Spatial Aspects of Structural Complexity

in Old-Growth Forests

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ABSTRACT

Old-growth forests typically have complex structures, including heterogeneous spatial arrangements as well as a diversity of individual structures. Two aspects of this spatial complexity are discussed and illustrated: (1) vertical distribution of foliage, often apparent as multiple layers; and (2) horizontal heterogeneity, often evident as canopy gaps and dense reproduction patches. Shifts in mortality processes from competitive-based mortality in young stands to agent-based mortality (i.e., insects, diseases, and wind) in older stands play an important part in the development of structural heterogeneity. Old temperate forests can be viewed as fine-scale structural mosaics in which all stand development processes are simultaneously present within the stand. An additional definition of *forest stand* that incorporates the entire structural mosaic of old-growth is needed.

Keywords: forest health; silviculture

Late-successional forests, including a broad spectrum of old-growth forests, consistently have high levels of structural complexity compared with early-successional forests, particularly stands managed for intensive timber production. This complexity includes a large variety of individual structures, such as a broad range of sizes and conditions of live trees, standing dead trees (snags), and boles on the forest floor (e.g., Spies et al. 1988; Lindenmayer et al. 2000). Such forests often include other structural features, such as well-developed and often diverse understories and thick forest floors.

This structural complexity is the key to many distinctive functional and compositional roles played by old-growth forests, such as habitat for biodiversity and regulation of energy and material cycles (e.g., Franklin et al. 1981; Spies, this issue). The diversity of structures and microclimates in an old-growth forest provides niches for a broad array of organisms. These structures constitute significant stores of energy, water, and nutrients and create protected environments that moderate responses to daily, seasonal, and annual fluctuations in environmental conditions.

Structural complexity in old-growth forests involves complex spatial arrangements of structures, however, as well as a diversity of individual structures. Heterogeneity, rather than uniformity, characterizes the spatial distribution of structures in old-growth forests. Two important dimensions of that spatial complexity are (1) the vertical distribution of canopy, often apparent as continuous or multiple layers of foliage; and (2) the irregular horizontal distribution of structures, often apparent as canopy gaps or forest openings and as dense patches of saplings and poles.

We focus in this article on spatial aspects of structural complexity rather than diversity in individual structures. We describe this heterogeneity and discuss some of the factors that contribute to its development in the even-aged stands that characterize forest regions with stand-replacement disturbances regimes, using the Pacific Coast forests of Douglas-fir and western hemlock *(Pseudotsuga menziesii* and *Tsuga heterophylla)* as our major example. We find a gradual evolution of (1) canopies from simple, top-loaded, single-layered canopies in young stands to the vertically continuous, bottom-loaded canopies in old forests; and (2) spatial heterogeneity from uniform young stands that are initially dominated by competitive processes to the fine-scale structural patchwork of old-growth forests. We also point out the comparable complexity that is continuously present in uneven-aged forests maintained by chronic, low- to moderate-intensity disturbance regimes, exemplified by many western pine forests. The presence of spatial heterogeneity in vertical and horizontal structure in late-successional forest stands appears broadly applicable to many forest types.

Mortality and Structural Development

Development of old-growth conditions in even-aged stands following stand-replacement disturbances involves many processes operating over several centuries (Franklin et al. 2002). Tree mortality is one of the important processes, but the agents, patterns, and

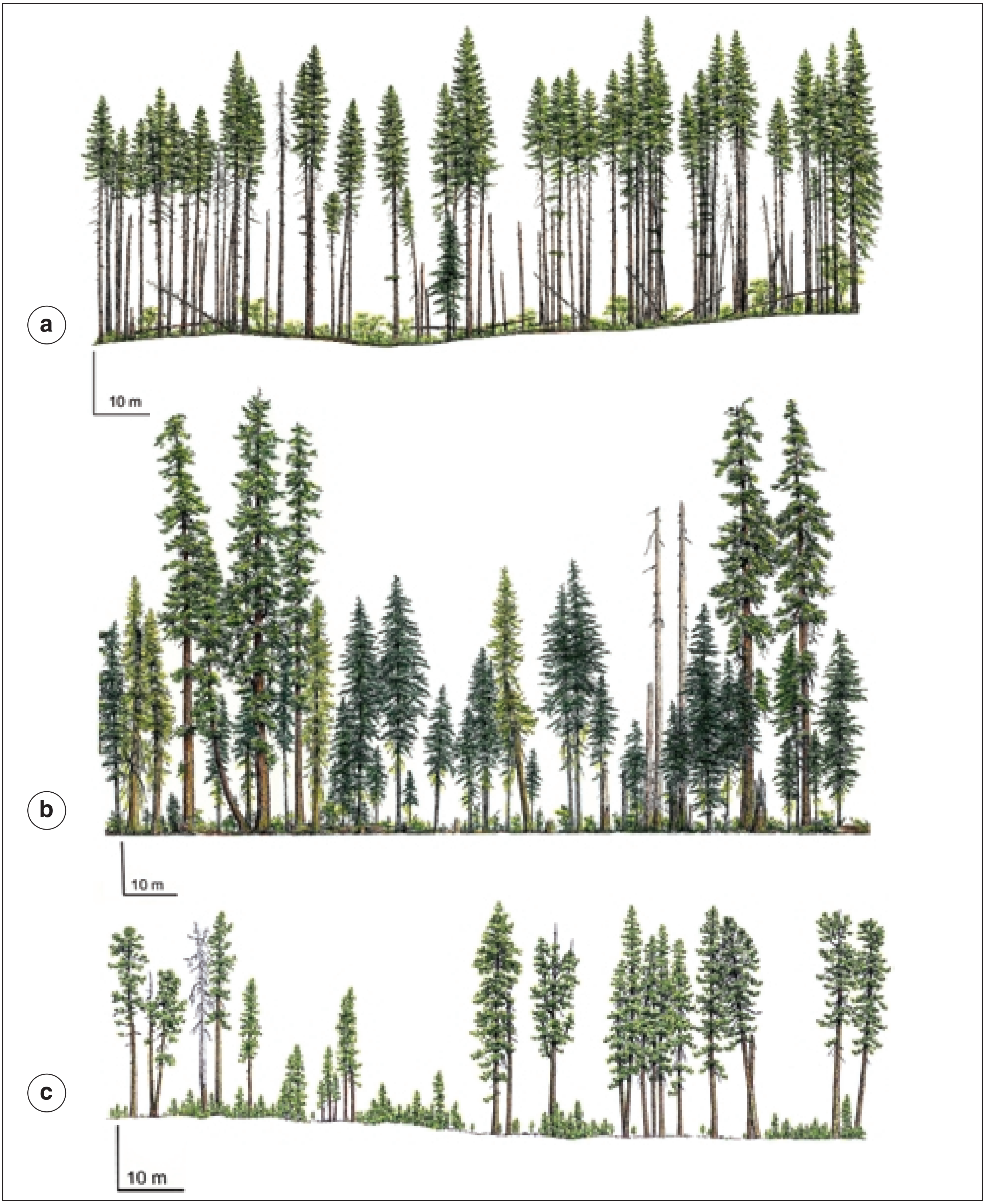

Figure 1. **Structural cross sections illustrate the structural heterogeneity of different forests: (a) maturing even-aged Douglas-fir stand developed following a 1902 wildfire in the southern Washington Cascade Range (Martha Creek drainage, Wind River Experimental Forest); (b) old-growth, 650-year-old stand of Douglas-fir, western redcedar, and western hemlock in the southern Washington Cascade Range (Cedar Flats Research Natural Area, Gifford Pinchot National Forest); (c) old-growth ponderosa pine stand in southeastern Oregon (Blue Jay Springs Research Natural Area, Winema National Forest).**

consequences of mortality undergo major changes during the evolution from young to old-growth forest. We review these briefly here because these changes in tree mortality processes have important consequences for the development of spatial heterogeneity.

Once canopy closure occurs, the young or early-successional forest is characteristically a relatively uniform stand in which competitive-based tree mortality is a dominant development process (Oliver and Larson 1990). Competitive-based mortality occurs predominantly in the smaller, suppressed trees. Because the intensity of the thinning process depends on stand density, competitive-based mortality contributes to the development of structural homogeneity within the young stand. Of course, stands initiated by some intense natural disturbance may have a legacy of surviving trees that do provide some spatial heterogeneity (Franklin 2000).

Pacific Coast Douglas-fir stands typically attain mature conditions between approximately 100 and 250 years. This midsuccessional stage is impressive: The forest is dominated by large but sound and thrifty Douglas-firs, which attain their ultimate height and crown spread during this stage (Franklin et al. 2002). Other structural features are poorly represented in such stands, such as amounts of coarse woody debris in the form of snags and boles on the forest floor and levels of decadence in live trees (Spies et al. 1988; Spies and Franklin 1991). Major transitions occur in developmental processes and conditions during the mature stage, however, including development of the shade-tolerant tree component of the stand and genera-

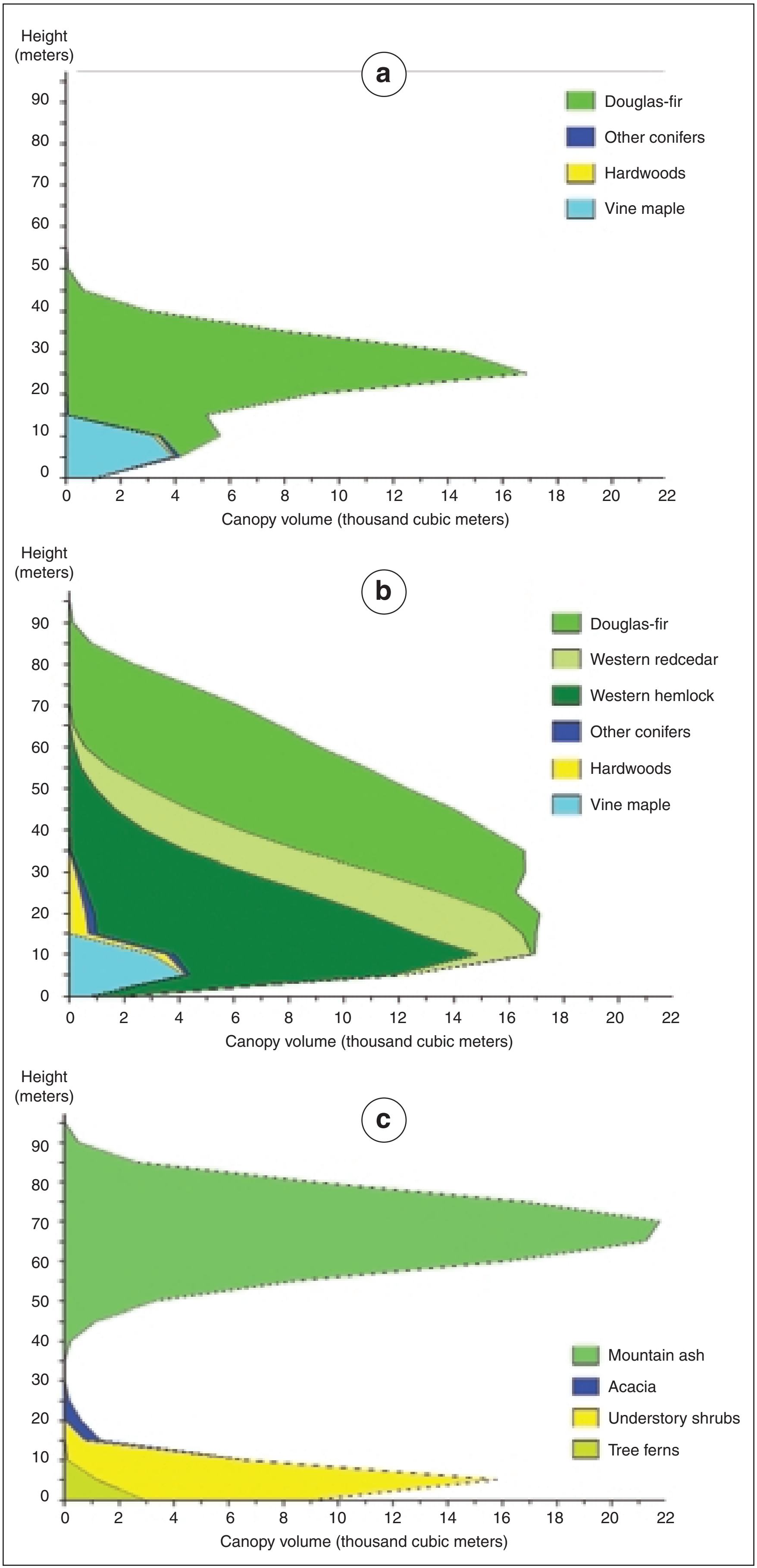

***Figure* 2. Canopy profiles illustrate the distribution of foliage in different forests: (a) even-aged, 100-year-old Douglas-fir stand in the southern Washington Cascade Range (Martha Creek, Wind River Experimental Forest); (b) old-growth Douglas-fir–western redcedar–western hemlock forest in the southern Washington Cascade Range (Cedar Flats Research Natural Area, Gifford Pinchot National Forest); (c) old-growth mountain ash stand in southeastern Australia.**

Figure 3. **Old-growth Douglas-firs are characterized by epicormic branch systems that result in reestablishment of crowns in the middle and lower bole: (a) epicormic branch development produces sprays of short branches that often extend ¼ or more around the circumference of the bole; (b) large epicormic branches typically provide excellent platforms for development of epiphytic communities and for birds and arboreal mammals, such as northern spotted owls and northern flying squirrels.**

tion of coarse woody debris and decadence in living trees. Of course, shade-tolerant trees, such as western hemlock, may be a part of the initial cohort on the site, especially in coastal regions.

An important shift in causes and consequences of mortality occurs during midsuccession as tree death from insects (notably Douglas-fir bark beetle, *Dendroctonus pseudotsugae*), diseases (especially root rots), and wind replaces competition as the dominant mortality process (e.g., Bible 2002). These agents typically result in mortality that is contagious (spatially aggregated) and kills many dominant trees. Hence, canopy gaps are created that contribute significantly to the development of the spatial heterogeneity that characterizes old-growth stands—the primary subject of this article.

Vertical Diversity and Complexity

Stand-replacement disturbances typically lead to establishment of a relatively even-aged young forest with a closed, single-layered canopy *(figs. 1 and 2);* as used here, *canopy* refers to all the foliage, from the ground to the top of the tree crowns. The single-layered canopy gradually moves upward as the trees grow taller and shading results in the death and gradual pruning of lower branches. As the stand approaches maturity, the overstory canopy thins, initially as a result of competitive thinning processes and then increasingly as a result of other agents of mortality, as noted in the preceding section.

A vertically continuous canopy gradually develops in response to the increased light levels within the stand as it moves into the mature or mid-successional stage. The growth response of shade-tolerant tree associates that have become established in the understory—western hemlock and western redcedar *(Thuja plicata),* for example—is the most important factor contributing to this development. These species move into intermediate and codominant positions in the canopy, gradually filling in the foliage gap that existed between overstory canopy and ground layer in the young stand. Douglas-fir stands in which establishment of shade-tolerant associates is delayed—and there are many natural examples—will have much slower development of the vertically continuous canopy.

Dominant Douglas-firs also contribute to development of canopy continuity, however, by producing epicormic branch systems. The occurrence of deep crowns on dominant Douglas-fir trees in old-growth stands was initially confusing to forest scientists (Franklin et al. 1981). The relatively shade-intolerant Douglas-firs are subject to intense natural pruning in dense young stands, so one early hypothesis was that the deep-crowned old-growth Douglas-firs must have been open-grown throughout their life. Subsequently, however, Douglas-fir trees were discovered to be very effective at redeveloping crowns from epicormic buds in the axils of branches and twigs (Ishii and Ford 2001). Epicormic branches develop in response to increased solar radiation on boles or to loss of primary branch systems and may become the dominant foliage-

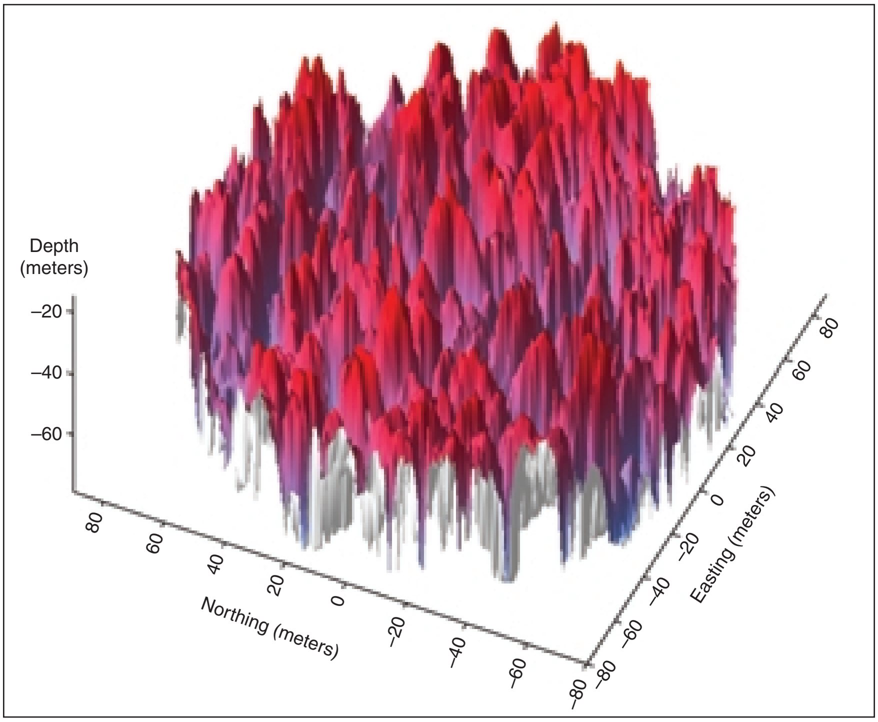

Figure 4. **Old-growth coniferous forest canopies typically display very rough and complex topographic surfaces, as illustrated by the 500-year-old forest at the Wind River Canopy Crane Research Facility in the southern Washington Cascade Range.**
Source: **Diagram courtesy of Geoffrey Parker, Smithsonian Institution.**

bearing branches in old Douglas-firs. In addition to regenerating the upper and extending the lower crown, the platformlike sprays of epicormic branches are excellent habitat for many arboreal animals and epiphytic plants *(fig. 3).*

Ultimately, the aging forest develops a canopy that differs greatly from that of young stands in its distribution, concentration, and roughness (Parker et al. 2002; Van Pelt and Nadkarni, in press). Foliage is vertically well-distributed and is concentrated in the lower half of the profile—that is, it is bottom- rather than top-loaded, as is the case with young stands (as in *fig. 2*). The rough surface topography of the old-growth canopy can be likened to rugged mountains with deep canyons and high peaks *(fig. 4),* contrasting markedly with the relatively smooth and continuous canopies of fully stocked young stands. The canopy is predominantly composed of foliage of shade-tolerant tree species, which are much more important in controlling the light environment at ground level than the dominant Douglas-fir trees. Both canopy architecture (e.g., roughness) and species composition contribute to the higher leaf areas—a characteristic more typical of older than of younger stands.

There are many variations on the theme of multilayered old-growth canopies, and the presence or absence of shade-tolerant associates is a critical element in these variations. For example, as stands of the shade-intolerant lodgepole pine *(Pinus contorta* var. *latifolia)* age, vertically continuous canopies will develop in a fashion similar to those in coastal Douglas-fir forests if shade-tolerant species, such as Rocky Mountain subalpine fir *(Abies bifolia)* and Engelmann spruce *(Picea engelmannii),* are present. On sites where shade-intolerant associates are absent, the lodgepole pine canopy ultimately thins to the point that lodgepole pine can reproduce, and much of this reproduction occurs in larger openings or canopy gaps within the stand.

Canopy architectures in the old-growth mountain ash *(Eucalyptus regnans)* and alpine ash *(E. delegatensis)* forests of southeastern Australia contrast with the preceding examples (Lindenmayer et al. 2000). These are very tall, shade-intolerant hardwoods with a fire-based life history similar to that of Douglas-fir. However, the tall mountain and alpine ash often lack shade-tolerant tree associates that can grow even into a midcanopy position in the stand. Old-growth stands of these species typically have an understory of small trees that develop a dense canopy that extends up to around 10 meters. Hence, old-growth ash stands are characterized by two canopy layers with a large intervening gap *(fig. 2c).*

Horizontal Heterogeneity

High levels of structural heterogeneity in the horizontal dimension are also characteristic of old-growth forests *(fig. 1).* This heterogeneity is often apparent in the form of forest gaps, which are created primarily by mortality in overstory trees, as noted earlier, and are often at the scale of 10 to 40 meters (one-quarter to one-half acre) (e.g., Bradshaw and Spies 1992).

The creation of gaps—as well as the overall thinning of the overstory—provide opportunities for establishment and development of shade-tolerant trees and other understory plant species. The canopy gaps contribute significantly to increased light availability well beyond the gap itself because of the sun angles found in mid-latitude forests (Van Pelt and Franklin 1999).

The old-growth forests that result from these processes consist of fine-scale structural mosaics, as illustrated by the old-growth forest at Cedar Flats *(fig. 1b).* Spatial heterogeneity—patchiness—has largely replaced the relative homogeneity of the young even-aged stand *(fig. 1a)* as a result of overstory mortality and associated regeneration and growth of shade-tolerant tree species. However, competitive-based mortality continues to be an important process within the old-growth stand in several forms, such as in dense patches of small trees; i.e., spatial patterns exist at multiple scales in these stands.

Development of the spatial heterogeneity in the old stand is most notably the result of chronic disturbances to the stand—wind, insect, and disease. Effectively, chronic disturbances have acted on the homogeneous even-aged stand that developed after a stand-replacement disturbance and created spatial heterogeneity.

Old forests on sites that are subject to low to moderate intensity of disturbances are characteristically maintained in a similar fine-scale structural patchwork. For example, most ponderosa pine *(Pinus ponderosa)* forests exhibit such a structure when subject to characteristic periodic wildfires of light to moderate intensity *(fig. 1c).* Fine-scale patchiness is consistently documented in spatial analyses in western North American ponderosa pine (e.g., Harrod et al. 1998) and mixed-conifer forests (e.g., Knight 1997; North et al., in press), with aggregation typically occurring at spatial scales that are much smaller than those proposed for group selection. Similarly, deciduous hardwood forests subject to chronic windthrow, such as the lenga *(Nothofagus pumilio)* forests of Tierra del Fuego, exist as fine-scale patch mosaics (Rebertus et al. 1997).

Chronic disturbances maintain these structurally complex forests unless and until an uncommon stand-replacement disturbance occurs. If chronic disturbances are eliminated, such as by fire suppression, multiple canopy layers can develop within the same structural patch, particularly if shade-tolerant species are present. Such multilayered conditions may be unsustainable, however, because they enhance the potential for stand-replacement fires.

Hence, late-successional or old-forest stands typically consist of fine-scale structural mosaics, whether they occur on sites characterized by stand- or gap-replacement disturbance regimes. There is a tendency for spatial aggregation, primarily in the smaller size classes; dominant trees may be evenly spaced (Moeur 1997). Multiple canopy layers are characteristic, but where forests lack shade-tolerant species (i.e., are characterized by shade-intolerant species), the canopy layers will typically be spatially displaced.

Conclusion

Old forests are structurally complex in the spatial distribution of structures as well as the variety of individual structures. These forests are spatially heterogeneous compared with young even-aged forests, which exhibit structural homogeneity. Old forests typically have multiple or continuous canopy layers and are "bottom loaded" in foliage mass, in contrast to the top-loaded canopies of young stands.

Old temperate forests can be viewed as fine-scale structural mosaics that are developed and maintained as a consequence of chronic disturbances. Forests subject to stand-replacement disturbances evolve through an even-aged cohort that is initially homogenized by competitive-based mortality before arriving at the developmental stage where chronic disturbances become the dominant influence on stand structure.

An additional definition of *forest stand* is needed that recognizes that the functional old-growth forest consists of a fine-scale structural mosaic in which all elements of the structural mosaic are needed to achieve a complete old-growth forest. The traditional definition of a *forest stand*—"a contiguous group of trees sufficiently uniform in age-class distribution, composition, and structure…to be a distinguishable unit" (Helms 1998)—is inappropriate for an old-growth forest if the small-scale structural patches characteristic of these forests are interpreted as separate stands.

The functional old-growth forest stand *is* the complete structural mosaic. Under this condition, all stand development processes are simultaneously present within the stand, from the initiating processes of disturbance, legacy creation, and cohort initiation through the creation of gaps by contagious mortality of overstory dominants (Franklin et al. 2002).

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