almost all cases, inducing heterogeneity at a fine scale (0.2 to 1 hectare) will be appropriate and help contribute to achieving biocomplexity, increasing resilience, and mitigating the forest health risks resulting from poor past management.

### **Decadence Management**

Decadence management includes retaining coarse woody debris on the ground throughout a major harvest area. Covers of more than 10 percent in dry-mesic Douglas-fir forest and more than 15 percent in mesic-hydric western hemlock forests seem reasonable targets. The smaller the diameters left and the closer the values are to 10 percent and 15 percent, the sooner the coarse woody debris will need to be augmented. Provision should be made for cavity trees during major harvests. These could include well- to moderately-decayed conifers more than 80 centimeters in diameter at breast height (d.b.h.),

**Figure 71**—Second-growth clumped legacy retention with hardwoods in an industrial forest. Photo by A. Carey.





lightly- to moderately-decayed trees more than 80 centimeters in d.b.h., live trees more than 50 centimeters in d.b.h. but with evidence of past damage to the top and a reiterated top; live trees more than 50 centimeters in d.b.h. that are sound can be left, topped above two to three whorls of live branches, and branches perpendicular to prevailing wind direction can be lopped to reduce wind resistance. The shorter and more decayed the trees are, the shorter time they will serve as a cavity tree. A well-decayed, short (greater than 5 meters), large snag may be used for nesting only occasionally by small secondary cavity-using birds or small mammals. Large lightly- to moderately-decayed live trees and dead trees will be used for nesting, roosting, perching, and denning often, and simultaneously, by a variety of cavity-using birds and mammals. Retaining deciduous trees to allow them to grow and later be overtopped and become snags (red alder) or to be maintained indefinitely and develop cavities while still alive (madrone and bigleaf maple) is an important aspect of decadence management.

During thinnings, trees with cavities or with high potential for cavities can be marked for retention. Some dominant live trees can be wounded (cavities excavated, lightning scars simulated, and crevices incised with a chainsaw—to more quickly provide cavities and crevices to wildlife and to provide the proximal cues to wildlife that such a tree may have cavities and crevices), topped, and released to promote continued height growth, allow a new crown to develop, accelerate development of epicormic branches, and initiate decay processes that can continue for decades to centuries. Some damage will be caused by the felling of trees and contribute to the decadence



**Figure 72**—Mixed hardwood-conifer legacy retention along streams and seeps in an industrial forest. Photo by A. Carey.

processes; second and third thinnings in older stands are more likely to promote decadence in some retained dominants. Inoculation with decay-causing fungi also works in some systems, and artificial cavity and nest structures can be used to promote early colonization of young forests by cavity-nesters and to benefit threatened species (Bellrose et al. 1964; Bull 1991; Bull et al. 1997, 1981; Carey 2002b; Carey and Gill 1983; Carey and Sanderson 1981; Carey et al. 1999d; Copeyon et al. 1991; Lewis 1998; McArdle et al. 1961; McComb and Noble 1981a, 1981b, 1981c; Parks et al. 1999). If, because of past management, coarse woody debris is sparse, some felled trees can be left to contribute to maintaining the 10 percent and 15 percent levels; if large fallen trees are absent, smaller trees can be aligned longitudinally and stacked as pyramidally to form coarse woody debris structures with large size and high surface area to promote high biological activity.

### **Rotation Age and Uneven-Age Management**

The longevity of Pacific Northwest conifers allows more flexibility in management than in many other forest types. Many of the techniques presented here can be used in restoration efforts to direct second-growth forests to trajectories that will eventually produce old forests with the biocomplexity of present-day old growth; active management may cease after 1 to 10 decades. Douglas-fir/western hemlock/western redcedar forests, redwood forests, and some other types can be actively managed indefinitely (more than 500 to 1,000 years) without the need for “creative destruction” or an event that leads to fundamental reorganization of the biotic community. Douglas-fir dominated forests can be thinned multiple times with gradual replacement with shade-tolerant trees; at some point, no more dominant Douglas-fir will be taken, a significant Douglas-fir presence can be maintained, and continuous removal and autogenic replacement of shade-tolerants can occur. Uneven-age management systems can be used, but regeneration of Douglas-fir may require group-selection harvests that are essentially small patch cuts around 1 hectare. Uneven-age management can be used in hemlock-cedar forests. At the other end of AIM for multiple values, variable-retention harvests on alternating 70- to 80-year and 130- to 150-year intervals (with no major harvests on unstable slopes, next to streams, and other areas of special value) can be combined with multiple variable-density thinnings to produce robust, resilient forests in landscapes dominated by late-seral complex forest with high capacity for biological diversity,

adaptation, and other environmental values while simultaneously contributing greatly to social and economic values. Severe ecological problems arise when rotation ages less than the above are used; rotation ages are prime determinants of cumulative effects in both space and time and determine, in large part, landscape character and potential for impacts on aquatic systems.

### Landscape Management

Rotation age does much to determine the nature of the shifting, steady-state mosaic of AIM landscapes. However, the stage must be set before the play unfolds. Stage setting includes geologic and geomorphologic analysis at the watershed scale to identify unstable slopes, fragile soils, fragile biotic communities, riparian areas, reserves, special landscape elements, transportation systems (including public access management), and zoning for equipment use. Once the stage is set, then the condition of the various ecosystems in the landscape must be evaluated. Then the need for, and potential of, various AIM strategies and techniques can be assessed and an AIM implementation plan developed. Care must be taken, however, not to make the

**Table 32**—Tree and shrub species of the Pacific Northwest with special attributes that are valuable ecologically

Conifers	Broadleaf	Shrubs
Douglas-fir	Bigleaf maple	Black hawthorn
Grand fir	Bitter cherry	California hazelnut
Incense cedar	Black cottonwood	Cascara
Lodgepole pine	Oregon ash	Devil's club
Mountain hemlock	Oregon white oak	Elderberry spp.
Pacific silver fir	Pacific dogwood	Evergreen huckleberry
Pacific yew	Pacific madrone	Huckleberry spp.
Ponderosa pine	Paper birch	Indian plum
Sitka spruce	Red alder	Manzanita spp.
Subalpine fir		Oceanspray
Western hemlock		Oregongrape spp.
Western redcedar		Rosa spp.
Western white pine		Salal
Yellow-cedar		Salmonberry
		Saskatoon
		Sitka alder
		Sitka mountain ash
		Snowberry spp.
		Vine maple
		Willow spp.

Source: Wilson and Carey [N.d.].

analysis and plan the driving goals; conservation of nature is the driving goal with environmental, social, and economic sustainability the ultimate goals. Care must be taken to avoid unnecessary zoning because zoning tremendously complicates efforts at restoration and sustainability (Carey et al. 1999c); the more constraints placed on the landscape, the less operational the landscape becomes. Care should be taken in formulating operating principles and instilling normative values for conducting on-the-ground operations for all involved from those setting specific objectives to those carrying out a narrow action on the ground. If longer rotations and good stage setting were used and the entire management group could come to consensus on a land ethic, much of present day zoning would be unnecessary in AIM landscapes. Similarly, collaborative management must be willing to accept short-term impacts and short-term risks to achieve long-term benefits and long-term risk reduction; overly zealous application of the precautionary principle often is a deliberate, conscious management decision to forego long-term increases in forest health and resilience to avoid short-term responsibility or controversy. If collaborative managers recognize their role as one of disturbance managers—to plan and implement disturbance to foster ecosystem and landscape resilience—some of the fear of short-term disturbance may be ameliorated (sidenotes 64, 65).

A question still being asked (but more rarely) in the Pacific Northwest is “Should old growth be actively managed?” Old-growth forests in the Pacific Northwest are unique, perishable, and irreplaceable (Carey 1998b). Old growth is a unique heterogeneous set of forests that developed under various unique sets of conditions over multiple physiographic and biogeographic regions over various time periods ranging from 250 to over 1,000 years. In any one locale, old growth tends to be of the same approximate age (and can be defined by that age) and to have arisen from one or more large-scale fires and to have been affected by a subsequent series of intermediate-scale disturbances by fire, wind, and disease. All old growth shows evidence of small-scale disturbances owing to disease, wind, fire, and decadence that provide a variety of structures from snags to gaps. The various disturbances that originated and shaped the development of old-growth ecosystems produced forests of dimensions in terms of size of structures, biodiversity, complexity, and emergent properties that have not been matched in managed forests. Managers will never be able to recreate the disturbance histories and geographically extensive contexts under which today’s old-growth forests developed; thus, these forests are irreplaceable. Even though old-growth forests are quite stable compared to younger stands,

**Sidenote 65**—Roles of scientists (Lach et al. 2003):

- Reporting science results that others use in making decisions
- Reporting and interpreting science results for others involved in decisions
- Working closely with managers and others in integrating science results into management decisions
- Actively advocating for specific and preferred natural resources decisions
- Making decisions about natural resources management and policy

**Sidenote 66**—President Clinton's five principles (Haynes and Perez 2001):

- Never forget human and economic dimensions
- Protect the long-term health of forests, wildlife, and water
- Use science that is sound, ecologically credible, and legally responsible
- Produce predictable and sustainable flows of timber and nontimber forest products
- Insist on collaboration, not confrontation

**Sidenote 67**—Lessons from the Northwest Forest Plan (Haynes and Perez 2001):

- A focus on individual species is necessary, but not sufficient.
- Elucidation of the key roles of species, species groups, and biotic communities is important to effective management.
- Providing for long-term evolutionary capacity is important.
- Intermittent streams are important in providing coarse woody debris and sediment to large streams.
- Legacies are important to aquatic communities.
- Collaborative adaptive management is necessary.
- Top down standards and guidelines do not work.
- Physiographic provinces differ in many ways.
- How timber is sold and contracted is as important as how much is sold.
- Communities differ.
- Nontimber forest products are important.
- Fungi are not old-growth dependent.
- Long rotations are good.

they still are susceptible to catastrophic disturbance, for example, the old growth destroyed by the eruption of Mount St. Helens, tsunamis on the Washington coast, catastrophic windstorms on the Olympic Peninsula, and fire throughout the Pacific Northwest. In addition, the old Douglas-fir that characterizes much of the Pacific Northwest old growth will all eventually die; the loss of Douglas-fir changes the nature of the stand from a successional stage to a quasi-climax stage dominated by shade-tolerant tree species. Thus, old growth is perishable. Science suggests that thoughtful management could produce complex forests that provide many of the functions of old growth and habitat for many of the species found in old growth. Of course, the full biodiversity associated with old growth will never be known. Complex forests created by managers will take hundreds of years to develop the stature of natural old growth. Thus, managers will never know if they were successful in recreating old growth. Thus, for all practical conservation purposes, managers cannot recreate old growth or manipulate old growth with predictable results. The public resistance to further destruction of the natural legacies in the Pacific Northwest suggests further harvesting of old growth will likely evoke more protests, sometimes destruction of equipment, and litigation.

## Common Questions

The last century of exploitation of natural resources and societal conflicts over the disposition of natural resources has been intense as large numbers of people moved westward across North America and as preindustrial countries developed. These issues culminated and permeated in forests and human communities in the Pacific Northwest (see, e.g., Behan 2001, Daily and Ellison 2002, Golden 1999, Harris 1996, Kemmis 2001, and Satterfield 2002). Many lessons have been rendered about ecology and the sociology of protection, restoration, maintenance, and utilization of biodiversity (sidenotes 66, 67). Whereas silviculture is occasionally questioned in the management of nonindustrial and industrial private forests, its use is coming under closer scrutiny in the management of public forests. In particular, the use of silviculture to achieve ecological benefits in second-growth forests in late-successional reserves has raised several questions. How can such questions, often based on the history of mismanagement and mistrust of agencies and experts, be answered? It appears the sociology of conservation needs more development than ecosystem management does. Dryzek (1992) describes the

three main institutions of our society (capitalism, “liberal” democracy, and the administrative state) as thoroughly inept as regards to ecology and conservation. There is no cookbook approach that will achieve intentionality; management must be site specific and in the context of a spatial hierarchy. Thus, I will list only management technique tactics that can be integrated into AIM for multiple values if and when the mechanism for achieving discussion, collaborative learning, and collaborative management replace adversarial, position-based jousting (see Thomas 2002 for further discussion of the “The Conflict Industry”).

The toolbox includes legacy retention and maintenance, planting and seeding, control of species composition, exotic species management, precommercial thinning, underplanting, variable-density thinning, coarse woody debris augmentation, cavity tree augmentation, variable-retention harvesting systems, and uneven-age management systems at the level of biotic communities. At the landscape level, management (sidenote 68) includes protection of special landscape elements; transportation systems; recreation opportunities and recreational access management; harvesting of timber and non-timber forest products; aquatic conservation strategies for wetlands, riparian areas, and unstable slopes; extractions of minerals and fossil fuels; locations and routing of highways, power lines, and communication towers; and reserves. Reserve management is a field unto itself: in the Pacific Northwest, 3 million hectares are in congressionally reserved lands; 3 million hectares have been administratively withdrawn into late-successional reserves, over 600,000 hectares have been constrained in adaptive management areas, and 1.1 million hectares are in riparian reserves, for 8.3 million hectares of federally administered forests on which management is restricted and tightly regulated. Federal lands available for collaborative management include 1.6 million hectares of “matrix” lands embedded in 7.7 million hectares of reserves (Haynes and Perez 2001). Additional state, county, and private lands have been constrained under designation as parks, habitat conservation plans, riparian buffer areas, and areas of unstable soil.

**Sidenote 68**—General principles of landscape management (Lindenmayer and Franklin 2002):

- Maintain connectivity.
- Maintain landscape heterogeneity.
- Maintain ecosystem complexity.
- Maintain intact aquatic systems.
- Spread risk—do not do the same thing everywhere.

### **Will Plantations Develop Into Old Growth?**

The answer to this question is “No,” for the very same reasons that old growth is unique and irreplaceable in the previous discussion. Will plantations in late-successional reserves develop into complex forests that have many of the attributes of old growth? The answer



to this question is a qualified “Yes, but it would take centuries.” There are two qualifications. First, and most obvious, is that there be no global climate change of sufficient magnitude to change the type of vegetation that would naturally occur in the region. Second, the speed at which second growth develops late-seral character depends on the multitude of factors that led to its current condition. The timber harvest that created the second growth was quite unlike the natural disturbance that led to old growth. Clearcutting, burning, and planting often produce simplified, depauperate forests that could take more than 250 years to develop conditions suitable for recolonization by late-seral species. The sooner the canopy closes and the longer it remains closed in a plantation, the less likely a wide variety of seeds of native species will be retained in the soil, including those of shade-tolerant trees (Halpern et al. 1999). In some cases, the existing stand may have to be destroyed by natural disturbances and replaced by a larger variety of trees before development can proceed. Monocultures of small, dense trees are often more susceptible to disease and wind than natural stands and lack resilience, as well as resistance. Partial cuttings and “sloppy” clearcuts that left substantial legacies from a preceding old-growth stand may function as habitat for many late-seral species within 10 to 200 years depending on the amount of disturbance at harvest and subsequent natural disturbances. The speed of colonization of simplified second-growth forest by missing elements of natural forest will depend on the size and context of the forest in question. Although, modern clearcuts on federal lands often were less than 15 hectares (an area that could be colonized rapidly if surrounded by intact natural systems), extensive areas cumulatively were clearcut over several decades, and recolonization of these areas could take much longer. A key point is that development toward old growth is not inexorable; multiple alternative, relatively long-lived states exist for naturally regenerated forests and are more likely with forests regenerated with conventional silviculture.

### **Is Active Management Better Than Leaving Second Growth Alone?**

The probability of active management accelerating the development of late-seral forest conditions will increase with the intentionality of the management and decrease with time since stand establishment. Certainly, precommercial thinning of densely stocked monocultures less than 20 years old is desirable, and its efficacy will increase with

provisions for favoring volunteer seedlings of additional tree species, including deciduous species and for favoring tall shrubs. Conventional commercial thinning is more likely to be deleterious than not. Thinnings that are too light or too heavy are likely to be deleterious. Biodiversity management with variable-density thinning favoring a diversity of species, cavity tree retention, coarse woody debris conservation, and underplanting, cavity-tree creation, and coarse woody debris augmentation, when warranted, should increase the probability that the ecosystem will quickly develop late-seral characteristics (Carey 2000b, 2001; Carey and Harrington 2001; Carey et al. 1999b; Thysell and Carey 2000, 2001a; Wilson and Carey 2000).

### **Will Active Management of Second Growth Produce Negative Effects?**

Short-term negative effects are unavoidable. Thinning will disturb the soil, kill trees, disrupt canopy connectivity, and reduce sporocarp production by belowground fungi. Thinning operations are destructive of plants and animals in the forest floor. Achlorophyllous mycotrophs (e.g., Indianpipe) may be negatively affected over the long term, but these negative impacts might be mitigated by leaving small unthinned patches within the stands. Thinning may decrease northern flying squirrel populations in the short term (less than 5 years). The same can be said of natural disturbances. Commercial thinning requires roads and use of heavy equipment within the forest with attendant disturbance effects. The positive benefits of thinning will most likely begin accruing after 5 years and could continue for a decade or more. Thus, active management for ecological values trades short-term negative effects for long-term gains. Commercial thinnings, by definition, remove biomass in the form of wood. Many second-growth stands contain many more stems than naturally young stands, and reduction in stem density is essential for a number of stand developmental processes. This reduction in biomass, however, can be at the expense of foregone standing dead trees, coarse woody debris recruitment, and total forest-floor organic matter with unintended negative consequences. Thus, high intentionality must be used in taking action to maintain (or enhance) decadence processes during thinning.

