Chapter 6
Wildlife

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6.1 Introduction

The central and southern Appalachian Mountain region is among the most biodiverse temperate zone regions in the world (Delcourt and Delcourt 1998; Olson and Dinerstein 2002; Pickering et al. 2002). For vertebrate wildlife, it is a region of particularly high diversity for fishes and amphibians (Etnier and Starnes 1993; Petranka 1998; Jenkins et al. 2015), and many northern breeding bird and small mammal species reach their southern extent in the region (Steele and Powell 1999; Merker and Chandler 2020). Red spruce (*Picea rubens*) and spruce-fir forests occupy a small proportion of the central and southern Appalachians and generally occur only at high elevations, which have comparatively harsh climates and typically small and ephemeral surface water systems (reviewed in Chap. 1). As a result of the restricted occurrence and limiting environmental conditions of high elevation red spruce and spruce-fir forests, wildlife diversity is comparatively low in these forest types. However, they represent optimal habitat for a variety of wildlife species, some

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of which have highly restricted distributions, and thus these forest types are important contributors to regional wildlife diversity (Fig. 6.1).

In this chapter, we review wildlife diversity in red spruce and spruce-fir forests of the central and southern Appalachians, with a focus on species that are strongly associated with these forest types. Sections are organized by taxonomic groups, including fish, herpetofauna (amphibians, reptiles), birds, mammals, and lastly, invertebrates. As discussed in Chap. 1, the extent of red spruce and spruce-fir forests in the region has been dramatically reduced since European settlement. Consequently, local occurrence and abundance of wildlife species that are strongly associated with these forest types has likely been greatly reduced (Chaplin et al. 2000; Diggins 2023). Our knowledge synthesis provides managers and biologists with a single reference to assist

Fig. 6.1 Habitat for the federally threatened Cheat Mountain salamander (*Plethodon nettingi*) in a high elevation red spruce (*Picea rubens*) forest in West Virginia. Photo by Donald Brown

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with identifying local wildlife species that would most benefit from restoration and management of these forest types.

6.2 Fish

Although the central and southern Appalachian Mountain region is known for its tremendous freshwater fish diversity (Etnier and Starnes 1993), fish assemblages that occur in small, high gradient first- and second-order headwater streams within red spruce and spruce-fir forests are fairly depauperate, particularly in the Blue Ridge region and the few red spruce forest occurrences in the Ridge and Valley region. Brook trout (*Salvelinus fontinalis*) are perhaps the most notable fish species in red spruce forests (see Sidebar 6.1) and occur throughout the Appalachian Mountains with their southern distributional terminus in northern Georgia where summer maximum water temperature does not exceed 21 °C (70 °F). Although a number of fish species co-exist with brook trout at lower elevations, the occurrence of fishes other than brook trout in red spruce stands above 1,200 m (3,900 ft) is limited; thus, many cold-water high elevation streams are commonly and appropriately known as *trout streams* because often the only fish inhabitants are brook trout (Fig. 6.2). A notable exception, the western blacknose dace (*Rhinichthys obtusus*) has been found at elevations of > 1,200 m (3,900 ft) in the Great Smoky Mountains National Park in North Carolina and Tennessee (Simbeck 1990).

Fig. 6.2 Brook trout (*Salvelinus fontinalis*) from a red spruce (*Picea rubens*) headwater stream in West Virginia. Photo by Chad Landress

Sidebar 6.1 Focal Species—Brook Trout (*Salvelinus fontinalis*)

Brook trout (*Salvelinus fontinalis*) in the central and southern Appalachians are glacial refugees at the southern extent of their range (Karas 1997). As cold-water specialists, brook trout are capable of occupying extreme headwaters at high elevations (Etnier and Starnes 1993; Jenkins and Burkhead 1994). The cold, clean waters flowing through and from expansive red spruce (*Picea rubens*) forests fed prime brook trout streams prior to the mid-1800s (Kennedy 1853; McNeill 1877; Zurbuch 2015). However, the exploitative logging and subsequent wildfires that reduced the extent of red spruce forest from the mid-1800s to 1930s (McNeill 1877; Yetter et al. 2021) degraded habitat through sedimentation, streambed scouring, and loss of forest shade, which increased stream temperatures and subsequently reduced the distribution and abundance of brook trout populations throughout the region (Marschall and Crowder 1996; Zurbuch 2015). Brook trout and red spruce share more contemporary environmental stressors as well, including increased headwater acidification from atmospheric deposition on already naturally acidic systems (Menendez 1976; Herlihy et al. 1993). These stressors can push brook trout to lower elevations, whereas warming waters from elevation drop and/or climate change chase them upslope into an increasingly narrow and restricted zone of remaining habitability (McDonnell et al. 2015, Zurbach 2015). In the central Appalachians, acidic runoff from surface coal mines is also a contemporary stressor that has degraded aquatic habitat quality and, in some instances, eliminated brook trout populations entirely (Petty et al. 2005, 2010). Throughout the central and southern Appalachians in red spruce forests, road culverts that limit or block passage represent a significant movement barrier to brook trout and other fish in many watersheds (Poplar-Jeffers et al. 2009). As a result, brook trout in the central and southern Appalachians today share the same fate as red spruce and the biotic communities therein: small, isolated, high elevation populations occupying a fraction of their historical range (Hudy et al. 2008) that are vulnerable to extirpation (Etnier and Starnes 1993; Kazyak et al. 2022) and consequently are in severe need of conservation and restoration (Habera and Moore 2005; Eastern Brook Trout Joint Venture 2018).

The shared histories, ecological intersections, and overlapping threats to brook trout and red spruce are striking and suggest that conservation and restoration efforts for each may be enhanced by more direct consideration of the other. Despite the obvious intersection between strategies (Clingerman 2008), we were unable to locate any examples where both brook trout and red spruce were explicitly considered together during conservation or restoration planning in the Blue Ridge portion of the southern Appalachians. In contrast, addition of limestone fines to ameliorate geologic, atmospheric, and mine-induced aquatic acidity to improve brook trout habitat conditions and populations has a long history of application in central Appalachian streams (Fig. 6.3;

Downey et al. 1994; Hudy et al. 2000), including in streams in red spruce forests (Zurbuch et al. 1996). Increases in stream pH from lime application have improved conditions for brook trout and other biota (Clayton et al. 1998), though full system recovery remains elusive with regard to water chemistry, disconnectivity of treated streams, macroinvertebrate recovery, physical barriers to fish movement, and thermal conditions in most red spruce-dominated watersheds (McClurg et al. 2007). Shingleton and Brown (2010) estimated that restoration of mine-impacted cold-water streams in West Virginia would provide > 300,000 additional angler-days with a considerable economic benefit. Reforestation of red spruce on former surface mines (Rhodes and Barton 2024) in West Virginia and red spruce forest enhancement and restoration throughout the central and southern Appalachians (Thomas-Van Gundy and Sturtevant 2014) are now being implicitly linked to improved brook trout habitat and populations (Ray and Pool 2018).

Low fish diversity should not be interpreted to mean that streams in high elevation red spruce and spruce-fir forests are unimportant to fish. Appalachian headwater streams are highly connected to their surroundings (Richardson 2019), and the condition of headwater forests impacts the quality and quantity of water delivered downstream to fish and other aquatic biota (MacDonald and Coe 2007). A headwater spruce-fir stand with its dense evergreen canopy provides cooling shade, and the thick, spongy forest floor of organic material and moss acts as a filter for organic and inorganic chemicals (Cormack 1949; Gregory et al. 1991; Ball et al. 2010; Zurbuch 2015). The cold, clean water flowing from these forests is important for a variety of fish species living downstream, including the economically important non-native wild trout fishery for rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) in the region (Ahn et al. 2000).

In the southern Appalachians, high elevation spruce-fir forests typically only contain brook trout and potentially blacknose dace. At slightly lower elevations, sculpin species such as the mottled sculpin (*Cottus bairdi*) are known to co-occur with brook trout (Jenkins and Burkhead 1994). In the Allegheny Mountains and Plateau portion of the central Appalachians, where the downslope limit of red spruce is 400–500 m (1,300–1,650 ft) lower than in the southern Appalachians, greater fish species richness can be found within the larger second- and third-order systems flowing through red spruce forests near the interface with northern hardwood forests (e.g., Blackwater River, Cherry River, Gauley River, Upper Greenbrier, Upper Shavers Fork, and Williams River in West Virginia). Fish therein can include: least brook lamprey (*Lampetra aepyptera*), American eel (*Anguilla rostrata*), white sucker (*Catostomus commersonii*), torrent sucker (*Thoburnia rhothoeca*), northern hogsucker (*Hypentelium nigricans*), bigmouth chub (*Nocomis platyrhynchus*), creek chub (*Semotilus atromaculatus*), central stoneroller (*Campostoma anomalum*), longnose dace (*Rhinichthys cataractae*), blacknose dace,

Fig. 6.3 Application of crushed limestone into a headwater stream impacted by acid deposition. Photo by Eric Gladwell

rosyface shiner (*Notropis rubellus*), New River shiner (*Notropis scabriceps*), rosyside dace (*Clinostomus funduloides*), cutlip minnow (*Exoglossum maxillingua*), river chub (*Nocomis micropogon*), mountain redbelly dace (*Chrosomus oreas*), common shiner (*Luxilus cornutus*), striped shiner (*Luxilus chrysocephalus*), pearl dace (*Margariscus margarita*), sharpnose darter (*Percina oxyrhynchus*), candy darter

(*Etheostoma osburni*), fantail darter (*Etheostoma flabellare*), mottled sculpin, Blue Ridge sculpin (*Cottus caeruleomentum*), Potomac sculpin (*Cottus girardi*), and the non-native brown trout and rainbow trout (Stauffer et al. 1995; Clayton et al. 1998; Petty et al. 2005).

6.3 Herpetofauna

Species richness of amphibians and reptiles is high and moderate, respectively, in the central and southern Appalachians relative to other regions in the U.S. (Jenkins et al. 2015). In particular, the Appalachians represent a global biodiversity hotspot for salamanders (Rissler and Smith 2010; Kozak 2017) and are the potential origin of the lungless salamander family Plethodontidae (Beachy and Bruce 1992). Although only a small proportion of herpetofaunal species in the central and southern Appalachians are strongly associated with red spruce or spruce-fir forests, these forest types are considered optimal habitat for some high elevation-endemic salamander species of conservation concern, such as the federally threatened Cheat Mountain salamander (*Plethodon nettingi*; Pauley 2022). In addition, many generalist amphibian and reptile species can be found in these forest types.

To identify herpetofaunal species associated with red spruce and spruce-fir forests, we consulted the Partners in Amphibian and Reptile Conservation (PARC) habitat management guidelines for the northeastern and southeastern U.S. (Bailey et al. 2006; Mitchell et al. 2006). PARC represents a broad partnership of herpetofaunal species experts from across research and management sectors in the U.S. and develops products useful for management of these species, such as designation of priority conservation areas and conservation action plans. The PARC guidelines provide species-specific associations with habitat types in defined geographic regions, including red spruce and spruce-fir forests, and qualitatively rank them as optimal/primary, suitable, marginal, and non-habitat. We excluded species only found in the northern Appalachians based on distribution maps in Powell et al. (2016) and reviewed the scientific literature for all species for which spruce-fir was designated as optimal habitat. The PARC guidelines list spruce-fir forests as habitat for 40 amphibian and 13 reptile species in the central and southern Appalachians (Table 6.1). Based on our assessment of the PARC habitat designations, we consider spruce-fir forests to be habitat for 40 amphibian and 12 reptile species, including optimal habitat for 7 amphibian species (all salamanders), suitable habitat for 23 amphibian and 4 reptile species, and marginal habitat for 10 amphibian and 8 reptile species.

6.3.1 Amphibians—Salamanders

The PARC guidelines consider spruce-fir forests to be optimal, suitable, and marginal habitat for 11, 19, and 2 salamander species, respectively (Table 6.1). After consulting

Table 6.1 Amphibian and reptile species considered to be associated with red spruce (*Picea rubens*) or spruce-fir forests in the central and southern Appalachian regions. Spruce-fir forests were qualitatively ranked as optimal, suitable, or marginal habitat for each species by Partners in Amphibian and Reptile Conservation (PARC) habitat management guidelines (Bailey et al. 2006; Mitchell et al. 2006). We reviewed the scientific literature for all species where spruce-fir was designated as optimal habitat in one or both of the PARC guidelines and modified habitat designations for several of the species. Many additional amphibian and reptile species have been documented in spruce-fir forests, but are not generally considered to be associated with the forest type. Scientific and common names follow Nicholson (2025) except where noted

Scientific name	Common name	Appalachia distribution	Spruce-fir association
Amphibians—Salamanders			
Ambystoma maculatum	Spotted salamander	Central/Southern	Suitable
Ambystoma opacum	Marbled salamander	Central/Southern	Suitable
Desmognathus aeneus	Seepage salamander	Southern	Suitable
Desmognathus carolinensis	Carolina mountain dusky salamander	Southern	Suitable
Desmognathus folkertsi	Dwarf black-bellied salamander	Southern	Suitable
Desmognathus fuscus	Northern dusky salamander	Central/Southern	Suitable
Desmognathus imitator	Imitator salamander	Southern	Optimal
Desmognathus marmoratus	Northern shovel-nosed salamander	Central/Southern	Suitable[e]
Desmognathus monticola	Northern seal salamander	Central/Southern	Suitable
Desmognathus ochrophaeus	Allegheny Mountain dusky salamander	Central/Southern	Optimal
Desmognathus ocoee	Ocoee salamander	Southern	Suitable
Desmognathus orestes	Blue Ridge dusky salamander	Central [c]/Southern ePara>ePara>	Suitable
Desmognathus organi[a]	Northern pygmy salamander	Southern	Optimal
Desmognathus quadramaculatus[b]	Black-bellied salamander	Central/Southern	Suitable
Desmognathus santeetlah	Santeetlah dusky salamander	Southern	Suitable
Desmognathus welteri	Black Mountain salamander	Central/Southern	Suitable
Desmognathus wrighti	Pygmy salamander	Southern	Optimal[f]
Eurycea bislineata	Northern two-lined salamander	Central	Suitable

(continued)

Table 6.1 (continued)

Scientific name	Common name	Appalachia distribution	Spruce-fir association
Eurycea wilderae	Blue Ridge two-lined salamander	Southern	Suitable
Gyrinophilus porphyriticus	Spring salamander	Central/Southern	Suitable[g]
Hemidactylium scutatum	Four-toed salamander	Central/Southern	Suitable
Notophthalmus viridescens	Eastern newt	Central/Southern	Suitable[g]
Plethodon cinereus	Eastern red-backed salamander	Central/Southern	Suitable
Plethodon glutinosus	Northern slimy salamander	Central/Southern	Marginal
Plethodon jordani	Red-cheeked salamander	Southern	Suitable
Plethodon nettingi	Cheat Mountain salamander	Central	Optimal
Plethodon punctatus	Cow Knob Salamander	Central	Suitable
Plethodon teyahalee	Southern Appalachian salamander	Southern	Marginal[h]
Plethodon wehrlei	Wehrle's salamander	Central/Southern[d]	Optimal
Plethodon welleri	Weller's salamander	Southern	Optimal[f]
Plethodon yonahlossee	Yonahlossee salamander	Southern	Suitable
Pseudotriton ruber	Red salamander	Central/Southern	Marginal
Amphibians—Anurans			
Anaxyrus americanus	American toad	Central/Southern	Suitable[i]
Dryophytes chrysoscelis	Cope's gray treefrog	Central/Southern	Marginal[i]
Dryophytes versicolor	Gray treefrog	Central/Southern[e]	Marginal
Lithobates clamitans	North American green frog	Central/Southern	Marginal
Lithobates palustris	Pickerel frog	Central/Southern ePara>ePara>	Marginal
Lithobates sylvaticus	Wood frog	Central/Southern	Marginal
Pseudacris brachyphona	Mountain chorus frog	Central/Southern	Marginal
Pseudacris crucifer	Spring peeper	Central/Southern	Marginal

(continued)

Table 6.1 (continued)

Scientific name	Common name	Appalachia distribution	Spruce-fir association
Reptiles—Squamates			
Coluber constrictor	North American racer	Central/Southern	Marginal
Crotalus horridus	Timber rattlesnake	Central/Southern	Marginal
Diadophis punctatus	Ring-necked snake	Central/Southern	Marginal
Lampropeltis triangulum	Eastern milksnake	Central/Southern	Suitable[j]
Storeria occipitomaculata	Red-bellied snake	Central/Southern	Suitable[j]
Thamnophis saurita	Eastern ribbonsnake	Central/Southern	Marginal
Thamnophis sirtalis	Common gartersnake	Central/Southern	Suitable
Reptiles—Turtles			
Chelydra serpentina	North American snapping turtle	Central/Southern	Marginal
Chrysemys picta	Painted turtle	Central/Southern	Marginal
Clemmys guttata	Spotted turtle	Central	Marginal
Glyptemys insculpta	Wood turtle	Central	Suitable
Terrapene carolina	Eastern box turtle	Central/Southern	Marginal

[a]In Bailey et al. (2006), species had not yet been described and was considered to be *Desmognathus wrighti*
[b]Pyron and Beamer (2022) proposed that *Desmognathus quadramaculatus* be split into four distinct species, which was adopted by Nicholson (2025): Kanawha black-bellied salamander (*D. kanawha*), Pisgah black-bellied salamander (*D. mavrokoilius*), Smoky Mountains black-bellied salamander (*D. gvnigeusgwotli*), and southern black-bellied salamander (*D. amphileucus*). Additional research is needed to clarify the geographic distributions and habitat preferences for the individual species
[c]Limited distribution within the central Appalachian region
[d]Limited distribution within the southern Appalachian region
[e]Listed as non-habitat in Mitchell et al. (2006) and optimal in Bailey et al. (2006)
[f]Listed as suitable in Mitchell et al. (2006) and optimal in Bailey et al. (2006)
[g]Listed as optimal in Mitchell et al. (2006) and non-habitat in Bailey et al. (2006)
[h]Listed as optimal in Bailey et al. (2006)
[i]Listed as optimal in Mitchell et al. (2006)
[j]Listed as marginal in Mitchell et al. (2006) and suitable in Bailey et al. (2006)

the scientific literature, we consider spruce-fir to represent suitable rather than optimal habitat for three of these species, northern shovel-nosed salamander (*Desmognathus marmoratus*), spring salamander (*Gyrinophilus porphyriticus*), and eastern newt (*Notophthalmus viridescens*), and marginal rather than optimal habitat for one of these species, southern Appalachian salamander (*Plethodon teyahalee*). The northern shovel-nosed salamander is a highly aquatic species that occupies forest streams over a large elevational gradient (300–1,680 m [990–5,500 ft]; Petranka 1998). Although this species can be found in high elevation red spruce forests, such as White Top Mountain in Virginia and Grandfather Mountain in North Carolina (Pope and Hairston 1947), they are not restricted to this forest type and their distribution appears to be most strongly influenced by aquatic habitat characteristics (Martof 1962). In fact, no literature that we consulted mentioned red spruce or Fraser fir (*Abies fraseri*) in relation to habitat for the northern shovel-nosed salamander. The spring salamander is a semi-aquatic species that occupies forest streams and adjacent terrestrial habitat over a large geographic and elevational (100–2,000 m [330–6,550 ft]) gradient (Petranka 1998). Spring salamanders can be found in spruce-fir forests (Bruce 1972), but similar to the northern shovel-nosed salamander, occurrence is most heavily influenced by aquatic habitat characteristics (Bruce 2003; Lowe 2005; Petranka and Smith 2005). The eastern newt is one of the most widely distributed salamanders in North America and has no elevational restriction (Petranka 1998). It is a wetland breeder with a terrestrial juvenile (red eft) stage and an aquatic adult stage. Eastern newts can be found in spruce-fir forests (Rinehart et al. 2009; Pauley 2015), but there is no evidence that this is a preferred forest type (DeGraaf and Rudis 1990). Southern Appalachian salamanders (*Plethodon teyahalee*) have a restricted distribution, occurring primarily in western North Carolina (Powell et al. 2016). This is a mid-elevation species that is typically found from 640 to 910 m (2,100–2,990 ft; Niemiller and Reynolds 2011), but the species does reach higher elevations in a few localities (Riddell and Sears 2015).

Byers et al. (2010) documented Jefferson salamanders (*Ambystoma jeffersonianum*) and long-tailed salamanders (*Eurycea longicauda*) in red spruce forests in West Virginia, but these species are not considered to be associated with spruce-fir in the PARC guidelines. Pauley (2022) documented only one long-tailed salamander during 40 years of salamander surveys in the high elevation red spruce forests of West Virginia, but he and his graduate students have found several green salamander (*Aneides aeneus*) populations in red spruce forests (Thomas Pauley, Marshall University, oral communication, May 3, 2023). Similarly, Mathews and Echternacht (1984) listed the southern red-backed salamander (*Plethodon serratus*) as known from spruce-fir forests in Great Smoky Mountains National Park, but it is also not considered to be associated with this forest type in the PARC guidelines. Though not spruce-fir forest obligates, PARC guidelines consider four salamanders to be common components therein: spotted salamander (*Ambystoma maculatum*), four-toed salamander (*Hemidactylium scutatum*), eastern red-backed salamander (*Plethodon cinereus*) in the central and southern Appalachians, and red-cheeked salamander (*Plethodon jordani*) in the southern Appalachians. Spotted salamanders and four-toed salamanders are wetland breeders, and thus are likely to be encountered in spruce-fir forest patches adjacent to wetlands (Pauley 2015; Millikin et al. 2019). In contrast, eastern red-backed salamanders and red-cheeked salamanders have a fully terrestrial lifecycle and are widely distributed within spruce-fir forests (DeGraaf and Rudis 1990; Dodd and Dorazio 2004; Kroschel et al. 2014).

We regard seven salamander species in the central and southern Appalachians as either spruce-fir obligates or those for which this forest type is considered optimal habitat. The imitator salamander (*Desmognathus imitator*) has a small geographic distribution at high elevations (900–2,024 m [2,950–6,640 ft]) in eastern Tennessee and western North Carolina (Powell et al. 2016) and has been documented on Great

Smoky, Balsam, and Plott Balsam Mountains (Petranka 1998). Mathews and Echternacht (1984) considered the imitator salamander to be truly indicative of spruce-fir forests in Great Smoky Mountains National Park. Though robust studies are lacking, this salamander is associated with forest seeps and adjacent terrestrial habitats (Tilley 1985; Dodd 2003).

The Allegheny Mountain dusky salamander (*Desmognathus ochrophaeus*; Fig. 6.4) occurs from extreme southwestern Québec to north-central Tennessee (Powell et al. 2016). This is a highly terrestrial species that occupies the largest elevational gradient of any *Desmognathus* species and occupies a wide variety of forest types (Hairston 1949). However, in North Carolina, Tilley (1973) found that Allegheny Mountain dusky salamander annual survival and growth rates were highest in the spruce-fir forest. In the central Appalachians, this is often one of the most abundant species in red spruce forests (Brooks 1948; Pauley 1980; Kroschel et al. 2014).

Historically, pygmy salamanders (*Desmognathus organi*) and northern pygmy salamanders (*Desmognathus wrighti*) were considered to be the same species (*D. wrighti*), with a geographic distribution restricted to the Blue Ridge from southern Virginia to northern Georgia (Harrison 2000). Crespi et al. (2010) concluded that the species are separated by the French Broad River, with pygmy salamanders occurring south and west, and northern pygmy salamanders occurring north and east of the river. These are two of the smallest and most terrestrial species of *Desmognathus*, with no aquatic larval stage (Petranka 1998; Bruce 2011). Although they can be found at elevations < 700 m (2,300 ft; Hocking et al. 2021), these two salamanders are most associated with spruce-fir forests at elevations > 1,600 m (5,250 ft; Hairston 1949; Crespi et al. 2003; Rossell et al. 2018). Occurrence records within

Fig. 6.4 Adult Allegheny Mountain dusky salamander (*Desmognathus ochrophaeus*) observed in a high elevation red spruce (*Picea rubens*) forest in Tucker County, West Virginia. Photo by Donald Brown

their distributions largely correspond to current and former occurrence of spruce-fir forests in the southern Appalachians (Bruce 1977; Harrison 2000; Crespi et al. 2003). Mathews and Echternacht (1984) considered the pygmy salamander to be the other salamander species characteristic of spruce-fir forests in Great Smoky Mountains National Park. Rossell et al. (2018) sampled populations of both species in North Carolina and compared relative abundances among three forest types that occurred at different elevations: spruce-fir (>1,645 m [5,400 ft]), northern hardwood (1,310–1,645 m [4,300–5,400 ft]), and mountain cove (<1,310 m [4,300 ft]). For the combined species data, relative abundance was higher in spruce-fir forest than mountain cove forest, but not significantly different from adjacent northern hardwood forest. However, captures of both species were highest in spruce-fir forest, in contrast to 14 of the 15 additional salamander species encountered. Because the forest types in this study differed by elevation, additional research is needed to determine the relative influences of forest type and elevation on density. Rossell et al. (2018) did not find that microhabitat characteristics differed for occupied locations among the forest types, and only coarse woody debris was a strong predictor of occurrence.

The Cheat Mountain salamander (Fig. 6.5) is restricted to high elevation forests in the Allegheny Mountains portion of the central Appalachians in eastern West Virginia (Pauley 2022). This is the most well-studied amphibian species in relation to associations with red spruce forests (see Sidebar 6.2). Although at present, Cheat Mountain salamanders do not occur exclusively in red spruce forests, presence is strongly associated with this forest type (Dillard et al. 2008a; Pauley 2022), and most contemporary occupied patches probably were red spruce prior to the exploitative logging and subsequent wildfire period (1890–1940) based on post-harvest assessments (Minckler 1945).

Sidebar 6.2 Focal Species—Cheat Mountain Salamander (*Plethodon nettingi*).

The Cheat Mountain salamander was first described in 1938 by Green (1938). At that time, the species was only known to occur at two high elevation localities in eastern West Virginia, Barton Knob (1,351 m [4,432 ft]) and Cheat Bridge (1,084 m [3,556 ft]). Between 1976 and 2016, Thomas K. Pauley surveyed > 1,300 areas in eastern West Virginia to define the geographic distribution of the Cheat Mountain salamander (Pauley 2022). These efforts resulted in the delineation of 81 geographically isolated populations located across a latitudinal and longitudinal distance of approximately 31 km and 84 km (19 mi and 52 mi), respectively, in eastern West Virginia. The lowest documented elevation of occurrence for this species is 805 m (2,640 ft; Pauley and Pauley 1997), and occurrence probability is strongly positively associated with elevation (Dillard et al. 2008b; Kroschel et al. 2014).

In the first publication for the Cheat Mountain salamander, the two known localities of occurrence were described as “originally covered with spruce

Fig. 6.5 Adult female Cheat Mountain salamander (*Plethodon nettingi*) with eggs observed in a high elevation red spruce (*Picea rubens*) forest in Tucker County, West Virginia. Photo by Donald Brown

forest" (Green 1938). Brooks (1948) further described the species' forest type association as "nearly pure stands of red spruce" and "forests in which red spruce is a prominent species." In many occupied areas, red spruce (*Picea rubens*) was replaced by eastern hemlock (*Tsuga canadensis*) and deciduous trees (e.g., yellow birch [*Betula alleghaniensis*]) following extensive clearcutting and wildfires that occurred in the late 1800s and early 1900s (Brooks 1948; Stephenson and Clovis 1983). Pauley (2008) hypothesized that Cheat Mountain salamanders survived the logging and fires in areas that contained large emergent rocks, but were extirpated elsewhere, resulting in the current fragmented distribution. Pauley (2022) recorded contemporary forest type at 195 known-occupied Cheat Mountain salamander sites, and found that 74.3% contained red spruce, with 55.4% of the sites dominated by red spruce. He found that 13.8% of sites did not contain either red spruce or eastern hemlock, indicating that whereas Cheat Mountain salamanders are associated with red spruce and to a lesser extent eastern hemlock, they have persisted in some forest patches that were clearcut and returned as northern hardwood forests.

A few studies have sought to quantitatively characterize Cheat Mountain salamander habitat using observational field data. Pauley (1998) surveyed seven habitat characteristics at two known-occupied sites paired with two unoccupied sites, analyzing each pair separately and found that three of the variables significantly differed between occupied and unoccupied sites, but each variable only differed for one of the site pairs. Air temperature was cooler at one occupied site, soil acidity was lower at one occupied site, and litter mass was higher at one occupied site. Dillard et al. (2008a) surveyed 18 habitat characteristics at 67 known-occupied sites and 37 random sites. They determined that probability of occurrence decreased with soil depth to rock and distance to emergent rocks and increased with bryophyte density and spruce-hemlock density. Brown et al. (2022) quantified soil moisture and soil pH at four occupied sites across their geographic distribution, adjacent forest patches where Cheat Mountain salamanders have not been detected, and nearby forest patches that represented seemingly high-quality habitat but lacked the species. They found that soil moisture was higher at occupied sites, but soil pH did not significantly differ.

Two studies have sought to quantify Cheat Mountain salamander habitat using ecological niche models. Dillard et al. (2008b) used 180 known-occupied locations and random locations within the species' geographic distribution to assess the influence of 13 environmental variables on occurrence probability. A logistic regression analysis indicated that landform and lithology variables were the strongest predictors of occurrence probability, with some additional support for vegetation variables. Specifically, occurrence was positively associated with sandstone, elevation, and red spruce, and negatively associated with slope and southwesterly aspects. A complementary classification tree analysis found that sandstone and annual precipitation were the strongest predictors of occurrence. Another study used 702 known-occupied locations and random background locations within the species' geographic distribution to assess the influence of 11 landscape and 3 climate variables on occurrence probability (Rucker et al. 2025). A random forest analysis found that 10 of the candidate variables were influential for occurrence of Cheat Mountain salamanders, including elevation, existing vegetation, heat load index, canopy cover, soil type, rock type, Euclidean distance to rocky habitat, annual mean temperature, temperature seasonality, and precipitation in the warmest quarter. The estimated relationships generally agreed with previous studies, with occurrence probability positively associated with sandstone, elevation, and red spruce-eastern hemlock, and negatively associated with distance to rocky habitat. The model characterized 6.6%, 23.2%, 12.4%, and 57.8% of area within the known Cheat Mountain salamander distribution with high-quality habitat, moderate-quality habitat, low-quality habitat, and non-habitat, respectively.

In summary, Cheat Mountain salamanders have been considered a red spruce-associated species since their discovery, and research to date has generally supported this association. However, it is not currently known if Cheat Mountain salamanders directly benefit from red spruce. It is plausible that other environmental conditions, such as temperature and moisture (which are strongly correlated with aspect and elevation) and soil/geological characteristics, are influencing occurrence of both species. This may explain why Cheat Mountain salamander populations have persisted in forest patches that were clearcut

> 100 years ago and no longer contain red spruce. Brown et al. (2022) hypothesized that low soil pH found in red spruce and eastern hemlock forests may reduce interspecific competition pressure from other *Plethodon* salamanders, particularly the eastern red-backed salamander (*Plethodon cinereus*), which prefers less acidic soils (Sugalski and Claussen 1997; Wyman and Hawksley-Lescault 1987). If so, Cheat Mountain salamanders may have a competitive advantage in red spruce and eastern hemlock stands as climatic changes increase the habitat quality of high elevation forests for competitor salamanders (Kroschel et al. 2014; Rucker et al. 2022).

The Wehrle's salamander (*Plethodon wehrlei*; Fig. 6.6) occurs from southwestern New York to northwestern North Carolina and northeastern Tennessee, with the largest portion of their distribution occurring in West Virginia (Powell et al. 2016). Wehrle's salamanders occur within, but are not wholly restricted to, high elevations in the central and southern Appalachians (Pauley 1978; Petranka 1998). To our knowledge, forest type associations for the species have not been investigated. In West Virginia, Brooks (1948) noted that Wehrle's salamander was often the most abundant salamander species encountered in mature red spruce forests, and Rucker et al. (2022) observed that it was among the three most common salamander species encountered over three decades in that forest type.

Weller's salamanders (*Plethodon welleri*) have a small, fragmented distribution in the Blue Ridge of the southern Appalachians, from southwestern Virginia (Whitetop Mountain and Mt. Rogers; Hoffman and Kleinpeter 1948) through northwestern North Carolina (Flat Top Mountain, Grandfather Mountain, and Unaka Mountain;

Fig. 6.6 Adult Wehrle's salamander (*Plethodon wehrlei*) observed in a high elevation red spruce (*Picea rubens*) forest in Tucker County, West Virginia. Photo by Donald Brown

Snyder 1946; Thurow 1963) and extreme northeastern Tennessee (Thurow 1963). They are typically found in high elevation spruce-fir forests (Petranka 1998), but also occur in deciduous and eastern hemlock (*Tsuga canadensis*)-dominated forests as low as 700 m (2,300 ft; Thurow 1963; Ronca et al. 2026). Bogert (1952) surveyed several mountains in southwestern Virginia and only encountered this species in spruce-fir on Mt. Rogers.

6.3.2 Amphibians—Anurans

The PARC guidelines consider spruce-fir forests to be optimal and marginal habitat for two and six anuran (i.e., frog and toad) species, respectively (Table 6.1). Spruce-fir is listed as optimal habitat and non-habitat for the American toad (*Anaxyrus americanus*) in the northeastern and southeastern PARC guidelines, respectively. This species is considered a terrestrial habitat generalist, with a preference for open deciduous forests and grasslands (Dodd 2013). American toads occur in red spruce and spruce-fir forests where present in their distribution (Karns 1992; Mazerolle 2004; Pauley 2015). DeGraaf and Rudis (1990) found that American toads used balsam fir (*Abies balsamea*) stands in New Hampshire, but relative abundance was significantly lower than in red maple (*Acer rubrum*) and northern hardwood stands. In Ontario, timber harvesting in red spruce forests did not influence relative abundance of American toads (Thompson et al. 2008). Given this species is a habitat generalist, we consider spruce-fir to be suitable, but not optimal, for the American toad.

Spruce-fir is also listed as optimal habitat and non-habitat for Cope's gray treefrog (*Dryophytes chrysoscelis*) in the northeastern and southeastern PARC guidelines, respectively. This species is considered a terrestrial habitat generalist, with a preference for deciduous forests and grasslands (Dodd 2013). Cope's gray treefrogs have been documented in red spruce forests in West Virginia (Pauley 2015), but to our knowledge, no studies indicate this is a preferred forest type. Byers et al. (2010) listed one additional anuran, northern leopard frog (*Lithobates pipiens*), that has been documented in red spruce forests in West Virginia, but it is not considered to be associated with this forest type in the PARC guidelines. The PARC guidelines do consider two anuran species, wood frog (*Lithobates sylvaticus*) and spring peeper (*Pseudacris crucifer*), to be characteristic species of spruce-fir forests, despite the habitat type not being considered optimal. Both of these species are wetland breeders, and thus are likely to be encountered in forest patches adjacent to wetlands (Pauley 2015; Lambert et al. 2021).

6.3.3 Reptiles—Squamates

The PARC guidelines consider spruce-fir forest to be suitable and marginal habitat for three and four squamate (i.e., snake and lizard) species, respectively, all of which are snakes (Table 6.1). Byers et al. (2010) listed seven additional snake species that have been documented in red spruce forests in West Virginia but are not considered to be associated with the forest type in the PARC guidelines. These include: eastern copperhead (*Agkistrodon contortrix*), common watersnake (*Nerodia sipedon*), smooth greensnake (*Opheodrys vernalis*), central ratsnake (*Pantherophis alleghaniensis*), queensnake (*Regina septemvittata*), Dekay's brownsnake (*Storeria dekayi*), and mountain earthsnake (*Virginia valeriae pulchra*). Two of these species, common watersnake and central ratsnake, have also been documented in spruce-fir forests in Great Smoky Mountains National Park in North Carolina and Tennessee (Mathews and Echternacht 1984). Eastern copperheads and queensnakes were not observed by Thomas Pauley during 40 years of salamander surveys in the high elevation red spruce forests of West Virginia (Thomas Pauley, Marshall University, written communication, February 24, 2024). The PARC guidelines consider four squamates to be characteristic species of spruce-fir forests, despite the habitat type not being considered optimal, including ring-necked snake (*Diadophis punctatus*), eastern milksnake (*Lampropeltis triangulum*), red-bellied snake (*Storeria occipitomaculata*), and common gartersnake (*Thamnophis sirtalis*).

6.3.4 Reptiles—Turtles

The PARC guidelines consider spruce-fir forests to be suitable and marginal habitat for one and four turtle species, respectively (Table 6.1). No turtles are considered to be characteristic species of spruce-fir forests. In Maine and southeastern Canada, alluvial spruce-fir is considered suitable habitat for the wood turtle (*Glyptemys insculpta*; Latham et al. 2023); however, we are unaware of any wood turtle populations occurring in red spruce forests in the central Appalachians, and the species does not occur in the southern Appalachians (Jones and Willey 2021). Eastern box turtles (*Terrapene carolina*) are rarely observed in red spruce forests in West Virginia (Thomas Pauley, Marshall University, written communication, February 24, 2024), but have been found in spruce-fir forests above 1,828 m [6,000 ft; Diggins et al. 2016).

6.4 Birds

Avian (bird) communities of high elevation red spruce and spruce-fir forests in the central and southern Appalachian Mountains are unique and distinctive in their species composition compared to adjacent, lower elevation forests (Rabenold 1978; Clipp et al. 2022). Reflecting the differences in dominant tree species as elevation increases, the bird community composition therein is quantitatively distinct from those of northern hardwood forests, oak-pine forests, and mixed mesophytic forests, which tend to be primarily comprised of birds associated with deciduous tree assemblages (Clipp et al. 2022). Red spruce forests support trailing-edge, breeding populations of boreal bird species (e.g., Blackburnian warbler [*Setophaga fusca*], blue-headed vireo [*Vireo solitarius*], winter wren [*Troglodytes hiemalis*]) more commonly encountered at higher latitudes in New England or southern Canada (Rabenold 1978, 1984; Alsop and Laughlin 1991; Gross 2010). These trailing-edge populations boost both regional diversity and species-level genetic diversity (Hampe and Petit 2005; Ferrari et al. 2018; Merker and Chandler 2020), but they are thought to be at high risk from climate change (Cahill et al. 2014; Rushing et al. 2020), leading to numerous species being listed as local or regional conservation priority species. Southern Appalachian spruce-fir forests also contain endemic subspecies such as Carolina dark-eyed juncos (*Junco hyemalis carolinensis*) and Appalachian black-capped chickadees (*Parus atricapillus practicus*; Rabenold 1984, Rabenold et al. 1998). Despite post-European settlement changes to red spruce and spruce-fir forests, bird assemblages have remained consistent over many decades in the central Appalachians (Stewart and Aldrich 1949; Hall 1984; Clipp et al. 2022) and the southern Appalachians (Brewster 1886; Alsop and Laughlin 1991; Rabenold et al. 1998).

Relative to the boreal bird communities of New England and Canada, the taxonomic composition in central and southern Appalachian red spruce and spruce-fir forests is simpler, with fewer Neotropical migrant songbirds and a notable dominance of species that are residents or short-distance migrants (including altitudinal migrants; Rabenold 1978, 1984). In addition, red spruce forests in the central Appalachians have higher avian richness than spruce-fir forests in the southern Appalachians. To illustrate, in red spruce stands of the Monongahela NF in eastern West Virginia, 45 bird species from 21 families were observed using point count surveys (Clipp et al. 2022), whereas observers counted 32 bird species from 18 families in southern Appalachian spruce-fir forests in North Carolina (Rabenold et al. 1998). Alsop and Laughlin (1991) reported 16 territorial species from 10 families in a virgin spruce-fir stand within the Great Smoky Mountains National Park in Tennessee.

6.4.1 Neotropical Migrant Songbirds

Neotropical migrant songbirds (i.e., long-distance migrants) occur in the U.S. or Canada during the breeding season (approximately late May to mid-July) and spend the non-breeding season in the Caribbean Islands, Central America, or South America. These songbirds comprise a relatively small proportion of central and southern Appalachian red spruce and spruce-fir forest bird communities. Although observers documented 18 Neotropical migrant species during breeding songbird point count surveys in central Appalachian red spruce forests, only three species were considered strongly associated with red spruce: blackburnian warbler, magnolia warbler (*Setophaga magnolia*), and Swainson's thrush (*Catharus ustulatus*; Table 6.2; Clipp et al. 2022). Blackburnian and magnolia warblers, in particular, have a long and consistent history (>70 years) of abundant detections at red spruce survey sites within the central Appalachians (Stewart and Aldrich 1949; Demeo 1999; Kahler and Anderson 2010). In the southern Appalachians, there are fewer breeding Neotropical migrant species; in addition to Blackburnian warblers, observers in spruce-fir forests have recorded relatively low numbers of black-throated green warblers (*Setophaga virens*), black-throated blue warblers (*Setophaga caerulescens*), veeries (*Catharus fuscescens*), and chestnut-sided warblers (*Setophaga pensylvanica*), the latter of which were associated with clearings and disturbed areas (Rabenold 1978, 1992; Alsop and Laughlin 1991).

The Blackburnian warbler (Fig. 6.7) is the primary Neotropical migrant associated with red spruce forests in both the central and southern Appalachians. In West Virginia, multiple studies have linked Blackburnian warblers with forest stands comprised of > 50% red spruce cover of poletimber to sawtimber (13–56 cm [5–22 in] DBH) size (Clipp et al. 2022), and the species' occurrence increases in tandem with those habitats (Bailey and Rucker 2021). Regionally, the Blackburnian warbler is listed as a moderate priority species by the Appalachian Mountains Joint Venture for the Appalachian Mountains Bird Conservation Region (Appalachian Mountains Joint Venture 2019).

In the central Appalachians, magnolia warblers (Fig. 6.7) and Swainson's thrushes are the two other relatively common Neotropical migrants with strong red spruce associations. As one of the most abundant breeding warblers in montane conifer forests of West Virginia, magnolia warblers are associated with understories of dense, young red spruce, eastern hemlock, and eastern white pine (*Pinus strobus*;

Table 6.2 List of breeding songbird species that are strongly associated with red spruce (*Picea rubens*) forests in the central and southern Appalachian Mountains along with the distribution in which they have been documented as indicator species (central Appalachians, southern Appalachians, or both regions) and their migratory status (long-distance migrant [LD], short-distance migrant [SD], or resident [R])

Scientific name	Common name	Appalachia distribution	Migratory status
Catharus guttatus	Hermit thrush	Central	R
Catharus ustulatus	Swainson's thrush	Central	LD
Certhia americana	Brown creeper	Southern	R
Haemorhous purpureus	Purple finch	Central	R
Junco hyemalis	Dark-eyed junco	Both	R
Loxia curvirostra	Red crossbill	Central	R
Poecile atricapillus	Black-capped chickadee	Southern	R
Regulus satrapa	Golden-crowned kinglet	Both	R
Setophaga coronata	Yellow-rumped warbler	Central	SD
Setophaga fusca	Blackburnian warbler	Central	LD
Setophaga magnolia	Magnolia warbler	Central	LD
Sitta canadensis	Red-breasted nuthatch	Both	R
Troglodytes hiemalis	Winter wren	Both	R
Vireo solitarius	Blue-headed vireo	Both	SD

Fig. 6.7 Adult male Blackburnian warbler (*Setophaga fusca*; left; photo by Derek Courtney) and adult male magnolia warbler (*Setophaga magnolia*; right; photo by Hannah Clipp) perched in a mature red spruce (*Picea rubens*) tree and red spruce sapling, respectively, from high elevation sites within the Monongahela NF, West Virginia

Bailey and Rucker 2021). In a recent indicator species analysis identifying individual bird species associated with central Appalachian forest types and cover classes, the magnolia warbler had the second highest indicator value for red spruce forest and the highest indicator value for stands with medium (10–50%) red spruce cover composition (Clipp et al. 2022). Although Swainson's thrushes are the rarest breeding thrush species in the central and southern Appalachians, they are also strongly associated with red spruce-dominated stands. The majority of their trailing-edge breeding population is restricted to high elevation red spruce and mixed forests in the Allegheny Mountains of West Virginia (Bailey and Rucker 2021). In 2000–2001, Kahler and Anderson (2010) recorded Swainson's thrushes only in red spruce stands within their study area in that region. Notably, there is consideration among the ornithological community that the Appalachian Mountain population is a distinctive subspecies in the olive-backed group of Swainson's thrush (*Catharus ustulatus appalachiensis*; Ramos and Warner 1980, Pyle 1997, Mack and Yong 2000). Uncommon Neotropical migrant species in the central Appalachians include Nashville warblers (*Leiothlypis ruficapilla*), northern waterthrushes (*Parkesia noveboracensis*), and olive-sided flycatchers (*Contopus cooperi*). All three species have small, extant breeding populations confined to higher elevations (>1,000 m [3,280 ft]) in the Allegheny Mountains and are found in a few known openings and edges of conifer forests, bogs, and/or shrub wetlands (Hall 1984; Gross 2010), though it is probable that olive-sided flycatchers are regionally extirpated as they are only known to intermittently breed at one location (Bailey and Rucker 2021). The olive-sided flycatcher is a moderate priority species for the Appalachian Mountains Bird Conservation Region and a locally high priority species for conservation in high elevation forests of the southern Blue Ridge Mountains (Hunter 2010).

6.4.2 Short-Distance Migrant and Resident Songbirds

Short-distance migrant songbirds (including altitudinal migrants) are found in the U.S. throughout their full annual cycles, but their breeding grounds tend to be at higher elevations or latitudes than their non-breeding grounds. Similarly, resident songbirds are present year-round in a given area, although individuals may migrate short distances. Combined, these two groups of songbirds comprise the majority of central and southern Appalachian red spruce and spruce-fir forest bird communities (Rabenold 1978, 1984). For breeding songbird point count surveys in red spruce forests of the central Appalachians, observers documented a total of 25 short-distance migrant or resident species (compared to 18 Neotropical migrant species; Clipp et al. 2022). Of those 25 species, 9 were considered to be strongly associated with red spruce forest: dark-eyed junco (*Junco hyemalis*), golden-crowned kinglet (*Regulus satrapa*), winter wren, blue-headed vireo, red-breasted nuthatch (*Sitta canadensis*), yellow-rumped warbler (*Setophaga coronata*), hermit thrush (*Catharus guttatus*), purple finch (*Haemorhous purpureus*), and red crossbill (*Loxia curvirostra*; Table 6.2; Clipp et al. 2022). In the southern Appalachians, dark-eyed juncos, golden-crowned kinglets, winter wrens, red-breasted nuthatches, black-capped chickadees, and brown creepers (*Certhia americana*) comprise the majority of individual birds in spruce-fir forests during the breeding season (Rabenold 1984; Alsop and Laughlin 1991; Rabenold et al. 1998), with the former three species having the densest breeding populations (Alsop and Laughlin 1991, Raynolds et al. 1999). Although most bird species are scarce in winter, a handful of resident species (e.g., dark-eyed juncos, red-breasted nuthatches, black-capped chickadees, brown creepers), along with occasional hardy species such as hairy woodpeckers (*Dryobates villosus*), blue jays (*Cyanocitta cristata*), and common ravens (*Corvus corax*), can be found year-round at the lower boundaries of red spruce forests in the central and southern Appalachians (Rabenold 1984). Winters can also bring irruptive, short-distance migrant finch species, including red crossbills (from populations that breed further north), evening grosbeaks (*Coccothraustes vespertinus*), and pine siskins (*Spinus pinus*; Strong et al. 2015).

Dark-eyed juncos, golden-crowned kinglets, and winter wrens are strongly associated with and abundant within red spruce and spruce-fir forests in the central and southern Appalachians, although dark-eyed juncos may also occur in mesic deciduous forests at lower elevations. At one study site in a spruce-fir forest stand in the southern Appalachians, dark-eyed juncos exhibited the highest breeding density of all species in both 1967 and 1985 surveys (Alsop and Laughlin 1991). Golden-crowned kinglets are year-round residents of high elevation red spruce and mixed forests in the Allegheny Mountains of West Virginia, with a close dependence on red spruce for nesting and foraging (Bailey and Rucker 2021). In a recent indicator species analysis identifying individual bird species associated with central Appalachian forests (Clipp et al. 2022), the golden-crowned kinglet had the highest indicator value for stands dominated by red spruce. Winter wrens are also associated with high elevation forests of the Allegheny Mountains and are likely benefited by maturation of protected red spruce forests and restoration efforts in this region (Bailey and Rucker 2021). Blue-headed vireos (Fig. 6.8) and red-breasted nuthatches are two additional species that are also strongly associated with red spruce and spruce-fir forests. In West Virginia, blue-headed vireo and red-breasted nuthatch populations are highest in red spruce, pine-dominated, mixed, and northern hardwood forests of the Allegheny Mountains; however, blue-headed vireos are not restricted to that region and can be found across much of the eastern and southern portions of the state at lower elevations (Bailey and Rucker 2021).

Yellow-rumped warblers (Fig. 6.8), hermit thrushes, purple finches, and red crossbills are associated with red spruce forests in the central Appalachians, but they occur in limited or low numbers in the southern Appalachians. In West Virginia, yellow-rumped warblers are restricted to breeding in higher elevation forests of pure or mixed red spruce and other montane conifers (Bailey and Rucker 2021). An indicator species analysis in Clipp et al. (2022) showed that the yellow-rumped warbler had the second highest and the purple finch had the highest relative abundance values, respectively, in red spruce-dominated stands. Hermit thrushes tolerate a broader range of habitat within montane northern hardwood and red spruce forests of West Virginia compared to the congeneric Swainson's thrush, but both species are most abundant at high elevations where red spruce is present (Bailey and Rucker 2021). Purple finch breeding records in West Virginia are mainly from the red spruce forest type (Bailey and Rucker 2021), although they will occasionally breed in mixed northern hardwood forests, near bogs, and in riparian areas (Wootton 2020). Red crossbills differ slightly in their life-history traits compared to the other highlighted bird species. They are conifer-obligate finches with bills adapted to extract seeds from conifer cones, and populations in the central and southern Appalachians are linked to conifer seed production and retention, exhibiting nomadic movements driven by food availability (Bailey and Rucker 2021). In the Allegheny Mountains of West Virginia, they are an uncommon breeding bird species that nests in dense conifers and is observed consistently in red

Fig. 6.8 Adult blue-headed vireo (*Vireo solitarius*; left) and adult male yellow-rumped warbler (*Setophaga coronata*; right) from Spruce Knob, an area with high amounts of red spruce (*Picea rubens*) in the Monongahela NF, West Virginia. Photos by Hannah Clipp

spruce. The red crossbill is a high priority species for the Appalachian Mountains Bird Conservation Region and a locally high priority species for conservation in high elevation forests of the southern Blue Ridge Mountains (Hunter 2010).

In the southern Appalachians, black-capped chickadees and brown creepers are associated strongly with spruce-fir forests. In contrast, black-capped chickadees and brown creepers in the central Appalachians are found in red spruce forests, but they are not restricted regionally to the forest type. For example, brown creepers occur more generally in mature mixed coniferous-deciduous forests within West Virginia (Bailey and Rucker 2021). The black-capped chickadee is a moderate priority species for the Appalachian Mountains Bird Conservation Region and a high priority species for high elevation forests of the southern Blue Ridge Mountains (Hunter 2010).

6.4.3 Raptors and Owls

Red spruce and spruce-fir forests provide habitat for several raptor and owl species. Sharp-shinned hawk (*Accipiter striatus*) and American goshawk (*Astur atricapillus*) are the two raptors most strongly associated with red spruce, as they both prefer coniferous forest for nesting (Bailey and Rucker 2021), and both are listed as priority species for the Appalachian Mountains Bird Conservation Region (Appalachian Mountains Joint Venture 2019). In particular, the American goshawk is a rare, apex raptor species of high elevation red spruce and northern hardwood forests in the Allegheny Mountains portion of the central Appalachians, but it does not occur in the southern Appalachians. Although American goshawks will nest in red spruce forests in the central Appalachians, they have become increasingly uncommon in recent years, and they face challenges from nest predation by fishers (*Pekania pennanti*) and mortality from West Nile virus (Bailey and Rucker 2021). Within the past decade, there have been only a few confirmed breeding pairs of American goshawks in West Virginia (Bailey and Rucker 2021).

The primary owl species that occur in central and southern Appalachian red spruce and spruce-fir forests are barred owl (*Strix varia*) and northern saw-whet owl (*Aegolius acadicus*). The latter species is the smallest owl in the region and requires heterogeneous montane coniferous and mixed forests with dense understory structure and well-diversified foliage structure (Milling et al. 1997; Gross 2010). In the central and southern Appalachians, northern saw-whet owls only breed at higher elevations, occupying habitat with large red spruce or eastern hemlock mixed with northern hardwoods (Simpson 1972a, Bailey and Rucker 2021). The northern saw-whet owl is a moderate priority species for the Appalachian Mountains Bird Conservation Region and a high priority species for high elevation forests of the southern Blue Ridge Mountains (Hunter 2010).

6.4.4 Game Birds

Ruffed grouse (*Bonasa umbellus*), American woodcock (*Scolopax minor*), and wild turkeys (*Meleagris gallopavo*) are the only game birds closely associated with red spruce and spruce-fir forests in the Appalachian Mountains. Ruffed grouse are decreasing in abundance throughout all forest types in the central and southern Appalachians due to forest maturation and low abundance of early successional/young forest habitat (Tirpak et al. 2006, Bailey and Rucker 2021). However, they are regularly encountered in red spruce and mixed forests, ecotones, wildlife opening edges, regeneration units, and canopy gaps within surrounding northern hardwood types, as they used these habitats for foraging and mating displays (Gross 2010). Simpson (1972b) found ruffed grouse to be common in spruce-fir on Mt. Mitchell in North Carolina from spring through mid-fall, but largely absent during the winter. The ruffed grouse is a moderate priority species for the Appalachian Mountains Bird Conservation Region.

American woodcock requires wetlands and early successional habitat, and they are also a species with decreasing populations within the eastern U.S. (Gross 2010). In the few areas with abundant wetland resources occurring in red spruce forests, primarily within the central Appalachians, such as Canaan Valley in West Virginia, American woodcock can be common. Goudy et al. (1970) considered Canaan Valley's population of American woodcock, at the time, to be one of the most heavily hunted in the U.S. However, as with ruffed grouse, loss of early successional shrub habitats and development have reduced habitat quality (Steketee et al. 2015; Bailey and Rucker 2021). Meanwhile, wild turkeys are also present and can be locally common in red spruce forests of the central and southern Appalachians (Michael et al. 2015), but the species is limited by hard mast availability and snow depth (Healy and Dickson 1992; McShea et al. 2007), making red spruce forests sub-optimal habitat.

6.5 Mammals

The mammalian biota of high elevation red spruce and spruce-fir forests in the central and southern Appalachians displays a boreal affinity, providing a window to past climatic and landscape conditions that existed across much of the Southeast and mid-Atlantic during the immediate post-Pleistocene and early Holocene. By 10,000 YBP, for example, the post-Pleistocene mammalian mega-fauna that invariably were associated with spruce-fir forests and high elevation open habitats was extinct—whether by the influx of Native Americans or the rapidly changing climate or both (Weigl and Knowles 1995). Still, very few extant mammalian species in present-day red spruce and spruce-fir forest can be considered obligates to that forest type—essentially only the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) and the snowshoe hare (*Lepus americanus*) in the central Appalachians, and the

Carolina northern flying squirrel (*Glaucomys sabrinus coloratus*) in the southern Appalachians.

Several species with more boreal, continental distributions occur down the spine of the Appalachians at higher elevations. Some of these species are associated with montane or boreal conifer and mixed forests (e.g., southern red-backed vole [*Myodes gapperi*], woodland jumping mouse [*Napaeozapus insignis*]). Most other species are not restricted to spruce-fir forests, such as masked shrew (*Sorex cinereus*), pygmy shrew (*Sorex hoyi*), water shrew (*Sorex palustris*), hairy-tailed mole (*Parascalops breweri*), red squirrel (*Tamiasciurus hudsonicus*), and fisher. Species with poor cold tolerance or those associated with old field/early successional habitats are uncommon in spruce-fir forests, such as Virginia opossum (*Didelphis virginiana*) and woodchuck (*Marmota monax*), though both have been observed at > 1,900 m (6,230 ft) in Great Smoky Mountains National Park (Linzey 1995). Aptly covered in other chapters, a changing climate from the end of the last glaciation to present, combined with anthropogenic disturbance of the habitat from forest harvesting, burning, and conversion to pastoral uses, as well as post-disturbance succession and forest maturation (for early successional species), has reduced the distributional extent and ecological integrity of these forests and in turn shaped the mammalian community present today.

6.5.1 Insectivores

Of the insectivorous mammals, seven of the eight species of shrew occurring in the region have been documented in red spruce and spruce-fir forests of the central and southern Appalachians (Ford et al. 2006). Based on approximately 38,000 pitfall trap-night surveys performed between 1979 and 2001 within red spruce forests in West Virginia and spruce-fir forests in North Carolina, Tennessee, and southwest Virginia, masked shrews represented 87% of the captures, whereas from a similar level of effort in regional northern hardwood forests, they comprised only 63% of the captures. Ford and Rodrigue (2001) found rock shrews in both red spruce forests and northern hardwood forests with a red spruce component in West Virginia where shaded, moss-covered talus and colluvial rock was present. Kirkland (1977) actually observed a higher abundance of rock shrews in recently cut (<5 years) red spruce stands than in uncut stands that were > 25 years since disturbance. Laerm et al. (2007a) listed streams draining spruce-fir, eastern hemlock-white pine, and high elevation bogs as the preferred habitat for water shrews. On the Ridge and Valley/Allegheny Front interface in Virginia, Pagels et al. (1998) noted that water shrews required cold, pristine headwater streams. Throughout much of their distribution, water shrews also are associated with American beaver (*Castor canadensis*) ponds (Beneski and Stinson 1987), so occurrence in high elevation ponds in West Virginia is probable. In the southern Appalachians, Linzey (2002) reported an observation of a water shrew in a small bog on Andrew's Bald, North Carolina at around 1,800 m (5,900 ft). For the three mole species in the region, the hairy-tailed mole is the most likely to be encountered in spruce-fir forests (Laerm et al. 2007b), with observations occurring in the Mt. Roger's area in Virginia (Linzey 2021) and Kuwohi Mountains (i.e., Clingman's Dome) in Great Smoky Mountains National Park (Linzey 1995).

6.5.2 Bats

Although considerable bat research has been conducted in the central and southern Appalachians (Britzke et al. 2003; Ford et al. 2005, 2016; Austin et al. 2018; O'Keefe et al. 2019; Rojas et al. 2019; Beilke et al. 2021; Johnson et al. 2021), little work, particularly mist-netting, has purposefully occurred in red spruce or spruce-fir forests. Many records have been chance observations (e.g., a big brown bat [*Eptesicus fuscus*] discovered roosting in Mt. LeConte Lodge in the Great Smoky Mountains National Park at an elevation of 1,920 m [6,300 ft]). Johnson et al. (2021) mist-netted widely on the Monongahela NF, West Virginia from 2003 to 2019, including some sites in red spruce forest, but did not report findings relative to forest cover type or elevation. De La Cruz et al. (2023a, b) created concordance probabilistic distribution maps that included contemporary and historical mist-net capture, day-roost, and acoustic recording records for northern long-eared bats (*Myotis septentrionalis*) and Indiana bats (*Myotis sodalis*) for the Monongahela NF in West Virginia and determined that the cool, high elevation red spruce forests were unsuitable as potential summer day-roosting or foraging habitat. Virginia big-eared bats (*Corynorhinus townsendii virginianus*) inhabit maternity caves and hibernacula in the northern hardwood-red spruce forest transition zone in West Virginia (Stihler 2011) and the Burke's Garden area in Tazewell County, Virginia, which may have been a northern hardwood-red spruce forest prior to European settlement (Hoffman 1950).

Prior to the introduction of white-nose syndrome (WNS; a disease that has decimated populations of many bat species in eastern North America), Francl et al. (2004) acoustically surveyed high elevation (900–1,100 m [2,950–3,610 ft]) wetlands within the red spruce forest zone in and adjacent to Canaan Valley, West Virginia. Although eight species were detected, little brown bats (*Myotis lucifugus*) accounted for 73% of all echolocation files. Post-WNS, Beilke et al. (2021) noted that bat activity attributable to the genus *Myotis* was greater in northern hardwood forests than in spruce-fir forests, in part due to structural clutter in the latter forest type. Similarly, Diggins and Ford (2022) conducted acoustic surveys at seven southern Appalachian *sky island* (1,585–1,920 m [5,200–6,300 ft] in elevation) spruce-fir stands in North Carolina from spring through fall, and found that 53% of bat passes were hoary bats (*Lasiurus cinereus*) and 20% were silver-haired bats (*Lasionycteris noctivagans*). Although these migratory species are present in the Southeast during the non-maternity fall-early spring season, summer activity higher than in the spring and fall migration period therein or as observed in the central Appalachians (Muthersbaugh et al. 2019) suggests that summer foraging and day-roosting indicative of maternity activity is occurring at high elevations in southern Appalachian spruce-fir forests. Only 2% of passes were attributable to bats in the genus *Myotis,* including the eastern small-footed bat (*Myotis leibii*), the threatened northern long-eared bat, and the endangered Indiana bat. Prior to WNS, Kerns and Kerlinger (2004) documented bat mortality at a wind-energy site in Tucker County, West Virginia along Backbone Mountain that was predominantly a high elevation northern hardwood-red spruce community. Even accounting for low detection probability due to rough terrain, bat mortality in the fall and spring migration periods were higher than most wind-energy sites in eastern North America. Eastern red bats (*Lasiurus borealis*) accounted for > 40% of the carcasses recovered, followed by hoary bats (18.5%) and tricolored bats (*Perimyotis subflavus*; 18.3%). No Indiana bats were observed and only six northern long-eared bats were observed (1.3% of total).

6.5.3 Lagomorphs and Rodents

Snowshoe hares occur in red spruce forests, particularly in young regeneration, openings, and forest stands with dense great laurel (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) over 20,000–40,000 ha (49,000–99,000 ac) in the high Allegheny portion of the central Appalachians of West Virginia (Chapman 2007c). Brooks (1955) indicated that snowshoe hares remained in West Virginia in the 1920s to 1940s and were never extirpated but were supplemented in 1949 with individuals from Wisconsin. Until recently, a small number of snowshoe hares persisted in the Laurel Fork area of Highland County, Virginia in dense second-growth thickets of red spruce, yellow birch (*Betula alleghaniensis*), *Rhododendron* spp., mountain laurel, and blackberry (*Rubus* spp.). This population was supplemented by released snowshoe hares from neighboring West Virginia, but post-release survival was low due to predation, averaging only about 24 days (Linzey 2021). Declines in the central Appalachians are attributed to reduced high elevation early successional habitat from forest maturation and climate change, specifically reduced duration and extent of snow cover when snowshoe hare pelage is white, increasing vulnerability to predation (Fies 1991; Michael et al. 1982; Diefenbach et al. 2016). Brooks (1955) noted that even in the first half of the twentieth century, the white winter pelage of snowshoe hares was somewhat of an ecological maladaptation for a region that even in snowy winters often had cycles of melting and limited snow cover.

Whether snowshoe hares historically occurred in the southern Appalachians is subject to debate (Linzey 1995). Merriam (1888) doubted they occurred in the Great Smoky Mountains, whereas Kellogg (1939) reported they were formerly present based on local residents' accounts of "hares" that turned white in the winter along the crest of mountains in spruce-fir forests. Additionally, Campbell et al. (2010) reported a museum record of snowshoe hare from Buncombe County, North Carolina. Although the Appalachian cottontail (*Sylvilagus obscurus*) occurs widely in the Appalachians in early successional habitat and forests with dense, usually ericaceous understories, the species appears to be more common in high elevation red spruce forests in the central Appalachians (Boyce and Barry 2007) and spruce-fir or eastern hemlock-white pine in the southern Appalachians, perhaps in part due to the absence of competition from the eastern cottontail (*Sylvilagus floridanus*; Chapman 2007a). Apodaca et al. (2020) conducted a range-wide assessment of Appalachian cottontails in western North Carolina and found that high elevation populations were associated with shrub and heath balds, but usually in closer proximity to spruce-fir than other forest types. Genetic analyses showed population structuring as a result of their disjunct distribution, and high predicted occupancy was associated with the high elevation *sky islands* in North Carolina where spruce-fir forests occur.

Red squirrels occur at mid to high elevations in the Blue Ridge of the southern Appalachians and the Blue Ridge, Ridge and Valley, and Appalachian Plateau sections of the central Appalachians. Generally, red squirrels require a conifer component, as they feed more heavily on conifer seeds than other sciurids (Linzey 2021). Despite being generally abundant in spruce-fir forests, Laerm and Webster (2007) believed the status of the species more widely in the southern Appalachians was unknown and that stressors to high elevation forests, such as eastern hemlock mortality from the hemlock woolly adelgid (*Adelges tsugae*) and Fraser fir mortality from the balsam woolly adelgid (*Adelges piceae*), are probably a threat to red squirrel populations. Eastern chipmunks occur in spruce-fir forests (Linzey 1995), but are less common due to the paucity of hard mast (Mengak and Laerm 2007b).

Two subspecies of northern flying squirrel (*Glaucomys sabrinus*) occur within spruce-fir forests (Miller 1936; Handley 1953). The Virginia northern flying squirrel occurs in the Allegheny Mountains of West Virginia and Highland County, Virginia (Fig. 6.9), and the Carolina northern flying squirrel occurs in the Blue Ridge portion of the southern Appalachians in western North Carolina, eastern Tennessee, and southwestern Virginia (Weigl et al. 1992; Stihler et al. 1995). Both are Pleistocene relicts that are strongly associated with forests with a high percent stand composition of red spruce, Fraser fir, balsam fir, or eastern hemlock (Weigl et al. 1992; Hughes 2006; Menzel et al. 2006; Ford et al. 2015, 2022; Diggins et al. 2017). Both subspecies were listed as federally endangered in 1985, although the Virginia northern flying squirrel was delisted in 2013 (see Sidebar 6.3). Occupancy probability for northern flying squirrels is highest in mature to old-growth forests with > 30% conifer and occurring above 900 m and 1,350 m (2,950 and 4,430 ft) in the central and southern Appalachians, respectively (Ford et al. 2007, 2015, 2022). Foraging home range size is strongly influenced by habitat quality, such that home ranges in stands with a high red spruce component were < 6 ha (15 ac; Ford et al. 2014; Diggins et al. 2017), whereas home ranges in northern hardwood stands with a small red spruce component were > 50 ha (120 ac; Menzel et al. 2006). Northern flying squirrels are flexible in their denning habits, but dreys (i.e., leaf nests) in conifers and cavities in hardwoods are typically used (Menzel et al. 2004; Diggins et al. 2015, 2017). Though their diet can be varied (Mitchell 2001), northern flying squirrels in the central and southern Appalachians are mycophagists that feed mainly on hypogeal fungi (i.e., truffles) that are associated with red spruce overstories and deep organic soils (Loeb et al. 2000; Diggins et al. 2020).

Fig. 6.9 Adult female Carolina northern flying squirrel (*Glaucomys sabrinus coloratus*) in a spruce-fir forest, William H. Silver Game Land, Haywood County, North Carolina. Photo by Clifton Avery, North Carolina Wildlife Resources Commission

Sidebar 6.3 Focal Species—Northern Flying Squirrel (*Glaucomys sabrinus*).

Two subspecies of northern flying squirrel (*Glaucomys sabrinus*) are strongly associated with red spruce (*Picea rubens*) and spruce-fir forests, the Virginia northern flying squirrel (*G. s. fuscus*) and the Carolina northern flying squirrel (*G. s. coloratus*). Both subspecies were listed as federally endangered in 1985 due to the drastic decline of spruce-fir forests following the exploitative logging period and the threat of climate change to remaining habitat (U.S. Fish and Wildlife Service 1990). The two subspecies are geographically isolated from contiguous populations in the northern Appalachians by approximately 500 and 1,000 km (310 and 620 mi), respectively. Arbogast et al. (2005) found that both Appalachian subspecies had lower levels of genetic variability and the presence of several private alleles compared to continental populations of northern flying squirrels in the northern U.S. and southern Canada.

The reduction of red spruce in the central Appalachians and spruce-fir in the southern Appalachians allowed for the increase of hard mast bearing tree species (i.e., oaks [*Quercus* spp.] and American beech [*Fagus grandifolia*]) that provided a high-energy cacheable food source for the southern flying squirrel (*Glaucomys volans*), an aggressive den site competitor to northern flying squirrels (reviewed in Diggins 2023). Moreover, southern flying squirrels harbor a parasitic nematode (*Strongyloides robustus*) that is deleterious to northern flying squirrels (Wetzel and Weigl 1994). Federal listing resulted in the initiation of long-term monitoring programs using artificial nest-boxes in North Carolina, Virginia, and West Virginia (Fig. 6.10). The monitoring programs have shown that, within their distributions, populations are stable for both subspecies (Reynolds et al. 1999; Ford et al. 2010, 2015). Apparent population stability, coupled with the majority of suitable habitat occurring on protected Federal or State lands, resulted in the Virginia northern flying squirrel being delisted in 2013, although it remains a state endangered animal in Virginia (Ford et al. 2022). Currently, improving northern flying squirrel habitat quality via red spruce planting or midstory release is one of the largest drivers of central and southern Appalachian red spruce restoration efforts (Thomas-Van Gundy and Sturtevant 2014; Rentch et al. 2016).

American beavers occur throughout the central and southern Appalachians, but owing to the small, high gradient streams in southern Appalachian spruce-fir forests, they are uncommon in that setting (Linzey 1995; Mengak and Laerm 2007a). The species was extirpated in Highland County, Virginia and eastern West Virginia by the 1850s, but populations were reestablished in the Allegheny Mountains by the 1940s through reintroduction efforts that began in 1911, and the species occurs in red spruce forests where, unlike the southern Appalachians, larger watercourses and numerous wetland complexes exist (Bailey 1954). Bonner et al. (2009) noted that American beaver-created or maintained wetlands were an important component supporting wetland plant diversity, and presumably, fish, amphibian, and avian diversity in the Canaan Valley area of West Virginia.

No other rodents in the central and southern Appalachians are strongly tied to spruce-fir forests. The small rodent community is dominated by deer mice (*Peromyscus maniculatus*), southern red-backed voles, and woodland jumping mice (Laerm and Castleberry 2007; Laerm and Pagels 2007; Pagels and Laerm 2007b; Linzey 2021). Rock voles (*Microtus chrotorrhinus*) can occur where moss-covered emergent rock and colluvium occur in mesic forests above 900 m (2,950 ft), including in red spruce and spruce-fir forests (Pagels and Laerm 2007a). For this species, Kirkland (1977) found greater abundances in red spruce forests than northern hardwood

Fig. 6.10 A researcher installs a nest-box for Carolina northern flying squirrels (*Glaucomys sabrinus coloratus*) in the Roan Mountain Highlands, Avery County, North Carolina. These artificial den structures are readily used by flying squirrels and constitute a valuable survey and monitoring tool. Photo courtesy of U.S. Fish and Wildlife Service

forests in West Virginia and determined that rock vole abundance increased dramatically in recent red spruce regeneration areas. Francl et al. (2008) observed that current red spruce forests within and surrounding the Canaan Valley area of West Virginia presented a barrier to genetic exchange among high elevation fields and wetlands for the meadow vole (*Microtus pennsylvanicus*), which likely expanded in abundance and distribution following the exploitative logging period. The presence of porcupines (*Erethizon dorsatum*) within historic times in the southern Appalachians is unclear (Linzey 1995). However, for the central Appalachians, sporadic observations in high elevation areas of western Maryland, northwestern Virginia, and northern West Virginia (including Spruce Knob) have been noted since the late 1800s (Goode 1879; Harman and Thoerig 1968). Moncrief and Fies (2020) determined that porcupines had established breeding populations in this part of the central Appalachians and were expanding southward.

6.5.4 Carnivores

No mammalian carnivore in the central or southern Appalachians is strongly tied to spruce-fir forests, but most extant species occur in this habitat type. Although speculative, red spruce forests in West Virginia and spruce-fir forests in the southern Appalachians may have served as localized refugia for species such as the American black bear (*Ursus americanus*) following European settlement and then subsequently after the exploitative logging period, due to their remoteness and low human population density. Throughout its continental distribution, the fisher is associated with boreal forest types, but not exclusively (Chapman 2007b). Miller and Kellogg (1955) believed the species originally ranged down into the southern Appalachians as far south as North Carolina and was probably extirpated by the mid-1800s in the central Appalachians (Linzey 2021). Fishers were reintroduced in two red spruce forest patches in West Virginia in 1969 (Pack and Cromer 1981), and over the subsequent decades have expanded their distribution in West Virginia and have recolonized western Maryland and northwestern Virginia (Moncrief and Fies 2015). Based on the success of the West Virginia reintroduction, a potential fisher reintroduction in Great Smoky Mountains National Park was considered, but ultimately was determined to be a potential threat to the Carolina northern flying squirrel (Weigl 2007).

6.5.5 Ungulates

White-tailed deer (*Odocoileus virginianus*) generally occur at low densities in spruce-fir forests (Linzey 1995), though abundance can be high in localized areas such as Canaan Valley, West Virginia owing to an abundance of improved pastures, early successional wetland, and refugia provided by hunting prohibition on state parks and private lands therein (Michael et al. 2015). Cherefko et al. (2015) noted that white-tailed deer herbivory damage on balsam fir seedlings and saplings in Canaan Valley was severe. Similarly, herbivory on bog Jacob's-ladder (*Polemonium vanbruntiae*), a rare wetland plant, reduced survival and prevented plant recolonization (Flaherty et al. 2018). Despite lower white-tailed deer densities in the red spruce-northern hardwood forest interface in West Virginia, relative browsing pressure on palatable woody browse species can be high in that setting (Campbell et al. 2006). Campbell et al. (2004) did not note any discernible winter "yarding" pattern of white-tailed deer in this habitat type, which has been documented in northern states, despite deep snow and cold temperatures in some winters in the central Appalachians.

Elk (*Cervus canadensis*) were extirpated in the southern Appalachians by the early to mid-1800s (Ganier 1928) and in the central Appalachians by the 1870s in Virginia and West Virginia (Linzey 2021; West Virginia Division of Natural Resources 2021). A reintroduction effort occurred during the 1920s and 1930s in Giles and Bland counties, Virginia, near red spruce habitat at Mountain Lake. The population persisted until 1974 when the combination of forest maturation and crop depredation made their occurrence untenable in the local community (Linzey 2021). Subsequently, elk were successfully reintroduced on the coalfields portion of the Appalachian Plateau on previously surface mined areas in Kentucky, Tennessee, Virginia, and West Virginia, where open grasslands are abundant and the risk of negative interactions with agricultural production is low (Lituma et al. 2021). Interestingly, the West Virginia Division of Natural Resources identified the high elevation areas on the Monongahela NF as the most ecologically suitable habitat for restoration efforts and long-term persistence (Enck and Brown 2005). Similarly, elk were reintroduced to the Cataloochee Valley, North Carolina portion of Great Smoky Mountains National Park in 2001 (Maehr et al. 2007). This small herd has slowly grown in numbers and expanded their distribution in the park as well as adjacent private land (Linehan and Palmer 2014). In 2018, the North Carolina Wildlife Resources Commission purchased 821 ha (2,029 ac) for the William H. Silver Gameland that has high elevation balds, meadows, and mixed red spruce-northern hardwood forests, in part to support expansion of the elk herd (North Carolina Wildlife Resources Commission 2023). Prior to herd expansion in the park, work by Hillard (2013) did not show a strong selection for high elevation habitat types in the Cataloochee Valley, but if the herd continues to grow and expand, potential use of high elevation grassy bald habitats in the spruce-fir forest matrix for foraging habitat and thermal refugia merits investigation.

6.5.6 Feral Swine

Russian wild boar/feral swine (*Sus scrofa*) accidently released from a game preserve on Hooper Bald, North Carolina in the 1920s became established in Great Smoky Mountains National Park by the 1940s (Linzey 1995). As poor thermoregulators, feral swine will often move into higher elevations in the park, including spruce-fir forest during the summer prior to hard mast drop, where their presence has been extremely deleterious to the flora (Bratton 1974). Though the National Park Service has maintained an aggressive control program over the decades, the species' fecundity and high adaptability has allowed it to persist. With additional feral swine releases by the public, the species recently became established in the spruce-fir and grassy balds in the Roan Mountain Highlands of North Carolina and Tennessee (Marquette Crockett, Southern Appalachian Highlands Conservancy, oral communication, 19 Oct 2023).

6.6 Invertebrates

The central and southern Appalachians represent the southern distribution limit for many northern invertebrate species, such as the murky flash-train firefly (*Photinus obscurellus*) and white-spotted sawyer beetle (*Monochamus scutellatus*), due to associations with plants found in high elevation red spruce and spruce-fir forests (Baker 1972; Faust 2017). Invertebrate communities are heavily influenced by local plant communities, relying on them for larval development, oviposition sites, microclimate generation, and habitat for prey. Because red spruce and spruce-fir systems of the central and southern Appalachians contain distinctive plant communities, they also host unique invertebrate assemblages (Niemelä et al. 1996; Bishop et al. 2009). Most documentation of invertebrates in these systems comes from research focusing on tree pest species, but the occurrence of many other invertebrate species can be inferred from the botanical composition of the forest understory. The majority of plants in red spruce and spruce-fir systems are angiosperms, the bulk of which are pollinated by insects. For example, blueberries (*Vaccinium* spp.), an important food supply for vertebrates, rely on pollination by bumble bees (*Bombus* spp.) to produce fruit, and rare flowers in these forest ecosystems, such as orchids, typically depend on bees or flies for pollination.

The high elevation streams and wetlands associated with red spruce and spruce-fir forests also harbor uncommon invertebrates such as the superb jewelwing (*Calopteryx amata*; Paulson and Dunkle 2021). Cool, acidic, nutrient poor waters can be inhospitable to more common, generalist species found at lower elevations, allowing specialist species such as the superb jewelwing to remain extant. High elevation streams are associated with higher stream gradients, increased scour, reduced catchment areas, and increased shading, resulting in smaller amounts of fine particulate matter (Cormack 1949; Vannote et al. 1980; Arbuckle and Downing 2002). They are also typically characterized by lower pH and reduced fish diversity (see Sect. 6.2). These conditions are unsuitable for many filter feeding invertebrates, such as mussels, which are impacted by limited food, substrates that are not conducive to burrowing, and reduced diversity of larval (glochidial) host fish (Arbuckle and Downing 2002; Modesto et al. 2018). Instead, aquatic invertebrate communities contain higher proportions of predatory invertebrates and *shredder* invertebrates (which feed on coarse organic matter, such as twigs, leaves, and needles, that fall into the streams) than streams at lower elevations (Vannote et al. 1980).

Pest insect associations with red spruce are well studied, as understanding the impacts these organisms have on red spruce ecosystems is critical for forest management. Important insect pests of red spruce include eastern spruce gall adelgid (*Adelges abietis*), pine leaf adelgid (*Pineus pinifoliea*), eastern spruce beetle (*Dendroctonus rufipennis*), European spruce sawfly (*Diprion hercyniae*), yellowheaded spruce sawfly (*Pikonema alaskensis*), and spruce budworm (*Choristoneura fumiferana*; Potter et al. 2019). These insects can damage host trees in various ways (e.g., defoliation, sap feeding), and the significance of damage ranges from minor to potentially lethal. Although these pest species are not exclusively red spruce specialists and may utilize various hosts (typically other *Picea*), red spruce is a potential host and may be the primary host, within the central and southern Appalachians.

Studies of non-pest insects and other invertebrates in red spruce and spruce-fir forests of the central and southern Appalachians are scarce. Nonetheless, notable non-pest invertebrates that associate with red spruce include numerous high elevation wetland species (Byers et al. 2007, 2010), the spruce-fir moss spider (*Microhexura montivaga*), stoneflies (*Plecoptera* spp.), and several land snails. While this chapter emphasizes major pest species, select non-pest insects are included where the literature supports their inclusion.

6.6.1 Insecta: Coleoptera

6.6.1.1 Eastern Spruce Beetle (*Dendroctonus Rufipennis*)

The eastern spruce beetle is a major pest of red spruce, preferentially boring into weak or windthrown spruce as these hosts make excellent nesting sites and represent a source of nutrition without the need to battle host defenses. During outbreak years, eastern spruce beetles become substantially more aggressive and will attack standing trees in numbers significant enough to overwhelm host defenses (Wallin and Raffa 2004; Fig. 6.11). This species may have up to three generations per year. Population size fluctuates intermittently, with peak densities capable of killing large numbers of spruce over a few years, followed by many years of relatively low impact.

Several organisms are strongly associated with the eastern spruce beetle. The beetle acts as a vector for multiple fungi including *Leptographium abietinum* (Six and Bentz 2003) and *Ceratocystis rufipenni* (Wingfield et al. 1997). Additionally, Cardoza et al. (2008) listed eight mites and six nematodes carried by eastern spruce beetles. *Leptographium abietinum* has a context-dependent mutualism with the eastern spruce beetle, as the fungi can weaken host defenses and synthesize sterols that are important to the beetle, but with a tradeoff of fewer eggs produced (Cardoza et al. 2008). *Ceratocystis rufipenni* is a particularly virulent fungus and represents a serious threat to infected trees (Six and Bracewell 2015). The nature of its relationship with the eastern spruce beetle is less clear, but presumably the fungus weakens the host tree, making invasion easier. While the specific nature of the phoretic mite and nematode associations described by Cardoza et al. (2008) are not fully known, it is known that

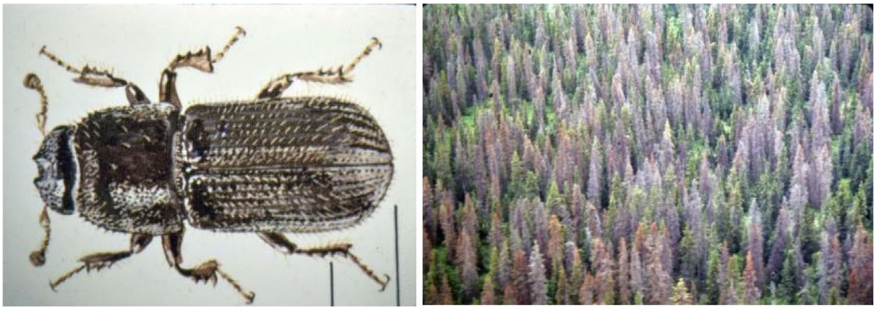

Fig. 6.11 Adult eastern spruce beetle (*Dendroctonus rufipennis* [left]) and an example of the potential for extensive spruce mortality caused by this species (white spruce [*Picea glauca*] in south-central Alaska [right]; photos by USDA Forest Service Forest Health Protection program)

one mite species, *Histiogaster arborsignis*, feeds on *L. abietinum* and likely transfers spores to eastern spruce beetles.

6.6.2 Insecta: Hemiptera

6.6.2.1 Eastern Spruce Gall Adelgid/Pineapple Gall Adelgid (*Adelges Abietis*)

The eastern spruce gall adelgid is an introduced species from Europe which typically does only minor damage, primarily aesthetic, to host trees (Fig. 6.12). As an entirely female species, reproduction is by parthenogenesis. Because it is a poor flier, dispersal potential is low. This often leads to individual trees being densely covered in galls while nearby trees have relatively few galls. Because gall abundance and volume are directly related to production of nymphal gallicolae, any factors that impact these gall parameters will also impact eastern spruce gall adelgid population size. Stems with larger, more numerous galls will have a larger number of gallicolae nymphs present, and these nymphs will be larger and possess greater fecundity than smaller individuals (Sopow and Quiring 1998, McKinnon et al. 1999). Gall density is typically highest on intermediate-sized mid-crown shoots or on upper-crown shoots after crown closure (Fidgen et al. 1994). Gall abundance and volume may be impacted by tree stress. For example, drought-stressed trees may show greater gall abundance, though reduced gall volume.

6.6.2.2 Balsam Woolly Adelgid (*Adelges Piceae*)

Balsam woolly adelgid is an exotic invasive insect that invaded North America in the early twentieth century and is a serious pest of trees in the *Abies* genus. The

Fig. 6.12 Example of pineapple-shaped galls caused by feeding activity of exotic invasive eastern spruce gall adelgids (*Adelges abietis*); photo by USDA Forest Service Forest Health Protection program

species has expanded to many of North America's fir populations, including the Appalachian Mountains (Montgomery and Havill 2014; Hrinkevich et al. 2016). Despite its specific epithet, this insect does not feed on *Picea* species. Balsam woolly adelgid has caused extensive fir mortality within its invasion distribution, resulting in altered stand composition of spruce-fir ecosystems (Ragenovich and Mitchell 2006). Notably, this includes extensive die-offs of Fraser fir in Great Smoky Mountains National Park in the 1960s and 1980s (Dull et al. 1988; Alsop and Laughlin 1991). Rapid reductions in canopy cover associated with fir die-offs can result in increased understory temperatures, drier soil conditions, and replacement of bryophyte, herbaceous, and shrub layers with more sun-tolerant plants, such as *Rubus* spp. (Potter et al. 2005; McManamay et al. 2011).

North American fir species respond to balsam woolly adelgid feeding by creating dense wood growth, causing reduced nutrient availability and subsequently a distinctive progression of foliage discoloration; first yellow, then red, and finally brown (Ragenovich and Mitchell 2006). Prolonged infestation can also cause curled crowns (Amman and Speers 1965). This species produces 2–4 generations per year, depending on weather conditions. While there is some evidence of sexual reproduction, creation of males generally requires an additional host tree species, which is not present in North America and is suspected to have gone extinct in its native range during a European interglacial period. Consequently, most reproduction is parthenogenic (Havill et al. 2021), with females producing more than 100 eggs that hatch into a mobile stage called crawlers. Crawlers feed in protected bark crevices on the trunk, near nodes, and bud bases (Varty 1956). Once feeding begins, they become immobile for the rest of their lives, secreting a protective, waxy coating that results in a distinctive woolly appearance. As the insect matures, this woolly coating increases in volume, allowing severe infestations to be identified from a distance.

Adults lay eggs underneath this woolly layer at the end of their lives. Generations are not synchronous and all life stages can be found on trees from April to November (Sidebottom 2019). However, crawlers are the only life stage to survive the winter.

6.6.2.3 Pine Leaf Adelgid (*Pineus Pinifoliae*)

The pine leaf adelgid has a complex life cycle which occurs on two different host plants and requires 2 years to complete (Drooz 1985). The primary host is either red spruce or black spruce (*Picea mariana*), and the secondary host is eastern white pine. In stands where both spruce species are present, pine leaf adelgids show a preference for red spruce (Howse and Dimond 1965). This alternation of host-dependence has important implications for population size. Dimond and Bishop (1968) showed that the relative proportions of primary and secondary hosts are an important predictor of population size. Because these insects are relatively poor fliers (Lowe 1966), dispersal capability is limited. Thus, population size is also likely limited by distance between primary and secondary hosts. Forest stands that possess a mixture of primary and secondary hosts in close proximity have the greatest potential for large population sizes.

Pine leaf adelgids feed from the host tree using piercing/sucking mouthparts. Populations tend to be highly synchronized, with nearly all individuals being on either the primary or secondary host in a given year (Lowe 1966, Dimond and Allen 1974). These insects infrequently outbreak, and the conelike galls of gallicolae do relatively little damage to the primary host. It is the secondary host, eastern white pine, that suffers significant damage due to exule feeding, particularly in the mid-crown (Lowe 1966). This damage may result in tree mortality in some instances (Dimond 1974). Feeding by exules creates a diagnostic growth pattern in the secondary host, with alternating reduced needle length and reduced shoot growth being a direct result of the pine leaf adelgid's 2-year life cycle (DeBoo et al. 1964).

6.6.3 Insecta: Hymenoptera

6.6.3.1 European Spruce Sawfly (*Gilpinia Hercyniae*)

The European spruce sawfly is an invasive pest of red spruce that may have up to three generations per year. Populations of European spruce sawflies are kept in check primarily by a virus (*Lefavirales*: Baculoviridae) mistakenly introduced alongside several biological control agents for the species in the 1930s (Morris 1958; Entwistle et al. 1983). There is evidence that small mammals consume cocoons of European spruce sawflies, with some areas seeing 40–50% of cocoons damaged by small mammals (Morris 1942). Tree mortality occurs gradually over outbreak periods, with the most mortality seen in host trees suffering losses of all old foliage and 75% of new foliage (Morris 1958). For example, Morris (1958) pointed to the work of

Fig. 6.13 Eggs (left) and feeding larvae (right) of the yellowheaded spruce sawfly (*Pikonema alaskensis*); photos by USDA Forest Service Forest Health Protection program

Reeks and Barter (1951) on the 1920s through 1930s outbreak of European spruce sawflies in Gaspé, Québec. In that study, tree mortality took 7 years to develop and another 5 years to reach peak loss rate. Reeks and Barter (1951) also found that trees under severe feeding stress experienced prolonged (e.g., post-infestation) reduction of growth in annual rings and tree height.

6.6.3.2 Yellowheaded Spruce Sawfly (*Pikonema Alaskensis*)

Yellowheaded spruce sawflies feed heavily on young needles of host spruce trees and may cause either reduced growth or outright mortality of host trees (Houseweart and Kulman 1976; Fig. 6.13). Younger trees and those growing in the open are preferred oviposition sites, and thus are at greatest risk of damage (Rose et al. 1994). This preference makes the yellowheaded spruce sawfly particularly damaging in spruce plantations (Bartelt et al. 1982). For example, Morse and Kulman (1984) investigated factors causing mortality of plantation white spruce (*Picea glauca*) in Minnesota. They attributed 65% of white spruce mortality in 5–12-year-old trees to yellowheaded spruce sawflies. Outbreaks occur frequently and may persist over several years (Katovich et al. 1995).

6.6.4 Insecta: Lepidoptera

6.6.4.1 Spruce Budworm (*Choristoneura Fumiferana*)

Spruce budworm densities are typically low and relatively little damage occurs to host trees in most years (Fig. 6.14). However, because spruce budworm population density is strongly associated with the extent of defoliation (Anderson and Sturtevant

Fig. 6.14 Larval (left) and adult (right) spruce budworms (*Choristoneura* sp.); photos by USDA Forest Service Forest Health Protection program

2011), these insects are capable of severely damaging or killing their hosts during outbreak years. These outbreaks also impact forest floor nutrient availability (Paré et al. 1993) and synergistically interact with other forest disturbances (e.g., fire) to restructure local environments (Bergeron and Leduc 1998). Population outbreaks occur approximately every 30 years, although this varies throughout the insect's range. For example, in New Brunswick, population outbreaks occur approximately every 35 years (Royama 1984).

Population density has two important effects on spruce budworm populations: triggering of dispersal behavior and negative impacts on body size and fecundity of adult moths (Bauce et al. 1994, Bakthavatsalam et al. 2016). Female spruce budworms are capable of autodetection (i.e., the detection of their own pheromones; Ross et al. 1979). While it may not seem intuitive that females would need this ability, it is likely that autodetection triggers dispersal behavior in females when population density is high (Bakthavatsalam et al. 2016). When densities are high, it is possible for new shoots to be totally consumed, forcing larvae to feed from older needles. Adult spruce budworm fecundity and body size are reduced in this circumstance (Bauce and Carisey 1996), and autodetection-triggered dispersal at high densities may alleviate this issue. When moths find themselves in heavily defoliated stands post-dispersal, these individuals may engage in a second dispersal flight.

The microsporidium (*Nosema fumiferanae*) is a lethal pathogen of spruce budworms that is transmitted between individuals orally or passed from mother to offspring through the egg (Eveleigh et al. 2007). This pathogen thrives when foliage nitrogen content is high (Bauer and Nordin 1988), which is optimal for spruce budworm development (Shaw and Little 1977). Consequently, those areas where spruce budworm populations outbreak may experience heavy transmission of this pathogen and subsequent steep population decline.

6.6.5 Arachnida: Araneae

6.6.5.1 Spruce-Fir Moss Spider (*Microhexura montivaga*)

The spruce-fir moss spider is the world's smallest tarantula, a mygalomorph spider with a body size ranging from 0.25 to 0.40 cm (0.10–0.16 in; Fig. 6.15). This spider is federally listed as endangered, one of four arachnids listed under the Endangered Species Act (Fridell 1995). It is endemic to six spruce-fir *sky islands* in the southern Appalachians (Coyle 1981, 1997, 2009; U.S. Fish and Wildlife Service 2001; Hedin et al. 2015). Spruce-fir moss spider habitat occurs under dense canopies of spruce-fir forests underneath bryophyte mats found on north-facing emergent rocky outcrops, cliffs, and colluvial boulders (Coyle 1997, 2009; U.S. Fish and Wildlife Service 2001). The main threat to spruce-fir moss spider populations is the loss of bryophyte mats through desiccation or disturbance. Bryophyte mats provide the spiders with relatively stable microclimates (Seaborn and Catley 2016). Shade-adapted bryophytes are sensitive to loss of overstory cover (Proctor 2000; Nelson and Halpern 2005); therefore, reduced canopy cover following balsam woolly adelgid-induced dieback events can dry out bryophyte mats. Climate change may also impact habitat through increased drought events or alteration in the patterns of cloud immersion events, an important source of moisture for high elevation bryophyte communities (Norris 1974). In the 1980s, population declines were observed at several sites via bryophyte mat desiccation events linked to drought and balsam woolly adelgid-induced dieback events (Coyle 2004, 2009). Since the rocky outcrops upon which bryophyte mats occur are a patchy resource and the types of moss and bryophytes favored by the spider are also patchily distributed, loss of habitat at one rocky outcrop could lead to extirpation at that site. Spruce-fir restoration activities that impact the overstory or directly impact bryophyte mats may impact spruce-fir moss spider habitat (Diggins and Ford 2020).

6.7 Wildlife Considerations for Management and Restoration Efforts

Forest management and restoration actions can have immediate and delayed positive and negative effects on wildlife (e.g., Thompson et al. 2003; Harper et al. 2016; Irwin et al. 2018). Species differ in habitat requirements, spatial and temporal activity patterns, and tolerance to ecological disturbances. Thus, it is not possible to make singular management recommendations for the benefit of all wildlife species. Rather, we suggest that it is incumbent on land and wildlife managers to consider the specific details of management actions during the development of site-specific management plans. Major considerations for wildlife include: (1) what species are present or likely to be present; (2) what action is to be conducted and what are all of its subcomponents (e.g., if timber is harvested, access road ground disturbance impacts would be a part

Fig. 6.15 Spruce-fir moss spider (*Microhexura montivaga*) documented on Roan Mountain. Photo by Gary Peeples

of the actions to consider); (3) when will the action occur; and (4) how much of the action will occur.

Understanding what species are present is perhaps the single most important consideration with regard to wildlife, as this may guide all subsequent discussions for conservation measures. The taxa lists included in this chapter provide useful guidance for identifying species likely to occur in a management unit, but obtaining species occurrence records for the area and performing site-specific wildlife surveys is optimal to validate occurrence. Identifying the action and all relevant subcomponents also is important, as this can help determine *what* species are likely to be affected and will help understand *how* species may be affected. Action timing is also important as some effects may be avoided entirely if the action is conducted at a time when species are not present in the disturbance area. How much of the action is to be performed will in large part determine the scope for potential effects, including the likelihood of direct impacts, how many individuals of each species may be impacted, and the potential for indirect effects on habitat quality.

Potential negative effects include mortality and injury as a direct result of management actions (e.g., crushing animals with equipment or falling trees), noise disturbances, and temporary habitat degradation (e.g., micro-site desiccation from overstory removal). For example, when conducting tree felling for red spruce release, the use of chainsaws could disturb nesting birds and cause nest abandonment (Ortega 2012), and the act of felling trees could impact microclimate quality for amphibians or spruce-fir moss spider (Diggins and Ford 2020; Brown et al. 2022). In this simple example, potential impacts to nesting birds can be avoided by conducting the tree removal outside of the nesting season, impacts to amphibians could be reduced by limiting the intensity of the tree removal and retaining coarse woody debris on the forest floor, and impacts to spruce-fir moss spider could be reduced by avoiding canopy gap creation treatments around rocky outcrops.

The wildlife species benefiting from red spruce restoration will change with age of the restored forests. For example, Stewart and Aldrich (1949) determined that Blackburnian warblers, magnolia warblers, golden-crowned kinglets, and dark-eyed juncos were the most common bird species in a mature second-growth red spruce stand in West Virginia, whereas only magnolia warblers and dark-eyed juncos were present in a young red spruce stand. In general, habitat quality will increase with stand age for most of the species of conservation concern associated with red spruce, such as Cheat Mountain salamanders, Virginia northern flying squirrels, and northern saw-whet owls (Simpson 1972a; Ford et al. 2022; Pauley 2022). As discussed in Sect. 7.2, benefits for downstream fish communities will also increase with maturity of the restored red spruce stands. Thus, from a wildlife perspective, red spruce restoration is largely a proactive management strategy to improve habitat quality in the long term.

References

Ahn S, De Steiguer JE, Palmquist RB et al (2000) Economic analysis of the potential impact of climate change on recreational trout fishing in the southern Appalachian Mountains: an application of a nested multinomial logit model. Clim Change 45:493–509

Alsop FJ III, Laughlin TF (1991) Changes in the spruce-fir avifauna of Mt. Guyot, Tennessee, 1967–1985. J Tenn Acad Sci 66:207–209

Amman GD, Speers CF (1965) Balsam woolly aphid in the southern Appalachians. J For 63:18–20

Amman GD, Laughlin TF (1991) Changes in the spruce-fir avifauna of Mt. Guyot, Tennessee, 1967–1985. J Forest 63:18–20

Anderson DP, Sturtevant BR (2011) Pattern analysis of eastern spruce budworm *Choristoneura fumiferana* dispersal. Ecography 34:488–497

Apodaca JJ, Diggins CA, Erb L (2020) Distribution, habitat preferences, and landscape genetics of Appalachian cottontail (*Sylvilagus obscurus*) in western North Carolina. Report WM-0323 to the North Carolina Wildlife Resource Commission, Raleigh, North Carolina

Appalachian Mountains Joint Venture (2019) Priority species. https://amjv.org/priority-species/. Accessed 26 Mar 2024

Arbogast BS, Browne RA, Weigl PD et al (2005) Conservation genetics of endangered flying squirrels (*Glaucomys*) from the Appalachian Mountains of eastern North America. Anim Conserv 8:123–133

Arbuckle KE, Downing JA (2002) Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. Can J Fish Aquat Sci 59:310–316

Austin LV, Silvis A, Ford WM et al (2018) Bat activity following restoration prescribed burning in the central Appalachian upland and riparian habitats. Nat Areas J 38:183–195

Bailey RW (1954) Status of beaver in West Virginia. J Wildl Manag 18:184–190

Bailey RS, Rucker CB (eds) (2021) The second atlas of breeding birds in West Virginia. Pennsylvania State University Press, University Park, Maryland

Bailey MA, Holmes JN, Buhlmann KA et al (2006) Habitat management guidelines for amphibians and reptiles of the southeastern United States. Partners in Amphibian and Reptile Conservation Technical Publication HMG-2, Montgomery, Alabama

Baker WL (1972) Eastern forest insects. USDA Forest Service Miscellaneous Publication No. 1175, Washington, DC
Bakthavatsalam N, Vinutha J, Ramakrishna P et al (2016) Autodetection in *Helicoverpa armigera* (Hubner). Curr Sci 110:2261–2267
Ball BA, Kominoski JS, Adams HE et al (2010) Direct and terrestrial vegetation-mediated effects of environmental change on aquatic ecosystem processes. Bioscience 60:590–601
Bartelt RJ, Jones RL, Kulman HM (1982) Evidence for a multicomponent sex pheromone in the yellowheaded spruce sawfly. Journal of Chemical Ecology 8:83–94
Bauce É, Carisey N (1996) Larval feeding behaviour affects the impact of staminate flower production on the suitability of balsam fir trees for spruce budworm. Oecologia 105:126–131
Bauce É, Crépin M, Carisey N (1994) Spruce budworm growth, development and food utilization on young and old balsam fir trees. Oecologia 97:499–507
Bauer LS, Nordin GL (1988) Nutritional physiology of the eastern spruce budworm, *Choristoneura fumiferana*, infected with *Nosema fumiferanae*, and interactions with dietary nitrogen. Oecologia 77:44–50
Beachy CK, Bruce RC (1992) Lunglessness in plethodontid salamanders is consistent with the hypothesis of a mountain stream origin: a response to Ruben and Boucot. Am Nat 139:839–847
Beilke EA, Blakey RV, O'Keefe JM (2021) Bats partition activity in space and time in a large, heterogeneous landscape. Ecol Evol 11:6513–6526
Beneski JT Jr, Stinson DW (1987) Sorex palutris. Mamm Species 296:1–6
Bergeron Y, Leduc A (1998) Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest. Journal of Vegetation Science 9:492–500
Bishop DJ, Majka CG, Bondrup-Nielsen S et al (2009) Deadwood and saproxylic beetle diversity in naturally disturbed and managed spruce forests in Nova Scotia. ZooKeys 22:309–340
Bogert CM (1952) Relative abundance, habitats, and normal thermal levels of some Virginian salamanders. Ecology 33:16–30
Bonner JL, Anderson JT, Rentch JS et al (2009) Vegetative composition and community structure associated with beaver ponds in Canaan valley, West Virginia, USA. Wetlands Ecol Manage 17:543–554
Boyce KA, Barry RE (2007) Seasonal home range and diurnal movements of *Sylvilagus obscurus* (Appalachian cottontail) at Dolly Sods, West Virginia. Northeast Nat 14:99–110
Bratton SP (1974) The effect of the European wild boar (*Sus scrofa*) on the high-elevation vernal flora in Great Smoky Mountains National Park. Bull Torrey Bot Club 101:198–206
Brewster W (1886) An ornithological reconnaissance in western North Carolina. Auk 3:94–112
Britzke ER, Harvey MJ, Loeb SC (2003) Indiana bat, *Myotis sodalis*, maternity roosts in the southern United States. Southeast Nat 2:235–242
Brooks M (1948) Notes on the Cheat Mountain salamander. Copeia 1948:239–244
Brooks M (1955) An isolated population of the Virginia varying hare. J Wildl Manag 19:54–61
Brown DJ, Rucker LE, Johnson C et al (2022) Microhabitat associations for the threatened Cheat Mountain salamander in relation to early-stage red spruce restoration areas. J Fish Wildl Manag 13:68–80
Bruce RC (1972) Variation in the life cycle of the salamander *Gyrinophilus porphyriticus*. Herpetologica 28:230–245
Bruce RC (1977) The pygmy salamander, *Desmognathus wrighti* (Amphibia, Urodela, Plethodontidae), in the Cowee Mountains, North Carolina. J Herpetol 11:246–247
Bruce RC (2003) Ecological distribution of the salamanders *Gyrinophilus* and *Pseudotriton* in a southern Appalachian watershed. Herpetologica 59:301–310
Bruce RC (2011) Community assembly in the salamander genus *Desmognathus*. Herpetol Monogr 25:1–24
Byers EA, Vanderhorst JP, Streets BP (2007) Classification and conservation assessment of high elevation wetland communities in the Allegheny Mountains of West Virginia. West Virginia Division of Natural Resources Report, Elkins, West Virginia

Byers EA, Vanderhorst JP, Streets BP (2010) Classification and conservation assessment of upland red spruce communities in West Virginia. West Virginia Division of Natural Resources Report, Elkins, West Virginia

Cahill AE, Aiello-Lammens ME, Fisher-Reid CM et al (2014) Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. J Biogeogr 41:429–442

Campbell TA, Laseter BR, Ford WM et al (2004) Movements of female white-tailed deer (*Odocoileus virginianus*) in relation to timber harvests in the central Appalachians. For Ecol Manage 199:371–378

Campbell TA, Laseter BR, Ford WM et al (2006) Abiotic factors influencing deer browsing in West Virginia. North J Appl for 23:20–26

Campbell JW, Mengak MT, Castleberry SB et al (2010) Distribution and status of uncommon mammals in the southern Appalachian Mountains. Southeast Nat 9:275–302

Cardoza YJ, Moser JC, Klepzig KD et al (2008) Multipartite symbioses among fungi, mites, nematodes, and the spruce beetle, *Dendroctonus rufipennis*. Environ Entomol 37:956–963

Chaplin SJ, Gerrard RA, Watson HM et al (2000) The geography of imperilment: targeting conservation toward critical biodiversity areas. In: Stein BA, Kutner LS, Adams JS (eds) Precious heritage: the status of biodiversity in the United States. Oxford University Press, New York, New York, pp 159–199

Chapman BR (2007a) Appalachian cottontail *Sylvilagus obscurus*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 243–246

Chapman BR (2007b) Fisher *Martes pennati*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 486–489

Chapman BR (2007c) Snowshoe hare *Lepus americanus*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 226–229

Cherefko C, Fridley C, Medsger J et al (2015) White-tailed deer and balsam woolly adelgid effects on balsam fir in Canaan Valley. Southeast Nat 14:218–231

Clayton JL, Dannaway ES, Menendez R et al (1998) Application of limestone to restore fish communities in acidified streams. North Am J Fish Manag 18:347–360

Clingerman JW (2008) Statewide analysis of brook trout (*Salvelinus fontinalis*) population status and reach-scale conservation priorities in West Virginia watersheds. West Virginia University, Morgantown, West Virginia, Thesis

Clipp HL, Brown DJ, Rota CT et al (2022) Distinct forest bird communities are strongly associated with red spruce-northern hardwood ecosystems in central Appalachia, USA. Ecol Ind 135:108568

Cormack RGH (1949) A study of trout streamside cover in logged-over and undisturbed virgin spruce woods. Can J Res 27:78–95

Coyle FA (1981) The mygalomorph spider genus *Microhexura* (Araneae, Dipluridae). Bull Am Mus Nat Hist 170:64–75

Coyle FA (1997) Status survey of the endangered spruce-fir moss spider, *Microhexura montivaga* Crosby & Bishop, on Mount LeConte. Report to the U.S. Fish and Wildlife Service, Asheville, North Carolina

Coyle FA (2004) Status survey of the endangered spruce-fir moss spider, *Microhexura montivaga* in the Great Smoky Mountains National Park. Report to the Great Smoky Mountains National Park, Asheville, North Carolina

Coyle FA (2009) Status survey of the spruce-fir moss spider, *Microhexura montivaga*. Report to the U.S. Fish and Wildlife Service, Asheville, North Carolina

Crespi EJ, Rissler LJ, Browne RA (2003) Testing Pleistocene refugia theory: phylogeographical analysis of *Desmognathus wrighti,* a high-elevation salamander in the southern Appalachians. Mol Ecol 12:969–984

Crespi EJ, Browne RA, Rissler LJ (2010) Taxonomic revision of *Desmognathus wrighti* (Caudata: Plethodontidae). Herpetologica 66:283–295

De La Cruz JL, Ford WM, Jones SC et al (2023a) Distribution of summer habitat for the Indiana bat on the Monongahela National Forest, West Virginia. J Southeast Assoc Fish Wildl Agencies 10:125–134

De La Cruz JL, Ford WM, Jones SC et al (2023b) Distribution of northern long-eared bat summer habitat on the Monongahela National Forest, West Virginia. J Southeast Assoc Fish Wildl Agencies 10:114–124

DeBoo R, Dimond J, Lowe J (1964) Impact of pine leaf aphid, *Pineus pinifoliae* (Chermidae) on its secondary host, eastern white pine. Can Entomol 96:765–772

DeGraaf RM, Rudis DD (1990) Herpetofaunal species composition and relative abundance among three New England forest types. For Ecol Manage 32:155–165

Delcourt PA, Delcourt HR (1998) Paleoecological insights on conservation of biodiversity: a focus on species, ecosystems, and landscapes. Ecol Appl 8:921–934

Demeo TE (1999) Forest songbird abundance and viability at multiple scales on the Monongahela National Forest, West Virginia. Dissertation, West Virginia University, Morgantown, West Virginia

Diefenbach DR, Rathbun SL, Vreeland JK et al (2016) Evidence for range contraction of snowshoe hare in Pennsylvania. Northeast Nat 23:229–248

Diggins CA (2023) Anthropogenically-induced range expansion as an invasion front in native species: an example in North American flying squirrels. Front Ecol Evol 11:1096244

Diggins CA, Ford WM (2020) Effects of surveying for the federally endangered spruce-fir moss spider (*Microhexura montivaga* Crosby & Bishop) on its bryophyte habitat. Southeast Nat 20:77–91

Diggins CA, Ford WM (2022) Seasonal activity patterns of bats in high-elevation conifer sky islands. Acta Chiropterologica 24:91–101

Diggins CA, Kelly CA, Ford WM (2015) Atypical den use of Carolina northern flying squirrels (*Glaucomys sabrinus coloratus*) in the southern Appalachian Mountains. Southeast Nat 14:44–49

Diggins CA, Higdon S, Ford WM (2016) High elevation record for eastern box turtle in the southern Appalachians. Herpetol Rev 47:454

Diggins CA, Silvis A, Kelly CA et al (2017) Home range, den selection and habitat use of Carolina northern flying squirrels (*Glaucomys sabrinus coloratus*). Wildl Res 44:427–437

Diggins CA, Castellano MA, Ford WM (2020) Hypogeous, sequestrate fungi (genus *Elaphomyces*) found at small-mammal foraging sites in high-elevation conifer forests of West Virginia. Northeast Nat 27:N40–N47

Dillard LO, Russell KR, Ford WM (2008a) Site-level habitat models for the endemic, threatened Cheat Mountain salamander (*Plethodon nettingi*): the importance of geophysical and biotic attributes for predicting occurrence. Biodivers Conserv 17:1475–1492

Dillard LO, Russell KR, Ford WM (2008b) Macrohabitat models of occurrence for the threatened Cheat Mountain salamander, *Plethodon nettingi*. Appl Herpetol 5:201–224

Dimond JB (1974) Sequential surveys for the pine leaf chermid, *Pineus pinifoliae*. University of Maine Life Sciences and Agriculture Experiment Station Technical Bulletin 68, Orono, Maine

Dimond J, Allen D (1974) Sampling populations of pine leaf chermid *Pineus pinifoliae* (Homoptera: Chermidae): III. Neosistentes on white pine. Canadian Entomologist 106:509–518

Dimond JB, Bishop RH (1968) Susceptibility and vulnerability of forests to the pine leaf aphid *Pineus pinifoliae* (Fitch) (Adelgidae). University of Maine Agricultural Experiment Station Bulletin 658, Orono, Maine

Dodd CK Jr (2013) Frogs of the United States and Canada. Johns Hopkins University Press, Baltimore, Maryland

Dodd CK Jr, Dorazio RM (2004) Using counts to simultaneously estimate abundance and detection probabilities in a salamander community. Herpetologica 60:468–478

Dodd CK Jr (2003) Monitoring amphibians in Great Smoky Mountains National Park. U.S. Geological Survey Circular 1258, Tallahassee, Florida

Downey DM, French CR, Odom M (1994) Low cost limestone treatment of acid sensitive trout streams in the Appalachian Mountains of Virginia. Water Air Soil Pollut 77:49–77

Drooz A (1985) Insects of eastern forests. USDA Forest Service Miscellaneous Publication No. 1426, Washington, DC

Dull CW, Ward JD, Brown HD et al (1988) Evaluation of spruce and fir mortality in the southern Appalachian Mountains. USDA Forest Service Southern Region Protection Report R8-PR 13, Atlanta, Georgia

Eastern Brook Trout Joint Venture (2018) Eastern brook trout roadmap to conservation. https://easternbrooktrout.org/about/reports/eastern-brook-trout-roadmap-to-conservation-2018/view. Accessed 11 May 2023

Enck JW, Brown TL (2005) Social feasibility of restoring elk to West Virginia. Report to the West Virginia Division of Natural Resources, Cornell University, Ithaca, New York

Entwistle PF, Adams PHW, Evans HF et al (1983) Epizootiology of a nuclear polyhedrosis virus (Baculoviridae) in European spruce sawfly (*Gilpinia hercyniae*): spread of disease from small epicentres in comparison with spread of baculovirus diseases in other hosts. J Appl Ecol 20:473–487

Etnier DA, Starnes WC (1993) The fishes of Tennessee. University of Tennessee Press, Knoxville, Tennessee

Eveleigh ES, Lucarotti CJ, McCarthy PC et al (2007) Occurrence and effects of *Nosema fumiferanae* infections on adult spruce budworm caught above and within the forest canopy. Agric For Entomol 9:247–258

Faust LF (2017) Fireflies, glow-worms, and lightning bugs: identification and natural history of the fireflies of the eastern and central United States and Canada. University of Georgia Press, Athens, Georgia

Ferrari BA, Shamblin BM, Chandler RB et al (2018) Canada warbler (*Cardellina canadensis*): novel molecular markers and a preliminary analysis of genetic diversity and structure. Avian Conservation and Ecology 13:8

Fidgen JG, Teerling CR, McKinnon ML (1994) Intra- and inter-crown distribution of the eastern spruce gall adelgid, *Adelges abietis* (L.), on young white spruce. Can Entomol 126:1105–1110

Fies ML (1991) Snowshoe hare. In: Terwilliger K (ed) Virginia's endangered species. McDonald and Woodward Publishing Company, Newark, New Jersey, pp 576–578

Flaherty KL, Grafton WN, Anderson JT (2018) White-tailed deer florivory influences the population demography of *Polemonium vanbruntiae*. Plant Biosyst 152:453–463

Ford WM, Rodrigue JL (2001) Soricid abundance in partial overstory removal harvests and riparian areas in an industrial forest landscape of the central Appalachians. For Ecol Manage 152:159–168

Ford WM, Menzel MA, Rodrigue JL et al (2005) Relating bat species presence to simple habitat measures in a central Appalachian forest. Biol Cons 126:528–539

Ford WM, Kelly CA, Rodrigue JL et al (2014) Late winter and early spring home range and habitat use of the endangered Carolina northern flying squirrel in western North Carolina. Endanger Species Res 2:73–82

Ford WM, Evans AM, Odom RH et al (2015) Predictive habitat models derived from nest-box occupancy for the endangered Carolina northern flying squirrel in the southern Appalachians. Endanger Species Res 27:131–140

Ford WM, Silvis A, Rodrigue JL et al (2016) Deriving habitat models for northern long-eared bats from historical detection data: a case study using the Fernow Experimental Forest. J Fish Wildl Manag 7:86–98

Ford WM, Diggins CA, De La Cruz JL et al (2022) Distribution probability of the Virginia northern flying squirrel in the high Allegheny Mountains. J Southeast Assoc Fish Wildl Agencies 9:168–175

Ford WM, McCay TS, Menzel MA et al (2006) Influence of elevation and forest type on shrew community assemblage and species distribution in the central and southern Appalachian Mountains. In: Merritt JF, Churchfield S, Hutterer R et al (eds) Advances in the biology of the shrews II. International Society of Shrew Biologists Special Publication No. 1, New York, New York, p 303–315

Ford WM, Mertz KM, Menzel JM et al (2007) Winter home range and habitat use of the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). USDA Forest Service Northern Research Station Research Paper NRS-4, Newtown Square, Pennsylvania

Ford WM, Moseley KR, Stihler CW et al (2010) Area occupancy and detection probabilities of the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) using nest-box surveys. In: Rentch JS, Schuler, TM (eds) Proceedings from the conference on the ecology and management of high elevation forests in the central and southern Appalachian Mountains. USDA Forest Service Northern Research Station General Technical Report NRS-P-64, Newtown Square, Pennsylvania, p 39–47

Francl KE, Ford WM, Castleberry SB (2004) Bat activity in central Appalachian wetlands. Georg J Sci 62:87–94

Francl KE, Glenn TC, Castleberry SB et al (2008) Genetic relationship of meadow vole (*Microtus pennsylvanicus*) populations in central Appalachian wetlands. Can J Zool 86:344–355

Fridell JA (1995) Endangered and threatened wildlife and plants: spruce-fir moss spider determined to be endangered. Fed Reg 60:6968–6973

Ganier AF (1928) The wildlife of Tennessee. J Tenn Acad Sci 3:10–22

Goode GB (1879) The occurrence of the Canada porcupine in West Virginia. Proc US Natl Mus 1:264–265

Goudy WH, Kletzly RC, Rieffenberger JC (1970) Characteristics of a heavily hunted woodcock population in West Virginia. Trans N Amn Wildl Nat Resour Conf 35:183–195

Green NB (1938) A new salamander, *Plethodon nettingi*, from West Virginia. Ann Carnegie Mus 27:295–299

Gregory SV, Swanson FJ, McKee WA et al (1991) An ecosystem perspective of riparian zones: focus on links between land and water. Bioscience 41:540–551

Gross DA (2010) Pennsylvania boreal conifer forests and their bird communities: past, present, and potential. In: Rentch JS, Schuler, TM (eds) Proceedings from the conference on the ecology and management of high elevation forests in the central and southern Appalachian Mountains. USDA Forest Service Northern Research Station General Technical Report NRS-P-64, Newtown Square, Pennsylvania, pp 48–73

Habera J, Moore S (2005) Managing southern Appalachian brook trout: a position statement. Fisheries 30:10–20

Hairston NG (1949) The local distribution and ecology of the plethodontid salamanders of the southern Appalachians. Ecol Monogr 19:47–73

Hall GA (1984) A long-term bird population study in an Appalachian spruce forest. Wilson Bull 96:228–240

Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. Ecol Lett 8:461–467

Handley CO Jr (1953) A new flying squirrel from the southern Appalachian Mountains. Proc Biol Soc Wash 66:191–194

Harman DM, Thoerig T (1968) Occurrence of the porcupine *Erethizon dorsatum* and the nutria *Myocastor coypus bonariensis* in western Maryland. Chesap Sci 9:138–139

Harper CA, Ford WM, Lashley MA et al (2016) Fire effects on wildlife in the central hardwoods and Appalachian regions, USA. Fire Ecology 12:127–159

Harrison JR III (2000) *Desmognathus wrighti* king pygmy salamander. Cat Am Amphib Reptil 704(1–704):7

Havill NP, Griffin BP, Andersen JC et al (2021) Species delimitation and invasion history of the balsam woolly adelgid, *Adelges* (*Dreyfusia*) *piceae* (Hemiptera: Aphidoidea: Adelgidae), species complex. Syst Entomol 46:186–204

Healy WM, Dickson JG (1992) Population influences. Environment 1:129–143
Hedin M, Carlson D, Coyle F (2015) Sky island diversification meets the multispecies coalescent – divergence in the spruce-fir moss spider (*Microhexura monitvaga*, Araneae, Mygalomorphae) on the highest peaks of southern Appalachia. Mol Ecol 24:3467–3484
Herlihy AT, Kaufmann PR, Church MR et al (1993) The effects of acidic deposition on streams in the Appalachian Mountain and Piedmont region of the Mid-Atlantic United States. Water Resour Res 29:2687–2703
Hillard EM (2013) Elk (*Cervus elaphus* L.) habitat selection in Great Smoky Mountains National Park. Thesis, Western Carolina University, Cullowhee, North Carolina
Hocking DJ, Crawford JA, Peterman WE et al (2021) Abundance of montane salamanders over an elevational gradient. Ecol Evol 11:1378–1391
Hoffman RL (1950) Records of *Picea* in Virginia. Castanea 15:55–58
Hoffman RL, Kleinpeter HI (1948) A collection of salamanders from Mount Rogers, Virginia. J Wash Acad Sci 38:106–108
Houseweart MW, Kulman HM (1976) Life tables of the yellowheaded spruce sawfly, *Pikonema alaskensis* (Rohwer) (Hymenoptera: Tenthredinidae) in Minnesota. Environmental Entomology 5:859–867
Howse GM, Dimond JB (1965) Sampling populations of pine leaf adelgid *Pineus pinifoliae* (Fitch): I. The gall and associated insects. Can Entomol 97:952–961
Hrinkevich KH, Progar RA, Shaw DC (2016) Climate risk modelling of balsam woolly adelgid damage severity in subalpine fir stands of western North America. PLoS ONE 11:e0165094
Hudy M, Downey DM, Bowman DM (2000) Successful restoration of an acidified native brook trout stream through mitigation with limestone sand. North Am J Fish Manag 20:453–466
Hudy M, Thieling TM, Gillespie N et al (2008) Distribution, status, and land use characteristics of subwatersheds within the native range of brook trout in the eastern United States. North Am J Fish Manag 28:1069–1085
Hughes RS (2006) Home ranges of the endangered Carolina northern flying squirrel in the Unicoi Mountains of North Carolina. Proc Annu Conf Southeast Assoc Fish Wildl Agencies 60:19–24
Hunter WC (2010) Bird conservation issues in high-elevation (red spruce-Fraser fir-northern hardwood) forests of the southern Blue Ridge. In: Rentch JS, Schuler, TM (eds) Proceedings from the conference on the ecology and management of high elevation forests in the central and southern Appalachian Mountains. USDA Forest Service Northern Research Station General Technical Report NRS-P-64, Newtown Square, Pennsylvania, p 212
Irwin LL, Riggs RA, Verschuyl JP (2018) Reconciling wildlife conservation to forest restoration in moist mixed-conifer forests of the inland northwest: a synthesis. For Ecol Manage 424:288–311
Jenkins RE, Burkhead NM (1994) Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland
Jenkins CN, Van Houtan KS, Pimm SL et al (2015) US protected lands mismatch biodiversity priorities. Proc Natl Acad Sci 112:5081–5086
Johnson C, Brown DJ, Sanders C et al (2021) Long-term changes in occurrence, relative abundance, and reproductive fitness of bat species in relation to arrival of white-nose syndrome in West Virginia, USA. Ecol Evol 11:12453–12467
Jones MT, Willey LL (eds) (2021) Biology and conservation of the wood turtle. Northeast Association of Fish and Wildlife Agencies, Petersburgh, New York
Kahler HA, Anderson JT (2010) Factors influencing avian communities in high-elevation southern Allegheny Mountain forests. In: Rentch JS, Schuler, TM (eds) Proceedings from the conference on the ecology and management of high elevation forests in the central and southern Appalachian Mountains. USDA Forest Service Northern Research Station General Technical Report NRS-P-64, Newtown Square, Pennsylvania, pp 94–103
Karas N (1997) Brook trout. Lyons & Burford, New York, New York
Karns DR (1992) Effects of acidic bog habitats on amphibian reproduction in a northern Minnesota peatland. J Herpetol 26:401–412

Katovich SA, McCullough DG, Haack RA (1995) Yellowheaded spruce sawfly–its ecology and management. USDA Forest Service North Central Forest Experiment Station General Technical Report NC-179, St. Paul, Minnesota

Kazyak DC, Lubinski BA, Kulp MA et al (2022) Population genetics of brook trout in the southern Appalachian Mountains. Trans Am Fish Soc 151:127–149

Kellogg R (1939) Annotated list of Tennessee mammals. Proc US Natl Mus 86:245–303

Kennedy PP (1853) The Blackwater chronicle. Refield Publishing, New York, New York

Kerns J, Kerlinger P (2004) A study of bird and bat collision fatalities at the Mountaineer Wind Energy Center, Tucker County, West Virginia: annual report for 2003. Curry & Kerlinger, LLC Report, Frostburg, Maryland

Kirkland GL Jr (1977) Responses of small mammals to the clearcutting of northern Appalachian forests. J Mammal 58:600–609

Kozak KH (2017) What drives variation in plethodontid salamander species richness over space and time? Herpetologica 73:220–228

Kroschel WA, Sutton WB, McClure CJW et al (2014) Decline of the Cheat Mountain salamander over a 32-year period and the potential influence of competition from a sympatric species. J Herpetol 48:415–422

Laerm J, Castleberry SB (2007) Deer mouse *Peromyscus maniculatus*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 337–341

Laerm J, Pagels JF (2007) Woodland jumping mouse *Napaeozapus insignis*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 426–429

Laerm J, Webster WD (2007) Red squirrel *Tamiasciurus hudsonicus*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 422–425

Laerm J, Ford WM, Chapman BR (2007a) American water shrew *Sorex palustris*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 109–112

Laerm J, Ford WM, Chapman BR (2007b) Hairy-tailed mole *Parascalops breweri*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 117–119

Lambert M, Drayer AN, Leuenberger W et al (2021) Evaluation of created wetlands as amphibian habitat on a reforested surface mine. Ecol Eng 171:106386

Latham SR, Sirén APK, Reitsma LR (2023) Space use and resource selection of wood turtles (*Glyptemys insculpta*) in the northeastern part of its range. Can J Zool 101:20–31

Linehan K, Palmer D (2014) Landowner views of elk in western North Carolina. Report to the North Carolina Wildlife Resources Commission, Raleigh, North Carolina

Linzey DW (1995) Mammals of the Great Smoky Mountains—1995 update. J Elisha Mitchell Sci Soc 111:1–81

Linzey DW (2002) Significant new mammal records from the Great Smoky Mountains National Park, Tennessee-North Carolina. J N C Acad Sci 118:91–96

Linzey DW (2021) The mammals of Virginia. McDonald and Woodward Publishing Company, Newark, New Jersey

Lituma CM, Cox JJ, Spear S et al (2021) Terrestrial wildlife in the post-mined Appalachian landscape: status and opportunities. In: Zipper C, Skousen J (eds) Appalachia's coal-mined landscapes. Springer, Cham, Switzerland, pp 135–166

Loeb SC, Tainter FH, Cázares E (2000) Habitat associations of hypogeous fungi in the southern Appalachians: implications for the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*). Am Midl Nat 144:286–296

Lowe JH Jr (1966) Biology and dispersal of *Pineus pinifoliae* (Fitch). Dissertation, Yale University, New Haven, Connecticut

Lowe WH (2005) Factors affecting stage-specific distribution in the stream salamander *Gyrinophilus porphyriticus*. Herpetologica 61:135–144
MacDonald LH, Coe D (2007) Influence of headwater streams on downstream reaches in forested areas. Forest Science 53:148–168
Mack DE, Yong W (2000) Swainson's thrush (*Catharus ustulatus*), ver 1.0. In: Poole AF, Gill FB (eds) Birds of the world. Cornell Lab of Ornithology, Ithaca, New York
Maehr DS, Cox JJ, Larkin JL (2007) Elk *Cervus elaphus*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 562–532
Marschall EA, Crowder LB (1996) Assessing population responses to multiple anthropogenic effects: a case study with brook trout. Ecol Appl 6:152–167
Martof BS (1962) Some aspects of the life history and ecology of the salamander *Leurognathus*. Am Midl Nat 67:1–35
Mathews RC, Echternacht AC (1984) Herpetofauna of the spruce-fir ecosystem in the southern Appalachian Mountain regions, with emphasis on the Great Smoky Mountains National Park. In: White PS (ed) The southern Appalachian spruce-fir ecosystem: its biology and threats. National Park Service Uplands Field Research Laboratory Research/Resources Management Report SER-71, Gatlinburg, Tennessee, pp 155–167
Mazerolle MJ (2004) Amphibian road mortality in response to nightly variations in traffic intensity. Herpetologica 60:45–53
McClurg SE, Petty JT, Mazik PM et al (2007) Stream ecosystem response to limestone treatment in acid impacted watersheds of the Allegheny Plateau. Ecol Appl 17:1087–1104
McDonnell TC, Sloat MR, Sullivan TJ et al (2015) Downstream warming and headwater acidity may diminish coldwater habitat in southern Appalachian Mountain streams. PLoS ONE 10:e0134757
McKinnon ML, Quiring DT, Bauce E (1999) Influence of tree growth rate, shoot size and foliar chemistry on the abundance and performance of a galling adelgid. Funct Ecol 13:859–867
McManamay RH, Resler LM, Campbell JB, McManamay RA (2011) Assessing the impacts of balsam woolly adelgid (*Adelges piceae* Ratz.) and anthropogenic disturbance on the stand structure and mortality of Fraser fir [*Abies fraseri* (Pursh) Poir.] in the Black Mountains, Noth Carolina. Castanea 76:1–19
McNeill D (1877) The last forest: tales of the Allegheny woods. McClain Printing Company, New York, New York
McShea WJ, Healy WM, Devers P et al (2007) Forestry matters: decline of oaks will impact wildlife in hardwood forests. J Wildl Manag 71:1717–1728
Menendez R (1976) Chronic effects of reduced pH on brook trout (*Salvelinus fontinalis*). J Fish Board Can 33:118–123
Mengak MT, Laerm J (2007a) American beaver *Castor canadensis*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 252–257
Mengak MT, Laerm J (2007b) Eastern chipmunk *Tamias striatus*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 417–421
Menzel JM, Ford WM, Edwards JW et al (2004) Nest tree use by the endangered Virginia northern flying squirrel in the central Appalachian Mountains. Am Midl Nat 151:355–368
Menzel JM, Ford WM, Edwards JW et al (2006) Home range and habitat use of the vulnerable Virginia northern flying squirrel *Glaucomys sabrinus fuscus* in the central Appalachian Mountains, USA. Oryx 40:204–210
Merker SA, Chandler RB (2020) Identifying global hotspots of avian trailing-edge population diversity. Glob Ecol Conserv 22:e00915
Merriam CH (1888) Remarks on the fauna of the Great Smoky Mountains; with description of a new species of red-backed mouse (*Evotomys carolinensis*). Am J Sci 36:458–460
Michael ED, Hahn BL, Hasen HJ (1982) Response of deer, hare, and grouse to whole-tree harvesting in central Appalachia. Proc Annu Conf Southeast Fish Wildl Agencies 36:627–633

Michael ED, Brown SL, Brown WS (2015) Historic game harvests in Canaan Valley and Tucker County, West Virginia. Southeast Nat 14:382–404

Miller GS Jr (1936) A new flying squirrel from West Virginia. Proc Biol Soc Wash 49:143–144

Miller GS Jr, Kellogg R (1955) List of North American recent mammals. United States National Museum Bulletin 205, Washington, DC

Millikin AR, Woodley SK, Davis DR et al (2019) Habitat characteristics in created vernal pools impact spotted salamander water-borne corticosterone levels. Wetlands 39:803–814

Milling TC, Rowe MP, Cockerel BL et al (1997) Population densities of northern saw-whet owls (*Aegolius acadicus*) in degraded boreal forests of the southern Appalachians. In: Duncan JR, Johnson DH, Nicholls TH (eds) Biology and conservation of owls in the northern hemisphere: 2nd international symposium. USDA Forest Service North Central Forest Experiment Station General Technical Report NC-190, St. Paul, Minnesota

Minckler LS (1945) Reforestation in the spruce type in the southern Appalachians. J Forest 43:349–356

Mitchell D (2001) Spring and fall diet of the endangered West Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). Am Midl Nat 146:439–443

Mitchell JC, Breisch AR, Buhlmann KA (2006) Habitat management guidelines for amphibians and reptiles of the northeastern United States. Partners in Amphibian and Reptile Conservation Technical Publication HMG-3, Montgomery, Alabama

Modesto V, Ilarri M, Souza AT et al (2018) Fish and mussels: importance of fish for freshwater mussel conservation. Fish Fish 19:244–259

Moncrief ND, Fies ML (2015) Report of first specimens of *Pekania pennanti* (fisher) from Virginia. Northeast Nat 22:N31–N34

Moncrief ND, Fies ML (2020) Recent records and range expansion of *Erethizon dorsatum* (North American porcupine) in Virginia. Northeast Nat 27:N21–N27

Montgomery ME, Havill NP (2014) Balsam woolly adelgid. In: Van Driesche R, Reardon R (eds) The use of classical biological control to preserve forests in North America. USDA Forest Service Forest Health Technology Enterprise Team Report FHTE-2013–2, Morgantown, West Virginia, pp 9–19

Morris RF (1958) A review of the important insects affecting the spruce - fir forests in the Maritime provinces. For Chron 34:159–189

Morris RF (1942) Preliminary notes on the natural control of the European spruce sawfly by small mammals. Can Entomol 74:176–202

Morse BW, Kulman HM (1984) Plantation white spruce mortality: estimates based on aerial photography and analysis using a life-table format. Can J For Res 14:195–200

Muthersbaugh MS, Ford WM, Powers KE et al (2019) Activity patterns in regional and long-distance migrant bat species during the fall and spring along ridgelines in the central Appalachians. J Fish Wildl Manag 10:180–195

Nelson CR, Halpern CB (2005) Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. Can J Bot 83:610–620

Nicholson, KE (committee chair) (2025) Scientific and standard English names of amphibians and reptiles of North America north of Mexico, with comments regarding confidence in our understanding. 9th edn. Society for the Study of Amphibians and Reptiles

Niemelä J, Haila Y, Punttila P (1996) The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. Ecography 19:352–368

Niemiller ML, Reynolds RG (2011) The amphibians of Tennessee. University of Tennessee Press, Knoxville, Tennessee

Norris DH (1974) Bryoecology of the Appalachian spruce–fir zone. Dissertation, University of Tennessee, Knoxville, Tennessee

North Carolina Wildlife Resources Commission (2023) Elk—North Carolina wildlife profiles. https://www.ncwildlife.org/Portals/0/Learning/documents/Profiles/Mammals/Elk-Species-Profile-FINAL.pdf. Accessed 20 Jan 2023

O'Keefe JM, Pettit JL, Loeb SC et al (2019) White-nose syndrome dramatically altered the summer bat assemblage in a temperate southern Appalachian forest. Mamm Biol 98:146–153
Olson DM, Dinerstein E (2002) The global 200: priority ecoregions for global conservation. Ann Mo Bot Gard 89:199–224
Ortega CP (2012) Effects of noise pollution on birds: a brief review of our knowledge. Ornithol Monogr 74:6–22
Pack JC, Cromer JI (1981) Reintroduction of fisher in West Virginia. In: Chapman JA, Pursley D (eds) Worldwide furbearer conference proceedings, vol 2. Frostburg State College. Frostburg, Maryland, pp 1431–1442
Pagels JF, Smock LA, Sklarew SH (1998) The water shrew, *Sorex palustris* Richardson (Insectivora: Soricidae), and its habitat in Virginia. Brimleyana 25:120–134
Pagels JF, Laerm J (2007a) Rock vole *Microtus chrotorrhinus*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 276–279
Pagels JF, Laerm J (2007b) Southern red-backed vole *Clethrionomys gapperi*. In: Trani-Griep M, Ford WM, Chapman BR (eds) Land managers guide to mammals of the south. The Nature Conservancy, Durham, North Carolina, pp 272–275
Paré D, Bergeron Y, Camiré C (1993) Changes in the forest floor of Canadian southern boreal forest after disturbance. J Veg Sci 4:811–818
Pauley TK (1978) Plants as indicators of occurrence of two sympatric *Plethodon* species. Bull Md Herpetol Soc 14:29–35
Pauley TK (1980) Amphibians and reptiles of the West Virginia mountains above 975 meters. W Va Acad Sci 50:84–92
Pauley BA (1998) The use of emergent rocks as refugia for the Cheat Mountain salamander. Thesis, Marshall University, Huntington, West Virginia, Plethodon nettingi Green
Pauley TK (2008) The Appalachian inferno: historical causes for the disjunct distribution of *Plethodon nettingi* (Cheat Mountain salamander). Northeast Nat 15:595–606
Pauley TK (2015) Amphibians in the Canaan Valley drainage. Southeast Nat 14:314–322
Pauley TK (2022) Forty-years of field notes: the Cheat Mountain salamander (*Plethodon nettingi*). Proc W Va Acad Sci 94:1–37
Pauley BA, Pauley TK (1997) Range and distribution of the Cheat Mountain salamander, *Plethodon nettingi*: an update. Proc W Va Acad Sci 69:3–4
Paulson DR, Dunkle SW (2021) A checklist of North American Odonata including English name, etymology, type locality, and distribution. https://www.odonatacentral.org/public/media/uploads/files/NA_Odonata_Checklist_2021_update.pdf. Accessed 26 Mar 2024
Petranka JW (1998) Salamanders of the United States and Canada. Smithsonian Books, Washington, DC
Petranka JW, Smith CK (2005) A functional analysis of streamside habitat use by southern Appalachian salamanders: implications for riparian forest management. For Ecol Manage 210:443–454
Petty JT, Lamothe PJ, Mazik PM (2005) Spatial and seasonal dynamics of brook trout populations inhabiting a central Appalachian watershed. Trans Am Fish Soc 134:572–587
Petty JT, Fulton JB, Strager MP et al (2010) Landscape indicators and thresholds of stream ecological impairment in an intensively mined Appalachian watershed. J N Am Benthol Soc 29:1292–1309
Pickering J, Kays R, Meier A et al (2002) The Appalachians. In: Mittermeier RA, Mittermeier CG, Gil PR et al (eds) Wilderness: Earth's last wild places. Conservation International, pp 458–467
Pope CH, Hairston NG (1947) The distribution of *Leurognathus* a southern Appalachian genus of salamanders. Fieldiana Zool 31:155–162
Poplar-Jeffers IO, Petty JT, Anderson JT et al (2009) Culvert replacement and stream habitat restoration: implications from brook trout management in an Appalachian watershed, U.S.A. Restor Ecol 17:404–413
Potter KM, Escanferla ME, Jetton RM et al (2019) Important insect and disease threats to United States tree species and geographic patterns of their potential impacts. Forests 10:304

Potter KM, Frampton J, Sidebottom J (2005) Impacts of balsam woolly adelgid on the southern Appalachian spruce-fir ecosystem and the North Carolina Christmas tree industry. In: Onken B, Reardon R (eds). Proceedings of the Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, USDA Forest Service Forest Health Technology Enterprise Team, Morgantown, West Virginia, pp 25–41

Powell R, Conant R, Collins JT (2016) Peterson field guide to reptiles and amphibians of eastern and central North America, 4th edn. Houghton Mifflin Harcourt, New York, New York

Proctor MCF (2000) Physiological ecology. In: Shaw AJ, Goffinet B (eds) Bryophyte biology. Cambridge University Press, Cambridge, England, pp 225–247

Pyle P (1997) Identification guide to North American birds: a compendium of information on identifying, ageing, and sexing “near-passerines” and passerines in the hand. Slate Creek Press, Bolinas, California

Pyron RA, Beamer DA (2022) Nomenclatural solutions for diagnosing ‘cryptic’ species using molecular and morphological data facilitate a taxonomic revision of the black-bellied salamanders (Urodela, *Desmognathus* ‘*quadramaculatus*’) from the southern Appalachian Mountains. Bionomina 27:1–43

Rabenold KN (1978) Foraging strategies, diversity, and seasonality in bird communities of Appalachian spruce-fir forests. Ecol Monogr 48:397–424

Rabenold KN, Fauth PT, Goodner BW et al (1998) Response of avian communities to disturbance by an exotic insect in spruce-fir forests of the southern Appalachians. Conserv Biol 12:177–189

Rabenold KN (1984) Birds of Appalachian spruce-fir forests: dynamics of habitat-island communities. In: White PS (ed) The southern Appalachian spruce-fir ecosystem: its biology and threats. National Park Service Southeast Region Research/Resources Management Report SER-71, Atlanta, Georgia, pp 168–186

Rabenold KN (1992) Bird communities of Great Smoky Mountains National Park: establishing monitoring protocol and measuring effects of disturbance. Report to the National Park Service, Gatlinburg, Tennessee

Ragenovich IR, Mitchell RG (2006) Balsam woolly adelgid. USDA Forest Service Forest Insect & Disease Leaflet 118, Washington, DC

Ramos MA, Warner DA (1980) Analysis of North America subspecies of migrant birds wintering in Los Tuxtlas, southern Veracruz, Mexico. In: Keast A, Morton ES (eds) Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, DC, pp 173–180

Ray S, Pool J (2018) Once degraded, West Virginia’s Monongahela National Forest is restored to glory. World Resources Institute, Washington, DC. https://www.wri.org/insights/once-degraded-west-virginias-monongahela-national-forest-restored-glory. Accessed 20 Jan 2023

Reeks WA, Barter GW (1951) Growth reduction and mortality of spruce caused by the European spruce sawfly, *Gilpinia hercyniae* (HTG.) (Hymenoptera: Diprionidae). For Chron 27:140–156

Rentch JS, Ford WM, Schuler TS et al (2016) Release of suppressed red spruce using canopy gap creation—ecological restoration in the central Appalachians. Nat Areas J 36:29–37

Reynolds RJ, Pagels JF, Fies ML (1999) Demography of northern flying squirrels in Virginia. Proc Southeast Assoc Fish Wildl Agencies 53:340–349

Rhodes BM, Barton CD (2024) Comparing the response of red spruce plantings on legacy coal mines and old-field restoration sites in the West Virginia highlands. Nat Areas J 44:65–75

Richardson JS (2019) Biological diversity in headwater streams. Water 11:366

Riddell EA, Sears MW (2015) Geographic variation of resistance to water loss within two species of lungless salamanders: implications for activity. Ecosphere 6:86

Rinehart KA, Donovan TM, Mitchell BR et al (2009) Factors influencing occupancy patterns of eastern newts across Vermont. J Herpetol 43:521–531

Rissler LJ, Smith WH (2010) Mapping amphibian contact zones and phylogeographical break hotspots across the United States. Mol Ecol 19:5404–5416

Rojas VG, Loeb SC, O’Keefe JM (2019) False-positive occupancy models produce less-biased occupancy estimates for a rare and elusive bat species. J Mammal 100:212–222

Ronca R, Winterton E, Davenport JM (2026) Bridging data gaps: evidence-based population assessment for an endemic amphibian of conservation concern. J Wildl Manag 2026:e70216
Rose AH, Lindquist OH, Syme P (1994) Insects of eastern spruces, fir and hemlock. Canadian Forest Service, Ottawa, Canada
Ross RJ, Palaniswamy P, Seabrook WD (1979) Electroantennograms from spruce budworm moths (*Choristoneura fumiferana*) (Lepidoptera: Tortricidae) of different ages and for various pheromone concentrations. Can Entomol 111:807–816
Rossell CR Jr, Haas IC, Williams LA et al (2018) Comparison of relative abundance and microhabitat of *Desmognathus organi* (northern pygmy salamander) and *Desmognathus wrighti* (southern pygmy salamander) in North Carolina. Southeast Nat 17:141–154
Royama T (1984) Population dynamics of the spruce budworm *Choristoneura fumiferana*. Ecol Monogr 54:429–462
Rucker LE, Brown DJ, Watson MB et al (2022) Long-term occupancy dynamics of the threatened Cheat Mountain salamander and its competitors in relation to linear habitat fragmentation. For Ecol Manage 505:119847
Rucker LE, Brown DJ, Strager MP et al (2025) Projected future changes in the geographic distributions of the threatened *Plethodon nettingi* and a potential competitor. Endanger Species Res 57:103–118
Rushing CS, Royle JA, Ziolkowski DJ Jr et al (2020) Migratory behavior and winter geography drive differential range shifts of eastern birds in response to recent climate change. Proc Natl Acad Sci 117:12897–12903
Seaborn T, Catley K (2016) Abiotic microhabitat parameters of the spruce–fir moss spider, *Microhexura monitvaga* Crosby and Bishop (Araneae: Dipluridae). Southeast Nat 15:16–75
Shaw GG, Little CHA (1977) Natural variation in balsam fir foliar components of dietary importance to spruce budworm. Can J for Res 7:47–53
Shingleton MV, Brown WS (2010) Wild trout restoration in acidified streams. In: Carline RF, LoSapio C (eds) Conserving wild trout. Proceedings of the wild trout X symposium, Bozeman, Montana, pp 304–310
Sidebottom J (2019) Balsam woolly adelgid Christmas tree notes. https://content.ces.ncsu.edu/balsam-woolly-adelgid#section_heading_4932. Accessed 16 Dec 2024
Simbeck DJ (1990) Distribution of the fishes of the Great Smoky Mountains National Park. University of Tennessee, Knoxville, Tennessee, Thesis
Simpson MB Jr (1972a) Annotated checklist of the birds of Mt. Mitchell State Park, North Carolina. J Elisha Mitchell Sci Soc 88:244–251
Simpson MB Jr (1972b) The saw-whet owl population of North Carolina's southern Great Balsam Mountains. Chat 36:39–47
Six DL, Bracewell R (2015) *Dendroctonus*. In: Vega FE, Hofstetter RW (eds) Bark beetles: biology and ecology of native and invasive species. Academic Press, London, England, pp 305–350
Six DL, Bentz BJ (2003) Fungi associated with the North American spruce beetle, *Dendroctonus rufipennis*. Can J for Res 33:1815–1820
Snyder RC (1946) *Plethodon welleri* from Flat Top Mountain, North Carolina. Copeia 1946:174
Sopow SL, Quiring DT (1998) Body size of spruce-galling adelgids is positively related to realized fecundity in nature. Ecol Entomol 23:476–479
Stauffer JR, Boltz JM, White LR (1995) The fishes of West Virginia. Proc Acad Natl Sci Phila 146:1–389
Steele MA, Powell RA (1999) Biogeography of small mammals in the southern Appalachians: patterns of local and regional abundance and distribution. In: Eckerlin RP (ed) Proceedings of the Appalachian biogeography symposium. Virginia Museum of Natural History Special Publication 7, Martinsville, Virginia, pp 155–165
Steketee AK, Wood PB, Gregg ID (2015) American woodcock habitat changes in Canaan Valley and environs. Southeast Nat 14:331–343
Stephenson SL, Clovis JF (1983) Spruce forests of the Allegheny Mountains in central West Virginia. Castanea 48:1–12

Stewart RE, Aldrich JW (1949) Breeding bird populations in the spruce region of the central Appalachians. Ecology 30:75–82

Stihler CW, Wallace JW, Michael ED et al (1995) Range of *Glaucomys sabrinus fuscus*, a federally endangered subspecies of the northern flying squirrel, in West Virginia. Proc W Va Acad Sci 67:13–20

Stihler CW (2011) Status of the Virginia big-eared bat (*Corynorhinus townsendii virginianus*) in West Virginia: twenty-seven years of monitoring cave roosts. In: Loeb SC, Lacki MJ, Miller DA (eds) Conservation and management of eastern big-eared bats: a symposium. USDA Forest Service Southern Research Station General Technical Report SRS-145, Asheville, North Carolina, pp 75–84

Strong C, Zuckerberg B, Betancourt JL et al (2015) Climatic dipoles drive two principal modes of North American boreal bird irruption. Proc Natl Acad Sci 112:E2795–E2802

Sugalski MT, Claussen DL (1997) Preference for soil moisture, soil pH, and light intensity by the salamander, *Plethodon cinereus*. J Herpetol 31:245–250

Thomas-Van Gundy MA, Sturtevant BR (2014) Using scenario modeling for red spruce restoration planning in West Virginia. J Forest 112:457–466

Thompson ID, Baker JA, Ter-Mikaelian M (2003) A review of the long-term effects of post-harvest silviculture on vertebrate wildlife, and predictive models, with an emphasis on boreal forests in Ontario, Canada. For Ecol Manage 177:441–469

Thompson ID, Baker JA, Jastrebski C et al (2008) Effects of post-harvest silviculture on use of boreal forest stands by amphibians and marten in Ontario. For Chron 84:741–747

Thurow GR (1963) Taxonomic and ecological notes on the salamander, *Plethodon welleri*. Univ Kans Sci Bull 44:87–108

Tilley SG (1973) Life histories and natural selection in populations of the salamander *Desmognathus ochrophaeus*. Ecology 54:3–17

Tilley SG (1985) *Desmognathus imitator* imitator salamander. Cat Am Amphib Reptil 359(1–359):2

Tirpak JM, Giuliano WM, Miller CA et al (2006) Ruffed grouse population dynamics in the central and southern Appalachians. Biol Cons 133:364–378

U.S. Fish and Wildlife Service (2001) Endangered and threatened wildlife and plants; designation of critical habitat for the spruce-fir moss spider. Fed Reg 66:35547–35566

U.S. Fish and Wildlife Service (1990) Appalachian northern flying squirrels (*Glaucomys sabrinus fuscus* and *Glaucomys sabrinus coloratus*) recovery plan. U.S. Fish and Wildlife Service, Hadley, Massachusetts

Vannote RL, Minshall GW, Cummins KW et al (1980) The river continuum concept. Can J Fish Aquat Sci 37:130–137

Varty I (1956) *Adelges* insects of silver firs. Her Majesty's Stationary Office Forestry Commission Bulletin No. 26, Edinburgh, Scotland

Wallin KF, Raffa KF (2004) Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. Ecol Monogr 74:101–116

Weigl PD (2007) The northern flying squirrel (*Glaucomys sabrinus*): a conservation challenge. J Mammal 88:897–907

Weigl PD, Knowles TW (1995) Megaherbivores and southern Appalachian grass balds. Growth Chang 26:365–382

Weigl PD, Knowles TW, Boyton AC (1992) The distribution and ecology of the northern flying squirrel *Glaucomys sabrinus coloratus* in the southern Appalachians. North Carolina Wildlife Resources Commission Nongame and Endangered Wildlife Program, Raleigh, North Carolina

West Virginia Division of Natural Resources (2021) West Virginia elk management plan. West Virginia Division of Natural Resources, Charleston, West Virginia

Wetzel EJ, Weigl PD (1994) Ecological implications for flying squirrels (*Glaucomys* spp.) of effects of temperature on the in vitro development and behavior of *Strongyloides robustus*. Am Midl Nat 131:43–54

Wingfield MJ, Harrington TC, Solheim H (1997) Two species in the *Ceratocystis coerulescens* complex from conifers in western North America. Can J Bot 75:827–834

Wootton JT (2020) Purple finch (*Haemorhous purpureus*), ver 1.0. In: Poole AF, Gill FB (eds) Birds of the world. Cornell Lab of Ornithology, Ithaca, New York

Wyman RL, Hawksley-Lescault DS (1987) Soil acidity affects distribution, behavior, and physiology of the salamander *Plethodon cinereus*. Ecology 68:1819–1827

Yetter E, Chhin S, Brown JP (2021) Sustainable management of central Appalachian red spruce. Sustainability 13:10871

Zurbuch PE (2015) Historic fishery of the Blackwater River. Southeast Nat 14:276–296

Zurbuch PE, Menendez R, Clayton JL (1996) Limestone neutralization of Dogway Fork, West Virginia, by means of a rotary-drum system. Restor Ecol 4:206–219