Chapter 5
Ecosystem Dynamics

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5.1 Introduction

Red spruce (*Picea rubens*)-dominated forest and woodland dynamics emerge from interactions among the life histories of the constituent species, biogeography, and impacts from historical anthropogenic and natural disturbances. In this chapter, we build on descriptions of species biology, community biogeography, and regional forest history to describe components of spruce-dominated ecosystem dynamics, including disturbance regimes and altered dynamics due to loss of key species from logging, invasive insects, pollution, or climate change. Our use of the term dynamics implies the influence of time on these processes, and at a minimum a disturbance regime should include descriptions of frequency and scale or patch size of disturbance events. In some areas or timeframes, pre-European settlement for instance, we may only have qualitative descriptions of disturbance regime components. Quantitative measures or qualitative descriptions may be used to help design restoration treatments or determine restoration success.

Higher elevations and steeper slopes of the central and southern Appalachians were some of the last to be impacted by wide-scale, exploitative logging (see Chap. 1). However, use of narrow-gauge railroads to reach even remote sites resulted in near complete removal of all economically viable trees in the region (Lewis 1998; Fig. 5.1).

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In addition to direct effects of exploitative logging, secondary events had significant effects on red spruce ecosystems. Common across the various anthropogenic disturbances is change from pre-Euro-American settlement frequency, scale, and magnitude of disturbance. Notable examples include changes in wildfire intensity, deer numbers, and domestic livestock grazing. Due to large amounts of logging slash and use of coal-fueled logging equipment, fires that occurred during and just after exploitative harvest were outside normal fire regime intensity and return interval. Deer numbers plummeted after exploitative logging, but rebounded with reintroductions and re-growth of the hardwood forest. Livestock grazing also occurred in many communities on constructed pastures and by free-range animals (Pyle and Schafale 1988).

Within the broad classification of the red spruce ecosystem, upland forest and woodland communities range from nearly pure red spruce to mixtures of red spruce and hardwood species. Generally, these forests are found on ridgetops, side slopes, and soils influenced by terrestrial processes. In the central Appalachians, these forests range across middle and upper elevations (1,070–1,400 m [3,500–4,500 ft]) and the highest elevations (above 1,370 m [4,500 ft]) on gentle slopes and on exposed ridges and summits (Fig. 5.2 and 5.3). Red spruce becomes mixed with northern hardwoods at lower elevations, but above 850 m (2,800 ft), where the climate is generally warmer. The southern Appalachian Mountains reach their highest elevations and greatest extent in eastern Tennessee, western North Carolina, and southwestern

Fig. 5.1 Construction of a railroad grade near Cranberry Glades, Pocahontas County, West Virginia, around 1911. Photo by USDA Forest Service

Virginia (Fig. 5.3). Red spruce forest can be found above about 1,370 m (4,500 ft) elevation, but only becomes widely dominant above 1,525–1,680 m (5,000–5,500 ft) elevation (Cogbill and White 1991). Ten named mountain areas in the southern Appalachians surpass the 1,680 m (5,500 ft) elevation threshold for continuous spruce forest, contain all of the southern Appalachian region's spruce-fir and red spruce forests, and are also referred to as *sky islands* (Table 5.1).

Red spruce forests also occur in small patches within the matrix of hardwood-dominated forests (central Appalachians) and *sky islands* (southern Appalachians). These wetland patches are largely found in landscape positions with low slope. Hydrologic regimes range from stream and river flooding to wetlands fed by groundwater seepage and rainfall. Protection of the hydrologic regime is important in sustaining the dynamics and ecosystem service of these wetland communities. For more detailed descriptions of community types for upland and wetland communities, see Chap. 4.

For this chapter, we reviewed and synthesized the literature on the dynamics of central and southern upland Appalachian red spruce and spruce-fir forests under five topics. We begin with a section on gap dynamics in old-growth forests that describes the natural dynamics of these forests and contrasting life strategies of the major tree

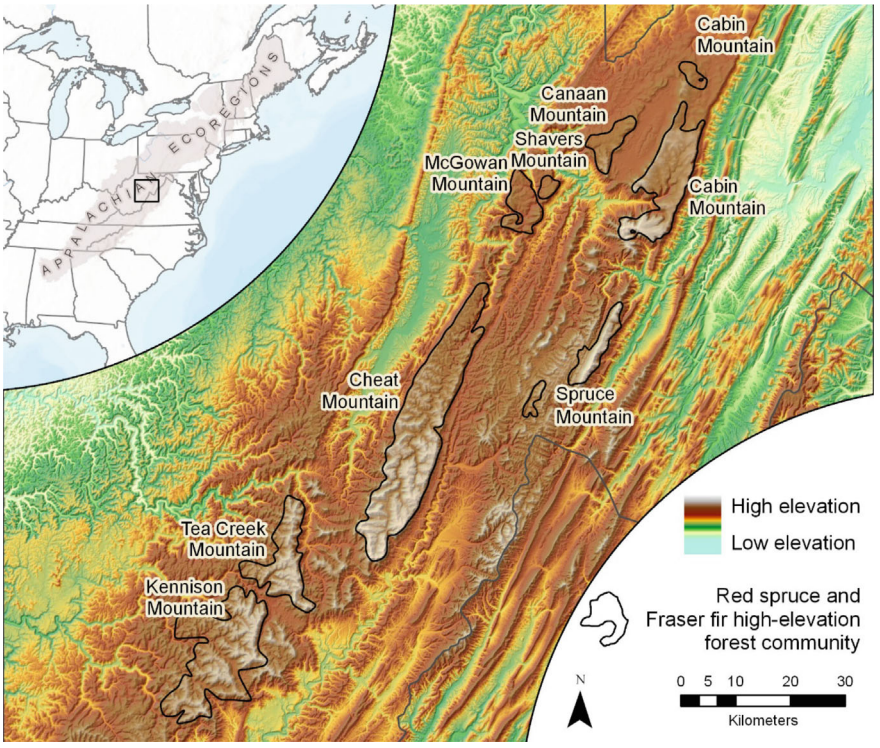

Fig. 5.2 Red spruce (*Picea rubens*) forests of the central Appalachians

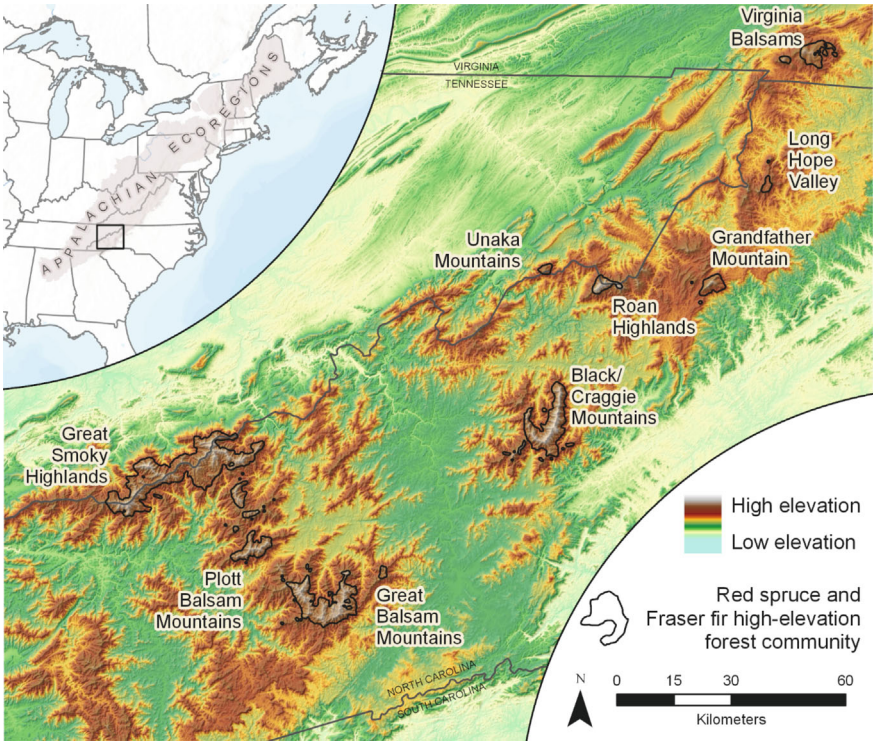

Fig. 5.3 Red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*) *sky islands* of the southern Appalachians

Table 5.1 Topographic characteristics of the ten mountain regions in the southern Appalachians that have spruce-fir or red spruce (*Picea rubens*) forest

Region	Area (km^2)	Number	Max. elev. (m)
Great Smoky Mountains	40.0	10	2,024
Great Balsam Mountains	29.4	20	1,954
Black Mountains and Black Craggies	26.8	6	2,037
Roan Highlands	8.8	3	1,916
Plott Balsam Mountains	5.7	1	1,918
Grandfather Mountain	1.1	1	1,818
Virginia Balsams (Mt. Rogers, Mt. Pisgah, and Whitetop)	0.48	5	1,743
Total	121.1	46	

Modified from White (1984). Area = area above 1,680 m (5,500 ft); Number = number of peaks in the site; Max. elev. = maximum elevation reached at the site

species: red spruce, Fraser fir (*Abies fraseri*), yellow birch (*Betula alleghaniensis*), and pin cherry (*Prunus pensylvanica*). We then discuss four topics that address human impacts on these dynamics: broad-scale logging and remnant old-growth forests; the balsam woolly adelgid (*Adelges piceae*); pollutant deposition and exposure; and climate change. We also discuss potential interactions among these disturbances, a topic that has been addressed directly in some studies we reviewed (e.g., Soulé et al. 2012; Stehn et al. 2013). Here, we treat these topics in terms of their potential impacts on community dynamics. In Chap. 2, several of the same topics are reviewed from the perspective of how they act as physiological stressors on red spruce individuals.

5.2 Disturbance Regimes

The impacts of disturbance regimes over time define ecosystem services and influence structure and composition at the landscape scale (see Sidebar 5.1). Disturbances interact with current vegetation, topography, climate and other factors, resulting in a range of landscape patterns. A disturbance regime, unlike a disturbance event, is defined by frequency, return interval, rotation period, size, intensity, severity, and residuals (Turner 2010). Additionally, a disturbance regime can be described by the agent or source, patterns, seasonality, duration, interactions, and variability of disturbances (Keane 2013).

Dynamics of spruce forests are linked to the biology of red spruce and co-occurring species. In general, red spruce has a shallow root system and is extremely shade tolerant compared to northern hardwood species. It is slow-growing and long-lived, but can respond to release; seeds need moist substrate for best germination (Blum 1990, see Chap. 2). These characteristics make red spruce susceptible to wind-throw, but enable it to regenerate from seeds or advance regeneration following disturbances and management actions that open the canopy or remove litter. However, saplings have greater net photosynthesis, leaf conductance, and xylem water potential on cloudy days compared to clear days, suggesting that red spruce may be less able than other species to respond to large disturbances that create high light, high vapor pressure deficits, and low soil moisture conditions (Berry and Smith 2013). This adaptation to low light levels and moist conditions means red spruce can be outcompeted by faster-growing species, especially following broad-scale disturbances. In general, dynamics of red spruce-dominated communities differ with the characteristics of associated species and the types and scales of disturbances. As these differ subtly between the central and southern Appalachian Mountains, we discuss the regions separately below.

Sidebar 5.1: Disturbance Regimes 101 Early tenets of ecology viewed succession as a sequential linear process whereby a plant community develops into a stable climax state controlled by climate (Clements 1936). This highly

deterministic idea (i.e., that there is an end point to succession) has largely been replaced by a more dynamic view of plant communities as described by H. C. Cowels, H. A. Gleason, and others (see historical overview by Kingsland 1991). Gleason (1926) contended that a plant association can be mapped, and that the association "…represents the result of an environmental sorting of a population…" that is, the species making up the community are all able to persist under the conditions at that location over time. One key difference between Clements and Gleason is the acknowledgement of disturbance and how it affects plant community development over time. In many ecosystems, communities are likely to experience multiple disturbances and may never reach a stable end point defined by Clements as climax. In both views, spatial and temporal scales are important but also often unstated.

For land managers working on time scales ranging from years to decades and spatial scales of tens to thousands of hectares, the principles of disturbance ecology are important to consider. Disturbance should be viewed as a series of events and not individual occurrences, and in aggregate they are fundamental to spatial and temporal heterogeneity across a landscape (Turner 2010). In disturbance ecology, disturbance regimes are defined by many factors including agent, frequency, return interval, size, intensity, severity, seasonality, and pattern (Table 5.2). Restoration actions designed to emulate natural disturbances benefit from an assessment of the historical range of variability in a landscape through determination of disturbance regimes for the area being considered for management (Engstrom et al. 1999; Greenberg and Collins 2016). For example, the information in Tables 5.3 and 5.4 give land managers an idea of the historic disturbance dynamics of red spruce-dominated forests.

Another important idea to consider is the concept of the shifting mosaic steady state of a landscape (Bormann and Likens 1979; Turner 2010). This concept integrates both time and space, describing various vegetation states of a landscape where individual stands are at different successional stages and changing over time, however, the proportion of the landscape in those successional stages remains constant (Turner 2010). In restoration, this idea can help define goals and frame monitoring efforts at the landscape scale. Monitoring of many restoration actions will focus on a sample of treated or planted trees, but landscape scale goals can also add to the determination of success or progress. For example, the Monongahela NF Forest Plan includes desired conditions for the spruce and spruce-hardwood forest restoration management prescription for tracking progress across age or successional classes. The desired conditions are stated as percentages of the area by successional stage, with 3–8% of the area in early successional habitat and 60–80% in late successional forest (USDA Forest Service 2006). As these forests trend toward multi-aged conditions, the spatial locations of those age classes will create a shifting mosaic of conditions.

Table 5.2 Definitions of terms related to disturbance regimes

Term	Definition
Agent	Factor or origin causing the disturbance (Keane 2013)
Frequency	How often an event occurs (Keane 2013); probability of an event, or the mean or median number of events per unit of time (Turner 2010)
Return interval	Mean or median time between events, the range or variability may also be important (Turner 2010)
Size	Area disturbed in an event, can be expressed in area or percentage of area (Turner 2010)
Intensity	Magnitude of the disturbance (Keane 2013); physical energy of or released by the event not the ecological impact (Turner 2010)
Severity	Effect or impact of the event on the community or a given component of the community (Turner 2010; Keane 2013)
Seasonality	Time of year the event occurs (Keane 2013)
Pattern	Spatial arraignment of disturbance effects (Keane 2013)

5.2.1 Canopy Gap Dynamics

Red spruce-dominated ecosystems of the central and southern Appalachians are driven largely by disturbances that result mainly in small canopy gaps after the death or injury of individual or groups of trees (Table 5.3). Disturbances that can lead to the downing of snags or living trees include wind-throws, ice storms (Nicholas and Zedaker 1989), and the debris avalanches and down-watershed flood scour that accompany intense rainfall events (Harmon et al. 1984; White et al. 1985). The humidity and dampness of high elevation forests mean that natural fires are rare. Post logging fires in the early 1900s, however, were significant and are described more fully below. Native insects and fungi might cause individual tree deaths, but do not cause stand-initiating disturbance to the forest canopy (Bruck et al. 1989; Blum 1990). However, there is a record of two large-scale damaging insect events in West Virginia during the broad-scale logging of the original forest. One outbreak period, from 1882 to 1886, was attributed to a spruce bark beetle (*Polygraphus rufipennis*) and a second, from 1890 to 1803, was attributed to a pine bark beetle (Hopkins 1899). Given that the damaging beetles were found during timber harvest, it is not clear whether these beetles had broad-scale impacts; in 1899, living spruce were healthy and free from insect damage (Hopkins 1899). The non-native balsam woolly adelgid, however, has significantly affected spruce-fir forests of southern Appalachian forests and is discussed more fully below.

5.2.1.1 Southern Appalachians

Although shade tolerant, both red spruce and Fraser fir also depend on canopy gaps for long-term survival and growth into the canopy. White et al. (1985) documented

Table 5.3 Estimates of major natural disturbances in the old-growth spruce-fir forests of Mt. Collins in the Great Smoky Mountains as reported in White et al. (1985). Note that the area affected only includes vegetation types and topographic positions appropriate for each disturbance type, and that year of the last event is as of 1985

Disturbance	Area affected (%)	Return interval (yr)	Recovery time (yr)
Fire	10^{-5}	$>10^7$	10^2
Debris avalanches			
Headwalls	1	10^2–10^3	10^2–10^3
Scour channels	1	10^2	10^2
Wind			
Windfall > 200 m^2	0.1	$>10^3$	10^2
Fir patches	10	50–75	20
Gaps < 200 m^2	5–20	10^2	50

the dynamics of an old-growth spruce-fir forest in the Great Smoky Mountains. This study is notable in that it used stands that had not yet suffered mortality from the balsam woolly adelgid and focused on the middle part of the gradient where red spruce, Fraser fir, and yellow birch are co-dominant (1,740–1,830 m [5,700–6,000 ft]). Small canopy gaps (≤0.02 ha [0.05 ac]) dominated the landscape and disturbance regime, with gap (complete or nearly complete reductions in canopy) creation rates of just under 1% of the canopy per year (see Table 5.3). Several methods were used to measure gaps and calculate opening size, and depending on the method used, gaps formed in the most recent decade covered 6–17% of the study area (Table 5.4). This translates to a return interval, at the scale of canopy trees, of between 111 and 178 years. As suggested by these results, red spruce and Fraser fir trees that have reached the canopy in southern Appalachian forests have been found to have periods of growth suppression and release that correlate with gap size (Reams et al. 1993; Wu et al. 1999). For example, periods of red spruce suppression averaged 19 years (range 4–79 years), while the duration of growth release periods averaged 29 years (Wu et al. 1999), which is consistent with a small gap disturbance regime and shade tolerance of this species.

Interestingly, for the small gaps studied by White et al. (1985), the species capturing a gap was not predictable from the size or age of that gap although the three main species had different competitive strategies. Fraser fir had the highest density of seedlings and saplings in the understory, but had a lifespan, and consequently a canopy residence time, only about half as long as red spruce (140 versus over 250 years). Red spruce was well distributed in forest understories but had lower density of seedlings and saplings. Korstian (1937) attributed this to the fact that red spruce seed crops come at longer intervals than those of Fraser fir (also see Nicholas et al. 1992; Johnson and Smith 2005). As might be expected from the difference in lifespan, however, red spruce held onto its place in the canopy (canopy residence time) about twice as long as Fraser fir. Yellow birch, moderately tolerant of shade, has small but widely dispersed seeds (Houle and Payette 1990) and seedlings had

Table 5.4 Summary of selected gap size characteristics and mortality rates in red spruce-dominated forests of the central and southern Appalachians from published literature

Location	Community type	Mean gap size (range) in m^2	Annual mortality	Proportion of area in gaps	Other information	Reference
West Virginia	Red spruce-northern hardwoods	53.4 (6.2–276.4)	1.4%	4.7%	Second-growth stands; gaps generally elliptical	Rentch et al. (2010)
West Virginia	Red spruce-northern hardwoods	50.6 (5–459)		7.6%	Second-growth; about 79% of gaps smaller than 75 m^2; average gap age 19 years (SE 6.8)	Lutz (2018)
Tennessee and North Carolina	Red spruce-Fraser fir		1%		Smaller trees experience higher mortality	Busing and Wu (1990)
Great Smoky Mountains NP/ Tennessee and North Carolina	Red spruce-Fraser fir	60–174		6–17% in gaps 1–10 years of age	Return interval of 111–178 years	White et al. (1985)
Great Smoky Mountains NP/ Tennessee	Red spruce-Fraser fir		2% of red spruce canopy trees		Compared mortality before and after adelgid-caused fir mortality	Busing and Pauley (1994)

very low survivorship in the shade but had the highest growth rates in gaps. In short, yellow birch compensates for a smaller starting size (little advance regeneration) with faster growth rates, whereas red spruce and Fraser fir start from larger sizes (advance regeneration), but have lower growth rates. Fraser fir captures most gaps, but the other two species can hold onto canopy positions twice as long.

In larger windfall gaps (>0.02 ha [0.05 ac]), on open soil after debris avalanche, and on flood scour along streams, pin cherry becomes important in spruce forest dynamics. This species, too, has distinctive life history characteristics, the most important of which is its ability to form a persistent soil seedbank of dormant seeds that can survive 100 or more years before germination (Tierney and Fahey 1998). In large disturbance patches, faster litter decomposition rates, due to higher forest floor temperatures from increased solar exposure, and less competition from larger trees result in higher soil solution nitrate, which triggers pin cherry germination (Marks 1974; Nyland et al. 2007). As a result of its rapid colonization, pin cherry serves to conserve nitrogen on watersheds (Marks 1974; Fahey et al. 1998; Nyland et al. 2007). Pin cherry growth rates are the highest and life span the shortest (<80 years) of the four species profiled here. The large disturbances that lead to pin cherry colonization are rare, however, and succession more often leads to dominance by red spruce, Fraser fir, and yellow birch.

Additional spruce-fir forest dynamic patterns are found on high summits, ridges, and upper slopes. On the highest summits in the southern Appalachians, where Fraser fir forms nearly pure stands (White et al. 1985), upper slopes are wind-exposed, and blowdowns affect larger patches of trees. Although seedling survival can be low in direct sunlight (Johnson and Smith 2005), Fraser fir forms a high density of seedlings and saplings so that, after wind disturbance, the ensuing stand of maturing trees is of similar heights and interlocking crowns, making the forest vulnerable to larger windthrow patches. Aerial photographs taken before balsam woolly adelgid invasion show these larger patches of windthrow in pure Fraser fir forest (Peter White, personal observation). Evergreen rhododendron (*Rhododendron* spp.) populations can also influence spruce-fir dynamics on upper slopes and convex ridges. These shrubs cast deep shade and produce thick, slow to decay, leaf litter, thereby acidifying soils (Nilsen et al. 1999; Wurzburger and Hendrick 2007). At least at small scales, this reduces tree seedling establishment and leads to stable shrub communities, called heath balds, on the most convex ridges and upper slopes (White et al. 2001). Several areas with severe logging impacts are dominated by *Rhododendron* thickets with some trees today, and it is unclear whether past logging altered the density of the heath shrubs. However, no evidence indicates that past logging altered the shrub pattern at the landscape scale (White et al. 2001; Woodbridge and Dovciak 2022).

5.2.1.2 Central Appalachians

In the central Appalachians, Fraser fir does not occur and balsam fir (*Abies balsamea*) is a very small component of spruce-dominated forests. Very few red spruce-dominated old-growth forests remain in the central Appalachian region for study

Fig. 5.4 Contemporary forest structure and composition at Gaudineer Scenic Area, Monongahela NF. Approximately 20 ha (50 ac) of this scenic area is virgin red spruce-northern hardwood forest. Many of the largest red spruce (*Picea rubens*) trees have died from natural causes. The complexity of the forest structure, size of trees on the forest floor, and standing snags are examples of old-growth conditions possible in this forest type. Photo by USDA Forest Service

of disturbance patterns or species composition (Fig. 5.4). A 1920 report based on timber inventory data collected for the West Virginia Pulp and Paper Company for its holdings in Pocahontas, Randolph, and Webster counties gives us a glimpse of the original red spruce forest's character (Sterling 1920). These lands, the headwaters of the Cheat and Elk rivers, included about 52,000 ha (130,000 ac) of cut over, burned, and unharvested forests. The primary purpose of the survey was to

quantify current reproduction on the cut over lands to calculate future value and growth of the second-growth forest. The virgin unharvested areas were described as small parcels with harvests occurring rapidly. Contracted foresters divided the area into three forest types based on dominant species (softwood, softwood-hardwood, and hardwood) and noted that existing reproduction under mature overstory generally matched the overstory in species composition. This suggests the original forest had reached understory reinitiation stage of development (Oliver and Larson 1996) and was a stable and self-sustaining community. Based on second-growth spruce-dominated forests and old-growth forests in other regions, and this glimpse of the unharvested areas of West Virginia, we can generalize that the pre-European settlement red spruce forests were dominated by a disturbance regime of small canopy gaps. As found in other forest types, it is likely that trees would have been taller and larger in old-growth forests and canopy gaps were likely larger on average compared to canopy gaps in current second-growth forests (Clebsch and Busing 1989; Ziegler 2000).

Canopy gap formation in second growth red spruce-northern hardwood forests of West Virginia is estimated to be about 1.4% of stand area per year based on ages of existing gaps (Rentch et al. 2010). Like in other red spruce-dominated forests, most gaps (65%) were created by the death of one or two trees; however, in the West Virginia study gaps were the result of the death of American beech (*Fagus grandifolia*) by beech bark disease (Rentch et al. 2010). Gap creation rates only tell part of the stand dynamics story even in forests dominated by a long lived and shade tolerant species such as red spruce. Gap closure rates differ by species composition of the stand. Where present, hardwoods in the canopy can quickly close a canopy gap by lateral expansion of branches. Consequently, existing red spruce seedlings and saplings will likely require more than one release event to reach the upper canopy status (Rentch et al. 2007). Gaps formed by the gradual decline and death of diseased trees, such as American beech following beech bark disease or eastern hemlock (*Tsuga canadensis*) following hemlock woolly adelgid (*Adelges tsug*ae), differ in character from gaps formed by sudden windthrow due to gradual changes in light levels. Additionally, repeated disturbances are more likely to expand existing gaps than create new gaps as trees on the edges of existing gaps are susceptible to uprooting by wind (Worrall et al. 2005).

The culmination of a disturbance regime dominated by small gap dynamics results in an uneven-aged forest structure with a reverse J-shaped distribution when stems per hectare are plotted by size class. To explore the structure of stands likely to be included in restoration efforts, a second growth (approximately 80 years old) red spruce-dominated forest in West Virginia was compared to an old-growth reference stand. Although the distribution of stem diameters showed second-growth structure and maximum DBH for red spruce trees was smaller than the reference stand, the study stand did have some characteristics of an old-growth forest, including similar basal area, snag density, and downed coarse woody debris (Schuler et al. 2002).

Although wind throw is the main creator of canopy gaps, ice storm damage is also very common in central hardwood and central Appalachian forests (Lafon 2016) and southern Appalachians (Nicholas and Zedaker 1989), and results in a disturbance

regime of intermediate severity (partial canopy removal or reduction) but potentially high frequency. The Appalachian Mountains are uniquely situated for continental air masses to interact with high elevation and complex terrain to produce weather events with heavy ice accumulations (Changnon and Karl 2003). Based on the analysis of climate and weather data, the Appalachian Mountains can experience up to four or five days with freezing rain annually (Changnon 2003). Combining tree ring records with documented accounts of ice storms in newspaper accounts has shown a return interval of 25 years for damaging ice events in southwest Virginia between 1914 and 1998 (Lafon and Speer 2002). Further, dendrochronology exposes a combination of ice storm effects on trees, with heavily damaged trees showing reduced growth and other stems showing increased radial growth (Lafon and Speer 2002). Even though the variation between sites and individual trees will occur, red spruce is considered resistant to ice or glaze damage (Lemon 1961) and in general this disturbance regime sustains shade tolerant and slow growing late successional forest species.

5.2.1.3 Influence of Rhododendron Species

Some upland communities dominated by red spruce include a significant heath family (*Ericaceae*) shrub component (Fig. 5.5). These communities are found at middle and lower elevations in red spruce-dominated and red spruce-northern hardwood forests, generally in sheltered locations such as concave sideslopes and cove landforms. While the canopy disturbance regime is still dominated by wind throw in these upland communities, the role of rhododendron species (predominantly *Rhododendron maximum*) is not trivial. Early descriptions of spruce communities noted that great laurel and red spruce combined to retain moisture and maintain cooler air temperatures (Allard and Leonard 1952). Studies in the southern Appalachians documented the influence of rhododendron species in lowering seedling density and light levels, and found limited recruitment of trees into gaps created where rhododendron dominated the shrub layer (Beckage et al. 2000). Rhododendron's ability to stabilize microsite shade, moisture, and temperature suggests that rhododendron could be considered a foundation species that adds stability in forests impacted by pests and climate change (Dudley et al. 2020).

Great laurel is widespread and abundant in the mountains of both the central and southern Appalachians, meeting the first criterion for a foundation species. Rhododendron species also can replace red spruce on toeslopes after fire, making red spruce reestablishment there more difficult due to negative impacts of dense rhododendron on soil and light, which hinders regeneration. Leaves and roots of great laurel are slow to decay and produce soils with lower nutrient levels, but higher organic matter, than those in sites without rhododendron (Beckage et al. 2000). Soil nitrogen, for example, is impacted by rhododendron through creation of compounds that inhibit nitrification (Wurzburger and Hendrick 2007). Although air under rhododendron thickets can be higher in moisture, soil moisture is lower (Clinton and Vose 1996), pH is lower, and aluminum content is higher (Horton et al. 2009) compared to deciduous overstories without rhododendron shrub layers. These conditions might also

Fig. 5.5 Example of a great laurel (*Rhododendron maximum*) understory in a red spruce (*Picea rubens*) forest along the Yellow Creek Trail in the Otter Creek Wilderness, Monongahela National Forest, Randolph County, West Virginia. Photo by Kelly Bridges

be expected in spruce forests, as red spruce also has recalcitrant leaf litter and the ability to acidify soils.

Once rhododendron is established it is difficult to remove either by natural disturbances or by management practices such as fire, cutting, or herbicide treatments (Harrell and Zedaker 2010). Consequently, rhododendron shrub layers afford resilience and resistance to changes in other ecosystem components even with loss or reduction of tree canopy (Beckage et al. 2000), although they also lower plant diversity and affect species composition through reduced seed germination and seedling recruitment (Stehn et al. 2011). Further, rhododendron's shallow rooting habit increases the potential for landslides when soils are saturated (Hwang et al. 2015), and severe droughts can lead to high fuel loading and flammability in dense rhododendron patches (Stottlemyer et al. 2009). However, current understanding of rhododendron effects on ecosystems is largely based on thickets in hardwood forests.

5.2.2 *Industrial Logging Era (1890–1940)*

Harvesting of the historical red spruce forest began in the late 1800s and became particularly intense from about 1920–1940 as roads and railroads penetrated even the most remote high elevations (Fig. 5.6; Pyle and Schafale 1988; Lewis 1998), resulting in clearcutting of whole watersheds. Accidental fires were frequent, but logged sites were also burned to remove slash, which, given the region's high rainfall, led to soil erosion. Many logged areas were burned twice (Korstian 1937). As a result, red spruce regeneration failed widely in the southern Appalachians due to loss of the seed bank and seed trees (Korstian 1937). In the Great Smoky Mountains, the lower limit of spruce-fir forests was displaced upward by approximately 200 m (650 ft) and the overall extent of this forest type was reduced by about one-third (Hayes et al. 2007) after broad-scale harvesting. Over a century after this historical logging, some logged, burned, and eroded slopes in the Smokies have not yet developed continuous tree cover (Lindsay and Bratton 1979; Peter White, personal observation).

Fig. 5.6 Sherwood Forest burn on the Pisgah NF; photo taken in April 1938. Bracken fern (*Pteridium aquilinum*) and blackberry (*Rubus* spp.) dominated the site after the fire and pin cherry (*Prunus pensylvanica*) is sparse or absent at this elevation (approximately 1,680 m [5,500 ft]). See Minckler (1939) for additional information. Photo by USDA Forest Service

The failure of post-logging regeneration has been related to several traits of red spruce: high fire sensitivity because of shallow roots, relatively thin bark early in life, slow growth rates, and resinous exudates (Korstian 1937). Further, red spruce requires damp substrates for seedling survival, and logging can reduce moisture in the forest floor (Brooks and Kyker-Snowman 2008). Mechanical disturbance from logging practices of the period damaged existing regeneration of red spruce and other shade tolerant species, and red spruce subsequently was outcompeted by hardwoods that sprouted prolifically from surviving root systems (unlike red spruce which do not sprout from roots or stumps) or those with light, wind-borne seed.

The few direct assessments of succession after logging have found both broadscale patterns and site-specific differences. Compared to those that were unlogged, logged sites in the southern Appalachians can have lower abundance of red spruce (Smith and Nicholas 1999; Soulé et al. 2012) and younger-aged spruce (Smith and Nicholas 1999), but higher tree diameter growth rates and recruitment into the canopy across all species (Smith and Nicholas 1999), as well as release of Fraser fir from the understory (Soulé et al. 2012). However, on Mt. Rogers in southwestern Virginia, maximum elevation is relatively low (1,747 m [5,700 ft]) and the elevation gradient from red spruce to Fraser fir dominance, which is typical in other areas of the southern Appalachians, does not occur. Here, logged stands, which ranged in age from 60 to 92 years, were found to be dominated by Fraser fir (importance value [i.e., the sum of relative density, relative frequency, and relative dominance] = 72), followed by red spruce (importance value = 21), mountain ash (*Sorbus americana*; importance value = 5.4), and yellow birch (importance value = 1; Stephenson and Adams 1984). Compared to a survey in the 1950s, mountain ash and yellow birch had increased in importance. Despite the observed site-level differences, Smith and Nicholas (1999) concluded that it likely would be many decades before the "forest communities resembled those in old growth areas."

From studies on second growth forests, we can construct general models of post-logging succession in which effects of logging vary with magnitude of logging and pre-logging composition (and thus elevation). These general dynamics for the main upland spruce communities are depicted in the conceptual state and transition models in Fig. 5.7. In the broad-scale logging era, red spruce failed to reproduce, or at least failed to reproduce as quickly as other species (Korstian 1937) where harvests were most intense. Where harvests occurred with partial removal of canopy trees and minimal soil and understory damage, post-logging forest dynamics depended on composition. If the understory was dominated by Fraser fir, as is typical at low and mid-elevations within the range of red spruce forests, then Fraser fir increased. If hardwoods were present in the overstory and understory, as is typical at lower elevations within the range of red spruce forests, hardwood sprouting and seedling establishment likely dominated the resulting young forest. In contrast, if large areas were cut, and particularly if the soil was damaged by fire and soil erosion, colonization by early successional species like pin cherry and blackberry (*Rubus* spp.) predominated. At higher elevations and in forests in which Fraser fir was a dominant or co-dominant and with advance Fraser fir regeneration, balsam woolly adelgid

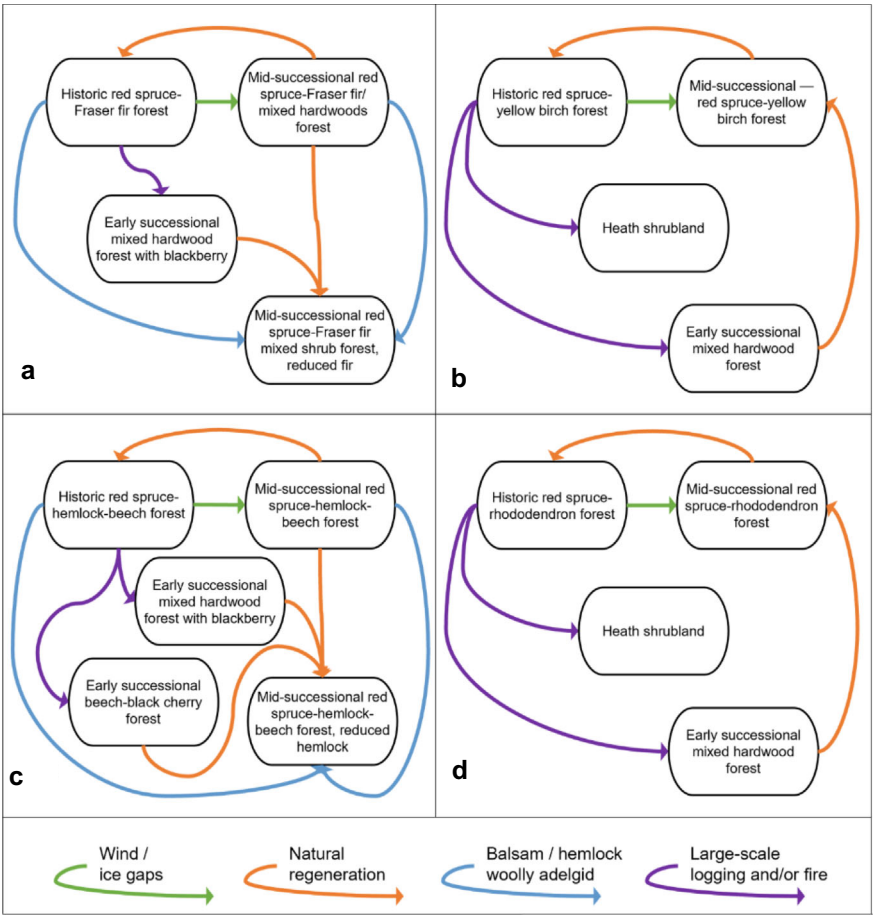

Fig. 5.7 Conceptual model of historical red spruce (*Picea rubens*)-dominated forest states and transitions through biotic and abiotic disturbances. Historical red spruce-Fraser fir (*Abies fraseri*) forest (A), historical red spruce-yellow birch (*Betula alleghaniensis*) forest (B), red spruce-hemlock (*Tsuga*)-beech (*Fagus*) forest (C), and historical red spruce-rhododendron (*Rhododendron*) forest (D)

creates a second episode of disturbance, leading to a recovering stand of young Fraser fir (further discussed in Sect. 5.2.3).

5.2.3 Balsam Woolly Adelgid—Southern Appalachians

The balsam woolly adelgid, a Eurasian invasive species, was first detected in the Black Mountains of North Carolina in 1957, apparently after it had been transported to the

region on infested nursery stock (Eagar 1984; McManamay et al. 2011). Over the next three decades, balsam woolly adelgids spread throughout the range of Fraser fir, causing near complete mortality of canopy Fraser fir trees (Allen and Kupfer 2000, 2001). While the balsam woolly adelgid has relatively minor effects on fir seedlings and saplings, mature trees typically succumb within seven years of infestation because this sap-sucking insect feeds in bark crevices that develop over time, setting off a wound reaction in fir stems that greatly damages the function of the sapwood (Eagar 1984). The adelgid disperses on wind currents and eddies produced by ridgelines which caused balsam woolly adelgid populations to settle first in the lower elevation part of the Fraser fir range, followed by movement upslope (Allen and Kupfer 2000, 2001). From its initial establishment, the geographic pattern of balsam woolly adelgid-caused mortality followed from its pattern of dispersal. For example, Allen and Kupfer (2000, 2001) used remote sensing imagery to document the pattern of Fraser fir mortality from 1988 to 1998 in the Great Smoky Mountains, finding nearly complete canopy tree mortality moving from east to west and from the lower elevation part of the Fraser fir range to higher elevations. As part of a larger assessment, aerial photography and ground-based sampling in the mid-1980s documented 26,610 ha (65,752 ac) of spruce-fir forest with 24% classed as severe mortality, 6% as heavy, and 70% as light mortality (Dull et al. 1988).

Smaller stems do not become vulnerable to the balsam woolly adelgid until they are large enough to develop bark crevices; thus, the initial waves of Fraser fir mortality left behind a high density of younger stems. These are now contributing to recovery of the Fraser fir population (Boner 1979; Smith and Nicholas 1998, 1999; Jenkins 2003; Moore et al. 2008; Bowers et al. 2010; Lusk et al. 2010; McManamay et al. 2011; Soulé et al. 2012; Stehn et al. 2013; Kaylor et al. 2017). For example, in spruce-fir forests of the Great Smoky Mountains, biomass was stable overall (around 260 megagrams [Mg]/ha [105 Mg/ac]), but Fraser fir biomass increased from 3.3 to 12.7 Mg/ha (1.3–5.1 Mg/ac) between 1993 and 2003 (Moore et al. 2008). However, Fraser fir recovery may be weaker in the lower part of its elevation range (McManamay et al. 2011).

It is uncertain whether patches of healthy Fraser fir will survive long enough to provide seeds for future generations and open the possibility of long-term persistence (Dale et al. 1991; Smith and Nicholas 2000; Moore et al. 2008). Eagar (1984) noted that the time to develop bark fissures is shorter than the time required for cone production, suggesting a likely decline of Fraser fir populations in the future despite perceived recovery. On the other hand, it is possible that the balsam woolly adelgid and Fraser fir will continue to coexist through a patch dynamic in which the balsam woolly adelgid becomes locally scarce (since it does not thrive on younger stems), allowing Fraser fir stands time to reproduce because there is a delayed recolonization by balsam woolly adelgids, resulting in increasing patchiness of Fraser fir populations. Additionally, clones of Fraser fir showed potential resistance to the balsam woolly adelgid through production of sesquiterpenes, which may be useful indicators of genetically resistant genotypes (Thomas et al. 2022).

Although the balsam woolly adelgid does not attack red spruce directly, the sudden loss of Fraser fir canopy has been shown to shift the cause of red spruce mortality

(Busing and Clebsch 1988; Busing et al. 1988; Busing and Wu 1990; Pauley and Clebsch 1990; Busing and Pauley 1994; Wu et al. 1999; Busing 2004). In spruce-fir forests of Great Smoky Mountains National Park, increases in red spruce tree mortality rates over time were attributed to the sudden death of Fraser fir exposing spruce to more wind damage, especially on exposed topographic positions (Busing 2004). Interestingly, dendrochronological analysis of those dead red spruce at Mt. Collins in the Great Smoky Mountains showed that mortality was not associated with reduced radial growth. This finding contradicts the hypothesis that acid rain was causing the red spruce mortality because, if acid rain was responsible, reduced radial growth would accompany increased mortality. The sharp increase of Fraser fir and red spruce mortality produced a large increase (93–132%) in red spruce sapling density (Busing et al. 1988). Nonetheless, live basal area in these stands declined by 50%.

5.2.4 Pollutant Deposition and Exposure

Pollutant deposition and exposure have been the subject of much research in the central and southern Appalachians (Eagar and Adams 1992; Rosenberg and Butcher 2010; see also Chap. 3). Pollutant deposition and exposure in the Appalachians increased from the 1960s to the 1980s and then declined from the 1990s onward, as the Clean Air Act (1970, as amended 1977 and 1990) led to reduction of emissions from industrial point sources in regions to the west and northwest of the Appalachians (Moore et al. 2002; Lawrence and Bailey 2021). Along with rainfall and cloud immersion, pollutant deposition and exposure increase with elevation. The elevation gradient has therefore been used to determine how spruce forests respond to various levels of exposure (e.g., Berry et al. 2014). Spruce-fir forests in the southern Appalachians are immersed in clouds 25–40% of the time and one third to one-half of all water at upper elevation sites derives from cloud immersion (Aneja et al. 1992; Reinhardt and Smith 2008). Cloud-intercepted water is more acidic (pH = 2.5–4.5) than rainwater (pH = 3.5–5.5; Aneja et al. 1992).

As reviewed in Chap. 3, acid exposure resulted in leached cation nutrients from red spruce needles, made soil cations vulnerable to leaching, reduced cation retention in soils, and led to a reduction in calcium to aluminum ratios to potentially toxic aluminum levels (e.g., McLaughlin et al. 1991). These effects were superimposed on soils that are naturally acidic and poorly buffered, and a number of studies have shown declining nutrient cations and low calcium to aluminum ratios that are correlated with toxicity in soils (Robarge et al. 1989; Joslin and Wolfe 1992; Bintz and Butcher 2007; Rosenberg and Butcher 2010; Stehn et al. 2013). There are five documented physiological effects of this acidification on red spruce (McLaughlin et al. 1993, 1995; McLaughlin and Percy 1999): (1) a decrease in cold hardiness and, at least in the northern Appalachians, subsequent winter damage (Thornton et al. 1994); (2) an increase in respiration and a decrease in photosynthesis (McLaughlin et al. 1990, 1991, 1993); (3) membrane disruption and foliar injury, including needle

speckling (DeHayes et al. 1999); (4) lessened response to water stress because of effects on leaf stomata (Borer et al. 2005); and (5) potential aluminum toxicity to growth of fine roots (Schier 1985). McLaughlin et al. (1995) tied many of these changes to reduced calcium availability, especially membrane-associated calcium. Work by Stehn et al. (2010, 2011, 2013) suggests heterogeneous effects of acidification that affect regeneration, including local hotspots of high nitrogen and increased competition, hotspots of aluminum levels toxic to sensitive species, and acidification that favors members of the heath family (e.g., *Rhododendron*) whose acidic and slow decaying leaf litter reinforces the acidification effect.

A similar loss of cations and decrease in the calcium to aluminum ratio in red spruce tissues as soils become acidified was found at Whitetop Mountain, Virginia (Joslin et al. 1992). In contrast, another study that sampled sites in Virginia, West Virginia, and Tennessee found that foliar and soil cations were only weakly correlated, aluminum levels were "well below toxic levels," and cation concentrations were not indicative of deficiencies (Bryant et al. 1997). However, the authors noted that they had no high elevation sites, suggesting that perhaps the greatest acidification results occur only at the highest elevations (>1,800 m [6,000 ft]). As described below, red spruce and spruce-fir forests are generally considered to be "healthy," with the most dramatic changes occurring during recovery from balsam woolly adelgid infestation and recovery from earlier exploitative logging. However, pollutant deposition and exposure, though at reduced levels since the 1990s, continues. Further, impacts from climate change are just beginning to be studied.

Although elevated mortality of red spruce was widespread in the northern Appalachians in the 1960s to the 1980s, Johnson et al. (1992), summarizing a decade of research on southern Appalachian forests, concluded that widespread mortality had not occurred in this region (e.g., Busing et al. 1988; McLaughlin et al. 1990, 1998; Cook and Zedaker 1992; Johnson et al. 1992; Busing and Pauley 1994; Smith and Nicholas 1999). Further, evidence for red spruce growth declines linked to pollution is mixed with some studies finding growth declines, particularly at the highest elevation study sites (McLaughlin et al. 1990, 1994, 1998; McLaughlin and Percy 1999; White et al. 2014), and some studies finding no growth declines (Busing and Wu 1990; Cook and Zedaker 1992; Busing 2004; Soulé 2011). Indeed, research since 2000 suggests that there is no ongoing decline in red spruce growth (Bowers et al. 2010; Lusk et al. 2010; Mathias and Thomas 2018). Nowacki et al. (2010), stated "no problems found for red spruce recruitment under current climate" and suggested that red spruce populations were increasing, perhaps recovering, albeit slowly, in some of the areas that had been lost during the wave of clearcut logging and logging slash fires in the late 1800s to early 1900s. In addition, a positive trend in radial growth rates of red spruce was found on Grandfather Mountain in the southern Appalachians (Soulé 2011). From these studies, it does not appear that pollutant deposition and exposure have, by themselves, caused a change in the dynamics of forests dominated or co-dominated by red spruce. However, research has also suggested that there is a more chronic, longer-term issue: ongoing ecosystem acidification. In the long-term, this could slow element recycling rates and has the potential to affect community dynamics in the future, particularly if tolerances of some species are exceeded and

species differ in their responses (Nodvin et al. 1995; Pardo et al. 2018). Acidification stress will likely interact with climate change. Further, stream ecosystems have experienced greater acidification effects and have had a slower response to recent reductions in pollutant emissions because differing rates of soil retention of sulfur and nitrogen pollutants create a lag in release and cycling of these nutrients (Pardo and Duarte 2007; Fakhraei et al. 2016), meaning forest restoration may fail to result in immediate changes in stream chemistry. Given these longer-term uncertainties, monitoring of key species and environmental factors will be needed.

5.2.5 Climate Change

Red spruce and spruce-fir forests are the highest elevation forested ecosystems in the central and southern Appalachians and are dependent on the cool and wet conditions that prevail at these elevations. As a result, they form a series of *sky islands* where mountains reach sufficient elevation, from Shenandoah National Park in Virginia and south to the high mountains of North Carolina and Tennessee. In the central Appalachians of West Virginia red spruce-dominated forests are found over larger areas and are less isolated, although still found at higher elevations. A straightforward expectation is that climate warming will cause these islands to become smaller as the ideal environmental conditions move to higher elevations (Potter et al. 2010). Red spruce and spruce-fir forests will likely disappear from mountains that are not tall enough to provide the environmental conditions necessary for these forests. For example, Walter et al. (2017) predicted that the area of habitat supportive of red spruce would decline from the present day to the year 2100, but "the magnitude of this decline depended on the level of carbon emissions, and there was considerable variability between climate models."Red spruce has been ranked as the most vulnerable of 40 tree species to climate change, followed by two other frequent associates of red spruce, yellow birch, and balsam fir (Rogers et al. 2016). Thus, red spruce and spruce-fir forests have frequently been called the most threatened forest ecosystem in the eastern U.S. (e.g., McLaughlin et al. 1998). Please also see Chap. 7 for more in-depth discussions of the topics covered here and for more information.

Current models for red spruce documented in the Forest Ecosystem Atlas (https://www.fs.usda.gov/nrs/atlas/tree/97) conclude that habitat suitability is expected to decline range-wide, and that red spruce is considered to have low adaptability to change and poor ability to adapt to climate change (Peters et al. 2020). However, red spruce climate adaptability can be explored at different scales. In the central Appalachian Mountains, climate forecasting results suggested that red spruce in northern latitudes on south aspects or central latitudes on north aspects will likely be the most resilient to future climate change due to increases in monthly minimum temperatures and extended growing seasons (Yetter et al. 2021). Site-specific dendroclimatic results and future growth projections can assist with identifying locations that are most suitable for future red spruce restoration activities.

Climate change has the potential to reduce the amount of area suitable for supporting red spruce, and thus effects of climate change on the distribution of suitable habitat is an important management consideration. However, research in northeastern spruce-fir forests supports the need to consider the historical range of spruce in predicting future distributions. Along these lines, Andrews et al. (2021) found that models that included historical data predicted persistence of spruce-fir, while models that did not include historical data predicted extirpation of spruce-fir forests. Further, mountain spruce-fir ecotones in New England have been found to be changing in complex ways, with some expanding downslope, rather than upslope (Foster and D'Amato 2015, 2018), likely due to ongoing response to historical disturbances. Declining range is not, however, the entire story, as researchers have noted that red spruce only partially occupies some suitable habitats because of past logging impacts (Walter et al 2017). There are opportunities to expand spruce and fir forests through restoration of sites where this forest failed to regenerate after the intense logging of the early 1900s (Morin and Widmann 2010; Nowacki et al. 2010; Yetter et al. 2021).

Although species distribution models have produced useful perspectives, more complex models that incorporate important factors like pollutant deposition, disturbance rates, demographic processes like seed production and establishment, competitive interactions (for example, with evergreen shrubs), and ecosystem processes such as nutrient cycling are needed. For example, Koo et al. (2011, 2014, 2015) built a more complex model to include these kinds of factors by adding demographic modeling and individual tree growth to a habitat model. Under climate change projections and three pollution scenarios (10% increase, no change, and 10% decrease) they found that lower elevation populations of red spruce are most at risk (Koo et al. 2015). Clouds and precipitation are important to these forests but harder to predict than temperature change. At the very least, ecological complexity and the uncertainty of future climate changes and emission levels make a strong case for further research and a long-term program of monitoring red spruce populations and environmental parameters, even as restoration efforts occur.

Because red spruce and spruce-fir forests are dependent on high moisture supply, the effect of climate change on precipitation and cloud immersion is critical (Berry et al. 2014). Red spruce radial growth can be positive with warmer temperatures as long as moisture is not limiting (Soulé 2011; Ribbons 2014), although warmer temperatures may increase competition with warm-adapted species moving into red spruce territory. Berry and Smith (2012, 2013) found that xylem water potentials decreased with lower cloud immersion and, as a result, photosynthesis, carbon gain, leaf conductance, and growth of seedlings and saplings decreased. Red spruce has also been found to grow faster when the previous winter and current growing season were warmer (Soulé 2011). There was a positive correlation with CO_2 and a negative correlation with sulfur and nitrogen oxide exposure (Soulé 2011). White et al. (2014) showed that the correlation between red spruce radial growth and temperature changed after logging, where the correlation was positive before the 1930s and then became negative, possibly because of an effect of logging on soil properties, leading to drier conditions during warm temperatures. As noted above, McLaughlin et al.

(1994) hypothesized that red spruce growth became insensitive to climate variation under acidification effects.

Some researchers have asserted that the average cloud ceiling sets the lower boundary of spruce-fir forests and, in a Vermont study, that climate change is causing that ceiling to move to higher elevations (Richardson et al. 2003). In the Great Smoky Mountains, low elevation sites tracked regional weather patterns more closely than high elevation sites, suggesting the importance of cloud immersion and high rainfall in buffering temperature change (Fridley 2009). Low elevations also warmed during regional warm periods, but high elevation sites experienced less warming. Red spruce and spruce-fir forests at lower elevations may be more vulnerable to the rate and magnitude of temperature change than those at higher elevations. Patterns of cloud immersion and precipitation will likely change as a function of climate change. However, this reasoning also depends on whether regionally warm periods are a good analogy for future warming—that is, the nighttime-daytime contrast in temperatures and seasonal differences in warming may be more important in future climates than they are in contemporary warm periods.

In complex mountain landscapes, the degree of climate change will not be constant across topographic gradients. Rather, the degree of change is itself a function of those topographic variables. Some sites may be relatively stable and resilient over time, while others change more dramatically. This question has been examined directly in the central and southern Appalachians. Temperature across the region at a 4 km (2.5 mi) scale showed clear differences in the degree of temperature variability in the years 1950–2005; mountaintops had more stable temperatures over time (Nelson 2017). Temperature sensitivity is a factor for choosing restoration sites using fine-scale environmental analysis and for continued monitoring of environmental change at small scales to analyze the effect of changing climates on active restoration.

Disjunct low elevation red spruce populations in wetlands may be particularly vulnerable to future climates that are drier and warmer. The Alarka Creek headwaters basin is among the lowest elevation and southernmost of these wetlands in the southern Appalachians (Schafale and Weakley 1990; White and Cogbill 1992; Collins et al. 2010). This site has a mixed canopy of red spruce, American serviceberry (*Amelanchier arborea*), sweet birch (*Betula lenta*), and other hardwoods, with red spruce more abundant than hardwoods in the larger size classes (Collins et al. 2010). The understory has a patchy, but dense, shrub layer of great laurel (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) on gully tops (Collins et al. 2010). Vegetation and tree ring analyses found that red spruce seedlings and saplings ranged from 0.5 to s4 m (1.6–13.1 ft) tall; overstory tree ages ranged up to 155 years with a linear population structure, suggesting steady spruce recruitment over the last hundred years (Collins et al. 2010). However, drops in diameter growth in the 1930s and late 1990s correlated with widespread drought and a regional pine beetle outbreak, respectively (Collins et al. 2010). Thus, while red spruce in sheltered basins with cold air drainage, such as the Alarka basin, may persist at lower elevations, they may be sensitive to periods of extreme drought or pest outbreaks.

5.3 Management Implications

Efforts are underway to restore and manage red spruce and spruce-fir forests using non-commercial and commercial methods (see Chaps. 8 and 9). Active restoration efforts rely, in part, on restoring historical disturbance regimes, including fine-scale canopy gaps and soil disturbance associated with tree blowdowns. Non-commercial actions include canopy release of red spruce stems to increase their height growth and accelerate their advancement to the overstory. These targeted treatments mimic the multiple release events resulting from ice storms and wind throw that make up the dominant disturbance regime of these forests.

In the central Appalachians, two examples of simulated stand-level forest management show potential success in increasing stand-level red spruce basal area and individual tree diameter growth through thinning. Using actual stand data, Schuler et al. (2002) compared two thinning treatments to no management over 50 years. The time to develop old-growth structural characteristics could be shortened by thinning smaller-sized trees and removing at most 50% of the existing basal area (Schuler et al. 2002). In a larger study involving more study areas, simulated treatments where 50% of the basal area was removed to release understory red spruce resulted in a near doubling of red spruce basal area (Rentch et al. 2007). The treatment in this simulation was a one-time release event or liberation cut where all trees that overtopped targeted red spruce were removed. A similar release of targeted red spruce from overtopping hardwoods was also tried in a field experiment in West Virginia (Rentch et al. 2016). Three levels of release were implemented on target red spruce trees of >2.54 cm (1 in) DBH, overtopping trees were killed through stem injection of herbicide, and height and DBH of target trees tracked for six years. The treatment that provided the highest level of release resulted in the largest change in height and DBH growth, although increases were of small magnitude (Rentch et al. 2016).

Traditional silviculture guides, developed without considering restoration, suggest single tree selection and group selection for commercial management (Blum et al. 1983). Even-aged practices are mentioned but a caution is given that planting may be necessary due to the failure of red spruce to compete (Blum et al. 1983). Red spruce has been successfully regenerated and managed using a variety of thinning or partial cutting methods in northern areas (e.g., Pothier and Prévost 2008; Olsen et al. 2014). Studies utilizing operational-scale treatments such as commercial timber harvesting to promote seedling development are lacking for the central Appalachian red spruce stands. Using commercial treatments to accelerate the development of advance spruce regeneration in hardwood-dominated stands can substantially shorten the time needed to increase the coverage of red spruce forest communities across the landscape. However, specific guidelines for promoting the development of advance reproduction and subsequent ascension into the canopy are lacking for central and southern Appalachian forests.

Unlike the red spruce forests of central and southern Appalachia, which are relatively rare and largely second growth, current red spruce-dominated forests in New England have undergone multiple harvests, resulting in simplified age structures and

altered species composition (Seymour 2005). To mimic natural stand dynamics in these forests with silvicultural practices, a hybrid system that combines shelterwood with reserves and group selection has been proposed. In this system, similar to the German *Femelschlag*, canopy gaps are created and over several cutting cycles are expanded in size (Seymour 2005). Ten-year results of this expanding-gap method of group selection in Maine show that larger gaps (>0.1 ha [0.25 ac]) favored mid-successional species and gaps smaller than that threshold favored shade tolerant species (Arseneault et al. 2011).

Given the unknowns, any restoration action for spruce forests will need to be adaptive to changing conditions and will benefit from intensive and detailed monitoring. Regardless of the restoration action chosen, non-commercial release of individual red spruce trees to commercial scale expanding gap shelterwood prescriptions should consider the range of attributes, such as gap size or return intervals, and not manage strictly for the average. More details of current restoration efforts are found in Chap. 8.

5.4 Knowledge Gaps and Research Needs

While silvicultural prescriptions for commercial management of red spruce-dominated forests are in use in forests in New England and Canada, demonstrated success for commercial scale management is lacking for the central and southern Appalachians. Management goals will differ when active management is used for restoration rather than production of pulp or lumber. Research efforts are underway at the Kumbrabow State Forest in West Virginia to test a version of expanding gap shelterwood (*Femelschlag*) harvest for restoration of red spruce at a commercial scale.

While environmental regulations have resulted in reduced deposition of sulfur and nitrogen, there may be lingering effects of pollutants on red spruce forests, and questions remain about the recovery of these systems from decades of acidic deposition. There are also gaps in our knowledge of the impacts other pollutants have had or are continuing to have on these forests. These effects could also amplify predicted impacts of climate change. Red spruce-dominated forests were refugia for past climate change events but impacts from current anthropogenic climate change might override this capacity.

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