5 Physical Influences on Habitat Patterns

Habitat elements, those pieces of the environment that in certain sizes, numbers, and distribution influence habitat quality for vertebrates, are not uniformly distributed across stands and forests. Some stands have high vertical diversity and others are rather simple in their vertical structure. Some support a deep litter layer and others virtually none. Browse quantity and quality vary tremendously depending on the plant species, growth rates, shade, and past browsing. So what is it that influences these patterns of habitat elements? In this chapter, we will explore the physical factors influencing patterns of habitat elements.

Although habitat is not simply vegetation, vegetation is shaped by natural disturbances and is the part of the environment that we can influence by silviculture and harvest planning. The patterns and dynamics of vegetation have a significant effect on the patterns and dynamics of habitat elements. Most of this chapter will focus on the physical processes influencing the pattern of vegetation and habitat elements associated with vegetation, and then in the Chapters 6 and 7 we will address how cultural features and disturbances change those patterns.

THE PHYSICAL ENVIRONMENT

Probably the greatest overriding effects of the physical environment on habitat quality for many species are those of geology, climate, soils, and topography on vegetation patterns. Associations between the physical environment and vegetation patterns are complex and they vary regionally. These associations have a significant influence on patterns of habitat elements such as vertical complexity, horizontal complexity, and forage resources. In the following subsections, we will cover both direct and indirect effects of physical factors that influence habitat quality for vertebrates. Although major factors are presented independently, it should be clear that all of these factors interact to a greater or lesser degree to influence habitat quality for species.

GEOLOGY

Vegetation structure and composition are often highly associated with the underlying geology. The glacial outwash materials of the northeast, the volcanic basalts of the Cascades, and the erosion of sedimentary rocks all interact with climate and animal activities to give rise to conditions for different plant communities. For instance, in the Klamath-Siskiyou Province of northwestern California and southwestern Oregon, diverse geologic conditions and soils produce a rich array of plant communities (Coleman and Krukeberg 1999). Soils developed from serpentinized rock may be relatively enriched in various toxic metals, including nickel, magnesium, barium, and chromium, and lacking in important nutrients such as calcium (Smith and Diggles 1999). Consequently, serpentine geology provides the basis for a unique plant structure and composition that includes Jeffrey pine savannas, xeric shrub types, and serpentine barrens, as well as hygric Darlingtonia fens (Coleman and Krukeberg 1999). Vegetation structure and composition, and habitat element characteristics are also related to surficial geology and topography over larger areas. For instance, the complex surficial geology and topography of northeastern Ohio created a variety of conditions favoring presettlement forests composed of American beech and maples on some sites and oaks and hickories on others (Whitney 1982). The structure of these forests and their ability to produce mast, browse, and other resources varies in part because plant species composition differs between sites with different geologic histories, slope, and aspect. The relationship between geology and plant associations is not always direct. Hypotheses were generated years ago that plant species richness (the number of plant species found in a particular area) is low in areas with low net primary productivity (in some cases due to nutrient restrictions) and also at high levels of productivity (where competition allows the most successful species to dominate) and is highest in areas of intermediate net productivity. But this hypothesis is not well supported; Adler et al. (2011) examined patterns among 47 plant communities on five continents and found no consistent relationships between net primary production and plant species richness. Of course, soil fertility and underlying geology are only two aspects of net primary production (the ability of a plant community to accumulate carbon), but the message is clear that there are many interacting processes driving the number of plant species on a site.

In addition to the effects that geology has on topography and soil formation, the interaction of geology with water can lead to direct effects on habitat for some species. Richards et al. (1996) reported that physical characteristics such as catchment area, clay soils, and glacial outwash materials had strong influence on stream habitat structure as some land use activities. Wilkins and Peterson (2000) related amphibian occurrence and abundance in headwater streams draining second-growth Douglas-fir forests to two geologic substrates: sedimentary and basalt formations. Streams traversing basalt had almost twice the abundance of the Pacific giant salamanders as streams flowing over marine sediments. They concluded that habitat quality for headwater amphibians in western Washington was strongly influenced by basin geology. In parts of North America, karst geology often occurs in association with limestone formations, or other carbonate rocks that dissolve more easily than surrounding rock formations (Figure 5.1). These karst geologies are prone to formation of caves, sink holes, and subterranean water flow. In Alaska, some species seem to seek karst features and the stable environment provided within caves (Baichtal 1993). Caves are used by a wide variety of species (Blackwell and Associates, Ltd. 1995). Deer are known to rest in the vicinity of

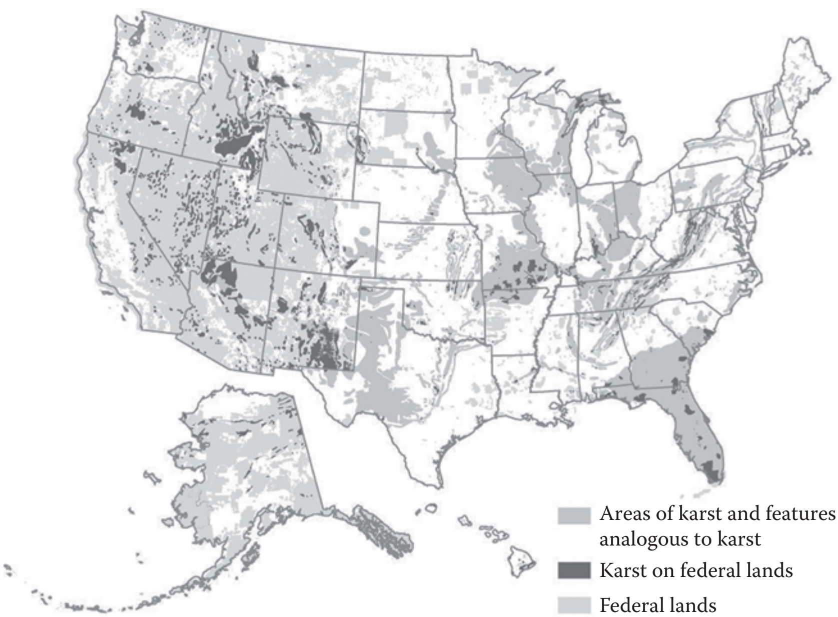

FIGURE 5.1 Locations of karst geology in the United States. These areas are prone to caves and subterranean streams and often require special consideration during forest management. (Reprinted from the National Cave and Karst Institute, USDI National Park Service.)

caves during both the summer, when air from the caves is cooler, and in winter, when cave entrance air is generally warmer (Blackwell 1995). Cave systems also are used by many species of bats for roosting and hibernation. Cave environments provide specific air circulation patterns, temperature profiles, humidity, cave structure, and locations relative to feeding sites that some species of bats require (Hill and Smith 1992).

Although manipulation of vegetation does not directly influence geological features such as caves and headwater streams, the microclimatic characteristics of these environments near the surface of the ground can be altered by forest manipulation. For instance, these associations provide managers an opportunity to consider headwater amphibian conservation strategies by prioritizing stream segments based on geology with respect to their likely amphibian fauna and providing more or less shade to these systems depending on the needs of the species being managed.

Topography: Slope, Aspect, and Elevation

Vertebrates use behavior to modify the ambient temperature around them and move themselves closer to their thermal neutral zone as they seek appropriate thermal cover. Invertebrates also seek topographic features when selecting habitat (Weiss et al. 1988). Quite often thermal cover may not only entail vegetative cover but also be located on particular aspects and slope positions that provide warmth or cooling. Variation in slope and aspect affect the spatial variability in solar radiation incident on the ground and also ground surface temperature and wind speeds (Porter et al. 2002). These areas of slope and aspect can particularly influence habitat quality for ectotherms (those species that regulate their body temperature by their behavior) (Thomas et al. 1999). Endotherms also can use behavior to modify their ambient environment. For instance, Pearson and Turner (1995) studied ungulates (deer, elk, and bison) in Yellowstone National Park and found that grazing occurred most often in burned areas at low elevation, drier sites, and on steep southerly slopes. In addition to the direct effects of slope and aspect on ambient temperature, forest vegetation can moderate extreme temperatures on those sites receiving direct sunlight, or lack of vegetation can cause cooler sites to be warmer in the day and cooler at night. Slope and aspect in combination with vegetation can influence snow depths and winter habitat quality for some species of ungulates (D'eon 2001), and large mammals will use topography as a form of hiding cover (Ager et al. 2003, Sawyer et al. 2007). Silvicultural activities that consider slopes and aspects as potential thermal environments or hiding cover for some species can significantly influence habitat quality for these species.

Volcanic extrusions in combination with glacial activities have left cliffs (nest sites for common ravens and peregrine falcons), caves (used by some bat species for hibernacula), and a diverse topography producing vegetation gradients over relatively small areas. Distributions of some animal species also follow the complex topographic features that resulted from glacial recession. For instance, the distribution of Bicknell's thrush is highly associated with the higher elevations in the Berkshires, Green, and White Mountains, Adirondacks and Catskills that generally represent rock formations resistant to the forces of the past glaciers.

Some species also benefit from improved nutrition in areas with certain topographic characteristics. The body weight of red deer in Norway was correlated with access to the variability in topography and aspects (Mysterud et al. 2001), likely due to the variability in plant species represented over a relatively small area. Vegetation patterns often are significantly influenced by changes that occur along elevational gradients. Changes in elevation of less than a meter influence vegetation patterns in bottomland hardwood forests (Wall and Darwin 1999). In mountainous terrain of the western United States and Canada, vegetation patterns are significantly structured by patterns of precipitation and temperature that change with elevation. As air is moved over mountains, it increases in elevation, cools, and moisture precipitates from the air as rain or snow. This *orographic precipitation* produces marked patterns in vegetation, which in turn influences the occurrence and abundance of some vertebrates (e.g., Terborgh 1977). For instance, the distribution of several species of reptiles and amphibians, such as Cascades frogs are highly associated with elevation, temperature, and snowfall in the Cascades Mountains. Some species of *Anolis* lizards also seem to separate along elevational gradients in tropical forests (Buckley and Roughgarden 2005). Elevation also can interact with other physical variables such as ultraviolet radiation due to ozone depletion (UV-B) to influence abundance of some species. Declines in California red-legged frog populations exhibit a strong positive association with elevation, as well as with percentage of upwind agricultural land use (i.e., chemicals), and local urbanization (Davidson et al. 2001). These declines in frog abundance along an elevational gradient are consistent with increased levels of UV-B radiation.

Soils

Maintaining long-term soil productivity in managed forests is critical to producing wood products and habitat elements (Fox 2000). Given the short-term positive effects of forest fertilization (Brockway 1983) and negative long-term effects of soil compaction (on certain soils) (Kozlowski 1999) on tree growth, it is easy to see that soil structure and composition are critical to sustaining various ecosystem services (Knoepp et al. 2000). Bedrock and surficial geology interact with climatic variables and hydrology to produce soils varying in their ability to support growth of certain species and clearly alter growth rates of trees. On sites where trees grow faster, large trees and vertical complexity can develop more quickly. Soil structure, nutrient composition, moisture content, and temperature clearly influence the vegetation species composition and quality of habitat elements such as tree species composition and browse quality. For instance, the chemical constituency of flowering dogwood and red maple foliage changes over subtle gradients of soil moisture and nutrient availability such that the production of phenolic compounds was highest on sites of greatest plant stress (Muller et al. 1987). Soils can also have direct effects on vertebrate habitat quality. The minerals available in some soils can meet direct dietary needs. Pabian and Brittingham (2011) found a positive relationship between soil calcium levels and ovenbird territory density, clutch size, and nest density in Pennsylvania forests. Species such as moose, deer, caribou, and band-tailed pigeons seek sodium-rich soils and springs to meet demands for this nutrient (e.g., Kennedy et al. 1995, Sanders and Jarvis 2000). Areas of eucalypt forest in Australia on high nutrient sites have trees with higher foliar nutrients, making them more suitable for some arboreal marsupials (Pausas et al. 1995). This relationship presents a challenge to forest managers wanting to maximize wood production and protect high-quality habitat for these species.

Burrowing animals are clearly affected by soil structure. As an example of the extensive nature of burrow systems, Askram and Sipes (1991) found approximately 16,000 holes and 7.5 km (4.7 miles) of above-ground runways per 0.4 ha (1 acre) created by voles in an orchard in the northwestern United States. Gopher tortoises are adept at making burrows in sandy coastal plain soils (Ultsch and Anderson 1986, Figure 4.9), Gapper's red-backed voles in boreal forests develop elaborate networks of burrows, and mountain beaver develop extensive burrow systems used by many other species. Regosin et al. (2003) suggested that small mammal burrow densities could influence abundances of spotted salamanders in northeastern U.S. forests. Ground-based logging equipment and other forest management activities can disrupt soil structure and reduce burrow availability. Protection of soils from disruption, compaction, and erosion can be a key step in providing habitat for many species that spend their time below ground.

Climate

Climatic conditions are a predominant force influencing the distribution of organisms. Temperature and precipitation, separately and in combination, have significant effects on vegetation patterns. The physical environment of North America has been altered by climatic processes extending hundreds of thousands of years into the past. Most notably glaciation and subsequent climate change have influenced surficial geology, soils, and hydrology over large parts of North America. For instance, about 12,000 years ago, there was a 2-km-thick chunk of ice sitting over much of the northern

United States and Canada. At that time, the sea level was considerably lower and forests once grew on parts of what is now the continental shelf. As climates changed, the receding glaciers left deeply scoured valleys, outwash plains, wind-blown deposits of sands, drumlins, and erosion-resistant ridges of granite and basalt. The distribution of tree species found in forests then was much different than it is today and patterns of forest species changed markedly as the glaciers receded (Figure 5.2, Jacobson et al. 1987). The soils that were left behind as glaciers receded represented a complex mosaic of sands, gravels, and clays that structures vegetative communities quite markedly.

Climatic conditions not only influence the vegetation patterns of a region but also directly influence the ability of species to survive in an area. Consider the geographic distribution of the northern copperhead in New England (Figure 5.3a). The northern limit of the geographic range for this species, an ectotherm sensitive to prolonged cold, closely corresponds with the mean dates of the first and last frost (Figure 5.3b).

Indeed many species of ectotherms are influenced by air, soil, or water temperatures in forests (e.g., Nussbaum et al. 1983, Welsh and Lind 1996). Some endotherms are also highly influenced by changes in ambient temperature. Temperature at roosts and maternity sites of some bat species seems to be particularly important for survival and growth of adults and young (Agosta 2002). In fact, there is even evidence that sex ratios of bats and some reptiles can be influenced by ambient temperatures (Ewert et al. 1994, Ford et al. 2002). Consequently, considering the effects of forest management on temperature regimes in forests can be quite important to providing adequate habitat for species such as these.

Moisture plays a critical role in structuring the patterns of vegetation and often is more important than temperature in structuring the regional environment (e.g., the Pacific Northwest). Clearly, precipitation and temperature are interrelated, particularly as they influence moisture stress on plants. Consider the map of moisture stress in Figure 5.4 for western Oregon. Moving from west to east, patterns of tree dominance changes from Sitka spruce and western hemlock in areas with low moisture stress, to Douglas-fir and western hemlock, to Douglas-fir and grand fir to Oregon oak and grand fir, as you move east along this gradient. Moisture stress seems to be an important factor associated with vegetation patterns over much of the northwest (Zobel et al. 1976, Ohmann and Spies 1998) and possibly the continent (Goward et al. 1985). Under predicted

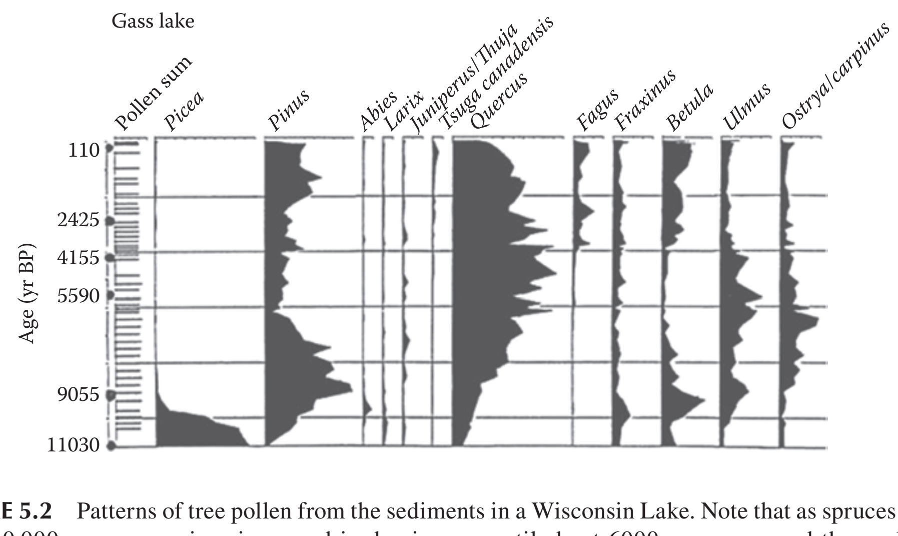

FIGURE 5.2 Patterns of tree pollen from the sediments in a Wisconsin Lake. Note that as spruces declined about 10,000 years ago, pines increased in dominance, until about 6000 years ago, and then oaks dominate. American beech did not begin to have a significant presence in the area until about 4000 years ago. (Reprinted from Webb, S.L. 1987. *Ecology* 68:1993–2005. With permission of the Ecological Society of America.)

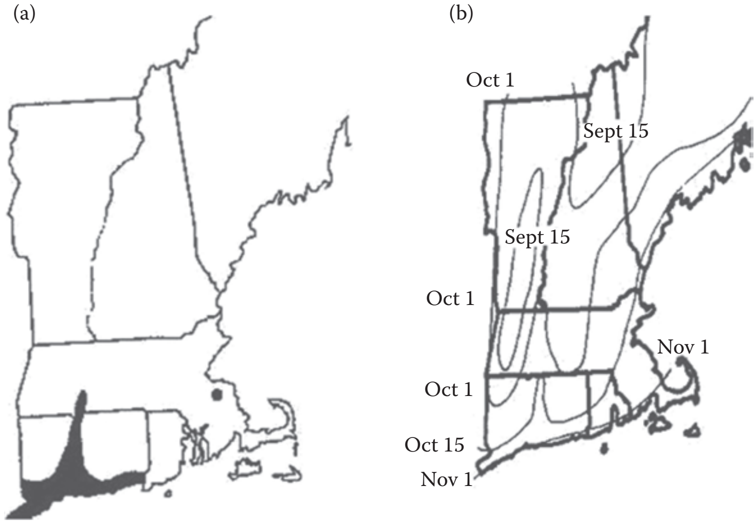

FIGURE 5.3 The geographic range of northern copperheads (a) and the isotherms for date of first frosts (b). (Reprinted from DeGraaf, R.M., and M. Yamasaki. 2001. *New England Wildlife: Habitat, Natural History, and Distribution*. University of Press of New England, Hanover, NH. With permission from the University Press of New England.)

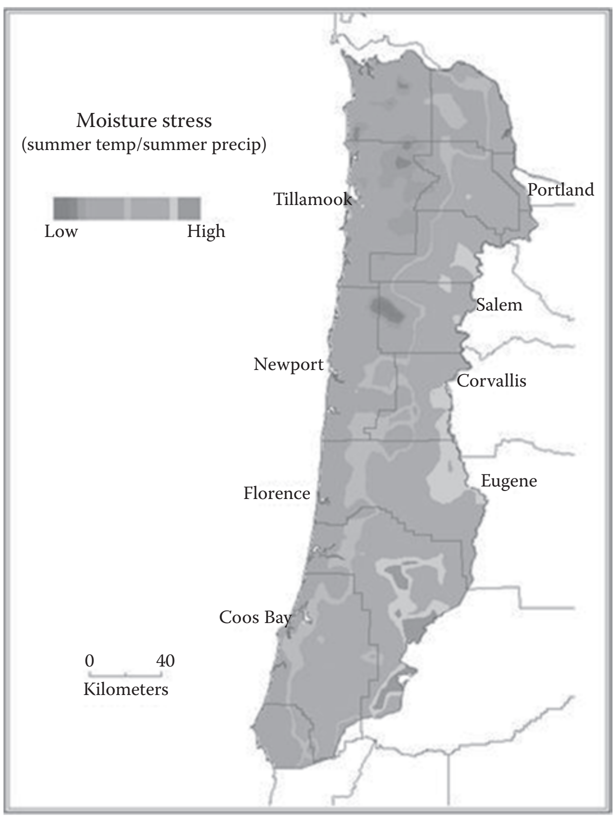

FIGURE 5.4 Map of moisture stress in the Oregon Coast Range. Plant communities seem to be structured in large part by this variable. (Reprinted from a figure developed by the USDA Forest Service Pacific Northwest Research Station Coastal Landscape Analysis and Modeling Study.)

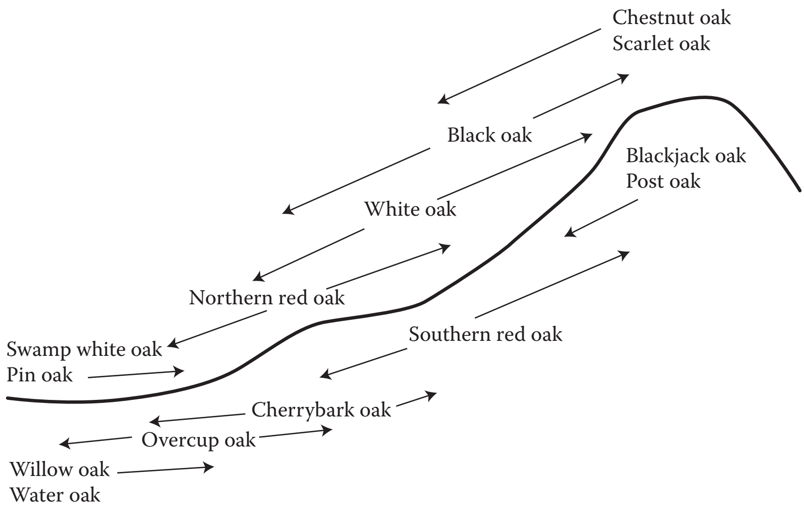

FIGURE 5.5 Gradient of oak species along a topographic and moisture stress gradient in the eastern United States.

climate change, increased moisture stress can lead to significant shifts in tree species distributions (Coops et al. 2011).

Local patterns of vegetation are also driven by moisture stress gradients (Figure 5.5). In the eastern United States, oak species segregate along topographic features that are related to a moisture stress gradient. Sites with standing water are dominated by pin oak and swamp white oak, and as you move upslope, these are replaced with northern red oak and white oak, then black oak, and finally chestnut oak and scarlet oak at the ridgetops. The ability of a forest to produce mast is highly influenced by site conditions that reflect moisture stress. Further it is important to recognize these patterns when regenerating forests during management. Matching plant species to sites is a key step in successfully regenerating a stand.

Precipitation also influences soil moisture and hydrology for an area (see previous and following sections) and consequently plays a key role in structuring habitat quality for many species. Recently though, there also have been noticeable effects of acid precipitation on habitat quality for species such as amphibians and waterfowl (Stenson and Ericksson 1989). The effects of acid deposition on vertebrates are complex. There are direct effects of reduced pH such as reduced reproduction or survival of fish and probably aquatic amphibians. There also are indirect effects, such as a shift of top predators from fish to invertebrates and a reduced decomposition rate due to decreased abundance of animals that contribute to the decomposition of organic matter by consuming wood, leaves, and other plant materials (detrivores) (Stenson and Ericksson 1989). In addition, productivity and turnover rate of nutrients can be reduced and there often is an increase in water transparency, which influences predation effectiveness. In addition, acid precipitation can have indirect effects on terrestrial systems through changes in vegetation structure and composition resulting from alteration of nutrient exchange capacity in the soils (Schreiber and Newman 1988).

There are also direct effects of rain (Waltman and Beissinger 1992) or snow (Kirchhoff and Schoen 1987) on habitat quality for many species. Many species seek shelter from precipitation due to the evaporative cooling effect on their bodies. Snow, in particular, can influence movements and choice of foraging and resting areas by deer and other ungulates (Nelson 1998).

In the past decade there has been increasing attention paid to the effects of climate change on conservation of biodiversity around the world. Predictions include significant changes in geographic ranges for species with narrow niches (a narrow range of conditions in which they can occur, especially at high latitudes and high elevations). But specific changes that we might see are difficult to predict because changes are a result of not only changes in the physical environment but also range shifts of competitors, predators, and diseases. To complicate things even more, changes in climate may lead to conditions that we have not seen before in a specific location or in former analog conditions (Fitzpatrick and Hargrove 2009). How will a species that is strongly influenced by climatic conditions, many reptile species for instance, respond to entirely new climatic conditions? Uncertainty in predictions of species ranges increases with the degree to which a species is highly associated with specific climatic conditions and the nonanalog conditions depart from the historic conditions under which a species has evolved.

Hydrology

Watersheds influence the physical structuring of the environment and consequently habitat elements and habitat quality for a number of species. We will spend much more time addressing issues of riparian vegetation and management on habitat elements in a later chapter. Clearly though, the proximity of habitat elements to water and groundwater conditions can influence vegetation patterns markedly. Some tree species are very well adapted to growing in flood-prone or saturated soils (e.g., baldcypress, eastern cottonwood, and water oak). Considering management effects on the regeneration and growth of these species is key to effective management for many bottomland species. In particular, waterfowl managers in the southern United States have used greentree reservoirs to provide timber and waterfowl habitat (Wigley and Filer 1989). Greentree reservoirs allow water levels to be manipulated in order to flood bottomlands in the winter to attract waterfowl feeding on acorns. Water then is drawn down during the growing season to allow rapid growth of oaks that are then harvested for timber.

The hydrologic features of an area can also have more direct effects on some species. Seeps and steep headwater streams provide large boulder and rock substrates, cool water, and highly aerated water that provide habitat for species such as spring salamanders in the east and torrent salamanders in the west (Sheridan and Olson 2003, Olson et al. 2007). As the watershed area increases, headwater streams that may be intermittent become permanently flowing. If there are no barriers to fish movement, we may find brook trout in the eastern streams and cutthroat trout in western streams, which in turn influence the distribution of salamanders in those streams. As the gradient (slope) of the stream declines and water volume increases, we see sediments deposited and more meandering stream courses. These mid-watershed stream reaches provide the substrate for dens for muskrats and beavers. Farther along the gradient where wide valley floors and annual floods characterize the large river systems, backwater sloughs, swamps, side channels, and flooded wetlands become important nest sites for species such as wood ducks, great-blue herons, and western pond turtles. In fact, the large bottomland hardwood forests of the Mississippi River floodplain and Gulf coast provide habitat for many species, including the ivory-billed woodpecker, which may have been recently rediscovered (although that remains to be confirmed). Finally, as the river empties into an estuary, the interface between fresh and salt water provides a set of conditions that are ideal for many species such as American black ducks, muskrats, and many species of wading birds.

Kettle holes that resulted from the melting of large ice blocks embedded in glacial soils may allow the formation of vernal pools. Vernal pools hold water for a period in the spring, but dry out later in the summer. These sites are key breeding habitat for species such as marbled salamanders and wood frogs. Large mountain lakes that result from scouring from glaciers also provide habitat for species such as loons, Cascade frogs, and common goldeneyes. Since each of these hydrologic features provides habitat for a different suite of species, each must be considered differently when managing adjacent forest lands.

Vegetation Patterns

Vegetation patterns are associated with these physical features of the environment. The potential vegetation of a region represents the dominant vegetation that would be present in a region in the

FIGURE 5.6 Potential vegetation of North America. (From Adams, J. *North America during the Past 150,000 Years*. Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN. http://www.esd.ornl.gov/projects/qen/nercNORTHAMERICA.html.)

absence of culturally induced changes (Figure 5.6). Clearly these vegetation patterns influence the patterns of habitat elements over the region. Wildlife habitat types have been delineated in many states and provinces to facilitate the understanding of historic and current patterns of vegetation and topography. For instance, in Oregon, 33 habitat types representing vegetation, water, and geologic features are a way of understanding how species might respond to these features (Figure 5.7). It should be clear by now, though, that these broad categories driven by physical forces may only be crudely related to the distribution of some species because every species has its own habitat requirements. Indeed, Cushman et al. (2008) found that habitat types were a very weak indicator of habitat for any particular species of bird. Indeed it is the interaction of individual plant species with the physical environment as well as the interactions with other species and other individuals of the same species that are better predictors of where a species might occur on a landscape.

Vegetation patterns that we see today were quite different historically. The changes in vegetation patterns resulting from glaciation and climate changes occurred relatively slowly in the past and

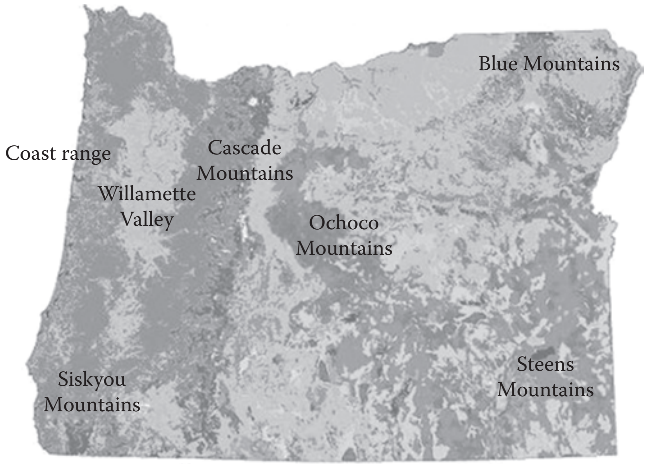

FIGURE 5.7 The mosaic of historic habitat types for the state of Oregon, US. These patterns have been changed through recent cultural activities associated with land use. (Redrafted from a map produced by the Institute for Natural Resources, Oregon State University. With permission.)

encompassed thousands of generations of vertebrates. The slow rate of change usually allowed species to adapt to these changes. Habitat selection certainly also would have been influenced by these changes and led to genetic advantages for those individuals most adaptable to the new conditions. Habitat selection also would have facilitated the changes in vegetation pattern. Movement of heavy-seeded tree species (e.g., oaks) was facilitated by birds and mammals (e.g., jays and squirrels). Similar dispersal mechanisms are seen in high altitude areas where whitebark pine occurs. Dispersal of whitebark pine seeds by Clark's nutcrackers may be critical to the long-term survival of both species as climates change (Schrag et al. 2008). The current distribution of vertebrates may be associated with vegetation patterns in a broad sense (e.g., mink frogs are associated with boreal forest) or temperature (Figure 5.3) or by the distribution of vegetation in conjunction with temperature (e.g., Carolina wren, see DeGraaf and Yamasaki 2001). For many species it is the interplay among these factors that led to regional patterns of distribution in vegetation, habitat elements, and geographic ranges of species.

The potential patterns of plant species are particularly important for many species because they represent the potential of a system to provide energy to the trophic levels within the ecosystem. Systems vary considerably in their production of biomass. Biomass represents stored energy sources for consumers and detritivores. Mature deciduous forests can support over 475 tons/ha (190 tons/acre) of biomass (Whittaker et al. 1974), while deserts support only 5–50 tons/ha (2–20 tons/acre) of biomass (Noy-Meir 1973). Consequently, human activities that influence the direct physical factors of geology, soils, climate, or hydrology, or vegetation patterns through land use, can have huge impacts on the distribution of vertebrates by changes in habitat quality.

SUMMARY

The physical factors of a region that include geology, soils, topography, climate, and hydrology interact to influence the potential for a region to support a plant community and the elements of habitat used by vertebrates. These physical factors also influence the quality of habitat for some species directly by their influence on providing suitable microclimates, burrowing substrates, cover, and stream features. The greatest effect of these physical factors is in structuring plant communities from continents to stands. It is the forest vegetation and the associated habitat elements that we can influence through forest management decisions. In Chapter 7, we will spend more time discussing the role of disturbance in driving patterns of vegetation across large regions.

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