4 Forest Structure and Composition

When a forester sees a forest she often will look at the tree species mix, the tree size, tree density, and other clues about how the stand might be managed to achieve wood products or other goals. When a wildlife biologist sees a forest, she sees evidence of deer browse, pellet groups on the forest floor, tracks in the mud, or nests in trees. To effectively manage habitat in a forest, the forester and the biologist must assess the sizes, numbers, and arrangement of a set of habitat elements, the building blocks for habitat within a stand or forest. *Habitat elements* are those pieces of the forest that in certain numbers, sizes, and arrangements meet the food or cover resources for a species. If these are highly variable within and among stands, then the needs for many species can be met. If they are very uniform, then the needs of only a few species can be met. The challenge to the forester and biologist is to walk into a stand and see the same habitat elements. In so doing, the biologist can explain why more or fewer of any set of them are needed to meet a species goal. Similarly, the forester can explain how silviculture might be used to achieve that goal.

FOOD AND COVER IN A CELLULOSE-MANAGED SYSTEM

Timber management has, for many years, been focused on producing wood products (cellulose) from managed forests. To maximize cellulose production, foresters want to be sure that the growing space for trees in a stand is fully utilized. Cellulose is quite indigestible for most species so unless the trees are allowed to decompose into forms of carbon that are digestible, maximizing timber production can lead to low levels of food for many species. To compensate for this lack of digestible energy, growing space could be allocated to other plant species or habitat elements, or the cellulose must be made available to more species through wood decomposition. Both of these choices result in a decrease in the production of wood for humans. Consequently, the decision to manage habitat elements must come with the understanding that providing some habitat elements in some stands or in some parts of some stands may come at a financial cost to the landowner. The manager must decide which habitat elements can be provided in a way that is compatible with the goals for managing the stand for cellulose, and which will come at a cost, and how much cost the landowner is willing to bear.

Generally, we think of providing these elements by altering the structure and composition of a stand. *Structure* refers to the physical features of the environment such as vegetation, soils, and topography. The complexity of the structure serves as both proximate cues in habitat selection as well as ultimate resources for cover (e.g., nesting sites, resting sites). *Composition* refers to the species of plants, types of soils, and other features that contribute complexity, for instance through plant species richness. It is the combination of vegetation structure and composition that managers can change through their management actions.

VERTICAL COMPLEXITY

Read any forest plan or silvicultural prescription and early on there will be reference to forest area: 10, 100, or 1000 ha. But to most animals, forests are not areas. Forests are volumes—they have three dimensions: length, width, and height. One characteristic of forest development that influences the diversity of animals within a stand is the distribution of the foliage vertically within the stand.

Some species use the foliage as a source of food either directly through herbivory (e.g., red tree voles in the Pacific Northwest) or indirectly by feeding on foliage-dwelling invertebrates (e.g., red-eyed vireos in hardwood forests of the southern United States).

Indeed, many bird species distribute themselves vertically within a forest to take advantage of food and cover resources while reducing competition among species for these resources (Figure 4.1). In some stands, the foliage is distributed only in one layer, such as a dense plantation where all of the live foliage is in one canopy layer with little foliage beneath it. These stands typically provide habitat for a narrow range of species, but can still be important for a few species (Titchenell et al. 2011). Mixed species stands have several tree and shrub species and often with foliage distributed in several layers (understory, midstory, overstory). These multilayer stands tend to support more species of vertebrates than a one-layer stand. Wet tropical forests and mixed mesophytic forests develop vertical complexity naturally because of the mixture of tree species that occur within them. The distribution of foliage can be influenced by the shade tolerance of the tree species in the stand. *Shade-tolerant* species are those that can survive under low light conditions. Shade-tolerant species use a strategy of survival and slow growth under low light until an opening or gap is provided in the tree canopy. When that gap occurs from tree fall or tree death, then the shade-tolerant species in that gap grow more rapidly to occupy the opening. These species can occupy lower levels in the stand for many years and often have deep crowns. Sugar maples, hemlocks, and American beech are examples of species that use this strategy. *Shade-intolerant* species do not survive under low light conditions and grow well only under full sunlight. Shade-intolerant species tend to grow rapidly once the seed has germinated. Because leaves are intolerant of shade, they tend to have smaller crowns in dense stands. Aspens, gray birch, and willows are examples of shade-intolerant species. A plantation of shade-tolerant species will have somewhat greater vertical complexity than a plantation of shade-intolerant species at a similar density simply because of the depth of the crowns of the trees.

Silviculture can be used to modify the vertical complexity in a stand in several important ways. Foresters usually will approach management of a stand using either even-aged or uneven-aged strategies. An even-aged stand is one in which most of the dominant trees—those trees comprising the uppermost canopy—are of a narrow range of ages. That is, they all began life at about the same time following a stand-replacement disturbance such as a fire, hurricane, or clearcut. If the trees are

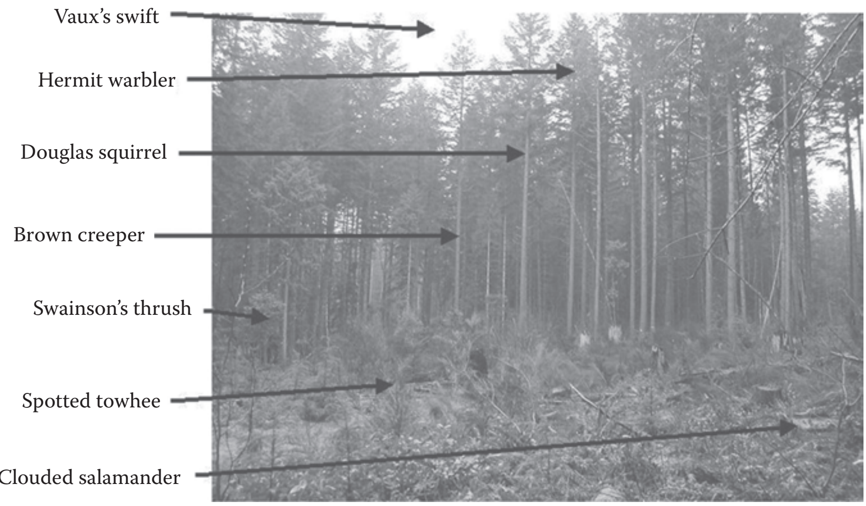

FIGURE 4.1 Vertical structure of a forest provides niches for many species. This is an example from the Willamette National Forest in Oregon.

all the same age and all the same species, then the tree heights will be very similar and many of the tree diameters will be similar (Figure 4.2). In plantations of one species, the distribution of tree diameters is often a bell-shaped curve. Foliage cover is also represented in one dominant layer and is a bell-shaped curve turned on its side (Figure 4.2).

Even-aged stands that contain a variety of species including those that are shade intolerant and others that are shade tolerant often have more complex diameter distributions and a vertical foliage structure (Figure 4.2). Slower-growing shade-tolerant species in the understory are ‘waiting’ for the intolerant species in the overstory to die. Consequently, the range of tree diameters, heights, and distribution of foliage is more complex than in a single species plantation.

Any disturbances, natural or silvicultural, that cause the diameter distribution of a stand to change from uniformity to uneven sized will lead to more vertical complexity within the stand. In particular, silvicultural practices that create regeneration sites, where seeds can germinate and grow, can result in an uneven-aged stand—one with many tree ages and sizes (Figure 4.2). If these trees of many ages also represent a variety of tree species, then trees with a variety of diameters and heights will be represented in the stand.

Vertical complexity is typically measured using an index to foliage height diversity (FHD). FHD is calculated in a manner similar to species diversity indices, by considering both the number of layers in a stand (comparable to the number of species) and the percent cover by foliage in each layer (comparable to the number of individuals of each species). Taller forests may have many layers and if they have foliage cover in each layer, then FHD will be high (e.g., an old tropical forest). Stands with short stature and all of the foliage in one or a few layers will have a low FHD (e.g., a young single-species plantation). MacArthur and MacArthur (1961) reported that bird species diversity (BSD) was associated with FHD in the temperate forests of the eastern United States. There is a

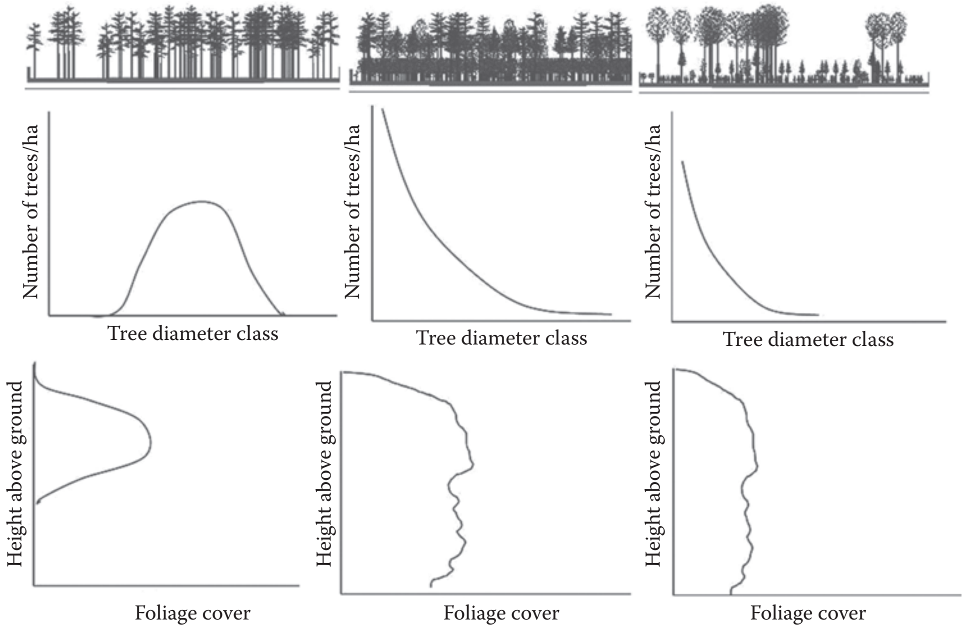

FIGURE 4.2 Even-aged, single species stands have a bell-shaped distribution of tree diameters, and one dominant vegetation layer (left). Even-aged mixed species stands have a skewed diameter distribution and a more complex vertical structure (middle). Uneven-aged stands have an inverse-J-shaped diameter distribution and a more complex vertical structure (right). Figures developed using Landscape Management Systems software. (McCarter, J.M. et al. 1998. *Journal of Forestry* 96(6):17–23.)

logical conclusion that increasing FHD could lead to an increase in BSD within the stand, but the BSD–FHD relationship has not been found consistently in other forests, such as tropical forests where competition among bird species may be important in structuring the community (Pearson 1975). Further, it is important to remember that not all species of animals benefit from vertically complex stands. Species such as northern goshawks and some bat species are very well adapted to forage beneath the canopy of large even-aged stands that have sufficient flight space beneath the canopy. In general, increasing the vertical complexity of a stand increases the potential number of niches for more species of birds (and possibly bats), but this generalization may not hold in some forest types and no single stand condition is best for all species. Nonetheless, Flather et al. (1992) found that a combination of indices of vertical and horizontal complexity were reliable indicators of bird community integrity in the eastern United States.

Horizontal Patchiness

The variability in tree size, species composition, dead wood, and other habitat elements is often related to the horizontal variability within a stand. Homogenous stands with evenly spaced trees and uniform canopies offer fewer niches so animal diversity is often lower in these uniform stands. The size of openings and arrangement within a stand may positively affect some species and negatively affect others. Chapin et al. (1997) found that American marten use of habitat was more influenced by the combination of vertical and horizontal complexity than by the species composition of the forest. Overwintering birds also seem to be associated with horizontal complexity in the southern United States (Zeller and Collazo 1995). Small openings or variability in tree spacing will likely have few adverse effects on most animal species and may benefit the maintenance and development of important ecological processes (Carey 2003). If openings or other discontinuities are larger than a species' home range, then we may begin to see species occupy the stand that otherwise would not occur there (DeGraaf and Yamasaki 2003), but there may be adverse effects of the openings on forest interior-associated species (Germaine et al. 1997). See Chapter 12 for more information on edge effects in forests.

Forage Availability and Quality

Forage for herbivores is influenced by many aspects of forest composition and structure. Conversely, the forest structure and composition can be significantly altered by herbivory. Vertebrate herbivores such as deer, elk, and moose typically *graze* more heavily on grasses (monocots) and forbs (herbaceous dicot plants) than on woody plants during the growing season. Herbaceous plants are more easily digested than woody plants and can represent 50%–80% of herbivore diets during the growing season. When cold weather or drought kills the upper portion of grasses and forbs, then vertebrate herbivores are forced to *browse* more heavily on woody plants. Browsing is concentrated on the new growth of the woody plants because that part is most easily digested. During the winter, browse can constitute over 90% of the diets of vertebrate herbivores, and for forest managers trying to regenerate forests, this level of browsing intensity can be a significant economic burden and have significant ecological effects. Krueger et al. (2009) indicated that not only can herbivory by white-tailed deer have a significant influence on future forest composition but herbivory interacts with disturbance (e.g., canopy gaps) to influence the spatial distribution of future forest composition.

That herbivores impact the trajectory of stand development is not surprising given the potential for intense browsing during winters. Animals that try to survive a long winter on woody browse face significant stress. Nearly all browsing vertebrates lose body mass during the winter (Mautz et al. 1976). Indeed, browse quality is important in slowing the rate of starvation but not preventing it. Providing high-quality grasses, forbs, and browse is important in the overwinter survival of many herbivores. Controlling the intensity of browse on tree seedlings is important in effectively regenerating forests.

During the growing season, stands that allow more sunlight to support grasses and forbs provide higher quality forage for many species. These grasses and forbs are typically found in greatest abundance beneath or between overstory trees in open stands (e.g., savannahs) or following a large disturbance such as a fire or clearcut. The species composition of a stand can have profound effects on animal diversity and use by various species. The digestibility of twigs and leaves can be affected by tree species composition (Mautz et al. 1976).

Each species of herbivore is selective of the species of grasses, forbs, and woody browse that they chose to eat. In so doing, herbivores such as deer and elk can have profound effects on forest structure and composition (Rooney and Waller 2003, Figure 4.3). The potential effects of selective browsing include shifts in tree species composition of the forest understory (Strole and Anderson 1992). For instance, white-tailed deer in Illinois preferred to browse on white oak and shagbark hickory; sugar maple was browsed less than would be predicted from its abundance (Strole and Anderson 1992). Horsley et al. (2003) found that bramble abundance in several silvicultural treatments; the density of striped maple in clearcuts; and birch, American beech, and red maple in thinned stands declined in abundance with increasing deer density. In Yellowstone National Park, elk preferentially browse on willows and aspens (Ripple et al. 2001) and moose in Newfoundland selected balsam fir, pin cherry, high-bush cranberry, and white birch over other plant species. Such selection may be influenced by the digestibility of the various plants, but not always. Mautz et al. (1976) compared digestibility among seven plant species eaten by white-tailed deer in the northeastern United States. They found higher levels of digestible energy in hobblebush, eastern hemlock, and balsam fir than in red maples, striped maple, mountain maple, or hazelnut. Despite these differences, white-tailed deer often feed heavily on maples in the winter in New England (Mautz et al. 1976) so factors other than simply digestible energy may be coming into play. Some plant species contain high levels of phenols that reduce their digestibility for many herbivores (Sinclair and Smith 1984, Friesen 1991). Plants that produce high levels of phenols gain some protection against herbivory, but the coevolution of plants and herbivores has resulted in plant defense mechanisms that are less effective for herbivores such as deer. In the battle of coevolution, mule deer have evolved to produce saliva that contains a substance (prolene) that binds with the phenols and reduces their effectiveness (Robbins et al. 1987, Austin et al. 1989). Other chemicals such as lignin and cutin can

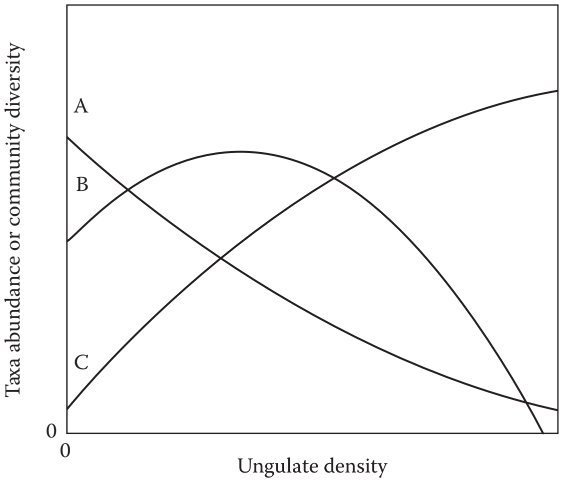

FIGURE 4.3 The change in taxa abundance or community diversity along an ungulate density gradient. Curve A is an idealized representation of taxa or communities that are adversely affected by browsing, and curve C represents taxa or communities that benefit. Curve B represents taxa or communities that benefit from intermediate ungulate densities. (Reprinted from *Forest Ecology and Management*, 181, Rooney T.P., and D.M. Waller, Direct and indirect effects of white-tailed deer in forest ecosystems, 165–176, Copyright 2003, with permission from Elsevier.)

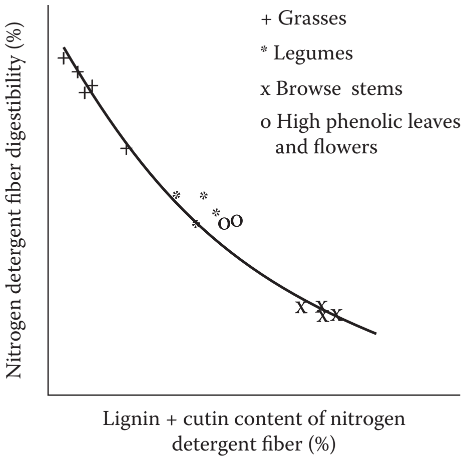

FIGURE 4.4 Plants with lower lignin and cutin have higher levels of digestibility than those with low levels for elk. (Redrafted from Hanley, T.A., C.T. Robbins, and D.E. Spalinger. 1989. Forest habitats and the nutritional ecology of Sitka black-tailed deer: A research synthesis with implications for forest management. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-230.)

influence digestibility as well. Plants with high content of lignin and cutin have lower digestibility than plants low in these compounds (Figure 4.4).

While some plants have chemical and physical defenses against herbivory (Farentinos et al. 1981), plants also respond to herbivory by altering growth rates. Among many grasses, forbs, and some shrubs, moderate levels of herbivory can actually stimulate growth above the levels of either undisturbed or heavily grazed or browsed plants (Belsky 1986, du Toit et al. 1990). It is widely assumed that browsed plants exhibit compensatory growth at the expense of reproduction and that herbivory, therefore, results in decreased seed production or smaller seed sizes (Belsky 1986).

Herbivores alter forest systems in ways other than consumption. They aid in the dissemination of seeds, and they may help to maintain site quality. Some plants are well adapted to dispersal on animals (e.g., bedstraws). Other plant species (e.g., dogwoods and cherries) are well adapted to scarification that results from passing through animal digestive systems and "direct-seeding" in a packet of fertilizer. Consequently, many fencerows are dominated by cherries, hawthorns, and dogwoods because birds often perch on fences after eating the fruits of these plant species.

Specialized herbivores that feed on fungi, called mycophagists, also play a role in ecological processes in forests. Through symbiotic relationships, mycorrhizal fungi aid vascular plants in the uptake of water and nutrients, and they can be particularly important to early plant growth and survival on harsh sites (Perry et al. 1989). Unlike most other fungi, these fungi produce fruits underground, and they do not rely on aerial spore dispersal as do other fungi. They seem, instead, to be well adapted to animal dispersal. Some fungi known as truffles are important components of the diets of some small mammals, particularly red-backed voles in the United States and woylies in Australia (Maser et al. 1978, Taylor 1992, Figure 2.5). These animals eat fruits and ingest spores, which then pass through the digestive system in a few days and are deposited at a new site. A new fungal mat may then grow from this site and ensure the presence and widespread distribution of mycorrhizae in the soil (Cork and Kenagy 1989). Mixing organic matter in the soil by these burrowing animals also is likely to influence decomposition rates and influences soil processes (Maser et al. 1978).

The activities of some herbivores can have tremendous impact on habitat for other species (Naiman 1988). The activities of American beaver, for example, create early successional riparian forest patches and pools in the stream that can be important to other species. For example, Suzuki and McComb (2004) found very different amphibian and mammal communities associated with areas in the Oregon Coast Range that were impacted by beavers compared with similar areas where beavers did not build dams. Other examples include black bears that kill patches of trees in plantations, pocket gophers that eliminate regeneration in patches, or elk herds that browse heavily next to riparian zones. All these activities create patchiness or heterogeneity in affected sites, and such patches can be the important resource areas for other species.

FRUIT PRODUCTION

Fruits that are produced in forests by woody and nonwoody plants provide a key food resource for many species of animals. *Hard mast* are those hard fruits that are produced annually but tend to be highly variable in their production (Healy et al. 1999). Seed production usually is greatest in large, open-grown trees. Generally, those plants in full sunlight with large crowns more regularly produce larger mast crops, but year-to-year variability is high (Healy et al. 1999). Providing a variety of hard mast-producing species in the stand may help to compensate for the variability in fruit production within any one species. For instance, the oaks in the United States are grouped into two subgenera: the white oaks (Leucobalanus) and red oaks (Erythrobalanus) (Figure 4.5). White oaks flower and are fertilized in the spring, the acorn matures in one growing season, and falls to the forest floor and germinates at the end of the growing season. Red oaks flower and are fertilized in the spring, but the acorn takes two growing seasons to mature before it falls to the forest floor. It then passes through a winter stratification period before germinating the following spring. Red oak acorn production is delayed 1 year after fertilization compared with white oak acorn production. If both red oaks and white oaks occur in a stand, then a late frost that kills flowers in one spring may affect white oak acorn production that fall, but red oaks may still produce abundant acorns from flowers fertilized during the previous year. Similarly, providing a variety of other hard mast-producing species such as hickories, beech, walnuts, and hazelnuts further reduces the risk of a complete mast failure in any one year. Unfortunately, one of the most reliable mast producers once dominant in eastern U.S. forests, American chestnut is now only a stump sprout in our forests due to the chestnut blight fungus. There is some hope that genomic approaches may lead to a recovery of American chestnuts once again (Wheeler and Sederoff 2009).

Soft mast are soft fruits such as berries and drupes. These food sources are high in energy and used by many animal species. In a study in South Carolina, McCarty et al. (2002) found that 50% of fruits on 17 species of plants were eaten by vertebrates. Since different trees and shrubs flower and produce fruit at different times of the year, again a variety of species is important. For instance,

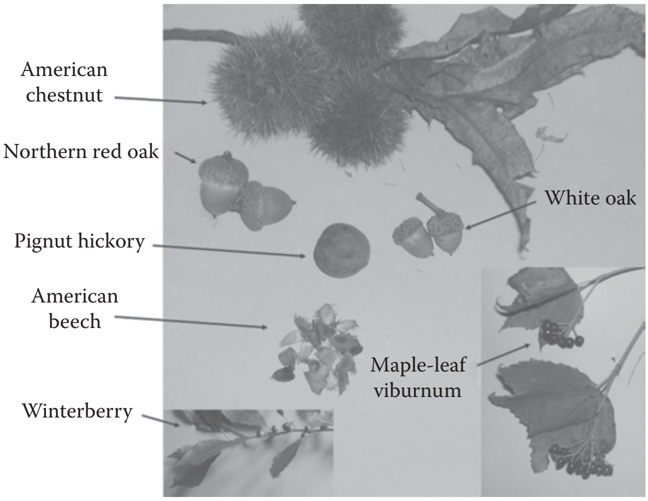

FIGURE 4.5 Examples of hard and soft mast foods for vertebrates.

serviceberries produce fruits early in the growing season, viburnums in late summer, and hollies retain fruit into the winter (Figure 4.5). These food sources may be particularly important in the winter when other digestible foods are in short supply. Soft mast production is greatest in most species where the fruit-producing plants are receiving full or nearly full sunlight (Wender et al. 2004). Plants in partial shade often allocate most energy to growth and not to fruit production. Consequently, providing patches of forest where sunlight can reach these plants may increase food availability and quality (Perry et al. 1999).

DEAD AND DAMAGED TREES

Trees provide a basis for food and cover resources for various species while they are alive and growing. The value of trees to some species wildlife extends well beyond this period, however, and for many species, the value of a tree only begins after the tree has died. Dead trees in various stages of decay offer sites for nesting, resting, and foraging for many species of vertebrates and invertebrates (Figure 4.6). Species vary in their use of dead wood size and decay classes (McComb and Lindenmayer 1999). Those species that use standing dead trees, or *snags*, are often separated into two groups. *Primary cavity nesters* are those species that can excavate a cavity in dead wood or trees with heart rot decay (Figure 4.7). Woodpeckers are the best example; indeed, most woodpecker species must excavate a cavity in a tree or snag before they will complete the nesting ritual (for instance, they will usually not nest in nest boxes unless the box is filled with sawdust so that they have something to excavate). *Secondary cavity users* use cavities that were created either by primary cavity nesters or in natural cavities (Figure 4.7). This group of species can be extremely diverse and includes parrots, tree frogs, tree-hole mosquitoes, and black bears. All of these species rely on either primary cavity nesters or trees with natural cavities for survival.

Snags go through a process of decay that allows primary cavity nesters to excavate cavities. Snags that are not well decayed are still hard wood and only a few species of woodpeckers can excavate in these snags. As the snags decay and become soft snags, other species can then excavate

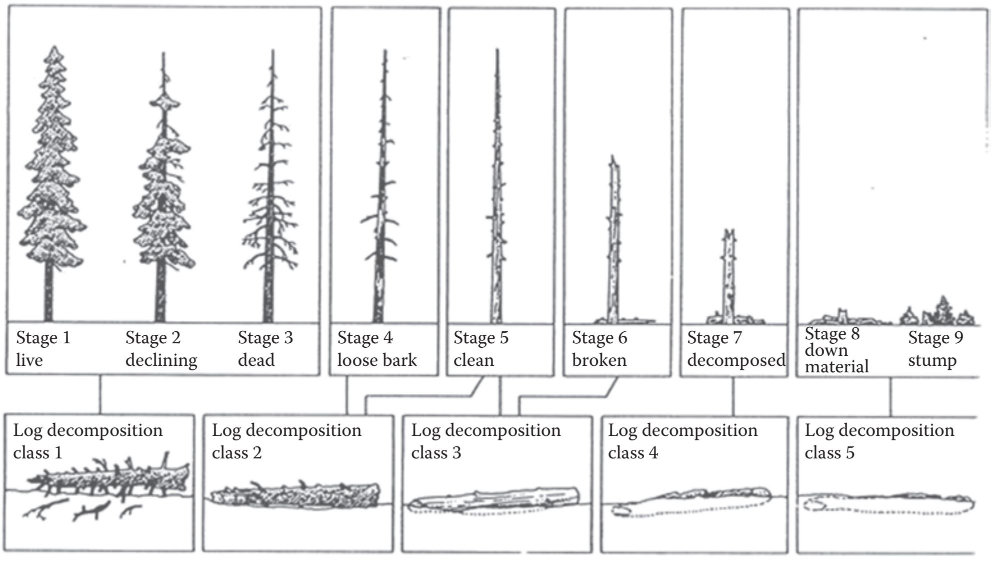

FIGURE 4.6 Stages of decay of trees and logs. As wood decays, the types of food and cover change for various species. (From Maser, C., R.G. Anderson, and K. Cromack, Jr. 1979. Wildlife habitats in managed forests: The Blue Mountains of Oregon and Washington. Pages 78–95. USDA For. Serv. Agric. Handb. No. 553.)

FIGURE 4.7 Primary cavity nesters have used this snag (left), and these cavities are now available to secondary cavity nesters. Secondary cavity nesters can also use cavities created by fungal decay, such as the one in this live tree used by porcupines (right).

in the snags. If snags of both types are provided in a stand, then there are more potential nest sites for more species. Snags are particularly important in conifer forests. Hardwood forests, especially with large trees, often have large dead limbs that provide many of the same benefits as snags.

Tree species vary in their propensity to decay following the death of a tree or a wound to a live tree. Some species tend to be more prone to forming *natural cavities* that result from tree injuries. Many of the conifers (e.g., pines) are poor producers of natural cavities. Tree cavities are important den sites for secondary cavity-using species (those species that cannot excavate their own cavity as woodpeckers do). Hollow trees are formed through top breakage and subsequent heart rot. Large hollow trees are especially important for species such as fisher, bears, and some species of bats and swifts. Species such as Oregon oak, Pacific madrone, and bigleaf maple in the western United States and red maples and blackgum in the southern United States seem to produce many natural cavities and dead limbs (effectively, elevated snags) that are used by cavity-nesting animals (McComb et al. 1986, Raphael 1987, Gumtow-Farrier 1991).

Fallen logs also provide cover and nesting sites for a wide range of species, including many amphibian and reptile species, small mammals, and a few species of ground nesting birds (Butts and McComb 2000). Large logs provide more cover and nesting opportunities for more species than small logs so the production of large trees that can fall to the forest floor should be given consideration during silvicultural activities (McComb 2003). Hollow logs can only occur if a hollow tree falls to the ground (they do not decay into hollow logs after they have fallen); so retention of some decaying hollow trees in a forest is necessary to provide hollow logs. Trees that fall into streams and lakes also play a role in habitat quality for many aquatic and semiaquatic species (Naiman et al. 2002). Logs in a stream divert water and cause pools either from plunging over the log or from scouring under the log. Dead wood also provides cover for fish and amphibians and is used as a substrate upon which some salamanders lay their eggs. Large logs also are often the basis for a beaver dam in a stream. More information on managing dead wood is provided in Chapter 12.

TREE SPECIES AND INVERTEBRATE ASSOCIATIONS

MacArthur and MacArthur (1961) also found that BSD is associated with plant species diversity within stands, probably because of the additional niche space provided in stands with more plant species. Vertebrates that feed on invertebrates associated with the leaves and needles of trees and shrubs select certain species over others for feeding (Holmes and Robinson 1981, Muir et al. 2002). Selection is probably dependent on the food resources available, competition among species, and the foraging adaptations of each species. Insect abundance and species richness tend to be higher in hardwood than conifer stands, but clearly there are species well-adapted to gleaning insects from both types of trees (Muir et al. 2002). Hardwood composition in conifer stands is associated with the abundance and occurrence of several bird species in the northwest United States (Huff and Raley 1991).

Tree species also vary in their ability to support bark-dwelling insects, an important overwintering food supply for some bird species (Mariani 1987). Rough-barked trees provide more cover for these insects and support higher insect biomass than smooth-barked trees (Brunell 1987) (Figure 4.8).

Tree Size and Density

Trees of different sizes play various roles as vertebrate habitat elements in stands. Seedlings provide browse for deer (much to the chagrin of some foresters!), nest sites for shrub-nesting birds, shade for forest floor amphibians, and hiding cover for many species of birds and mammals. Saplings provide browse for larger herbivores such as moose, and pole-sized trees may provide cover for ungulates. Large trees, especially those that grow beyond marketable size, can significantly influence the quality of a stand as habitat for some species. Trees in some managed stands are designated as legacy trees and left to grow to maturity and die through natural processes (Carey and Curtis 1996). For instance, Douglas-firs >125 cm (50 in.) in dbh (diameter at breast height) are used by marbled murrelets (Singer et al. 1991), red tree voles, and northern spotted owls. Large trees also add to the vertical structure within forests.

Large trees that add large surfaces of deeply fissured or scaly bark are used by bark-foraging birds such as brown creepers (Mariani 1987) and they support lichens, an important food source for species such as northern flying squirrels (Martin 1994). Designating a variety of tree species as legacy trees in forests would provide a range of growth rates and bark surfaces and contribute to complexity in the stand. These legacy trees provide an ecological link to the previous stand structure and composition.

Tree density also influences the production of many habitat elements. Dense stands with many trees may exclude sunlight from the forest floor, producing an open sub-canopy condition. Sparsely stocked savannah stands leave much sunlight and moisture available for grasses, forbs, and browse. Manipulation of stand density is probably the most significant influence that a forester can have on habitat availability for a wide variety of species (Carey 2003).

FIGURE 4.8 Example of a rough-barked tree (white oak, left) that supports higher densities of overwintering invertebrates than a smooth-barked tree (red maple, right).

FOREST FLOOR LITTER AND SOIL

Forest floor and below-ground conditions influence habitat quality for ground-foraging and burrowing species. The type and depth of leaf litter have been shown to be associated with the community structure and abundance of invertebrates (Bultman and Uetz 1982). Consequently, the leaf litter characteristics are associated with species that find food or cover on the forest floor, such as ovenbirds in the northeastern United States (Burke and Nol 1998). Insectivorous mammals also are assumed to be associated with litter type and depth. Leaf litter has been adversely affected by several invasive nonnative species, such as earthworms that can cause a reduction in leaf litter on the forest floor, and the loss of leaf litter is associated with declines in species such as amphibians. Maerz et al. (2009) reported that this effect may in part be due to declines in populations of small arthropods, which are an important food source for the salamanders.

Some terrestrial mammals and amphibians remain active below-ground during the summer. For instance, red-backed salamanders use earthworm burrows (Caceres-Charneco and Ransom 2010), and rough-skinned newts use logs and burrow systems of voles and shrews as summer daytime refuges (McComb and Chambers, unpublished data). Burrow systems of mountain beavers, gopher tortoises, and pocket gophers are used by many other species (Maser et al. 1981, Figure 4.9). These below-ground conditions are often not considered during forest management so the next time that you walk through a forest, think of the unseen animal community that lives beneath your feet.

Proximity to Water

Intermittent and permanent streams, seeps, springs, vernal pools, ponds, swamps, marshes, and lakes all provide water in a setting that can be critical to habitat quality for many species of aquatic and semiaquatic organisms. Although we have little control over how close a stand or forest is to water, we do have control over the function of the water body as habitat for a variety of species. For aquatic and semiaquatic species, the temperature, sediment load, and chemical concentrations in water may be influenced by the surrounding forest. Trees and shrubs over the water influence the temperature of the water by providing shade, by the influx of nutrients through litter fall, and by the degree of erosion through root strength. Some species of amphibians require clear, cold water for survival and have greatest fitness in water bodies where there are no fish (predators) (Lowe and Bolger 2002). These non-fish-bearing streams often are overlooked as a potential habitat for animals because they may be dry at some times of the year and may appear no different than the surrounding uplands. In many settings, especially on federal lands in the United States, buffer strips are provided to retain habitat for species associated with these sites (Vesely and McComb 2002). More information on managing riparian areas is provided in Chapter 11.

FIGURE 4.9 Gopher tortoises are associated with certain soil conditions and their burrows are used by a wide variety of other species. (Photo by Mike Jones. With permission.)

CASE STUDY ON PLANT RESPONSE TO HERBIVORES, OR, IT IS A (CHEMICAL) WAR OUT THERE!

Some plants produce chemicals in their leaves and twigs that reduce consumption by herbivores (herbivory). Others produce spines, thorns, and physical barriers to herbivory. Consequently, the effect that herbivores have on plant communities can be altered depending on the ability of the plants to cope with or avoid being eaten. A well-known herbivore, beaver, cuts trees of a range of sizes to feed on the bark and to use in building dams. They are selective of certain sizes and species of plants that they cut and so influence the riparian forest composition and structure considerably. A study by Martinsen et al. (1998) examined interactions between beaver, leaf beetles, and cottonwoods. Cottonwoods felled by beavers sprout vigorously, and these sprouts contain higher levels of defensive compounds than the original stem that was cut. This is an important chemical strategy for the cottonwood because it can repel generalist herbivores (those that eat a wide variety of plants), but not a specialist insect herbivore, the leaf beetle, that sequesters these chemicals for its own defense. Martinsen et al. (1998) found 15 times as many adult beetles on resprouts following beaver cutting as on uncut cottonwoods. Resprout cottonwoods have twice the concentration of phenolic chemicals as uncut stems. Several indices of beetle fitness were also higher on resprout growth than on uncut cottonwoods. This is fascinating but what does this have to do with managing habitat in forests? There are several implications from this work. Phenols are highly toxic to some mammals. As little as 1 g of some phenolic compounds can kill a human (Budavari 1989). Phenolic concentrations are often higher in juvenile plants than in mature plants. For instance, snowshoe hares prefer to feed on mature willows and poplars, avoiding juvenile trees. Through plant breeding or nursery practices, if nursery stock can be developed that contain higher levels of phenolic compounds, then seedling damage by herbivores could be reduced. But it may not be that simple. Deer saliva contains a glycoprotein that has large amounts of proline, glycine, and glutamate/glutamine that binds with tannins, and potentially other defensive compounds, to reduce the effectiveness of these compounds. So although increasing defensive compound concentrations in seedlings may be a reasonable strategy to reduce some forms of herbivory, it may not work well for all herbivores.

In addition, this study points to the fact that browse is not browse is not browse. Species vary in their production of these defensive compounds and hence in the quality of browse for herbivores. And individual plants vary in production of these chemicals depending on if they have already been browsed, if they are growing rapidly or slowly, or growing in shade or sun (Martinsen et al. 1998). Consequently, we can create literally tons of browse per hectare following a clearcut, but if the species composition is such that the resulting browse is of low quality then herbivores may be at a disadvantage eating this browse compared with another site with higher quality, but less quantity of browse.

SUMMARY

Managing habitat for vertebrates in forests often entails manipulating a set of habitat elements that are important to many species. The sizes, density, and distribution of plants; vertical structure; horizontal complexity; forage; dead wood, large trees; leaf litter; soil; and water contribute to habitat quality for many species. Habitat is not just vegetation but includes soils, water, and below-ground structure. Managers have control over the structure and composition of vegetation; so by manipulating the density, sizes, and distribution of trees and shrubs in a stand, foresters can have a tremendous influence on the availability of these habitat elements to vertebrates. Further, manipulation of vegetation can also influence the quality of these habitat elements. Browse resources that are high in lignin, cutin, phenols, and tannins reduce digestibility for many herbivores. Managing in a way that provides not only abundant browse resources but high-quality browse resources can have the biggest benefit to ungulates. Similarly, providing large pieces of dead wood or large decaying trees and stands representing a range of vertical and horizontal complexities can also benefit a wide variety of species.

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