Chapter 7
Climate Change Implications and Adaptation Solutions



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7.1 Historical and Contemporary Climate Change Responses of Red Spruce

7.1.1 The Climatic Niche of Red Spruce

Aspects of red spruce's climatic niche and its relation to the biogeography of the species are covered in Chap. 1. Our emphasis here is on red spruce's interaction with its biophysical environment in terms of a *changing* climate, what this might illuminate about the nature of its climate sensitivities, and how it may respond to future climate change. We approach this from an interdisciplinary viewpoint that integrates perspectives across biological, temporal, and spatial scales not often discussed together in the same work. We first briefly summarize key features of red spruce's climate preferences and tolerances, as they relate to the ensuing discussion of its realized and potential responses to climate changes, past, present, and future.

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The Appalachian Mountains span a diverse range of environmental conditions in terms of precipitation patterns, humidity, mean and extreme temperatures, and length of growing season. The climatic niche of red spruce has been described as cool, moist, and temperate, as reflected by its distribution at mid to high elevations within the Appalachians and along the cool, humid coastal areas of Maine and the Atlantic Canadian provenances (Fig. 7.1; Day 2000; Dumais and Prévost 2007). Red spruce is not, as it is sometimes described, a boreal tree species or one that is preferentially found in the coldest microclimates available within the geography it inhabits. Perhaps the most easily defined and visible aspect of red spruce's climatic niche is that its distribution generally exhibits a latitude-elevation relationship, with central and southern Appalachian spruce forests confined to the highest elevations in the region, typically above 1,000 m and 1,600 m (3,280 ft and 5,250 ft), respectively (Cogbill and White 1991, Byers et al. 2010). In their analysis of latitude-elevation relationships of Appalachian spruce-fir forests, Cogbill and White (1991) found the spruce-fir/deciduous ecotone to closely follow a mean July isotherm of 17.1 °C (62.8 °F). High temperatures (>32 °C [90 °F]) during the growing season inhibit photosynthesis of red spruce seedlings and saplings and can cause irreversible foliar injury in mature trees (Day 2000; Dumais and Prévost 2007). This is consistent with red spruce favoring environments with low vapor pressure deficits, characterized by moderate temperatures and high humidity (Day 2000). Red spruce is also sensitive to extreme cold and shows moderate levels of mid-winter freezing hardiness among conifers, even compared to co-occurring balsam fir (*Abies balsamea*; Strimbeck et al. 2007, 2015). Red spruce foliage is especially susceptible to winter freezing injury as a result of dehardening that occurs during prolonged temperatures >0 °C (32 °F), followed by rapid return of sub-freezing temperatures (Schaberg 2000). Detailed descriptions of red spruce's physiological tolerances as they relate to climate are presented in Sect. 7.2.

In comparison to the northern part of its range, the climate inhabited by red spruce in the central and southern Appalachians is characterized by milder summer and winter temperatures, longer frost-free period and growing season length, lower

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Fig. 7.1 High-elevation red spruce community after an ice storm in Tucker County, West Virginia. Photo by Matthew Fitzpatrick

amplitude of mean monthly temperature variation across the year, enhanced precipitation, lower snowfall, and frequent orographic-derived cloud cover (Cogbill and White 1991). Red spruce reaches its largest size and has its greatest growth potential in the southern portion of the range (King and Stupka 1950). The persistence of red spruce in the southern extent of the range is likely dependent on ecophysiological adaptations to cloud forest conditions that mitigate climatic conditions near the physiologically determined limits of its range. In the context of a warming climate, the climatic niche of red spruce suggests that as temperatures increase, southern portions of its range may become too warm, especially when combined with increasing frequency of drought and associated increases in vapor pressure that, collectively, are likely to decrease climatic suitability and could lead to extirpation of populations at both local and regional scales. In contrast, portions of the northern range currently limited by severe winter cold are likely to increase in suitability as long as sufficient moisture remains available. Detailed projections of the future climatic niche of red spruce are discussed in Sect. 7.3.

7.1.2 The Paleoecological Perspective: What Does the Pollen Record Tell Us About the Response of Spruce to Climate Change?

The paleoecological record of the last ice age provides a unique opportunity to examine how species have responded to rapid climate change and thereby can provide a glimpse of what might be expected in the future, even if the analogy between climate change in the past and that expected in the future is less than perfect. Fortunately, the ice age history of spruce is relatively well documented, with the important caveat that, due to limitations in assigning fossil material to species, most inferences are limited to the genus level (*Picea*; unless otherwise noted, we use the term spruce in this section to refer to all species in the genus). Nonetheless, available fossil evidence suggests spruce responded relatively quickly to climate changes during the Last Glacial Maximum (approximately 22,000 YBP) and has largely tracked its climatic niche in the process. It therefore is not surprising that the predictions of change in the distribution of spruce from ecological niche models (ENM), which attempt to fit a statistical model to the climatic niche, tend to be in good agreement with observed changes in spruce abundance inferred from fossil pollen records (Veloz et al. 2012), and therefore lend support to the use of ENMs to forecast the potential response of spruce to future climatic changes. In this section, we first summarize relevant past climatic trends and then discuss how spruce appears to have responded to warming according to changes in fossil pollen abundance through time, as well as some limited evidence of the responses of red spruce specifically.

7.1.2.1 Climatic and Vegetation Changes Since the Last Glacial Maximum

The Quaternary period, which began 2.58 million YBP, was characterized by colder temperatures than the present and encompassed about 30 cycles of glaciation with expanded ice sheets in the northern hemisphere (Marshall 2009). Whereas cooling typically occurred gradually over periods of 50,000–100,000 years, the interglacials, which were comparatively short at 10,000–20,000 years, were characterized by relatively rapid climate warming and associated environmental changes that were more disruptive to vegetation than the cooling periods (Davis 1981). The last glaciation started approximately 100,000 YBP, and by the Last Glacial Maximum about 22,000 YBP, the Laurentide ice sheet extended into central Illinois, northern Pennsylvania, and southern New England. The Last Glacial Maximum terminated with a sudden steep temperature rise beginning about 16,000 YBP. The interglacial reached its warmest period during the Holocene Climatic Optimum at 8,500–5,000 YBP. From a conservation (and modeling) perspective, the paleoecological record makes it clear that during these periods of climatic upheaval, plant taxa responded individually and opportunistically to Quaternary environmental changes rather than migrating as

intact forest communities (Williams et al. 2004). Existing plant communities disassembled as individual taxa migrated at different rates and along different routes such that forest communities rarely exhibited constant species composition for more than 2,000–3,000 years at a time during the interglacials (Davis 1981).

Spruce pollen is abundant in the fossil record and suggests that *Picea* was among the most responsive to changes in climate and also among the first trees to colonize recently deglaciated regions (Watts 1979; Davis 1981; Williams et al. 2004). *Picea*'s propensity for rapid migration in response to climate change helps explain the relative stability of its niche through time, suggesting that changes in the distribution of spruce were closely linked to changes in climate and that the genus was able to largely track rapid climate changes (Veloz et al. 2012). The late Quaternary vegetation history of North America was characterized by rapid north–south, but also east–west shifts in plant distributions (Williams et al. 2004). The center of abundance of spruce pollen over the past 22,000 YBP has shifted several times between eastern and western North America according to pollen records (Williams et al. 2004). Range shifts of red spruce likely remained restricted to the eastern part of the continent but still were rapid and substantial according to modeling (Thibaut Capblancq and Susanne Lachmuth et al. unpublished manuscript).

7.1.2.2 Geographic Distribution of Spruce During the Last Glacial Maximum

The eastern Laurentide Ice Sheet was fringed by tundra in the continental interior (Jackson et al. 2000), and alpine communities also covered the Appalachian ridges up to several hundred km south of the glacial limit (Watts 1979; Davis 1981). Multiple lines of evidence suggest spruce occurred in the cold, dry, and windy conditions near the glacial margin as spruce logs were found to have been overridden by the oscillating ice front while still growing in Ohio (Watts 1979 and citations therein). Moreover, spruce macrofossils in Pennsylvania 60 km (37 mi) south of the ice sheet and at 200 m (656 ft) elevation indicate the proximity of the tree limit (Watts 1979), which was formed by open spruce forest or spruce tundra along most of the Laurentide and Cordilleran ice sheets (Watts 1979; Williams et al. 2004). Macrofossils analyzed by Jackson and Overpeck (2000) also confirmed that the occurrence of spruce in the continental interior ranged from very close to the ice margin (in particular in the Ohio Valley) south into east-central Louisiana. However, given the current distribution of red spruce and the species' sensitivity to extreme cold, it is likely populations close to the ice sheets were white spruce (*Picea glauca*) and/or black spruce (*Picea mariana*).

In the South, vegetation appears to have remained relatively stable from 22,000 to 13,500 YBP. In this period, a spruce refugium stretched from the Great Plains, where spruce codominated with larch (Davis 1981), to the eastern Coastal Plain (Jackson et al. 2000; Williams et al. 2004). In the lower Mississippi Valley, spruce pollen reached maximum abundance, likely reflecting the presence of Critchfield's spruce (*Picea critchfieldii*), which also occurred in Georgia (Jackson et al. 2000). Despite its seemingly high abundance in the Southeast in the past, Critchfield's

spruce is now extinct and represents the only documented plant extinction from the last ice age in North America, though the cause of its extirpation remains unresolved. When still extant, Critchfield's spruce was associated with oak (*Quercus* spp.) and other nonboreal species, a plant assemblage with no close modern analog (Jackson et al. 2000). Spruce abundance was low in the Carolinas, Georgia, and eastern Tennessee and the genus was absent from the central and southern Appalachian highlands (Davis 1981), even though these areas were not glaciated (White and Cogbill 1992). All members of the genus *Picea* were absent from the central and southern Appalachians and the absence of red spruce specifically is supported by both pollen records (Delcourt and Delcourt 1988) and ENM hindcasts and demogenetic simulations (Thibaut Capblancq and Susanne Lachmuth et al., unpublished manuscript). This is also consistent with Davis (1981), who described the distribution of *Picea* in eastern North America as a belt stretching from the Mississippi Valley to the East Coast, excluding the mountainous region of the southern Appalachians. According to Watts (1979), red spruce occurred along the southern edge of this belt for its entire east–west extent. ENM hindcasts and demogenetic simulations (Thibaut Capblancq and Susanne Lachmuth et al., unpublished manuscript) delineate this belt as the glacial refugium of red spruce, which was largely maintained in its east–west extent during northward migration until approximately 15,000 YBP.

7.1.2.3 Rapid Shifts in Spruce Distribution During the Late Pleistocene and Early Holocene

With the onset of warming around 15,000 YBP, which probably increased the length of the growing season (Watts 1979), spruce proved to be an aggressive pioneer as it rapidly spread northward into the tundra of the Great Lakes Region (Davis 1981). In New England, the earliest records of spruce date to between 16,500 and 14,000 YBP (Davis and Jacobson 1985), with recalibrated dates in Lindbladh et al. (2003). Lindbladh et al. (2007) suggested that around 14,000–13,000 YBP a transition from open white spruce forest-tundra to closed black spruce-dominated forest occurred. Lindbladh et al. (2003, 2007), who applied a palynological method to distinguish red spruce from white spruce and black spruce (Lindbladh et al. 2002), also suggested that red spruce was largely absent from New England before 12,000 YBP during the immediate post-glacial in which climate was characterized by high seasonality and extreme low winter minimum temperatures. While it remains difficult to distinguish whether the increase in spruce pollen after 12,000 YBP was primarily red spruce or if black spruce was also increasing in abundance at this time, the timing aligns well with ENM hindcasts (Thibaut Capblancq and Susanne Lachmuth et al., unpublished manuscript), which suggest that red spruce rapidly colonized this region between 12,000 and 10,000 YBP.

Evidence suggests that climate initially hindered red spruce colonization of higher elevations in the central and southern Appalachians (Watts 1979; Davis 1981), and that the expansion front was likely formed mostly by white spruce, followed by black spruce. Watts (1979) claimed to have distinguished red spruce pollen from

other *Picea* species and documented a sudden massive increase of red spruce around 11,000 YBP at a site in the Appalachians of southern Pennsylvania (Crider's Pond, 40° N), where members of the *Picea* genus occurred as early as 15,200 YBP. Watts (1979) also found red spruce and no other members of the genus in a sample dated to 11,100 YBP from the southcentral Appalachians (Potts Mountain, Virginia, 37.5° N).

Around 12,500 YBP during the Pleistocene-Holocene transition, cold, dry, and windy Pleistocene climates were replaced by warmer and more humid climates (White and Cogbill 1992). In the south, lowland spruce populations declined (Williams et al. 2004) and the open spruce forest and forest tundra were replaced with species-rich conifer-hardwood forests (Watts 1979). At a continental scale and genus level, peak abundances of spruce pollen occurred in the eastern interior until 14,000 YBP, then shifted to western Canada as a consequence of asymmetrical retreat of the Canadian ice sheet and did not move back to eastern Canada until around 7,000 YBP (Williams et al. 2004).

7.1.2.4 Near Loss of Midcontinent Spruce During the Holocene Climatic Optimum and Its Sudden Reappearance Afterward

During the Holocene Climatic Optimum, spruce nearly disappeared entirely from its midcontinent belt when temperatures peaked between 9,000 and 4,000 YBP (White and Cogbill 1992; Lindbladh et al. 2003). In the Appalachians, spruce-fir forests shifted upwards by 200–500 m (656–1,640 ft; White and Cogbill 1992). White and Cogbill (1992) suggested that red spruce may have survived this time period in damp lowlands, on steep rocky slopes, and/or in the northeastern Maritime region, after which time spruce suddenly re-emerged and presumably expanded to the Appalachian slopes ca. 2,000 YBP. Similarly, Lindbladh et al. (2003) and citations therein suggest a disappearance of spruce from the lowlands in New England during the Holocene Climatic Optimum followed by an increase in abundance 1,000–500 YBP, probably indicative of red spruce. Further south, Lindbladh et al. (2003) also noted that "the presence of a continuous *Picea* pollen curve (identified as *P. rubens*) at a high-altitude site (Cranberry Glades) in the Appalachian Mountains of West Virginia (Watts 1979) raises the possibility that the species survived the generally warm and dry middle Holocene climate in cool, moist microhabitats at suitable altitudes there."

7.1.3 Contemporary Evidence of Red Spruce Responses to Climate Change

There have been mixed reports of how the distribution and abundance of red spruce in natural forested stands have responded to contemporary climate trends over the last

century. Some of this complexity appears to reflect the confounding of the climate signal, which has generally been progressively warmer, with other temporal changes such as recovery from past land-use history and atmospheric pollution (e.g., acid rain). Initial evidence of red spruce range contraction came from upslope shifts of the deciduous/coniferous ecotone in Vermont between 1964 and 2004 (Beckage et al. 2008). The position of this ecotone is highly correlated with mid-summer temperatures (Hamburg and Cogbill 1988; Cogbill and White 1991). However, later studies documented widespread regional trends of a subsequent downslope movement of red spruce and associated conifer forests throughout New England (Foster and D'Amato 2015; Wason and Dovciak 2017), including some of the same areas where upslope movement was previously documented (Verrico et al. 2020). This re-colonization of lower elevations has principally been attributed to recovery from historical anthropogenic land-use history, which negatively impacted low-elevation red spruce, and reductions in atmospheric pollution since passage of the Clean Air Act (Wason and Dovciak 2017; Verrico et al. 2020).

Other evidence of growth responses of red spruce to contemporary climate comes from dendroecological studies. Here again, the response to climate change is complicated. In western Massachusetts, where red spruce is at the southern margin of its distribution in New England, climate warming trends over the past century resulted in reductions in annual growth rings, particularly associated with the previous year's July maximum temperature (Ribbons 2014). In contrast, positive associations between annual growth rings and summer temperatures (both current and previous year's) were reported elsewhere in New England, despite a similar climate trend of regional warming (Wason et al. 2017; Kosiba et al. 2018). In the central Appalachians, tree-ring chronologies of red spruce from three stands in West Virginia showed evidence of recovery from historical atmospheric pollution and increased growth linked to higher CO_2 concentration and warmer April temperatures, the latter likely reflecting a positive phenological response to climate warming (Mathias and Thomas 2018). Another dendroclimatic study of red spruce from 18 sites throughout the Monongahela NF in West Virginia also found tree-ring growth was positively associated with warmer April temperatures, as well as warmer autumn temperatures (Yetter et al. 2021). However, this same study documented negative growth responses to warming summer temperatures, and climate change projections forecasted an overall reduction in growth in response to warm-temperature stress under future climates (Yetter et al. 2021). These projections are in line with most red spruce ENMs for this region, which generally predict a range contraction in response to increasing temperatures (summarized in Sect. 7.3.1.1).

7.2 Ecological, Physiological, and Evolutionary Perspectives on Climate Adaptation in Red Spruce Ecosystems

Here we summarize what is known about the responses of red spruce ecosystems to climate and climate change, looking across scales including the level of communities of interacting species and the physiological scale of tree stress response. We finish this section with a summary of recent research on red spruce local adaptation to climate, and the traits and genes that have been discovered as underlying this adaptation. Our intent is to impart a detailed understanding of the current distribution of climate-adapted diversity in red spruce, as a preface to Sect. 7.3, which explores model predictions of how this diversity is likely to interact with a changing climate over the next century.

7.2.1 Red Spruce Communities, Species Interactions, and Climate Change

Red spruce communities, and the unique biodiversity they contain, occupy the highest-elevation habitats and the coolest climatic niches in the central and southern Appalachians and are clearly at risk due to climate change. Warming and possible drying of habitats will negatively impact many species that are adapted to the cool, moist conditions prevailing within the red spruce ecosystem. Extreme events, including floods, droughts, and severe storms will also place new stresses on species struggling to adapt to changing conditions.

The majority of foundational tree species in the red spruce ecosystem are predicted to decline as the climate changes, based on modeling by the USDA Forest Service (Table 7.1; Iverson et al. 2012; Peters et al. 2020). As these foundational tree species decline, cascading effects on specialist species are anticipated. For example, the Cheat Mountain salamander (*Plethodon nettingi*; Fig. 7.2) depends upon the moist, cool, mossy, rock-strewn forest floor of red spruce forests, and with a home range of just a few m^2, has very limited ability to disperse (Pauley 2022). Virginia northern flying squirrels (*Glaucomys sabrinus fuscus*) depend on red spruce and red spruce-northern hardwood forests with abundant snags, mature trees, lichens, and mosses (Menzel et al. 2006; Ford et al. 2022). Certain snails, such as the Spruce Knob threetooth (*Triodipsis picea*), live in moist or wet areas associated with calcium-poor soils common to the red spruce ecosystem. This species accumulates calcium in its shell, which upon its death becomes a key available nutrient for birds and small mammals (Dourson and West Virginia Division of Natural Resources 2015). Larvae of the salt-and-pepper looper moth (*Syngrapha rectangula*) feed on the needles of red spruce, balsam fir (*Abies balsamea*), and eastern hemlock (*Tsuga canadensis*), and these larvae in turn form a key food source for birds (Opler et al. 2010).

Table 7.1 Modeled climate change adaptability (biological and disturbance factors) and capability (adaptability, predicted range shift, and abundance) scores for common dominant trees in the red spruce ecosystem

Common name	Scientific name	Adaptability	Capability	Traits that increase adaptability	Traits that decrease adaptability
Red spruce	*Picea rubens*	Low	Poor	Environmental habitat specificity; shade tolerance	Fire topkill; seedling establishment
Balsam fir/Fraser fir	*Abies balsamea/ Abies Fraseri*	Low	Fair	Shade tolerance	Insect pests; fire topkill; drought
Eastern hemlock	*Tsuga canadensis*	Low	Poor	Shade tolerance	Insect pests; drought
Yellow birch	*Betula alleghaniensis*	Medium	Fair	Dispersal	Fire topkill; insect pests; disease
Red maple	*Acer rubrum*	High	Very good	Seedling establishment, environment habitat specificity, edaphic specificity, shade tolerance, dispersal	None
American beech	*Fagus grandifolia*	Medium	Good	Shade tolerance	Insect pests; fire topkill
Yellow buckeye	*Aesculus flava*	High	Poor	Shade tolerance	Drought; seedling establishment; fire topkill; environment habitat specificity; dispersal

Adapted from Peters et al. (2020) and Iverson et al. (2012)

The relative risk of local extirpation of plant and animal species due to climate change was assessed by Byers and Norris (2011) for 185 taxa in West Virginia using NatureServe's Climate Change Vulnerability Index (Young et al. 2011). Thirty-seven of these taxa are associated with red spruce ecosystems. Climate change vulnerability assessments involve describing the severity and scope of exposure that species experience and combining this with species' sensitivity and capacity to adapt to climate change (Foden et al. 2019). Inputs to the assessment are downscaled projections of future climate, natural history data for each species, and distributional data for the species and its habitat. Of the 37 red spruce-associated species assessed, thirteen are globally rare, twelve are rare in West Virginia, and twelve are common (Table 7.2).

All of the globally rare species assessed were determined to be vulnerable to climate change, including two species, Cheat Mountain salamander and glade spurge



Fig. 7.2 Adult Cheat Mountain salamander (*Plethodon nettingi*) in a high-elevation red spruce (*Picea rubens*) forest in Tucker County, West Virginia. Photo by Donald Brown

(*Euphorbia purpurea*), which scored *Extremely Vulnerable.* Of the state-rare species assessed, half (six) were determined to be vulnerable to climate change, five were presumed stable, and one was predicted to increase. Of the common species, eight were presumed stable, one was predicted to increase, and the following were determined to be vulnerable to climate change: red spruce, black cherry (*Prunus serotina*), sugar maple (*Acer saccharum*), and brook trout (*Salvelinus fontinalis*).

Several factors were key to influencing climate change vulnerability in this species assemblage, including natural barriers to dispersal (mountaintop location with low-elevation barriers to the north), physiological thermal niche, physiological hydrologic niche, and historical hydrologic niche. For amphibians and some plants, dispersal ability was a strong limiting factor. Thirteen of the 37 species assessed, including red spruce, black cherry, and many of the more mobile taxonomic groups such as birds and butterflies, were predicted to shift their range northward and disappear from West Virginia.

On the positive side, red spruce communities have several key characteristics that are likely to impart resilience in the face of climate stress and other stresses. For one, they occur on large tracts of relatively well-connected landscapes. The red spruce ecosystem as a whole, including both forested and wetland communities, contains high levels of biodiversity, which means that even with some extinctions, there may be enough connected threads of the ecosystem left to function. The southwest to northeast orientation of the mountains, and the connectivity of natural habitats between low and high elevations, may allow some rapidly dispersing species to migrate northward or, in some cases, upward as the climate envelope shifts. Regardless of what happens to the individual species in the red spruce ecosystem, the landscape itself is

Table 7.2 Climate change vulnerability assessment of selected species inhabiting red spruce (*Picea rubens*) ecosystems in West Virginia (WV)

Common name	Scientific name	Conservation status	Climate change vulnerability	Relationship to red spruce ecosystems
Alder flycatcher	*Empidonax alnorum*	WV vulnerable	Highly vulnerable; range may shift out of WV	Associate; also occurs in other habitats
Allegheny crayfish	*Orconectes obscurus*	Apparently secure	Presumed stable	Associate; also occurs in other habitats
Allegheny woodrat	*Neotoma magister*	Globally vulnerable	Moderately vulnerable	Associate; also occurs in other habitats
American woodcock	*Scolopax minor*	WV vulnerable	Presumed stable	Associate; also occurs in other habitats
Appalachian brook crayfish	*Cambarus bartonii cavatus*	Secure	Presumed stable	Associate; also occurs in other habitats
Bear Creek slitmouth snail	*Stenotrema simile*	Globally imperiled	Moderately vulnerable	Associate; also occurs in other habitats
Big River crayfish	*Cambarus robustus*	Apparently secure	Presumed stable	Associate; also occurs in other habitats
Black cherry	*Prunus serotina*	Secure	Moderately vulnerable; range may shift out of WV	Associate; also occurs in other habitats
Black dash	*Euphyes conspicua*	WV critically imperiled	Moderately vulnerable; range may shift out of WV	Associate; also occurs in other habitats
Blackgum	*Nyssa sylvatica*	Secure	Increase likely	Associate; also occurs in other habitats
Blue crawfish	*Cambarus monongalensis* (mountains)	Globally vulnerable	Moderately vulnerable	Associate; also occurs in other habitats
Bog copper	*Lycaena epixanthe*	WV critically imperiled	Moderately vulnerable; range may shift out of WV	Obligate (wetlands)

(continued)

Table 7.2 (continued)

Common name	Scientific name	Conservation status	Climate change vulnerability	Relationship to red spruce ecosystems
Brook trout	*Salvelinus fontinalis*	Secure	Highly vulnerable	Associate; also occurs in other habitats
Cheat Mountain salamander	*Plethodon nettingi*	Globally imperiled	Extremely vulnerable	Close associate
Elk River crayfish	*Cambarus elkensis*	Globally imperiled	Moderately vulnerable	Associate; also occurs in other habitats
Fisher	*Martes pennanti*	WV vulnerable	Presumed stable; range may shift out of WV	Associate; also occurs in other habitats
Glade spurge	*Euphorbia purpurea*	Globally vulnerable	Extremely vulnerable	Obligate (wetlands)
Monongahela Barbara's-buttons	*Marshallia pulchra*	Globally imperiled	Moderately vulnerable	Associate; also occurs in other habitats
Mountain earthsnake	*Virginia valeriae pulchra*	Globally vulnerable	Highly vulnerable; range may shift out of WV	Associate; also occurs in other habitats
New River crayfish	*Cambarus chasmodactylus*	WV vulnerable	Presumed stable	Associate; also occurs in other habitats
Northern goshawk	*Accipiter gentilis*	WV critically imperiled	Presumed stable; range may shift out of WV	Associate; also occurs in other habitats
Northern saw-whet owl	*Aegolius acadicus* (breeding)	WV imperiled	Moderately vulnerable; range may shift out of WV	Close associate
Northern saw-whet owl	*Aegolius acadicus (*wintering)	WV vulnerable	Increase likely	Associate; also occurs in other habitats
Olive-sided flycatcher	*Contopus cooperi*	WV critically imperiled	Presumed stable; range may shift out of WV	Obligate (openings and wetlands)

(continued)

Table 7.2 (continued)

Common name	Scientific name	Conservation status	Climate change vulnerability	Relationship to red spruce ecosystems
Pink-edged sulphur	*Colias interior*	WV critically imperiled	Moderately vulnerable; range may shift out of WV	Close associate (openings)
Pitch pine	*Pinus rigida*	Secure	Presumed stable	Associate; also occurs in other habitats
Red maple	*Acer rubrum*	Secure	Presumed stable	Associate; also occurs in other habitats
Red spruce	*Picea rubens*	Apparently secure	Highly vulnerable; range may shift out of WV	Obligate
Rock crawfish	*Cambarus carinirostris*	Secure	Presumed stable; range may shift out of WV	Associate; also occurs in other habitats
Sanborn's crayfish	*Orconectes sanbornii*	Apparently secure	Presumed stable	Associate; also occurs in other habitats
Shriver's frilly orchid	*Platanthera shriveri*	Globally critically imperiled	Highly vulnerable	Associate; also occurs in other habitats
Southern rock vole	*Microtus chrotorrhinus carolinensis*	Globally vulnerable	Moderately vulnerable	Associate; also occurs in other habitats
Southern water shrew	*Sorex palustris puctulatus*	Globally vulnerable	Moderately vulnerable	Associate; also occurs in other habitats
Spruce Knob threetooth snail	*Triodopsis picea*	Globally vulnerable	Moderately vulnerable	Close associate
Sugar maple	*Acer saccharum*	Secure	Moderately vulnerable	Associate; also occurs in other habitats

(continued)

Table 7.2 (continued)

Common name	Scientific name	Conservation status	Climate change vulnerability	Relationship to red spruce ecosystems
Swainson's thrush	*Catharus ustulatus*	WV critically imperiled	Moderately vulnerable; range may shift out of WV	Close associate
Virginia northern flying squirrel	*Glaucomys sabrinus fuscus*	Globally imperiled	Highly vulnerable	Close associate

Adapted from Byers and Norris (2011)

likely to continue to support important conservation targets for the foreseeable future (Byers et al. 2010).

7.2.2 Physiological Responses to Seasonal and Annual Variation in Climate

7.2.2.1 Gas Exchange and Environmental Conditions

Photosynthetic rates in red spruce follow ambient air temperature, achieving the highest rates in midsummer, declining in the autumn, and reducing to zero under freezing conditions. Red spruce trees are able to efficiently photosynthesize over a wide optimum temperature range (16–32 °C [61–90 °F]), with sharp declines at temperatures >32 °C (90 °F; Vann et al. 1994; Day 2000). Specific rates are dependent on leaf nutrition, hydration status, and genetics, though the photosynthetic response to air temperature is very predictable (Fig. 7.3). The species is very responsive to warming in the winter and can photosynthesize any time the air temperature is above freezing for a few hours (Schaberg et al. 1998). Winter photosynthesis is limited by water availability in the foliage and inhibition from the accumulation of carbohydrates (Schaberg 2000), so it is not a primary means of carbon capture in northern regions, but the long season with temperatures permissive for photosynthesis is likely relevant to growth in the southern end of the range. The rapid response of photosynthesis to increasing temperature may confer growth advantages over deciduous trees and, in mixed forests, permit enhanced carbon capture in the understory before spring leaf-out. However, the warm conditions that permit photosynthesis also lead to a reduction in cold tolerance and a vulnerability to injury if there is a rapid return to very cold temperatures (Schaberg 2000).

Red spruce is characterized by comparatively low stomatal conductance or degree of stomatal opening, which relates to gas exchange and water loss. This results in low to moderate growth rates and conservation of water in dry conditions. Photosynthesis and stomatal conductance in red spruce are less sensitive to low vapor pressure deficit than other conifers (Day 2000), enabling them to capture carbon during periods of high humidity (Reinhardt and Smith 2008). It has been hypothesized that elevation, temperature, and cloud cover combine to define where red spruce is abundant across its range (Cogbill and White 1991). In studies of high and low-elevation saplings near Mt. Mitchell, North Carolina, Berry et al. (2019) found that immersion in clouds resulted in higher leaf water potential and rates of photosynthesis, especially in the afternoon, even though lower light conditions prevailed. Immersion in clouds also helped to maintain leaf hydration which allowed for higher photosynthetic rates throughout the day. Evidence that cloud levels are rising from the central to northern Appalachians (but not southern Appalachians) could exacerbate drought stress for

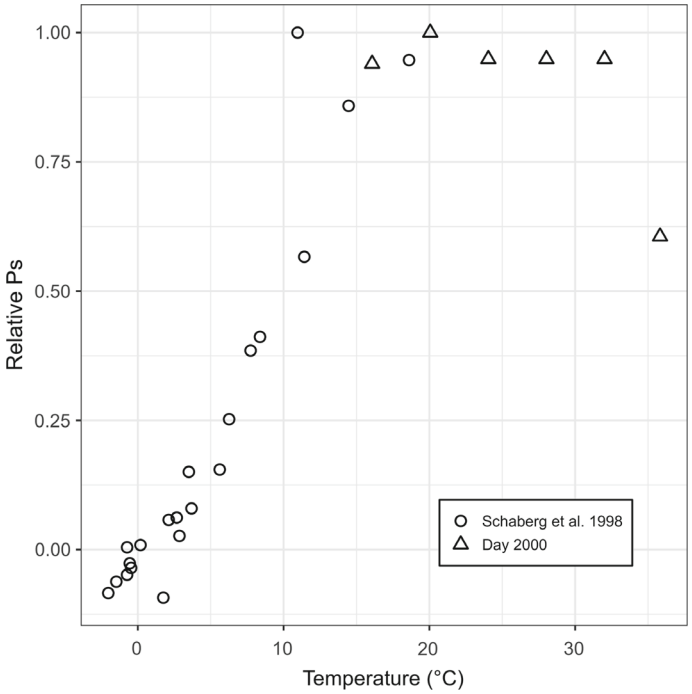


Fig. 7.3 Relative red spruce (*Picea rubens*) photosynthesis (Ps) where the maximum value is normalized to 1 (per study) follows a predictable pattern from negative to near zero at air temperatures of 0 °C (32 °F), and rises to an optimum range from 16 to 32 °C (61–90 °F), before declining

red spruce (Richardson et al. 2003). Climate change scenarios that lead to diminished cloud levels and high vapor pressure deficit would likely be detrimental to productivity.

7.2.2.2 Light Response

Red spruce is a late-successional species with adaptations to low-light environments. Compared to its sister species black spruce, red spruce has lower quantum yield or efficiency in bright light and greater thermal energy dissipation efficiency, which offer a greater degree of photoprotection and resulting photoinhibition (Major et al. 2003). In low light, red spruce exhibits a higher photochemical efficiency than other conifers allowing it to take advantage of fleeting sunflecks, though light saturation of photosynthesis can occur at levels as low as 250 μmol m^{-2} m s^{-1} or 1/8 that of full sunlight in the understory (Alexander et al. 1995). Seedlings grown under 50% shade cloth experienced light-saturated photosynthesis at levels between 600

and 1,000 μmol m^{-2} m s^{-1} (J. Butnor, unpublished data). Seedlings and advance-regeneration understory trees can be stressed by sudden exposure to bright light as may occur with clearcutting (Dumais and Prévost 2007). For this reason, gradually increasing light through multiple entries or gap creation is recommended for releasing suppressed red spruce in the understory (Rentch et al. 2016).

7.2.2.3 Response to High Temperatures and Drought

Based on the distribution of the species on the landscape, red spruce is favored in cool, moist environments and microsites (Koo et al. 2014a, b). On a physiological level, red spruce is unable to efficiently photosynthesize at temperatures above 32 °C (90 °F; Day 2000) and severe cellular damage has been reported for temperatures between 32 and 40 °C (90 and 104 °F; Vann et al. 1994). Red spruce's low stomatal conductance limits transpirational cooling. Air temperatures at elevations where red spruce occurs in the southern Appalachians seldom exceed these thresholds. For example, a series of data loggers on Mt. Mitchell (North Carolina) that were installed across eight elevations from 1,024 to 2,027 m (3,360–6,650 ft) found the maximum hourly air temperature at the summit never surpassed 21.2 °C (70.2 °F) during a 3-year period (2018–2020), while the lowest elevation experienced a maximum temperature of 29.8 °C (85.6 °F; Table 7.3). However, seed beds in full sunlight and exposed surfaces after disturbances can easily exceed lethal temperatures (Gray and Spies 1997), and leaf temperatures in full light can be several degrees warmer than ambient air, emphasizing the species' need for cool establishment conditions.

Drought affects the growth patterns of most woody plants, including red spruce, though relatively low stomatal gas exchange limits water loss during dry conditions (Day 2000). Red spruce is noted for shallow rooting and requiring ample moisture for seedling germination and establishment (Blum 1990), which likely are responsible for its drought vulnerability. Prior-season heat and drought stress have been correlated with growth declines and susceptibility to injury from cold and other abiotic stressors (Kosiba et al. 2018).

7.2.2.4 Freezing Injury

Populations adapted to cold climates typically have greater cold tolerance, though seasonal acclimation to cold temperatures determines the susceptibility to injury at specific times (Bigras and Colombo 2013). Acclimation is a complex biochemical process where changes in intracellular carbohydrates, solutes, proteins (particularly dehydrins), antioxidants, and lipid membranes are initiated by environmental cues and function to protect cells from freezing (Kalberer et al. 2006; Strimbeck et al. 2008, 2015). Tree species from warm temperate mountains may be injured by winter temperatures between −25 and −35 °C (−13 and −31 °F), while true boreal species can survive temperatures in excess of −80 °C (−112 °F; Strimbeck and Schaberg 2009).

Table 7.3 Mean, maximum, minimum, January (mean), and August (mean) air temperature (temp) and maximum vapor pressure deficit (VPD; kilopascals [kPa]) statistics based on weather station data collected hourly from eight elevations at Mt. Mitchell, North Carolina, 2018–2020 (J. Butnor and C. Maier, USDA Forest Service, Southern Research Station, unpublished data)

Elevation (m [ft])	Mean temp (°C [°F])	Maximum temp (°C [°F])	Minimum temp (°C [°F])	January temp (°C [°F])	August temp (°C [°F])	VPD (kPa)
2,027 (6,650)	6.3 (43.3)	21.2 (70.2)	−22.2 (−8.0)	−3.4 (25.9)	13.8 (56.8)	1.7
1,914 (6,280)	7.2 (45.0)	22.6 (72.7)	−21.3 (−6.3)	−2.3 (27.9)	14.5 (58.1)	1.9
1,807 (5,928)	8.0 (46.4)	23.4 (74.1)	−20.2 (−4.4)	−1.3 (29.7)	15.2 (59.4)	2.0
1,699 (5,574)	8.3 (46.9)	23.0 (73.4)	−18.9 (−2.0)	−1.0 (30.2)	15.4 (59.7)	1.9
1,543 (5,062)	9.4 (48.9)	23.8 (74.8)	−17.4 (0.7)	−0.1 (31.8)	16.7 (62.1)	1.9
1,377 (4,518)	10.6 (51.1)	28.0 (82.4)	−17.4 (0.7)	0.8 (33.4)	17.8 (64.0)	2.6
1,217 (3,993)	11.5 (52.7)	28.3 (82.9)	−18.0 (−0.4)	1.4 (34.5)	18.7 (65.7)	2.8
1,024 (3,360)	11.9 (53.4)	29.8 (85.6)	−17.0 (1.4)	2.1 (35.8)	18.8 (65.8)	3.3

Red spruce foliage is only marginally cold-tolerant (e.g., −35 to −50 °C [−31 to −58 °F] in Vermont mid-winter conditions), compared to the sympatric species balsam fir, which can survive freezing in liquid nitrogen after acclimation (DeHayes et al. 1990; Schaberg et al. 2000; Strimbeck et al. 2015). These temperatures may seem unrealistic in the warming central and southern Appalachians, but extensive evaluation of red spruce cold tolerance has only been done on material acclimated to the temperatures of the northern Appalachians, where extreme low temperatures may be 10–20 °C colder than in the southern portion of the range. A red spruce provenance trial planted near Colebrook, New Hampshire that included collections from North Carolina, West Virginia, and Pennsylvania did not find strong relationships between climate of origin and either cold tolerance or winter injury for these southern provenances (DeHayes et al. 1990). Mid-winter cold hardiness of red spruce may be reduced by as much as 14 °C after a thaw of ≥3 days, opening a window for freezing injury (Strimbeck et al. 1995), after which trees may require several weeks to return to pre-thaw cold hardiness. This highlights the tradeoff between the risk of freezing injury versus the benefit of additional carbon gain (Schaberg 2000), especially for productivity of understory red spruce before deciduous trees leaf out in the spring.

A variety of abiotic factors have been shown to affect red spruce physiology in ways that impact susceptibility to cold injury. During the severe red spruce declines in the 1980s, symptoms analogous to winter injury of foliage were commonly observed

and related to air pollution and acid rain (Johnson and Siccama 1983; DeHayes et al. 1990; Vann et al. 1992). Low-pH conditions were found to alter the mobility of Al ions in the soil, which affected Ca nutrition in red spruce, leading to winter injury under otherwise nonlethal temperatures (Shortle et al. 1997; DeHayes et al. 1999; Driscoll et al. 2001).

7.2.2.5 Physiological Component of Recent Gains in Productivity

Over the past decade, there have been numerous reports of increases in general health and radial growth, combined with downslope migration of red spruce (Foster and D'Amato 2015; Kosiba et al. 2018; Mathias and Thomas 2018), and the last major winter injury event was in 2003 (Lazarus et al. 2004). Dramatic reductions in atmospheric deposition of nitrate and sulfate associated with red spruce decline have helped ameliorate winter injury, and warmer temperatures outside of the typical growing season have increased photosynthesis and growth (Kosiba et al. 2018). Between 1980 and 2020, the concentration of CO_2 in the atmosphere has increased by more than 20% (National Oceanic and Atmospheric Administration 2023), making photosynthesis more efficient by increasing the differential between atmospheric CO_2 concentration and CO_2 inside the leaf, leading to increased water-use efficiency. Using stable isotopes, Mathias and Thomas (2018) found that red spruce growth more than doubled in the central Appalachians since 1989, an effect they attributed largely to reduced sulfate deposition and increased atmospheric CO_2.

7.2.3 Evidence and Nature of Adaptation to Climate in Red Spruce

7.2.3.1 Local Adaptation to Climate in Common Garden Studies

Local adaptation is the product of an evolutionary process by which natural selection favors individuals with genetically based trait values that maximize fitness (e.g., survival, growth, reproduction) under local environmental conditions. A strict definition of local adaptation posits that locally adapted genotypes have higher fitness in their native environment than genotypes originating from other environments (Kawecki and Ebert 2004). Local adaptation to climate is commonly observed in forest trees (Savolainen et al. 2007), often studied using provenance trials or common gardens, and has been shown to be present in the genus *Picea* in relation to different climatic drivers. For example, white spruce is locally adapted to the frequency of extreme drought events (Depardieu et al. 2021), Sitka spruce (*Picea sitchensis*) and black spruce are locally adapted to the length of the growing season (Mimura and Aitken 2010; Rossi 2015), and Norway spruce (*Picea abies*) shows variation in both

height and diameter associated with source-locality genetic make-up (Milesi et al. 2019).

Two recent studies showed that red spruce is no exception to the ubiquity of local adaptation to climate among spruce species (Capblancq et al. 2022; Prakash et al. 2022). Prakash et al. (2022) conducted a common garden study (Fig. 7.4) in which seed was sampled from >300 mother trees representing 65 geographically diverse localities throughout the geographic distribution of red spruce (Fig. 7.5). This sampling captured variation naturally present across three geographically and genetically differentiated ancestry groups: (1) the northern Appalachians, (2) the Allegheny and Pocono plateaus of Pennsylvania, and (3) the central and southern Appalachians (Capblancq et al. 2020a). Seedlings from each family (>5,000 total) were planted into three common gardens located along a latitudinal gradient in Burlington, Vermont; Frostburg, Maryland; and Asheville, North Carolina. By monitoring vegetative phenology (spring bud break and autumn bud set) and height growth over 2 years, Prakash et al. (2022) showed the presence of significant heritable genetic variation in these traits (H^2 from 0.075–0.408), as well as strong plasticity in trait expression across the different common garden sites. Growing plants from different source climates together under common garden conditions revealed significant genetic differentiation in phenology among the ancestry groups, with seedlings from the central and southern Appalachians exhibiting the latest bud break and bud set across all garden sites, while seedlings from the northern ancestry group had the earliest phenology (Prakash et al. 2022). This somewhat counterintuitive result (i.e., southern genotypes with delayed phenology relative to northern genotypes under common garden conditions) is a frequent observation in other tree species and reflects the warmer and more variable winter temperatures commonly encountered in southern regions that select for genotypes that require a large number of growing degree days to accumulate before breaking dormancy (Thibault et al. 2020). Phenology traits also showed a high degree of plasticity in response to climatic differences between the garden sites, occurring earlier in the growing season at the North Carolina garden for both bud break and bud set relative to the two more northern gardens. Interestingly, plasticity in bud break was significantly correlated with climate of origin, with southern seedlings expressing higher bud break plasticity compared to northern seedings (Prakash et al. 2022). Recent analyses have demonstrated that the genetic differentiation among ancestry groups in bud break and bud set phenology, as well as in bud break plasticity, reflect local adaptation of these traits to climate (A. Prakash and S. Keller, unpublished manuscript).

Evidence of locally adaptive bud phenology at a finer spatial scale within the southern Appalachian region comes from a common garden greenhouse study using 32 seed families collected along replicated altitudinal gradients in Great Smoky Mountains National Park, Tennessee and Mt. Mitchell State Park, North Carolina (Butnor et al. 2019). Seedlings from high-elevation sources set bud up to 10 days earlier than low-elevation sources, but no clinal variation was observed for bud break (Butnor et al. 2019). The accelerated bud set of high-elevation sources closely paralleled the earlier bud set observed for high-latitude sources by Prakash et al. (2022),



Fig. 7.4 Red spruce (*Picea rubens*) common garden experiment at the University of Maryland Center for Environmental Science, Appalachian Lab in Frostburg, Maryland. Photo by Matthew Fitzpatrick

confirming that this trait serves as a local adaptation to growing season length in red spruce.

A further demonstration of local adaptation of red spruce populations to their source climates comes from Capblancq et al. (2022). Using the same experimental seedlings reported in Prakash et al. (2022), Capblancq et al. (2022) analyzed height growth over two years of growth in the common gardens and related these to the difference between source climate and the climate of the common garden (a.k.a., climate transfer distance). They showed a highly significant negative correlation between the magnitude of climate transfer distance and seedling height growth in the common gardens over 2 years, thus demonstrating local adaptation in red spruce linked to gradients of temperature and precipitation (Fig. 7.6). Further, because the climate of the garden sites was generally warmer and drier than most of the source climates for the seedlings (especially the North Carolina site), the climate transfer analysis by Capblancq et al. (2022) provides a much-needed experimental assessment of how red spruce will respond to a warming climate, using a space-for-time proxy for climate change. However, this experiment only addressed seedling performance and may or may not be indicative of fitness at later life stages.

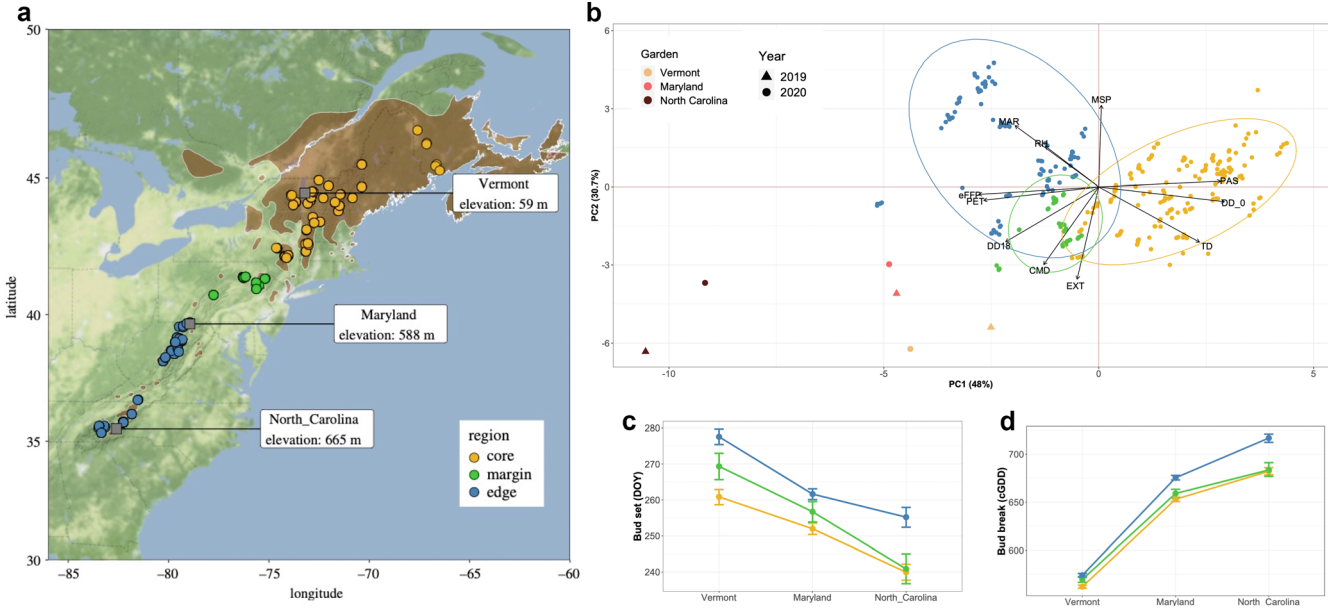


Fig. 7.5 Regional differentiation in quantitative genetic variation in phenology traits along climatic gradients in red spruce (*Picea rubens*). **a** Genetic ancestry groups sampled in the northern Appalachians (yellow, *core*), Allegheny and Pocono plateaus (green, *margin*), and central and southern Appalachians (blue, *edge*) are genetically differentiated at the molecular level (Capblancq et al. 2020a). Seeds from each of these populations were grown as seedlings and planted into three common garden locations (gray squares) in Vermont, Maryland, and North Carolina. **b** The genetic ancestry groups inhabit different climatic zones, based on a principal component analysis of 11 climate variables: mean summer precipitation (MSP), precipitation as snow (PAS), degree-days per year <0 °C (32 °F; DD_0), temperature continentality (TD), extreme summer temperature (EXT), climate moisture deficit (CMD), degree-days per year >18 °C (64 °F; DD_18), potential evapotranspiration (PET), estimated frost-free period (eFFP), mean annual solar radiation (MAR), and mean annual relative humidity (RH). **c** Mean bud set versus day of year (DOY) in 2019 by genetic ancestry group and common garden site. **d** Mean bud break versus cumulative growing degree days >0 °C (32 °F; cGDD) in 2020. Values represent means ± SE. Figures used with permission of The Royal Society (U.K.), from Prakash et al. (2022); permission conveyed through Copyright Clearance Center, Inc.

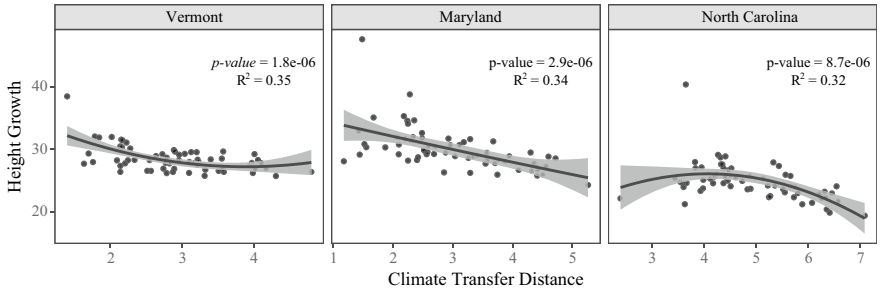


Fig. 7.6 Association between climate transfer distance based on a principal component analysis of 11 climate variables (see Fig. 7.5) and red spruce (*Picea rubens*) seedling fitness represented by mean height growth per source locality at the three common garden sites. The significance of the association was tested in each garden using a quadratic regression; the resulting p-values for the quadratic term and R^2 are shown on each panel. Lines show model predictions and the gray areas show the 95% confidence intervals. Figure used with permission of John Wiley & Sons, from Capblancq et al. (2022); permission conveyed through Copyright Clearance Center, Inc.

Other common garden studies with evidence of genetically based climate adaptation come from red spruce provenance trials established by foresters in the mid-twentieth century, which are now mature enough to provide informative data on adult tree responses. These trials were located in the northern part of the range (Morgenstern et al. 1981; Wilkinson 1990), but since many incorporated at least a few central or southern Appalachian seed sources, they provide valuable evidence of genetic differentiation in quantitative traits between southern and northern populations and evidence for local adaptation to their respective climates. For example, Li et al. (2020) used height and diameter measurements on mature trees established in six historical provenance trials in eastern Canada's Acadian forests to evaluate if red spruce is likely to persist under climate change in this region. The trials were established in the early 1960s in New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland by the Canadian Forest Service and its collaborators, and each included trees from the same 30 provenances. Except for the two provenances from West Virginia, the locations of origin were all located near the northern range edge or fell within the northern range core in New Brunswick, Nova Scotia, and Maine. Remeasurements from 2013 revealed that temperature-related climate variables played a greater role than precipitation in the growth response of red spruce to climate transfer distance between provenance origin and trial site (Li et al. 2020). Interestingly, under these northern climates, trees showed a significant positive growth response to climate transfer into warmer temperatures, in particular to increases in the length of the growing season, although climate transfers into shorter growing seasons decreased tree size, likely as a result of frost damage (Li et al. 2020). Trees from provenances with a shorter growing season were smaller in size and benefited more from warming than southern provenances, which in turn reacted negatively to cooling.

The findings of Li et al. (2020) indicate that red spruce is cold-limited at its northern range edge, and might at least temporarily benefit from climate warming

in these regions, and imply that northward assisted migration of southern populations might help mitigate climate change effects. The positive effect of mean annual temperatures did not peak, probably due to the fact that none of the experimental sites had a warmer climate than the southernmost West Virginia provenances. Mean annual precipitation had no significant effect, and the positive effects of increased moisture availability (measured, for example, as climatic moisture deficit) were weak but increased the explanatory power of the temperature-related variables. Due to the location of the experiments in the Canadian Maritime provinces, trees received abundant precipitation and were likely not water-limited. In conclusion, Li et al. (2020) provided evidence of the importance of growing season length and other temperature-related climatic conditions for red spruce growth and highlighted the role that phenotypic plasticity and local adaptation may play in its climate change response. However, the study design, which included a limited number of southern provenances and no trial sites in the central or southern Appalachians, limits our ability to draw conclusions regarding how climate warming or increased drought might affect growth of adult red spruce in these regions.

7.2.3.2 Gene-Environment Association Studies Reveal Genes Under Climatic Selection

Local adaptation in red spruce has also been investigated using genomics, which allowed the identification of genes linked to climatically driven divergent selection and revealed the distribution of adaptive genetic variation across the species' range (Fig. 7.7). Three main interconnected axes of adaptation to climate are described for temperate and boreal coniferous species: drought tolerance (Moran et al. 2017), cold hardiness (Howe et al. 2003; Chang et al. 2021), and phenological timing of growth and dormancy (Gyllenstrand et al. 2007). In red spruce, genes involved in all three adaptive pathways were found to be under selection using genome scan methods (Capblancq et al. 2022). The identified candidates included, for example, the FPA gene which regulates the phenology of flowering time in *Arabidopsis thaliana* (Schomburg et al. 2001) and could control the same process in red spruce in response to temperature variation across the latitudinal range or along altitudinal gradients. Various genes associated with drought and heat tolerance were also identified as important potentially adaptive genes in red spruce, especially including genes involved in the abscisic acid pathway. Abscisic acid is known to initiate responses to drought stress (Hamanishi and Campbell 2011), with high abscisic acid concentration acting as a signal for plants to close their stomata and prevent water loss (Moran et al. 2017). Interestingly, some drought resistance genes were also shown associated with pathogen resistance in Norway spruce (Capador-Barreto et al. 2021) and in red spruce, with the gene At4g33300 identified as one of the most important candidate genes.

The geographic distribution of candidate adaptive alleles is particularly interesting in red spruce. Climatically driven divergent selection has resulted in a clear differentiation between southern and northern ancestry groups (Fig. 7.8). Climate-associated



Fig. 7.7 Red spruce (*Picea rubens*) cuttings collected for DNA extraction and sequencing for use in genomic analyses (photo by Matthew Fitzpatrick)

alleles, which make up just a small proportion of the overall diversity within the genome, show strong clinal differentiation of central and southern Appalachian populations compared to populations in the northeastern part of the range. The climate-adaptive alleles contained within the central and southern Appalachian gene pool make this region very important for future conservation and management plans, particularly in the context of assisted migration (Aitken and Bemmels 2016). The presence of warm-adapted alleles in the southern portion of red spruce's range suggests this region could be an important source of seed for assisted migration strategies and highlights the importance of preserving in situ populations that contain unique functional but also genetic diversity.

In addition to adaptive genetic divergence, there is a clear difference in the neutral genetic composition of the central and southern Appalachians from the fragmented

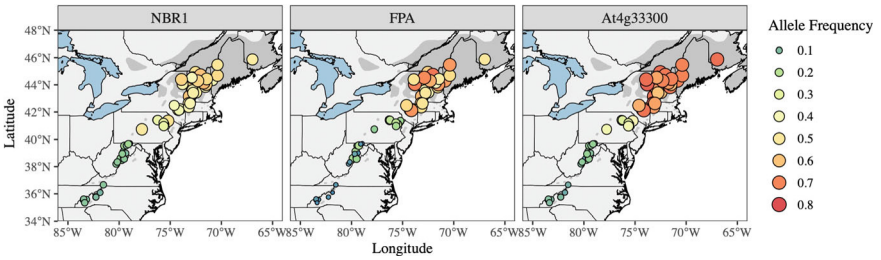


Fig. 7.8 Among-population variation in red spruce (*Picea rubens*) climate-adaptive alleles for three candidate genes identified through gene-environment association analysis. Figure used with permission of John Wiley & Sons, from Capblancq et al. (2022); permission conveyed through Copyright Clearance Center, Inc.

midlatitude region in Pennsylvania and the northeastern region in New England and Canada (Capblancq et al. 2020a). While the estimated genetic difference is relatively low between these regional populations ($F_{ST} < 0.03$), it points to a lack of gene flow along the latitudinal gradient and thus a poor natural dispersal capacity.

In conclusion, recent work on the genetics of climate-adaptive variation has shown that red spruce forests of the central and southern Appalachians are an important pool of adaptive genetic diversity that could become a key component of future genetically informed management programs. However, these forests are already adapted to the warmest portion of the species' climatic niche, which may present constraints to adaptation under warmer future climates. Maintaining high connectivity and gene flow among forest patches will likely be an important consideration for facilitating red spruce persistence in the southern part of its range.

7.3 Adaptation and Management of Red Spruce in a Dynamic Climate

7.3.1 Future Forecasts: What Do Models Suggest About the Future of Red Spruce?

While not without shortcomings, forecasting models offer one of the best methods available to anticipate what the future might hold for natural systems. To date, numerous studies have used models to forecast how red spruce could be impacted by expected changes in climate over the next several decades. While most studies have focused on modeling red spruce's response at the species level, recent studies have begun to consider local adaptation to climate and population-level responses (e.g., Lachmuth et al. 2024). Despite differences in techniques and data, these studies generally depict a gloomy future for red spruce in the central and southern Appalachians. However, recent studies incorporating genomic data and local adaptation to climate

suggest that some populations could persist through this century. In this section, we summarize studies that have used models to forecast the potential impacts of climate on red spruce and what these studies suggest in light of important uncertainties, caveats, and assumptions.

7.3.1.1 Species-Level Models

Numerous studies have used various implementations of ENMs to forecast changes in the potential distribution of red spruce in response to climate change. ENMs are empirical models that combine observations of species occurrence (e.g., presence-absence records) with abiotic covariates that describe important habitat characteristics. Habitat predictors typically include measures of precipitation and temperature and, occasionally, soils or other abiotic correlates (Elith and Leathwick 2009). Once fitted, these models can be forecasted to scenarios of future climate to estimate potential changes in distribution, abundance, or habitat suitability (Guisan and Thuiller 2005).

To describe future climate conditions, modeling studies use forecasts from general circulation models. These forecasts, typically generated as part of assessment reports from the Intergovernmental Panel on Climate Change, span a range of possible emission scenarios and different periods in the future. Best modeling practices dictate that studies should consider climate forecasts from multiple general circulation models (to capture variation between models) and emission scenarios (to explore how different assumptions about future emissions impact forecasts). The typical periods to which models are forecasted are mid-century (2050) and end-of-century (2080). Studies therefore often report results for multiple models and time periods.

Model forecasts based on the worst-case emission scenarios typically project near-complete loss of red spruce habitat from the southern Appalachians by the end of the twenty-first century (Iverson et al. 2008; Stanton 2009; Beane and Rentch 2015; Walter et al. 2017; Yetter et al. 2021). Under the best-case emission scenarios, models generally also forecast overall declines in habitat suitability in the central and southern Appalachians, but the magnitude and extent of these declines tend to be not as severe (e.g., Mosher 2020).

Regions where models suggest red spruce could maintain suitable habitats, especially into the late twenty-first century and regardless of the severity of expected climate change, represent potential climate refugia and areas to focus restoration efforts. For the southern Appalachians, potential refugial locations include Big Bald, Beech Mountain, Plott Balsam Mountain, Sugar Mountain, and Elk Knob (Mosher 2020). For West Virginia, refugial areas reside primarily in Pocahontas and parts of Randolph and Pendleton counties, which contain the Monongahela NF (Beane and Rentch 2015). The broad agreement in forecasted declines in habitat suitability across studies that used different methods, general circulation models, and emission scenarios suggests conservation and restoration efforts in the region will be challenging under ongoing climate change (Walter et al. 2017).

Given their relative simplicity, computational efficiency, and modest data requirements, ENMs are the class of models most often used to forecast potential changes in species distributions in response to climate change. However, these correlative models often lack incorporation of important biological processes such as plasticity, evolution, and dispersal. Mechanistic models offer an alternative to purely empirical ENMs that can incorporate aspects of biological processes into forecasts and a few such models have been developed for red spruce. For example, Rentch et al. (2007) used the NE-TWIGS growth model and the Forest Vegetation Simulator to forecast changes in red spruce abundance in 10-year intervals from 2005 to 2106. The simulations showed initial, early increases in abundance after 10–20 years, followed by declines starting around 2050, and that areas above 1,035 m (3,395 ft) supported the highest total basal area. Prasad et al. (2020) combined predictions from ENMs with a dispersal simulation in an effort to forecast actual changes in occurrence of 25 eastern North American tree species rather than simply potential shifts in habitat suitability. The study provided summaries of the amount of habitat expected to be lost and gained in the U.S. and Canada. Even under moderate emissions, Prasad et al. (2020) reported that red spruce would colonize only 36% of newly suitable habitats, nearly all of which were in Canada, while red spruce habitat would be lost in most other regions. Koo et al. (2011a, 2011b) applied a mechanistic model for red spruce habitat in a series of papers. For example, Koo et al. (2011b) generated submodels that fed into a primary model in order to fully describe the distribution of red spruce based on available and plausible data. This method aimed to assess both direct and indirect, and within- and across-scale, interactions to more accurately portray red spruce habitat. The simulations suggested that at lower elevations (1,450–1,700 m [4,757–5,577 ft]) red spruce exhibits more complex interactions with the environment. Empirical studies by the same group were then able to connect temperature, precipitation, and pollution with tree-ring growth (Koo et al. 2011a). The combination of increased acid rain, temperature, and cloud frequencies negatively impacted suitability the most at higher elevations (Koo et al. 2014a, b). Pollution had an overall negative effect on red spruce regardless of elevation, but the magnitude of impact was less at higher elevations and importantly had more of an impact than did climate change.

7.3.1.2 Population-Level

Species-level ENMs do not take intra-specific differentiation into account and therefore do not consider how local adaptation to climate will influence how different populations could respond to climate change (Aitken et al. 2008). As a promising tool for closing this research gap, the concept of genomic offset (Fitzpatrick and Keller 2015; Capblancq et al. 2020b) allows the incorporation of genomic information into climate change impact assessments and forecasts of climate change responses at the level of populations. Based on model predictions of genomic turnover along environmental gradients, genomic offsets quantify the expected disruption of

existing genotype-environment associations (i.e., the degree of maladaptation populations will likely experience under future environmental conditions; Capblancq et al. 2020b). As such, estimates of the genomic offset a population may experience in situ if the local environment changes (local offset, sensu Gougherty et al. 2021) provide a valuable predictive tool for risk assessment at the population level (Rellstab et al. 2021), and have been applied to a variety of taxa (Dauphin et al. 2020; Gougherty et al. 2021; Nielsen et al. 2021).

For red spruce, Lachmuth et al. (2024) used genomic offset analyses in combination with habitat suitability predictions from classical ENMs. Importantly, the offset models incorporated genomic markers that were linked to genetic loci likely involved in climate adaptation (Capblancq et al. 2022), with common garden experiments being used to validate whether genomic offsets based on these loci had a significant negative effect on growth performance (see also Prakash et al. 2022). The forecasted genomic offsets and changes in habitat suitability from ENMs were mostly driven by changes in temperature-related climatic variables and predicted drastic shifts of suitable habitat to areas north of the current range (Fig. 7.9). However, these projected northward shifts in habitat were driven primarily by populations found in the northern portion of red spruce's range and in the isolated margin populations in Pennsylvania. In contrast to many existing forecasts based on ENMs that did not consider local adaptation, genomic offsets suggested that populations in the central and southern Appalachians might be able to persist in situ owing to specific local climate adaptations, at least under moderate climate change (Lachmuth et al. 2024). Such strong local adaptation is common in both climatically marginal populations that experience strong selection pressure as well as at the equatorial edges of species ranges, where local adaptation has had a longer time to develop (Bontrager et al. 2021).

7.3.1.3 Interpreting Model Forecasts

Ecological niche models require a number of simplifying assumptions and are sensitive to the species occurrence and environmental data used in model fitting. For these reasons, ENM-based forecasts should be interpreted with caution. Perhaps most relevant to modeling the future of red spruce in the central and southern Appalachians is that many of the stands occupying the lowest elevations, and therefore the warmest habitats, have been extirpated by logging and land-use change (Adams and Stephenson 1989). For this reason, ENMs may overestimate the extent of future habitat loss since the data available for model fitting are likely skewed somewhat towards occurrences in high-elevation, cooler and more mesic habitats. In addition, ENMs typically use relatively coarse-grained climate data that do not characterize microclimates that could allow persistence in areas that otherwise become unsuitable.

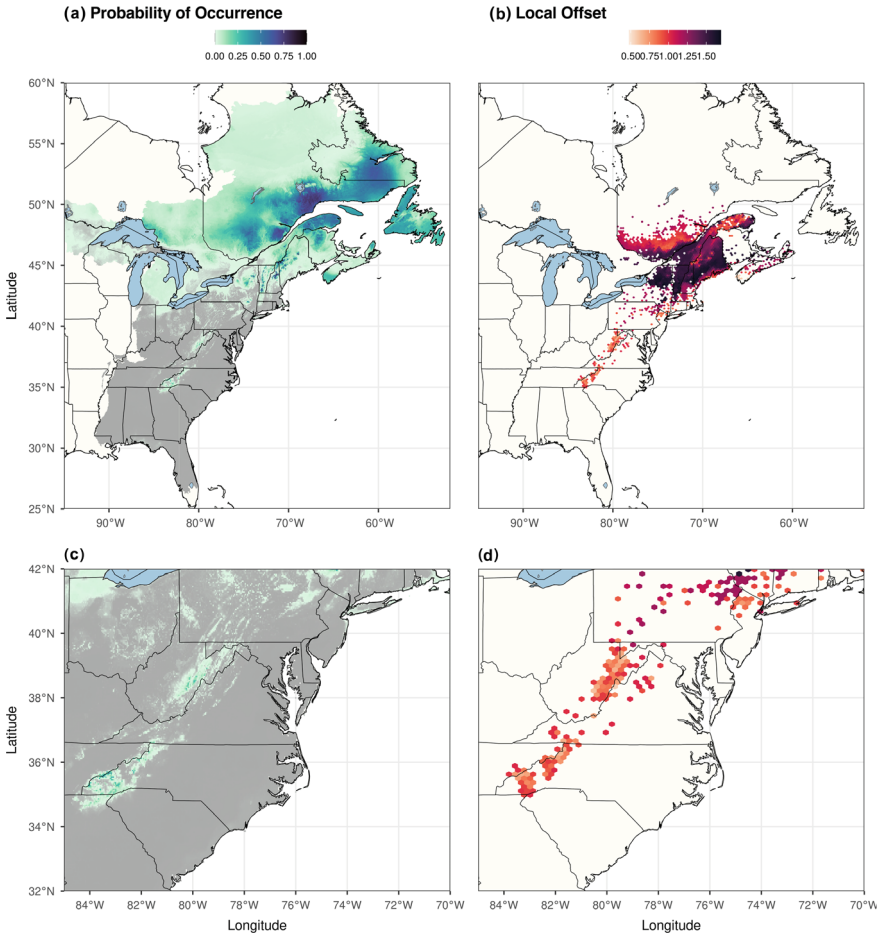


Fig. 7.9 Species versus population-level climate change impact forecasts for red spruce (*Picea rubens*) by the end of the twenty-first century under moderate greenhouse gas emissions (Shared Socio-economic Pathway SSP2-45; Masson-Delmotte et al. 2021). **a** Projection of red spruce occurrence probability (i.e., climate suitability) as predicted by an ensemble of ENMs. Dark gray corresponds to near-zero climate suitability. **b** Genomic offsets of grid cells with contemporary red spruce occurrence (hex map for increased readability). Offsets estimate the disruption of existing genotype-environment associations red spruce populations may experience under climate change. Higher offset values reflect a higher degree of expected mal-adaptation and thus climate change vulnerability. Panels **c** and **d** correspond to those of **a** and **b**, but cropped to the central and southern Appalachians to show greater detail

7.3.2 *Importance of Conserving Genetic Diversity in Situ and in Restoration Strategies for Adaptability to Future Climate Change*

Red spruce genetic variation provides the essential basis for adaptation and resilience to environmental stress and change (Potter et al. 2017), conveying adaptive capacity for future response, the loss of which can be detrimental to the ability of a tree species to survive (Schaberg et al. 2008; Jump et al. 2009). The findings of Prakash et al. (2022) of low to moderate genetic variation and geographic differentiation for phenology and growth traits (Fig. 7.5) suggest that some potential exists to respond to selection and that future climate adaptation will depend on the availability of regional genetic variation in the species. At the same time, the three distinct red spruce ancestry groups, which are associated with different geographic regions of its distribution, exhibit low effective population sizes associated with a sustained population decline across the range of the species (Capblancq et al. 2020a). Lower genetic diversity and higher inbreeding in the fragmented central and southern Appalachian populations of red spruce have been associated with lower germination rate, shorter height, and reduced seedling fitness (Capblancq et al. 2021).

In situ (on site) conservation for tree species such as red spruce is generally considered more efficient for preserving genetic diversity than are ex situ (off site) methods, encompassing the identification of species and areas to protect, the actual protection of an appropriate area, the monitoring of the species or population, and the preparation of management plans (Food and Agriculture Organization of the United Nations 2014). Importantly, protecting or restoring populations in situ is a more evolutionarily dynamic approach because the species or population of interest can maintain its full range of evolutionary and ecological functions and processes while remaining more likely to track the environmental changes to which it must adapt (Rajora and Mosseler 2001). In the medium- to long-term, the restoration of red spruce forests may be necessary in response to past anthropogenic disturbances (e.g., logging, fire, atmospheric pollution), as well as the future potential for widespread mortality resulting from climate change or an insect or disease infestation. Given that red spruce may be vulnerable to as-yet-unknown exotic pests and pathogens, it may be advisable to conserve germplasm that is broadly representative of locally adapted genotypes (Potter et al. 2019). That germplasm could then be used to restore or augment degraded populations in parts of the red spruce distribution. Forest restoration is a complex and relatively young discipline, however (Jacobs et al. 2015).

While forest restoration efforts may successfully conserve the genetic resources of a target tree species, there is also a risk that they could fail. It is important, therefore, that the collection and propagation of germplasm ensure a broad genetic base of restored tree populations, that genetic material is matched to restoration sites where it is likely to be adapted based on current and future site conditions, and that restoration objectives include landscape-level planning (Thomas et al. 2014; Prakash et al. 2024). Specifically, it is critical that planting material represents a

minimum level of intraspecific diversity to ensure that the restored plant species will be able to survive and produce viable offspring (Thomas et al. 2014). Such a focus on capturing and even enhancing regional-scale genetic diversity in restoration plantings has become a recent focus in the central Appalachians and should be considered a critical strategy for in situ conservation alongside optimizing local adaptation under current and future climates (Prakash et al. 2024). This maximization of genetic diversity during in situ restoration is especially important for red spruce, which exhibits overall low genetic diversity compared to other similar tree species (e.g., wind-pollinated conifers), likely due to its demographic history of long-term population decline (Capblancq et al. 2020a).

7.3.3 The Potential for Assisted Migration / Gene Flow to Manage Red Spruce Vulnerability to Climate Change

In the past, conservation and reforestation have largely relied on local seed sources following a "local is best" paradigm (O'Neill and Gómez-Pineda 2021). However, it has also become increasingly clear that forest trees, which are characterized by long generation times and limited dispersal, will not be able to realize rapid in situ evolutionary adaptation or track favorable climates by dispersing to new locations given the velocity of the predicted climatic changes (Aitken et al. 2008; Dauphin et al. 2020). This time delay in natural response is expected to result in increased susceptibility to pest infestations, lower productivity, and reduced carbon sequestration (O'Neill and Gómez-Pineda 2021) and will also limit the prospects of in situ management (Dumroese et al. 2015). Considering these threats, assisted migration—an approach that was long mostly considered for rescuing rare and declining species from the brink of extinction (Hoegh-Guldberg et al. 2008)—has received increasing attention in forestry research (Castellanos-Acuña et al. 2018; Benomar et al. 2022) and practice (Park et al. 2018; O'Neill and Gómez-Pineda 2021). The measures summarized as *assisted migration* comprise both assisted gene flow within and assisted colonization beyond the current geographic distribution of a species (Aitken and Whitlock 2013; Aitken and Bemmels 2016). The potential goals of management through assisted migration range widely from re-introductions of species in parts of their historical ranges; reinforcement (building up an existing population), which may or may not include genetic material better adapted to future climatic conditions; assisted range expansion; and assisted long-distance migration (Dumroese et al. 2015).

Given the projected decline in habitat suitability throughout its current range and the projected northward shift of suitable habitats, red spruce could benefit from proactive measures. More than a decade ago, Byers and Norris (2011) suggested in their climate change vulnerability assessment that innovative and unconventional measures such as assisted migration should at least be discussed for highly vulnerable species, including red spruce. Iverson et al. (2019) combined habitat suitability models, migration simulation models, and analyses of biological species attributes

and disturbance factors to assess the potential of 125 tree species in the eastern U.S. to migrate or infill naturally into suitable habitats over the next 100 years, with explicit reference to assisted migration planning. Due to its presumed low adaptability, the estimated capability of red spruce to cope with climate change across its U.S. range was estimated as "poor" (Massachusetts, New Hampshire [under RCP8.5], New York [under RCP4.5], Vermont, West Virginia) or "very poor" (Connecticut, North Carolina, New York [under RCP8.5], Pennsylvania, Tennessee, Virginia). Only Maine and New Hampshire (under RCP4.5) reached a ranking of "fair." The only states for which the study saw a potential of filling additional, currently unoccupied habitat were Maine, New York (under RCP4.5) and West Virginia (Fig. 7.10). Georgia, Maryland, and Wisconsin were considered currently unoccupied and of unknown potential. Estimates of current and potential future habitat, coping capability, and migration summaries can be downloaded for a variety of geographies from the USDA Forest Service Climate Change Atlas (https://www.fs.usda.gov/nrs/atlas/), providing a valuable resource for assisted migration planning. However, the Iverson et al. (2019) assessment was based on classical species-level ENMs and did not take local adaptation to climate into account. Just as with in situ risk assessments, we can use genomic offset metrics to leverage the informational value of landscape genomics and select source populations that are likely best adapted to future conditions in a potential recipient area, or conversely, sites where seed from an existing population are likely to thrive in the future (Lachmuth et al. 2024). In addition, landscape genomic analyses allow for identification of the underlying climate adaptations and genetic markers responsible for the matches between donor populations and recipient sites.

For red spruce, landscape genomic analyses by Lachmuth et al. (2024) suggest that both assisted gene flow within the current range and assisted colonization beyond the current northern range limit become necessary to protect substantial parts of the

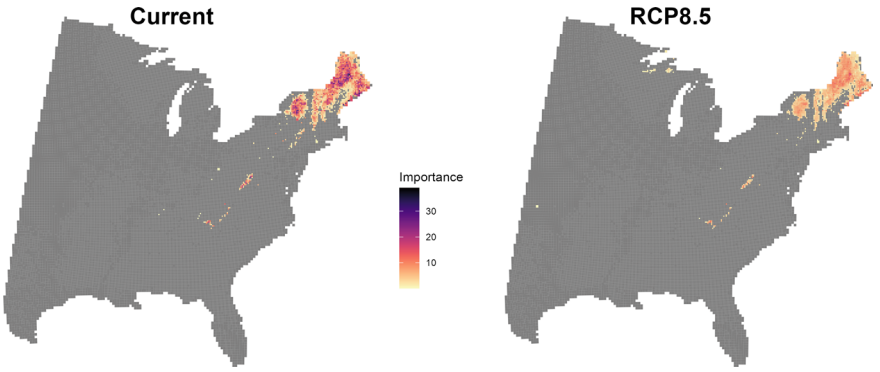


Fig. 7.10 Current predicted (left) and forecasted (right) importance values (a measure of abundance) for red spruce (*Picea rubens*). The forecasted importance values represent a combination among three general circulation models and assuming high emissions (RCP8.5) for the period 2070–2099. Original maps made using data from Peters et al. (2020)

gene pool under climate change. For central and southern Appalachian populations, the analyses confirmed the potential for in situ persistence and potential reforestation or augmentation of existing populations with local seed sources from populations that harbor genotypes adapted to high potential evapotranspiration (PET). The findings further suggest that southern edge populations with adaptations to comparably low PET could serve as donors for assisted migration into the Adirondacks, the Green and White Mountains, and the Canadian Maritime provinces. Moreover, the Maritime provinces may serve as refuges for more southerly populations, including those currently located in Pennsylvania, with adaptations to comparably low chilling degree-days and low precipitation as snow as well as adaptations to low PET and low continentality. The most drastic northward shift of suitable habitat into Ontario and Québec is predicted for red spruce populations with adaptations to high chilling degree-days and high precipitation as snow as well as low PET and high continentality, currently occurring in the northern core of the range. The findings suggest that conserving the genetic resources harbored by these populations would require assisted long-distance migration into a different country and into habitat not currently occupied by the species. This scenario is certainly the most complex case for intervention through assisted migration and requires careful consideration of both risks and benefits, while considering the interests and values of diverse stakeholders (Hagerman and Kozak 2021). Moreover, variability among different climate change emissions scenarios and choice of climatic predictors in modeling add uncertainty to the forecasts, particularly for the southern and central Appalachians, which need to be considered in conservation planning (Lachmuth et al. 2023).

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