OVERVIEW OF THE PHYSIOGRAPHY AND VEGETATION OF VIRGINIA

Virginia Dept. of Conservation and Recreation, Division of Natural Heritage

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OVERVIEW OF THE PHYSIOGRAPHY AND VEGETATION OF VIRGINIA

The natural communities treated on this web site are the products of geological, climatic, and biological factors interacting over time on Virginia's landscape. While a thorough treatment of these influences is well beyond the scope of this overview, a basic understanding of them is essential to developing a deeper appreciation of the diverse habitats and plant species distributions in the state that combine to form recognizable vegetation types. Why certain plants grow where they do and how they came to occupy those habitats are topics of great interest in most geographic regions, and Virginia is no exception. Its flora contains substantial groups of species with affiliations to northern regions, the Southeast, the Midwest, and endemic habitats of the Appalachians, as well as many distinctive within-state distribution patterns. This chapter attempts to outline 1) the basic environmental parameters that determine which species can grow in Virginia and their status in different parts of the state; 2) the history of plant migrations, vegetation change, and human impacts on the flora since the late Wisconsin glacial maximum 18,000 years ago; and 3) the current distribution of vegetation and natural communities in the state.

Physiographic Setting of the Vegetation and Flora

Virginia is situated in the middle portion of the East Coast of the United States, approximately equidistant between Maine to the north and Florida to the south. Its boundary encloses 109,624 sq km (42,326 sq mi), including 2590 sq km (1000 sq mi) of inland water and 4475 sq km (1728 sq mi) of coastal water over which the Commonwealth of Virginia has jurisdiction. Roughly triangular in shape, the state extends 755 km (469 mi) east to west and 323 km (201 mi) north to south at its widest points. Maximum elevation is reached on the adjacent Southern Blue Ridge peaks of Mount Rogers (1746 m/5729 ft) and Whitetop (1682 m/5520 ft), while its minimum relief is found on the Eastern Shore and in the Embayed Region of southeastern Virginia (0 m/0 ft, or mean sea level). Virginia is bounded on the east by the Atlantic Ocean, on the north and east by Maryland and the District of Columbia, on the west by West Virginia and Kentucky, and on the south by Tennessee and North Carolina. Politically, the state is divided into 95 counties and 41 independent cities, a few of which rival most counties in size.

Stretching east to west from the Atlantic Ocean well into the Appalachian Mountains, Virginia spans five of the more than 20 major physiographic provinces defined for North America (Fenneman 1938) — Coastal Plain, Piedmont, Blue Ridge, Ridge and Valley, and Appalachian Plateaus — making it one of the most topographically diverse states in the East. Virginia's considerable latitudinal range (36º30 ′ N–39º30 ′ N), vertical relief (sea level to 1746 m [5729 ft]), and variety of geological settings contribute to a significantly wide range of landforms, soils, and microclimates supporting correspondingly diverse vegetation and flora.

The northern and central sections of Virginia are drained by the Atlantic-slope watersheds of the Potomac, Rappahannock, York, and James rivers, which flow to the Chesapeake Bay (Fig. 1). In southeastern and south-central Virginia, surface drainage is via the watersheds of the Chowan and Roanoke rivers, which flow into North Carolina and hence to the Atlantic. Southwest of the upper

Roanoke and James watersheds, the New River flows in a northerly direction across southwestern Virginia, draining substantial portions of the Blue Ridge and Ridge and Valley provinces before exiting the state at the West Virginia border; it is a tributary of the Kanawha River (Ohio River drainage). The mountains of far southwestern Virginia are drained by the Pound River, Russell Fork, Levisa Fork, and other north-flowing tributaries of the Ohio River drainage and by the Clinch River, Powell River, and forks of the Holston River, southwest-flowing tributaries of the Tennessee River drainage.

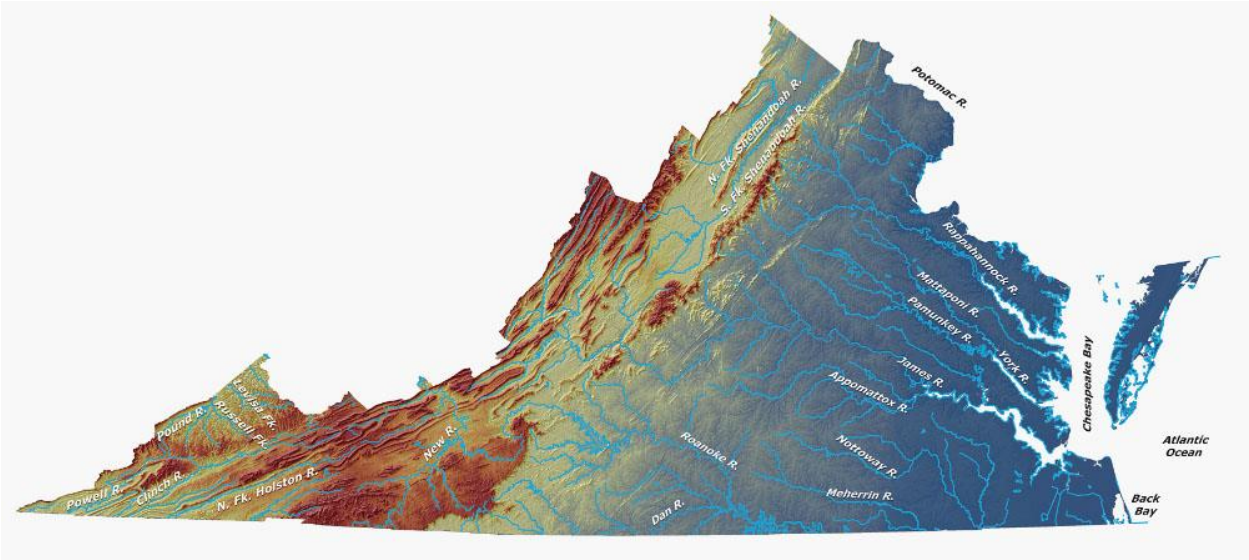

Fig. 1. Shaded relief map showing Virginia's physiography and surface hydrology. Click image for larger version.

Climate

The overall climate of Virginia is classified as humid subtropical, denoting a seasonal regime of warm to hot summers and mild winters, along with sufficient precipitation to support temperate broadleaf and mixed forest vegetation (Woodward and Hoffman 1991). However, within-state variation in temperature, precipitation, and length of the growing season is dramatic. Much of the temperature gradient is related to elevation and distance from the coast, with oceanic influences moderating the climate of near-coastal areas. The length of the growing season thus ranges from more than 250 days along the southeastern Virginia coast to fewer than 150 days at higher elevations in western Virginia (Crockett 1972). Average annual precipitation varies from approximately 850 mm (33.5 in) to 1270 mm (50 in), with the highest averages in far southeastern and far southwestern Virginia, and the lowest averages in the Ridge and Valley of northwestern Virginia (Hayden 1979). Average annual snowfall is less than 250 mm (10 in) in the Coastal Plain and less than 500 mm (20 in) west of the Blue Ridge (Ruffner 1980). Snowfalls greater than 250 mm (10 in) are infrequent in most parts of the state. Late spring and summer thunderstorms are frequent in all parts of the state and are occasionally severe. Tornadoes, tropical storms, and hurricanes are infrequent but can produce extensive damage to vegetation from high winds and flooding.

Considerable topographic heterogeneity, especially in western Virginia, induces a wide gradient of local weather conditions and microclimates. As a rule, the average temperature decreases 6.4° C (11.5° F) with every 1000-m (3280-ft) increase in elevation (Woodward and Hoffman 1991); thus sub-boreal to boreal microclimates prevail at some of the highest elevations. Local topography can also greatly modify precipitation patterns. The southwest-to-northeast-trending Appalachian ridges, in particular, cause prevailing westerly or southwesterly air masses to rise and release most of their precipitation on the windward side of the mountains. Thus, the low annual average precipitation in the Ridge and Valley

region of northwestern Virginia is the result of that area's being in a rain shadow of the higher Allegheny Mountains, to the west. A similar process of orographic lift is responsible for the high annual precipitation in the mountains of far southwestern Virginia, which induce rainfall from southwesterly air masses as they move into the state. Less frequent weather systems generated by Atlantic storms track across Virginia from east to west, producing heavy precipitation as they rise over the inner Piedmont and Blue Ridge. Such local conditions exert strong control over the types of vegetation and relative abundance of individual plant species in specific areas of the state.

In addition to these types of large-scale, topographically induced climatic patterns, microclimatic variation exerts considerable influence on plant life at much smaller scales. For instance, on sheltered north-facing slopes, temperatures and solar radiation may be reduced and soil moisture availability increased compared with conditions on the exposed south-facing slopes of the same ridge.

Geological History

Geologic substrates and the soils weathered from them have a profound influence on the distribution and diversity of plants in Virginia. In combination with climatic factors, the physical, hydrological, and chemical characteristics of rocks and soil frequently determine which species can colonize, grow, and disperse in a given area or habitat. Those interested in detailed information about Virginia's geological history and physiographic evolution are referred to the excellent Internet resources of the College of William and Mary's Department of Geology (*http://web.wm.edu/geology/virginia/index.php?svr=www*) and James Madison University's Department of Geology and Environmental Sciences (*http://csmres.jmu.edu/geollab/vageol/vahist/index.html*), as well as the many professional bulletins and papers published by the U.S. Geological Survey and the Virginia Department of Mines, Minerals, and Energy. Most of the following summary has been synthesized from information contained in those sources.

The tectonic evolution of continents is described in terms of Wilson cycles—the opening and closing of oceans and marginal seas and the attendant rifting and collision of the adjacent continental landmasses to form mountains, whose ultimate erosion furnishes the sedimentary detritus that fills adjacent basins and begins the cycle anew. The rocks of our area record a series of Wilson cycles. The earliest events in Virginia's geological history are represented by meso-Proterozoic igneous and metamorphic rocks in the core of the Blue Ridge physiographic province. These rocks record volcanism and mountain-building events that occurred more than a billion years ago, when the supercontinent of Rodinia was assembled, while somewhat younger, neo-Proterozoic rocks along the flanks of the Blue Ridge record the rifting and breakup of that landmass and the opening of a proto-Atlantic ocean that eventually covered the entire present-day state. Thousands of meters of beach sand, followed by limestone and dolostone, were deposited along the continental shelf throughout Virginia during the first part of the Paleozoic Era. Beginning about 475 million years ago (Ma), however, a series of exotic microcontinents and island arcs collided with and were accreted to the eastern edge of the continent, each such event generating volcanism, folding, and uplift of mountains along the suture. The closing of the proto-Atlantic ocean culminated 250–300 Ma with the arrival of the southern supercontinent of Gondwanaland, whose collision with North America produced the Alleghenian Orogen and the supercontinent of Pangaea. This signature event folded most of the rocks east of the Allegheny Plateau, including the Ridge and Valley, and produced large thrust sheets that were transported westward by tens of kilometers, in the process throwing up a proto-Appalachian range of mountain peaks that spanned the entire region and is thought to have been as high as 6100 m (20,000 ft) at the close of the Paleozoic Era.

Areas west of the Blue Ridge, however, continued to act as sedimentary basins well into the time of the Alleghenian Orogen, receiving large pulses of sediment that coincided with each mountain-building event further east and generating a section of Paleozoic sedimentary rocks 3000–6000 m (10,000–20,000 ft) thick beneath the Allegheny Plateau. Drainage was predominantly westward through what is now Virginia during the middle and late Paleozoic Era. Land plants, in the form of small, nonvascular sporophytes, first appeared during the Ordovician Period, around 450 Ma. The earliest fossil records of vascular plants date from the Silurian Period (~ 420 Ma), and this group diversified greatly during the remainder of the Paleozoic. During the Pennsylvanian and Mississippian periods (collectively known as the Carboniferous Period, 360–300 Ma), forests of huge ferns and gymnosperms grew in coastal swamps and peat bogs in a subequatorial region now represented by the Allegheny Plateau and western Ridge and Valley. Repetitive cycles, in which these Carboniferous swamp forests alternated with periods of tidal and fluvial sedimentation, produced immense beds of organic material that were buried beneath younger sediments and eventually consolidated and compacted into numerous coal seams.

During the Mesozoic Era (250–65 Ma), the supercontinent rifted apart, opening the modern Atlantic Ocean Basin and initiating the development of east-flowing rivers. By the late Jurassic Period (160–145 Ma) a shallow sea covered what is now eastern Virginia, and during the Cretaceous a seaward-thickening wedge of fluvial, estuarine, and marine sediments was deposited on the continental margin. Flowering plants appeared, becoming widespread and dominant by the late Cretaceous (100–70 Ma). Deposition in a coastal environment continued throughout the Tertiary Period (65–2 Ma), punctuated by periods of erosion as the shoreline fluctuated. Uplift and eastward tilting of the region occurred episodically during the Tertiary, producing the modern Appalachian Mountains and Allegheny Plateau. The climate of the early Tertiary was tropical or subtropical but shifted back to a cooler temperature regime late in the period. The vegetation and flora changed accordingly, and, by the late Tertiary, forests of broad-leaved tree species were well established in parts of eastern North America (Delcourt et al. 1993).

During the mid-Tertiary, an asteroid or a comet crashed into the Atlantic Ocean in the vicinity of what is now the southern Chesapeake Bay, near the present-day town of Cape Charles on the Eastern Shore. The impact fractured bedrock to a depth of 11 km (7 mi) and a width of 137 km (85 mi), forming a massive structure known as the Chesapeake Bay impact crater (Powars 2000). Millions of tons of seawater and debris were ejected into the atmosphere and vaporized, likely followed by a huge tsunami, widespread fires, a prolonged period of darkness and acidic precipitation, and, ultimately, atmospheric cooling. This event and its aftermath were the probable cause of a mass extinction about 33 Ma during the Eocene Epoch.

The Pleistocene Epoch (2.5–0.1 Ma) saw repeated southward advances of continental glaciers accompanied by cold and wet conditions alternating with warm, temperate interglacial stages. Each glacial advance tied up enormous volumes of water in ice sheets as thick as 3 km (1.9 mi), resulting in lowered sea levels and accelerated down-cutting of drainage systems south of the glacial boundary. During interglacial periods, coastal plains that had been extensively exposed during glacial maxima, as well as near-coastal river valleys, were drowned by rising sea levels. Although the area that is now Virginia was not covered by the Pleistocene ice sheets, their great size generated major climatic and multiple-scale erosional effects that shaped many of the state's present landforms. Dramatic alternations of climatic conditions during the Pleistocene were also accompanied by vast plant migrations and changes in vegetation cover, which are well known only for a period from the maximum of the last North American glaciation (the Wisconsin, about 18,000 years ago) through the Holocene Epoch (10,000 years ago to the present).

This brief outline of geological history is far from complete and is intended mainly to demonstrate that the rocks and sediments now underlying Virginia constitute a nearly complete cross section of the geological timescale from the Proterozoic to the present and comprise an array of physical and chemical substrate types. The state's five physiographic provinces, while defined primarily on the basis of gross surficial landforms and topography, have their structural basis in these underlying rocks and sediments.

Physiographic Provinces

The physiographic provinces that intersect Virginia are generally defined by their relative elevation, relief, geomorphology, and lithology (Fig. 2). Beginning at sea level, at the eastern edge of the state, the surface of Virginia rises gradually in elevation and increases in irregularity until it reaches its maximum elevation and ruggedness in the western part of the state. From west to east, the major physiographic divisions are the Appalachian Plateaus, the Ridge and Valley, the Blue Ridge, the Piedmont Plateau, and the Coastal Plain. Each province, in turn, is divisible into subregions (Fig. 3) using geological and topographic features, climate, biota, or some combination of these factors. Geologists, physiographers, and biogeographers often differ slightly in their delineation of regional boundaries and subregions. We will consider the subregional divisions that are the most useful in describing large-scale vegetation patterns in the state.

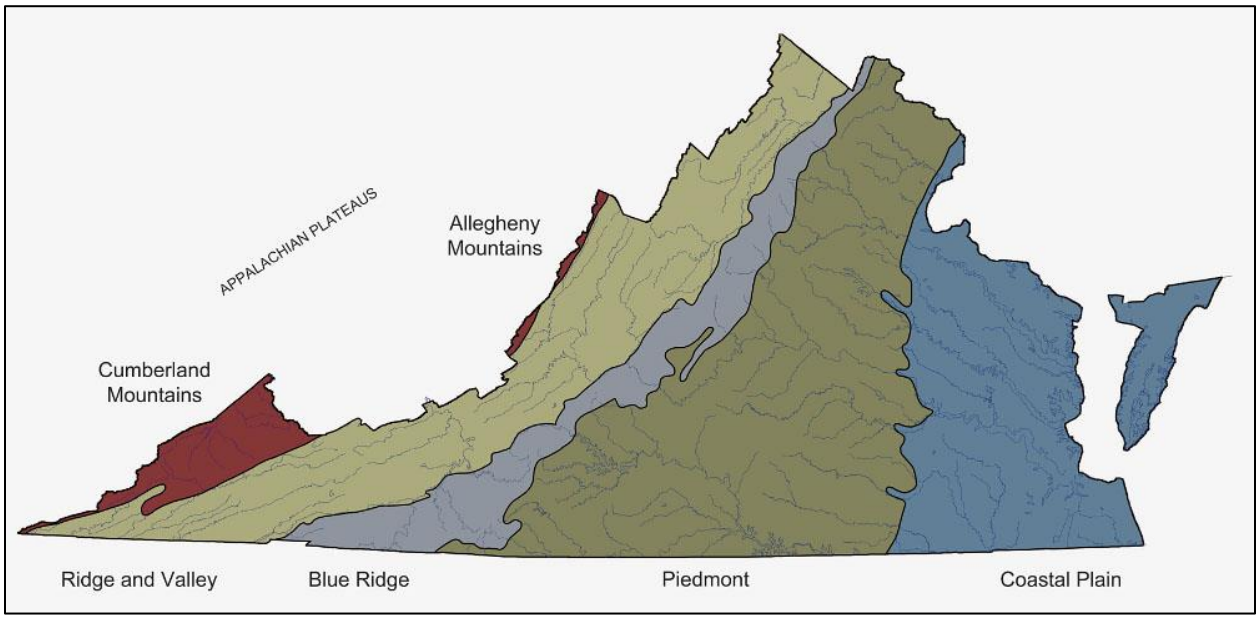

Fig. 2. Physiographic provinces of Virginia. Provincial boundaries follow Keyes et al. (1995). Click image for larger version.

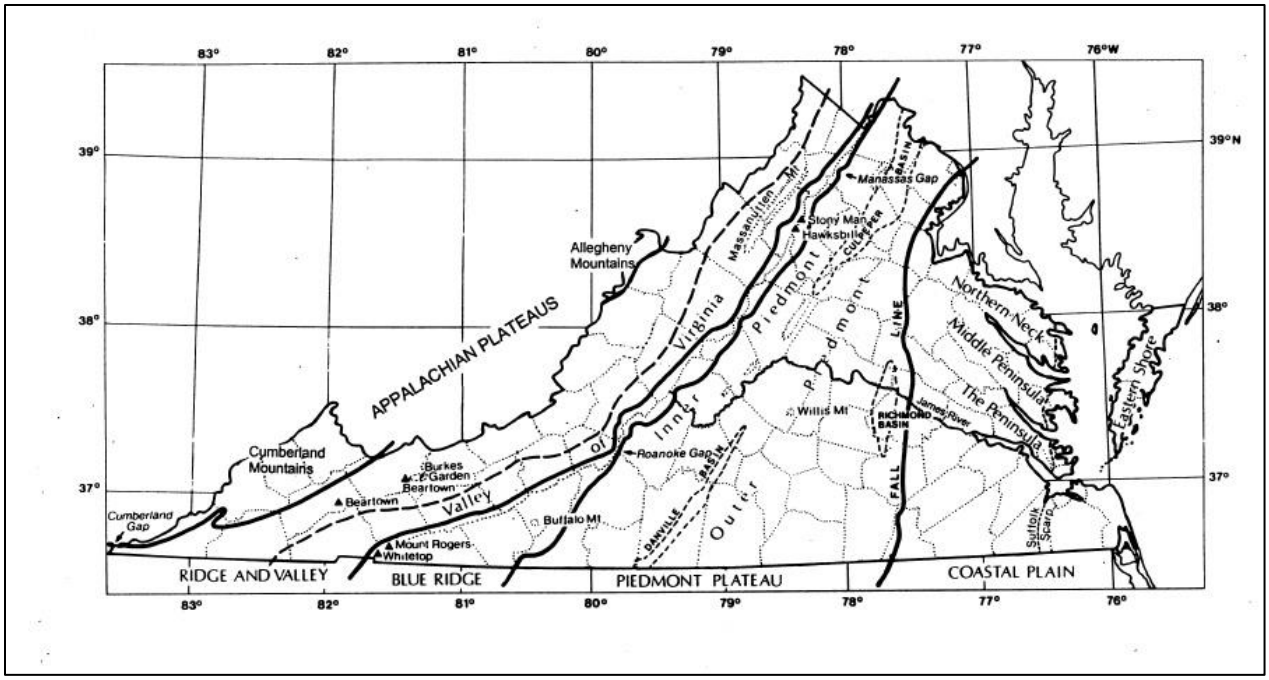

Fig. 3. Physiographic provinces and subregion features. Modified from Woodward and Hoffman (1991), with copyright permission. Click image for larger version.

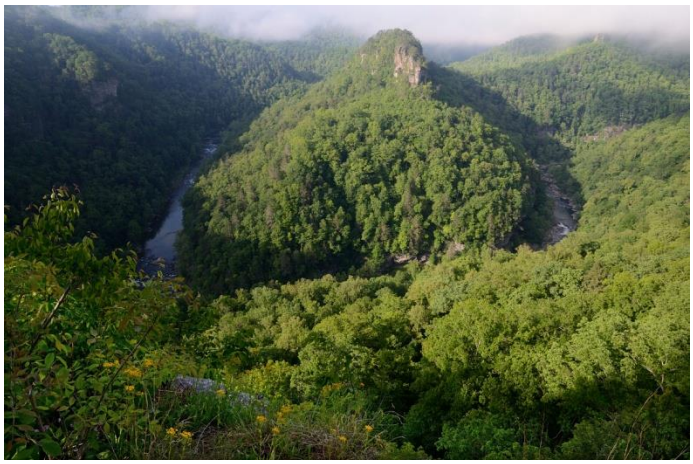

Fig. 4. Deep stream incision of horizontal sandstones has produced spectacular gorges in the Cumberland Mountains. Russell Fork Gorge, Breaks Interstate Park. Photo © DCR-DNH, Gary P. Fleming

Paleozoic sedimentary rocks — sandstones, shales, siltstones, limestones, and dolostones — underlie both the Appalachian Plateaus and the Ridge and Valley in western Virginia, with the two provinces distinguished more by structural differences than by lithology. The Appalachian Plateaus graze two areas of western Virginia: the westward-extending part of far southwest Virginia that lies northwest of the Clinch River valley in the **Cumberland Mountains**, and the easternmost ridge of the **Allegheny Mountains** (Allegheny Mountain proper) from Allegheny County to the northwest corner of Highland County. Both areas contain closely spaced mountain ranges with deep intervening valleys. Underlying rocks are mildly folded or nearly horizontal sandstones, shales, and limestones of Devonian, Mississippian, and Pennsylvanian age. These strata were deposited in the huge Paleozoic sedimentary basin that lay west of the rising Appalachian Mountains and that was uplifted during the Alleghenian Orogen and, more recently, the Tertiary. Modern landforms resulted from uplift and warping of the sedimentary strata followed by deep and intricate stream incision of uplifted, plateau-like erosional surfaces (Fig. 4). Elevations exceeding 1200 m (4000 ft) are attained in both subregions. Pennsylvanian coal beds are common in the Cumberland Mountains and have been extensively mined.

Fig. 5. Tightly spaced ridges and valleys west of Roanoke in Craig County. Photo © DCR-DNH, Gary P. Fleming.

Most of western Virginia lies within the Ridge and Valley province, which was developed from slightly older rocks deposited in the same Paleozoic basin that formed the Cumberland and Allegheny Mountains. In this part of the basin, however, the sedimentary deposits were extensively folded and thrust-faulted during the Alleghenian orogeny. The alignment of ridges and valleys was determined by the long axes of the folds, while differential erosion of underlying bedrock formations controlled the structural development of landforms. The present landscape of the region is characterized by long, parallel, narrow, even-crested ridges rising above intervening valleys of varying size, the largest and easternmost of which is the **Valley of Virginia**, or **Great Valley**. The linear strike ridges are generally underlain by more resistant sandstones and quartzites, whereas valleys and low knobs are underlain by less resistant limestones, dolostones, and shales. Much of the Ridge and Valley lies at low to middle elevations (< 1070 m/3500 ft), with scattered peaks along the higher ridges reaching elevations from 1200 to 1436 m (4000 to 4710 ft).

The Ridge and Valley is divisible into subregions based on topographic and geological features. The Great Valley, lying at the western foot of the Blue Ridge, is actually a series of different watershed valleys of various width and valley-floor elevation. The portion in northwestern Virginia, known as the Shenandoah Valley and drained by the Shenandoah River and its tributaries, approaches 48 km (30 mi) in width locally. A prominent, isolated range of medium-elevation ridges known as the Massanutten Mountains runs down the center of the Shenandoah Valley for approximately 80 km (50 mi). In west-central Virginia and southwestern Virginia, the Great Valley is successively drained by the James, Roanoke, New, and Holston rivers, narrowing considerably over much of this range as ridges on the west intrude toward the Blue Ridge. West of the Great Valley is a subregion of high, closely spaced, parallel ridges capped by very resistant Silurian sandstones, with narrow intervening valleys frequently connected by water gaps (Fig. 5). Two of the largest ridges are Shenandoah Mountain, which runs for 95 km (59 mi) in northwestern Virginia and attains a maximum elevation of 1340 m (4397 ft), and Clinch Mountain, which dominates the southwestern Virginia Ridge and Valley for a length of 140 km (87 mi) and reaches 1436 m (4710 ft) elevation.

Fig. 6. View of the Clich Valley/Knobs region from Powell Mountain in Scott County. Photo © DCR-DNH, Gary P. Fleming.

Valleys underlain by limestone (composed primarily of calcium carbonate) and dolostone (containing magnesium carbonate in addition to calcium carbonate) are frequent throughout western Virginia and often contain karst topography, with numerous sinkholes and caves caused by dissolution of the underlying bedrock by water. However, between Clinch Mountain and the Cumberland Mountains in Russell and Scott counties in far southwestern Virginia is an area of some 1300 sq km (500 sq mi) in which the more resistant dolostones form prominent low ridges and knobs above less resistant calcareous shales and limestones (Fig. 6). There is little acidic sedimentary rock in this distinctive subregion, through which the Clinch River has cut a magnificent valley lined with precipitous bluffs, palisading cliffs, and deep, sheltered coves. The **Clinch Valley/Knobs** sector of the Ridge and Valley is arguably the richest area for plant growth and species diversity in the province.

The Blue Ridge is underlain by ancient (Proterozoic) continental basement rocks that were faulted, uplifted, and deformed during three discrete orogenies. This province is usually divided into two subregions based on physiography and elevation. From Roanoke Gap northward, the **Northern Blue Ridge** consists of a narrow, irregularly weathered series of peaks underlain by a core of resistant granites, gneisses, and metabasalt (greenstone), with resistant metasedimentary rocks (quartzite, metasiltstone, phyllite) exposed on the western flank. Maximum elevation in the Northern Blue Ridge is 1288 m (4225 ft) on Apple Orchard Mountain, just south of the James River. Much of the Northern Blue Ridge geology is dominated by base-rich metabasalt of the Catoctin Formation and by granitic and gneissic formations containing large amounts of pyroxene and other mafic minerals. As a result, this region has a prevalence of fertile soils, basic rock outcrops, and an overall richness of vegetation unique among the state's middle- to high-elevation areas.

South of Roanoke Gap, the Blue Ridge broadens into a more gently rolling plateau as wide as 80 km (50 mi) that is bordered on the southeast by a pronounced escarpment abruptly descending to the Piedmont. Towering above the southwest side of the plateau are the Balsam Mountains, Virginia's most extensive high-elevation landscape occupying portions of Smyth, Grayson, and Washington counties. This **Southern Blue Ridge** section is underlain by a variety of ancient igneous and metamorphic rocks, with occasional granitic promontories such as Point Lookout Mountain (1387 m/4550 ft) and mafic monadnocks such as Buffalo Mountain (1210 m/3971 ft) punctuating the broad, central plateau. The Balsam Mountains encompass approximately 88 sq km (34 sq mi) above 1220 m (4000 ft) and 11.5 sq km (4.5 sq mi) above 1525 m (5000 ft), where climatic conditions and vegetation comparable to boreal regions of the north prevail (Rheinhardt and Ware 1984). Here, elevations reach 1682 m (5520 ft) at Whitetop and 1746 m (5729 ft) at Mount Rogers, the two highest points in Virginia.

The Piedmont is a rolling to locally hilly landscape that lies between the Blue Ridge on the west and the Coastal Plain on the east. The land surface of the province slopes gradually from a general elevation of about 300 m (1000 ft) near the Blue Ridge to roughly 50 m (160 ft) on its eastern border. In the

southern part of the state, the Piedmont reaches a width of about 280 km (175 mi), gradually narrowing to approximately 75 km (45 mi) in northern Virginia. The underlying geology consists largely of resistant metamorphic and igneous rocks, some of them blocks of exotic terrane, that have undergone a history of deposition, uplift, deformation, and erosion that is complex and difficult to interpret. However, except in dissected or foothill areas, most of the province is covered by a thick mantle of soil and saprolite that has weathered in place for millions of years and obscured much of the geologic parent material, while losing many of the original chemical constituents, notably base metals.

Fig 7. Isolated inner Piedmont foothills in western Albemarle County. Photo © Gary P. Fleming.

The Piedmont can be divided into western (inner) and eastern (outer) zones by topographic features. The **inner Piedmont** is part of the geological Blue Ridge anticlinorium and is underlain by the same rocks as the latter but is here treated as part of the physiographic Piedmont. It contains the steeply rolling to hilly belt lying just east of the Blue Ridge, including a number of more or less isolated monadnocks or foothill ranges (Fig. 7) that reach elevations of about 300 m (1000 ft) to more than 600 m (2000 ft). These ridges, such as the Bull Run Mountains in northern Virginia, the Southwest Mountains near Charlottesville, and Smith Mountain southwest of Lynchburg, are ecological outliers of the Blue Ridge in terms of plant habitats. The **outer Piedmont** comprises the eastern two-thirds of the province, including several low, nearly level Mesozoic basins (e.g., the Culpeper, Richmond, and Danville basins). The latter are remnants of Triassic to Jurassic rift valleys that were intruded by magma (now diabase and basalts) and filled with sediments (now siltstones and sandstones) eroded off the Appalachians.

The eastern edge of the Piedmont is known as the **Fall Zone**, an area roughly 32 km (20 mi) wide where the change in geology from crystalline bedrock to the unconsolidated sediments of the Coastal Plain accelerates the down-cutting of streams, creating a low escarpment with high-gradient flows along the major watercourses. Rivers that cross the Fall Zone characteristically have dramatic rapids and falls such as those seen along the James River in Richmond, the Rappahannock River west of Fredericksburg, and the Potomac River west of Washington, D.C. Much of the prominent stream incision along the Fall Zone resulted from changes in base level in response to Pleistocene fluctuations in sea level.

The Atlantic Coastal Plain stretches from Cape Cod south to Florida, extending east from the Fall Zone to the Atlantic Ocean. In Virginia, its inner edge roughly corresponds to the route of Interstate 95 between Washington, D.C., and Emporia. Virginia's Coastal Plain is a low-relief, terraced landscape that slopes gently toward the Atlantic Ocean from its highest elevations at the fall line (~ 75 m/250 ft). Geologically, this province is a young landscape, sculpted during the last few million years by the repeated rising and falling of sea level during several cycles of Pleistocene glaciation. The Coastal Plain is underlain by a wedge of Cretaceous and Tertiary sediments that increases in thickness from a feather edge at the Fall Zone to thousands of meters at the offshore edge of the North American continental shelf. Soils tend

to be sandy, although deposits of terrace gravels, marine clays, silt, and fossiliferous shells are extensive in places. Most streams draining the eastern portion of the Coastal Plain are estuaries in river valleys drowned by Holocene sea-level rise and now subject to tidal fluctuations (Delcourt et al. 1993). The largest rivers flowing across the Coastal Plain—the Potomac and James—are tidal upstream to the Fall Zone. South of the James, the larger rivers such as the Meherrin, Nottoway, and Blackwater are non-tidal and have broad floodplains with large swamps that are flooded for considerable parts of the year.

Fig. 8. Tidal estuaries with fringing marshes are characteristic of the Coastal Plain. Accokeek Creek, Stafford County. Photo © DCR-DNH, Gary P. Fleming.

Like the Piedmont, the Virginia Coastal Plain is often divided into western (inner) and eastern (outer) sections based on topographic features. The **inner Coastal Plain** is a broad upland, gently dissected by streams but quite rugged where short, high-gradient streams have incised steep ravine systems. Four large tidal rivers—the Potomac, Rappahannock, York, and James—drain the northern part of the inner Coastal Plain, flowing southeastward into the Chesapeake Bay and dividing the area into three prominent peninsulas. The Northern Neck is the peninsula between the Potomac and Rappahannock rivers, while the Middle Peninsula lies between the Rappahannock and the York. The area between the York and James rivers is simply referred to as The Peninsula. In areas of greater topographic relief, down-cutting of the inner Coastal Plain rivers is producing actively eroding riverside cliffs of exposed sediments that often contain large shell beds and fossils. In areas of lower relief, the rivers are typically bordered by extensive tidal marshes and swamps (Fig. 8).

The **outer Coastal Plain** is an undulating to nearly flat landscape marked by several ancient marine terraces bounded by scarps that mark former Pleistocene shorelines. South of the James River, the outer Coastal Plain lies within the Mid-Atlantic Embayed Region, a region of sounds, embayments, and flatwoods stretching from Back Bay, Virginia, to the Neuse River in North Carolina. In Virginia, the

Embayed Region includes the Great Dismal Swamp and the North Landing and Northwest rivers, all northern extensions of Currituck Sound. A line through the town of Suffolk north to Gloucester Courthouse and Westmoreland County on the Potomac roughly marks the boundary between the inner and outer coastal plains. East of this line, the outer Coastal Plain does not exceed 18 m (60 ft) in elevation and includes the Embayed Region, the western shore of the Chesapeake Bay, a narrow strip along the Potomac, and the **Eastern Shore,** representing the southern end of the Delmarva Peninsula. Lying on the eastern edge of the Eastern Shore, and continuing south of the Chesapeake Bay, is a chain of large bay and marsh complexes and barrier islands with both active and stabilized dunes. These islands are dynamic landscapes that are constantly buffeted by powerful winds and waves, generally eroding on the ocean side and accreting on the sound side.

Fig. 9. Infrared aerial view of the Great Dismal Swamp, with Lake Drummond in its southern portion. Photo: © Commonwealth of Virginia 2009.

The Embayed Region contains several topographic and hydrologic features not found elsewhere in Virginia. The Great Dismal Swamp (Fig. 9) includes nearly 500 sq km (200 sq mi) in the state that is covered by superficial to deep Holocene peat deposits and saturated or seasonally flooded by fluctuating groundwater (Oaks and Whitehead 1979). Lake Drummond, a 1287-ha (3180-acre) body of water with a maximum depth of about 2 m, punctuates the interior of the swamp and is one of just two natural lakes in the state (Marshall 1979). Although it has been determined that the lake was formed about 4000 years ago, the nature of its origin and development is uncertain. A meteor impact, a deep peat fire, and the solution and collapse of underlying calcareous strata, singly or in combination, are considered the most likely scenarios (Levy 2000).

The Northwest and North Landing rivers and Back Bay are tributaries of Currituck Sound located east of the Dismal Swamp and represent the upper limits of estuarine systems in drowned Holocene valleys (Copeland 1983). They were formerly influenced by diurnal tides, but now lie beyond the upstream limits of lunar tides due to the closure of various inlets on the Outer Banks within the past 350 years. However, since these water bodies are now oversized for the amount of water they carry, low velocities allow wind tides to predominate over riverine flows for short periods of time (Stanley 1992). Strong winds from the southeast move water northward from Currituck Sound into Back Bay and the two rivers, flooding the fringing marshes and swamps. Conversely, strong north to west winds result in lower water levels. Because wind influences are irregular, the frequency and duration of wind tides are also highly variable and cause fluctuations in salinity regimes from strictly freshwater to oligohaline.

Soils

Virginia soils formed from a broad range of parent materials and, in most cases, developed under the influence of vegetation for thousands to millions of years. Consequently, the numerous classified soil types that cover the state exhibit great variation in depth, textural and mineral composition, organic matter content, water-holding capacity, pH, fertility, and other characteristics. The fine level of soil classification used by agencies such the Natural Resources Conservation Service (NRCS), along with the heterogeneity of some classification units, makes direct correlation between vegetation or plant species diversity and specific soil types elusive. For practical vegetation or plant ecology work, a broader interpretation of soils, related to their structural and chemical characteristics, is often more useful.

Several of the major soil orders recognized by soil scientists are well represented in Virginia (USDA-NRCS 1999). The most prevalent are the Ultisols, representing strongly leached, infertile mineral soils that formed under deciduous, coniferous, or mixed forest and woodland vegetation and that have well-developed red or yellow-red subsurface clay horizons. Weathered from a variety of parent materials, these soils are typically strongly to extremely acidic and deficient in calcium, magnesium, potassium, and total base saturation, their reddish color resulting from the accumulation of insoluble iron oxides. Ultisols are the most characteristic red clay soils of the warm-humid southeastern United States and are widespread in Virginia, especially in the Piedmont and Coastal Plain. Both Alfisols and Inceptisols are widely but somewhat locally distributed in the mountains and Piedmont. Alfisols formed under hardwood forest cover but generally have not been leached to such a degree as Ultisols and have a clay-enriched subsoil and greater native fertility. They are common in areas underlain by basic and calcareous rocks and are typically much younger than Ultisols. Inceptisols are mineral soils of relatively recent origin, characterized by weak profile development. Varying widely in composition, texture, and fertility, they are often found on erosive slopes, young geomorphic surfaces, and resistant parent materials. In Virginia, Inceptisols are most prevalent on the rocky ridges and steep slopes of the Appalachians and western Piedmont foothills. Inceptisols classified as frigid soils (average annual temperature < 8.3º C [47º F]) are prevalent in the Balsam Mountains, the Allegheny Mountain portion of Highland County, and several other high-elevation montane landscapes in Virginia.

Entisols and Histosols occur much less extensively in the state, the former constituting soils lacking any profile development and consisting of materials unaltered from their original state. Examples of Entisols include soils of Coastal Plain sandhills and dunes, as well as many types of unconsolidated alluvial soils repeatedly altered by flooding. Histosols are deep, poorly drained organic soils consisting of muck, peat, or combinations thereof that are usually highly deficient in plant nutrients. The most extensive occurrences of this soil order are in the Great Dismal Swamp, but small patches occur locally throughout the Coastal Plain. Spodosols, soils formed under coniferous forests and in which organic matter and aluminum, leached from the upper horizons, have accumulated in a subsoil horizon, are known from a few poorly drained sandy flats of the Coastal Plain. They are also likely to occur under the spruce and fir forests at the highest elevations of Mount Rogers and Whitetop, based on their documentation in similar environments of the Great Smoky Mountain in North Carolina and Tennessee (White et al. 1993).

Soil chemistry data collected by ecologists of the Virginia Department of Conservation and Recreation's Division of Natural Heritage from more than 3400 vegetation plots in all regions of the state show strong correlations between geological substrate, pH, and base cation levels. These data demonstrate that soils weathered from most Coastal Plain sediments and silica-rich sedimentary or metasedimentary rocks of the Piedmont and mountains have consistently low pH (often 4.5 or less), low calcium and magnesium content, and high iron and aluminum levels, characteristics consistent with the prevalent infertile, red clay Ultisols that occur throughout the state and with some Inceptisols formed on acidic sedimentary

rocks. On the other hand, soils weathered from some sandstone, siltstone, metasiltstone, and shale formations may be moderately to strongly calcareous due to the presence of calcium concretions or calcareous materials in the sediments from which they were formed. Such soils are locally prevalent in the Piedmont Mesozoic (Triassic) Basins, the Ridge and Valley, and the Cumberland Mountains.

Soils weathered from igneous and metamorphic rocks of the Piedmont and Blue Ridge are highly variable in their chemistry. The felsic granites, gneisses, and other metasedimentary rocks tend to produce Ultisols of low fertility, but granitic rocks that contain significant amounts of pyroxene, amphibole, hornblende, or other dark minerals produce more base-rich soils. Metabasalt, amphibolite, actinolite schist, diabase, and gabbro are chemically similar mafic igneous or metamorphic rocks that underlie discrete areas of these provinces and contribute to soil chemistries that are somewhat intermediate in composition. Many soils originating from mafic parent materials are deep, well-drained, and relatively fertile, but a subset develops impermeable subsoils of shrink-swell clays that impede drainage and rooting. Alternately waterlogged during wet periods and rock-hard during droughts, such hardpan soils are most frequent in gentle Piedmont landscapes and significantly influence the vegetation growing on them.

There is a common misconception among ecologists and botanists that mafic substrates produce soils that are circumneutral, i.e., having a pH of about 7.0. This is usually not the case, however, because, as these substrates weather, concentrations of the acidic elements iron, aluminum, and manganese increase in the soil, lowering the pH by their chemical weathering and replacing the exchangeable base cations (calcium, magnesium, potassium) that are leached. Of 480 plots sampled by the Division of Natural Heritage on Piedmont and Blue Ridge mafic sites, fewer than 10% had soils with pH greater than 6.0, and the mean soil pH was 5.0, only marginally higher than the mean pH of 4.8 for soils of all 1694 Piedmont and Blue Ridge plots. On the other hand, mean calcium and magnesium were 32% and 50% higher in the mafic-soil plots than the mean values for all plots of these regions. Thus it is typical for soils weathered from mafic substrates to be strongly acidic yet also to have considerably higher base status than do soils from many other substrates. The only consistently circumneutral or moderately alkaline soils in Virginia are those weathered from carbonate formations of limestone and dolostone in the Ridge and Valley and Cumberland Mountains of western Virginia. These soils also have the highest mean calcium levels (2850 ppm) in Virginia, along with significantly lower than average iron and aluminum levels. Exceptional soils over carbonate rocks can have calcium that ranges to 9000 ppm, and dolomitic soils can exceed 1500 ppm magnesium. Extraordinarily high calcium levels have also been recorded from soils of inner Coastal Plain ravines that have down-cut into Tertiary or Quaternary shell deposits and from fertile alluvium in large-river floodplains of the Piedmont and mountains.

Despite strong correlations between parent material and soil fertility, the dynamics of soil chemistry are complex, variable at small spatial scales, and often influenced by a host of site-specific factors, including past land use, leaching of bases, colluvial processes, and the transportation of dissolved bases into concave land forms by groundwater. In determining the role of soil in the ecology of vegetation or individual plants, there is simply no substitute for the careful collection, field characterization, and laboratory analysis of soil samples from specific study sites.

Developmental Setting of the Flora

Present-day vegetation assemblages and species distributions in Virginia have developed since the maximum extent of the last continental glaciation during the late Wisconsin era, roughly 18,000 years ago (yr BP). At that time, the North American Laurentide ice sheet extended south to about lat 41°N into what is now northern Pennsylvania, and to about lat 40°N in central Ohio and Indiana to the west,

imposing a boreal climate on the mid-Atlantic and Central Appalachian region. Since about 16,500 yr BP, a fluctuating but gradually warming climate has fundamentally changed conditions for plant life and initiated a period of large-scale plant migrations and redistribution of vegetation in eastern North America (Delcourt and Delcourt 1993; Prentice et al. 1991). During the later part of this period, vegetation changes on the landscape have been influenced less by climatic changes and increasingly by human activities. Paleoecologists have been able to reconstruct specific changes in vegetation during the late Wisconsin and Holocene by analyzing the pollen record preserved in peat deposits. Such palynological studies have been conducted on data collected from seven sites in Virginia: 1) the entrance to the Chesapeake Bay (Harrison et al. 1965); 2) the Great Dismal Swamp (Whitehead 1972); 3) Saltville Valley in Smyth County (Ray et al. 1967); 4) Potts Mountain Pond in Craig County (Watts 1979); 5) Browns Pond in Bath County (Kneller and Peteet 1993); 6) Hack (Spring) Pond (Fig. 10) in Augusta County (Craig 1969); and 7) Quarles Pond in Augusta County (Craig 1969). Although no studies have been done at Piedmont and Blue Ridge sites, the Virginia studies and those conducted in adjacent states depict remarkably similar trends in post-Wisconsin vegetational change.

Fig. 10. Spring Pond, August County, a large spring-fed sinkhole pond that is one of seven palynological study sites that has helped reconstruct the vegetational history of Virginia. Photo © DCR-DNH, Gary P. Fleming.

Late Pleistocene and Early Holocene

Full-glacial vegetation in our area consisted largely of cold, species-poor, northern pine-spruce woodland, or taiga, with alpine tundra vegetation occupying areas of permafrost at the middle to high elevations of the Appalachians and closed boreal forests in lower, more favorable landscape positions (Delcourt and Delcourt 1986). Northern pines included *Pinus banksiana* (Jack Pine) and *P. resinosa* (Red Pine), while spruces probably included *Picea rubens* (Red Spruce), *P. mariana* (Black Spruce), and *P. glauca* (White Spruce). During the glacial maximum, severe climatic conditions and repeated freeze-thaw cycles in the Appalachians accelerated geomorphic processes such as mass wasting, debris

avalanches, and the downslope movement of rock fragments and soil, forming extensive exposed boulderfields and filling poorly drained valley depressions with mineral soil (Delcourt and Delcourt 1988). Evidence from several sites indicates that such processes maintained areas of pioneer shrub and herb vegetation, as well as bogs, ponds, and other open wetlands in sediment-filled depressions, which formed mosaics with the boreal woodlands and forests. On the Coastal Plain, extensive wind-driven landscape disturbances probably maintained a patchwork of open taiga, sand barrens, and ephemeral bogs amid the boreal forest. Vast areas of sediments exposed along the Atlantic coast during sea-level minima probably supported small patches of other temporally unique, non-forest vegetation types. It is also possible that the climate of these exposed near-coastal areas was somewhat modified by slightly warmer oceanic influences, allowing opportunities for the persistence and migration of southern and low-elevation species (Christiansen 1988; Sorrie and Weakley 2001).

During the late-glacial period from 15,500 to 12,500 yr BP, considerable variation in climatic conditions and vegetation was no doubt present both longitudinally and latitudinally in Virginia, just as it is today. For instance, in the Ridge and Valley, the pollen record indicates that closed spruce-pine forest occupied the Shenandoah Valley region in west-central Virginia, with increasing amounts of *Pinus strobus* (Eastern White Pine), *Betula* (birch), and *Quercus* (oak) after 12,700 yr BP (Craig 1969). However, at Saltville in the southwestern Ridge and Valley, the vegetation was more diverse and included *Pinus banksiana–Populus* (Jack Pine–Aspen) stands on sandstone ridges, bottomland forests of Red Spruce, *Abies balsamea* (Balsam Fir), and *Larix* (Tamarack); open wetland glades dominated by boreal shrubs and graminoids; and a mesophytic hardwood forest somewhat akin to today's northern hardwoods (Ray et al. 1967).

In the mid-Atlantic region, both geomorphic processes and vegetation patterns were locked into a glacial climate until about 12,500 yr BP, when the effects of climatic amelioration following the northward-retreating ice sheets began to result in widespread changes. These changes were driven not only by climate but by a shift from predominantly colluvial to alluvial geomorphic processes, allowing closed forests to invade formerly unstable land surfaces and the development of extensive sediment and peat deposits, marshes, ponds, and alluvial glades along streams. In the outer Coastal Plain, sediments and rising ocean levels filled the once high-gradient river valleys and began the formation of our current tidal estuaries. Concurrently, boreal species retreated northward and to higher elevations in the mountains, while species that had been pushed far south of the region during the full-glacial climate moved into the area along corridors that included the river valleys of the Ridge and Valley and the Atlantic Coastal Plain. Vegetation in all areas changed gradually from boreal forest to forests dominated by oaks, *Castanea dentata* (American Chestnut), *Carya* (hickory), and *Pinus* (southern pines), often through intermediate phases in which both boreal and warm-temperate trees occurred in mixture with *Tsuga canadensis* (Eastern Hemlock), *Fagus* (beech), Eastern White Pine, birch, and other northern hardwoods (Delcourt et al. 1993). Hemlock dominated the forests at Saltville and at Shady Valley, Tennessee (just south of Damascus, Virginia), but abruptly declined at both sites about 4500 yr BP (Delcourt and Delcourt 1986). In the Great Dismal Swamp of southeastern Virginia, vegetation changed from a northern pine-spruce assemblage from 12,000 to 10,000 yr BP, to a beech-hemlock-birch assemblage 10,600 to 8200 yr BP, to an oak–hickory–temperate hardwoods assemblage 8200 to 3500 yr BP, and finally to a *Taxodium-Nyssa* (baldcypress-tupelo) swamp assemblage about 3500 yr BP (Whitehead 1972).

The earliest evidence of humans in Virginia dates to about 17,000 yr BP, from a site along the Nottoway River in southeastern Virginia. This date challenges the long-prevailing theory that North America was initially colonized by people who entered via a land bridge between Siberia and Alaska, and hence

southward through a corridor between the Cordilleran and Laurentide glaciers that opened 14,500 and 13,000 yr BP (Egloff and Woodward 2006). It now seems likely that some of the colonization was via boat and subsequent migration north from Central and South America. Regardless of exactly how they arrived, American Indians inhabited Virginia for most of the late Wisconsin and the Holocene, their cultures evolving with the changing climate and vegetation.

The initial Paleo-Indian period, from about 17,000 to 10,000 yr BP, corresponds to the late-glacial and early Holocene period, when the climate was still boreal or nearly so. Indians of this time were essentially nomadic hunters who lived in small groups and relied heavily on megafauna (woolly mammoth, mastodons, caribou, bison) that inhabited the cold landscape. By the start of the Archaic period, 10,000 yr BP, the megaherbivores had migrated out of the region or become extinct. Over the next seven millennia, Indian cultures adapted to the warming climate and increasingly deciduous forests. Small game such as deer, along with fruits and nuts, became important food sources. Wood became a major resource, and different types of stone were quarried for various purposes. Fire was a critical tool used extensively for clearing land, range management, hunting, and agriculture (Trigger 1978; Pyne 1982; Mann 2005). Extensive burning favored the physiologically adapted oaks and pines, as well as their soil requirements for seed germination, while eliminating thin-barked, fire-intolerant competitors like maples and beech. By all accounts, Indian fires, in combination with natural, lightning-caused fires, were key ecological factors in the development of Holocene oak and southern pine forests, savannas, and grasslands in Virginia and throughout the Southeast (Van Lear and Waldrop 1989; Abrams 1992; Skeen et al. 1993; Delcourt and Delcourt 1998; Frost 1998).

Middle and Late Holocene

During the middle Holocene, from about 8500 to 4000 yr BP, the Hypsithermal Interval (also known as the Xerothermic Period or the post-glacial thermal optimum) saw a warmer, drier climate in much of eastern North America. Different regions may have been affected at different times or for periods of different durations, but during this interval the midwestern prairie peninsula reached its greatest eastern extent, and mid-Atlantic vegetation likely assumed a more xerophytic character. Changes that occurred in and east of the Appalachians during the Hypsithermal are poorly known, but increased pine and charcoal in some pollen records may constitute evidence of them (Scirvani 2003). Boreal species, then persisting as outliers on some of the higher Appalachians, were likely pushed upward in elevation and suffered many local extinctions as well as increased disjunction into relict populations (Ware 1999). Some ecologists have also hypothesized that isolated populations of prairie species now found in the mid-Atlantic reached this area during the Hypsithermal from the west or southwest, either via distributions that were more continuous or by moderate-distance dispersal between patches of open xeric habitat (DeSelm and Murdock 1993; Thorne 1993; Laughlin 2004). The effects of ongoing fires, both deliberately set and natural, would have enhanced the expansion of open woodland and prairie-like habitats in Virginia under a warmer and drier climatic regime, at least at lower elevations.

The Hypsithermal also saw the transition of Indian cultures during the Archaic period, when settlements and populations grew and tribes practiced more concentrated resource management that included fire, clearing, quarrying and other activities that directly influenced plants and vegetation. By the late Archaic (~ 4000 yr BP), Virginia Indians numbered in the tens of thousands and increasingly located their settlements in and along floodplains and riparian areas, where rich soils were conducive to small-scale slash-and-burn agriculture (Egloff and Woodward 2006). A cooling trend also began during the late Archaic, when virtually all the components of the present-day native Virginia flora were in place and began to undergo minor shifts in distribution in response to the new climatic conditions. These conditions continued into the Woodland period of Indian cultures (3200–400 yrs BP), during which

settlements and agricultural practices grew even larger and became more permanent. Despite this sedentary trend, Indians utilized virtually all parts of Virginia for hunting and other resource extraction, and fire was still an important tool and a pervasive ecological force on the landscape.

About 500 years ago, Indian populations suffered a sudden collapse, apparently the result of the continent-wide spread of smallpox and other diseases introduced by Spanish explorers (Mann 2005). In some areas, populations decreased 90–95%, and large areas of formerly burned, cleared, or cultivated land were left unmanaged or fallow. A likely consequence of Indian depopulation was that the first European settlers encountered many forests that had been free of disturbance for 100 years or more and were denser and more closed-canopy than those of the earlier Archaic and Woodland periods. Nevertheless, early explorers and settlers reported some areas of open forest, savanna, and grassland that had persisted or were still being maintained by surviving tribes (Allard and Leonard 1962; Brown 2000; Maxwell 1910).

European Settlement to Present

The post-settlement history of Virginia plant life is one of far-reaching human influence leading to extensive ecological and floristic changes that continue today. It began as a 300-year period of agricultural and timber exploitation (1630–1930) before entering a phase of forest recovery and renewal (1930–1980) (Scirvani 2003). Since 1980, Virginia's vegetation and flora have seen both the positive benefits of increased conservation awareness and activity and the negative impacts of urbanization, habitat loss, forest decline, pathogens, and invasive non-native plants.

In 1630, forest covered 96% of Virginia's land area, or nearly 10 million ha (25 million acres) (Virginia Department of Forestry 2011). Over the first 230 years of European settlement much of the land was cleared for agriculture at one time or another, especially in the Coastal Plain and Piedmont. On poorer soils, attempts at cultivation were usually short-lived, and those areas reverted to forest. Thus, during this initial 230-year period of settlement, an average forest cover of 40–60% was maintained across Virginia (Scirvani 2003). Areas left in forest were cut for domestic uses and commonly subjected to free-ranging cattle and hogs (Woodward and MacDonald 1991; Martin and Boyce 1993). Soil depletion and erosion during this time were severe and led to massive sediment loading in floodplains and bottomlands. During the nineteenth century, accessible oak forests in the Ridge and Valley, Blue Ridge, and northern Piedmont were repeatedly cut for tanbark and processed into charcoal to fuel the furnaces of an active iron industry (Orwig and Abrams 1994; USDA Forest Service unpublished data). Most of the older forests remaining in the Piedmont and Coastal Plain at the time of the Civil War were destroyed to fill both armies' prodigious needs for construction lumber and firewood. Natural, accidental, and intentionally set fires continued to burn forests and fields at irregular intervals throughout this era, since there were no effective ways of stopping or controlling them once started.

Following the Civil War, construction of new railroads in western Virginia provided the impetus for major expansion of coal mining in the Cumberland Mountains. Larger-scale timber operations also began in the less accessible parts of the Virginia mountains, where most of the remaining old-age forests were located. Migration of the timber industry southward toward the end of the nineteenth century led to a peak in timber production in 1909, when only 14 million acres, or 55% of the state, was forested (Scirvani 2003; Virginia Department of Forestry 2011). Many of the remote mountain areas were logged using narrow-gauge railroads and cable logging techniques. Entire mountainsides, denuded by clear-cutting and covered with slash, were commonly devastated by accidental fires (Clarkson 1964). The introduced Chestnut Blight Fungus (*Cryphonectria parasitica*) arrived in 1910 and over the next 20 years decimated populations of *Castanea dentata* (American Chestnut), a tree that had made up 20–25% of

the Appalachian forests. During the entire period of exploitation and continuing well after, approximately 42% of Virginia's original 970,000 ha (2.4 million acres) of wetlands were lost to ditching, draining, filling, conversion to farmland, development, and impoundments (USGS 1997). Many of the remaining wetlands were damaged by livestock, industrial pollution, logging, and other intrusive land-use practices.

By 1930, Virginia's forest resources had been seriously depleted, and the condition of most land and natural vegetation in the state had been degraded. By that time, a number of initiatives for conserving forest land had begun, including the establishment of the George Washington and Jefferson National Forests, the Virginia State Forest system, Shenandoah National Park, and other parks. The onset of the Great Depression saw the widespread abandonment of farmland and the re-establishment of young forests. By the mid-1940s, the tools for effective fire suppression were in place in many areas, and a massive advertising campaign, led by the U.S. Forest Service and its mascot, Smokey Bear, had been launched to educate the public about the dangers of forest fires. The effort was a huge success, as the total acreage burned annually statewide and the average size of individual fires decreased 95% and 98% respectively from 1925 to 1991 (Orwig and Abrams 1994).

Management of forests for sustained yields, increasingly under the guidance of professional foresters, contributed to an 800,000-ha (2 million–acre) increase in forest cover by 1980. In 1940, during the initial phase of this recovery period, 43% of Virginia forests were classified as a pine type, and the planting of monospecific stands of *Pinus taeda* (Loblolly Pine) became a prevalent practice in eastern Virginia during the 1960s and 1970s. However, a steep decline of natural pine types (especially *Pinus echinata*, Shortleaf Pine) and their replacement by oaks led to a greater percentage of hardwood coverage by 1980 (Scirvani 2003).

In the 1980s, more stringent laws slowed but did not stop the loss and degradation of wetlands. Also, land conservation programs of federal and state agencies and private organizations such as The Nature Conservancy began to create systems of wilderness areas, special biological areas, and natural area preserves designed specifically to protect biodiversity. These have expanded to provide habitat protection for many of Virginia's rarest plants, animals, and natural communities. However, the past three decades have also seen a permanent loss of more than 100,000 ha (300,000 acres) of forest land, fragmentation of much additional forest acreage, and loss of other habitat types to development (Scirvani 2003). Moreover, decades of nearly complete exclusion of fire have precipitated widespread fundamental changes in forest and woodland composition and a loss of species diversity. Naturally open woodlands that require periodic burning to maintain their structure, such as the *Pinus serotina* (Pond Pine)/evergreen shrub pocosins of the Coastal Plain and the *Pinus rigida* (Pitch Pine)–*Pinus pungens* (Table Mountain Pine)/*Quercus ilicifolia* (Bear Oak) woodlands of the mountains, have in most cases been replaced via ecological succession by dense, nearly closed forests. In addition, many plants that benefit from fire have undergone serious declines and local extirpations. Compounding these problems, Whitetail Deer (*Odocoileus virginianus*) populations have exploded in many parts of Virginia, further reducing tree seedling survival, herbaceous composition and cover, and forest understory structure over large areas (W.M. Knox 1997; McShea and Rappole 1997; Rheinhardt et al. 2000).

Among forests in every region of Virginia the dominant oaks are now in the process of being replaced by mesophytic, fire-intolerant trees such as *Acer rubrum* (Red Maple), *Acer saccharum* (Sugar Maple), *Fagus grandifolia* (American Beech), *Betula lenta* var. *lenta* (Sweet Birch), *Betula alleghaniensis* (Yellow Birch), *Fraxinus americana* (White Ash), and *Pinus strobus* (Eastern White Pine). *Carya* spp. (hickories) are physiologically closer to oaks but more shade-tolerant, and are also recruiting heavily in oak forests

on many sites, especially those with base-rich soils. The oak replacement species vary by region but typically dominate the understory of all but the driest oak stands, cast dense shade, produce moisture-holding litter, and create an environment inhospitable to fire, oak regeneration, and the growth of diverse shrubs and herbs (Nowacki and Abrams 2008). Cutting of such a stand only accelerates the replacement of oaks by releasing the non-oak understory trees, increasing opportunities for gap invaders such as *Liriodendron tulipifera* (Tulip-poplar), and further reducing the possibility of oak recruitment. Increased efforts to use prescribed burning for biodiversity conservation and commercial forest management hold promise for reversing this trend. Yet, to a great extent, these changes will have to be accepted as part of the continuing coevolution of vegetation and human culture, because it is improbable that fire can be restored to anything like its pre-settlement scope on the modern, developed landscape.

Insect and fungal pathogens and invasive non-native plants have increasingly plagued Virginia's vegetation and flora in recent decades. Around 1950, on the heels of the chestnut blight calamity, the European Dutch Elm Disease fungi (*Ophiostoma ulmi* and *O. novo-ulmi*) arrived in Virginia and, by the late 1970s, had caused extensive mortality of both *Ulmus americana* (American Elm) and *Ulmus rubra* (Slippery Elm). The Hemlock Woolly Adelgid (*Adelges tsugae*), a non-native insect also first reported in the 1950s, remained at low population levels for decades, before its numbers increased exponentially to devastate Eastern Hemlock stands throughout the mountains and Piedmont in the 1980s and 1990s. The past three decades have witnessed large outbreaks of the non-native Gypsy Moth (*Lymantria dispar*) in northern and western Virginia, leading to the defoliation and locally extensive mortality of oaks. The symptoms of what is now known to be the Dogwood Anthracnose Fungus (*Discula destructiva*) began to be noticeable in Virginia forests in the early 1980s. Since then the fungus, also suspected of being non-native, has rampantly infected forest stands and caused the mortality of millions of *Cornus florida* (Flowering Dogwood) trees. The ecological consequences of such pathogens are potentially severe, especially when vegetation composition, structure, and forest-floor microhabitats are radically altered by the removal of overstory or understory dominants such as oaks, hemlock, and dogwood. In addition, habitats and food resources for various animals and songbirds are inexorably reduced or degraded by the loss of such important wildlife-resource plants.

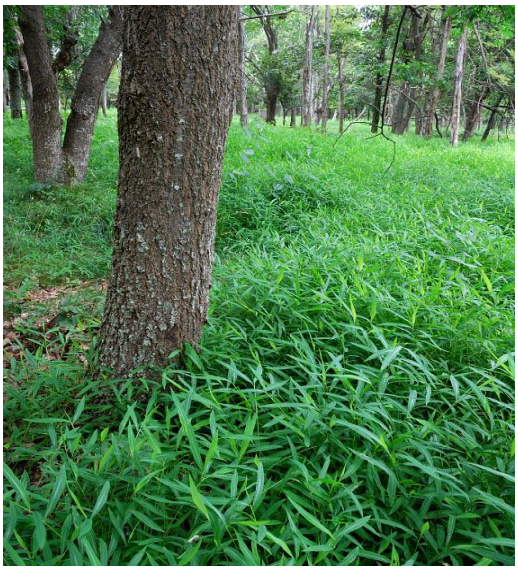

Fig. 11. A forest over-run by *Microstegium vimineum* (Japanese stiltgrass). Shenandoah National Park, Madison County. Photo © Gary P. Fleming.

In recent decades, naturalized non-native plant species have exerted an ever greater influence on the composition of Virginia's plant communities and the ecological dynamics of the state's flora. This trend can be difficult to quantify, but two site-specific examples can serve as illustrations. In the Bull Run Mountains, a foothill range in the northern Virginia Piedmont, the percentage of non-natives increased from 15% in a 1943 flora (Allard and Leonard 1943) to 20% in an updated flora 59 years later (Fleming 2002) that covered a considerably smaller and more wooded area. In 1943, *Lonicera japonica* (Japanese Honeysuckle) was the only non-native identified as a serious threat to native vegetation. By 2002, numerous non-natives that were not in the 1943 flora were widespread and common in the area. Foremost among these was *Microstegium vimineum* (Japanese Stiltgrass, Fig. 11), arguably the most abundant, invasive, and rapidly spreading non-native plant in Virginia today. Aside from the greater percentage of non-native

species and their greater prevalence in the area's natural communities, other non-native species, present in 1943, occurred in far greater numbers by 2002. For instance, *Alliaria petiolata* (Garlic Mustard), now abundant in floodplains and mesic, fertile forests throughout the area, was reported by Allard and Leonard (1943) as "infrequent" around old homesites in one area.

A similar but even more dramatic example of this trend is found in the flora of the highly urbanized Washington, D.C., area, where the percentage of non-native species doubled from 17.9% in a 1919 flora (Hitchcock and Standley 1919) to 35.6% in a more recent Washington-Baltimore regional flora (Shetler and Orli 2000, 2002). As in the Bull Run Mountains, Japanese Honeysuckle was the only non-native recognized as "abundant everywhere" in the 1919 flora, and many now familiar and widespread species were not mentioned. The dates of first documentation for the species of more recent arrival can be identified through collections at the Smithsonian Institution's U.S. National Herbarium, including *Rubus phoenicolasius* (Wineberry, first collected in 1933), *Persicaria longiseta* (Long-bristled Smartweed, 1937), *Lespedeza cuneata* (Sericea Lespedeza, 1938), *Berberis thunbergii* (Japanese Barberry, 1945), *Lonicera maackii* (Amur Honeysuckle, 1959), *Euonymus alatus* (Winged Euonymus, 1968), Japanese Stiltgrass (1969), *Celastrus orbiculatus* (Oriental Bittersweet, 1973), and *Persicaria perfoliata* (Mile-a-minute Vine, 1982).

Many familiar non-native plants reached North America during the early post-settlement era, arriving either as unintentional stowaways, propagules in packing materials, or deliberate introductions for medicinal or culinary uses. Additional non-natives escaped early horticultural plantings and became naturalized. However, the more recent onslaught of introductions is a growing consequence of the globalization of human culture and the removal of many barriers to the worldwide migration of weedy species. At the regional and local scales, roads now encroach into even the most remote areas, fragmenting the landscape and creating isolated forest stands that are highly susceptible to edge and interior disturbances, and providing vectors for the dispersal of weeds. Thus, non-native plants have increased and, in some cases, become pervasive in natural communities largely because of human-caused landscape disturbances.

Contemporary Vegetation and Natural Communities

After four centuries of land clearing, farming, timber removal, mining, and, ultimately, modern infrastructure and urban development, Virginia's landscape today is as much the product of our cultural history as our natural heritage. A land that, pre-settlement, was 96% forested with many old-age trees and contained 970,000 ha (2.4 million acres) of wetlands, the state today is about 63% forested with 570,000 ha (1.4 million acres) of wetlands. Although about three-quarters of the wetlands are forested, only 58% of the uplands are forested, and approximately 25% of those forests are pine plantations or early-successional pine and pine-hardwood stands; the remaining hardwood stands are mostly less than 100 years old. The 42% of the uplands that is not forested is predominantly agricultural. About 8% of Virginia's land area is developed, and only 20% is in relatively large, unfragmented blocks of natural lands of very high or outstanding ecological integrity (Fig. 12; Weber 2007). Approximately 1.3 million ha (3.1 million acres), covering about 12.4% of the state, are in national forest, national park, national wildlife refuge, state forest, state park, and other publicly accessible park and preserve lands devoted to multiple uses (e.g., conservation, recreation, timber management, hunting). Only 378,000 ha (933,900 acres), covering 3.6% of the state, are in conservation lands devoted specifically to biodiversity protection.

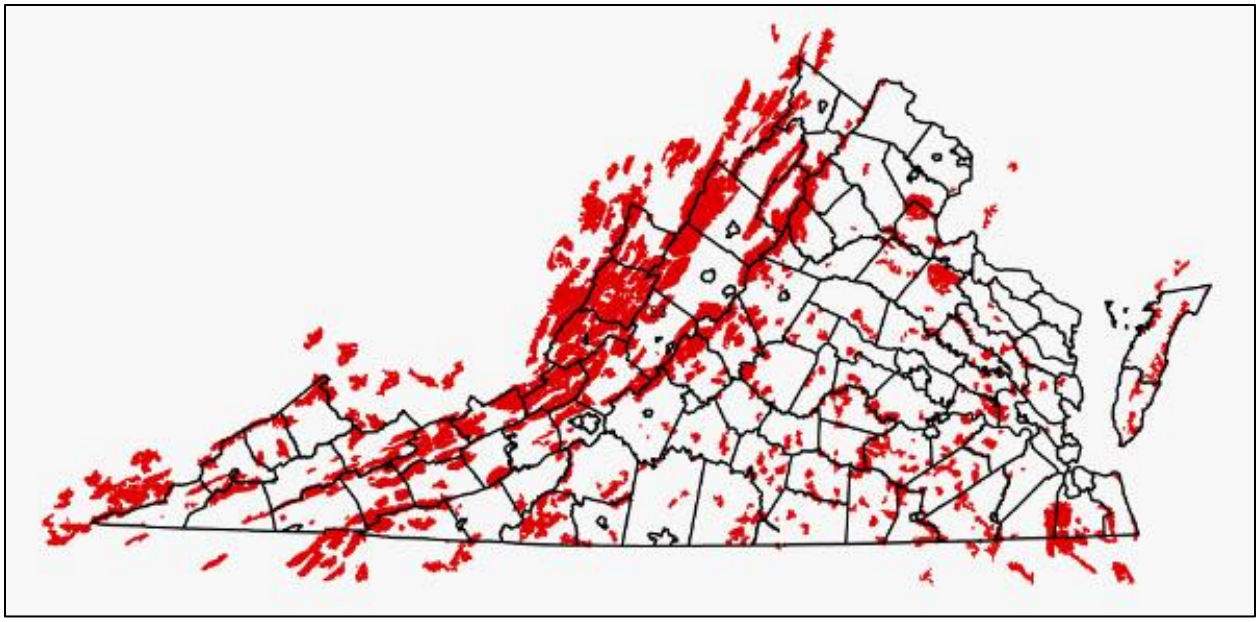

Fig. 12. Large blocks of relatively unfragmented natural lands with very high to outstanding integrity are shown in red (see Weber 2007). These blocks are heavily concentrated in the central Ridge and Valley and Northern Blue Ridge region. Click image for larger version.

There is no question that most remaining patches of older forest differ greatly from their counterparts of the pre-settlement and early post-settlement eras. Forests today are much denser, the result of repeated cutting, regeneration, coppice sprouting, and prolonged absence of fire. Many stands also exhibit low herbaceous cover and diversity that are artifacts of heavy shading and decades of increasing herbivory by large populations of Whitetail Deer (Côté et al. 2011; Russell et al. 2001). Many of our rare, non-forested vegetation types such as sandhill woodlands, pocosins, outcrop barrens, seepage bogs, and fens have been greatly reduced and in some cases nearly extirpated by wetland destruction, grazing, lack of fire, and other impacts. Composition of natural vegetation has also changed following human intrusions, the alteration of disturbance regimes, and the reduction or elimination of species by pathogens. Most important, more than 20% of the current flora was not even present in Virginia when European settlement began, and recently naturalized non-natives are now components, sometimes prevalent, of many natural communities.

Although no portion of Virginia's landscape has altogether escaped direct or indirect human impacts, areas of fairly old forest and good examples of many environmentally specialized vegetation types remain throughout the state, often in isolated patches. It is these plant communities and their habitats that provide ecologists with valuable data for assessing which assemblages of species likely constitute the longer-lasting or more stable, climax stages of vegetation development; the role that disturbance regimes play in that development; the role animals that live in and interact with vegetation play; and which environmental factors underlie the occurrence of similar groups of species at different sites on the landscape. Comprehensive inventories of these communities also may reveal stands that represent outstanding examples of community types and may indicate which types are rare and in need of protection or restoration.

Regional Context

There have been a number of attempts to characterize the eastern North American temperate broadleaf and mixed forests in regional-scale classifications, but one of the best known is that of Braun (1950), who recognized nine regions defined by the tree association that marks the late-successional vegetation

in each. Despite its age, Braun's classification has much ecological and floristic merit when applied to Virginia, which intersects four of the nine forest regions. The Mixed Mesophytic Forest Region only grazes the western edge of Virginia and corresponds closely with the unglaciated Appalachian Plateaus (Cumberland and Allegheny Mountains). According to Braun (1950), this region is (or at least was) covered mostly by a species-rich forest with dominance by various combinations of mesophytic trees, including *Acer saccharum* (Sugar Maple), *Fagus grandifolia* (American Beech), *Tilia americana* var. *heterophylla* (White Basswood), *Aesculus flava* (Yellow Buckeye), *Liriodendron tulipifera* (Tulip-poplar), *Tsuga canadensis* (Eastern Hemlock), *Quercus rubra* (Northern Red Oak), and others. More restricted oak and pine communities occupy drier sites on the sandstone ridges and outcrops, while higher-elevation areas support forests of a more northern character. The mixed and varied mesophytic forest with outliers of dry oak and pine vegetation described by Braun fit Virginia's Cumberland Mountains well, but the Allegheny Mountain portion is less diverse and contains high-elevation areas where Red Spruce and northern hardwood forests prevail.

Braun's Oak-Chestnut Forest Region includes the Virginia Ridge and Valley, Blue Ridge, inner Piedmont foothills, and northern third of the Piedmont. The natural vegetation of this region was formerly characterized by various mixtures of oaks and *Castanea dentata* (American Chestnut), with smaller inclusions of mixed mesophytic forests, high-elevation forests, oak-pine woodlands, and various specialized non-forest vegetation types. Following the elimination of the American Chestnut as an overstory tree by the Chestnut Blight Fungus by about 1940, this region is now mostly described as Appalachian oak, oak-pine, or oak-hickory-pine forest (Küchler 1964; Skeen et al. 1993; Stephenson et al. 1993). Despite the loss of the American Chestnut, this region holds together well due to its distinctive physiography and Appalachian floristics. There is little evidence, however, that the chestnut was important in forests typical of carbonate rock (limestone and dolostone) substrates of the region, and the overall vegetation of limestone or dolomitic valley slopes in Virginia may be closer to that of Braun's more westerly Oak-Hickory and Western Mesophytic Forest Regions.

The central and southern Piedmont and the Coastal Plain north of the James River lie within Braun's Oak-Pine Forest Region, an area floristically dominated by low-elevation species of southern affinity. It is a vegetation region so altered by human utilization that several pines characteristic of regeneration following disturbance — *Pinus echinata* (Shortleaf Pine), *Pinus taeda* (Loblolly Pine), and *Pinus virginiana* (Virginia Pine) — are ubiquitous among hardwoods. In the Virginia part of this region, forest cover now varies from about 40% to 60%, a sizeable portion of which consists of monospecific plantations of Loblolly Pine, pine or mixed forests that have followed agricultural abandonment, and successional forests in which pines are mixed with oaks, *Liquidambar styraciflua* (Sweetgum), and *Acer rubrum* (Red Maple) due to repeated cutting. Potential late-successional forests in this area include stands of mixed oaks on the drier sites and mixed stands of American Beech, *Quercus alba* (White Oak), and *Liriodendron tulipifera* (Tulip-poplar) on more mesic sites. Much of Braun's oak-pine region in Virginia has been more recently treated as part of a regional Oak–Hickory-Pine Forest (Skeen et al. 1993), emphasizing the importance of hardwoods such as hickories and Tulip-poplar in both pre-settlement forests and current late-seral forests in the absence of disturbance.

Braun's Southeastern Evergreen Forest reaches its northern extent in the southeastern Virginia Coastal Plain, south of the James River. This region extends over much of the South Atlantic and Gulf Coastal Plains and is essentially defined by the ranges of *Pinus palustris* (Longleaf Pine) and maritime forests of *Quercus virginiana* (Live Oak), as well as inclusions of the great southeastern swamp forests dominated by *Taxodium distichum* (Baldcypress) and *Nyssa* spp. (tupelos). Although much altered and somewhat

attenuated at its northern limits, the Virginia portion of this region is quite distinct in its overall vegetation and floristics. More recently, ecologists have characterized nearly the same region as the "Southern Mixed Hardwood Forest" in deference to the potential late-seral, mesophytic hardwood associations that can become prevalent in the absence of fire and other disturbances (Ware et al. 1993).

Contemporary Vegetation and Natural Communities of the Physiographic Provinces

While Braun's classification remains an ecologically viable framework for putting Virginia's vegetation in a larger perspective, it is almost entirely focused on forests and is not adequate to describe the great variety of plant communities that occur at the spatial scale of a state. For the purposes of an introductory discussion of vegetation and natural communities, we will rely on the basic concepts and terminology of the ecological group and community type levels in the Natural Communities of Virginia classification detailed elsewhere on this web site. This classification is consistent with the standards of the U.S. National Vegetation Classification (Grossman et al. 1998) and based on 26 years of quantitative plot data collected from representative stands of natural vegetation throughout Virginia (Fleming et al. 2013). The concept of an ecological community embraced by the National Vegetation Classification and the Virginia state classification is based on total floristic composition, including trees, shrubs, and herbs. This approach contrasts with many ecological studies in which only trees or woody vegetation have been used to define the structure and composition of communities or cover types. The two approaches are not mutually exclusive, and each has its advantages and disadvantages for specific applications.

The physiographic provinces of Virginia provide an excellent framework in which to discuss the general patterns of vegetation in the state, as well as the distribution of specific plants that are good indicators of various natural communities. Differences in climate, soils, and overall habitat conditions in each province greatly influence the distribution of plants and the assemblages of plants that represent natural communities. Although many species are wide-ranging in Virginia, differences in the overall vegetation of the Coastal Plain, Piedmont, and Appalachian provinces are pronounced and apparent. To a great extent, these variations reflect the influences of two larger biogeographic floras: that of the northern North American and Appalachian region and that of the southeastern Atlantic and Gulf slopes and coastal plains. Plants and vegetation characteristic of each region are well represented in Virginia, which is situated at latitudes at which these great floras intermingle. The patterns of distribution, however, are not simplistic, nor do the provincial boundaries represent hard and fast vegetational boundaries. Gradations in species distributions and larger-scale vegetation patterns are evident both on a north-south axis, related primarily to regional climate and the history of climatic changes and plant migrations, and on an east-west axis, related primarily to topography and local climate.

The Appalachian Plateaus

The Appalachian Plateaus province in Virginia can be divided into two sections that are distinctive in their geography and vegetation.

Cumberland Mountains Section

The Cumberland Mountains, in far southwest Virginia, consist mostly of medium-elevation ridges and narrow intervening valleys that collectively cover about 4% of the state. Eighty-one percent of the section in Virginia is forested, and 95% of the forests are of deciduous hardwoods; the remainder represents local areas where *Tsuga canadensis* (Eastern Hemlock) and *Pinus* spp. (pines) are intermixed. Palustrine wetlands are small and sparse, making up less than 0.1% of the area. About 7% of the Cumberland Mountains is developed, primarily around the valley towns of Big Stone Gap, Coeburn, Norton, and Wise. Twenty-three percent is in unfragmented blocks of natural lands with very high to

outstanding ecological integrity (Weber 2007). The George Washington and Jefferson National Forests and other public lands cover about 12% of the Cumberland Mountains. Only 7300 ha (18,120 acres), or 1.8% of the area, is in conservation lands protected for biodiversity.

Throughout the Cumberland Mountains, mesophytic cove forests and more or less mesophytic mixed oak and oak-hickory forests cover most of the mountain slopes and valleys that are not cleared. Magnolias — including *Magnolia acuminata* (Cucumber-tree), *Magnolia fraseri* (Fraser Magnolia), *Magnolia tripetala* (Umbrella Magnolia), and *Magnolia macrophylla* (Bigleaf Magnolia) — are prominent in most vegetation types, and species of Southern Appalachian affinity such as *Astilbe biternata* (Appalachian False Goat's-beard), *Convallaria pseudomajalis* (American Lily-of-the-valley), *Clethra acuminata* (Mountain Pepperbush), *Eubotrys recurva* (Mountain Fetterbush), *Eutrochium steelei* (Appalachian Joe-pye-weed), *Galax urceolata* (Galax), *Hexastylis arifolia* var. *ruthii* (Appalachian Little Brown Jug), *Rhododendron calendulaceum* (Flame Azalea), *Trillium sulcatum* (Southern Red Trillium), and *Veratrum parviflorum* (Mountain Bunchflower) are widespread components of the flora.

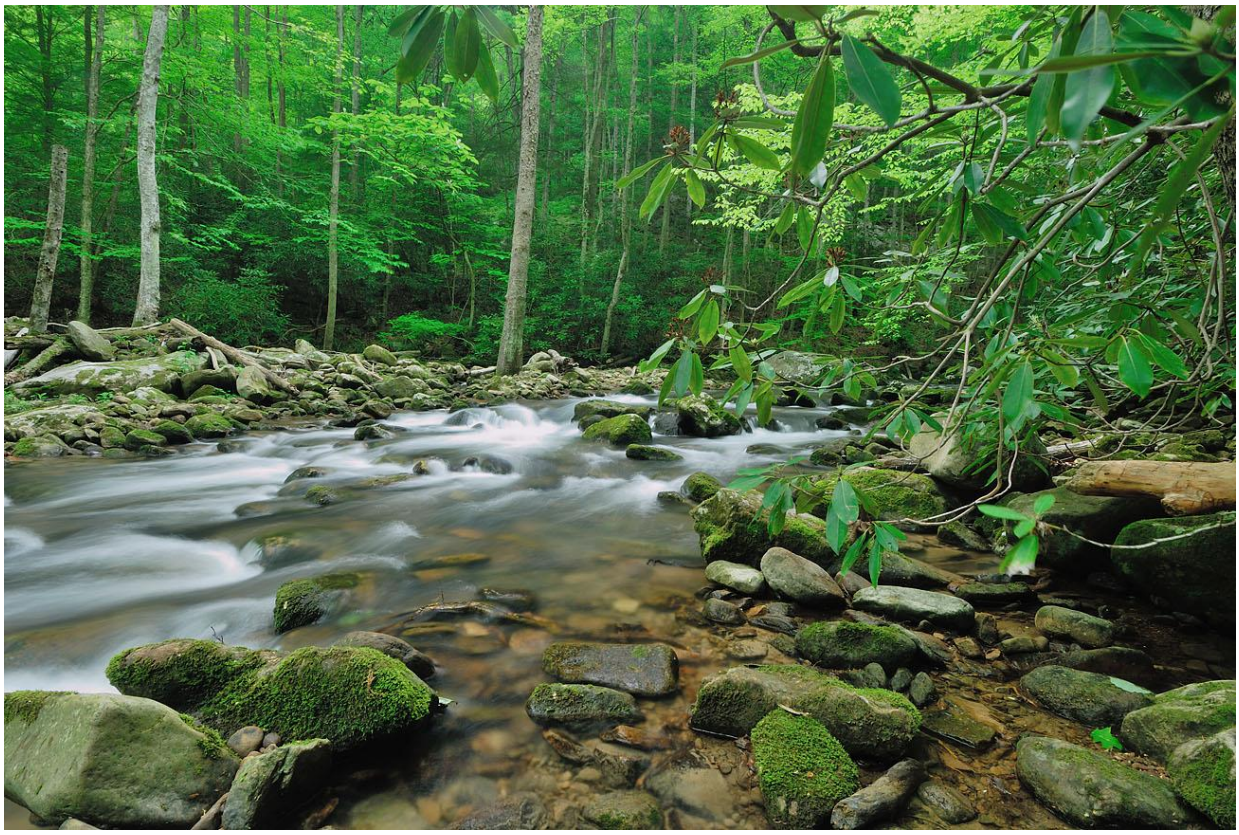

Fig. 13. Acidic cove forest along Little Stony Creek, Scott County. Photo © DCR-DNH, Gary P. Fleming.

The cove forests are divisible into two distinct ecological groups: acidic cove forests (Fig. 13), occurring on nutrient-poor soils originating mostly from sandstone colluvium and alluvium; and rich cove forests, occurring on base-rich soils weathered from limestone and other calcareous substrates. Acidic cove forests are characterized by stands of *Rhododendron maximum* (Great Rhododendron), which forms enormous evergreen shrub colonies beneath mixed overstories of *Liriodendron tulipifera* (Tulip-poplar), Cucumber-tree, *Fagus grandifolia* (American Beech), Eastern Hemlock, *Betula lenta* var. *lenta* (Sweet Birch), *Acer rubrum* (Red Maple), and various oaks. A variety of often sparse mesophytic ferns and herbs occurs in openings among the shrubs. Rich cove forests, by contrast, typically have a rather sparse shrub layer beneath a canopy dominated by more nutrient-demanding trees, especially *Acer saccharum*

(Sugar Maple), *Tilia americana* var. *heterophylla* (White Basswood), *Aesculus flava* (Yellow Buckeye), and *Carya cordiformis* (Bitternut Hickory). The herb layer of these forests is dense and exceedingly lush with spring ephemerals and colonial, nutrient-demanding forbs, including *Caulophyllum thalictroides* (Blue Cohosh), *Laportea canadensis* (Wood Nettle), *Hydrophyllum canadense* (Canada Waterleaf), *Hydrophyllum macrophyllum* (Hairy Waterleaf), *Impatiens pallida* (Yellow Jewelweed), *Trillium* spp. (trilliums), *Prosartes lanuginosa* (Yellow Mandarin), *Prosartes maculata* (Spotted Mandarin), *Dicentra canadensis* (Squirrel Corn), *Uvularia grandiflora* (Large-flowered Bellwort), *Delphinium tricorne* (Dwarf Larkspur), and many others.

On the drier ridge slopes and summits, species-poor oak/heath forests of *Quercus montana* (Chestnut Oak), other oaks, and ericaceous shrubs such as *Kalmia latifolia* (Mountain Laurel), *Eubotrys recurva* (Mountain Fetterbush), *Vaccinium* spp. (blueberries), and *Rhododendron catawbiense* (Catawba Rhododendron) are fairly common. On the driest, most fire-prone ridge spurs and sandstone-capped summits, oak/heath vegetation gives way to pine-oak/heath woodlands of *Pinus rigida* (Pitch Pine), *Pinus virginiana* (Virginia Pine), *Pinus echinata* (Shortleaf Pine), and ericaceous shrubs.

A number of natural communities associated with localized environmental conditions occur in the Cumberland Mountains. High-elevation habitats are sparse in the region, but Stone Mountain reaches 1287 m (4223 ft) at High Knob, and northern hardwood forests of Sugar Maple, American Beech, *Betula alleghaniensis* (Yellow Birch), and *Prunus serotina* var. *serotina* (Black Cherry) find suitable niches on a few high, north-facing slopes of this ridge. Mid-slope bands of the Greenbrier Limestone formation occur on Cliff Mountain, Cumberland Mountain, Little Stone Mountain, Powell Mountain, and other ridges, supporting distinctive dry-mesic and dry calcareous forests and woodlands. Some of the calciphilic species that are common in these community types include *Quercus muehlenbergii* (Chinquapin Oak), *Acer nigrum* (Black Maple), *Cercis canadensis* var. *canadensis* (Eastern Redbud), *Frangula caroliniana* (Carolina Buckthorn), *Helianthus hirsutus* (Hairy Sunflower), *Diarrhena americana* (Eastern Beakgrain), *Polymnia canadensis* (Whiteflowered Leafcup), *Heuchera longiflora* (Long-flowered Alumroot), *Solidago sphacelata* (Limestone Goldenrod), and *Carex purpurifera* (Limestone Purple Sedge). Rare natural communities of the Cumberland Mountains include acidic woodlands of *Pinus echinata* (Shortleaf Pine), *Quercus stellata* (Post Oak), and *Carya* spp. (hickories) on steeply sloping sandstone pavements; Appalachian bogs; spray cliffs; and sparsely vegetated cliff faces with grottoes supporting such characteristic “rock-house” specialties as *Heuchera parviflora* (Small-flowered Alumroot) and *Silene rotundifolia* (Sandstone Fire Pink).

Allegheny Mountains Section

The Allegheny Mountains section covers less than 1% of the state on the eastern flank of Allegheny Mountain along the west-central border with West Virginia. Ninety-six percent of the section in Virginia is forested, and 96% of the forests are of deciduous hardwoods; the remaining 4% represents local areas where *Picea rubens* (Red Spruce), *Tsuga canadensis* (Eastern Hemlock), or *Pinus* spp. (pines) are prevalent. About 0.1% of the area is classified as palustrine wetlands. Approximately 3% of the Allegheny Mountains has been developed in low-density residential areas, and 80% is in unfragmented blocks of natural lands with very high to outstanding ecological integrity (Weber 2007). The George Washington and Jefferson National Forests and a few small tracts of other public lands cover about 77% of the Allegheny Mountains. A total of 4374 ha (10,808 acres), or 11% of the area, consists of conservation lands protected for biodiversity.

Over most of its length in Virginia, the narrow band of this province supports montane mixed oak and oak-hickory forests, with smaller inclusions of cove forest (both acidic and rich) and dry oak/heath

forest. In the vicinity of Paddy Knob (elevation 1365 m/4477 ft) in Bath and Highland counties, there is a small area that lies above 1200 m (4000 ft), with patches of northern hardwood forest occupying sheltered slopes. However, much of the Paddy Knob area has been disturbed by clearing, grazing, and clear-cutting. The province broadens into a more extensive high-elevation area in the northwest corner of Highland County, where several ridge spurs exceed 1200 m (4000 ft) elevation. Although most of this area lies below 1200 m, its location adjacent to the highest portion of the Allegheny Mountains in West Virginia contributes to a dramatically cooler and wetter climate than in areas immediately to the east in Virginia. Second-growth northern hardwood forest (Fig. 14) of *Prunus serotina* var. *serotina* (Black Cherry), *Acer saccharum* (Sugar Maple), *Fagus grandifolia* (American Beech), *Betula alleghaniensis* (Yellow Birch), *B. lenta* var. *lenta* (Sweet Birch), *Quercus rubra* (Northern Red Oak), and Eastern Hemlock is the prevalent natural community throughout this highland landscape, with patches of Red Spruce forest occupying both the higher valley bottoms and ridgetops (Bailey and Ware 1990). Magnificent high-elevation cove forests of Yellow Birch and *Rhododendron maximum* (Great Rhododendron) line the valleys of Laurel Fork and other streams, while oak-dominated forests are generally confined to small patches on the warmest, south-facing slopes.

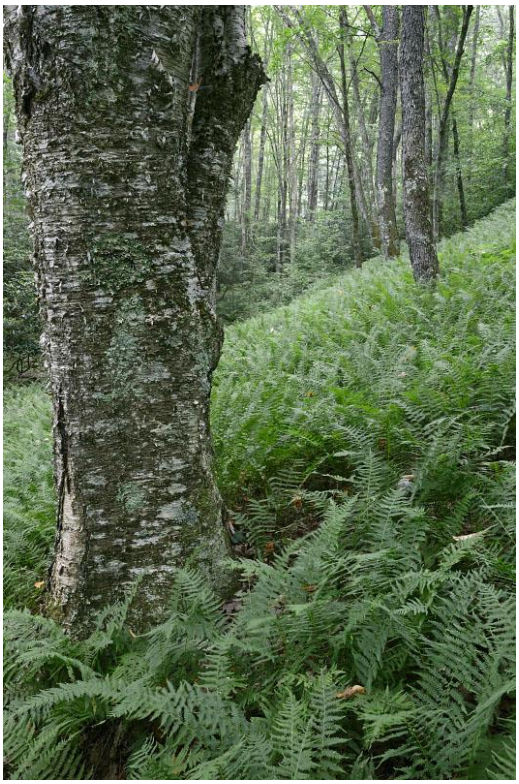

Fig. 14. Northern hardwood forest along Laurel Fork on Allegheny Mountain in Highland County. Photo © DCR-DNH, Gary P. Fleming.

Among the many species of northern affinity that abound throughout the Allegheny Mountain/Laurel Fork area of Highland County but rarely occur elsewhere in Virginia are *Dendrolycopodium dendroideum* (Prickly Tree-clubmoss), *Spinulum annotinum* (Stiff Clubmoss), *Cinna latifolia* (Slender Wood Reedgrass), *Milium effusum* var. *cisatlanticum,* (Tall Millet Grass), *Schizachne purpurascens* (Purple Oatgrass), *Carex arctata* (drooping woodland Sedge), and *Scirpus hattorianus* (Northern Bulrush).

The high-elevation valley floors of northwest Highland County contain stream headwaters with abundant groundwater seepage and two rare community types: a high-elevation seepage swamp co-dominated by Red Spruce, Eastern Hemlock, and Yellow Birch, and an Appalachian bog community containing many rare and localized herbaceous species such as *Solidago uliginosa* var. *uliginosa* (Bog Goldenrod), *Sparganium emersum* (Narrow-leaf Bur-reed), *Glyceria grandis* var. *grandis* (American Mannagrass), and *Epilobium leptophyllum* (Narrow-leaved Willowherb).

The Ridge and Valley Province

The Ridge and Valley is the most extensive of the Appalachian provinces in Virginia, covering about 25% of the state. Forests cover 63% of the Virginia Ridge and Valley, and 88% of the forests are of deciduous hardwoods; the remainder is mixed or evergreen forest in which *Pinus* spp. (pines), *Tsuga canadensis* (Eastern Hemlock), and, rarely, *Picea rubens* (Red Spruce) are prominent components. Palustrine wetlands cover less than 0.1% of the area. Much of the 37% of the province that is not forested is devoted to cattle grazing and production of feed grains. About 8% of the Ridge and Valley is developed, with a number of medium-sized urban areas concentrated around valley cities such as Winchester,

Harrisonburg, Staunton, Lexington, Blacksburg, and Abingdon. Thirty-four percent of the province is in unfragmented blocks of natural lands with very high to outstanding ecological integrity (Weber 2007). Public lands, primarily the George Washington and Jefferson National Forests, cover about 24% of the province. Only 109,916 ha (271,607 acres), or 4.3% of the Ridge and Valley, consists of conservation lands protected for biodiversity.

The topographic, floristic, and natural community diversity of the Ridge and Valley generally decreases from south to north through the state. The southwestern Virginia portion, lying southwest of Roanoke, contains the largest areas of high-elevation terrain and carbonate-rock (limestone and dolostone) geology in the province. As in the Cumberland Mountains, Southern Appalachian taxa and community types are characteristic of the southwestern Virginia Ridge and Valley. Between the New River and the Roanoke River is a transition zone in which Southern Appalachian vegetation types give way to floristically less diverse communities typical of the Central Appalachian region. The northern two-thirds of the Virginia Ridge and Valley contain extensive lower-slope areas, secondary ridges, and knobs underlain by Ordovician, Silurian, and Devonian shales. The northern part of the province is one of the driest areas of the state, as the high Allegheny Mountains to the west capture much of the precipitation of eastward-moving fronts and air masses.

Fig. 15. Spruce forest with *Rhododendron maximum* (Great Rhododendron) understory at Beartown, Clinch Mountain, Tazewell County. Photo © DCR-DNH, Gary P. Fleming.

Forested ridges of the southwest Virginia Ridge and Valley are dominated by various oak/heath and montane mixed oak forests in which *Quercus montana* (Chestnut Oak) is a characteristic species in mixture with other oaks and mesophytic hardwoods. On the higher ridgetops (generally above 1060 m/3500 ft elevation), Chestnut Oak drops out, and forests dominated by *Q. rubra* (Northern Red Oak) form large patches (Stephenson and Adams 1989). Both acidic and rich cove forests similar in composition to those of the Cumberland Mountains are common on sheltered slopes, in hollows, and along stream valleys. Stands of northern hardwood forest are scattered at high elevations of Clinch Mountain in several counties and Salt Pond Mountain in Giles County. Forests of Red Spruce (Fig. 15) and Red Spruce–northern hardwood mixtures are confined to the two Clinch Mountain Beartowns, which reach elevations of 1436 m (4710 ft) and 1429 m (4689 ft) in Russell and Tazewell counties, respectively. This suite of forest communities is generally distributed along topographic-moisture and elevation gradients, with less influence by soil nutrients due to the generally acidic character of the parent bedrock on most ridges (Lawrence et al. 1999).

Vegetation of the northern part of the Ridge and Valley is dominated by dry oak/heath forests of Chestnut Oak, *Quercus coccinea* (Scarlet Oak), *Quercus velutina* (Black Oak), and *Quercus alba* (White Oak), with variable mixtures of *Kalmia latifolia* (Mountain Laurel), *Gaylussacia baccata* (Black Huckleberry), *Vaccinium* spp. (blueberries), *Menziesia pilosa* (Minniebush), *Pieris floribunda* (Evergreen Mountain Fetterbush), and other ericads forming thick shrub layers. On sandstone cliffs and xeric ridge

spurs, constant drought and frequent historical fires have fostered the development of extensive pine–oak/heath forests and woodlands composed of fire-tolerant and fire-dependent species such as *Pinus rigida* (Pitch Pine), *P. pungens* (Table Mountain Pine), *Quercus ilicifolia* (Bear Oak), and inflammable heaths. Many ridges also contain large talus fields of deeply piled and minimally weathered sandstone boulders vegetated mostly with lichens such as *Lasallia papulosa, Lasallia pensylvanica, Dimelaena oreina,* and *Umbilicaria muhlenbergii.* On the more weathered edges of such block fields, as well as on talus where organic matter has accumulated, woodlands of gnarled and stunted *Betula lenta* var. *lenta* (Sweet Birch) have pioneered the slow reclamation by vascular plants of these habitats, which are relicts of periglacial freeze-thaw processes.

The boulderfields and floristically depauperate oak and oak-pine vegetation types are nearly ubiquitous on dry ridges underlain by various sedimentary rocks, broken only in areas where the more calcareous sandstone, shale, or siltstone formations prevail. These somewhat more calcareous substrates support species-rich montane oak-hickory forests, of which *Carya* spp. (hickories), *Fraxinus americana* (White Ash), *Ostrya virginiana* (Eastern Hop-hornbeam), and a great diversity of nonericaceous shrubs and shade-tolerant forbs and graminoids are important components. Northern Red Oak forests and northern hardwood forests are quite local and inextensive in the northern Ridge and Valley but do occur on portions of Shenandoah Mountain and other high ridges that reach or approach 1200 m (4000 ft) elevation. Red Spruce stands are confined to very small areas on the summits of Jack Mountain (Sounding Knob) in Highland County at 1295 m (4250 ft) elevation and Shenandoah Mountain in Rockingham County at 1100 m (3600 ft) elevation.

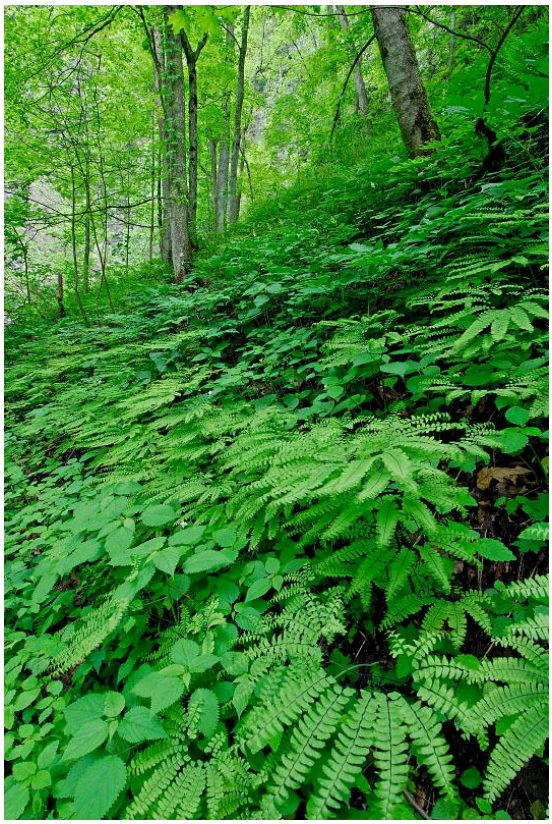

Fig. 16. Rich cove forest, Natural Tunnel State Park, Scott County. Photo © DCR-DNH, Gary P. Fleming.

Low-elevation shale ridges and knobs are prominent features of the central and northern parts of the Virginia Ridge and Valley, and their vegetation cover varies somewhat from the usual provincial patterns. Although oak/heath and pineoak/ heath types are common, acidic oak-hickory forests occupy large areas with slightly more mesic and fertile soils. These oak-hickory forests differ from those on the higher ridges in that they contain a greater proportion of White Oak, as well as *Cornus florida* (Flowering Dogwood), *Cercis canadensis* var. *canadensis* (Eastern Redbud), and numerous herbaceous plants that are restricted to lower elevations. Also forming extensive stands in the shale districts are Eastern White Pine–hardwood forests in which *Pinus strobus* (Eastern White Pine) shares dominance with oaks. This community type is clearly increasing and replacing oak and oak-hickory stands throughout the Ridge and Valley with the demise of fire, which readily kills the thin-barked White Pine saplings.

Throughout the Ridge and Valley, vegetation of valleys, lower ridge slopes, and knobs underlain by limestone and dolostone has been extensively altered by clearing and use of these fertile sites for agriculture and grazing. However, patches of the natural calciphilic vegetation

remain in some areas, the largest of which are the more resistant dolostone hill complexes such as the Clinch River/Knobs region in far southwestern Virginia and the Pedlar Hills east and southeast of Blacksburg. Cove forests in such areas are extraordinarily rich (Fig. 16) and contain obligate calciphiles and low-elevation species not found in the mountain coves; examples include *Staphylea trifolia* (Bladdernut), *Jeffersonia diphylla* (Twinleaf), *Trillium sessile* (Toadshade), *Cystopteris bulbifera* (Bulblet Fern), *Carex jamesii* (James's Sedge), and *Polemonium reptans* var. *reptans* (Spreading Jacob's Ladder). Dry-mesic calcareous forests of *Acer saccharum* (Sugar Maple), *Acer nigrum* (Black Maple), oaks, and hickories cover the average slopes, giving way to dry calcareous forests and woodlands on the warmer aspects and thin-soiled rocky slopes. The latter, which vary from open forests to very open, stunted woodlands of *Quercus muehlenbergii* (Chinquapin Oak), *Quercus shumardii* (Shumard Oak), *Juniperus virginiana* var. *virginiana* (Eastern Redcedar), White Ash, Eastern Redbud, *Frangula caroliniana* (Carolina Buckthorn), and *Rhus aromatica* var. *aromatica* (Fragrant Sumac), constitute one of Virginia's most species-rich vegetation types because of their high diversity of herbaceous plants. In addition to calciphiles, examples of dry woodlands on dolostone contain *Echinacea laevigata* (Smooth Coneflower), *Parthenium auriculatum* (Glade Wild Quinine), *Packera paupercula* var. *appalachiana* (Appalachian Ragwort), and several other diagnostic species that behave as obligate magnesiophiles, at least in this region.

The Ridge and Valley is well endowed with rare natural communities of specialized environmental settings. Conditions on the driest southwest-facing slopes, where exposed and shallow limestone or dolostone bedrock severely limit moisture and root penetration, can permanently retard the establishment of woody vegetation and support drought-tolerant herbaceous vegetation. Dominated by warm-season bunch-grasses such as *Schizachyrium scoparium* var. *scoparium* (Little Bluestem), *Andropogon gerardii* (Big Bluestem), *Sorghastrum nutans* (Indian Grass), and *Bouteloua curtipendula* var. *curtipendula* (Side-oats Grama), these Appalachian limestone/dolostone barrens (Ludwig 1999) are clearly related to the true prairie vegetation of the Midwest and, in fact, contain a number of species that are disjunct from more western ranges and habitats. Other rare natural communities of calcareous upland habitats in the province include rocky slope forests, with *Thuja occidentalis* (Northern Whitecedar) co-dominating among Eastern Hemlock, Eastern White Pine, and calciphilic hardwoods, and calcareous cliffs, dominated by Northern Whitecedar scrub or sparse lithophytic herbs.

Fig. 17. *Eriogonum allenii* (Shale Barren Wild Buckwheat) blooming on a Massanutten Mountain shale barren, Shenandoah County. Photo © DCR-DNH, Gary P. Fleming.

Shale barrens (Platt 1951; Braunschweig et al. 1999; Fig. 17) are probably the best known Central Appalachian outcrop, or barren, community, being essentially endemic to the Ridge and Valley from south-central Pennsylvania through western Maryland and northeastern West Virginia to Craig and Montgomery counties in Virginia. Since the mid-1990s, several barrens have been discovered by Virginia Natural Heritage ecologists on Cambrian metashales of the Harpers Formation in the central Virginia Blue Ridge. These barrens have proved environmentally and floristically indistinguishable from classic barrens of the Ridge and Valley Paleozoic shales. Most shale barrens occur on very

steep side slopes with thick but relatively weak shale strata that are continually undercut by a subtending stream. Less common variants, occurring on steep spur ridge crests and other stabilized shale slopes, are sometimes referred to as shale ridge balds or shale ridge prairies. Soil consisting of deep, exposed, rapidly eroding shale fragments (channery) subject to intense insolation is an important edaphic control in these habitats. Shale-barren vegetation is somewhat variable but generally characterized by very open woodlands of stunted trees, especially *Pinus virginiana* (Virginia Pine) and Chestnut Oak, with a suite of typical xerophytic grasses and forbs, shale-barren endemics, and near-endemics forming a sparse herb layer. Many of the most noteworthy species of shale barrens are disjunct from further west or have their closest relatives in the West (Keener 1983). Six strict shale-barren endemics – *Boechera serotina* (Shale Barren Rock Cress), *Clematis albicoma* (White-haired Leatherflower), *Clematis viticaulis* (Millboro Leatherflower; endemic to Virginia), *Eriogonum allenii* (Shale Barren Wild Buckwheat; Fig. 17), *Oenothera argillicola* (Shale Barren Evening-primrose), *Packera antennariifolia* (Shale Barren Ragwort) – along with several near-endemics, are prominent members of these natural communities.

Sandstone side slopes in the Ridge and Valley also produce localized acidic woodlands and barrens where steeply dipping pavements of Silurian strata have been exposed through weathering. Depending on the calcium content of their outcropping sandstone, these woodlands vary from Virginia Pine and Chestnut Oak woodlands with sparse ericads and acidophilic rock herbs, to more diverse woodlands with *Quercus stellata* (Post Oak), *Q. marilandica* var. *marilandica* (Blackjack Oak), *Carya glabra* (Pignut Hickory), *Juniperus virginiana* var. *virginiana* (Eastern Redcedar), and patches of warm-season grasses and subcalcareous forbs.

Although wetlands cover an insignificant percentage of the Ridge and Valley, they include some of the rarest small-patch vegetation types in the state. Seepage swamps, Appalachian bogs, calcareous fens, calcareous spring marshes, and wet prairies all fall into this category, but two other of the region's rare wetlands are particularly deserving of mention. Montane depression wetlands include natural seasonal ponds of ridge tops, slope benches, and valley floor alluvial fans that have formed through the sagging of landslide masses or solution of underlying bedrock. These exceptionally rare wetlands support unique shrub and herbaceous communities containing a number of globally and state-rare plants.

A special group of depression wetlands, known as the Shenandoah Valley sinkhole ponds (Fleming and Van Alstine 1999; Fig. 18), occurs on deep alluvial fans in Augusta, Rockingham, and Page counties that were deposited over carbonate rocks along the foot of the Blue Ridge during the Pleistocene. Solution of the underlying dolostone and reworking of surficial material by streams have resulted in the development of numerous natural ponds varying in size from less than 0.04 ha (0.1 acre) to more than 1.5 ha (3.7 acres). The extraordinary combination of solution features overlain by acidic colluvium and alluvium from metasedimentary rocks of the Blue Ridge has created edaphic conditions similar to those of certain Coastal Plain wetlands. Pollen profiles from bottom sediments in two Augusta County ponds demonstrate the continuous existence of wetlands over the past 15,000 years (Craig 1969). Most ponds in the Shenandoah Valley complexes experience seasonally fluctuating water levels. Clay weathered from metasiltstone and phyllite alluvium impedes drainage, but most ponds draw down as the growing season progresses and evapotranspiration increases. The hydroperiods of many ponds are irregular and unpredictable, varying with the size and depth of the basin, the degree of shading, and local groundwater conditions. Soils vary from organic to clay-rich; their low pH, calcium, and magnesium levels, combined with very high aluminum levels, have been hypothesized as a condition that impairs assimilation of macronutrients by plants (J.S. Knox 1997). Three rare and apparently endemic natural community types occur in the Shenandoah Valley ponds, and their flora is notable for its high

percentage of rarities and of disjuncts with both Coastal Plain and northern affinities (Harvill 1973, 1992).

Fig. 18. *Helenium virginicum* (Virginia Sneezeweed) is endemic to sinkhole ponds in the Shenandoah Valley and Missouri. Photo © DCR-DNH, Gary P. Fleming.

Finally, a small valley in southwestern Virginia near Saltville in Smyth County harbors perhaps the rarest of all wetland habitats and plant communities in Virginia. Here, several basins flooded by groundwater discharging through Mississippian-aged salt deposits support inland salt marshes (Ogle 1981) dominated by *Bolboschoenus robustus* (Saltmarsh Bulrush) and *Juncus gerardii* (Blackfoot Rush), species disjunct from the Atlantic Coastal Plain estuaries. Several other halophytic disjuncts have been found at this site, which has been disturbed historically by industrial salt mining, hydrologic alterations, and grazing.

The Blue Ridge

The Blue Ridge Mountains in western Virginia cover about 11% of the state. Seventy-four percent of the province in Virginia is forested, and 88% of the forests are of deciduous hardwoods; the remainder is mixed or evergreen forests in which *Pinus* spp. (pines), *Tsuga canadensis* (Eastern Hemlock), and *Picea rubens* (Red Spruce) are prominent components. Approximately 0.1% of the area is classified as palustrine wetlands. Much of the 7% of the province that is developed is concentrated around Roanoke and several small cities in the Shenandoah Valley at the western foot of the ridge. Thirty-eight percent of the Blue Ridge is in unfragmented blocks of natural lands (Fig. 19) with very high to outstanding ecological integrity (Weber 2007). Public lands, including the George Washington and Jefferson National Forests and Shenandoah National Park, constitute about 27% of the province. A total of 111,976 ha (276,697 acres), or 9.8% of the Blue Ridge, is in conservation lands protected for biodiversity.

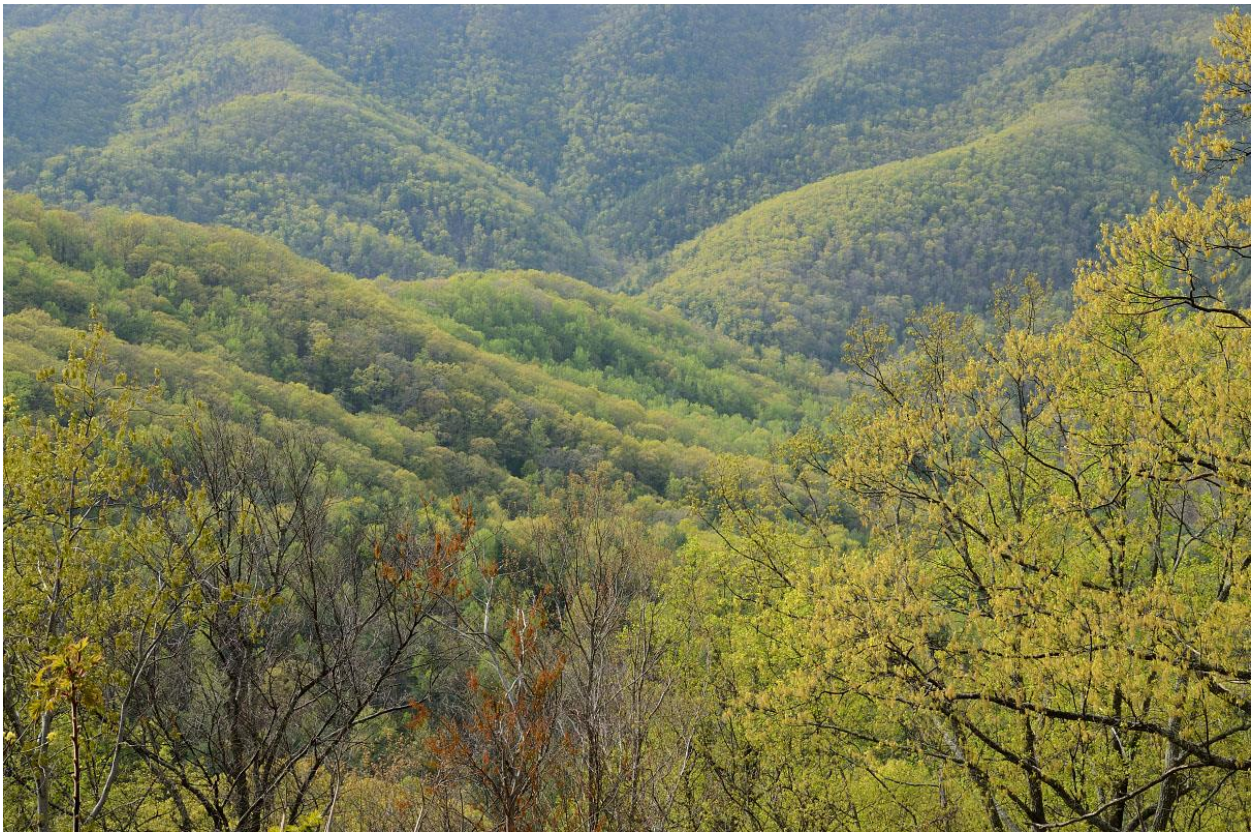

Fig. 19. The Blue Ridge has the highest percentage of unfragmented natural lands, public lands, and conservation lands managed for biodiversity among Virginia's four largest provinces. Photo © Gary P. Fleming.

Much like the Ridge and Valley, the Blue Ridge in Virginia changes in topographic character and decreases in floristic and natural community diversity from south to north. In this province, however, the change is more abrupt and strongly correlated with the great geomorphologic differences noted earlier between the Southern Blue Ridge, south of Roanoke, and the much lower and narrower section to the north. Since these sections differ in many ways, they will be discussed separately.

Southern Blue Ridge Section

Much of the rolling, Southern Blue Ridge plateau has been cleared or supports disturbed early-successional forests in which *Pinus strobus* (White Pine) is a prevalent tree. Cattle pastures are ubiquitous, but some fields are used for hay production. On the more heavily forested eastern escarpment and prominent ridges like Buffalo Mountain and the Iron Mountains, the vegetation is similar to that of the southwestern Virginia Ridge and Valley, with a diverse mixture of community types of strong Southern Appalachian affinity. Northern hardwood forests appear on north slopes at the highest elevations (above 1200 m or 4000 ft) of the Iron Mountains, Buck Mountain, and Point Lookout Mountain, becoming the prevalent community above 1070 m (3500 ft) over the entire Balsam Mountains massif in Smyth, Grayson, and Washington counties. This forest has a more southern flavor than the northern hardwood forests of the Ridge and Valley, with Southern Appalachian endemics such as *Aesculus flava* (Yellow Buckeye), *Magnolia fraseri* (Fraser Magnolia), *Ageratina altissima* var. *roanensis* (Appalachian White Snakeroot), *Eurybia chlorolepis* (Mountain Wood Aster), *Eutrochium steelei* (Appalachian Joe-pye-weed), and *Nabalus roanensis* (Roan Mountain Rattlesnake-root) being important components.

Fig. 20. The fern- and bryophyte-covered floor of a red spruce forest at 1615 m (5300 ft) elevation on Whitetop, Smyth County. Photo © DCR-DNH, Gary P. Fleming.

Virginia's most extensive stands of Red Spruce and spruce-fir forests occupy the highest elevations of the Balsam Mountains, on Whitetop (1682 m/5520 ft) and Mount Rogers (1746 m/5729 ft) but are virtually all second-growth (Adams and Stephenson 1991). The Southern Appalachian *Abies fraseri* (Fraser Fir) dominates above 1650 m (5400 ft) on Mount Rogers, with Red Spruce forests extending down to around 1500 m (5000 ft) (Stephenson and Adams 1984). Fraser Fir is absent on Whitetop, from which it was likely extirpated during the Hypsithermal period (Ware 1999). Instead, forests dominated by Red Spruce (Fig. 20) or a spruce–northern hardwoods mixture cover much of the area above 1500 m (5000 ft), extending somewhat lower in a few places. Joining *Vaccinium erythrocarpum* (Southern Mountain Cranberry) and other Southern Appalachian endemics in these forests are familiar species of northern latitudes and boreal forests — e.g., *Viburnum lantanoides* (Hobblebush), *Dryopteris campyloptera* (Mountain Wood Fern), *Cinna latifolia* (Slender Wood Reedgrass), *Clintonia borealis* (Bluebead Lily), and *Oxalis montana* (White Wood-sorrel) — which must have had wider distributions in Virginia during the late Wisconsin and early Holocene but are now isolated in disjunct high-elevation enclaves that meet their climatic requirements. Sadly, these forests are now stressed by the insect pathogen balsam woolly adelgid (*Adelges piceae*), as well as air pollution and acid rain, to such an extent in some areas that many of the larger firs and spruces are dead or exhibiting die-back symptoms (White et al. 1993).

Fig. 21. Southern Appalachian Grassy Bald on Whitetop, Grayson County. Photo © DCR-DNH, Gary P. Fleming.

Smaller-patch upland communities of high Southern Blue Ridge habitats include high-elevation cove forests, high-elevation boulderfield forests, high-elevation mafic barrens, and Southern Appalachian shrub and grassy balds. Though disturbed and enlarged by much human activity, the best example of the latter occurs on the upper south and west slopes of Whitetop (Fig. 21). High-elevation mafic barrens are known only from Buffalo Mountain in Virginia and from Bluff Mountain and Mount Jefferson in North Carolina. Several rare, small-patch wetland communities are also found in the province. In the Balsam Mountains, a high-elevation Appalachian bog community occurs in headwater valleys of the Wilburn Ridge–Pine Mountain area, harboring *Ilex collina* (Long-stalked Holly) and several other rare species. In Grayson County, a portion of the plateau known as the Glades is underlain by a suite of ultramafic rocks that produce strongly acidic soils with low calcium-to-magnesium ratios. Here, over a

long period of human disturbance, extraordinarily rare mafic fen and ultramafic woodland vegetation has managed to survive in small patches. The latter consists of open stands of *Pinus rigida* (Pitch Pine), *P. strobus* (Eastern White Pine), and *Quercus stellata* (Post Oak), beneath which grows an enigmatic herbaceous assemblage of *Andropogon gerardii* (Big Bluestem), *Schizachyrium scoparium* var. *scoparium* (Little Bluestem), *Packera paupercula* var. *paupercula* (Balsam Ragwort), *Thalictrum revolutum* (Skunk Meadow-rue), *Stenanthium leimanthoides* (Pinebarrens Death-camas), and others. Mafic fens in the Glades (Fig. 22) include both low-statured shrublands of *Alnus serrulata* (Smooth Alder) with low herbaceous vegetation and taller, more diverse shrublands with coarser herbaceous growth. Diagnostic species of this vegetation include *Vaccinium macrocarpon* (Large Cranberry), *Sanguisorba canadensis* (Canada Burnet), *Helenium brevifolium* (Short-leaf Sneezeweed), *Parnassia grandifolia* (Bigleaf Grass-of-Parnassus), *Solidago uliginosa* var. *uliginosa* (Bog Goldenrod), *Scirpus expansus* (Woodland Bulrush), and *Calamagrostis canadensis* var. *canadensis* (Bluejoint).

Fig. 22. Mafic fen dominated by *Sanguisorba canadensis* (Canadian burnet) at The Glades, Grayson County. Photo © DCR-DNH, Gary P. Fleming.

Northern Blue Ridge Section

The northern section of the Blue Ridge is a relatively narrow, irregularly weathered series of peaks that only occasionally exceed 1200 m (4000 ft) elevation and therefore lack any substantial high-elevation areas. Attenuated northern hardwood and hemlock–northern hardwood forests dominated mostly by *Betula alleghaniensis* (Yellow Birch) occupy sheltered north slopes and deep ravines only at the highest elevations. Northern Red Oak forests are more extensive on broad ridge crests and brows above about 900 m (3000 ft) elevation.

The western flank of the Northern Blue Ridge is underlain by siliciclastic metasedimentary rocks — Cambrian quartzites, metasiltstones, and phyllites that are similar to and only slightly older than the acidic Paleozoic rocks of the Ridge and Valley. Topography and vegetation of the western flank are essentially similar to those of the Ridge and Valley strike ridges, with dry oak/heath, pine-oak/heath, and acidic boulderfield vegetation prevalent. The acidic cove forests of this area differ considerably from those of the Southern Blue Ridge and Ridge and Valley in that *Rhododendron maximum* (Great Rhododendron), for reasons that are not clear, becomes infrequent to rare on the Blue Ridge north of

Roanoke. In some central Blue Ridge coves, *Rhododendron catawbiense* (Catawba Rhododendron), normally a plant of drier habitats, moves downslope along with *Kalmia latifolia* (Mountain Laurel) to replace Great Rhododendron as a typical evergreen shrub of the mesophytic forest.

Fig. 23. Rich montane oak-hickory forest on metabasalt, Shenandoah National Park, Greene County. Photo © DCR-DNH, Gary P. Fleming.

Except on its metasedimentary western flank, the Northern Blue Ridge is mostly mantled with base-rich soils and rocks weathered from underlying metabasalt (greenstone) and calc-alkaline granites and gneisses. Mesophytic, species-rich montane oak-hickory forests cover large areas, interspersed with hollows supporting rich cove forests of *Liriodendron tulipifera* (Tulip-poplar), *Tilia americana* var. *americana* (American Basswood) and *Tilia americana* var. *heterophylla* (White Basswood), *Fraxinus americana* (White Ash), *Acer saccharum* (Sugar Maple), *Carya cordiformis* (Bitternut Hickory), *Ulmus rubra* (Slippery Elm), and a dense, nutrient-demanding herb flora (Johnson and Ware 1982). *Quercus rubra* (Northern Red Oak) is the most characteristic tree of the rich oak-hickory forests (Fig. 23), usually in mixed stands with *Carya ovalis* (Red Hickory), *Carya ovata* (Shagbark Hickory), *Quercus alba* (White Oak), and White Ash. Beneath the trees, *Actaea racemosa* (Common Black Cohosh), *Thalictrum coriaceum* (Appalachian Meadow-rue), *Collinsonia canadensis* (Richweed), and other colonial forbs patch-dominate herb layers that can rival that of the rich cove forests in density and luxuriance.

Several rare community types are associated with or endemic to the basic rocks of the Northern Blue Ridge. High-elevation areas in this province produce some of Virginia's best examples of high-elevation boulderfield woodlands dominated by Yellow Birch, *Sorbus americana* (Mountain-ash), and *Polypodium appalachianum* (Appalachian Rockcap Fern), and the only known examples of high-elevation greenstone barrens and mafic nonvascular boulderfields. High-elevation greenstone barrens contain a patch mosaic of shrubs, herbaceous vegetation, and lichen-covered rock on exposed outcrops that are blasted by severe winds, low temperatures, and ice during the winter and subject to extreme insolation and drought during the summer. Diagnostic species of the community include a curious mix of widespread, Appalachian, and northern taxa, including *Physocarpus opulifolius* var. *opulifolius* (Eastern Ninebark), *Diervilla lonicera* (Northern Bush-honeysuckle), *Avenella flexuosa* (Wavy Hairgrass), *Solidago randii* (Rand's Goldenrod), *Hydatica petiolaris* (Cliff Saxifrage), and *Hylotelephium telephioides* (Allegheny Stonecrop). Several long-range boreal disjuncts found in patches of this community are no doubt Pleistocene relicts, including *Sibbaldia tridentata* (Three-toothed Cinquefoil), *Juncus trifidus* (Highland Rush), *Conioselinum chinense* (Hemlock Parsley), *Huperzia appressa* (Appalachian Fir Clubmoss), and *Trisetum spicatum* (Alpine Oatgrass). Characteristic lichens of the few known high-elevation greenstone nonvascular boulderfields (Fig. 24) include *Stereocaulon glaucescens, Lasallia papulosa, Chrysothrix chlorina, Usnea halei, Aspicilia cinerea, Diploschistes scruposus, Porpidia* spp., *Rhizoplaca subdiscrepens,* and numerous other crusts. Geographically isolated boreal-alpine lichen species that are present on these boulderfields include *Cladonia coccifera, Melanelia stygia, Microcalicium arenarium, Parmelia omphaloides, Porpidia tuberculosa, Rhizocarpon geographicum,* and *Umbilicaria caroliniana.*

Fig. 24. High-elevation metabasalt boulderfield dominated by lichens, some of them boreal-alpine species disjunct in Virginia. Shenandoah National Park, Page County. Photo © DCR-DNH, Gary P. Fleming.

At lower elevations of the Northern Blue Ridge, xerophytic vegetation occurring on south- or southwest-facing mid-slope outcrops of metabasalt and granitic rocks is somewhat akin to that of the calcareous woodlands and barrens of the Ridge and Valley. Central Appalachian basic woodlands (so named for their affiliation with basic rocks) are stunted, open stands of White Ash, *Carya glabra* (Pignut Hickory), and *Juniperus virginiana* var. *virginiana* (Eastern Redcedar), under which grows a species-rich flora of dry-site shrubs, grasses, and forbs. The characteristic species of these woodlands include *Rhus aomatica* var. *aromatica* (Fragrant Sumac), *Muhlenbergia sobolifera* (Rock Muhly), *Elymus hystrix* (Bottlebrush Grass), *Solidago ulmifolia* (Elm-leaf Goldenrod), *Phacelia dubia* var. *dubia* (Appalachian Phacelia), *Allium cernuum* (Nodding Onion), and *Pycnanthemum incanum* var. *incanum* (Hoary Mountain-mint). On the largest outcrops, woody species are greatly reduced, and mostly herbaceous barrens of *Schizachyrium scoparium* var. *scoparium* (Little Bluestem), *Carex pensylvanica* (Pennsylvania Sedge), *Sorghastrum nutans* (Indian Grass), *Sporobolus clandestinus* (Rough Dropseed), *Muhlenbergia capillaris* (Long-awn Hairgrass), *Cheilanthes lanosa* (Hairy Lip Fern), and numerous xerophytic forbs have developed. *Phemeranthus teretifolius* (Roundleaf Fameflower), *Polygonum tenue* (Slender Knotweed), *Trichostema brachiatum* (False Pennyroyal), and *Woodsia ilvensis* (Rusty Woodsia) are among the typical lithophytic species found in rock crevices and bryophyte mats of these communities.

Mafic fen vegetation similar to that of the Southern Blue Ridge is known from several small wetland areas near Big Meadows in Shenandoah National Park. The Northern Blue Ridge is also the stronghold in the state for the Central Appalachian basic seepage swamp (Fig. 25), a saturated forest community that develops only in large headwater seeps over mafic and calcareous rocks. This vegetation type is similar to other seepage swamps but has a larger component of characteristic nutrient-demanding hydrophytes. Among the latter, *Fraxinus nigra* (Black Ash), *Caltha palustris* (Marsh Marigold), *Carex*

bromoides ssp. *bromoides* (Common Brome Sedge), *Micranthes pensylvanica* (Swamp Saxifrage), and the rare *Poa paludigena* (Bog Bluegrass) are particularly diagnostic of the community.

Fig. 25. Central Appalachian Basic Seepage Swamp in a Northern Blue Ridge stream-head. G.R. Thompson Wildlife Management Area, Fauquier County. Photo © DCR-DNH, Gary P. Fleming.

The Piedmont

The Piedmont is Virginia's largest physiographic province, comprising about 39% of the state. Approximately 3% of the region is classified as palustrine wetlands. Sixty-one percent is forested, including 59% of the uplands and 63% of the wetlands. Among the upland forests, 68% are deciduous hardwood stands, while 32% are evergreen and mixed forests that include *Pinus taeda* (Loblolly Pine) plantations and natural pine-hardwood successional stands. About 8% of the Piedmont is developed, including large urban areas around Washington, D.C., Fredericksburg, Richmond, and Lynchburg. Only 9% of the province consists of unfragmented blocks of natural lands with very high to outstanding ecological integrity (Weber 2007). Public lands cover less than 3% of the province. Only 38,116 ha (94,186 acres) of the Piedmont, or 0.9%, is in conservation lands protected for biodiversity.

The vegetation of the Piedmont Plateau has been severely altered by a long history of clearing, agriculture, logging, and other anthropogenic disturbances. There is some evidence from the writings of early explorers that open, savanna-like woodlands and grasslands occupied parts of the Piedmont at the beginning of European settlement (Maxwell 1910; Allard and Leonard 1962; Brown 2000). Presumably, both natural fires and fires deliberately ignited by Indians to drive game and clear land played important roles in maintaining savannas and grasslands pre-settlement. Few traces of such vegetation remain today except in managed preserves and military base training areas subject to frequent prescribed or incendiary fires. Outside of the increasingly large urban and suburban areas, the province has a patchwork of secondary forests, pastures, and fields used for the production of feed grains or tobacco.

Most Piedmont forests have a history of repeated cutting or have regenerated on former agricultural lands, some of which were abandoned more than 150 years ago. Recently disturbed Piedmont forests tend to have a large component of pines and shade-intolerant hardwoods. In the northern Piedmont, *Pinus virginiana* (Virginia Pine) and *Liriodendron tulipifera* (Tulip-poplar) are prevalent early-successional trees. In the central and southern Piedmont, *Pinus echinata* (Shortleaf Pine) and *Liquidambar styraciflua* (Sweetgum) increase greatly in abundance, along with Loblolly Pine in the eastern part of the province.

Fig. 26. Mixed oak/heath forest on a dry, infertile upland in the southern Piedmont of Prince Edward County. Photo © DCR-DNH, Gary P. Fleming.

The composition of more mature hardwood forest communities varies with soils and topography. Upland forests of the western monadnocks resemble those of the Blue Ridge. Over most of the Piedmont, dry, nutrient-poor soils support oak/heath forests (Fig. 26), while more mesic and basic upland soils usually support oak-hickory forests. *Quercus alba* (White Oak) is a ubiquitous dominant in both groups, sometimes occurring in nearly pure stands but more often in mixtures with other oaks. The latter tend to sort out along a moisture gradient, with *Q. rubra* (Northern Red Oak) and *Q. velutina* (Black Oak) most important on submesic sites; *Q. montana* (Chestnut Oak), *Q. coccinea* (Scarlet Oak), and *Q. falcata* (Southern Red Oak) most important on drier sites; and *Q. stellata* (Post Oak) and *Q. marilandica* var. *marilandica* (Blackjack Oak) important only on the most xeric, drought-prone sites, especially those with impermeable hardpan soils.

Positive correlations between the abundance of *Carya* spp. (hickories), overall species richness, higher soil pH, and exchangeable base cation levels have been demonstrated by several Piedmont studies (Farrell and Ware 1991; Ware 1992; Cole and Ware 1997; Fleming 2002, 2007). Oak/heath forests typically have few hickories, few herbaceous species, and an understory consisting mainly of *Acer rubrum* (Red Maple), *Nyssa sylvatica* (Black Gum), and deciduous ericads such as *Vaccinium pallidum* (Early Lowbush Blueberry) and *Gaylussacia baccata* (Black Huckleberry). At the other end of the gradient, basic oak-hickory forests are restricted to sites underlain by mafic rocks such as amphibolite, metabasalt, diabase, or gabbro; usually have overstories with a major hickory component; have few or no ericaceous shrubs; and have a much greater diversity of understory and herbaceous species. Plants diagnostic of basic oak-hickory forests in the Piedmont include *Carya ovata* (Shagbark Hickory), *Fraxinus americana* (White Ash), *Cercis canadensis* var. *canadensis* (Eastern Redbud), *Actaea racemosa* (Common Black Cohosh), *Chrysogonum virginianum* var. *virginianum* (Green-and-gold), *Salvia urticifolia* (Nettle-leaf Sage), *Triosteum angustifolium* (Lesser Horse-gentian), *Ruellia purshiana* (Pursh's Wild-petunia), and *Muhlenbergia sobolifera* (Rock Muhly).

Acidic oak-hickory forests are intermediate in composition and widespread in the province on acidic and subacidic soils that have greater moisture-holding capacity and somewhat higher base status than those favored by oak/heath forests. Hickories are common in them but often occur mainly in the understory. Acidic oak-hickory forests usually have some patches of ericaceous shrubs, but these are subordinate to *Cornus florida* (Flowering Dogwood), *Viburnum acerifolium* (Maple-leaf Viburnum), and other non-

ericaceous understory species. The herb flora is often well developed with dry-mesophytic forest generalists such as *Hylodesmum nudiflorum* (Naked-flowered Tick-trefoil), *Polygonatum biflorum* var. *biflorum* (Solomon's-seal), and *Maianthemum racemosum* ssp. *racemosum* (Eastern Solomon's-plume). Oak-hickory forests throughout the Piedmont are suffering from fire exclusion, a paucity of oak regeneration, and invasion of the understory by saplings of Red Maple, *Fagus grandifolia* (American Beech), and other shade-tolerant, potential oak-replacement trees that were once confined to sheltered, fire-protected sites but are now dispersing widely on uplands.

Fig. 27. Large *Fagus grandifolia* (American Beech) dominate a mesic mixed hardwood forest in Fairfax County. Photo © DCR-DNH, Gary P. Fleming.

Mesic mixed hardwood forests (Fig. 27) of American Beech, White Oak, Northern Red Oak, and Tulip-poplar are common in moist, acidic-soil ravines throughout the Piedmont and appear to be gradually replacing oak-hickory forests on many upland sites due to fire exclusion and the drastic declines in oak recruitment. Lower strata of these forests are often quite open and characterized by species such as *Ilex opaca* var. *opaca* (American Holly), *Polystichum acrostichoides* (Christmas Fern), *Parathelypteris noveboracensis* (New York Fern), and other mesophytic generalists. More localized rich mesophytic forests are confined to ravines and river slopes underlain by mafic or calcareous rocks. In addition to the trees of the mesic mixed hardwood forests, overstories of these basic mesic forests often contain White Ash, *Carya cordiformis* (Bitternut Hickory), *Tilia americana* (Basswood [both varieties]), *Quercus muehlenbergii* (Chinquapin Oak), *Acer saccharum* (Sugar Maple), and, in the southern counties, *Acer floridanum* (Southern Sugar Maple). With dense understories of *Asimina triloba* (Common Pawpaw) and *Lindera benzoin* (Spicebush), along with high cover of nutrient-loving herbs such as Common Black Cohosh, *Asarum canadense* (Wild Ginger), *Adiantum pedatum* (Northern Maidenhair Fern), *Podophyllum peltatum* (Mayapple), *Tiarella cordifolia* (Foamflower), *Jeffersonia diphylla* (Twinleaf), *Dicentra cucullaria* (Dutchman's Breeches), *Erythronium americanum* (Yellow Trout Lily), *Uvularia perfoliata* (Perfoliate Bellwort), and *Sanguinaria canadensis* (Bloodroot), the basic mesic forests are the Piedmont analogues of the Appalachian rich cove forests.

Small-patch forest communities that are scattered in the Piedmont include Eastern White Pine–hardwood forests similar to those of the Ridge and Valley, occurring mostly in the central part of the province; Eastern Hemlock–hardwood forests confined to steep, acidic, north-facing bluffs along larger streams and rivers; and mixed forests of American beech and oaks with dense evergreen understories of American Holly and *Kalmia latifolia* (Mountain Laurel), also restricted to sheltered bluffs and ravine slopes with extremely acidic soils. The Fort Pickett military installation in the southern Piedmont and Quantico Marine Base in the northern Piedmont both contain large training areas that have experienced frequent incendiary fires for at least 70 years (Fleming et al. 2001). These areas contain vegetation patchworks of open forests, savanna-like woodlands (Fig. 28), grasslands, and open seepage bogs that may replicate conditions on Piedmont landscapes that burned under a regime of natural fires and fires

intentionally set by Indians during much of the Holocene. The world's largest known population of *Rhus michauxii* (Michaux's Sumac), a globally rare southeastern endemic shrub, is associated with the frequently burned woodlands at Fort Pickett.

Fig. 28. Grassland savanna at Fort Pickett (Nottoway County) that has experienced frequent fires for about 75 years. Photo © DCR-DNH, Gary P. Fleming.

Alluvial forests of *Acer saccharinum* (Silver Maple), *Platanus occidentalis* (Sycamore), *Ulmus americana* (American Elm), *Acer negundo* var. *negundo* (Eastern Boxelder), *Celtis occidentalis* (Common Hackberry), *Betula nigra* (River Birch), and other flood-tolerant trees are well developed along the larger rivers that traverse the Piedmont, particularly the Potomac, the Rappahannock, the James, and the Roanoke. Floodplain sloughs and backswamps that are not too deeply flooded often contain communities in which hydrophytic oaks—e.g., *Quercus palustris* (Pin Oak), *Quercus bicolor* (Swamp White Oak), *Quercus phellos* (Willow Oak), *Quercus lyrata* (Overcup Oak), and *Quercus michauxii* (Swamp Chestnut Oak)—are important overstory species, and *Carex* spp. (sedges) form large colonies in the herb layer. In addition to being one of the largest rivers that crosses the Piedmont, the Potomac River is one of the few Atlantic slope rivers that has not been altered by high dams and reservoirs, leaving intact both its natural flooding regime and its riverside topography sculpted by millennia of erosion. Thus, the high-gradient Potomac Gorge (Fig. 29) in the Fall Zone west of Washington, D.C., contains the most extensive and diverse examples of flood-scoured depositional bars, outcrops, and prairies in the state (Fleming 2007).

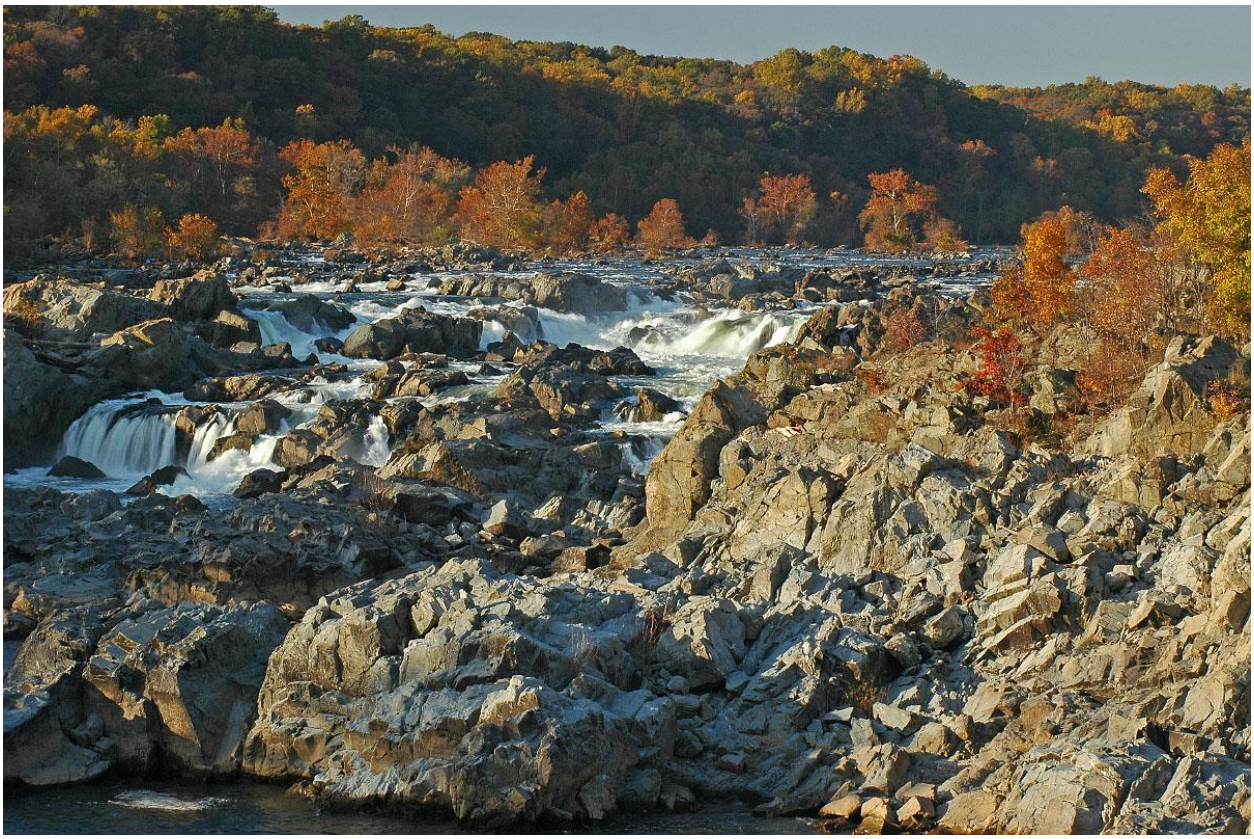

Fig. 29. The Potomac Gorge west of Washington, D.C. contains extensive and diverse occurrences of flood-scoured bars, outcrops, and prairies. Great Falls, Fairfax County. Photo © DCR-DNH, Gary P. Fleming.

Fig. 30. Piedmont Mafic Barren on actinolite schist at Bald Knob, Franklin County. Photo © DCR-DNH, Gary P. Fleming.

Because it has less topographic variation than the Appalachian region and many fewer wetlands than the Coastal Plain, the Piedmont has relatively low vegetation diversity and limited habitats supporting rare vegetation assemblages. Special habitats, however, are not entirely lacking. Granitic flatrocks and a suite of lithophytic plants that grow on them belong to a group of communities endemic to the southeastern Piedmont (Shure 1999). They reach their northern extent in a six-county area of south-central Virginia, where four flatrock endemics or near-endemics — *Cyperus granitophilus* (Granite Flatsedge), *Diamorpha smallii* (Small's Stonecrop), *Isoetes piedmontana* (Piedmont Quillwort), and *Portulaca smallii* (Small's Purslane) — reach their northern limits (Berg 1974; Belden 1998). Outcrop barrens on mafic and ultramafic rocks are also widely scattered in the Piedmont, most notably on diabase in the northern Virginia Triassic Basin and on Bald Knob, a spectacular monadnock of actinolite schist in Franklin County (Fig. 30). The rare *Phemeranthus piedmontanus* (Piedmont Fameflower) (Ware 2011), which is endemic to just a few Piedmont sites in southern Virginia and northern North Carolina, is an abundant component of the barrens on Bald Knob.

Another rare community found strictly in the southern and central Piedmont is a hardpan forest of gentle uplands with poorly permeable clay subsoils (hardpans) weathered from slates or fine-grained mafic rocks. Forest growth on these uplands is significantly impeded by a combination of poor drainage and shrink-swell soils that are alternately waterlogged and droughty and limit root penetration due to their thick hardpan horizons. Post Oak and *Carya glabra* (Pignut Hickory) are the most characteristic canopy trees in somewhat stunted stands, while *Ulmus alata* (Winged Elm) and *Juniperus virginiana* var. *virginiana* (Eastern Redcedar) are usually common in a subcanopy layer. In closed stands, there is often little herbaceous growth, while more open stands support large patches of xerophytic graminoids such as *Danthonia spicata* (Poverty Oatgrass), *Piptochaetium avenaceum* (Eastern Needlegrass), and *Scleria oligantha* (Fewflowered Nutrush). Shallow, seasonally flooded, upland depression swamps are also frequently associated with hardpan soils and are widely scattered over the entire Piedmont. In northern Virginia, Pin Oak, Swamp White Oak, and Red Maple are the most characteristic trees occupying the depressions, while Willow Oak, Sweetgum, and Overcup Oak are more typical in the central and southern Piedmont.

The Coastal Plain

The Coastal Plain covers about 21% of the state. Among all the provinces, it has the greatest area and diversity of wetlands, with palustrine wetlands covering about 18% of the region and estuarine wetlands covering about 4%. Forty-six percent of Virginia's Coastal Plain is forested, including 38% of the uplands and 75% of the wetlands. Among the upland forests, 45% are deciduous hardwood stands while 55% are evergreen and mixed forests that include extensive plantations of *Pinus taeda* (Loblolly Pine) and some natural pine-hardwood successional stands. About 9% of the Coastal Plain is developed, including large urban areas in the Richmond, Newport News–Hampton, and Norfolk–Virginia Beach areas. Only 13% of the province consists of unfragmented blocks of natural lands with very high to outstanding ecological integrity (Weber 2007), and the only large concentrations of such blocks are in the Great Dismal Swamp and on Fort A.P. Hill Military Reservation. Public lands comprise less than 8% of the province. A total of 106,223 ha (262,481 acres), or 4.4%, of the Coastal Plain is in conservation lands protected for biodiversity.

The upland forests that originally covered much of the Virginia Coastal Plain have been so extensively cleared or altered that it is difficult to determine which species and community types were originally prevalent. The wetlands of the province have fared better than the upland forests and still support a great variety of natural communities. The diversity of wetlands in this region spans a range of freshwater to mesohaline, lunar-tidal and wind-tidal estuaries; tidal and palustrine swamps; non-riverine groundwater-saturated flats; seasonally flooded ponds and depressions; seepage-slope wetlands; saturated peatlands; and various tidal and non-tidal aquatic habitats.

In addition to the physiographic distinctions between the inner and outer subregions of the Coastal Plain, phytogeographers (e.g., Braun 1950) also tend to recognize northern and southern divisions of the province, between which the James River serves as a rough boundary. South of the James, a number of southern species and vegetation types reach or approach their northern range limit. Natural communities entirely or largely restricted to the southern part of the Coastal Plain in Virginia are Longleaf Pine/scrub oak sandhills, Pond Pine woodlands and pocosins, Baldcypress-tupelo swamps, non-riverine swamp forests, and peatland Atlantic White-cedar forests. Fewer vegetation types are restricted to the northern part of the province, although both tidal freshwater marshes and tidal hardwood swamps occur only along the James River and other estuarine rivers to the north.

Much of the contemporary Coastal Plain upland forest consists of plantations or successional stands of Loblolly Pine and of secondary pine-hardwood forests that have developed after repeated cutting or agricultural abandonment. Early-successional mixtures of pine and *Liquidambar styraciflua* (Sweetgum) are ubiquitous. The most mature hardwood stands on mesic uplands are characterized by associations of *Fagus grandifolia* (American Beech), several oaks, and *Ilex opaca* var. *opaca* (American Holly) (Ware 1978; Dewitt and Ware 1979). Patches of drier oak-dominated forest and steep bluffs with dense forests of *Quercus montana* (Chestnut Oak), beech, and *Kalmia latifolia* (Mountain Laurel) are locally common in the dissected inner Coastal Plain north of the James River.

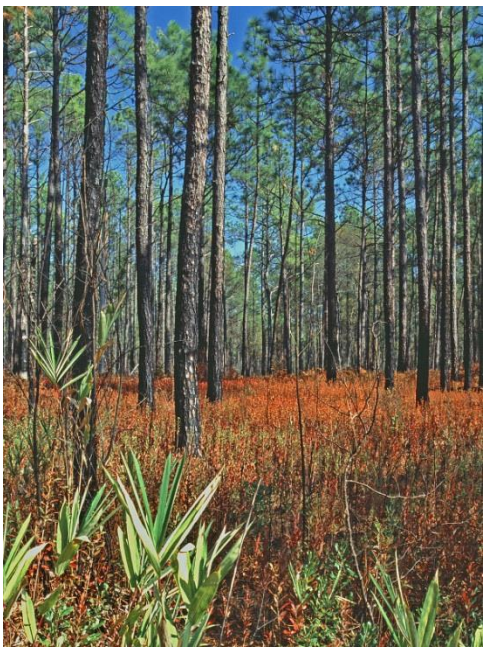

Fig. 31. Longleaf Pine woodland managed by prescribed fire at Blackwater Ecological Preserve, Isle of Wight County. Photo © DCR-DNH, Gary P. Fleming.

South of the James, the Coastal Plain is thought to have experienced frequent natural fires pre-settlement (Frost 1995). Fire-maintained forests and woodlands, dominated by *Pinus palustris* (Longleaf Pine) (Fig. 31), may have been widespread before European settlement, but little trace of them remains. The only remnants are associated with deep sandhill deposits along the Nottoway and Blackwater rivers in southeastern Virginia. In addition to Longleaf Pine, diagnostic species of the sandhill vegetation include a number of state-rare species and species reaching their northern or southern range limits, e.g., *Quercus laevis* (Turkey Oak), *Kalmia angustifolia* (Sheep Laurel), *Vaccinium crassifolium* (Creeping Blueberry), *Pyxidanthera barbulata* var. *barbulata* (Common Pyxie-moss), *Polygonella polygama* var. *polygama* (October-flower), *Lithospermum caroliniense* (Golden Puccoon), *Pediomelum canescens* (Hoary Scurfpea), and *Calopogon pallidus* (Pale Grass-pink). The primary area of Longleaf Pine development in Virginia may always have been in this sandhill belt, with the remainder of the southeastern Coastal Plain located in a transitional zone where Longleaf Pine originally occurred in mixtures with other pines and oaks (Ware et al. 1993).

Rare upland forest communities occur on ravine slopes and estuary-fronting bluffs that have down-cut into Tertiary shell deposits or lime sands or are mantled with deposits of massive pre-settlement shell middens (Ware and Ware 1992). Soils of these habitats have extraordinarily high levels of calcium and support a number of calciphilic species that are very infrequent or rare on the Coastal Plain, some of them disjunct from the inner Piedmont and the mountains (Harvill 1965, MacDonald 2000). Such species of the calciphilic flora include *Quercus muehlenbergii* (Chinquapin Oak), *Tilia americana* var. *heterophylla* (White Basswood), *Magnolia tripetala* (Umbrella Magnolia), *Euonymus atropurpureus* (Eastern Wahoo), *Hexalectris spicata* var. *spicata* (Crested Coralroot), *Campanula americana* (Tall Bellflower), *Solidago flexicaulis* (Broad-leaved Goldenrod), *Thalictrum dioicum* (Early Meadow-rue), *Scutellaria ovata* ssp. *ovata* (Heart-leaf Skullcap), *Mitella diphylla* (Two-leaved Miterwort), *Corallorhiza wisteriana* (Spring Coralroot), and *Verbesina virginica* var. *virginica* (White Crownbeard). Seepage swamps in the bottom of these calcareous ravines are saturated with calcareous groundwater and contain other disjuncts such as *Caltha palustris* (Marsh Marigold), *Carex tetanica* (Rigid Sedge), *Dirca palustris* (Leatherwood), *Pedicularis lanceolata* (Swamp Lousewort), and *Veratrum viride* (American False-hellebore).

The maritime zone of the outer Coastal Plain is vegetated with a unique suite of pine and pine-hardwood forests, dune woodlands and scrub, dune grasslands, and sparse beach vegetation — communities well adapted to deep sands, periodic salt spray, and oceanic storm impacts. The typical development of maritime vegetation proceeding along a gradient from the beach inland starts with the upper beaches and overwash flats that support a sparse assemblage of *Cakile edentula* (American Sea Rocket), *Salsola kali* (Saltwort), and a few other salt-tolerant, succulent annuals (Fig. 32). The foredune and ocean-facing secondary dunes usually support more stabilized grasslands dominated by combinations of *Ammophila breviligulata* (American Beach Grass), *Panicum amarum* var. *amarum* (Bitter Seabeach Grass), *Uniola paniculata* (Sea Oats), *Panicum amarum* var. *amarulum* (Southern Seabeach Grass), *Spartina patens* (Saltmeadow Cordgrass), *Schizachyrium littorale* (Seaside Little Bluestem), *Triplasis purpurea* var. *purpurea* (Purple Sandgrass), *Solidago sempervirens* var. *sempervirens* (Seaside Goldenrod), and a few other species. With increasing distance from the shoreline, more protected back dunes become vegetated with evergreen shrublands — primarily of *Morella pensylvanica* (Northern Bayberry) or *M. cerifera* (Wax Myrtle). In far southeastern Virginia, low, wind-mounded *Quercus virginiana* (Live Oak) is the usual dominant of maritime scrub. On very high, xeric back dunes, a rare maritime woodland of stunted Loblolly Pine and *Hudsonia tomentosa* (Sand Heather) occurs at several sites.

Fig. 32. Sparse upper beach/overwash flat vegetation dominated by succlent annuals *Cakile edentula* (Amerian Sea Rocket) and *Salsola kali* (Saltwort). Fishermans Island, Northampton County. Photo © DCR-DNH, Gary P. Fleming.

Fig. 33. Live Oak – Loblolly Pine Forest at False Cape State Park, City of Virginia Beach. Photo © DCR-DNH, Gary P. Fleming.

Maritime forests that occupy the most protected dunes and sand flats have been much reduced by clear-cutting and coastal development. South of the Chesapeake Bay in Virginia Beach city, most maritime forests are mixed stands of Live Oak and Loblolly Pine (Fig. 33), but a large and unusual example of a mixed deciduous maritime forest has been preserved in the ancient dune system at First Landing State Park. The most mature maritime forests of the Eastern Shore generally consist of Loblolly Pine in mixtures with *Prunus serotina* var. *serotina* (Black Cherry) and several oaks. Maritime-zone wetlands include some of the state's rarest natural communities, including sea-level fens, interdune ponds and wet grasslands, and maritime swamp forests.

The great bottomland swamp forests of the southeastern United States (Sharitz and Mitsch 1993) extend into the Virginia Coastal Plain along the Blackwater, Nottoway, and Meherrin rivers, and smaller non-tidal streams south of the James. The wettest backswamps and sloughs along streams that originate in the Piedmont and carry large sediment loads (often referred to as brownwater swamps; Fig. 34) have silty, relatively fertile soils and vegetation dominated by *Nyssa aquatica* (Water Tupelo), *Taxodium distichum* (Baldcypress), *Fraxinus caroliniana* (Carolina Ash), and numerous herbs adapted to draw-down habitats characterized by hydrologic regimes that vary from seasonally flooded to nearly dry over the course of the growing season. Swamps along smaller, strictly coastal streams with relatively low sediment deposition (often referred to as blackwater swamps) have sandy, organic-rich soils and are usually dominated by *Nyssa biflora* (Swamp Tupelo), with or without Baldcypress, and acidophilic shrubs such as *Clethra alnifolia* (Sweet Pepperbush). Less deeply flooded bottomland terraces and shallow sloughs in the major river floodplains support more mixed forests of *Quercus lyrata* (Overcup Oak), *Quercus laurifolia* (Laurel Oak), *Carya aquatica* (Water Hickory), *Fraxinus pennsylvanica* (Green Ash), and

other hardwoods, often with an herb layer dominated by sedges and grasses. Mature forests on the highest terraces that flood infrequently harbor stands of *Quercus michauxii* (Swamp Chestnut Oak), *Quercus pagoda* (Cherrybark Oak), *Carya ovata* (Shagbark Hickory), and such shrubs of well-drained alluvium as *Ilex decidua* var. *decidua* (Deciduous Holly), *Carpinus caroliniana* (American Hornbeam), and *Vaccinium elliottii* (Mayberry).

Fig. 34. Seasonally flooded bottomland swamp along the Nottoway River in Southampton County. Photo © DCR-DNH, Gary P. Fleming.

In the northern Coastal Plain, where the major rivers are tidal along most of their length across the province, alluvial swamp forests are less well developed and mostly restricted to smaller-order streams. In addition, north of the James, Baldcypress, Water Tupelo, and other southern species quickly become infrequent or drop out, leaving dominance of the wettest swamps to *Acer rubrum* (Red Maple), Green Ash, and Swamp Tupelo.

Non-alluvial wetlands of the Coastal Plain include depression swamps and seasonal ponds; non-riverine wet flatwoods and swamps; seepage swamps and bogs; peatland *Chamaecyparis thyoides* (Atlantic White-cedar) forests; and pocosins of *Pinus serotina* (Pond Pine) and evergreen shrubs such as *Lyonia lucida* (Shining Fetterbush) and *Ilex glabra* (Inkberry) (Stevens and Patterson 1998). Most of these communities and their habitats have been altered or destroyed by post-settlement disturbances and are now rare. Sphagnous seepage bogs reported historically have all been overgrown or obliterated by changes in land-use, and this community type now exists only in frequently burned training areas of the Fort A.P. Hill military base (Caroline County) and in artificially maintained power-line swales. Several complexes of depression swamps and ponds have escaped draining and clearing, but most of these forested wetlands have been altered by clearcutting. Acidic seepage swamps with abundant *Magnolia*

virginiana (Sweetbay), occurring in saturated headwaters of the inner Coastal Plain, remain more numerous though widely threatened with destruction by beaver impoundments. This wetland forest community is the Coastal Plain home of the federally listed endangered plant *Helonias bullata* (Swamp-pink).

Fig. 35. Non-riverine Wet Hardwood Forest dominated by mature oaks. Stumpy Lake, City of Virginia Beach. Photo © DCR-DNH, Gary P. Fleming.

On the flat, outer Coastal Plain and more extensive terraces elsewhere, extensive imperfectly drained soils that were seasonally saturated by perched water tables must have once supported large stands of non-riverine wet hardwood forest dominated by hydrophytic oaks (Fig. 35). Widespread ditching, draining, and timber cutting have reduced this community to small, secondary patches or replaced it with early-successional stands of Loblolly Pine, Red Maple, and Sweetgum. The best remnants are forests with dominance shared by Swamp Chestnut Oak, Cherrybark Oak, Laurel Oak, Willow Oak, and, in the northern Coastal Plain only, *Quercus palustris* (Pin Oak). *Arundinaria tecta* (Switch Cane) and *Leucothoe axillaris* (Coastal Dog-hobble) are characteristic understory species in stands south of the James River, while more northern non-riverine wet hardwood stands contain Sweet Pepperbush, *Eubotrys racemosa* (Fetterbush), and *Vaccinium formosum* (Swamp Highbush Blueberry). Related, but seasonally flooded, non-riverine swamp forest is found primarily on large peat deposits of the Great Dismal Swamp and its vicinity, where extensive ditching, canal construction, large-scale commercial logging, and deep peat fires have inexorably reduced its quality and extent.

Wetland communities subject to diurnal or irregular tidal flooding occur along estuarine rivers and on non-riverine flats that border the Chesapeake Bay and the Eastern Shore. A special class of oligohaline tidal wetlands that is influenced by wind-driven tides occurs along the shores of Back Bay, the North Landing River, and the Northwest River in the Embayed Region of far southeastern Virginia. In riverine settings, where freshwater flows are intermixed with tidal saltwater inflows, community composition changes along a halinity gradient from an upstream freshwater zone, through an intermediate oligohaline zone, to a downstream zone where the increasing influence of saltwater produces

mesohaline conditions. Salt marshes on the large non-riverine flats are generally associated with mesohaline to polyhaline conditions (Fig. 36). These latter communities are best developed on the Eastern Shore (Accomack and Northampton counties), where they occupy several thousand hectares of essentially flat plains, especially on the Atlantic side.

Fig. 36. Expansive salt marsh on Chesapeake Bay side of the Eastern Shore. Marks and Jacks Island, Accomack County. Photo © DCR-DNH, Gary P. Fleming.

Fig. 37. *Pontederia cordata* (Pickerelweed) flowering in a tidal freshwater marsh along Ashton Creek, Chesterfield County. Photo © DCR-DNH, Gary P. Fleming.

In Virginia, the largest and most diverse tidal freshwater marshes (Fig. 37) have developed on sediments deposited by large meanders of the Pamunkey and Mattaponi rivers, although outstanding examples also occur in the Potomac, Rappahannock, Chickahominy, and James river estuaries. Among their most common species are *Zizania aquatica* var. *aquatica* (Wild Rice), *Peltandra virginica* (Arrow-arum), *Pontederia cordata* (Pickerelweed; Fig. 37), *Persicaria punctata* (Dotted Smartweed), *Leersia oryzoides* (Rice Cutgrass), *Persicaria arifolia* (Halberd-leaf Tearthumb), *Bidens laevis* (Smooth Bur-marigold), and *Bidens*

trichosperma (Tall Swamp Marigold). *Spartina cynosuroides* (Big Cordgrass) is the most abundant and characteristic species of oligohaline marshes, with typical associates of *Hibiscus moscheutos* (Swamp Rosemallow), *Kosteletzkya pentacarpos* (Seashore Mallow), *Typha angustifolia* (Narrow-leaf Cattail), *Schoenoplectus americanus* (Olney Threesquare), *Sagittaria lancifolia* var. *media* (Bull-tongue Arrowhead), *Eleocharis fallax* (Creeping Spikerush), and *E. rostellata* (Beaked Spikerush), the latter two species primarily in wind-tidal marshes. Mesohaline and polyhaline communities are salt marshes of low stature and species richness, generally dominated by combinations of *Spartina alterniflora* (Salt-marsh Cordgrass), *Distichlis spicata* (Saltgrass), Saltmeadow Cordgrass, *Juncus roemoerianus* (Black Needle Rush), and *Bolboschoenus robustus* (Saltmarsh Bulrush).

Tidal hardwood swamps co-dominated by *Fraxinus profunda* (Pumpkin Ash), Green Ash, Swamp Tupelo, and a diverse shrub flora occur in irregularly flooded zones along the freshwater reaches of tidal rivers (Rheinhardt 1992). Less common are oligohaline tidal woodlands with open stands of Baldcypress over dense swards of *Carex hyalinolepis* (Shoreline Sedge). Smaller-patch estuarine communities include irregularly flooded salt-scrub vegetation dominated by *Baccharis halimifolia* (High-tide Bush) and *Iva frutescens* (Marsh-elder) and a range of freshwater to mesohaline aquatic beds dominated by submersed aquatics such as *Ceratophyllum demersum* (Common Hornwort) and *Zannichellia palustris* (Horned Pondweed). Salt flats (Fig. 38), or salt pannes, are irregularly tidal, hyperhaline flats and depressions with compact peat soils that accumulate salt as tidal inputs evaporate. Usually located within or at the edge of larger salt marshes, they support low vegetation of succulent halophytes, especially *Salicornia virginica* (Jointed Glasswort), *Salicornia bigelovii* (Dwarf Glasswort), *Sarcocornia pacifica* (Woody Glasswort), and *Limonium carolinianum* (Sea Lavender).

Fig. 38. Salt flat dominated by *Salicornia bigelovii* (Dwarf Glasswort). Fishermans Island, Northampton County. Photo © DCR-DNH, Gary P. Fleming.

Tidal wetlands are biologically productive systems that improve water quality, provide resources for numerous fish and wildlife species, and act as buffers against storm surges and shoreline erosion. Although historical losses have occurred through outright destruction, the biggest current threats to tidal wetlands are chronic sea-level rise and the rampantly invasive non-natives *Phragmites australis* ssp. *australis* (Common Reed) and *Murdannia keisak* (Marsh Dewflower).

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