Ecological Concepts and Diversity of Old-Growth Forests

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Above: Old-growth white pine–hemlock *(Pinus strobus–Tsuga canadensis)* in the Upper Peninsula of Michigan.

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ABSTRACT

An ecological understanding of old-growth requires a multiscale perspective, ranging from individual trees to regions. A consensus on a single general ecological definition of old-growth will never be reached, but that should not preclude the development of specific definitions needed by managers. Old-growth forests share many attributes, such as spatial heterogeneity, but they also differ in many ways. Given the complexity and dynamics of forests, efforts to conserve biodiversity must be sensitive to the diversity of old-growth forests and must consider forests of all developmental stages, not just old-growth. One implication is that forest policies and management practices may need to be as diverse as the old-growth forests they address.

Keywords: biodiversity; policy

What picture comes to mind when you hear the term *old-growth forest?* To many it is a forest that has grown for centuries without human disturbance and now is a stand of massive, towering trees with jumbles of large decaying tree boles; deep shade pierced by shafts of sunlight; and dense patches of herbs, shrubs, and saplings that perhaps conceal rare species. Such a forest is as awe inspiring as it is biologically rich. It may contain the largest trees, the oldest trees, the most at-risk forest species, and the largest accumulation of carbon per hectare of any forest type on earth. Given this picture, it is not difficult to understand why old-growth forests have become charismatic ecosystems in the debate about forest biodiversity.

Although this picture fits many old-growth forests, it does not fit all of them—or even most of them. Policymakers and managers are struggling to respond to the diverse definitions of these forest ecosystems. Some of the challenges stem from the fact that, despite their shared attributes, like high spatial heterogeneity, these forests also differ in many respects. For example, tree sizes, longevity, wood decay rate, tolerance of shade and fire, and disturbance frequency can differ by an order of magnitude among species and forest types (Harmon et al. 1986).

The diversity of old-growth forests types makes it impossible to use the same policies and management practices everywhere. In this article I briefly review ecological concepts of old-growth, propose some ways to think about the diversity of old-growth forests, and identify policy and management implications of this diversity.

The Conceptual Basis

Old-growth forests have multiple meanings and values in ecological, social, and economic arenas. In many cases it is the social values, such as aesthetic and spiritual qualities, that drive public debates about old-growth. To many people the ecological and biodiversity concerns are secondary to the idea that they just don't want large, old trees cut down. Even though issues of social values lie at the heart of many old-growth controversies, ecological perspectives must be taken into account if new policies are to lead to successful management on the ground.

Ecological concepts and definitions of old-growth form a basis for old-growth policy and management. The most basic definition of *old-growth* is simply a forest containing old trees. The "growth" part of the name dates back to the early days of forestry in the United States, when trees were viewed primarily as a crop, or a "growth" (Fernow 1891). Since then, *old-growth* has acquired ecological and social meanings and relatively widespread public recognition (although not necessarily scientific understanding). One example of an ecologically based definition is the generic definition of the USDA Forest Service (Anonymous 1989):

Table 1. Ecological and spatial scales relevant to policy and management for old-growth forests.

Scale	Examples of attributes
Individual tree (species specific)	Tree size, longevity, crown form, decay in living trees, bark thickness, wood decay rate
Stand or patch of trees	Tree size variation, horizontal patchiness, vertical foliage distribution, species composition, live and dead biomass, rates of mortality and regeneration, gap formation and closure rates
Landscape (mosaic of stands)	Patch size distributions, disturbance regimes, spatial patterns of forest developmental stages, soil and topographic influences
Region (mosaic of landscapes)	Variation in forest structure and composition in relation to climate, disturbance regimes, vegetation history

Figure 1. **Crown form development from young to old-growth in Douglas-fir on productive sites in western Washington (left to right: 50, 150, 300, 500, 700 years).**
Source: **Courtesy of Robert Van Pelt.** ***Note:*** **Human figures included for scale.**

Old-growth forests are ecosystems distinguished by old trees and related structural attributes. Old-growth encompasses the later stages of stand development that typically differ from earlier stages in a variety of characteristics, which may include tree size, accumulations of large dead woody material, number of canopy layers, species composition, and ecosystem function.

If the forests of North America are screened with this definition, the result is a population of forests that is diverse in structure, dynamics, and composition. Understanding the diversity of old-growth forests requires a multiscale ecological and spatial perspective, including distinction of tree species, stands and patches, landscapes, and regions (Spies and Franklin 1996) *(table 1).*

At its most fundamental level, an old-growth forest is the product of structures and processes associated with the maturation and senescence of a population of trees. Consequently, the life history characteristics (e.g., maximum size, age, growth rates, shade tolerance, and decay rates of wood) of those tree species have a strong influence on the characteristics of old-growth at stand, landscape, and regional levels. Individual trees develop forms and structures through genetic, physiological, and ecological processes of growth, senescence, death, and subsequent decay. In their youth, for example, many trees have a strong central stem and a conical crown, but with age they develop a more open, irregularly spreading or decurrent crown (Zimmermann and Brown 1971) *(fig. 1).* The open, individualistic crowns that form as trees age are perhaps the most distinctive feature of old-growth forests.

The generic ecological model of old-growth is best developed at the stand scale. For more than 50 years, beginning with a seminal paper by Watt (1947), ecologists have used a simple four-stage model to characterize forest stand development, with the last stage corresponding to old-growth or a relative steady state in which shade-tolerant canopy species replace themselves through regeneration in canopy gaps (Oliver and Larson 1990) *(table 2).* In this model, *old-growth* is synonymous with a *climax forest*—the last stage of forest development (i.e., structural change) and succession (i.e., compositional change) in which the forest community is self-perpetuating and relatively stable in the absence of stand-replacement disturbance. However, *old-growth* has also been applied to forests dominated by long-lived early seral dominants, such as Douglas-fir *(Pseudotsuga menziesii)* and ponderosa pine *(Pinus ponderosa),* or by short-lived seral species, such as aspen *(Populus* sp.) or jack pine *(Pinus banksiana)* (Franklin and Spies 1991; Spies and Franklin 1996; Frelich 2002). All of these old-growth forests, whether composed of shade-tolerant or seral species, share a relatively high degree of structural complexity that originates from structural elements, including decurrent crowns, canopy gaps, dead wood, and patchy understories.

Table 2. Examples of models of Douglas-fir stand development and old-growth.

Typical stage age (years)	Four-stage model (e.g., Oliver and Larson 1990)	Eight-stage model (Franklin et al. 2002)
0		Disturbance and legacy creation
	Stand initiation	Pioneer cohort establishment
20		
		Canopy closure
30	Stem exclusion	
		Biomass accumulation and competitive exclusion
80	Understory reinitiation	
		Maturation
150	Old-growth	
		Vertical diversification
300		
		Horizontal diversification
800		
		Pioneer cohort loss
1,200		

Pioneering work on old-growth forest ecology in Douglas-fir forests of the Pacific Northwest has emphasized structural features of old-growth, such as dead wood and vertical foliage diversity, instead of tree species composition. Forest structure is more diagnostic of stand development than is composition, because many forests—including black spruce *(Picea mariana)* and lodgepole pine *(Pinus contorta)*—develop structurally following disturbance but change little in composition. Forest structure is a critical attribute because it is the substrate for other organisms and processes. Compared with old forests, young natural forests have simpler structure, and intensively managed forest plantations are very simple.

Recently, ecologists have looked more closely at the standard four-stage model and found it wanting when it comes to elucidating the changes in forest structure that occur in the later stages of forest development *(table 2).* Franklin et al. (2002) have proposed an eight-stage model. These stages, none of which are termed "old-growth," incorporate changes in spatial heterogeneity and the role of disturbances that leave legacies of old-growth structures in young forests.

The four-stage model and even the recent eight-stage model are most obvious in forests with stand dynamics characterized by infrequent, stand-replacement disturbances that result in moderate to large, relatively distinct patches of forest. These models may not appear to be applicable to forests where stand dynamics are characterized by frequent, low-severity disturbances that create small patches, such as ponderosa pine forests or spruce-hemlock *(Picea sitchensis–Tsuga heterophylla)* forests. The models nevertheless apply in these situations because large stand-replacement disturbances still occur, albeit infrequently, and because the spatial disturbance and regeneration processes operate largely at the scale of small patches or small groups of trees. At the typical "stand" scale (10 to 100 hectares) these forests are a shifting mosaic that does not exhibit the strong directional structural changes over time that are characteristic of forests subject to stand-replacement disturbances (Spies and Turner 1999). This fine-grained shifting mosaic also occurs in the later stages of stand development in forests characterized by stand-replacement disturbances, like coastal Douglas-fir or, in the eastern United States, red pine *(Pinus resinosa),* as the large patches of the original cohort are broken up by disturbances and the regeneration of more shade-tolerant species.

Landscape and regional perspectives are also needed to more fully understand and manage old-growth (Parker et al. 2000). Disturbance regimes and climate can influence the spatial pattern of forest development and the time allowed for trees and stands to mature before they are killed. The amount of old-growth in a landscape and the level of complexity that develops in older stands are constrained by the disturbance regime of the landscape. Where stand-replacement disturbances occur at frequencies that are less than about half the age at which tree species of a forest reach maturity, old-growth conditions will be uncommon or rare in the landscape (Spies and Turner 1999).

For example, taking the fire frequency–age class model of Van Wagner (1978), old-growth would be less than 10 percent, on average, in a landscape with a disturbance frequency of 50 years and forests that require 150 years to develop into old-growth. The range of variation in the percentage of old-growth in a landscape or region also varies with the size of area considered and the disturbance regime of the region (Wimberly et al. 2000). At broad scales old-growth stands become one piece of a spatially and temporally interconnected, ever-changing mosaic. Stands that have old-growth structures today may not have them in the future after disturbances from wind, fire, pathogens, and humans, whereas areas that are now lacking old-growth may develop old-growth conditions in the future.

Old-growth aspen *(Populus tremuloides)* in the Rocky Mountains of western Colorado.

Definitions for Policy and Management

The conceptual models of stand development and old-growth, like all models, are simplifications of reality that help us make sense of a seemingly chaotic natural world. However, when it comes to policy and management issues, and when lines are drawn on maps and silvicultural decisions are made about particular stands and landscapes, the conceptual models are of limited value. Policymakers and managers typically need specific definitions of old-growth: tree species, tree diameters, snag and down wood sizes and volumes, and measures of patch size and vertical diversity. Tree age can be used in relatively even-aged forests, but in multiaged forests an average age or dominant age will not have much value in defining old-growth. In response to management needs, specific definitions of old-growth have been developed for several forest types (Old-Growth Definition Task Group 1986; Harms 1996; Wells et al. 1998)). These definitions, which are typically based on attributes of stand structure, composition, and age, can be used to estimate the amount of old-growth in an area and to map its distribution.

However, the definitions become arbitrary when the line between forests that are and are not old-growth must be determined. Stand development is a continuous process that lacks clear thresholds or abrupt changes in structure that can be considered diagnostic of the beginning of the old-growth stage (Spies and Franklin 1988; Hunter and White 1997). The picture is further complicated by the fact that old-growth includes many distinctive structural components that do not all change at the same rate and may not all be present in

Ecological Characteristics of Old-Growth

This classification illustrates the diversity of old-growth based on characteristics of space, time, and structure.

Development time. Long: requires centuries to millennia to develop as a result of poor site conditions and very slow growth and establishment. Intermediate: requires centuries to develop because of long lifespans of species, low site quality, or slow growth rates. Short: requires decades to develop because of short lifespans of dominant tree species.

Structure. Low: small trees with short life spans (<250 years), low-density stands, low dead wood because of high decay rates. Moderate: small to medium-sized trees with short lifespans, low to moderate accumulations of dead wood. High: large to very large trees with long lifespans (>250 years), moderate to high accumulations of dead wood.

Patch size. Fine-grained: dominant tree species typically regenerate in small canopy gaps and disturbance patches (<1 ha). Coarse-grained: dominant trees typically regenerate in moderate to large stand replacing disturbances (>1 ha). Mixed: combination of both fine- and coarse-grained disturbances regenerate the dominant tree species.

Stability. Short-term transient: old-growth stages exist for decades before successional change or stand-replacement disturbance. Long-term transient: old-growth stages typically exist for one to several centuries before successional change or stand-replacement disturbance. Surface-fire dependent: stands can persist for centuries as long as surface fires burn with a frequency of decades or less. Enduring: old-growth stages exist for centuries to millennia because canopy trees can regenerate in canopy gaps.

Development time	*Structure*	*Patch size*	*Stability*	*Examples of forest types*
Long	Low	Mixed	Enduring	Pinyon-juniper, subalpine white pines, dwarf black spruce
Intermediate	Moderate	Fine-grained	Enduring	Balsam fir, black spruce
Short	Moderate	Coarse-grained	Short-term transient	Aspen, red alder, jack pine, black spruce, sand pine
Intermediate	High	Coarse-grained	Long-term transient	Douglas-fir, ponderosa pine, white pine, red pine, Atlantic white cedar
Intermediate	High	Fine-grained	Surface fire dependent	Ponderosa pine, oak-hickory, longleaf pine, Douglas-fir–incense cedar
Intermediate	High	Fine-grained	Enduring	Beech-maple, hemlock-spruce

every stand. This continuous and variable nature of structural development has led some to call for using an index of "old-growthness" that would allow the threshold for identifying old-growth to be moved depending on the management objective (Spies and Franklin 1988).

Setting definition thresholds by age or structure influences the perception of how much old-growth is in a landscape. Hunter and White (1997) point out that, if rarity is the impetus to conserving old-growth and if the definition of old-growth is arbitrary, old-growth should be defined in a way that keeps it rare but not too rare. If old-growth is defined more broadly so that it is relatively common, it may be less valuable from a biodiversity perspective.

Using evidence of human activity as a criterion for old-growth is controversial. This perspective had its roots in the use of the term *virgin forest,* which has a long history of association with *old-growth forest.* If stands are defined largely on the basis of structural development, the source of the disturbance (e.g., human or fire) is irrelevant as long as the diagnostic features are present. However, human disturbances often remove wood or vegetation and reduce the structural variability that is typical of many naturally developed older forests.

The issue of human influence is moot in most forest regions where past logging and agriculture have removed old-growth forests (Foster et al. 1996) or where activities by native peoples have altered the structure and composition of many so-called virgin forests (Denevan 1992). Whether a forest can be defined as old-growth if it has had a history of human disturbance is where the boundaries of social values and ecological science become especially blurry and arbitrary. Degree of human influence is a characteristic that could also be included in an index of old-growthness.

Diversity of Old-Growth Forests

As forest ecologists have learned more about forest dynamics and about old forests in particular, they have become more sensitive to the variations that occur in the later stages of forest development. Characterizations of old-growth from a region where old-growth is distinctive and relatively common can dominate the thinking in other regions where old-growth is rare and poorly studied. Thus descriptions of old-growth Douglas-fir have sometimes been used as a model for old-growth age and structure in other forest types, which may not be appropriate depending on the ecological characteristics of the other forests (Lugo 1997).

The diversity of old-growth reflects the diversity of forest types and their environments. Old-growth types vary in terms of lifespans of the dominant tree species, disturbance regime, presence or absence of human disturbance, shade tolerance, and longevity and age structure (Spies and Franklin 1996; Frelich 2002). No generally accepted framework exists for understanding the diversity of old-growth types. Such a framework might be helpful in promoting a better understanding of the complexity of the old-growth phenomenon in the minds of the public, policymakers, and managers.

As a framework to illustrate the diversity of types, I use four ecological characteristics—development time, structure, patch size, and stability (see "Ecological Characteristics of Old-Growth"), selected to emphasize characteristics important for planning and managing old-growth at multiple scales. *Development time* is the time required for old-growth to redevelop following stand-replacement disturbance. *Structure* refers to the degree of development of phytomass and structural components. *Patch size* is the size of opening needed to regenerate the dominant tree species (but not the overall pattern of vegetation, which is typically a multiscale mosaic in old-growth). *Stability* refers to the duration of the old-growth stages given successional change and the occurrence of stand replacement disturbances.

Some short-term transient old-growth types, such as aspen and jack pine, may exist for only a few decades before the dominant trees die and are replaced by more shade-tolerant species, which then develop into another type of old-growth over time. Some low-stature old-growth types, such as white-bark pine *(Pinus albicaulis),* form open stands of small trees that do not develop the live and dead structural characteristics often associated with old-growth at the stand level but do exhibit old-growth structure at the tree level. Fine-grained, enduring old-growth types, such as beech–sugar maple *(Fagus grandiflolia* and *Acer saccharum),* can exist for centuries to millennia—until a stand-replacement disturbance occurs or climate change occurs—in a relatively small area because the trees are tolerant enough to replace themselves in small to medium canopy gaps. Old-growth ponderosa pine on moist sites can also persist for long periods but requires frequent surface fires to keep out shade-tolerant species and regenerate the canopy species.

Variation in the four characteristics presumably affects such forest processes as carbon sequestration, nutrient cycling, habitat selection by animals, and resistance to fire, wind, and other disturbances. However, we know relatively little about how these ecological functions vary across old-growth types.

Policy and Management Implications

I conclude by listing some implications for policymakers and managers.

- A consensus on the wording of an ecological definition of old-growth will never be reached and may not be desirable, given the diversity of forests. Multiple general definitions, however, are needed.
- Specific definitions and maps of old-growth, based on measurable structural features and biophysical site conditions (e.g., plant association groups) and prepared by local experts, are needed for forest types within regions.
- Use of indices instead of binary classes is essential in dealing with the continuous nature of forest structural development, in dealing with multiple definitions, and for making it clear that ours is not a black-and-white world.
- At some point in the process of developing specific definitions, the boundaries of what is and what is not old-growth become arbitrary. Other criteria, such as risk (including ecological, social, and economic risks) and uncertainty, can then be used to help decide whether to err on the side of inclusion or exclusion.
- Old-growth varies in terms of effort required for conservation and restoration, significance for biological diversity, and threat by direct or indirect human activities.
- Some types of old-growth have been threatened by too much disturbance (e.g., logging of Douglas-fir–western hemlock in the Pacific Northwest), while others are threatened by too little disturbance (e.g., fire suppression in some ponderosa pine forest types in the West).
- High buildups of woody fuel are natural in many old-growth forest types. However, some old-growth types are at risk from stand-replacement disturbances because of uncharacteristically high fuel loads.
- It will be easier to incorporate old-growth elements in managed forests in some forest types than others. For example, old-growth types maintained by canopy gap disturbances, such as northern hardwoods, may be more easily imitated through group selection and other silvicultural activities than types characterized by large, infrequent, severe disturbances. However, old-growth elements can be maintained in managed stands within stand-replacement forest types through application of new silvicultural practices (Franklin et al. 2002).
- Given the complexity of old-growth and uncertainties about management effects, a one-size-fits-all approach should be avoided. Forest reserves and active management both will be necessary.
- Old-growth management and policy issues differ regionally. In the eastern United States, where old-growth is rare or absent, goals for future old-growth are especially difficult to define. In these situations, restoration will lead to a type of old-growth that differs in structure and composition from old-growth forests of the past. In the western United States and Alaska, where old-growth is relatively abundant, management goals have been setasides of existing old-growth. However, long-term strategies are needed that provide for a dynamic population of old-growth stands within landscapes subject to wildfire, pathogens, and climate change.
- Given the complexity of forests, conserving forest biodiversity is more than just conserving something called

"old-growth." It means conserving or imitating processes that create diversity in all stages of forest development, at many spatial and temporal scales.

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