Northern Flying Squirrel

Glaucomys sabrinus (Shaw, 1801)

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CONTENT AND TAXONOMIC COMMENTS

Twenty-five subspecies are currently recognized (Hall 1981, Wells-Gosling and Heaney 1984) and two occur in the South: the Carolina northern flying squirrel (*G. s. coloratus*) and the Virginia northern flying squirrel (*G. s. fuscus*). The literature was reviewed by Wells-Gosling and Heaney (1984).

DISTINGUISHING CHARACTERISTICS

The northern flying squirrel is the larger of the two flying squirrels in the South, both of which are characterized by a furred patagium extending from front to hind limbs and a long, flattened tail. The measurements are: total length, 256-274 mm; tail, 108-160 mm; hind foot, 34-39 mm; ear, 16-20 mm; weight, 90–140 g. The dental formula is: I 1/1, C 0/0, P 2/1, M 3/3 = 22 (Figure 1). The pelage is thick and silky, gray with brownish to rusty wash dorsally and grayish to buffy white ventrally, with the base of the hairs slate gray. The sides of the head are often grayish with a buffy wash. The tail is bicolored cinnamon to blackish dorsally, especially near the tip, and buffy to gray ventrally (Wells-Gosling and Heaney 1984). The northern flying squirrel is distinguished from the southern flying squirrel, G. volans, by its larger size, greater adult weight, and gray base of its ventral hairs. The northern flying squirrel cranium is larger (>36 mm) than that of the southern flying squirrel. Of the two extant subspecies in the South, G. s. coloratus tends to be larger and has a somewhat longer tail (134 mm) than G. s. fuscus (115 mm; Reynolds et al. 1999). See keys for details.

CONSERVATION STATUS

The U. S. Fish and Wildlife Service (U. S. Department of the Interior 1993, 2007) lists *G. s. coloratus* and *G. s. fuscus* as Endangered. The northern flying squirrel has a global rank of Secure (NatureServe 2007). However, the species is Imperiled in North Carolina and Critically Imperiled in Virginia. It is unranked in Tennessee. Significant status reviews are provided in Linzey (1983), Weigl (1987), Fies and Pagels (1991), and Weigl et al. (1999).



Figure 1. Dorsal, ventral, and lateral view of cranium and lateral view of mandible of *Glaucomys sabrinus* from Fairbanks County, Alaska (USNM 242499, female).

DISTRIBUTION

The northern flying squirrel occurs throughout most of boreal and sub-boreal North America from Alaska east to Labrador and south to the Cascades, northern Rockies, Lake States and Upper mid-Atlantic to the Catskill Mountains in New York and the Pocono Mountains and Allegheny Plateau in extreme northern Pennsylvania (Wells-Gosling and Heaney 1984, Merritt 1987). Significant southern distributional extensions include the Coast Ranges and Sierra Nevada through southern California. Disjunct populations occur in the Black Hills of South Dakota, the Allegheny Mountains of West Virginia and Virginia, and the southern Blue Ridge in North Carolina, Tennessee and Virginia (Miller 1936, Wells-Gosling and Heaney 1984, Merritt 1987, Whitaker and Hamilton 1998, Linzey 1995, Browne et al. 1999, Reynolds et al. 1999, Odom et al. 2001; Figure 2). Regionally, G. s. *fuscus* occurs at high elevations in the Allegheny Mountains of Highland County, Virginia on the George Washington National Forest and more widely in eastern West Virginia in Grant, Greenbrier, Pendleton, Pocahontas, Randolph, Tucker and Webster counties on or near the Monongahela National Forest (Pagels et al. 1990, Fies and Pagels 1991, Stihler et al. 1987, Stihler et al. 1995, Reynolds et al. 1999, Odom et al. 2001; S. Jones, U. S. Fish and Wildlife Service, personal communication). In the southern Blue Ridge, G. s. coloratus is distributed along several high elevation massifs in and around the Great Smoky Mountains National Park, Blue Ridge Parkway, and Pisgah, Nantahala, and Cherokee National Forests in Avery, Buncombe, Graham, Haywood, Jackson, McDowell, Mitchell, Swain, Transylvania, Watauga, and Yancey counties, North Carolina and Blount, Carter, Monroe, and Sevier counties, Tennessee. Potential high elevation habitat also occurs in Caldwell and Macon counties, North Carolina and Cocke, Johnson, and Unicoi counties, Tennessee although those areas have been unsurveyed or surveys have failed to document their presence (Linzey 1995, Weigl et al. 1999; M. Cantrell, U. S. Fish and Wildlife Service, personal communication; B. Stiver, National Park Service, personal communication; P. Wyatt, Tennessee Wildlife Resources Agency, personal communication). Northern flying squirrels also occur in and around the Mt. Rogers-Grayson Highlands area of Grayson and Smyth counties, Virginia on the Jefferson National Forest (Reynolds et al. 1999). These specimens are referable to *G. s. coloratus*, although Fies and Pagels (1991) and Sparks (2005) suggested they could be intergrades between G. s. coloratus and G. s. fuscus.

ABUNDANCE STATUS

The species is very rare in the South and population densities in occupied habitat are unknown. Prior to Federal listing, 30 specimens from eight localities were known from the central and southern Appalachians. The number of collection localities has been expanded greatly with approximately 1,200 individuals caught in West Virginia and > 1,000 individuals



Figure 2. Distribution of *Glaucomys sabrinus* in the South: (1) *G. s. coloratus;* (2) *G. s. fuscus.*

caught in North Carolina, Tennessee, and Virginia since 1985 (Reynolds et al. 1999, Weigl et al. 1999; C. Stihler, West Virginia Department of Natural Resources, personal communication). However, Fies and Pagels (1991) suggest fewer than 250 individuals remain in Virginia. Both *G. s. coloratus* and *G. s. fuscus* have demonstrated yearly population fluctuations at some monitoring sites (Weigl et al. 1999; C. Stihler, West Virginia Department of Natural Resources, personal communication).

PRIMARY HABITATS

Throughout its range, the northern flying squirrel inhabits a variety of boreal coniferous and mixed hardwood forest habitats (Wells-Gosling and Heaney 1984). In the South, the species is a Pleistocene relict restricted to montane boreal or northern hardwoods communities at the highest elevations of the central and southern Appalachians. Montane boreal habitats in the southern Blue Ridge occupied by G. s. coloratus are dominated by conifers such as red spruce (Picea rubens) and Fraser fir (Abies fraseri), whereas those occupied by G. s. fuscus in the Allegheny Mountains are dominated by red spruce and eastern hemlock (Tsuga canadensis). Northern hardwood and northern hardwood-montane boreal forest ecotones occupied by northern flying squirrels in both areas are comprised of overstories of yellow birch (Betula alleghaniensis), sugar maple (Acer saccharum), red maple (A. rubrum), American beech (Fagus grandifolia), and black cherry (Prunus serotina), along with the aforementioned conifers. Captures of G. s. fuscus in the Alleghenies have ranged in elevation from approximately 900–1400 m (Stihler et al. 1995, Reynolds et al.

1999) whereas those of G. s. coloratus in the southern Blue Ridge generally have occurred at elevations above 1500 m (Browne et al. 1999). One individual was recorded in the Great Smoky Mountains National Park at 1230 m (Weigl 1968). Northern flying squirrels in the central and southern Appalachians have been documented in a variety of stand ages and conditions (Payne et al. 1989, Weigel and Osgood 1974), but mature forest conditions in the northern hardwood-montane boreal ecotone on north-facing slopes with large trees, numerous snags, high volumes of coarse wood debris, and abundant lichens and hypogeal fungi are believed to be optimal (Reynolds et al. 1999, Weigl et al. 1999, Loeb et al. 2000, Schuler et al. 2002, Hackett and Pagels 2003). Odom et al. (2001) found that increased elevation and close proximity to the presence of red spruce and eastern hemlock were the best predictive variables between occupied and unoccupied habitat for G. s. fuscus in the Allegheny Mountains at the landscape-level. At the stand-level, forests with 35% montane conifer overstories, primarily red spruce, are very indicative of occupied habitat (Ford et al. 2004). Individual home ranges are variable, ranging from 1.2–51.4 ha for G. s. coloratus in North Carolina (Weigl et al. 1999, Weigl et al. 2002) and 5 ha to > 100 ha for *G. s. fuscus* in West Virginia (Urban 1988, Menzel et al. 2006b). Most northern flying squirrel activity occurs from shortly after sunset until midnight (Weigl et al. 2002). Home range size probably varies by habitat structure quality and seasonal food abundance. Males tend to have larger home ranges than females, particularly in late winter at the onset of breeding (Weigl et al. 1999). Both subspecies typically den in cavities in live hardwoods and snags. Yellow birch and American beech are two of the most preferred den tree species. Leaf or "drey" nests in conifers such as red spruce also are common (Weigl et al. 1999, Weigl et al. 2002, Menzel et al. 2004), particularly in the warmer months (Urban 1988). Both Hackett and Pagels (2003) and Menzel et al. (2004) reported that northern flying squirrels routinely utilize den trees near trails, old logging roads or railroad grades; occupied den trees and snags tended to be larger and taller than surrounding stems. Northern flying squirrels will readily occupy artificial nest boxes (Reynolds et al. 1999). Both natural and artificial dens are lined with bark, moss or grass, particularly shredded yellow birch bark. Unlike the southern flying squirrel, large aggregations of individuals sharing a single nest typically does not occur (Fies and Pagels 1991).

REPRODUCTION

Little is known about the reproductive habits of the northern flying squirrel in the South and most information is gleaned from trap or nest box capture data. In both North Carolina and Virginia, testicular males have been reported from December into the spring months. Single litters of 2–4 are usually born March through June, but offspring can be born as late as September (Weigl et al. 1999). Gestation is approximately 37 days and weaning occurs at about 2 months, though young may remain with the female for some time. In part because year-to-year recapture rates are low in regional monitoring programs (Reynolds et al. 1999), actual longevity in the central and southern Appalachians is unknown. Elsewhere, it is though to be < 4 years (Wells-Gosling and Heaney 1984).

FOOD HABITS

Throughout its range, northern flying squirrels feed on a diversity of conifer and hardwood seeds and cones, buds, fruits, insects, bird eggs and nestlings and even tree sap (Hall 1981, Carey et al. 1999, Weigl et al. 1999); however, the sporocarps of mycorrhizal fungi such as the genera *Elaphomyces*, and lichens are among the most important foods in the central and southern Appalachians (Weigl 1968, Weigl 1978, Wells-Gosling and Heaney 1984, Weigl et al. 1999, Mitchell et al. 2001). In North Carolina, hypogeal fungal presence is closely correlated with the presence of red spruce in the overstory (Loeb et al. 2000). The year-round abundance of fungi and lichens may provide a steady food supply and reduce competition with other sciurids that depend upon hard mast such as northern red oak (Quercus rubra) acorns. Mitchell et al. (2001) found significant use of American beechnuts by G. s. fuscus in West Virginia during autumn. Northern flying squirrels spend large amounts of time on the ground indicative of foraging efforts for fungi during evening activity periods (Urban 1988).

ASSOCIATED SPECIES

The northern flying squirrel is frequently found in association with typical montane boreal small mammals in the central and southern Appalachians including the northern short-tailed shrew (*Blarina brevicauda*), smoky shrew (*Sorex fumeus*), masked shrew (*S. cinereus*), deer mouse (*Peromyscus maniculatus*), Allegheny woodrat (*Neotoma magister*), and red-backed vole (*Clethrionomys gapperi*). Other sciurids with which northern flying squirrel may be syntopic include the southern flying squirrel and red squirrel (*Tamiasciurus hudsonicus*).

VULNERABILITY AND THREATS

Despite numerous new collection records, the realization of larger populations than once believed, and as a potential candidate for down-listing, the northern

flying squirrel remains one of the rarest mammals in the southern United States. In part, the species rarity is an artifact of the natural contraction of northern forest communities in the Appalachians following the end of the last Ice Age to what are now relictual habitat islands (Browne et al. 1999, Arbogast et al. 2005). Regionally, many red spruce forest stands were destructively logged and altered by post-harvest fire at the turn of the 20th century, reducing this forest type's extent by up to 90% (Korstian 1937, Schuler et al. 2002), leading many to characterize this forest type as among the most endangered in North America (White et al. 1993). This habitat change and fragmentation undoubtedly has had serious negative impacts on northern flying squirrels. There is evidence of reduced genetic heterozygosity in G. s. coloratus from natural and human-induced isolation that has exposed sub-populations to a high risk of inbreeding depression (Browne et al. 1999). Current efforts are underway to fully assess the conservation genetic status of both subspecies in the region (J. Sparks, Virginia Commonwealth University, personal communication). Increased abundance of northern red oak and American beech following modification of these habitats probably has provided an infusion of cacheable, high-energy foods that allow southern flying squirrels to tolerate the climatically difficult and energetically expensive conditions at high elevations in the central and southern Appalachians (Weigl et al. 1999, Odom et al. 2001). In turn, range expansions of the competitively aggressive southern flying squirrel may have displaced northern flying squirrels locally at some sites (Weigl 1978, Weigl 1987, Fies and Pagels 1991). Moreover, many southern flying squirrels chronically harbor a parasitic nematode, Strongyloides robustus, which is believed to be seriously debilitating when passed to northern flying squirrels in these interspecific contact zones (Weigl 1978, Weigl 1987, Pagels et al. 1990). Weigl et al. (1999) noted a decline in northern flying squirrel numbers and reproductive activity following a steady increase in S. robustus infection and a series of mild winters in the Roan Mountain area on the North Carolina-Tennessee border. Fortunately, most identified northern flying squirrel habitat in the central and southern Appalachians occurs on public lands that are protected from further intentional anthropogenic perturbation. There are some indications that the ecotone between red spruce and northern hardwood forests is either stabilizing or decreasing in elevation to more approximate its former extent (Busing et al. 1988, Schuler et al. 2002). Still, infestations and spread of the balsam woolly aphid (Adelges piceae) and hemlock adelgid (A. tsugae) that threaten Fraser fir and eastern hemlock, as well as high atmospheric acid deposition, and continued global climate change continue to threaten the remaining structure, extent and integrity

of northern flying squirrel habitat patches in the region (Nicholas et al. 1992, Barker et al. 2002, Menzel 2006*a*). On private land, surface mining, forest management, second-home and recreational development, and wind-energy development are potential threats to northern flying squirrel populations and their habitats (Weigl et al. 1999, Schuler et al. 2002). Currently, *G. s. fuscus* is the focal species of several Habitat Conservation Plans on private lands in the Allegheny Mountains (S. Jones, U. S. Fish and Wildlife Service, personal communication).

MANAGEMENT SUGGESTIONS

Conditions that continue to promote or enhance mature forest conditions with an abundance of large trees, numerous snags, and mesic, micro-habitats in montane boreal and northern hardwood forests in the central and southern Appalachians should be maintained. Activities that convert or fragment occupied forest areas should be avoided, as should the use of prescribed fire in northern flying squirrel habitats. Techniques to effectively monitor population and demographic trends beyond current nest box programs also need to be developed (Odom et al. 2001). Odom and McNab (2000) showed that digital terrain modeling could successfully predict current and potential montane boreal and northern hardwood habitats in the southern Blue Ridge to guide habitat protection efforts and prioritize where habitat restoration activities should occur. Opportunities for ecological restoration of degraded former habitats through silvicultural manipulation of hardwoods to encourage red spruce release and eventual overstory/ stand dominance to expand or link occupied patches have been proposed but remain untested (Schuler et al. 2002).

REFERENCES

- Arbogast, B. S., R. A. Browne, P. D. Weigl and G. J. Kenazy, 2005. Conservation genetics of endangered flying squirrels (*G. lavcamys*) from the Appalachian mountains of eastern North America. Animal Conservation 8:123–133.
- Barker, M., H. Van Miegroet, N. S. Nicholas, and I. F. Creed. 2002. Variation in overstory nitrogen uptake in a small, high-elevation southern Appalachian spruce-fir watershed. Canadian Journal of Forest Research 32:1741–1752.
- Browne, R., P. D. Weigl, J. Kelly and M. Steele. 1999.
 Mountaintops as islands: I. Genetic variation among southern Appalachian populations of the endangered northern flying squirrel, *Glaucomys sabrinus* (Mammalia: Sciuridae). Pages 205–214 *in* R. Eckerlin, editor.
 Proceedings of the Appalachian Biogeography Symposium. Virginia Museum of Natural History Special Publication No. 7. Martinsburg, Virginia, USA.

Busing, R. T., E. E. Clebsch, C. C. Edgar, and E. F. Pauley. 1988. Two decades of change in a Great Smoky Mountains spruce-fir forest. Bulletin of the Torrey Botanical Club 115:25–31.

Carey, A. B., J. Kershner, B. Biswell, and L. Dominguez de Toledo. 1999. Ecological scale and forest development: Squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildlife Monograph 142:1–71.

Fies, M. L., and J. F. Pagels. 1991. Northern flying squirrel *Glaucomys sabrinus fuscus* Miller. Pages 538–584 *in*K. Terwilliger, editor. Virginia's endangered species. McDonald and Woodward, Blacksburg, Virginia, USA.

Ford, W. M., S. L. Stephenson, J. M. Menzel, D. R. Black and J. W. Edwards. 2004. Habitat characteristics of the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the Central Appalachian Mountains. American Midland Naturalist 152:430-438.

Hackett, H. M. and J. F. Pagels. 2003. Nest site characteristics of the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*) in southwest Virginia. American Midland Naturalist 150:321-331.

Hall, E. R. 1981. The mammals of North America. Volume 2. John Wiley and Sons, New York, New York, USA.

Korstian, C. F. 1937. Perpetuation of spruce on cut-over and burned lands in the higher Southern Appalachian Mountains. Ecological Monographs 7:125–167.

Linzey, D. W. 1983. Status and distribution of the northern water shrew (*Sorex palustris*) and two subspecies of northern flying squirrel (*Glaucomys sabrinus coloratus* and *Glaucomys sabrinus fuscus*). Final report under U. S. Fish and Wildlife Service Contract No. 14-16-005-79-068.

Linzey, D. W. 1995. Mammals of Great Smoky Mountains National Park – 1995 Update. Journal of the Elisha Mitchell Scientific Society 111:1–81.

Loeb, S. C., Tainter, F. H., and E. Cázares. 2000. Habitat associations of hypogeous fungi in the southern Appalachians: Implications for the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*). American Midland Naturalist 144:286–296.

Menzel, J. M., W. M. Ford, J. W. Edwards and M. A. Menzel. 2004. Nest tree use by the endangered Virginia northern flying squirrel in the Central Appalachian Mountains. American Midland Naturalist 151:355-368.

Menzel, J. M., W. M. Ford, J. W. Edwards and L. J. Ceperley. 2006*a*. A habitat model for the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the central Appalachian Mountains. USDA Forest Service Research Paper-NE-729.

Menzel, J. M., W. M. Ford, J. W. Edwards and T. M. Terry. 2006b. 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.

Merritt, J. F. 1987. Guide to the mammals of Pennsylvania. University of Pittsburgh, Pennsylvania, USA. Miller, G. S., Jr. 1936. A new flying squirrel from West Virginia. Proceedings of the Biological Society of Washington 49:143–144.

Mitchell, D. 2001. Spring and fall diet of the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). American Midland Naturalist 146:439–443.

NatureServe. 2007. An online encyclopedia of life [Database]. Version 6.1. Association for Biodiversity Information. http://www.natureserve.org/.

Nicholas, N. S., S. M. Zedaker, C. Edgar, and F. T. Bonner. 1992. Seedling recruitment and stand regeneration in spruce-fir forests of the Great Smoky Mountains. Bulletin of the Torrey Botanical Club 119:289–299.

Odom, R. H. and W. H. McNab. 2000. Using digital terrain modeling to predict ecological types in the Balsam Mountains of western North Carolina. USDA Forest Service Research Note SRS-8.

Odom, R. H., W. M. Ford, J. W. Edwards, C. W. Stihler, and J. M. Menzel. 2001. Developing a habitat model for the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the Allegheny Mountains of West Virginia. Biological Conservation 99:245–252.

Pagels, J. F., R. P. Eckerlin, J. R. Baker, and M. L. Fies. 1990. New records of the distribution of the intestinal parasites of the endangered northern flying squirrel, *Glaucomys sabrinus* (Mammalia: Sciuridae), in Virginia. Brimleyana 16:73–78.

Payne, J. L., D. R. Young, and J. F. Pagels. 1989. Plant community characteristics associated with the endangered northern flying squirrel, *Glaucomys sabrinus*, in the southern Appalachians. American Midland Naturalist 121:285–292.

Reynolds, R. J., J. F. Pagels and M. L. Fies. 1999. Demography of northern flying squirrels in Virginia. Proceedings of the Annual Conference of Southeast Association of Fish and Wildlife Agencies 53:340–349.

Schuler, T. M., W. M. Ford, and R. J. Collins. 2002. Successional dynamics and restoration implications of a montane coniferous forest in the central Appalachians, USA. Natural Areas Journal 22:88–98.

Sparks, J. L. 2005. Genetic variability, pathogen susceptibility, subspecies identity, and conservation of the endangered northern flying squirrel (*Glaucamys sabrinus*) in Virginia. Thesis, Virginia Commonwealth University, Richmond, Virginia, USA.

Stihler, C. W., K. B. Knight, and V. L. Urban. 1987. The northern flying squirrel in West Virginia. Pages 176–183 *in* R. A. Odum, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the Third Southeastern Nongame and Endangered Species Conference. Georgia Department of Natural Resources, Atlanta, Georgia, USA.

Stihler, C. W., J. L. Wallace, E. D. Michael, and H. Pawelczyk. 1995. Range of (*Glaucomys sabrinus fuscus*), a federally endangered subspecies of the northern flying squirrel in West Virginia. Proceedings of the West Virginia Academy of Science 67:13–20.

- U. S. Department of the Interior, Fish and Wildlife Service. 2007. Southeast Region 4. http://www.endangered.fws.gov/wildlife/html.
- U. S. Department of the Interior, Fish and Wildlife Service. 1993. Endangered and threatened wildlife and plants. U. S. Government Printing Office, Washington, D. C., USA.
- Urban, V. 1988. Home range, habitat utilization, and activity of the endangered northern flying squirrel. Thesis, West Virginia University, Morgantown, West Virginia, USA.
- Weigl, P.D. 1968. The distribution of the flying squirrels *Glaucomys volans* and *G. sabrinus*: An evaluation of the competitive exclusion idea. Dissertation, Duke University, Durham, North Carolina, USA.
- Weigl, P. D. 1978. Resource overlap, interspecific interactions, and the distribution of flying squirrels, *Glaucomys volans* and *G. sabrinus*. American Midland Naturalist 100:83–96.
- Weigl, P. D. 1987. Glaucomys sabrinus coloratus (Handley) Pages 12–15 in M. K. Clark, editor. Endangered, threatened and rare fauna of North Carolina. Part 1. A reevaluation of the mammals. Occasional Papers of the North Carolina Biological Survey, Raleigh, North Carolina, USA.

- Weigl, P. D., and D. W. Osgood. 1974. Study of the northern flying squirrel, *Glaucomys sabrinus*, by temperature telemetry. American Midland Naturalist 92:482–486.
- Weigl, P. D., T. W. Knowles, and A. C. Boynton. 1999. 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 Special Publication, Raleigh, North Carolina, USA.
- Weigl, P. D., R. S. Hughes, and D. C. Battle. 2002. Study of northern flying squirrel populations along the Cherohala Skyway: Questions of fragmentation and ecology in the southernmost part of the range. Final Report to the U. S. Fish and Wildlife Service, Region 4.
- Wells-Gosling, N. and L. R. Heaney. 1984. Glaucomys sabrinus. Mammalian Species 229:1–4.
- Whitaker, J. O., Jr., and W. J. Hamilton, Jr. 1998. Mammals of the Eastern United States. Cornell University, Ithaca, New York, USA.
- White, P. S., E. Buckner, J. D. Pattillo, and C. V. Cogbill.
 1993. High-elevation forests: Spruce-fir forests, northern hardwood forests, and associated communities. Pages 305–337 *in* W. H. Martin, S. G. Boyce, and A. C. Echternacht, editors. Biodiversity of the southeastern United States: Upland terrestrial communities. John Wiley and Sons, New York, New York, USA.