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## II Vertical structure

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Looking up at a 50 meter tall *Ceiba pentandra* in Panama, or a 60 meter dipterocarp in Borneo, or a 70 meter Douglas-fir (*Pseudotsuga menziesii*) in Oregon, you know that forests are, above all, vertical. Even in short forests the dimension from ground to canopy includes layers of foliage, gradients of microclimate, and a diversity of plants and animals that respond to that vertical structure. Human use of forests alters those layers, those gradients, and those arrays of plants and animals. In a world where more and more forest is disturbed, our goal in this chapter is to develop an understanding of vertical structure and its relation to biodiversity, and to suggest ways that forest management can maintain the vertical structure that supports biodiversity.

The study of animals and vertical structure has at least an 80 year history. Early in this century ecologists visualized strata in forests and recognized that different animals frequented different strata (Shelford 1912). At mid-century ecologists took another step, showing that differences in the complexity of vertical structure could explain differences among forests in diversity of birds (MacArthur and MacArthur 1961). While later studies showed that more than vertical structure is needed to explain diversity (James and Wanner 1982), no one disputes that a vertically complex forest generally supports more species than a simple forest. Meanwhile, foresters have increased their knowledge of how forest development and management determine vertical structure (Oliver and Larson 1996), and at century's end ecologists and foresters are applying these accumulated insights to conservation (DeGraaf et al. 1992, Franklin et al. 1997).

In this chapter we: (a) define vertical structure in forests, (b) discuss factors that determine vertical structure, (c) describe how particular plants and animals are influenced by vertical structure, (d) present examples of the connection between vertical structure and species richness, and (e) discuss how forest management affects vertical structure and therefore species richness, illustrating this with a case study.

### What vertical structure is

Vertical structure is the bottom to top configuration of above-ground vegetation within a forest stand (a relatively homogeneous area of forest with a common history of development). One can think of vertical structure as vegetation complexity, and horizontal variation among stands as vegetation heterogeneity (August 1983, McCoy and Bell 1991).

Of course it is often difficult to separate vertical and horizontal components. For instance, variation in vertical structure produces horizontal patchiness: in a grassland–shrubland–forest mosaic, addition of a vegetation layer makes a new kind of patch (Roth 1976). Furthermore, the degree of horizontal patchiness can change with vertical position in a stand. In some well-developed tropical forests the understory is comparatively homogeneous and the canopy is heterogeneous. At 2 m above ground there may be about 1000 small tree crowns in a hectare, each about 2 m<sup>2</sup> in area, at 40 m there may be 12 tree crowns, each about 500 m<sup>2</sup>, and at middle levels, between these extremes, there will be intermediate numbers of trees and crown sizes (Terborgh 1992).

Among stands vertical structure varies in terms of canopy and tree height, branching patterns, abundance of different plant life forms (trees, shrubs, herbs, vines, epiphytes), arrangement of leaves on branches, and the amount and distribution of twigs, branches, and leaves (Parker 1995; Figure 11.1). There is a controversy about whether defined vegetation strata exist (Smith 1973), but we will use 'strata' for convenience; what is important is that vertical structure varies and can be measured. Some researchers draw profiles of forests based on measurements in particular areas; others use quantitative data to draw statistically representative profiles or graphs showing the distribution of foliage, basal area, or stem density within different height intervals (Knight 1963, Popma *et al.* 1988; Figure 11.2). European foresters have developed methods for obtaining profile data (Blondel and Cuvillier 1977, Kruijt 1989).

To compare foliage profiles among forests, MacArthur and MacArthur (1961) rendered the density and height distribution of foliage into a single statistic, 'foliage height diversity' (FHD). The density of foliage was measured within various height intervals above ground (MacArthur and Horn 1969), and these data were used to calculate FHD with the Shannon-Weiner Diversity Index ( $H'$ ), to take into account both the total density of foliage and its distribution along the height gradient. Thus  $FHD = -\sum f_i \log_2 f_i$ , where  $f_i = d_i/D$ ,  $d_i$  = the density of foliage in layer  $i$ , and  $D$  = the total density of foliage over all layers in the vertical profile. The most diverse ver-



Fig. 11.1. The vertical structure of different forest types (greatly generalized): (left) tropical, (middle) temperate deciduous, and (right) boreal conifer forests.

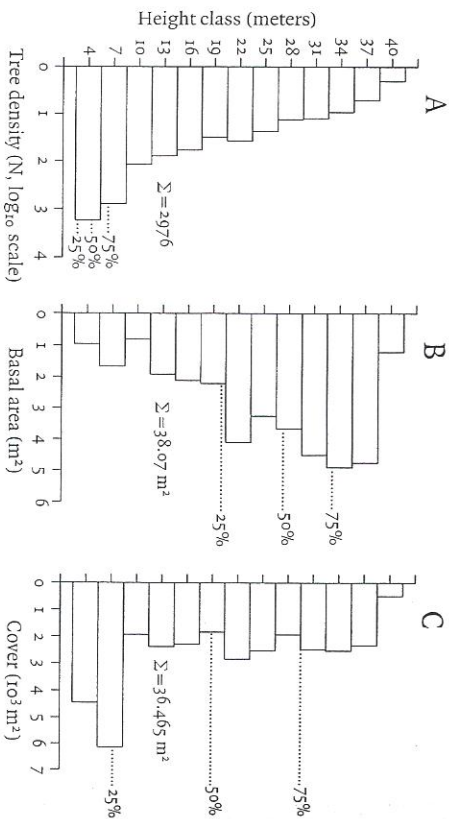


Fig. 11.2. The vertical distribution of various structural features in one hectare of tropical forest in Veracruz, Mexico (for all trees  $\geq 1$  cm DBH): (a) tree density (number of trees whose top height reaches particular height intervals), (b) basal area (amount contributed by trees whose top height reaches particular height intervals), and (c) foliage cover. (Adapted from Popina et al. 1988, with permission from Kluwer Academic Publishers.) Cumulative percentages for each parameter are shown: 75% of all individuals were  $\leq 6$  m tall; 50% of total basal area was contributed by trees  $> 2.6$  m tall; there was a distinct layer of foliage contributed by dense understory palms, while overstory foliage was evenly distributed. The upper limit of each height class interval is included in that class.

tical structure (highest FHD) has foliage evenly distributed among many layers. As we shall see, FHD often explains variation in bird species diversity, but the exceptions highlight other correlates of diversity.

Forests are also compared on the basis of leaf area index (LAI), the mean area of leaves stacked up above a unit of ground area. We do not discuss LAI further. LAI tends to reflect site productivity (Hedman and Binkley 1988), which may correlate with species richness, but productivity versus species richness is not our subject. Moreover, LAI is poorly related to forest height and FHD (Aber 1979), important parts of our subject.

### Variation in vertical structure

#### FOREST TYPE AND SITE CONDITIONS

Every forest type has a different vertical structure, almost by definition, due to the particular climate, soil, tree species, and plant life forms that produce a definable type. Boreal forests composed of pagoda-form

conifers have different profiles from temperate zone forests of laterally branching trees, or tropical forests with umbrella-crowned emergents (Figure 11.1). Structure can get exceptionally complex near the equator. To the many tree growth forms in tropical forests (Hallé et al. 1978) are added the complexity of vines, epiphytes, stranglers, and palms. However, even at one latitude the variety of vertical structures is wide.

The taller a forest is, generally the more complex will be its structure (Brown 1991), simply because there are more possible vertical positions for foliage. The vertical availability of light, however, can organize the vertical distribution of foliage in different ways, depending on forest height and angle of the sun. For example, in forests in the southeastern United States understory trees tend to grow up to, and form a stable layer at, the height where rays of light passing at generally low angles through holes in the upper canopy converge to form a spatially uniform light field (Figure 11.3; Terborgh 1985). This mechanism tends to limit complexity compared with profiles in taller tropical forests, where light passing through canopy holes at higher angles can pass farther down the longer vertical gradient, producing a more complex light environment and vertical distribution of foliage.

Site conditions can also affect vertical structure. In southern Wisconsin forests foliage profiles (and species) shift, on a mesic-xeric gradient, from nearly a monolayer foliage distribution on the most mesic sites, to increasingly uniform distribution at medium sites, to a distinctly two-layer distribution, of upper canopy and dense shrub layer, at the most xeric sites (Aber et al. 1982). Site fertility, however, did not clearly affect vertical structure in Piedmont hardwood forests in North Carolina (Hedman and Binkley 1988). Instead, vertical profiles in these stands reflected stand composition, age structure, and history.

#### SUCCESSION AND STAND DEVELOPMENT

Vertical structure changes markedly during forest succession. Early successional stands have simple structure, but as succession proceeds, inherent differences in height growth between regenerating tree species produce strata and more complex vertical structure. At Hubbard Brook, New Hampshire, for example, stratification results from differential growth rates during succession by species cohorts of pin cherry (*Prunus pensylvanica*), sugar maple (*Acer saccharum*), and beech (*Fagus grandifolia*), in descending order (Bicknell 1982). Similarly, black ash (*Fraxinus nigra*) outgrows elm (*Ulmus americana*) in Great Lakes forests (Guldin and Lorimer



Fig. 11.3. A schematic diagram showing how light availability can organize vertical structure in some mature forests. (Adapted from Terborgh 1992, with permission of W. H. Freeman and Company.) Light passing through canopy gaps during a day produces a cone of light within the forest. Where these cones intersect in the understory there is a spatially uniform light field. Understory trees tend to grow up to, and form a stable layer at, this height. Between the canopy and this layer, light is more variable and vegetation sparser.

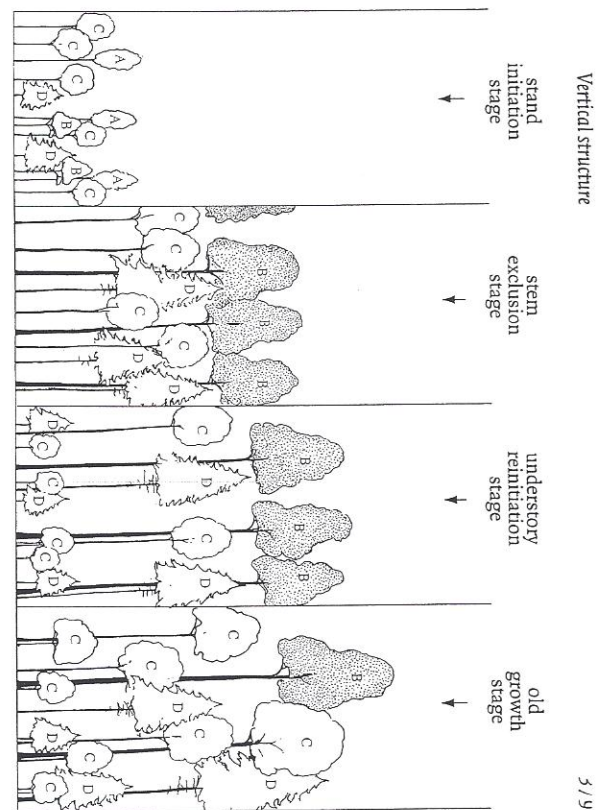


Fig. 11.4. Schematic diagram showing how vertical structure develops during succession in some forests. After stand initiation, differentiation of crown height and form results from variable height growth and mortality among individual trees and from contrasting species-specific architectures that are increasingly apparent as trees mature. Differentiation of canopy trees permits increased light below and the initiation of an understory stratum. There are multiple cohorts and maximum vertical complexity in old growth. In central New England, USA, typical tree species in this sequence would be, as designated by letters in the diagram: A, black birch (*Betula lenta*), B, red oak (*Quercus rubra*), C, sugar or red maple (*Acer saccharum*, *A. rubrum*), D, hemlock (*Tsuga canadensis*). (Adapted from Oliver 1981, with permission from Elsevier Science.)

1985), and secondary species top primary species during succession in Ghana (Swaine and Hall 1983), thereby differentiating strata during regrowth.

As the overstory layer matures, it becomes more horizontally heterogeneous and vertically complex due to thinning and to differential height growth and shaping of crowns (Figure 11.4). This permits more light to penetrate lower levels, and in response an understory layer develops, further complicating vertical structure (Oliver 1980). Yet when complexity increases with forest age it is not necessarily manifested by more and distinct foliage layers. In 12 New Hampshire stands ranging from three to 57 years old, plus one at 200 years, foliage did concentrate into strata through year 30, but later became more evenly distributed from forest floor to canopy (Aber 1979). In older forest stands, big trees die, leaving large gaps where vertical structure redevelops through a process similar to the stand-scale succession just described. The staggered timing and horizontal pat-

terning of this gap-phase regeneration produces variation in vertical structure within a stand (Oliver and Larson 1996) (also see Chapter 4).

Some forests become less vertically complex with time. The giant, emergent figs (*Ficus insipida*) and spanish cedar (*Cedrela odorata*) that colonize early in succession along the Río Mannu, Peru, eventually die and are replaced by shorter, more shade-tolerant species (Foster *et al.* 1986). On a longer time scale (100 000 years), soil weathering and leaching in tall Queensland rainforest eventually stunted the vegetation (Walker *et al.* 1981), and some forests become sphagnum bogs (Oliver and Larson 1996). Having discussed what vertical structure is and how and why it varies among forests, we next consider how vertical structure affects plants and animals. Understanding those mechanisms will help us manage forests for biodiversity. In a later section we will relate these mechanisms to patterns of species richness.

### Effects of vertical structure: mechanisms

The vertical organization of forest vegetation has various direct effects on animals and plants. The vertical arrangement of flowers, fruits, and foliage is the vertical arrangement of food for some animals, as well as the arrangement of sites for nesting, resting, perching, basking, and mating (Bell *et al.* 1991). For stranglers, vines, and epiphytes it is the vertical arrangement of substrate for attachment.

The vertical organization of forest vegetation also has indirect effects on animals and plants, because it affects internal stand microclimates and the distribution of animal prey (Bell *et al.* 1991, Robinson and Holmes 1982). From canopy top to forest floor there are gradients of decreasing light and wind, increasing humidity, and increasing (night) or decreasing (day) temperature (Chiarello 1984). The slopes of these gradients are usually not smooth but change markedly at heights of foliage concentrations that intercept light and interrupt air movement. Thus profile complexity produces complexity in internal stand microclimate, and profile differences among stands produce different arrays of microclimates. The range of microclimatic values in tall forests may be greater than in short forests, while the gradient may be less steep.

During stand development, changes in vertical profiles alter the vertical array of microclimates. In a chronosequence of tulip-poplar (*Liriodendron tulipifera*) forests, light transmittance to the ground was lowest through the dense regeneration in young stands. It increased at about 50 years as

the regeneration grew taller, permitting growth of an understory, then decreased in stands of 65–340 years, as the understory formed a dense layer (Brown and Parker 1994).

### EXAMPLES: DIRECT EFFECTS

The distribution of animals that eat plants is directly influenced by the vertical location of plant food. The most productive layer is the upper canopy, exposed to light that stimulates leaf, flower, and fruit production (Terborgh 1992) and attracting numerous insects (Sutton 1983) and birds (Stiles 1983). This active surface is better visualized not as a level, upper-canopy stratum but as a foliage–light interface (*cf.* Stiles 1983) that follows the outer contours of the canopy trees and descends into the gaps between them (Chapter 4). Also, a more detailed look at the distribution of insect herbivores reveals that many are more attracted to lower strata with softer, more edible, shade leaves than to upper canopy leaves (Lowman 1995) that may be leathery to resist desiccation.

Large arboreal herbivores are directly affected by vertical structure because they require adequate support for their bodies and appropriate configurations of vegetation for their movements (Pounds 1991). For instance, in tropical forests monkeys tend to be found well above ground level, where there are thicker branches, rather than in the more continuous, but thin and weak, branches of lower levels (Terborgh 1992). In Surinam, body sizes and locomotion of different monkey species are related to the forest strata they use (Fleagle and Mittermeier 1991), and in India the giant squirrel (*Ratufa indica*) requires a certain amount of canopy continuity for travel through the forest (Datta and Goyal 1996).

Foraging of insectivorous birds is also directly affected by vertical structure. In West Virginia, a forest that had regrown after logging in the early 1900s was taller and had a larger vertical span of relatively foliage-free area beneath the main canopy than did a forest regrown since clearcutting in 1958 (Maurer and Whitmore 1981). In the older forest Acadian flycatchers (*Empidonax virens*) preferentially sallied for flying insects in the sub-canopy open space, whereas in the young forest they were more broadly distributed vertically and used other foraging techniques to cope with the lack of open area. In Belize, some forest birds seem to adjust their foraging height depending on overall forest height (Mallory and Brokaw *in press*), and different European warbler species prefer different vegetation structures to which their particular leg morphologies are adapted (Winkler and Leisler 1985).

#### EXAMPLES: DIRECT/INDIRECT EFFECTS

Plants create the vertical structure in forests, but they are also influenced by it. Epiphytes are plants that grow on other plants but are not otherwise parasitic. They include many dicot species, especially orchids and bromeliads, as well as mosses and lichens. Epiphyte distribution is influenced directly and indirectly by vertical structure. For example, in Connecticut (Hale 1965) and Jamaica (Kelly 1985), particular epiphyte species are found in characteristically different vertical locations on trees and at different places on branches, presumably because they are confined to certain substrates that are suitable both for attachment (direct effect) and for light and humidity (indirect effect). In turn, the vertical distribution of certain bromeliad species determines the vertical distribution of particular mosquito species that breed in them (Pitendrigh 1948).

Insects and other invertebrates are finely tuned to the variation in physical and biological factors associated with vertical complexity (Speight and Wainhouse 1989). Species of *Anopheles* mosquitoes in Panama frequent different levels in the forest corresponding to differences in humidity (Bates 1944), and there is pronounced vertical stratification of arthropods, correlated with architectural and microclimatic variables in Missouri oak-hickory (*Quercus-Carya*) forest (Dowdy 1947) and other temperate forests (Davidson 1930, Fichter 1939, Adams 1941).

We have seen how the height of understory trees is limited by the angle of light passing through the upper layer of some forests (Figure 11.3). This indirect effect would also select for plant species adapted to reach maturity in the light climate at that level, such as dogwoods (*Cornus* spp.) and redbud (*Cercis canadensis*) in North American forests (Terborgh 1985). Similarly, in a developing stand, the continuous canopy of the early phase may allow only shade-tolerant plant species below it. However, the heterogeneous canopy of later phases permits more light penetration, ranging in area from sunflecks that sustain forest floor herbs (Anderson et al. 1969) to large gaps where light-demanding tree species establish (Denslow 1987). Although gaps are productive spots for some species, damage to the upper canopy can decrease abundances of animals adapted to shaded understory. Hurricane Hugo in Puerto Rico destroyed much forest canopy, raising temperatures, reducing humidity, and consequently depressing the abundances or changing distributions of understory snails, walking-sticks, a frog (*Eleutherodactylus portoricensis*), and Anolis lizards (Reagan 1991, Willig and Camillo 1991, Woolbright 1991).

We have now reviewed some mechanisms by which particular features

of vertical structure in forests affect the distribution of particular plant and animal species. That enables us to understand the next topic: how vertical structure affects the number of species that coexists in forests.

#### Effects of vertical structure: species richness

In general, the more vertically diverse a forest is the more diverse will be its biota, for two main reasons. First, a more complex habitat contains more kinds of microclimates and microhabitats for more species. For instance, we have seen how different epiphytes and lizards prefer different kinds of substrates, at different vertical locations, for attachment or perching; the more kinds of those substrates included in a forest, the more kinds of epiphytes and lizards there can be. Second, it follows that a more complex vertical structure, supporting more kinds of plants and animals, provides more diverse food resources for more diverse consumers (Malcolm 1995). Yet there are exceptions to this relationship between vertical complexity and species richness, because other factors, such as biogeographic patterns and differential response to habitat structure among taxonomic groups, also influence richness.

Whereas relatively many studies describe the vertical distributions of species in forests, fewer take the next step and show that forests differing in vertical complexity also differ in species richness. However, the examples below illustrate the generally positive correlation of complexity with richness in all forest types and for all taxonomic groups that have been studied, but also illustrate some exceptions.

#### PLANTS

For plants vertical complexity is in itself an expression of species richness, because complexity is in part an expression of the variety of plant life forms and species-specific morphologies (Terborgh 1992, Aiba and Kohyama 1996). In tall tropical forests the variability of light conditions in middle layers (Figure 11.3) contributes to a higher species richness of trees in the middle strata as compared with other strata, and as compared with temperate forests with more uniform light conditions beneath the canopy (Terborgh 1992). The species-specific preferences of epiphytes for vertical positions and substrates probably contributes to such high diversity as the 77 species in 17 families found on three neighboring, 45–50 m tall trees in French Guiana (Freiberg 1996). Epiphytes contribute a large part of the

plant species richness of tropical and temperate forests (Rose 1974, Gentry and Dodson 1987) and, in turn, support a rich fauna (Gerson and Seward 1977, Nadkarni and Matelson 1989).

#### MAMMALS AND REPTILES

Mammal and reptile species richness in tropical forest often reflects vertical complexity. For example, seven co-occurring squirrels in Africa differ in their use of the vertical vegetation column (Emmons 1980). In Venezuela the richness of mammal species is correlated with the increasing vertical complexity from savanna to tall forest, related to increasing potential food resources (August 1983). Surprisingly, the increased richness was in mainly terrestrial species, not arboreal species. Small mammal species richness and abundance in Brazil were correlated with density of understory vegetation (Malcolm 1995). In this case understory density was higher in disturbed forests. Intercontinental differences in the richness of gliding mammals and reptiles may be attributed to intercontinental differences in vertical structure. In taller Indo-Malaysian forests there are more gliding species than in Africa or America, perhaps because this mode of travel is more rewarding where launching from taller trees permits longer glide distances (Dudley and DeVries 1990). As a final example, species of *Anolis* lizards in Puerto Rico coexist partly by choosing different perch types that are stratified by height in the forest (Reagan 1992).

#### BIRDS

Birds are the best studied group in relation to vertical structure in forests. The association between bird species diversity (BSD) and foliage height diversity (FHD, see above) has been demonstrated in many places. BSD, like FHD, is calculated using  $H'$ , to take into account both the total number of species present and the evenness of their abundances. The most diverse bird community (highest BSD) has birds evenly distributed among many species, and this community is frequently found in forests with the most diverse vertical structure (highest FHD), in which foliage is evenly distributed among many layers.

BSD was positively correlated with FHD in, for example, the northeastern United States (MacArthur and MacArthur 1961), Illinois (Karr 1968), Australia (Recher 1969), Scandinavia (Rov 1975), and Scotland (Moss 1978). The Scottish study showed that the more complex forests were used

by small numbers of many bird species, rather than large numbers of few species, explaining why BSD was better correlated with FHD than were simply the numbers of species or of individual birds. The intercontinental consistency of these results suggests that the relationship is not due merely to the kinds of birds in these forests but to the universal process of diversification to fill niches in complex habitats (Recher 1969). Moreover, BSD is correlated with FHD because FHD is not only an index of the vertical complexity of foliage layers, but because it tends to be correlated with other components of habitat diversity important to birds, such as the greater variety of bark and leaf types that generally occur in older, more vertically complex forests (Holmes *et al.* 1979).

FHD is not always a good predictor of BSD, because other factors contribute to diversity. In various British studies on the correlation of BSD with FHD, it was sometimes not clear if it was vertical structure itself that affected diversity, as opposed to something else correlated with FHD, such as tree species composition, site, or altitude (Avery and Leslie 1990). The importance of additional factors is obvious from the fact that there are more birds in Amazonian forests than in Panamanian, Puerto Rican, and North American forests of similar FHD (Terborgh and Weske 1969). Furthermore, within a region the correlation between FHD and BSD may be misleading. On a gradient from 500 to 3500 m elevation in eastern Peru both BSD and FHD declined, but this was due mostly to a decline in the richness of insectivorous birds; nectarivores did not decline and frugivores declined only slightly, because foods of these two groups are less related to FHD than is the food of insectivores (Terborgh 1977). A more dramatic exception to the expected correlation between BSD and FHD is the greater number of Argentine bird species in scrub-cedar (*Austrocedrus chilensis*) vegetation than in adjacent, more vertically complex southern beech (*Nothofagus* spp.) forest (Ralph 1985). It appears that scrub-cedar habitat, although vertically simpler, draws birds from a wider area of similar habitat, to which more species may have adapted, than does the more complex beech forest (see Engstrom *et al.*, 1984, for a similar example).

#### SUCCESSION, VERTICAL STRUCTURE, AND SPECIES RICHNESS

Because more vertically complex forests usually contain more species than simpler forests do, and because vertical complexity generally increases with forest age, it follows that species richness usually increases

with succession (Chapter 4). The species richness of beetles and bugs increased with succession from old field to forest in Britain; even as plant species diversity declined in later stages, beetle and bug richness increased as vertical complexity increased (Southwood *et al.* 1979). Similarly, the density and, presumably, species richness of arthropods increases with forest age and vertical complexity in Douglas-fir forests in Oregon (Schowalter 1995). Species richness of birds increases during succession in various European forests (Głowaciński and Järvinen 1975, Turcek 1957).

However, when richness increases with succession, it is not necessarily monotonic, partly because the increase in vertical complexity with succession may not be monotonic. For example, in northern hardwoods and spruce-fir (*Picea-Abies*) forests in the United States, the number of animal species is high in regenerating stands, drops in the pole stage, when the canopy is fairly uniform and the understory is suppressed, then increases to a maximum in mature and overmature stands, as canopy structure diversifies and the understory develops (DeGraaf *et al.* 1992). It is important to understand the connections between succession, vertical complexity, and species richness in forests, because forest management usually maintains much forest area in early- and mid-successional stages. In the next section we discuss the impacts of logging on vertical structure and, briefly, the value of agroforestry for biodiversity.

### Forest management, vertical structure, and biodiversity

#### FORESTRY

Our review of the literature suggests, as a generalization with exceptions, that tall, mature forests contain the most vertical complexity and that vertical complexity is positively correlated with species richness. Thus ideal management to conserve species richness within a stand is probably to let it attain maturity and not disturb it. Still, the most species-rich stand will lack some species characteristic of vertically simpler stands. For example, in northern hardwoods forest some bird species prefer recently logged stands (Lent and Capen 1995), and in this forest type no single stand structure is preferred by all species (DeGraaf *et al.* 1992). Therefore, to conserve biodiversity across landscapes it is best to maintain a collection of stands of different vertical structures, as produced by natural disturbances (wind, fire, flood, etc.) that create a mosaic of

different-aged successional stands. This suggests that the best management for biodiversity over a landscape would mimic the natural disturbance regime to which the local biota are adapted, including creation of early successional stands with simple vertical structure. It will not, however, be possible to exactly mimic natural disturbance and regeneration in forests managed for timber. After all, the very idea of silviculture is to alter nature, to promote the abundance and growth of preferred tree species and harvest some of them before their natural deaths (Putz and Viana 1996). With care, however, native plants and animals can be maintained in logged landscapes.

Forestry systems are of three basic types that differ in their effects on vertical structure at the stand and landscape levels (Chapter 2). In single-cohort systems all trees are harvested over a certain area, in the practice known as clearcutting. In two-cohort systems most or many trees are cut in a stand but individuals or patches of trees are retained uncut. In multi-cohort systems single, or small groups of, trees are selectively felled at scattered locations in a stand. What are the impacts of these various systems on vertical structure?

In single-cohort systems, clearcutting trees in patches initiates secondary succession, during which vertical structure develops as described earlier. At the stand level clearcutting initially simplifies vertical structure. Post-harvest planting or thinning may further simplify vertical structure by limiting species composition and therefore tree form, or by creating a cohort of same-sized trees. Alternatively, thinning can accelerate stand differentiation and development of vertical structure (DeBell *et al.* 1997). The biggest potential problem in single-cohort systems is that stands with vertical structure typical of old growth may never be allowed to develop, if harvest rotation period is too short (Curtis 1997), or will be too small or isolated to support viable populations of dependent organisms. Yet if there is a range of stand ages (vertical structures), including old growth, and treatments do not overly homogenize seral stages, species richness might be maintained over the landscape, although the relative abundances of organisms will differ from what they would be in a pristine system. The impact on biodiversity of single-cohort systems that create a landscape mosaic of different-aged stands is treated in Chapter 4, but keep in mind that a differentiating feature of the stands, and one significant for biodiversity, is vertical structure.

In two-cohort systems, retention of scattered single trees or patches of trees diversifies the vertical structure of subsequent regenerating stands (Franklin *et al.* 1997), as typically occurs with natural disturbances, which



destroy stands but leave scattered old trees or tree patches. This legacy of vertical structure has direct, positive effects on biodiversity; for example, in New England oak-pine (*Quercus-Pinus*) forests, leaving 'bull pines' provides hawks and herons with perches and nest sites (DeGraaf *et al.* 1992). Retention has indirect effects also, because retained vertical structure ameliorates microclimatic extremes in harvested areas and hastens re-establishment of later-successional conditions. Studies in Oregon and Tasmania suggest that retained trees enhance species richness in regenerating forests (Hansen *et al.* 1991, Taylor and Haesler 1995). A strength of the two-cohort system is how flexibly it can be adjusted in terms of amount, location, and dispersion of retained vertical structure, according to forest type and management goals (Franklin *et al.* 1997). For instance, retention well suits the goals of shelterwood systems, in which understory and lower canopy trees are removed and replaced by seedlings of desirable species under the shelter of canopy trees, and of seedtree systems, in which scattered trees are left to provide seed for a new stand.

In multi-cohort systems selection cutting of single trees produces a finer-grained mosaic of vertical structures than single- or two-cohort systems do. Instead of initiating secondary succession in whole stands, single tree selection initiates gap-phase regeneration. The resulting stand mimics unlogged forest with natural treefall gaps, except that gaps and regenerating patches are more frequent. Group selection generally creates more large gaps than in a natural forest but not on the scale of clearcutting. Thus the impact on vertical structure of multi-cohort systems varies according to how many trees are taken per unit area and time (Whitman *et al.* 1997), yet the range in vertical structures among stands will not be so great as in single- or two-cohort systems.

At the stand level in a multi-cohort system, vertical complexity and species richness may be higher than in any seral stage in other systems. Nevertheless, species richness may be less than in old growth, especially due to impacts of felling and removal of canopy trees on the vertical structure in lower strata. Compared with the patchy environment created by the crowns of large, diversely shaped canopy trees, the understory is structurally and climatically uniform (Terborgh 1992). The felling of a large tree disrupts that uniformity by direct physical damage and by raising light levels, increasing temperature variation, reducing humidity, and encouraging dense growth near the ground. This, and log removal along the ground, alter the understory habitat and can reduce numbers of some understory species (Lambert 1992, and see Case Study below). However, as with clearcutting, some species benefit, for example, frugivores that take

advantage of increased fruiting stimulated by light penetrating the broken canopy (Johns 1988).

Canopy biota are certainly also affected by selection cutting. In Brazil, cutting of only eight trees per ha reduced canopy cover from 80% to 43% (Uhl and Viera 1989). Such damage disrupts arboreal pathways of upper strata animals (Datta and Goyal 1996). Liana cutting to reduce felling damage (Putz 1991) would moderate this disruption, but would also eliminate the pathways and vertical complexity contributed by those lianas. Perhaps more serious is that selection cutting often removes the largest trees, valuable for epiphytes and some animals. For example, selection cutting of large Norway spruce (*Picea abies*) significantly alters relative abundances of lichen species in northern Sweden (Essen and Renhorn 1996). To mitigate negative impacts in multi-cohort management, tree felling should not greatly exceed natural treefall rates, some large trees should be retained, and loggers should practice reduced impact methods for felling and skidding (Pinard and Putz 1996). The best animal indicators of logging impacts may be arthropods, due to their fine-scale associations with vertical structure and rapid response to disturbance (Kremen *et al.* 1993, Niemela 1997).

#### AGROFORESTRY

Agroforestry is a production system that yields crops from both canopy trees and other plant life forms growing in the same site, or at least retains trees to benefit an understory crop. Though less vertically complex than most natural forests, agroforests are usually far more complex and rich in plants and animals than is conventional agriculture of annual crops. In one region of Brazil at least 60 plant species are used in different agroforestry systems. Some of these systems combine commercial timber trees, fruit trees, palms, shrubs, vines, and herbs (Subler and Uhl 1990).

A widespread agroforestry system is the cultivation of coffee (*Coffea* spp.), an understory tree, under a canopy of taller trees, but this system is threatened by new techniques that simplify its vertical structure (Perfecto *et al.* 1996). Coffee is traditionally grown either in natural forest cleared of its understory or where canopy trees are planted, along with other plants such as bananas (*Musa* spp.). Both systems provide a vertically complex vegetation that supports a high diversity of other plants and many groups of animals. Given the large area in the world devoted to coffee, these traditional, vertically complex plantations conserve many species. However, new, high-yield strains of coffee, grown in full sun in vertically simple

plantations of coffee monoculture, have already replaced half the area of coffee planted in northern Latin America. Not only are all upper strata and dependent organisms eliminated in 'sun coffee' plantations, but the remaining coffee stratum itself is much poorer in species due, in part, to its harsher microclimate without a buffering upper canopy.

#### Case study: Effects of silvicultural treatments on vertical structure and birds in Venezuela

Three different silvicultural treatments were applied to a forest in southern Venezuela, each with different impacts on vertical structure and the species richness of birds (Mason 1996). The first treatment was selection cutting, in which about 2.3 trees/ha ( $7.3 \text{ m}^3 \text{ wood/ha}$ ) were removed, with no further treatment. The second was selection felling followed by bulldozing of 'enrichment strips', 3 m wide and 1000 m long, separated by about 50 m of logged forest, and planted with seedlings of commercial species. The bulldozed trees were shoved beyond the 3 m width into the forest. The third treatment was low intensity selection cutting, followed by cutting of all woody vines at ground level.

Working in replicate  $200 \times 200 \text{ m}$  plots following each treatment, and in primary forest, Mason mist-netted birds in two long sessions within a period of 1.75 years. Mist-nets were set in the understory of the unlogged forest matrix of each treatment, not in the directly affected sites. He also measured canopy height, canopy openness, and understory stem density in each treatment and the primary forest.

Over the 1.75 years Mason mist netted 3783 birds of 117 species, and discovered that birds were strongly affected by two of the silvicultural treatments. Compared with primary forest, bird assemblages were significantly different in selectively logged forests, even more different in the forest with enrichment strips, but not different in very selectively logged forest where vines were cut. The logged forests generally had lower, more open canopies and denser understories than did the primary forest. Differences in mist-netted bird assemblages were best correlated with understory stem density: as stem density increased, bird assemblages increasingly diverged from the assemblage in primary forest. Percent canopy openness was also, but less strongly, correlated with changes in bird assemblages.

We can understand the differences in these bird assemblages by looking at impacts on different feeding guilds and how the foraging habits

and preferred foods of those guilds may have been affected by changes in vertical structure. Hummingbirds benefited from logging, presumably because upper canopy openings increased light in the understory, stimulating flowering that provides nectar and attracts insects, both eaten by hummingbirds. The response of frugivores to logging was mixed: some increased and others decreased. Fruit is a patchy resource even in primary forest, thus changes in vertical structure due to logging may not have significantly changed the distribution or abundance of this resource. In fact, as with nectar, logging may increase fruit abundance by permitting more light to penetrate the forest and stimulate reproductive activity in the understory.

The biggest impact was on insectivorous birds, whose foraging mode is often closely tied to vegetation structure. For example, of 22 antbird species found in primary forest, 12 species were less abundant in the selectively logged area, four were absent, two were equal in numbers, and four were more common. Differences between primary and logged forest with enrichment strips were greater: six species were less abundant, nine were absent, and seven were more abundant. The response of sally-feeding flycatchers was similar to that of antbirds: of 22 species present in primary forest, 14 were less abundant or absent in selectively logged forest or in logged forest with enrichment strips.

In this Venezuelan forest a significant portion of the understory bird community was less abundant or even absent, while a few species increased, after selective logging and silvicultural treatments that affect vertical structure. Opening the canopy changed the understory microclimate and promoted increased plant density and perhaps plant reproductive density. The degrees of change in canopy openness and understory density were correlated with changes in the avifauna. Logging followed by clearing of enrichment strips had the most impact on vertical structure and birds. Because the strips were only 50 m apart this treatment affected both the immediate impact zones and the intervening forest understory. Low intensity logging followed by vine cutting had little effect on understory birds, perhaps because vine cutting altered vertical structure little.

#### Summary

Vertical structure is the bottom to top spatial configuration of above-ground vegetation within a forest stand. Vertical structure is depicted in profile diagrams and sometimes quantified as 'foliage height

diversity', a measure based on the Shannon-Weiner Diversity Index. Each forest type has a different vertical structure due to differences in height and shape of trees and other plant life forms composing a forest. Within a forest type, vertical structure and complexity vary with successional stage and site conditions. Generally, forests become more vertically complex with age, because they become taller, trees differentiate in height and crown form, and large trees die, initiating gap-phase regeneration.

Vertical structure directly affects biota because it constitutes the arrangement of attachment sites for epiphytes and foraging, perching, and nesting sites for animals. Vertical structure indirectly affects biota because it controls internal stand microclimates to which animals and plants respond, and it influences the distribution of prey for carnivores and insectivores.

In general, the more vertically complex a forest is the more species-rich it is, and both parameters usually increase with succession. Vertical complexity is in part an expression of plant species richness, and it further creates variation in microclimate, substrate, and food resources that support other biota. The best known example is the frequently observed positive correlation between foliage height diversity and bird species diversity in forests, to which, however, there are exceptions.

Clearcutting in single-cohort forest management systems creates a landscape mosaic of stands of different ages and vertical structures. Overall, this system may support a diversity of species adapted to the different successional stages. However, single-cohort systems may reduce species richness if the complex vertical structure of old growth becomes too rare in the landscape. Long rotations can permit development of old-growth vertical structure, while thinning can hasten its development. Retention of scattered old trees or tree patches in two-cohort systems enriches the regenerating stand with vertical structure typical of later successional stages and can accelerate its development. Selection felling of single or grouped trees in multi-cohort systems may diversify vertical structure within a stand and therefore benefit some species, just as natural treefall gaps do. However, the frequency of felled tree gaps and cutting of large trees may exceed the frequency of natural gaps and death of large trees and have negative impacts on animals and plants that depend on relatively continuous canopy pathways, uniform understory conditions, or large trees. Agroforestry in the tropics maintains vertically and biologically diverse strands of overstory trees and other plant life forms.

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### Further readings

Further reading on vertical structure, biodiversity, and forest management should start with Hunter (1990), who wrote on these same subjects. For a discussion of various ways vertical structure can be defined and quantified, a good article is Popma et al. (1988). The variety of vertical structures among different forest types, how structure changes during forest development, and effects of management are shown in detail by Oliver and Larson (1996). Terborgh (1992) describes vertical structure in temperate and tropical forests and its relationship to species diversity. Suggestions on how partial retention harvesting (Franklin et al. 1997), rotation length (Curtis 1997), and thinning (DeBell et al. 1997) can maintain vertical structure and biodiversity in managed forests are presented in Kohn and Franklin (1997).

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