Chapter 1
History and Biogeography

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The flora of the eastern United States is a fortuitous grab bag of species, the survivors of 16 to 18 glacial-interglacial cycles.
-Davis 1981

1.1 Introduction

Red spruce (*Picea rubens*) is a coniferous tree native to the eastern U.S. (Fig. 1.1), ranging from eastern Canada and New England south along the Appalachian Mountains, where it occurs in disjunct populations in Pennsylvania, West Virginia, Virginia, North Carolina, and Tennessee. Red spruce-dominated forests (i.e., ≥ 50% of the canopy trees are red spruce) occur in near-boreal regions in the northern U.S. and Canada, temperate forests in the central part of their range, and montane *sky islands* in the southern part of their range. Temperature and moisture drive the distribution of red spruce, with latitudinal dynamics driving the distribution in the northern part of the range and elevational and climatic complexes driving the distribution in the southern parts of the range (White and Cogbill 1992). For example, red spruce occurs at sea level north of the St. Lawrence River and at over 1,700 m (5,500 ft) in elevation in the southern Appalachians.

The distribution of red spruce has oscillated over time with climatic changes and disturbance factors—the latter having profound effects over the last 150 years due to Euro-American activities, specifically logging and human-ignited wildfires (Korstian 1937; Clarkson 1964; Pielke 1981). How these disturbances have affected red

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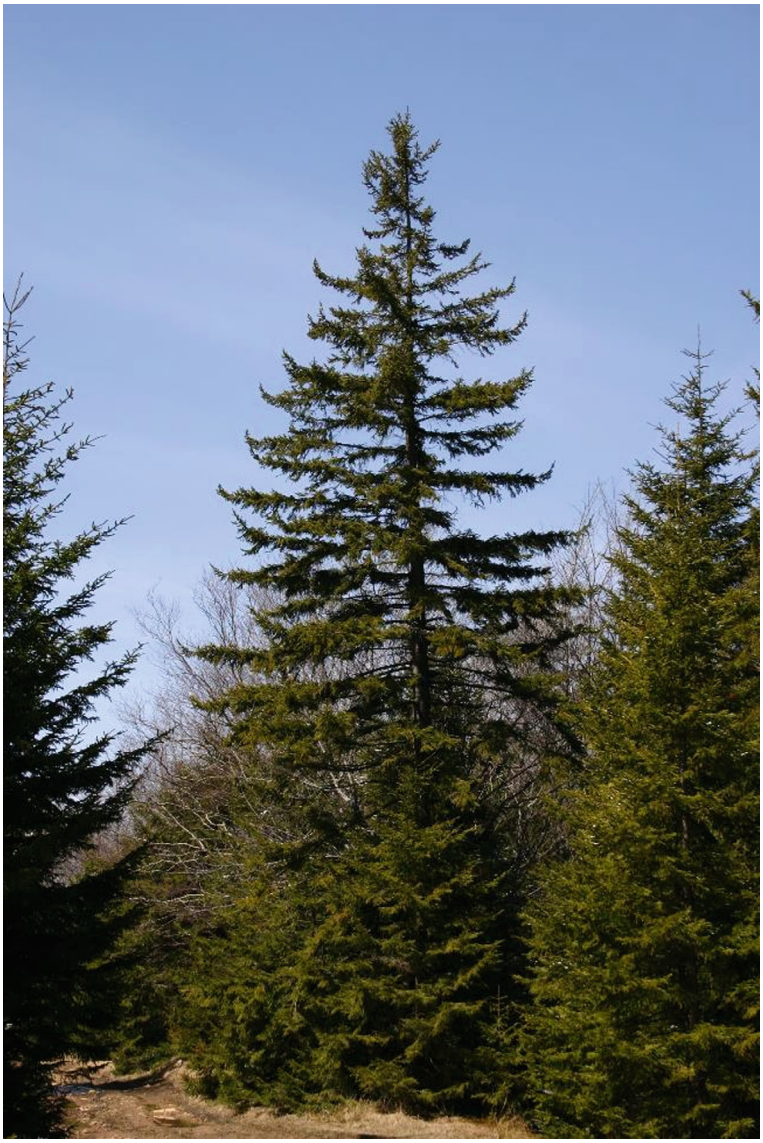

Fig. 1.1 Red spruce (*Picea rubens*) on Cabin Mountain, West Virginia (photo by Marquett Crockett)

spruce genetics are described more fully in Sect. 7.2.3 of Chap. 7. Active management and restoration of red spruce forests requires an understanding of their history and factors influencing their biogeography. For example, this information may help to determine how stressors such as climate change may influence the future distribution of red spruce forests (see Chap. 7). In this chapter, we discuss past and

current geographic distributions of red spruce and review how environmental factors influence occurrence of the species throughout its range.

1.1.1 Distribution

1.1.2 Paleohistory

During the last glacial maximum 18,000 YBP, ice sheets covered the continent north of Pennsylvania and New Jersey including parts of the continental shelf exposed by the lowered sea level. Beyond a narrow treeless zone in front of the ice, the land in eastern North America was covered with an open boreal woodland of spruce (*Picea* spp.) species (Delcourt and Delcourt 1981; Davis 1983). Closed-canopy conifer forests occurred further south to at least the Carolinas, with pine (*Pinus* spp.) becoming dominant. In the southeastern U.S., mixed hardwood forests were found consisting of all the common tree species surviving today, with the addition of another temperate spruce (*Picea critchfieldii*), which was common and widespread during the Pleistocene, but did not survive through the Holocene (Jackson and Weng 1999). With climatic warming and glacial retreat marking the end of the Pleistocene (Fig. 1.2), the trees closest to the retreating glacial edge subsequently migrated slowly northward. Pollen core and macrofossil data indicate that primarily white spruce (*Picea glauca*), followed by black spruce (*Picea mariana*), invaded the recently deglaciated land. This forest passed the former glacial front at 14,000 YBP in present-day Pennsylvania and expanded to northern latitudes, arriving north of the St. Lawrence River around 9,000 YBP.

In about 9,000 years, the spruce forest had migrated < 750 km (466 mi) from the maximum glacial extent to the present boreal region. Nearly all areas along this northward expansion zone were dominated by a boreal spruce ecosystem for approximately 2,000 years, including co-dominant species such as jack pine (*Pinus banksiana*) and aspens (*Populus* spp.). As this boreal spruce forest retreated north, pollen counts of any spruce species dropped precipitously starting at 9,000 YBP within the southern U.S. Across the eastern U.S., all areas then had a zone of temperate species (white pine [*Pinus strobus*], eastern hemlock [*Tsuga canadensis*], and northern hardwoods), with a marked hiatus of any spruce pollen from 8,000 to 2,000 YBP (Davis 1983). Spruce pollen then rose dramatically in New York, northern New England, and the coastal regions at northern latitudes, indicating the rapid expansion of red spruce in the last 2,000 years (Spear 1989; Jackson and Whitehead 1991). This southward expansion of spruce corresponds to (and was undoubtedly driven by) a cooler and wetter climate, known as the neoglacial period (see Fig. 1.2 and Fig. 1 in Abrams and Nowacki 2015).

Red spruce is closely related to black spruce, but diverged presumably through geographic isolation when driven south by colder climates and glacial advances in the mid-Pleistocene (ca. 400,000 YBP; Jaramillo-Correa and Bosquet 2003). The

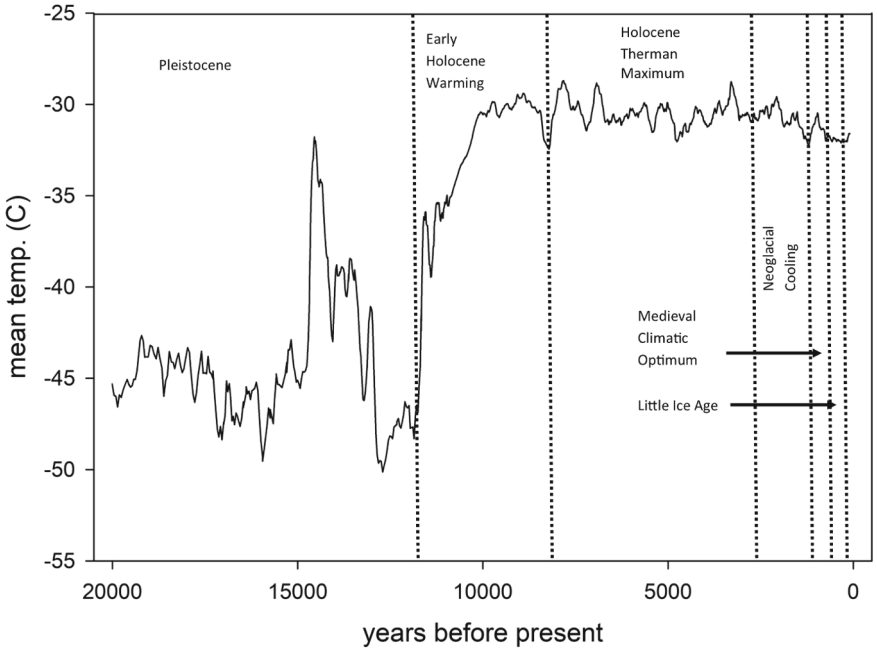

Fig. 1.2 Mean air temperature (°C) in the northern hemisphere based on central Greenland ice core data (GISP2 Ice Core; Alley 2004) spanning 20,000 YBP

species must have gone through subsequent geographic separation during several interglacial cycles. After isolation at the end of the last glacial maximum, red spruce overlapped with black spruce and hybridized during the early Holocene (Bashalkhanov et al. 2023), and now these species readily hybridize, especially in the northeastern extent of its range (Manley 1972; Perron and Bousquet 2003; Jaramillo-Correa and Bousquet 2005). The genetic structure of red spruce shows a geographic pattern confirming the general history of Holocene migrations after the last glacial maximum. There are three ancestry groups of red spruce haplotypes (Capblancq et al. 2020; see Chap. 7). The first genotype covers separated, high-elevation forests from the central and southern Appalachians. The second genotype combines the entire northern contiguous distribution including the Catskill Mountains. The third genotype from geographical intermediate Pennsylvania (Pocono Mountains, Bear Meadows) is divergent from the southern sites but contains elements from the intermediate northern sites. The genetic data, together with biogeographic, paleohistoric, and the non-montane setting, support the idea that the Pennsylvania populations are distinct from either the northern or southern mountains and not remnant populations left behind from a northern migration.

Red spruce pollen was only weakly represented in southern Pennsylvania and Massachusetts in the early Holocene prior to 11,000 YBP (Watts 1979; Lindbladh et al. 2003). Confirmed historical occurrence of red spruce north of Pennsylvania

began during the early stages of the Holocene Thermal Maximum, wherein continuous red spruce pollen occurred in several extreme coastal sites in Maine and with macrofossils at mid-elevations in the northern Appalachian Mountains. During the mid and late stages of the Holocene Thermal Maximum (9,000–2,000 YBP), spruce pollen had low scattered abundance in the Adirondack and White Mountains, but sediment samples had significant spruce macrofossils. Although pollen can be a poor indicator of tree abundance (Abrams and Nowacki 2019), macrofossils in both the White Mountains and the Adirondacks indicate that spruce had a continuous, but not dominant, presence at an elevational range of 850–1,150 m (2,800–3,800 ft) through the mid-Holocene (Spear 1989; Jackson and Whitehead 1991).

Although the late-Pleistocene refugia for red spruce are unclear, they were south of the maximum extent of glacial ice, including presently submerged surfaces along the Atlantic shoreline (approximately 120 m [400 ft] below current sea level). Judging from the prominence and current outliers east of the Appalachian Mountains, red spruce survived the glaciations cryptically somewhere between New Jersey and the Carolinas. Red spruce refugia were most likely cool, foggy coastal areas, possibly including the exposed and unglaciated continental shelf that is now below sea level. Red spruce most likely migrated north as part of the post-glacial boreal spruce wave. The spruce-dominated woodlands near the glacial maximum at 13,000–10,500 YBP contained American mastodons (*Mammut americanum*) and predominantly white spruce macrofossils just south of retreating glaciers and in Pleistocene coastal regions (Feranec et al. 2021). Although minor and mixed with the two other spruce species, pollen evidence indicates that red spruce was present in Massachusetts and Maine at 11,000–10,000 YBP (Lindbladh et al. 2003). Limited evidence also indicates red spruce pollen at 10,000–9,000 YBP in south-central Pennsylvania in the rearguard of the post-glacial spruce migration (Watts 1979). Then, for at least the second time, red spruce was restricted to refugia from 8,000–3,000 YBP. This is well after the boreal white and black spruces had migrated north or remained as isolated remnants in wetlands. Spruce pollen deposited in the mid-Holocene in montane and coastal habitats of south-central Pennsylvania was not identified to species, but was most likely red spruce because of the site conditions and because white and black spruces were restricted to isolated wetlands at that time (Schauffler and Jacobson 2002).

One refugium for red spruce in the hiatus was certainly along the Atlantic coast in the Canadian Maritimes and coastal Maine, where spruce pollen was moderate and continuous in the mid-Holocene (Schauffler and Jacobson 2002). It is likely that red spruce survived inland in interior valleys or moist, cool conditions similar to the present-day lakeshore, streamside, swamp, or bog margin habitats of relict populations, such as Mann's bog and War Spur in Virginia. Red spruce also survived in mixed forests such as isolated patches from Maine to New York, where it then had a rapid and synchronized population explosion in the last 2,000 years. Importantly, there was too little time for spruce to have migrated from known refugia along the coast, so spruce must have been in place before the late-Holocene expansion. Regardless of the refugia, the recent rise of spruce pollen throughout the area south of the current boreal forest zone was not due to black spruce expansion during the Neoglacial Cooling Period of the late-Holocene. The spruce pollen resurgence over

the last 2,000 years was undoubtedly red spruce expanding to occupy its current continuous range in the north during this cool period.

According to Watts (1979), spruce pollen is missing from mid-Holocene sediment cores at lower elevation sites in Virginia and Pennsylvania, apparently indicating no evidence of red spruce movement across the gap between the southern and northern mountains known as the Pennsylvania Saddle (Nowacki et al. 2010). The source for the handful of current spruce remnant sites within this saddle is unclear, because both red and black spruce are morphologically, genetically, and palynologically problematic at peripheral populations (e.g., at Bear Meadows, Pennsylvania; Morgenstern and Farrar 1964; Gordon 1976; Bobola et al. 1996; Capblancq et al. 2020). What is certain is that there was no northern migration of red spruce along the continuous uplands. The spruce range in West Virginia occurs beyond the current range of black spruce, thus interpretation of spruce pollen is unambiguous. Unfortunately, the few pollen diagrams available in West Virginia are at low elevations and even those where red spruce presently grows (e.g., Cranesville Swamp [Cox 1968], Cranberry Glades [Watts 1979]) display a spruce pollen hiatus in the mid-Holocene. In poorly drained sites or valleys with cold air drainages, red spruce in West Virginia can be found down to 760 m (2,500 ft) elevation (Cogbill and White 1991), with individual red spruce witness trees found as low as 509 m (1,670 ft; Thomas-Van Gundy et al. 2012). Regardless, red spruce obviously survived in the moist, cool environments on the higher mountains through the Holocene and is now abundant on the four ridges that are over 1,190 m (3,900 ft) elevation in West Virginia.

Unfortunately, there is little pollen or macrofossil evidence to show the migration history of red spruce at the southern end of the range. Therefore, any surmise about the Holocene history of the southern Appalachians is based primarily on the current biogeography. In the early Holocene, the highest elevations of the Appalachian Mountains had a periglacial environment above forests at lower elevations, leaving frost-riven substrates which were presumably treeless (Delcourt and Delcourt 1985). As the climate warmed, the surrounding spruce-pine forest moved north and the only remnant stands, presumably red spruce together with the endemic Fraser fir (*Abies fraseri*), remained in the southern Appalachians.

Given the lack of paleoecological information for the southern Appalachians, the geographic setting of the current forest has been used to interpret the past. Whittaker (1956) hypothesized that the spruce forest in the southern Appalachians expanded to higher elevations during the Holocene Thermal Maximum Period. Climatic fluctuations during this mid-Holocene warming period may have caused the loss of spruce from peaks less than 1,740 m (5,710 ft) in elevation in the Great Smoky Mountains (Whittaker 1956), which hosts the most southern populations of red spruce. Subsequently, a cooler, moister climate of the Neoglacial Cooling Period may have led to downslope expansion of spruce to 1,370 m (4,500 ft) within the southern Appalachians. While this 1,370 m (4,500 ft) adjustment may be locally true, spruce also occurs at this latitude at lower elevations (e.g., Long Hope Creek Bog at 1,320 m [4,330 ft], Alarka Laurel Bog at 1,265 m [4,150 ft]; 35.34° N; both in North Carolina). Regardless, the elevational zone is relatively abrupt latitudinally and by elevation as evidenced by the southwestern limit at Double Spring Gap (1,678 m [5,505 ft]) on the

Tennessee-North Carolina ridge in the Great Smoky Mountains and the lower limit of the small spruce cap on Whitetop Mountain (1,684 m [5,525 ft]) in Virginia. Spruce has apparently persisted on all mountain *sky islands* in the southern archipelago through the Holocene and the spruce community held its ground on rocky summits with shallow soils in the cloudy and cool orographic conditions.

It is speculated that there were at least three Pleistocene refugia for red spruce: near the northeastern coast, to the east of or within the southern mountains, and somewhere near the ice margin in between the southern mountains and eastern coast. From these sites, red spruce expanded, maintaining low abundance especially at the northern limits where today it overlaps with black spruce. All of the northern sites greatly expanded in the last 2,000 years as the cool and cloudy mountain conditions recreated the ancestral moist coastal environment. The genetic heritage indicates a divergence in the early Holocene (roughly 9,000 YBP; Capblancq et al. 2020), which would indicate that all three ancestry groups existed at that time along the East Coast. This is consistent with the pollen data and post-glacial refugia as the three spruce regions became distinct around 8,000 YBP (Gaudreau 1988; see Sidebar 1.1 for a perspective on pollen data). The present-day distribution and the convergence of the montane occurrences with the cool, moist, lowlands clearly reflect evolutionary and biogeographic history of red spruce as it segregated from its boreal, continental parent that has a wide ecological range.

Sidebar 1.1 Individual species migration, lag times, and ephemeral forest communities

Through analysis of pollen preserved in sediment cores, we can make educated guesses about the response of vegetation to the last ice age and changes in species abundances through the Holocene. While we are accustomed to thinking of these forests as groups of species adapted to similar climate and disturbance regimes, it is important to remember that tree species respond in an individualist manner when expanding into new territory and can colonize at differing rates. Given the huge distances involved, and the slow colonization rates of some species (for instance, those with heavy seeds), there are likely periods of time when a species' response lags behind the availability of suitable habitat. The individualistic nature of this response also means that many modern forest communities are very young, in geologic terms, with component species that may have only arrived a few thousand years ago. Also, past species combinations apparent in the pollen and fossil record may also have been relatively ephemeral in geologic terms.

1.1.3 Pre-Euro-American Extent

Before Euro-American settlement (see Sidebar 1.2), red spruce occurred in eastern North America and ranged from the interior of Ontario, Canada to the coast of eastern Canada and New England, then followed the Appalachian Mountains southward, forming disjunct populations in Pennsylvania south through Tennessee and North Carolina (Fig. 1.3), similar to the present-day geographic distribution of red spruce (Bailey and Ware 1990; White and Cogbill 1992). The red spruce forests located in Virginia in the transition between the Ridge and Valley and the Allegheny Plateau physiographic provinces are small and isolated relict stands (e.g., War Spur, Mann's Bog) compared to red spruce forests in the Allegheny Mountains and southern Blue Ridge Mountains. Relict populations also occur in Maryland and Pennsylvania, as well as at lower elevations in North Carolina (e.g., Alarka Bog).

Sidebar 1.2 Indigenous people in red spruce forests

While our discussion of factors affecting the current distribution of red spruce focused on events known to greatly impact the forest—glaciation and broad-scale timber harvesting by European settlers—the history of these forests includes Indigenous people. Pre-European history in the eastern U.S. is divided into five cultural periods by anthropologists and archaeologists: Pre-clovis, Paleoindian, Archaic, Woodland, and Contact. No pre-Clovis sites are known in West Virginia. However, the pre-Clovis Meadowcroft Rockshelter site is approximately 200 km (124 mi) north of spruce-dominated forests in West Virginia. Only one Paleoindian (12,000 to 10,000–8,000 YBP) projectile point has been found on the Monongahela National Forest (host to the largest extent of contiguous red spruce forests in the central Appalachians) on a tributary of the Greenbrier River. Paleoindian occupation in the larger central Appalachian region likely occurred after the less complex terrain of the Coastal Plain and Piedmont regions were occupied (Lane and Anderson 2001). The Archaic Period (10,000–3,000 YBP) is characterized by shifts in climate, vegetation, and technology with an increase in occupation of upland sites by the Middle Archaic (Custer 1990). In the uplands of the central Appalachians, however, much more is known about early humans during the Woodland Period (3,000–1,000 YBP). This multi-part period is defined in part by developments in ceramics, mortuary rituals, native plant cultivars, and the construction of earthworks. In the Late Woodland period, Indigenous settlements in West Virginia increased in number and size.

Two well-documented sites within or adjacent to the Monongahela NF help frame the early human use and occupation of the uplands of the central Appalachians. While the Mouth of Seneca site, a Late Woodland village (1,600–1,000 YBP), is not located within the historical range of red spruce-dominated forests, it shows that people did make their home here. At this

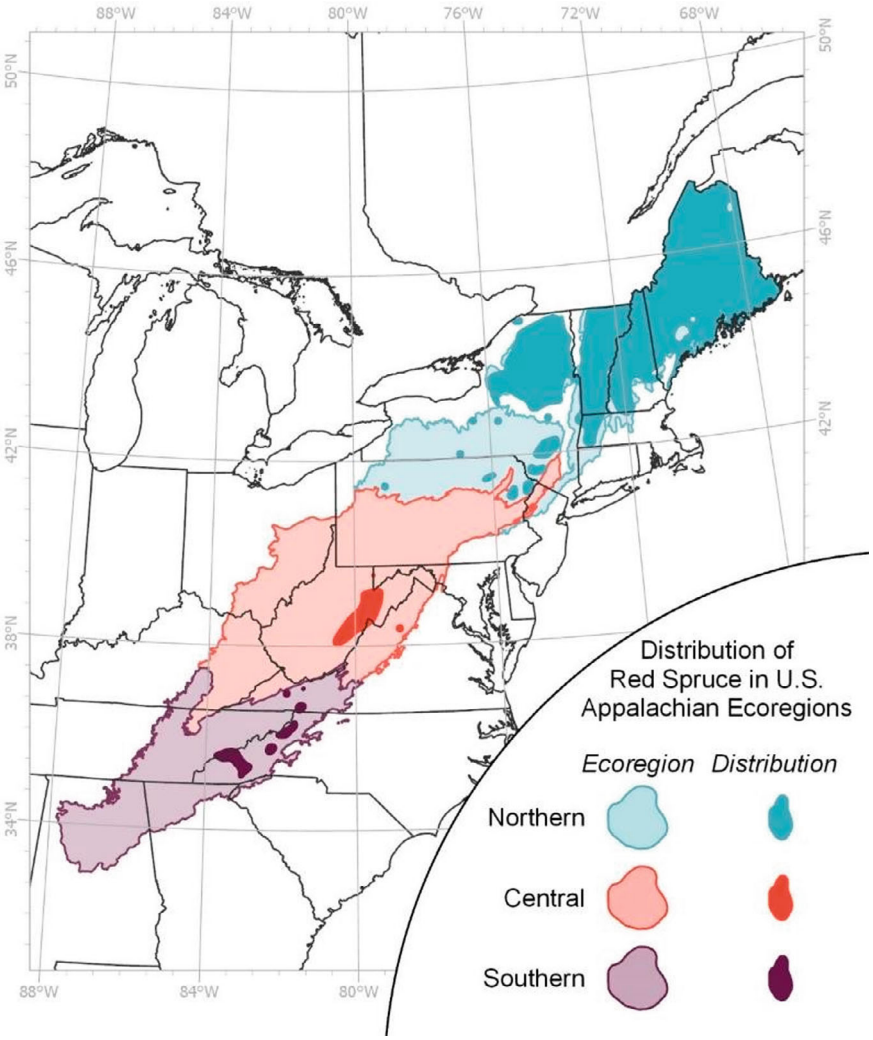

Fig. 1.3 Present-day distribution of red spruce (*Picea rubens*) in the eastern U.S. and Appalachian ecoregions as defined in this book. The depiction of the distribution in the southern Appalachians is exaggerated for visibility at this scale

upland site, the remains of deer and food plants including walnut, hickory, blueberry, huckleberry, cherry, and squash are found. This village site may have been occupied annually for short periods before more substantial shelters were built.

The Hyre Mound site near Huttonsville, West Virginia, lies in the Tygart Valley approximately 10 km (6 mi) from the Cheat Mountain range where red spruce persists. Recent analysis of this Middle to Late Woodland site confirmed extensive human occupation in the valley and suggests that Indigenous people here participated in the broader practices of the Eastern Woodlands culture (Rosencrance and Hirshman 2021). The reevaluation of lithic materials at this site further explores procurement strategies that linked people north and south along major drainages, including an important economic connection between the Greenbrier and Tygart River valleys. An over-land connection between these two drainages would take people across the higher elevations through red spruce-dominated forests. Upland archaeology is hampered by generally shallower sites than those at lower elevations or ones with gentler topography and upland sites often lack stratigraphic context making determinations of cultural chronology difficult. Indigenous people appear to have had less of a presence in West Virginia beginning in the 1700s, possibly because of the introduction of European diseases and the presence of Europeans themselves (Lesser 1993). However, early European settler accounts continued to document the presence of indigenous groups in the uplands of West Virginia engaged in hunting and resisting European settlements (Lesser 1993). European settlement of the area that would become the Monongahela National Forest began about this time (early to mid-1700s) and the low population densities of indigenous people led to the European idea that the uplands west of the Allegheny Front were not permanently settled (Henderson 1992). We now know this is not true and many are striving to recover this important history.

Although the pre-Euro-American geographic distribution of spruce-fir forests were distributed similar to today, red spruce-dominated forests occurred over larger extents in the pre-European landscape. While an estimate of extent for the entire range of red spruce is unknown, regional estimates for the central and southern Appalachians are available. Methods such as witness trees (Thomas-Van Gundy and Strager 2012; Thomas-Van Gundy et al. 2012), the presence of soils with spodic properties (Nauman et al. 2015, see Chap. 3), and historical data from early published reports (Hopkins 1891; Korstian 1937) can be used to determine historical locations of red spruce. Habitat suitability models may also reveal areas that were most likely favorable to red spruce, but where it may no longer occur (Nowacki and Wendt 2010; Beane et al. 2013; Koo et al. 2014; Andrews et al. 2022), potentially giving insight to pre-logging distributions throughout most of the red spruce's range.

Prior to exploitative logging at the turn of the twentieth century, there was an estimated 200,000 ha (494,200 ac) of red spruce-dominant forests in the central Appalachians, although if red spruce-northern hardwood forests are included estimates rise to about 1.2 million ha (2.96 million ac; Hopkins 1899; Fig. 1.4). The historical extent of red spruce in the southern Appalachians was about 405,000 ha

(1 million ac; Korstian 1937), with the largest extent in the Great Smoky Mountains at the most southern tip of red spruce's range. However, other estimates for the combined area of spruce occurrence in the central and southern Appalachians are only about 600,000 ha (1.5 million ac; Minckler 1940). Variation in the estimated area of red spruce occurrence may depend on whether both red spruce-dominated stands and red spruce-northern hardwood stands were included in those estimates (Pyle 1984).

In the central Appalachians, red spruce was seldom found below 700 m (2,300 ft) and most abundant above 900 m (2,900 ft), where soil and moisture conditions are favorable (Hopkins 1899). Red spruce forests before logging were restricted to elevations above 900 m (2,900 ft), with pure stands of red spruce likely above 1,200 m (3,900 ft) in Virginia (Pielke 1981). However, some have noted that Pielke's (1981) description of red spruce extent was based on lumber products which could have included hemlock, but labeled as spruce (Bailey and Ware 1990), potentially explaining the documentation of spruce lumber produced in states where the species was not considered to occur, such as Delaware. An analysis of witness trees from deeds and grants mainly dating in the 1800s documents individual red spruce trees at lower elevations, approximately 500 m (1,650 ft; Thomas-Van Gundy et al. 2012). In the southern Appalachians, red spruce occurred at elevations $\geq$ 1,375 m (4,500 ft; Korstian 1937), with Fraser fir becoming dominant above 1,800 m (5,900 ft; Pyle and Schafale 1988). Although there are many peaks with elevations greater than 1,375 m (4,500 ft), red spruce only occurs on peaks greater than 1,680 m (5,500 ft) in elevation (Cogbill and White 1991), highlighting the idea that past glacial and interglacial events influenced the pre-Euro-American distribution of red spruce in the region. Fraser fir typically dominates summits above 1,820 m (5,950 ft; Cogbill and White 1991), although the most northern extent of Fraser fir on Mt. Rogers in Virginia occurs below 1,700 m (5,580 ft).

1.1.4 Current Extent

Broad-scale clearcut logging occurred between 1870 and 1940 throughout the Appalachians, with sites in the northern Appalachians logged earlier followed by sites in the central and southern Appalachians (Fig. 1.5; Pinchot 1898; Korstian 1937; Pyle and Schafale 1988; Stephenson 1993). Logging in the northern extent of the range still occurs today, but commercial timber harvest in spruce forests in the central and southern Appalachians is limited (Nowacki et al. 2010). Logging since the nineteenth century removed most of the large merchantable spruce throughout the red spruce range (Korstian 1937; Westveld 1953; Hayes et al. 2007). Industrial clearcut logging resulted in an uphill elevational contraction of red spruce in mountainous regions (Pielke 1981; Busing et al. 1993; Hayes et al. 2007). Red spruce's current geographic distribution is similar to pre-Euro-settlement times, although its extent and density within those distributions have been greatly diminished due to anthropogenic activities.

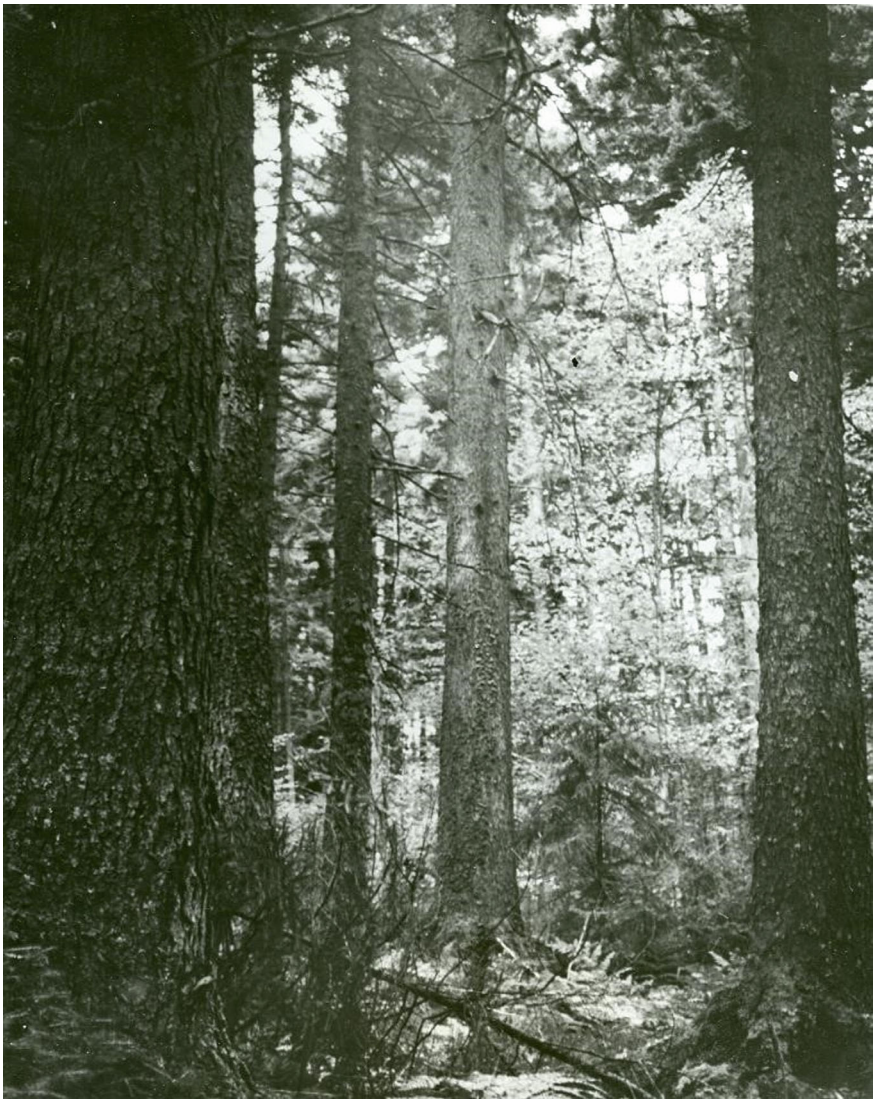

Fig. 1.4 Old-growth red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*) forest in 1936 on the Nels Wilson Tract, Monongahela NF, Randolph County, West Virginia. Photo by USDA Forest Service

The complete removal of overstory trees and accumulation of logging slash made both logged and adjacent unlogged red spruce forests susceptible to large, high-severity wildfires (Figs. 1.6 and 1.7). Fires were historically rare in the original montane spruce forests (Cogbill 2000), but in extreme multi-year drought events, spruce can fuel large wildfires (e.g., 1947 in southwest Maine and Mt. Desert Island).

Fig. 1.5 Residual red spruce (*Picea rubens*) trees left after logging on the Roaring Plains, Canaan Mountain, Tucker County, West Virginia, Monongahela NF, July 1938 (Minckler 1939). Note the absence of branches on the windward side. Photo by USDA Forest Service

However, this was thought to be even rarer in the southern Appalachians due to near-continual cloud deposition and frequent precipitation (see Sect. 1.4.2). Some sites, such as Dolly Sods in West Virginia in 1930 and Graveyard Fields in North Carolina in 1925, were converted from spruce-dominated forests to grasslands, shrublands, and boulder fields by logging-associated stand-replacing fires. Approximately 100 km^2 (39 mi^2) of spruce forests were consumed in the 1930 Dobbins Slashings Fire at Dolly Sods, a high-severity fire that burnt through logging debris and consumed thick duff layers down to bedrock. Almost a century later, neither Dolly Sods nor Graveyard Fields have recovered to their pre-fire vegetation condition, remaining in early successional states. At sites where fires were not severe enough to prevent forest reestablishment, logging and subsequent fires removed seed sources (i.e., mature trees, seedbanks) and changed soil and microclimate conditions, allowing faster growing northern hardwoods to easily outcompete and dominate sites formerly occupied by old-growth spruce forests (Pinchot 1898; Korstian 1937; Pielke 1981). The anthropogenically-induced species turnover from red spruce to northern hardwoods especially occurred at lower elevations in mountainous regions (Busing et al. 1993; Hayes et al. 2007) and increased mixed forests in flatlands and broad mountaintops (Boucher et al. 2006).

Fig. 1.6 Sherwood Forest burn on the Pisgah NF, April 1938 (approximate elevation of 1,830 m [6,000 ft]; Minckler 1939). The view is from near the top of Black Mountain facing northeast across the burn site. Remnants of spruce-fir can be seen at upper left. The foreground is a grassy bald and the darker areas down slope to the right regenerated with blackberry (*Rubus* spp.) and pin cherry (*Prunus pensylvanica*; photo by USDA Forest Service)

Regional estimates for loss of spruce-fir in the central and southern Appalachian Mountains are 50–95% and 35–60%, respectively (Stephenson 1993; Noss et al. 1995; Nowacki and Wendt 2010). Although losses of red spruce have not been specifically calculated for the northern Appalachians, climatic niche modeling indicates suitable habitat where red spruce may have been extirpated due to Euro-American logging and other land-use activities (Andrews et al. 2022). In West Virginia, red spruce occurred over about 300,000 ha (740,000 ac) in 1865 and was subsequently reduced to about 90,000 ha (220,000 ac) by 1899 and about 24,000 ha (60,000 ac) by the 1990s (Hopkins 1899; Stephenson 1993). In the Great Smoky Mountains, the lowest latitudinal population of red spruce experienced an estimated 45–50% loss of red spruce extent across the *sky island* landscape due to logging (Pyle 1984; Hayes et al. 2007). Estimates of spruce loss in refugia sites, such as Limberlost and War Spur in Virginia, due to logging are unknown. However, it is likely refugia also suffered decreases in extent or complete extirpation due to logging (Pielke 1981), especially since they are in minimally suitable habitats at elevations where hardwood forests are typically dominant. The drastic loss of red spruce-dominant forests is the

Fig. 1.7 Red spruce (*Picea rubens*) regeneration on Black Mountain, Monongahela NF, August 1938 (approximate elevation 1,370 m [4,500 ft]; Minckler 1939). This area was clearcut but not burned. Photo by USDA Forest Service

main reason why these forests in central and southern Appalachians are considered two of the most endangered forested ecosystems in the U.S. (Noss et al. 1995).

When red spruce was removed from mixed woods there was a profound lack of initial spruce regeneration given the competition with fast-growing, early successional hardwoods such as birch (*Betula* spp.) and black cherry (*Prunus serotina*), particularly in the central Appalachians (Nowacki et al. 2010). This "Westveld paradox" (Westveld 1930, 1953) resulted in restriction of the red spruce range and a sharpening of the coniferous/deciduous ecotone after logging. This sharpened ecotone is more obvious in the southern Appalachians, which may also have to do with the prevalence of mixed forests being more common in the flatter areas in the northern latitudes versus mountainous southern latitudes due to strong elevational gradients. In mountainous locations, logging activities shifted the lower elevational distribution upwards throughout its range. For example, in the Great Smoky Mountains prior to logging, red spruce was generally found above 1,513 m (4,964 ft) with minimal elevational limits down to 1,285 m (4,216 ft), but logging caused a 200 m (650 ft) upslope contraction in the upper and lower minimal elevational distribution of red spruce (Hayes et al. 2007). The logging-driven loss of red spruce at lower elevations and the potential for red spruce to occur at lower elevations is apparent in relict populations.

For example, Alarka Bog spruce forest in North Carolina sits at 1,220 m (4,000 ft; Collins et al. 2010), approximately 150 m (500 ft) lower than minimal elevations of red spruce at other sites.

Anthropogenic land uses may have also shifted the dominance of red spruce in the overstory, resulting in mixed forests, especially in the central Appalachians and northern parts of the red spruce range (Korstian 1937; Boucher et al. 2006). Within mountainous regions, the loss of overstory red spruce dominance may be driven by elevation, but not latitude depending on localized factors such as pre-logging forest composition and post-logging conditions (i.e., loss of seedbank, colonization distance of hardwoods). However, where red spruce forests suffered uphill contractions due to logging, regeneration currently indicates a recolonization of areas occupied before Euro-American activities, despite a warming climate (Busing et al. 1993; Nowacki et al. 2010; Rollins et al. 2010; Foster and D'Amato 2015; Wason and Dovciak 2017). Past land use may represent a stronger driver of red spruce elevational shifts than climate change at some sites (Iverson et al. 2008; Foster and D'Amato 2015; Danneyrolles et al. 2019), although some areas have experienced uphill shifts in northern hardwood-spruce ecotones since the 1960s (Beckage et al. 2008).

Current populations of red spruce seem stable throughout the geographic distribution of the species, including in the most southern latitudes (Nowacki et al. 2010). Nevertheless, climatic factors may influence the downhill shift of red spruce, wherein more pronounced shifts downslope to recolonize historical areas may be limited or hindered by warmer temperatures at lower elevations (Wason and Dovciak 2017). Therefore, past anthropogenic activity and climate change may interact and alter the future extent and distribution of red spruce (see Chap. 7). Within the central and southern Appalachians, most red spruce forests occur on state or federal land, are habitat for species of conservation concern, and are largely not available for commercial timber harvest (see Chap. 6). Presently, silvicultural activities on public lands in the central and southern Appalachians are generally restricted to treatments that promote red spruce restoration as guided by management plans (e.g., USDA Forest Service 2006; Rentch et al. 2016).

1.2 Topographical Influences

One of the main drivers influencing the geographic distribution of red spruce is topography (White and Cogbill 1992) and conditions associated with topography like soil depth and moisture (Murphy 1917). Variation in topographical factors interacting with climatic, edaphic, and biotic factors influences where species occur across the landscape (Braun 1950). Topographic features such as elevation, aspect, and landform shape (e.g., sheltered coves, exposed ridgelines) influence microclimate conditions (e.g., temperature, moisture, solar exposure), and may influence factors driving disturbance at local and regional scales (see Chap. 5), and potential climate change refugia (Stark and Fridley 2022).

Elevation interacting with latitude is a major driver of the red spruce distribution with occurrences at lower elevations corresponding to higher latitudes. The lower elevational limit of spruce-fir forests increases in elevation with decreasing latitude (i.e., southward) along the Appalachian Mountain chain (Cogbill and White 1991; White and Cogbill 1992). Red spruce currently ranges from sea level to 1,065 m (3,494 ft) in elevation in Canada and the northern Appalachians, 700–1,100 m (2,300–3,600 ft) in the Adirondack Mountains of New York, 915–1,480 m (3,000–4,850 ft) in the Allegheny Mountains of the central Appalachians, and 1,370–2,037 m (4,500–6,680 ft) in the southern Appalachians. However, relict sites in the Blue Ridge Mountains in North Carolina occur at 1,220 m (4,000 ft; Collins et al. 2010) and in the Ridge and Valley in Virginia at 975 m (3,200 ft; Adams and Stephenson 1991). In the central Appalachians, red spruce has been reported at elevations down to 822 m (2,697 ft). These relict populations and lower elevational distributions indicate potential lower elevational distributions prior to Euro-American disturbance (see Sect. 1.2.3). Indicator species analysis of red spruce witness tree locations in the mountains of east central West Virginia showed significant associations with higher elevations, moderate moisture (based on a moisture index), low topographic roughness (for example, stream channels, wetlands, or broad ridges) toeslope positions, and northeastern aspects (Thomas-Van Gundy and Strager 2012). These associations differed by ecological subsection. For example, red spruce was associated with lower elevations and valley landforms in the western Allegheny Mountain subsection (Thomas-Van Gundy and Strager 2012). It should be noted that elevation is closely correlated with climate, negatively with mean annual temperature and growing degree days, and positively with number of frost days (Nowacki and Wendt 2010). Although categorized as a topographic feature, elevation largely controls vegetation expression through climate.

Aspect influences insolation, moisture, and temperature, wherein a similar elevation on a south-facing slope is drier and hotter (more xeric) than the same elevation on a north-facing slope (more mesic). The cooler, moister microclimates on north-facing slopes likely explain why aspect is a predictor of the lower elevational limits of red spruce. For example, red spruce can occur 120–200 m (400–650 ft) lower in elevation on north-facing compared to south-facing slopes (Davis 1930; Brown 1941; Rheinhardt and Ware 1984; Hayes et al. 2007). Current spruce-fir forests on Mt. Rogers occur above 1,500 m (4,920 ft) on northern aspects, 1,600 m (5,250 ft) on aspects facing northwest, west, or south, and 1,700 m (5,580 ft) on southwestern aspects (Rheinhardt and Ware 1984), highlighting the variation in elevation limits of dominant spruce-fir stands on a single mountain.

1.3 Climatic Environment

The geographic distribution of red spruce corresponds to the Appalachian Mountain chain, an area of ecological diversity and climatic complexity located between the Mississippi River basin, the Great Lakes region, and the Atlantic Ocean. The

complexity of the topographic and climatic interactions found here are often simplified to differences in elevation and the orographic effect when prevailing west-to-east air masses intersect with the roughly north–south trending mountain chain. A recent broad-scale analysis across the Appalachian Mountains at airports on an east-to-west transect determined that westerly winds were observed 54.5% of the time on average (Kutta and Hubbart 2019). This data was derived north of our focal areas; however, the Appalachian Mountains could be described as having a bidirectional rain shadow. Flash flooding and winter storms, including icing events, are associated with air currents from the east (Kutta and Hubbart 2019). However, this work is based on surface winds which often do not reflect wind direction at higher latitudes.

1.3.1 Temperature

Within the range of red spruce estimated by Little (1971), the mean annual temperature ranges from 2.0 to 13.5 °C (35.6–56.3 °F; USDA Forest Service Climate Change Atlas, version 4). The gross range of temperature estimates can be narrowed by using climate stations within red spruce sites. The average annual temperature envelope of red spruce, utilizing an extension of Little's range and calibrating for stations at elevation in the mountains, ranges from 0.7 to 9.7 °C (33.3–49.5 °F). Additionally, the annual temperature regime is misleading as it does not account for winter or summer temperatures, which differ in the amplitude of variation around those seasonal means. Based on logistic regression, mean annual temperature almost exclusively explains red spruce occurrence in the northern Appalachians, whereas snowfall is the principal driver in the central and southern Appalachians (Nowacki et al. 2010).

The temperature parameter most closely correlated with spruce occurrence is the peak summer (i.e., July) temperature with a range of 12.9–20.3 °C (55.2–68.5 °F; mean = 18.2 °C [64.8 °F]) across the red spruce range (Cogbill and White 1991; Wason et al. 2017). Many summer temperature parameters covary with the peak, but July temperature was also the highest rated of 38 environmental variables used to predict the importance value of red spruce (USDA Forest Service Climate Change Tree Atlas, version 3). The red spruce climatic envelope is closely aligned with temperature observed at the northern hardwood-red spruce ecotone, which has a peak summer temperature of 16.6–17.5 °C (61.9–63.5 °F) and a corresponding growing season (>5 °C [41 °F]) of 160–238 days (Cogbill and White 1991). Because the southern mountains have a less continental temperature regime (thus lower amplitude) than the northern lowlands, the summer peak (July) temperature is more important in defining red spruce habitat than the annual average.

The mean minimum winter temperatures (January) are substantially warmer in the south (-6 °C [21 °F] at Newfound Gap, elevation 1,536 m [5,039 ft]) than in the north (-17 °C [1 °F] at Mt. Mansfield, elevation 1,205 m [3,953 ft]). Although the absolute minimum temperatures in winter are lower in the north (-40 °C [-40 °F]), a similar minimum temperature (-35 °C [-31 °F]) was recorded at Grandfather Mountain, North Carolina in 1985. However, extremes in the south are likely less

frequent and of shorter duration than the north. Since absolute minimum temperatures are typically observed in cold air drainages (e.g., coves, closed valleys), the same phenomenon of frost pockets allows occurrence of red spruce in lower elevation sites in the southern Appalachians, especially on northern aspects.

Despite the shorter summer photoperiod, the southern montane red spruce forests at lower latitudes receive more photosynthetically active radiation in the growing season (around 1,750 $\mu mol \bullet m^{-2} \bullet s^{-1}$; Reinhardt and Smith 2008) than northern mountains (around 1,300 $\mu mol \bullet m^{-2} \bullet s^{-1}$; Richardson et al. 2004). In general, red spruce forests have dense evergreen foliage (7–12 m^2/m^2 leaf area indices for unthinned forests in Maine; DeRose and Seymour 2012), which efficiently captures this energy leaving dark and open understories, typically dominated by mosses. Southern red spruce forests, however, have enhanced growing conditions at the same July average temperature with a longer growing season, greater precipitation, and increased energy input than northern forests. Additionally, the less extreme minimum winter temperatures and decreased snowfall reduce the stress on southern trees (Cogbill and White 1991).

Climate is inherently complex in mountainous regions, thus predicting impacts of climate change is equally difficult (see Chap. 7). Paradoxically, some trends might contrast what is expected from rising global temperatures. For instance, in West Virginia, Kutta and Hubbart (2018) found that recent reductions in diurnal temperature range and vapor pressure deficit may lead to increased relative humidity, cloud cover, and soil moisture which, in turn, support cool-adapted, mesophytic species such as red spruce. Similar resistance to climate warming was found on Mt. Washington in New Hampshire due to insulating factors such as thermal inversions and high incidence of cloudiness (Seidel et al. 2009).

1.3.2 Cloud Immersion

Even casual observers of red spruce forests of the central and southern Appalachian Mountains recognize that the topographic position of these forests, higher elevation and moist air masses, results in cloud cover. Red spruce is prominent in cloudy environments along coastal regions or in the mountains. A widely distributed network of regional monitoring stations has shown a cloud base typically forms at 800 and 1,200 m (2,600 and 3,950 ft) in the Adirondacks and northern Appalachian Mountains and between 1,000 and 1,400 m (3,300 and 4,600 ft) in the southern Appalachians (Mohnen 1992). Cloud deposition from orographic clouds (resulting from moist air forced upwards by mountains) provides additional moisture and cooler daytime temperatures to these forests in the summer, along with other ecophysiological benefits (see Chap. 2). At Yarmouth on the coast of Nova Scotia, around 15% of the summer hours are foggy (Environment Canada: Canada national climate data and information archive, https://climate.weather.gc.ca/historical_data/search_historic_data_e.html) and coastal Maine is immersed in fog 9–20% of the time during the summer months (Jagels 1986). Similarly, with orographic clouds, the northeast

mountains have increasing immersion from 17–19% of the day at 748–1,025 m (2,450–3,360 ft) in elevation (Mohnen 1992; Miller et al. 1993), rising through 37–50% of the day at 1,000–1,500 m (3,280–4,920 ft; Lovett and Reiners 1986, Mohnen and Vong 1993, Roberti 2011) to a peak of 57% of all hours at 1,917 m (6,289 ft) on Mt. Washington (Seidel et al. 2007).

In the southern Appalachians, cloud immersion occurs during 55–75% of growing season days (Reinhardt and Smith 2008; Berry and Smith 2012). Like the mountainous areas in the northern Appalachians, the number of cloud-immersed days in the southern Appalachians varies with elevation, with cloud immersion occurring 56% of days at sites at 1,510 m (4,950 ft) and 75% of days at 1,960 m (6,430 ft) during the growing season (Berry et al 2014). Cloud immersion typically occurs in the morning and usually lasts for more than 2 h in the southern Appalachian Mountains (Berry and Smith 2012). Unfortunately, there are no published reports on cloud immersion for red spruce sites in the central Appalachians, however a meso-scale analysis of airport weather data shows cloud immersion is a common event along ridgelines in the mid-Appalachian Mountains (Kutta and Hubbart 2019).

Beyond the effects of cooling, when cloud immersion is accompanied by orographic winds, moisture deposited on spruce foliage subsequently drips to the ground, also called fog drip. This can increase water input by an estimated 50–100% of the rain gauge precipitation and results in an estimated 300–400 cm (120–160 in) per year of additional moisture at high elevations in both the northern and southern Appalachian Mountains (Lovett et al. 1982; Miller et al. 1993; Shubzda et al. 1995; Reinhardt and Smith 2008), influencing plant physiology (see Chap. 2). However, a more recent study found much lower amounts of fog interception in the southern Appalachians than previously reported (3–8% of rainfall), which may be related to foliar uptake (Praskievcz and Sigdel 2023).

1.3.3 Precipitation and Ice

Annual precipitation across the range of red spruce varies by location. Total annual precipitation ranges from 86 cm (34 in; northern interior) to 206 cm (81 in; southern Appalachian Mountains). However, localized amounts of precipitation vary depending on elevation. Winter also produces snow, which accounts for roughly 10% of the annual precipitation in the southern mountains, rising to 25% in the central Appalachians, 30% in the northern Appalachians, and 40% at the northern limits in Québec. Ice storms with freezing rain typically accumulating 2 cm (0.8 in) of ice on contact with branches occur sporadically (typically 2–3 times per decade), but cause major damage to the canopy, especially to deciduous trees just adjacent to spruce forest (Nicholas and Zedaker 1989; Rhoads et al. 2002; Boyce et al. 2003; Lafon 2004).

During cold winter temperatures, the conditions of cloud immersion, wind, and an intercepting surface combine to produce rime deposition. Supercooled cloud droplets entrained by the wind impact on objects such as foliage and instantly freeze as frost

feathers growing into the wind. This is commonly observed as a *frost line* with white encased vegetation on mountain sides above the cloud base. In the Vermont mountains, the additional deposition of water contained in rime (60 cm [23.6 in]) in winter is roughly equal to the amount of water in the 60 cm (23.6 in) of snow deposited in the same period (Ryerson 1990). As in summer, the amount of water deposited in the high mountains in winter is up to double the amount measured as precipitation.

Red spruce is adapted to shedding heavy snow load, rime, or ice deposit, but tree height growth can be limited by broken branches or foliage damage in windy conditions at high elevations. More significant damage to red spruce and fir species are found with the regular wind-blown sleet or lofted ice (ice blast akin to sand blast) at high elevations, which abrades exposed branches and causes pruning of exposed foliage resulting in canopy flagging or stunted krummholz.

1.4 Summary

The last glacial maximum (approximately 20,00 YBP) influenced the genetics and biogeography of the modern red spruce species. Analysis of palaeobotanical data shows periods of increase and decrease in abundance through the Pleistocene and Holocene. While red spruce was pushed south by glaciation and moved north as the climate warmed, there were also refugia along the east coast. Red spruce occurs across a variety of latitudes and physiographic regions within its geographic distribution, with temperature, precipitation, cloud deposition, and elevation influencing occurrence throughout its range. Red spruce can be separated into five main zones: southern Appalachians, central Appalachians, northern Appalachians, coastal, and interior forests. Each region hosts distinct precipitation regimes that influence presence and unique disturbance regimes that influence stand dynamics. Each region also hosts different unique floral and faunal communities (see Chaps. 4 and 6 and Sidebar 1.3), with co-dominant tree species varying across the zones.

High moisture and cool growing season temperatures define red spruce sites for both past and present forests. This has implications for the impacts of contemporary climate change on these forests and for designing active restoration treatments. While we have evidence that red spruce is currently regaining ground lost to hardwood species after the exploitative pre-industrial logging period, this response could be impacted by changes in precipitation and summer air temperatures associated with anthropogenic climate change. Red spruce, as an evergreen, appears to benefit by cloud immersion compared to hardwood species, although potential climate change impacts to orographic cloud formation are difficult to estimate and quantify. Understanding the past of red spruce may help in understanding how climate change may impact this important tree species and the associated species found within its forests.

Sidebar 1.3 Ecological classification and mapping

In this book we use or reference several ecological community classification systems. The ecoregional boundary in Fig. 1.3 is based on the EPA's Ecoregions of North America, the NRCS system of Ecological Site Descriptions is described in Chap. 3, and the International Vegetation Classification system is used in Chap. 4 to describe the red spruce-associated communities. The overall goal of any classification system is to define, describe, and map repeated patterns, often in support of conservation and management efforts. Developing restoration actions using defined ecological units should aid in prioritizing where to act and allow for predictable results.

Classification systems should be hierarchical, that is the varying scale of ecological units should nest and build on each other with logical and consistent boundaries. Ecological communities are defined as the community of organisms and the physical environment. The physical environment defines the space the ecosystem occupies. This space can be described by independent variables of bedrock geology, geomorphic processes, and regional climate that influence the dependent variables of surface geology, landform, and local climate, which further combine to influence soil, site morphometry, and vegetation (Fig. 1.8). When relationships can be described between independent and dependent variables, independent variables may be useful for predicting dependent variables.

Ecological classification and mapping systems have shared characteristics, as all are developed to depict and describe the patterns and placement of ecosystems across multiple scales. The capacity of the land to support some action may also be included in these classification systems as many were first developed for specific management purposes, such as agricultural productivity or identification of geological hazards. The classification system used may be based on the preferences of individual managers or agencies and organizations. National Forest System lands are classified and mapped under the Terrestrial Ecological Unit Inventory system codified in the USDA Forest Service manual, handbook, and accompanying technical guide (Winthers et al. 2005). Other CASRI and SASRI partners may have different agency direction or no preference for a certain system.

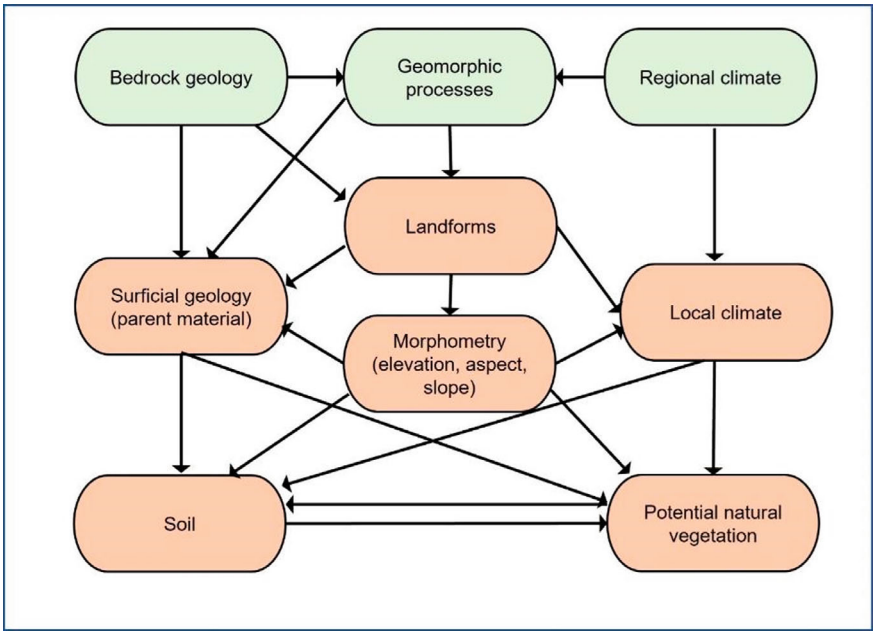

Fig. 1.8 A conceptual depiction of the general relationships between landscape elements. Elements are considered independent (light green shading) or dependent (light orange shading). Figure adapted from Winthers et al. (2005)

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