

Appalachian northern flying squirrels and high elevation spruce-fir ecosystems: An annotated bibliography

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Carolina Northern Flying Squirrel at Whitetop Mountain, VA (Photo Credit: C.A. Diggins)

North American boreal forest communities exist at the southernmost extent of their range in the Appalachian Mountains of the eastern United States. On high-elevation peaks and ridges in the central and southern Appalachian Mountains, this forest type represents a unique assemblage of boreal (northern) and austral (southern) latitude species following the end of the Pleistocene glaciation. Although south of the actual glaciated area, as the glaciers retreated and the climate warmed, boreal forests retreated northward and to cooler, high-elevation sites in the Appalachians. In the southern Appalachians, these boreal forest communities are dominated by red spruce (*Picea rubens*)-Fraser fir

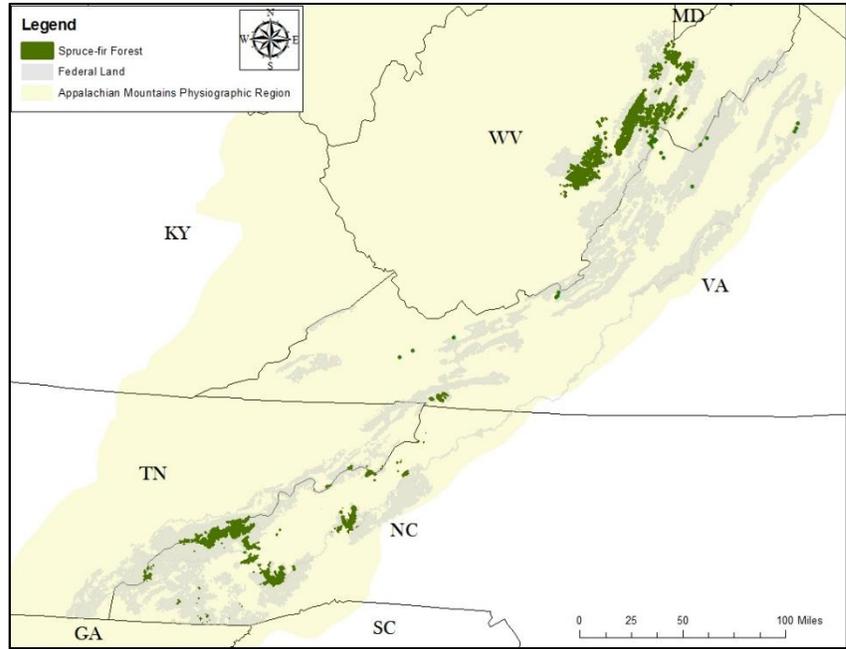


Figure 1. Distribution of red spruce-fir forests in the central and southern Appalachian Mountains. Most Virginia sites are represented by dots, indicating the presence of a red spruce stand, not indicative of the limited area.

(*Abies fraseri*) in southwestern Virginia, western North Carolina, and eastern Tennessee occurring above elevations of 4500 feet (Figure 1). In the central Appalachians, red spruce forests along with some small stands of balsam fir (*A. balsamea*) occur in eastern West Virginia and northwestern Virginia above elevations of 3000 feet (Figure 1). Red spruce- Fraser fir forests in the southern Appalachians are isolated from red spruce forests in the central Appalachians, while both forest types are isolated from the contiguous red spruce-balsam fir forests in the northeastern United States and Canada. In the central Appalachians, due to the broad topography of the Allegheny Mountains, this forest type is more contiguous locally than in the southern Appalachians. The more dramatic topography and lower latitude in the southern Appalachians has fragmented this forest type into highly disjunct “sky islands”. Railroad expansion followed by exploitative timber harvesting and widespread burning in the late 1800s – early 1900s reduced the extent and connectivity of these boreal forests in the central and southern Appalachians. In the southern Appalachians, public land acquisition during the early 1920s by the U.S. Forest Service and in the 1920s-1940s by the National Park Service, increased the protected area of red spruce-Fraser. Because the majority of spruce-fir forests in the central and southern Appalachians occur on federal lands, much of the red spruce-fir forest type has been protected from harvesting for many decades. However, beginning in the 1960’s stressors such as acid atmospheric deposition and the presence of the exotic balsam wooly adelgid (*Adelges piceae*) threatened the health and viability of red spruce and Fraser fir, respectively. Although impacts from deposition have lessened with improvements in air quality and adelgid infestations are less apparent as the current Fraser fir cohort is still too young, climate change is believed to be the ultimate threat to this forest type. Most climate change projection models predict the widespread extirpation of most extant red spruce-Fraser fir over the next century.

The subsequent discovery of another northern latitude species, the northern flying squirrel (*Glaucomys sabrinus*), was made in West Virginia in 1936 by G.S. Miller and in North Carolina in 1953 by C.O. Handley, extending the known range of this species southwest by approximately 700 miles. Two distinct subspecies, Virginia northern flying squirrel (VNFS; *G. s. fuscus*) and Carolina northern flying squirrel (CNFS; *G. s. sabrinus*) occur in the central and southern Appalachians, respectively (Figure 2). Both subspecies largely are associated with high-elevation red spruce or red spruce-Fraser fir forests. CNFS and VNFS were listed by the U.S. Fish and Wildlife Service (USFWS) as endangered in 1985 due to 1) lack of ecological and distributional knowledge in the Appalachians, 2) the reduced extent and health of their associated montane boreal habitat, and 3) den site competition with and parasite transmission by syntopic southern flying squirrels (*G. volans*).

Monitoring of CNFS and VNFS

Initial efforts to understand the distribution of northern flying squirrels in the southern and central Appalachians began in the late 1970s by Donald Linzey. He conducted a 2-year study using nest box surveys at sites in Maryland, North Carolina, Tennessee, Virginia, and West Virginia to confirm occurrence of northern flying squirrels. Linzey’s survey sites included previously known sites in North Carolina and West Virginia.

State nest box monitoring programs began in 1985 in West Virginia and Virginia after both subspecies became listed. Seminal work on CNFS throughout western North Carolina and some sites in Tennessee was conducted by Peter Weigl in the late 1980s – early 1990s. Weigl’s work increased knowledge of distribution of this subspecies in North Carolina and expanded on aspects of this subspecies biology and life history traits. His work became the basis for the North Carolina Wildlife Resources Commission (NCWRC) nest box monitoring program that began in 1996.

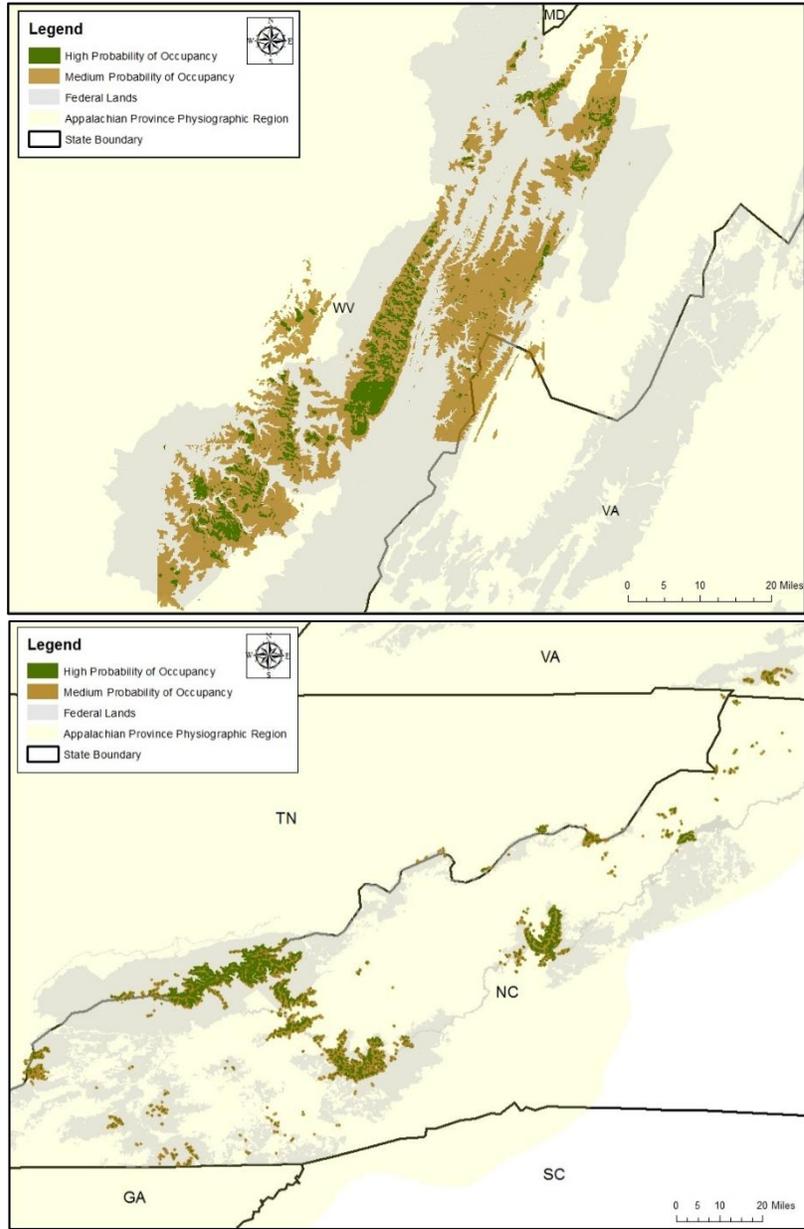


Figure 2. Probability of northern flying squirrel habitat occupancy in the central (above) and southern Appalachians (below).

VNFS was initially delisted by the USFWS in 2006 and subsequently re-listed in 2008 following litigation in opposition of delisting. In 2013, VNFS was officially delisted a second time from the List of Threatened and Endangered Wildlife and Plants by the USFWS. West Virginia Department of Natural Resources (WVDNR) is continuing their long-term nest box monitoring program as part of De-listing Monitoring under the Endangered Species Act (ESA). The NCWRC is continuing long-term nest box monitoring as part of ESA Recovery Monitoring, but efforts to monitor northern flying squirrels using nest boxes was discontinued by Virginia Department of Game and Inland Fisheries (VDGIF) in 1996 after extremely low capture rates. Subsequent nest box monitoring of northern flying squirrels in Virginia was conducted by U.S. Forest Service, George Washington-Jefferson National Forest personal at the Mt. Rogers National Recreation Area (MRNRA) on Whitetop Mountain and Mt. Rogers until 2006. In Tennessee, the Cherokee National Forest (CNF) Conducted nest box surveys in the Unaka Mountains in the 1990s. Nest boxes on the Tennessee side of Roan Mountain were established in 2009 and are continue to be checked by CNF personnel.

Table 1. Categories for Northern Flying Squirrel Papers. *Papers directly related to the central and southern Appalachian Mountains.

	Number Corresponding to Northern Flying Squirrel Paper
Life History/Behavior	22, 29, 30, 32, 33*, 43*, 49*, 87*, 95, 115, 116, 117, 118, 119, 120, 133*, 146*, 152, 153, 155, 157*, 162*, 163, 164, 166
Population Dynamics/Demography	12, 13, 14, 15, 19, 20, 45, 51, 55, 67, 74, 89, 95, 106, 107, 109*, 113, 121, 123, 124, 126, 128, 129, 155, 156, 168
Genetics	1*, 2*, 7, 9*, 40, 41, 61, 62, 130*, 164
Food habits	4, 8*, 18, 19, 21, 24, 26, 31, 33*, 39, 47, 66, 71, 74, 76, 77, 78, 79, 86*, 88, 100, 101, 102, 103, 105, 143, 154, 157, 164, 169
Competitors (Ecology/Habitat Use)	6*, 24, 27, 38, 40, 41, 42, 44, 50*, 51, 52, 53, 62, 65, 94, 95, 105, 106, 107, 108, 110*, 124, 131, 132, 133*, 134, 135, 136, 137, 139, 140, 141, 142, 153, 154, 159*, 162*
Parasites/Disease	27, 64, 91*, 97, 130*, 161*, 162*, 165
Distribution/Occupancy	10*, 33*, 48*, 49*, 63*, 69*, 72*, 73*, 81*, 85*, 90*, 91*, 98*, 133*, 134*, 144, 145, 159*, 162*, 164
Habitat Characteristics/Use	5, 12, 19, 20, 23, 28, 33*, 34*, 35*, 36*, 37*, 45, 46*, 52, 53, 56, 57, 58, 59*, 67, 73*, 80*, 81*, 82*, 83, 84, 89, 90*, 92*, 93, 94, 95, 98*, 99*, 104, 107, 108, 112, 113, 123, 125, 126, 127, 129, 133*, 134*, 138*, 144, 146*, 157*, 159*, 161*, 162*, 164, 166, 168
Survey Techniques/Monitoring	3, 16, 17, 37*, 43*, 68, 70, 75, 109*, 111, 114, 133*, 138*, 149*, 153, 167
Habitat Fragmentation/Loss	60*, 104, 120, 122, 161*
Forest Management	11, 13, 14, 15, 30, 45, 51, 53, 54, 55, 67, 74, 78, 84, 104, 106, 127
Conservation/Status	25, 33*, 60*, 72*, 130*, 147*, 148*, 149*, 150*, 151*, 160*

Annotated Bibliography

Our goal was to create an annotated bibliography of published research and observations pertaining to the distribution, ecology, and biology of northern flying squirrels, their competitors (i.e., southern flying squirrels), and red spruce and red spruce-Fraser fir forests in the central and southern Appalachian Mountains, respectively. Herein, we have summarized pertinent research from peer-reviewed scientific journal articles, theses, dissertations, government research and technical reports, and conference proceedings. Research on northern flying squirrels extends throughout the range of this species in North America, but importance is placed on research that occurred in the central and southern Appalachians. Research on red spruce, Fraser fir, and balsam fir are taken from northern, central, and southern Appalachians, although emphasis is placed on studies from the latter two areas.

Papers are divided into two groups: Northern Flying Squirrel Papers and Appalachian Spruce-Fir Papers. Papers in each category are listed alphabetically and have a corresponding identification number. For both sections, the papers are organized into categories (i.e., life history, habitat associations) by their corresponding number (Table 1 and 2). Some papers are cross-listed in more than one category. Northern Flying Squirrel Papers are found from page 6 – 36 and Appalachian Spruce-Fir Papers are found from page 36 – 62.

Common names of species are used throughout the bibliography, although hypogeous fungi and squirrel parasites are described by their scientific names. Scientific names of flora, fauna, and insects are provided in Table 3.

Table 2. Categories for Appalachian Spruce-Fir Papers.

Number Corresponding to Appalachian Spruce-Fir Papers	
Forest Stand Characteristics (e.g., density, growth, structure)	1, 3, 4, 8, 15, 16, 17, 24, 27, 28, 30, 32, 37, 42, 46, 53, 54, 55, 62, 67, 69, 71, 72, 75, 79, 80, 81, 84, 87, 88, 89, 92, 93, 105, 106, 111, 112, 116, 118, 119, 120, 121, 123, 131, 132, 134, 136
Community Dynamics and Characteristics (e.g., floristics, succession)	3, 5, 11, 26, 28, 31, 32, 38, 39, 41, 65, 66, 73, 80, 85, 88, 93, 94, 95, 103, 104, 105, 109, 115, 116, 117, 124, 125, 126, 137
Forest Processes (e.g., nutrient cycling, cloud immersion, soil chemistry)	12, 14, 20, 22, 23, 25, 38, 49, 50, 52, 68, 69, 74, 78, 83, 84, 90, 95, 96, 104, 110, 112, 122, 127, 130, 133
Distribution	2, 11, 18, 19, 21, 35, 36, 40, 58, 59, 61, 63, 77, 86, 92, 104, 135
Pests/Disease/ /Pollution/Climate Change/Disturbance	4, 6, 7, 9, 10, 13, 14, 16, 18, 22, 23, 24, 25, 27, 28, 29, 30, 34, 35, 38, 43, 44, 45, 46, 47, 48, 51, 55, 56, 57, 60, 61, 63, 65, 67, 68, 70, 73, 74, 75, 76, 78, 85, 95, 96, 97, 113, 115, 116, 119, 121, 123, 132, 134, 138
Historical Range, Stand Dynamics, and Landuse	11, 21, 26, 31, 37, 39, 40, 56, 58, 61, 63, 72, 81, 82, 99, 100, 101, 102, 120, 133, 134
Forest Management	7, 15, 42, 62, 64, 72, 81, 82, 83, 105, 114, 129, 131
Conservation/Status	13, 18, 19, 64, 91, 92, 135

Table 3. Common names and scientific names for flora and fauna described in Northern Flying Squirrel Papers and Appalachian Spruce-Fir papers.

Common Name	Scientific Name
<i>Animals</i>	
Cotton mouse	<i>Peromyscus gossypinus</i>
Eastern chipmunk	<i>Tamias striatus</i>
Eastern grey squirrel	<i>Sciurus carolinensis</i>
Fox squirrel	<i>Sciurus niger</i>
Northern flying squirrel	<i>Glaucomys sabrinus</i>
Carolina northern flying squirrel	<i>G. s. coloratus</i>
Virginia northern flying squirrel	<i>G. s. fuscus</i>
Red squirrel	<i>Tamiasciurus hudsonicus</i>
Red-cockaded woodpecker	<i>Picoides borealis</i>
Rock vole	<i>Microtus chrotorrhinus</i>
Short-tail shrew	<i>Blarina brevicauda</i>
Southern flying squirrel	<i>Glaucomys volans</i>
Southern red-backed vole	<i>Myodes gapperi</i>
White-footed mice	<i>Peromyscus leucopus</i>
Woodland jumping mouse	<i>Napaeozapus hudsonicus</i>
<i>Woody and Herbaceous Species</i>	
American beech	<i>Fagus Americana</i>
American chestnut	<i>Castanea denata</i>
Balsam fir	<i>Abies balsamea</i>
Black cherry	<i>Prunus serotina</i>
Blackberry spp.	<i>Rubus spp.</i>
Douglas-fir	<i>Pseudotsuga menziesii</i>
Eastern hemlock	<i>Tsuga canadensis</i>
Eastern white cedar	<i>Thuja occidentalis</i>
Fire cherry	<i>Prunus pennsylvanica</i>
Fraser fir	<i>Abies fraseri</i>
Great rhododendron	<i>Rhododendron maximum</i>
Mountain ash	<i>Sambucus canadensis</i>
Northern red oak	<i>Quercus rubra</i>
Norway spruce	<i>Picea abies</i>
Red maple	<i>Acer rubrum</i>
Red pine	<i>Pinus resinosa</i>
Red spruce	<i>Picea rubens</i>
Southern mountain cranberry	<i>Vaccinium erythrocarpum</i>
Yellow birch	<i>Betula alleghensis</i>
<i>Insects</i>	
Balsam woolly adelgid	<i>Adelges piceae</i>
Hemlock woolly adelgid	<i>Adelges tsugae</i>
Southern pine beetle	<i>Dendroctonus frontalis</i>

NORTHERN FLYING SQUIRREL PAPERS

1. **Arbogast, B.S. 2007. A brief history of the new world flying squirrels: Phylogeny, biogeography, and conservation genetics. *Journal of Mammalogy* 88(4): 840-849.** Summary of current understanding of evolutionary origin and biogeographic history of the North American flying squirrels. Discusses the phylogeographic structures of northern flying squirrels and southern flying squirrels, including the two Appalachian subspecies of northern flying squirrel.
2. **Arbogast, B.S., R.A. Browne, P.D. Weigl, and G.J. Kenagy. 2005. Conservation genetics of endangered flying squirrels (*Glaucomys*) from the Appalachian mountains of eastern North America. *Animal Conservation* 8: 123-133.** Assessment of the genetic status of northern flying squirrel populations restricted to the central and southern Appalachian Mountains. Results show both populations of Virginia and Carolina northern flying squirrels possess private alleles and have significantly lower levels of genetic variability compared to populations of northern flying squirrels in other regions of the country. These results support the evolutionary divergence of these two geographically isolated northern flying squirrel populations.
3. **Althoff, D.P., and P.S. Althoff. 2001. Monitoring southern flying squirrel populations with nest boxes. *Ohio Journal of Science* 101(2): 2-11.** Evaluation of a nest box program to monitor population changes of southern flying squirrels in southeastern Ohio. Found that nest boxes are a suitable to detect changes in squirrel productivity and habitat occupancy, but this method is not validated for monitoring population change.
4. **Anderson, J. 2003. The relationship between the production of hypogeous sporocarps and the density and diet of northern flying squirrels in western hemlock forests of coastal British Columbia. M.S. thesis. University of British Columbia, Vancouver, BC, Canada.** An intensive year-round study to determine the abundance of hypogeous truffle species and truffles preferentially consumed by northern flying squirrels. Diet of flying squirrels was determined by fecal samples. Despite intensive 2-year field sampling of truffles, flying squirrels consumed nine additional truffle taxa than was found in the field. Additionally, *Elaphomyces* spp. made up 93% of field samples, but were under-represented in fecal samples. Presence of plant material in the majority of the diet throughout the year suggests a somewhat generalist diet.
5. **Bakker, V.J., and K. Hastings. 2002. Den trees used by northern flying squirrels (*Glaucomys sabrinus*) in southeastern Alaska. *Canadian Journal of Zoology* 80: 1623-1633.** Assessment of den sites used by northern flying squirrels. Over 73% of dens were located in cavities. Flying squirrels may select for trees with indicators of cavity presence, such as snags and larger diameter trees with cavity features. Retention of snags and older trees with cavity features during forest management activities may be important to ensure denning habitat for flying squirrels.
6. **Bendel, P.R., and J.E. Gates. 1987. Home range and microhabitat at partitioning of the southern flying squirrel (*Glaucomys volans*). *Journal of Mammalogy* 68(2): 243-255.** Home range, denning, and microhabitat information on southern flying squirrels in

western Maryland. Has descriptions of species and size of denning trees in northern hardwood forests, including cavity entrance heights. Microhabitat within the core-activity centers had greater understory density versus denning microhabitat.

7. **Bidlack, A.L., and J.A. Cook. 2001. Reduced genetic variation in insular northern flying squirrels (*Glaucomys sabrinus*) along the North Pacific Coast. *Animal Conservation* 4: 283-290.** Investigation of genetic diversity of northern flying squirrels across southeast Alaska. Genetic analysis supports the designation of flying squirrels on the Alexander Archipelago from populations of flying squirrels on mainland southeast Alaska. Island flying squirrels exhibits significantly reduced genetic variation compared to mainland populations, possibly due to genetic isolation on islands. These findings are similar to disjunct Carolina northern flying squirrel populations in the southern Appalachians, which are isolated from contiguous northern flying squirrel populations in the north.
8. **Bird, C., and C. McCleneghan. 2005. Morphological and functional diversity of ectomycorrhizal fungi on Roan Mountain (NC/TN). *Southeastern Naturalist* 4: 121-132.** Comparison of ectomycorrhizal and hypogeous fungi in northern hardwood and Red spruce-Fraser fir forests on Roan Mountain. *Elaphomyces granulatus* and *E. muricatus* was found in red spruce-Fraser fir forests. The only hypogeous fungi found in northern hardwood forests were *E. muricatus*, although *E. muricatus* is most strongly associated with Fraser fir. Although a higher number of ectomycorrhizal morphotypes were found in spruce-fir forests versus the northern hardwood, some fungi symbiotic with red spruce-Fraser fir stands were also present in adjacent northern forests, suggesting there may be buffering between these two forest types.
9. **Browne, R. A., Weigl, P. D., Eagleson, E., Kelly, J., & Steele, M. 1999. Mountaintops as islands: genetic variation among southern Appalachian populations of the endangered northern flying squirrel, *Glaucomys sabrinus*. Pp 205-213 in *Proceedings of the Appalachian biogeography symposium*. Eds. Eckerlin, R. Special Publication Volume 7, Virginia Museum of Natural History, Martinsville, VA.** Compared allozymic analyses for northern flying squirrel populations in the Southern Appalachian Mountains versus the western United States. Found that Appalachian flying squirrels had decreased polymorphism, heterozygosity, and genetic fragmentation.
10. **Campbell, J.W., M.T. Mengak, S.B. Castleberry, and J.D. Mejia. 2010. Distribution and status of uncommon mammals in the Southern Appalachian Mountains. *Southeastern Naturalist* 9(2): 275-302.** Distribution of Carolina northern flying squirrels in the southern Appalachians according to museum records, publications and natural heritage data. Map shows the restricted range this species.
11. **Carey, A.B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. *Ecological Applications* 5(3): 648-661.** A study of the habitat factors that influence sciurid abundance in the Pacific Northwest forests. Indicate that large snags and patches of dense ericaceous shrubs are important for high densities of northern flying squirrels.
12. **Carey, A.B. 1996. Interactions of northwest forest canopies and arboreal mammals. *Northwest Science* 70: 72-78.** Identified which canopy habitat components are important to arboreal mammals. Indicate that northern flying squirrel populations are lower in younger

forest stands and may use drey nests more frequently and move longer distances to foraging sites within these habitat types.

13. **Carey, A.B. 2000. Ecology of northern flying squirrels: Implications for ecosystem management in Pacific Northwest, USA. Pp 45-61 in Biology of Gliding Mammals. Eds. Goldingay R.L., and J.S. Scheibe. Filander Verlag, Fürth, Germany.** Northern flying squirrel population densities are higher in unmanaged forests versus managed forests. Habitat components that may be important for sustaining flying squirrel populations include coarse woody debris, ericaceous shrubs, abundance of cavity trees, and heterogeneity in habitat vertical and horizontal habitat structure.
14. **Carey, A.B. 2000. Effects of new forest management strategies on squirrel populations. Ecological Applications 10(1): 248-257.** Northern flying squirrel populations are greater in old-growth and with passive management with legacy tree retention versus intensive timber management strategies. The potential of active, intentional ecosystem management may be beneficial for flying squirrels if management includes legacy retention, variable-density thinning, and management for decadence.
15. **Carey, A.B. 2001. Experimental manipulations of spatial heterogeneity in Douglas-fir forests: effects on squirrels. Forest Ecology and Management 152: 13-30.** Determined how populations of flying squirrels, chipmunks, and red squirrels are influenced by timber treatments in the Pacific Northwest. Northern flying squirrel populations decrease after a manipulation, but effects tend to be short term. Increasing biocomplexity of second-growth forest may be possible by using variable-density thinning, retention of legacies, and decadence management.
16. **Carey, A.B. 2002. Response of northern flying squirrels to supplementary dens. Wildlife Society Bulletin 30(2): 547-556.** Used nest boxes as supplementary dens for northern flying squirrels in Douglas-fir stands in Washington State. Flying squirrel use of nest boxes increased over a 5 year period. Nest boxes were primarily used by pregnant and nursing females, although proportions of adult females did not increase. Concluded that den sites are not a limiting factor for flying squirrels in Puget Trough.
17. **Carey, A.B., B.L. Biswell, and J.W. Witt. 1991. Methods for measuring populations of arboreal rodents. General Technical Report PNW-GTR-273. Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture, Portland, OR.** Discussed methods for trapping northern flying squirrels from experience gained in the Pacific Northwest. Trapping should be done in spring or fall. Two traps should be placed at each station: one on the ground and one up on a tree bole. Live-trapping and mark-recapture methods can help determine population densities.
18. **Carey, A.B., W. Colgan III, J.M. Trappe, and R. Molina. 2002. Effects of forest management on truffle abundance and squirrel diets. Northwest Science 76(2): 148-157.** Compared truffle abundance and squirrel diets in thinned and old-growth forests. Mean standing crop biomass of truffles did not vary between the two stand types, although the dominant truffle genus varied both field samples and fecal samples. Truffle diversity was higher in old-growth forests than thinned forests. High consumption of plant material was

found in northern flying squirrel diets in thinned forests versus old-growth. Flying squirrels also consumed a greater diversity of truffles than was found in intensive field sampling.

19. **Carey, A.B., J. Kershner, B. Biswell, and L.D. De Toledo. 1999. Ecological scale and forest development: Squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. *Wildlife Monographs* 142: 1-71.** Assessment of habitat factors correlated with squirrel used of forests in three different seral stages in the Pacific Northwest. Habitats used by northern flying squirrels had high decadence and complex canopy stratification. Variation of flying squirrels populations in stands with different seral stages was attributed to decadence, habitat breadth, and moisture-temperature gradient values. Individual flying squirrel home ranges tended to have overlapping foraging patches. Foraging patches were smaller in late-seral forests versus managed stands, where flying squirrels occurred at higher densities.
20. **Carey, A.B., T.M. Wilson, C.C. Maguire, and B.L. Biswell. 1997. Dens of northern flying squirrels in the Pacific Northwest. *Journal of Wildlife Management* 61(3): 684-699.** Described dens of northern flying squirrels in the Pacific Northwest, including tree species, status, and nest types. The majority of dens were located in live trees. Individuals used multiple dens and denning partners varied by den site. In sites with low squirrel populations (i.e., managed forests), flying squirrels used a wider variety of den types and traveled further between dens versus flying squirrels in higher populated old-growth forests. Den selection and den switching may be influenced by availability of denning sites, proximity to foraging locations, behavioral aspects (i.e., predator avoidance, parasite avoidance, energetic restrictions, social aggregation), and specific habitat elements.
21. **Cazares, E., D.L. Luoma, M.P. Amaranthus, C.L. Chamber, J.F. Lehmkuhl. 1999. Interaction of fungal sporocarps production with small mammal abundance and diet in Douglas-fir stands of the southern Cascade Range. *Northwest Science* 73: 64-76.** Linked fungal sporocarp production with mycophagy of small mammals. Truffles exhibit strong seasonal effects (i.e., a species of hypogeous fungi may fruit prolifically in the spring, but truffle production during other seasons may be substantially lower). Truffles were the primary food item in the diet for northern flying squirrels and they consumed *Gautieria* spp. more frequently than other species of truffles. Spatial and temporal patterns of truffles consumption by flying squirrels may be influenced by sporocarp availability, density of the small mammal community, and food item preferences.
22. **Cotton, C.L., and K.L. Parker. 2000. Winter activity patterns of northern flying squirrels in sub-boreal forests. *Canadian Journal of Zoology* 78: 1896-1901.** Determined winter activity of northern flying squirrels during foraging bouts during the winter in British Columbia. Activity bouts ranged from 0.52 to 13.7 hours, although 70% of all time periods foraging bouts were < 6 hours. No long activity bouts (> 1.9 hours) were observed during nighttime temperatures below -4°F. Some flying squirrels foraged during one bout in the middle of the night. Other flying squirrels exhibited bimodal activity patterns, with the first occurring within 2 hours after dark and the second occurring within 2 hours of dawn: the prevalence of these bouts were related to lower temperatures. The duration and timing of foraging bouts were adjusted according to sunset/sunrise and air temperature. Reduction of time active during winter and adjustment of timing of activity during low winter temperatures may serve as an energy conservation technique.

23. Cotton, C.L., and K.L. Parker. 2000. Winter habitat and nest trees used by northern flying squirrels in subboreal forests. *Journal of Mammalogy* 81(4): 1071-1086. Determined core nest areas and winter den trees for northern flying squirrels in British Columbia. Males exhibited larger average maximum distance moved between nest trees versus females. Overlap of core nest areas occurred during aggregation and when squirrels denned solo, suggesting an overlap of home ranges during the winter. Den tree selection was variable with tree size (i.e., dbh and height) and tree age, although they tend to select larger trees within younger stands. Denning sites mostly occurred in mesic and mesic-wet sites.
24. Currah, R.S., E.A. Smreciu, T. Lehesvirta, M. Niemi, and K.W. Larsen. 2000. Fungi in the winter diets of northern flying squirrels and red squirrels in the boreal mixedwood forest of northeastern Alberta. *Canadian Journal of Botany* 78: 1514-1520. Estimated winter diet of northern flying squirrels. Winter diets compared to summer diets confirm fungi are more important in summer diet. In boreal forests, flying squirrels are mycophagous on a year-round basis. Other items consumed in the winter diet include plant material and insects.
25. Deiulis, M. 2013. Time for judicial enforcement of ESA recovery plans?...“When [squirrels] fly”. *Boston College Environmental Affairs Law Review* 40(3): 29-44. Discusses the delisting of the Virginia northern flying squirrel in 2008 and subsequent legal action taken by non-profit groups. U.S. Fish and Wildlife Service (FWS) was sued by Friends of Blackwater for not fulfilling all criteria in the recovery plan to determine species recovery. FWS appealed the court decision because the recovery plan criteria was not considered legally binding.
26. Dubay, S.A., G.D. Hayward, and C.M. del Rio. 2008. Nutritional value and diet preference of arboreal lichens and hypogeous fungi for small mammals in the Rocky Mountains. *Canadian Journal of Zoology* 86: 851-862. Northern flying squirrels are known to consume lichens and hypogeous fungi, but nutritional value of these food items are unknown. Lichens are higher in calcium, but hypogeous fungi are higher in nitrogen, lipids, fibers, potassium, and phosphorus. Although flying squirrels consume lichen, they prefer hypogeous fungi in feeding trials. Lichens may be consumed in higher amounts in winter, but do not supplement enough nitrogen to the squirrels. Therefore the consumption of lichen and nitrogen year-round is necessary to maintain flying squirrels.
27. Espenshade, J.L., and R.L. Stewart. 2013. Prevalence of *Strongyloides robustus* in tree squirrels (*Sciuridae*) in south-central Pennsylvania and potential impacts for the endangered northern flying squirrel, *Glaucomys sabrinus*. *Journal of Student Research* 2(1): 43-47. Quantified prevalence of *Strongyloides robustus* in Eastern grey squirrel, red squirrel, and southern flying squirrel to determine the potential for other sympatric Sciurids to transmit *S. robustus* to northern flying squirrels. Infestation was found in all three species, highlighting the potential for other Sciurids to infect northern flying squirrels with *S. robustus*.
28. Evans, A. 2013. Modeling the distribution of northern hardwoods in Carolina northern flying squirrel (*Glaucomys sabrinus coloratus*) recovery areas of the southern Appalachians. M.S. thesis. Virginia Polytechnic Institute and State

University, Blacksburg, VA. Modeled northern hardwood forests in western North Carolina and southwestern Virginia by examining terrain data and patterns of northern hardwood occurrence using field data. Results indicate that latitude, elevation, aspect, and landform index are predictors of northern hardwoods on a regional, multi-state scale. The Elevation + Landform Index model correctly predicted northern hardwood presence at 78.2% of sites. This model created a predictive map of distribution of northern hardwood forests in Carolina northern flying squirrel recovery areas.

29. Ferron, J. 1983. Scent marking by cheek rubbing in the northern flying squirrel (*Glaucomys sabrinus*). *Canadian Journal of Zoology* 61: 2377-2380. Scent marking by cheek rubbing is used by northern flying squirrels to maintain the animal's familiarity with its home range. This behavior may also be used in intraspecific communication within grooming, denning, or feeding sites.
30. Flaherty, E.A., W.P. Smith, S. Pyare, and M. Ben-David. 2008. Experimental trials of the northern flying squirrel (*Glaucomys sabrinus*) traversing managed rainforest landscapes: perceptual range and fine-scale movements. *Canadian Journal of Zoology* 86: 1050-1058. Dispersal of northern flying squirrels may be related to the distance an individual can perceive a particular feature on the landscape. The perceptual range of flying squirrels is less in second-growth forests than clearcuts. While orienting around clearcuts, squirrels following the clearcut edge and paused more in their movements. Navigating through this habitat type may lead to higher energetic costs of dispersion.
31. Flaherty, E.A., M. Ben-David, and W.P. Smith. 2010. Diet and food availability: implications for foraging and dispersal of Prince of Wales northern flying squirrel across managed landscapes. *Journal of Mammalogy* 91(1): 79-91. Analyzed the diet of the northern flying squirrel using stable isotope and fecal analysis. Both types of analysis showed that flying squirrels ate conifer seeds and lichens. Fungi constituted the majority of the diet. Flying squirrels also consumed macroinvertebrates, but not berries. The major diet items were more prevalent in old-growth forests than second-growth forests or clearcuts. Therefore, there may be limited food available in managed habitats.
32. Flaherty, E.A., M. Ben-David, and W.P. Smith. 2010. Quadrupedal locomotor performance in two species of arboreal squirrels: Predicting energy savings of gliding. *Journal of Comparative Physiology B* 180: 1067-1078. Studied the energy expenditure of quadrupedal locomotion of northern flying squirrels and fox squirrels. Found that flying squirrels are poorly adapted to this type of locomotion versus fox squirrels.
33. Ford, W.M., and J.L. Rodrigue. 2007. Northern flying squirrel. Pp. 389-394 in *The Land Manager's Guide to Mammals of the South*. Eds. Trani, M.K., W.M. Ford, and B.R. Chapman. Nature Conservancy, Durham, NC. Summary of the ecology and conservation of the northern flying squirrel in the southeastern United States. Discusses taxonomy, distinguishing characteristics, conservation status, distribution, abundance status, primary habitats, reproduction, food habits, associated species, vulnerability and threats, and management suggestions.
34. 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(2): 430-438.** Assessment of occupied versus unoccupied habitat of Virginia northern flying squirrels. Found that stands occupied by northern flying squirrels had significantly higher montane conifer importance values and lower presence of northern red oaks than unoccupied sites. This study supports the link between montane conifers and northern flying squirrels in the Appalachian Mountains.
35. **Ford, W.M., K.N. Mertz, J.M. Menzel, and K.K. Sturm. 2007. Winter home range and habitat use of the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). Research Paper NRS-4, Northern Research Station, Forest Service, United State Department of Agriculture, Newtown Square, PA.** Assessed home range size and habitat use of Virginia northern flying squirrels in West Virginia. Determined that winter home range sizes of males were larger than summer and fall home range sizes, while this was the opposite for females. Flying squirrels foraged in both red-spruce dominated forests and northern hardwood forests, but selected red-spruce dominated forests and open areas greater than expected based on availability. Male flying squirrels routinely crossed ski slopes and roads, although this was not observed in females.
36. **Ford, W.M., C.A. Kelly, J.L. Rodrigue, R.H. Odom, D. Newcomb, L.M. Gilley, and C.A. Diggins. 2014. Late winter and early spring home range and habitat use of the endangered Carolina northern flying squirrel in western North Carolina. Endangered Species Research 23: 73-82.** Conducted telemetry surveys on Carolina northern flying squirrels in Pisgah National Forest to assess habitat use. Found that squirrels used red spruce stands with canopies >65 ft more than expected based on availability at both the landscape and home range scales. Supports previous research that squirrels in the Appalachians use northern hardwood stands for denning and red spruce stands for foraging and denning.
37. **Ford, W.M., K.R. Moseley, C.W. Stihler, and J.W. Edwards. 2010. Area occupancy and detection probabilities of the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) using nest-box surveys. Pp. 39-47 in Proceedings from the conference on the ecology and management of high-elevation forests in the central and southern Appalachian Mountains. Eds. Rentch, J.S., and T.M. Schuler. General Technical Report NRS-P-64. Northern Research Station, Forest Service, U.S. Department of Agriculture, Newtown Square, PA.** Estimated occupancy and detection probabilities of Virginia northern flying squirrels in West Virginia based on long-term nest box monitoring data. Detection probability is constant using nest boxes in high-, medium-, and low-ranking quality habitats. Concluded that nest box monitoring would successfully determine post-delisting monitoring requirements for this subspecies.
38. **Fridell, R.A., and J.A. Litvaitis. 1991. Influence of resource distribution and abundance on home-range characteristics of southern flying squirrels. Canadian Journal of Zoology 69: 2589-2593.** Compared distribution and abundance of mast-producing trees and potential den sites with the size and composition of southern flying squirrel home ranges in New Hampshire. Large hickories and beeches were abundant in core use areas versus random sites. Male home ranges had higher densities of large oak trees, while female home ranges had higher densities of snags. Home range size was larger for males versus females and home range sizes were 1.5 – 2.0 times larger than home range estimates from southern portions of southern flying squirrel range.

39. Gabel, A., C. Ackerman, M. Gabel, E. Krueger, S. Weins, and L. Zierer. 2010. Diet and habitat of northern flying squirrels (*Glaucomys sabrinus*) in the Black Hills of South Dakota. *Western North American Naturalist* 70(1): 92-104. Assessed habitat and diet of the northern flying squirrel from fecal samples in South Dakota in mixed deciduous/coniferous and coniferous forests. Captures of squirrels were correlated with the volume of downed wood and number of snags present. Hypogeous fungi was a frequent component in the diet with *Rhizopogon* spp. the most frequent of the spores observed. Fungal spores of 5 other genus of hypogeous fungi were also detected.
40. Garroway, C.L., J. Bowman, T.J. Cascaden, G.L. Holloway, C.G. Mahan, J.R. Malcolm, M.A. Steele, G. Turner, and P.J. Wilson. 2010. Climate change induced hybridization in flying squirrels. *Global Change Biology* 16: 113-121. Determined potential of hybridization between southern flying squirrels and northern flying squirrels in Ontario and northwestern Pennsylvania. Southern flying squirrel recently exhibited a northern range expansion increasing the chance of sympatry with northern flying squirrels. Recent evidence of hybridization between the two species was documented.
41. Garroway, C.L., J. Bowman, G.L. Holloway, J.R. Malcolm, and P.J. Wilson. 2011. The genetic signature or rapid range expansion by flying squirrels in response to contemporary climate warming. *Global Change Biology* 17: 1760-1769. Investigated a recent range expansion of 125 miles by southern flying squirrels in Canada. Evidence of allele frequencies exhibiting a latitudinal gradient and richness of alleles decreasing along the line of expansion for southern flying squirrels occurred, although no genetic bottleneck were observed. Therefore, rapid range expansion can cause an abrupt reduction in genetic diversity driven by a serial founder effect, regardless of high gene flow during the range expansion.
42. Garroway, C.J., J. Bowman, and P.J. Wilson. 2013. Complex social structure of southern flying squirrels is related to spatial proximity but no kinship. *Behavioral Ecology and Sociobiology* 67: 113-122. Examined social structure of southern flying squirrels by testing the role of kinship and familiarity in predicting social structure by monitoring nest groups. Individuals nested with specific individuals more often than expect by chance and relationships were stable and persisted across seasons and years. Prior familiarity was related to the amount of time individuals spent time in winter aggregations, not kinship as previously believed.
43. Gilley, L.M. 2013. Discovery and characterization of high-frequency calls in North American flying squirrels (*Glaucomys sabrinus* and *G. volans*): Implications for ecology, behavior, and conservation. Ph.D. dissertation. Auburn University, Auburn, AL. Seminal work describing and characterizing the ultrasonic calls of northern and southern flying squirrels. Found that lab recorded calls of northern and southern flying squirrels are differentiable qualitatively and quantitatively, which is important if surveying for these species where they are sympatric. Conducted first field surveys using passive and active recording on both northern and southern flying squirrels in western North Carolina. Demonstrated the potential of this method as a surveying tool.

44. Gilmore, R.M., and J.E. Gates. 1985. Habitat use by the southern flying squirrel at a hemlock-northern hardwood ecotone. **Journal of Wildlife Management** 49(3): 703-710. Determined habitat use and home range of southern flying squirrels in western Maryland using mark-recapture data from nest boxes. Few snags occurred around used nest boxes versus unused nest boxes, while habitat around used nest boxes has a higher diversity of tree and shrub species.
45. Gomez, D.M., R.G. Anthony, J.P. Hayes. 2005. Influence of thinning of Douglas-fir forests on population parameters and diet of northern flying squirrels. **Journal of Wildlife Management** 69(4): 1670-1682. Investigated how thinning young Douglas-fir forests in Oregon influenced density, survival, body mass, movements, and diets of northern flying squirrels. Flying squirrel densities were positively related to biomass and frequency of fungal sporocarps, which was the major portion in the squirrels' diet. Flying squirrel densities in young, structurally simple forests were comparable to densities observed in late-successional forests. Their results indicate that commercial thinning does not have measurable short-term effects on flying squirrels.
46. 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(2): 321-331. Assessed nest site use of Carolina northern flying squirrels at Mt. Rogers National Recreation Area in Virginia. Nest site characteristics varied and flying squirrels used a diversity of nest types, including subterranean dens. In old forest stands, nest sites has greater downed wood, lower snag densities, lower live-tree density, and lower shrub cover than in second-growth forest stands.
47. Hall, D.S. 1991. Diet of the northern flying squirrel at Sagehen Creek, California. **Journal of Mammalogy** 72(3): 615-617. Analyzed fecal samples from northern flying squirrels to assess food habits of this species in the Sierra Nevada Mountains. Fungal spores were observed in all fecal samples and a total of 22 fungal genera occurred across all samples, although at different rates depending on the season. When snow covered the ground, lichens were consumed in higher frequencies.
48. Handley, C.O. 1953. A new flying squirrel from the southern Appalachian Mountains. **Proc. Biol. Soc. Washington** 66: 191-194. Describes the first records of northern flying squirrel in North Carolina and Tennessee and describes the new subspecies.
49. Handley, C.O. 1978. Mammals: Northern flying squirrel. Pp. 513-516 *in* Proceedings of the Symposium on Endangered and Threatened plants and animals of Virginia. Eds. Linzey, D.W. Virginia Polytechnic Institute and State University, Blacksburg, VA. Reviews the distribution in Virginia and life history of northern flying squirrels. States that this species is secretive and not often observed, but can sometimes be located by high-pitched, insect like chirps, potentially referencing other accounts that flying squirrels may produce ultrasonic calls. Also discusses the status of the northern flying squirrel in Virginia and hypothesizes it must be on the verge of extirpation.
50. Healy, W.M., and R.T. Brooks. 1988. Small mammal abundance in northern hardwood stands in West Virginia. **Journal of Wildlife Management** 52(3): 491-496. Described small mammal communities in northern hardwood forests in Randolph and

Tucker counties, West Virginia. Common captures included southern red-backed voles, white-footed mice, short-tailed shrew, woodland jumping mice, Eastern chipmunk, southern flying squirrel, and rock vole although capture rates varied among forest stand age.

51. **Holloway, G.L., and J.R. Martin. 2006. Sciurid habitat relationships in forests managed under selection and shelterwood silviculture in Ontario. *Journal of Wildlife Management* 70(6): 1735-1745.** Examined Sciurid densities in managed and unmanaged stands in Ontario. Northern flying squirrel densities were significantly lower in recently harvested shelterwoods versus old growth forests, whereas densities were correlated with density of spruce, hardwood trees, and snags in conifer dominated stands. Densities of flying squirrels were positively associated with increased mast tree densities at the landscape level.
52. **Holloway, G.L., and J.R. Malcolm. 2007. Nest-tree by northern and southern flying squirrels in central Ontario. *Journal of Mammalogy* 88(1): 226-233.** Studied denning of northern and southern flying squirrels in partially harvested forests in Ontario. Northern flying squirrels used snags, declining trees, and healthy trees in conifer forests, with the majority of nesting sites used on ≥ 3 occasions were snags. The majority of nesting sites used by southern flying squirrels were in declining trees, although snags were also used. Nesting sites were limited in sites in recently harvested sites due to fewer cavity trees and snags.
53. **Holloway, G.L., and J.R. Malcolm. 2007. Northern and southern flying squirrel use of space within home ranges in central Ontario. *Forest Ecology and Management* 242: 747-755.** Determined home range and habitat use of northern and southern flying squirrels in partially harvested forests in Ontario. Northern flying squirrel core areas seemed to be associated with foraging activity, while southern flying squirrel core areas were located near nest trees. Food resources in selectively harvested stands appeared to provide sufficient short-term food resources for southern flying squirrels, but northern flying squirrels were not found in partially logged stands where there was a reduction of snags and decadent trees.
54. **Holloway, G.L., and W.P. Smith. 2011. A meta-analysis of forest age and structure effects on northern flying squirrel densities. *Journal of Wildlife Management* 75(3): 668-674.** Clarified the impact of clearcut and partial logging effects on northern flying squirrels using a meta-analysis of studies from North America. Found that forestry practices negatively influence flying squirrel abundance, resulting in potential short- and long-term consequences. Snag densities may be related to decreased flying squirrel densities in managed stands.
55. **Holloway, G.L., W.P. Smith, C.B. Halpern, R.A. Gitzen, C.C. Maguire, and S.D. West. 2012. Influence of forest structure and experimental green-tree retention on northern flying squirrel (*Glaucomys sabrinus*) abundance. *Forest Ecology and Management* 285: 187-194.** Assessed responses of northern flying squirrels to retention harvest at varying levels and spatial patterns in Oregon and Washington. After harvest, the relative abundance of flying squirrels decreased. Still, squirrel densities were significantly higher in treatments with higher retention rates. Local structure (e.g., basal area) and landscape-scale variables influence squirrel abundance and may determine the threshold response of squirrels to varying levels of retention harvest. Study results concur with previous studies that suggest flying squirrels are sensitive to logging at multiple scales.

56. Hough, M.J., and C.D. Dieter. 2009. Home range and habitat use of northern flying squirrels in the Black Hills, South Dakota. *American Midland Naturalist* 162(1): 112-124. Described home range and habitat use in an isolated population of northern flying squirrel in the Black Hill National Forest. Home ranges of females were smaller than that of males. Flying squirrels used ponderosa pine proportionally higher relevant to availability and selected areas with larger trees and higher canopy cover within their home ranges.
57. Hough, M.J., and C.D. Dieter. 2009. Resource selection habitat model for northern flying squirrels in the Black Hills, South Dakota. *American Midland Naturalist* 162(2): 356-372. Created a resource selection habitat model for northern flying squirrels in Black Hills National Forest based on habitat variables at used habitat locations versus random locations. Northern flying squirrels used habitats with higher precipitation, close to streams, presence of aspen, northwest aspect, higher density of live trees and snags, and higher basal area of snags than random sites. The model produced a map indicating the probability of habitat use that could be applied to management with the National Forest.
58. Hough, M.J., and C.D. Dieter. 2009. Summer nest tree use by northern flying squirrels in the Black Hills, South Dakota. *American Midland Naturalist* 162(1): 98-111. Described denning ecology of northern flying squirrels in Black Hills National Forest. Flying squirrels denned in dreys and cavities in live trees, and snags in cavities. Distance between consecutive nest sites were located farther for males versus females. The majority of nests were in cavities. Based on availability, flying squirrels selected snags and larger trees higher than expected.
59. Hughes, R.S. 2006. Home ranges of the endangered Carolina northern flying squirrel in the Unicoi Mountains of North Carolina. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 60: 19-24. Estimated home ranges for Carolina northern flying squirrels in high-elevation Eastern hemlock-mixed hardwood and northern hardwood forests in the Unicoi Mountains in North Carolina. On average, winter home ranges were larger than summer home ranges. Found squirrels did not cross the Cherohala Skyway and that roadways may act as a barrier to this population. The study also provides preliminary insights to flying squirrel associations with atypical habitats.
60. Kelly, C.A., C.A. Diggins, and A.J. Lawrence. 2013. Crossing structures reconnect federally endangered flying squirrel populations divided for 20 years by road barrier. *Wildlife Society Bulletin* 37(2): 375-379. Evaluated the use of crossing-poles to reconnect Carolina northern flying squirrel populations fragmented by the Cherohala Skyway. Utilized camera traps and telemetry of relocated squirrels, and nest box recaptures to determine road crossings and use of crossing-poles. First example of structure-assisted road crossings in a North American gliding mammal.
61. Kiesow, A.M., L.E. Wallace, and H.B. Britten. 2011. Characterization and isolation of five microsatellite loci in northern flying squirrels, *Glaucomys sabrinus* (Sciuridae, Rodentia). *Western North American Naturalist* 71(4): 553-556. Developed microsatellite primers for northern flying squirrels in the Black Hills. These populations show low heterozygosity and a significant departure from the Hardy-Weinberg equilibrium.

62. Kiesow, A.M., E.M. Monroe, and H.B. Britten. 2012. Genetic structure of the arboreal squirrels (*Glaucomys sabrinus* and *Tamiasciurus hudsonicus*) in the North American Black Hills. *Canadian Journal of Zoology* 90: 1191-1200. Identified genetic structure of isolated populations of northern flying squirrels and red squirrels in three regions of the Black Hills, North Dakota. Used microsatellite loci to determine genetic variability, substructure, and gene flow. Similar to other isolated species, both species exhibited allelic diversity and observed heterozygosity. Squirrel movements within the Black Hills may be restricted by unsuitable habitat and topography, although both species experience within population gene flow to some extent.
63. Knowles, T.W., M.A. Steele, and P.D. Weigl. 1989. Mammals: *Glaucomys sabrinus*. Pp 113-114 in Survey of rare and endangered vertebrates of the Blue Ridge Parkway in North Carolina. National Park Service Report, Asheville, NC. Describes the general characteristics, distribution, habitat, and locations on or near the Blue Ridge Parkway. Previous locations reported from Roan Mountain, Mt. Mitchell, and Great Smoky Mountains. In 1987 and 1988, trapping efforts had captures of northern flying squirrels expanded known range with new sites at Waterrock Knob, Beartrap Gap, Devils Courthouse, Brush Fence Ridge, Pisgah Campground, and Grandfather Mountain.
64. Krichbaum, K., C.G. Mahan, M.A. Steele, G. Turner, and P.J. Hudson. 2010. The potential role of *Strongyloides robustus* on parasite-mediated competition between two species of flying squirrels (*Glaucomys*). *Journal of Wildlife Diseases* 46(1): 229-235. Assessed parasite communities of southern and northern flying squirrels in two populations: 1) in Pennsylvania where both species are sympatric and 2) in New York where southern flying squirrels are absent. *Strongyloides robustus* was present in Pennsylvania northern flying squirrels, but not in New York northern flying squirrels, supporting previous research of parasite-mediated competition between the two species.
65. Laves, K.S., and S.C. Loeb. 2006. Differential estimates of southern flying squirrel (*Glaucomys volans*) population structure based on capture method. *American Midland Naturalist* 155(1): 237-243. Compared two methods to determine southern flying squirrel effects on red-cockaded woodpecker reproductive success. Obtained captures of flying squirrels from trapping and woodpecker nest tree cavities. Found that flying squirrel capture rates were higher per cavity inspection versus trap night. The study suggests that utilizing one capture method may not truly represent population size or structure of southern flying squirrels.
66. Lehmkuhl, J.F., L.E. Gould, E. Cazares, and D.R. Hosford. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. *Forest Ecology and Management* 200: 49-65. Quantified the relationship between ectomycorrhizal fungi sporocarp diversity and diets of northern flying squirrels in dry interior montane forests in the Pacific Northwest. Truffle biomass, diversity, and richness varied between dry open ponderosa pine forests, mesic young mixed-conifer forests, and mesic mature mixed-conifer forests. Found truffle diversity varied between the fall and spring. Fall flying squirrel diets were composed of 23 genera of fungi and 22% plant material, with *Rhizopogon* the most abundant genus in the diet.

67. Lehmkuhl, J.F., K.D. Kistler, J.S. Begley, and J. Boulanger. 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. *Ecological Applications* 16(2): 584-600. Tested hypotheses about regional and local abundance patterns of northern flying squirrels by quantifying habitat characteristics and squirrel density, population trends, and demography in eastern Washington. Home range size and recruitment varied depending on habitat quality. High recruitment rates were strongly associated with truffle biomass and understory species richness, while survival was associated with understory species richness and lichen biomass and snow depth negatively influenced survival.
68. Lindenmayer, D.B., A. Welsh, C. Donnelly, M. Crane, D. Michael, C. Macgregor, L. McBurney, R. Montague-Drake, and P. Gibbons. 2009. Are nest boxes a viable alternative source of cavities for hollow-dependent animals?: Long-term monitoring of nest box occupancy, pest use and attrition. *Biological Conservation* 142: 33-42. Determined the effectiveness of nest boxes with a long-term experimental study in southeastern Australia. They quantified occupancy of nest boxes by arboreal marsupials, infestation by pest invertebrates, and nest box attrition. They found the majority of nest boxes were never used and nest boxes occupied at higher rates in younger versus older stands. Infestations of invertebrate insects and box collapse were highest in younger forests. Study results suggest that locations where nest boxes are established should be carefully selected.
69. Linzey, D.W. 1984. Distribution and status of the northern flying squirrel and the northern water shrew in the southern Appalachians. Pp. 193-200 in *The southern Appalachian spruce-fir ecosystem: Its biology and threats*. Eds. P.S. White. Research/Resources Management Report SER-71. Great Smoky Mountains National Park, National Park Service, U.S. Department of Interior, Gatlinburg, TN, USA. Describes current knowledge of the Carolina northern flying squirrel at time of publication. Only three localities of this species was known from Yancey Co., NC (4 specimens near Mt. Mitchell) and Sevier and Carter Co., TN (2 specimens from Great Smoky Mountains National Park and 13 specimens from Roan Mountain, respectively). Set up the first nest box survey for this species in Maryland, Virginia, West Virginia, North Carolina, and Tennessee. Did not capture any individuals in nest boxes within the Great Smoky Mountains National Park.
70. Loeb, S.C., G.L. Chapman, and T.R. Ridley. 1999. Sampling small mammals in southeastern forests: The importance of trapping in trees. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 53: 415-424. Assessed how trapping in trees influenced capture rates of arboreal mammals versus only using ground traps. Conducted study in Upper Coastal Plain of South Carolina. When arboreal traps are included in a trapping effort, southern flying squirrels was found to be co-dominant with cotton mice, whereas when only ground traps were considered cotton mice was dominant.
71. Loeb, S.C., F.H. Tainter, and E. Cazares. 2000. Habitat associations of hypogeous fungi in the southern Appalachians: Implications for the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*). *American Midland Naturalist* 144(2): 286-296. Microhabitat and macrohabitat of hypogeous fungal sporocarps (i.e., truffles) was

assessed in suitable habitat for northern flying squirrels in North Carolina. The most common species found was *Elaphomyces granulatus*. Red spruce was the most important tree associated with plots with truffles. Truffles are ephemeral and of a patchy distribution.

72. Mahan, C.G., M.A. Steele, M.J. Patrick, and G.L. Kirkland. 1999. **The status of the northern flying squirrel (*Glaucomys sabrinus*) in Pennsylvania.** *Journal of the Pennsylvania Academy of Science* 73(1): 15-21. Examined current and historical data to determine the status of the northern flying squirrel in Pennsylvania. Comparisons between historical and current data indicate that this species may be drastically declining in the state. Decline may be linked to loss and fragmentation of old-growth forests. Makes recommendations for future research and conservation of this species.
73. Mahan, C.G., J.A. Bishop, M.A. Steele, G. Turner, and W.L. Myers. 2010. **Habitat characteristics and revised gap landscape analysis for the northern flying squirrel (*Glaucomys sabrinus*), a state endangered species in Pennsylvania.** *American Midland Naturalist* 164(2): 283-295. Examined habitat at the local and landscape level to quantify habitat characteristics of the northern flying squirrel in Pennsylvania. Flying squirrels preferred stands with mature mix conifers adjacent to a permanent water source. No flying squirrels were captured in pure conifer stands. Redefined Pennsylvania Gap Analysis for flying squirrel habitat.
74. Manning, T., J.C. Hagar, and B.C. McComb. 2012. **Thinning of young Douglas-fir forests decreases density of northern flying squirrels in the Oregon Cascades.** *Forest Ecology and Management* 264: 115-124. Measured impact of commercial thinning on northern flying squirrels approximately 11-13 years after thinning young Douglas-fir forests. Thinning decreased flying squirrel densities, although densities were significantly lower in heavily thinned versus lightly thinned stands. Density was positively related to density of large snags and negatively related low understory shrub percent cover.
75. Maser, C., R. Anderson, and E.L. Ball. 1981. **Aggregation and sex segregation in northern flying squirrels in northeastern Oregon, an observation.** *Murrelet* 62(2): 54-55. Examined at northern flying squirrels aggregations in nest boxes. They found sexes were segregated 97% of the time, where nest boxes were favored by males.
76. Maser, C., and Z. Maser. 1988. **Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon.** *Great Basin Naturalist* 48(3): 358-369. Assessed mycophagy in squirrel species in Oregon. Found that northern flying squirrels is almost exclusively a fungivore and may link vital ecological processes within temperate coniferous forests.
77. Maser, C., Z. Maser, J.W. Witt, and G. Hunt. 1986. **The northern flying squirrel: A mycophagist in southwestern Oregon.** *Canadian Journal of Zoology* 64: 2086-2089. Collected fecal samples of northern flying squirrels in the Pacific Northwest. Identified hypogeous fungi from the genera Basidiomycetes, Ascomycetes, and Zygomycetes in fecal samples. Found that squirrel food habits were generally related to the seasonal availability of hypogeous fungi.

78. Maser, C., J.M. Trappe, and R.A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* 59(4): 799-809. Discussed the interrelationship between small mammals and mycorrhizal fungi, addressing assumptions about small mammals, forest management practices, and forest health.
79. Maser, Z., C. Maser, and J.M. Trappe. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. *Canadian Journal of Zoology* 63: 1084-1088. Analyzed digestive tracts of northern flying squirrels in Oregon. Fungi and lichens composed of 90% or more of the consumed items. Twenty genera of hypogeous fungi were identified and this fungal groups is considered a major food source to northern flying squirrels.
80. 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(2): 355-368. Compared denning sites of Virginia northern flying squirrels to randomly selected den trees in West Virginia. Squirrels used an average of 3.6 nest trees/month, frequently switching nesting sites. The majority (69%) of nests were in cavities, although drey nests were also used (31%). Results indicated that flying squirrels may not be as specialized in nest tree selection as previously reported.
81. Menzel, J.M., W.M. Ford, J.W. Edwards, and L.J. Ceperley. 2005. A habitat model for the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the central Appalachian Mountains. Research Paper NE-729. Northeastern Research Station, Forest Service, U.S. Department of Agriculture, Newtown Square, PA. Factors important from previous telemetry studies and distribution data from nest boxes was used to developed a habitat occupancy map for Virginia northern flying squirrels in the Allegheny Mountains in the central Appalachians. Habitat characteristics, such as elevation, aspect, and forest cover type were obtained from radio-collared squirrels. This habitat model may help facilitate ecosystem-based management for multiple sensitive species within high-elevation red spruce and red spruce-northern hardwood forests in West Virginia.
82. Menzel, J.M., W.M. Ford, J.W. Edwards, and T.M. Terry. 2006. Home range and habitat use of the vulnerable Virginia northern flying squirrel *Glaucomys sabrinus fuscus* in the central Appalachian Mountains, USA. *Oryx* 40(2): 204-210. Examined home range size and habitat use of Virginia northern flying squirrels in high-elevation forests in West Virginia. Male flying squirrels had larger home ranges than female. Flying squirrels used red/Norway spruce, mixed red spruce-northern hardwood, and open habitats higher than their availability on the landscape.
83. Meyer, M.D., D.A. Kelt, and M.P. North. 2005. Nest trees of northern flying squirrels in the Sierra Nevada. *Journal of Mammalogy* 86(2): 275-280. Assessed nest tree preferences of northern flying squirrels in the Sierra Nevada Mountains. Squirrels selected nest trees larger in diameter versus surrounding trees. Snags were utilized more often relative to their availability compared to live trees. The majority of nest tree sites were close to riparian habitat.
84. Meyer, M.D., D.S. Kelt, and M.P. North. 2007. Microhabitat associations of northern flying squirrels in burned and thinned forest stands of the Sierra Nevada. *American*

Midland Naturalist 157(1): 2002-211. Used trap stations in managed forests stands to determine microhabitat associations of northern flying squirrels. Probability of flying squirrels captures was positively associated with increased litter depth and canopy cover, and decreasing distance to creeks. Thicker litter depth may be associated with increased truffle abundance, canopy cover may provide protection from predators, and creeks may provide foraging and nest habitat.

- 85. Miller, G.S. 1936. A new flying squirrel from West Virginia. Proc. Biol. Soc. Washington 49: 143-144.** Describes first record of northern flying squirrel in West Virginia, extending the known range approximately 400 miles southwest.
- 86. Mitchell, D. 2001. Spring and fall diet of the endangered West Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). American Midland Naturalist 146(2): 439-443.** Determined diet of Virginia northern flying squirrels in West Virginia. Spring diet consisted of tree buds, lichens, and hypogeous fungi, whereas the fall diet consisted of hypogeous fungi, epigeous fungi, and beechnuts. Epigeous fungi belonged the families *Boletaceae*, *Strophariaceae*, and *Russulaceae*, while the majority of hypogeous fungi was from the genus *Elaphomyces*.
- 87. Murrant, M.N., J. Bowman, C. J. Garroway, B. Prinzen, H. Mayberry, and P.A. Faure. 2013. Ultrasonic vocalizations emitted by flying squirrels. PloS one 8(8): e73045.** Confirmed anecdotal reports of North American flying squirrels to produce ultrasonic sounds. Calls recorded suggest flying squirrels use ultrasonic calls for communication and may be an important aspect of their social biology that is still poorly understood.
- 88. North, M., J. Trappe, and J. Franklin. 1997. Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. Ecology 78(5): 1543-1554.** Sampled fruiting bodies epigeous and hypogeous fungi biomass and animal consumption. Determined that hypogeous fungi may be a year-round food source versus the ephemeral nature of epigeous fungi.
- 89. O'Connell, A.F., F.A. Servello, J. Higgins, and W. Halteman. 2001. Status and habitat relationships of northern flying squirrels on Mount Desert Island, Maine. Northeastern Naturalist 8: 127-136.** Captured northern flying squirrels in older conifer and conifer-hardwood stands outside a large area burned in 1947. Found higher seedling density at capture locations. Southern flying squirrel reported at study site during 20th century, but this species was not captured during surveys.
- 90. 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.** Used nest box captures of Virginia northern flying squirrels to build a habitat model in the Allegheny Mountains. Topographic conditions and proximity to conifer forests were evaluated to develop a logistic regression model to delineate potential habitat. Overall model performance was equivocal, but presence was related to the proximity of conifer forests.

91. Pagels, J.F., R.P. Eckerlin, J.R. Baker, and M.L. Fies. 1990. New records of the distribution and the intestinal parasites of the endangered northern flying squirrel, *Glaucomys sabrinus* (*Mammalia: Sciuridae*), in Virginia. *Brimleyana* 16: 73-78. Expanded the distributional knowledge of northern flying squirrels in Virginia, where the only previous specimen was trapped on Whitetop Mountain in 1959 by Charles Handley. Additional specimens were found in Grayson and Highland Counties, including a squirrel that was predated on by a mink. Specimens were examined for parasites and found to have *Strongyloides robustus*, the first record of this species parasitizing northern flying squirrels in Virginia.
92. Parrish, N.D.A. 2012. Habitat analysis of a disjunct population of the Carolina northern flying squirrel (*Glaucomys sabrinus coloratus*). M.S. thesis, Western Carolina University, Cullowhee, NC. Created a potential habitat model for Carolina northern flying squirrels in the Unicoi Mountains. Used vegetation surveys and molecular techniques to show how flying squirrels used their habitat. Found squirrels foraged on common fungi, utilized other habitat patches in the study area similar to known occupied patches. Flying squirrels may not persist in hardwood forests as Eastern hemlocks continue to decline from hemlock woolly adelgid.
93. Patterson, J.E.H. 2012. Nest site characteristics and nest tree use by northern flying squirrels (*Glaucomys sabrinus*) in southwestern Alberta, Canada. *Northwest Science* 86(2): 144-150. Examined nest tree and nest site use by northern flying squirrels. Found the majority of nest sites were in cavities in large snags and aspens. Flying squirrels selected nest sites with less surrounding canopy cover and in closer proximity to larger snags versus random sites.
94. Patterson, J.E.H., and J.R. Malcolm. 2010. Landscape structure and local habitat characteristics as correlates of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus* occurrence. *Journal of Mammalogy* 91(3): 642-653. Investigated occurrence of northern flying squirrel and red squirrel a fragmented forest-agricultural matrix in Ontario. Found flying squirrels occurrence was positively correlated with patch size, while red squirrels occurrence was positively correlated with conifer tree basal area. Although no fragment 'effect' was found for red squirrels, flying squirrels were not found in habitat patches < 72 acres and the ideal patch size for occupancy was 119 acres.
95. Patterson, J.E.H., and S.J. Patterson. 2010. Multiple annual litters in *Glaucomys sabrinus* (northern flying squirrel). *Northeastern Naturalist* 17(1): 167-169. Documented multiple litters during a single year to an individual northern flying squirrel in southern Ontario, Canada. The first litter was in May and the second in September, indicating that flying squirrel may have greater population growth potential than previously thought.
96. Patterson, J.E.H., S.J. Patterson, and J.R. Malcolm. 2007. Cavity nest materials of northern flying squirrels, *Glaucomys sabrinus*, and North American red squirrel, *Tamiasciurus hudsonicus*, in a secondary hardwood forest of southern Ontario. *Canadian Field-Naturalist* 121(3): 303-307. Inspected composition of nesting material used by northern flying squirrels and red squirrels. Majority of nest for both species were composed of shredded eastern white cedar bark. Mean depth of nesting material was 4.8 in

across all nesting sites with no significant difference between seasons or species. Use of shredded cedar bark may reduce parasite loads in the nest.

97. Pauli, J.N., S.A. Dubay, E.M. Anderson, and S.J. Taft. 2004. ***Strongyloides robustus* and the northern sympatric populations of northern (*Glaucomys sabrinus*) and southern (*G. volans*) flying squirrels.** *Journal of Wildlife Diseases* 40(3): 579-582. Determined presence of *Strongyloides robustus* in fecal samples of northern and southern flying squirrels in Wisconsin. Occurrence of *S. robustus* infection in northern flying squirrels in Wisconsin was drastically lower than its prevalence in populations to the south. Most northern documentation of *S. robustus*.
98. Pelton, M.R. 1984. **Mammals of the spruce-fir forest in Great Smoky Mountains National Park.** Pp. 187-192 *in* **The southern Appalachian spruce-fir ecosystem: Its biology and threats.** Eds. P.S. White. **Research/Resources Management Report SER-71. Great Smoky Mountains National Park, National Park Service, U.S. Department of Interior, Gatlinburg, TN, USA.** Summarizes mammal species associated with red spruce-Fraser forests in the Great Smoky Mountains. States that no single species is totally dependent on this forest type, but several species, including the northern flying squirrel, have ranges closely associated with the distribution of red spruce-Fraser fir forests in the southern Appalachians and maybe be negatively affected by loss of red spruce-Fraser fir habitat.
99. Pyane, 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(2): 285-292. Assessed overstory and understory vegetation and physical parameters at site occupied by Virginia and Carolina northern flying squirrels in the southern Appalachian Mountains. Red spruce was always present in the overstory. Southern sites had greater densities of Fraser fir and American beech, whereas northern sites had greater densities of red spruce and yellow birch. Sites were located on mesic north-facing slopes or in sheltered coves. Understory vegetation and densities were highly variable among sites, therefore is a poor indicator of flying squirrel presence.
100. Pyare, S., and W.S. Longland. 2001a. **Mechanisms of truffle detection by northern flying squirrels.** *Canadian Journal Zoology* 79: 1007-1015. Evaluated how northern flying squirrels locates truffles of hypogeous fungi by evaluating olfactory chemicals produced by truffles, presence of coarse wood debris, and foraging memory of the flying squirrel. Olfaction and presence of logs were important in successful foraging of truffles. The majority of sites surveyed for truffles fruited at the same location in subsequent years, making memorization of these foraging sites potentially important to flying squirrel foraging success.
101. Pyare, S., and W.S. Longland. 2001b. **Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old growth forests of the Sierra Nevada.** *Journal of Mammalogy* 82(3): 681-689. Investigated consumption patterns of hypogeous fungi by 6 small mammals, including northern flying squirrels. Found that flying squirrels dispersed the greatest diversity of hypogeous fungi species versus the other species studied. Spring and fall diets of flying squirrels varied in frequency of occurrence and number of genera consumed.

102. Pyare, S., and W.S. Longland. 2002. Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. **Canadian Journal of Forest Research** 32: 1016-1024. Determined relative abundance of truffles, preferred food items, and microhabitat structure on northern flying squirrels occurrence in old-growth forests in California. At trap stations, truffle 'digs' were more abundant near actual flying squirrels capture sites. Microhabitat variables obtained from trap stations had higher understory cover, although coarse woody debris did not determine flying squirrels occurrence.
103. Pyare, S., W.P. Smith, J.V. Nicholls, and J.A. Cook. 2002. Diets of northern flying squirrel, *Glaucomys sabrinus*, in Southeast Alaska. **Canadian Field-Naturalist** 116: 98-103. Examined the diet of northern flying squirrels during snow-free periods in Southeast Alaska and compare that population's diet to populations in the western contiguous United States. Found that epigeous fungi and vegetation were more frequent food items than hypogeous fungi. Flying squirrels consumed a small number of truffle genera and consumed truffles less frequently versus flying squirrels in the western United States.
104. Pyare, S., W.P. Smith, and C.S. Shanley. 2010. Den use and selection by northern flying squirrels in fragmented landscapes. **Journal of Mammalogy** 91(4): 886-896. Assessed den use and its associated habitat at multiple spatial scales for northern flying squirrels on Prince of Wales Island. Juveniles' core denning areas were substantially larger than adults, although adults used double the number of nest sites per month as juveniles. Flying squirrels primarily used cavities in snags and live trees and selected den sites were in the largest diameter trees and snags. Silvicultural practices, such as clear-cut logging, and the creation of an early-successional habitat matrix influenced den use and selection by flying squirrels.
105. Ransome, D.B., and T.P. Sullivan. 1997. Food limitation and habitat preference of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus*. **Journal of Mammalogy** 78(2): 538-549. Analyzed food limitation and habitat preference of two species of Sciurids via a food supplementation. Found densities in treated stands for both species was almost double that of densities in control stands, while estimated of northern flying squirrels was higher in old-growth stands versus control stands. Populations of both species appeared to be limited by food and second-growth stands were not suboptimal habitat.
106. Ransome, D.B., and T.P. Sullivan. 2002. Short-term population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in commercially thinned and unthinned stands of coastal coniferous forest. **Canadian Journal of Forest Resources** 32: 2043-2050. Effects of commercial thinning on short-term population dynamics was assessed for two species of Sciurids in British Columbia. Found that densities of northern flying squirrels was higher in unthinned versus thinned stands, while the opposite was observed for red squirrels. Other parameters (e.g., abundance, recruitment, survival) were not affected, therefore commercial thinning had no negative short-term effects on population dynamics for either species.
107. Ransome, D.B., and T.P. Sullivan. 2003. Population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in old-growth and second-growth stands of coastal

- coniferous forest. Canadian Journal of Forest Resources 33: 587-596.** Used mark-recaptured to determine habitat preferences and population dynamics of two Sciurid species in old-growth and mature second-growth forest stands in British Columbia. Results indicated no difference between old-growth and mature second-growth stands for various parameters (e.g., density, mass of males, survival) for either species, although recruitment was higher for red squirrels in second-growth stands. Observed late-fall/early winter breeding for northern flying squirrels and age exceeding 3.5 years.
- 108. Ransome, D.B., and T.P. Sullivan. 2004. Effects of food and den-site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. Journal of Mammalogy 85(2): 206-215.** Inspected the effects of food and den site supplementation on population dynamics of two species of Sciurids. Survival of northern flying squirrels was significantly higher on grids with food supplementation. Occupancy rates of nest boxes was higher in stands supplemented with food versus stands with only nest boxes. Food supplementation may have increased populations leading to higher rates of nest box use in those stands.
- 109. Reynolds, R.J., J.F. Pagels, and M.L. Fies. 1999. Demography of northern flying squirrels in Virginia. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 53: 340-349.** Conducted long-term monitoring for northern flying squirrels in Virginia for 11 years. Majority of individuals were captured in Grayson and Smyth counties, although additional captures occurred in Highland County. Mean litter size was 2.5 and sex ratio was 1.4 males/females. Mean body mass was 109.8 g for adult males and 120.6 g for adult females. Males became reproductively active in December. Litters were observed at the earliest in March and at the latest in October.
- 110. Reynolds, R.J., M.L. Fies, and J.F. Pagels. 2009. Communal nesting and reproduction of the southern flying squirrel in montane Virginia. Northeastern Naturalist 16(4): 563-576.** Surveyed nest boxes at high elevation areas to study breeding habitats and communal nesting of southern flying squirrels in areas where they are typically sympatric with northern flying squirrels. Aggregation size ranged from 2 -12 individuals, although aggregation size appeared to be larger during the winter months. In mixed-age aggregations, females were more numerous than males, but in adult aggregations males were more abundant than females. Breeding season was from late January to early December. Two distinct parturition peaks occurred in early spring and late summer.
- 111. Risch, T.S., and M.J. Brady. 1996. Trap height and capture success of arboreal small mammals: Evidence from southern flying squirrels (*Glaucomys volans*). American Midland Naturalist 136(2): 346-351.** Assessed influence of three trap heights on arboreal mammal capture success. The majority of captures (86%) were southern flying squirrels. Low trap heights (6.5 ft) captured half as many squirrels as medium and high trap heights. Trapping in trees at higher trap heights may produce more captures and setting traps at 15 - 16.5 ft is recommended to increase capture success.
- 112. Ritchie, L.E., M.G. Betts, G. Forbes, and K. Vernes. 2009. Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic. Forest Ecology and Management 257: 1920-1929.** Using a spatially explicit local scale distribution model, occurrence of northern flying squirrels is influenced by independent effects of

landscape composition and configuration in New Brunswick. Occurrence was more frequent in old forest, mixed coniferous-deciduous microhabitat composition, and greater amounts of habitat cover within home-range scale. Probability of occurrence was lower at sites surrounded by greater proportions of early-successional habitat, although patch size and edge contrast were not important. Landscape composition is a more important factor for determining flying squirrel occurrence versus landscape configuration.

113. **Rosenberg, D.K., and R.G. Anthony. 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. *Canadian Journal of Zoology* 70: 161-166.** Compared annual recapture rates, body mass, sex ratio, and density of northern flying squirrels in second-growth and old-growth forests in the Oregon Cascades. Average densities varied between stands, although body mass and annual recapture rates were similar between forest types. Densities did not correlate with habitat characteristics in either stand type, indicating that flying squirrels may be habitat generalists not species associated with old-growth stands.
114. **Rosenberg, D.K., and R.G. Anthony. 1993. Difference in trapping mortality rates of northern flying squirrels. *Canadian Journal of Zoology* 71: 660-663.** Described trapping mortality rates of northern flying squirrels in western Oregon. Trap mortality rates are relatively low (7%), although mortality rates varied between sex and age with juvenile females experiencing the highest mortality rates and adult males the lowest. Behavioral responses to trapping may be effected by weather and related to stress thresholds.
115. **Sawyer, S.L., and R.K. Rose. 1985. Homing in and ecology of southern flying squirrel *Glaucomys volans* in southeastern Virginia. *American Midland Naturalist* 113(2): 238-244.** Relocated southern flying squirrels to determine homing ability. Captured squirrels in nest boxes and then relocated individuals. Flying squirrels were able to successfully return home when displaced 0.6 miles. Noted flying squirrel use of nest boxes directly after installation and aggregation of flying squirrels within nest boxes. Observed males were scrotal in late December and young were born in late February-early March and September-October.
116. **Scheibe, J.S., and J.H. Robins. 1998. Morphological and performance attributes of gliding mammals. Pp. 131-144 in *Ecology and evolutionary biology of tree squirrels*. Eds. Steele, M.A., J.F. Merritt, and D.A. Zegers. Special Publication No. 6, Museum of Natural History, Martinsville, VA.** Compared morphological differences between gliding, arboreal, and ground-dwelling mammals. Also calculated cost effectiveness of gliding for southern flying squirrels. Found that gliding and arboreal mammals have longer tails than ground-dwelling mammals, although tail length increases with body size more rapidly for gliders versus arboreal mammals. Concluded gliding contains an energetic advantage for small gliders (i.e., flying squirrels), but a disadvantage for larger gliders (i.e., *Petaurista* spp.).
117. **Scheibe, J.S., W.P. Smith, J. Bassham, and D. Magness. 2006. Locomotor performance and cost of transport in the northern flying squirrel *Glaucomys sabrinus*. *Acta Theriologica* 51(2): 169-178.** Evaluated the locomotor performance of northern flying squirrels to determine if gliding locomotion is energetically cheaper than quadrupedal locomotion. Mean glide distance ranged from 41 – 47 ft (maximum glide distance = 213 ft). Gliding performance did not vary between males and females. Used

models of transport cost to conclude that gliding typically expends less energy than quadrupedal locomotion.

118. **Scheibe, J.S., K.E. Paskins, S. Ferdous, and D. Birdsill. 2007. Kinematics and functional morphology of leaping, landing, and branch use in *Glaucomys sabrinus*. *Journal of Mammalogy* 88(4): 850-861.** Assessed takeoff and landing forces, angle of attack, and velocity profiles over short glides of northern flying squirrels. Found initial velocity, terminal velocity, and landing force increased with increasing glide distance. Northern flying squirrels did not demonstrate high levels of agility when traversing small branches.
119. **Smith, J.R., D.H. Van Vuren, D.A. Kelt, and M.L. Johnson. 2011. Spatial organization of northern flying squirrels, *Glaucomys sabrinus*: Territoriality in females? *Western North American Naturalist* 71(1): 44-48.** Analyzed home range overlap among northern flying squirrels to assess their spatial organization. Extensive home range overlap was found in females. Results suggest that females share foraging areas, but may be territorial in other portions of their home range (i.e., den trees). Habitat fragmentation could also impeded dispersal, causing crowding in suitable habitat.
120. **Smith, M.J., M.G. Betts, G.J. Forbes, D.G. Kehler, M.C. Bourgeois, and S.P. Flemming. 2011. Independent effects of connectivity predict homing success by northern flying squirrel in a forest mosaic. *Landscape Ecology* 26(5): 709-721.** Studied landscape connectivity effects on northern flying squirrels by translocating squirrels various distances (0.1 – 2.4 miles) from their home range across a forest matrix representing habitat loss and fragmentation. Flying squirrels demonstrated a high rate of homing success in landscapes with higher connectivity. Homing time depending on sex and distance the individual was translocated.
121. **Smith, M.J., G.J. Forbes, and M.G. Betts. 2011. Evidence of multiple annual litters in *Glaucomys sabrinus* (northern flying squirrel). *Northeastern Naturalist* 18(3): 386-389.** In New Brunswick, observed northern flying squirrels had first litter attempts in early June and second attempts were in mid-August. Flying squirrels will attempt a second litter when their first litter of the year has been successfully reared. Females can be lactating and pregnant simultaneously. Polyestry may be common for this species during certain years.
122. **Smith, M.J., G.J. Forbes, and M.G. Betts. 2013. Landscape configuration influences gap-crossing decisions of northern flying squirrel (*Glaucomys sabrinus*). *Biological Conservation* 168: 176-183.** Tested the gap-crossing decisions of northern flying squirrels in southern New Brunswick by translocating individuals across non-forest gaps and recording individual movement patterns to return to its original core area. Found the majority of flying squirrels avoided crossing gaps and moved through the forest to return home. Flying squirrels took longer to return home if the gap was greater than 335 m. Costs associated with crossing gaps (e.g., predation) is a potential reason individuals avoided gaps even when it resulted in returning home quicker while expending less energy.
123. **Smith, W.P. 2007. Ecology of *Glaucomys sabrinus*: Habitat, demography, and community relations. *Journal of Mammalogy* 88(4): 862-881.** Review of habitat, demography, and community dynamics of northern flying squirrels. Density is limited by

food and, to a lesser extent, suitable den sites. Local abundance is correlated with density of large trees and snags, shrub and canopy cover, old-growth forest features, and hypogeous fungi abundance. Fundamental niche of flying squirrels may be broader than suggested by earlier research, although disturbances that reduce structural complexity, canopy cover, or large trees may negatively affect flying squirrel populations.

124. **Smith, W.P. 2012. Flying squirrel demography varies between island communities with and without red squirrels. Northwest Science 86(1): 27-38.** Compared northern flying squirrel demography between islands where red squirrels were and were not present. Found increased home range sizes, lower population and breeding female density, and lower recruitment on the island where flying squirrels was sympatric with red squirrels. Presence of red squirrels may reduce the availability of nesting cavities for flying squirrels, influencing population parameters.
125. **Smith, W.P. 2012. Sentinels of ecological processes: The case of the northern flying squirrel. BioScience 62(11): 950-961.** Discusses northern flying squirrels as a forest obligate that facilitates critical symbiotic relationships and is an important prey item North American forests. Reviews habitat use and the role of flying squirrels as a sentinel of forest ecosystem process and conditions over geological and ecological time scales.
126. **Smith, W.P., S.M. Gende, and J.V. Nichols. 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rainforests of southeastern Alaska. Journal of Mammalogy 85(4): 663-674.** Investigated northern flying squirrel habitat relations by examining micro- and macro-habitat in old-growth forests. Density of large trees, abundance of *Vaccinium* species, snag density, and decreased understory cover positively correlated with microhabitat use, although these factors varied depending on forest type. Macrohabitat use variation was explained by presence of large trees, percent moss cover, and volume of downed woody debris. Probability of captures were higher in stands with increases in mean density of 10 large trees/ha. Findings indicate that flying squirrels in Alaska ecologically differs from populations in the Pacific Northwest.
127. **Smith, W.P., S.M. Gende, and J.V. Nichols. 2005. The northern flying squirrel as an indicator species of temperate rain forest: Test of a hypothesis. Ecological Applications 15(2): 689-700.** Evaluated the suitability of northern flying squirrels as a management indicator species in southeastern Alaska by modeling if flying squirrel habitat was an emergent property of old-growth rain forest. Density of large trees and *Vaccinium* species understory cover explained variation in microhabitat use. Concluded flying squirrels may not be suitable as a management indicator species in Alaska due to its generalist lifestyle.
128. **Smith, W.P., and J.V. Nichols. 2003. Demography of the Prince of Wales flying squirrel, and endemic of southeastern Alaska temperate rain forest. Journal of Mammalogy 83(4): 1044-1058.** Quantified demography of northern flying squirrels in spruce-hemlock and peatland-scrub-mixed-conifer forests. Age, sex, mean body mass, overwinter survival, percentage of reproductive females, and percentage of juveniles were similar between habitat types, but summer survival varied between habitat types and among years. Although spruce-hemlock forests are considered primary habitat for flying squirrels in Alaska, peatland-scrub-mixed-conifer forests support higher densities of flying squirrels compared to other managed and unmanaged forest types in the Pacific Northwest.

129. **Smith, W.P., and D.K. Pearson. 2007. Estimated persistence of northern flying squirrel populations in temperate rain forest fragments of Southeast Alaska. *Biological Conservation* 137: 626-636.** Evaluated the efficacy of habitat reserves for northern flying squirrel in Alaska using demographic and litter size data. Modeled persistence and time to extinction in different size reserves. Determine the minimum patch size in old-growth spruce-hemlock forests to sustain a flying squirrel population at high probability with low demographic variability was 1430 acres for 25 years, 12,500 acres for 50 years, and 195,000 acres for 100 years. Concluded that small, isolated habitat reserves could not sustain populations of flying squirrels for more than 25 years with no immigration.
130. **Sparks, J.L. 2005. Genetic variability, pathogen susceptibility, subspecies identity, and conservation of the endangered northern flying squirrel (*Glaucomys sabrinus*) in Virginia. M.S. thesis, Virginia Commonwealth University, Richmond, VA.** Examined population genetics of northern flying squirrels from subspecies in three locations. Flying squirrels at Mt. Rogers, VA were less inbred than expected. Compared inbreeding and level of parasite infection between populations on Mt. Rogers and Whitetop Mountain, VA. Found the Whitetop Mountain population was more inbred and had higher parasite load (although not statistically significant) than the Mt. Rogers population. Concluded habitat fragmentation increases susceptibility to inbreeding and higher parasitism.
131. **Stapp, P. 1992. Energetic influences on the life history of *Glaucomys volans*. *Journal of Mammalogy* 73(4): 914-920.** Evaluated seasonal and geographic variation in energetics of southern flying squirrels versus other sympatric Sciurids. In the winter, flying squirrels had a greater body mass than during the summer. There was no seasonal differences in basal metabolic rate or conductance. The gliding, nocturnal life-style of flying squirrels may be the reason it has lower basal metabolic rates than other Sciurids of similar size.
132. **Stapp, P., P.J. Pekins, and W.W. Mautz. 1991. Winter energy expenditure and the distribution of southern flying squirrels. *Canadian Journal of Zoology* 69: 2548-2555.** Measured oxygen consumption and energy expenditure of southern flying squirrels to construct daily energy budgets and better understand cold tolerance and current distribution of this species. Flying squirrels had a lower basal metabolism and rate of heat loss that expected based on mass. Huddling in groups reduced energy expenditure by 27-36% and insulated nests decreased heat loss by 37%. Additional thermoregulatory costs and decreased abundance of hard mast prevent flying squirrel occupancy north of its current range.
133. **Stihler, C.W., K.B. Knight, and V.K. Urban. 1987. The northern flying squirrel in West Virginia. Pp. 176-183 in *Proceedings of the Third Southeast Nongame and Endangered Species Symposium*. Eds. Odum, R.R., K.A. Riddleberger, and J.C. Dozier. University of Georgia, Athens.** Monitored for Virginia flying squirrels using nest boxes and live traps to document the distribution of this subspecies. Also obtained ecological data on this subspecies, including life history, basic biological data, home range size, interactions with southern flying squirrels, trapping success, and nest box use. Seminal data on this subspecies in West Virginia.
134. **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.** Analyzed capture data of Virginia northern flying squirrels from 11 years of nest box surveys in West Virginia. Produced 769 captures at 81 sites in six counties. Flying squirrels has been capture at elevations between 2860 – 4648 ft. Improved distribution data and habitat associations of this subspecies in West Virginia.
135. **Taulman, J.F., and K.G. Smith. 2003. Home range and habitat selection of southern flying squirrels in fragmented forests. Mammal Biology 69: 11-27.** Determined habitat selection and home range size of southern flying squirrels in Arkansas by capturing and radiocollaring squirrels. Home ranges of males were larger than females and home ranges were relatively small in home ranges abundant with hard mast. Flying squirrels were not found to be forest generalists, as previously described, but sensitive to forest disturbance and selective in habitat use.
136. **Taulman, J.F., and K.G. Smith. 2004. Home range, habitat selection, and population dynamics of southern flying squirrels in managed forests in Arkansas. Pp. 71-75 in Ouachita and Ozark Mountains symposium: Ecosystem management research. Eds. Guldin, J.M. General Technical Report SRS-74, Southern Research Station, Forest Service, U.S. Department of Agriculture, Asheville NC.** Assessed the effects of experimental harvest on southern flying squirrels population dynamics, home range size, and habitat selection in the Ouachita National Forest using nest box surveys. Squirrel densities declines in all harvested stands and increased in control stands. Home ranges were similar between males and females in harvested stands, although home range size was smaller in harvested stands with higher hard mast production.
137. **Taulman, J.F., K.G. Smith, and R.E. Thill. 1998. Demographic and behavioral responses of southern flying squirrels to experimental logging in Arkansas. Ecological Applications 8(4): 1144-1155.** Investigated the effects of even-aged and uneven-aged forestry practices on southern flying squirrel population responses using nest-box surveys. Found that squirrel densities declined in harvested stands and increased in control stands. Use of nest boxes increased in harvested stands, highlighting the reduction in denning habitat within these stands after harvest.
138. **Terry, T.M. 2004. Glaucomys sabrinus fuscus habitat and nest box use in West Virginia with management recommendations for Kumbrabow State Forest. M.S. Thesis. West Virginia University, Morgantown, WV.** Analyzed long-term nest box data of Virginia northern flying squirrels in West Virginia and habitat use of flying squirrels at Kumbrabow State Forest. Found that flying squirrels may be a generalist when selecting for nest trees. Found that occupancy rates of nest boxes were extremely low (1.5%) and may not be an effective method for determining the range of flying squirrels in West Virginia.
139. **Thomas, R.B., and P.D. Weigl. 1998. Dynamic foraging behavior in the southern flying squirrel (Glaucomys volans): Test of a model. American Midland Naturalist 140(2): 264-270.** Studied foraging behavior of southern flying squirrels in North Carolina. Found that flying squirrels consume more hickory nuts versus acorns at lower temperatures and a declining photoperiod.

140. **Thorington, K.K., J.D. Metheny, M.C. Kalcounis-Rueppell, and P.D. Weigl. 2010. Genetic relatedness in winter populations of seasonally gregarious southern flying squirrels, *Glaucomys volans*. Journal of Mammalogy 91(4): 897-904.** Assessed winter aggregations of southern flying squirrels to determine if individuals nest with kin. The majority of individuals were highly related to a nest mate, indicating flying squirrels prefer forming winter aggregations with relatives.
141. **Thorington, K.K., and P.D. Weigl. 2011. Persistence of southern flying squirrel winter aggregations: role of kinship, familiarity, and intruder squirrels. Journal of Mammalogy 95(2): 1005-1012.** Used a laboratory experiment to determine how intruder flying squirrels influenced winter aggregations of southern flying squirrels depending on the relation and familiarity of the intruder to nesting group. Related groups were more tolerant of an intruder. Unrelated groups were initially not tolerant of intruders, although as colony-wide familiarity increased intruders were accepted in these groups.
142. **Thorington, K.K., and P.D. Weigl. 2011. Role of kinship in the formation of southern flying squirrel winter aggregations. Journal of Mammalogy 92(1): 179-189.** Conducted a laboratory experiment to determine if familiar flying squirrels or kin were preferred when forming nest aggregations. Found kinship was the main factor influencing aggregation formations, although familiarity became a significant factor towards the end of the study.
143. **Thysell, D.R., L.J. Villa, and A.B. Carey. 1997. Observations of northern flying squirrel feeding behavior: Use of non-truffle food items. Northwestern Naturalist 78(3): 87-92.** Hypothesized northern flying squirrels may consume at a higher rate than is indicated by fecal pellet analysis. Observed flying squirrels consuming non-truffle items, including epigeous fungi, fruits, seeds, and conifer seedlings. These food items may be important in marginal habitat or in areas with low truffle abundance.
144. **Trudeau, C., L. Imbeau, P. Drapeau, and M.J. Mazerolle. 2011. Site occupancy and cavity use by the northern flying squirrel in the boreal forest. Journal of Wildlife Management 75(7): 1646-1656.** Measured factors influencing site occupancy and cold-weather nesting sites in northwestern Quebec by northern flying squirrels. Found that none of the considered habitat variables (e.g., cavity availability, downed woody debris) explained site occupancy. Both sexes used tree cavities, external nests, and ground nests. During cold weather, females preferred ground nests and males preferred external nests. These findings do not support the hypothesis that tree cavities are a limiting factor to flying squirrels in cold environments because this species seems to be a generalist and opportunistic.
145. **Trudeau, C., L. Imbeau, P. Drapeau, and M.J. Mazerolle. 2012. Winter site occupancy patterns of the northern flying squirrel in boreal mix-wood forests. Mammalian Biology 77: 258-263.** Used nest box occupancy to explain site occupancy of northern flying squirrels from mid-winter to early spring in northwestern Québec, Canada. Determined that flying squirrels are not a habitat specialist of late-seral conifer forests.
146. **Urban, V. 1988. Home range, habitat utilization, and activity of the endangered northern flying squirrel. M.S. thesis. West Virginia University, Morgantown, WV.** Conducted trapping and radio-telemetry surveys at Stuart Knob to determine home range, nesting, and activity levels. Found radio-collared squirrels exclusively used drey nests and no

cavity nesting was observed. Fern cover was positively associated with core areas within home ranges. Temperature was positively correlated with activity, while precipitation and moonlight caused decreases in activity. Squirrels exhibited 2 periods of activity during the night.

147. **USFWS. 1985. Final rule for listing Carolina Flying Squirrel and Virginia Flying Squirrel as endangered. 50 FR 27002, July 1, 1985.** Official listing for both Appalachian subspecies under the Endangered Species Act. Indicates reasons for listing, factors affecting the species, and critical habitat.
148. **USFWS. 1990. Appalachian northern flying squirrel (*Glaucomys sabrinus fuscus* and *Glaucomys sabrinus coloratus*) recovery plan. Annapolis Field Office, U.S. Fish and Wildlife Service, U.S. Department of Interior, Annapolis, MD.** Official document describing the reasonable actions determined to recover and/or protect Virginia and Carolina northern flying squirrels under the Endangered Species Act. These subspecies were listed because little was known about their population status, natural history, and primary habitat, high-elevation red spruce forests, in the southern and central Appalachians is endangered due to industrial logging and red spruce decline.
149. **USFWS. 2007. Post-delisting monitoring plan for the West Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). Fish and Wildlife Service, U.S. Department of Interior, West Virginia Field Office, Elkins, WV.** A 10-year framework for post-delisting monitoring of Virginia northern flying squirrels under the Endangered Species Act. Primary monitoring focus is on 1) habitat status and trends, and 2) implementation of habitat management plans and agreements. Additionally, monitoring distribution and persistence using presence/absence surveys from nest boxes and live trapping. Written after a proposed ruling to attempt to remove this subspecies from the Endangered Species Act on December 19, 2006.
150. **USFWS. 2013. Carolina Northern Flying Squirrel (*Glaucomys sabrinus coloratus*) 5-year review: Summary and evaluation. Southeast Region, Asheville Ecological Services Field Office, Asheville, NC.** Reviewed the recovery criteria and delisting criteria of Carolina northern flying squirrels have been met and determined these criteria have been met. Updated biology, habitat, life history, demography, population trends, genetics, distribution, and habitat conditions for this subspecies. Concluded flying squirrels should remain listed as Endangered and made recommendations for future actions pertaining to this subspecies.
151. **USFWS. 2013. Endangered and threatened wildlife and plants: Reinstatement of removal of the Virginia Northern Flying Squirrel from the list of Endangered and Threatened wildlife. Federal Register 78(42): 14022.** Final ruling to delist the Virginia northern flying squirrel from the Endangered Species List on March 4, 2013. Reinstated previous attempt to delist this subspecies on August 26, 2008.
152. **Vernes, K. 2001. Gliding performance of the northern flying squirrel (*Glaucomys sabrinus*) in mature mixed forest of eastern Canada. Journal of Mammalogy 82(4): 1026-1033.** Calculated glide parameters for northern flying squirrels observed in the field in New Brunswick. Flying squirrels had a glide angle of 26.8° and glide ratio of 1.98. On

average, males glided further than females (62 ft and 47 ft, respectively). Majority of glides were with the slope of the terrain. Horizontal glide distance ranged between 10.5 and 147 ft, although the majority of glides were between 16 and 82 ft.

153. **Vernes, K. 2004. Breeding biology and seasonal capture success of northern flying squirrels (*Glaucomys sabrinus*) and red squirrels (*Tamiasciurus hudsonicus*) in southern New Brunswick. *Northeastern Naturalist* 11(2): 123-136.** Determined capture success and reproductive status for northern flying squirrels and red squirrels in Fundy National Park. Found capture success of both species was positively correlated with maximum daily temperature, although capture rates of each species varied with the season. Males of both species became scrotal in winter and spring and females became pregnant and lactated in late spring and summer. Flying squirrels may have an additional breeding season in the fall.
154. **Vernes, K., S. Blios, and F. Bärlocher. 2004. Seasonal and yearly changes in consumption of hypogeous fungi by northern flying squirrels and red squirrels in old-growth, New Brunswick. *Canadian Journal of Zoology* 82: 110-117.** Examined seasonal consumption of hypogeous fungi by northern flying squirrels and red squirrels in an old-growth mixedwood forest in Fundy National Park. Found that diet was dependent on season and year, although higher diversity of hypogeous fungi were detected in summer diets. The majority of fungi detected were Ascomycetes and Basidiomycetes. Fungi may represent an important food source for both species of squirrel.
155. **Villa, L.J., A.B. Carey, T.M. Wilson, and K.E. Gos. 1999. Maturation and reproduction of northern flying squirrels in Pacific Northwest Forests. General Technical Report PNW-GTR-444. Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture, Olympia, WA.** Developed methods to determine age and reproductive condition of northern flying squirrels. Determined three age classes and reproductive conditions can be determined in the field.
156. **Waters, J.R., and C.J. Zabel. 1995. Northern flying squirrel densities in fir forests of northeastern California. *Journal of Wildlife Management* 59(4): 858-866.** Assessed northern flying squirrel densities in managed and old spruce forests in Lassen National Forest. Found flying squirrel densities were higher in older versus shelterwood stands. Body mass did not vary between stand types, but capture rates of juveniles were higher in old stands. Found hypogeous fungi was an important part of the diet and frequency of hypogeous sporocarps was linked to flying squirrel densities. Concluded flying squirrels are not an old-growth specialist, but silvicultural practices may negatively influence densities.
157. **Wheatly, M. 2007. Fungi in summer diets of northern flying squirrels (*Glaucomys sabrinus*) within managed forests of western Alberta, Canada. *Northwest Science* 81(4): 265-273.** Determined dietary fungal diversity consumed by northern flying squirrels in managed forest stands during late August to September. Found the majority of fecal samples contained hypogeous fungal spores, with the most frequently consumed fungi from the genera *Cortinarius*, *Gastroboletus*, and *Hysteragium*. Indicate that diets may shift from epigeous fungi in the winter to hypogeous fungi in the summer.

158. Weigl, P.D. 1974. Study of the northern flying squirrel, *Glaucomys sabrinus*, by temperature telemetry. *American Midland Naturalist* 92(2): 482-486. Used temperature telemetry to determine activity patterns and home ranges of northern flying squirrels in North Carolina and Pennsylvania. Found squirrels were active after civil twilight and directly before dawn. Factors that delayed the onset of the first activity bout were high winds, mist, and heavy rain, although these factors did not affect the length of the first activity bout. Home ranges were smaller in North Carolina than Pennsylvania. Flying squirrels utilized cavities and drey nests, although only the former were observed in North Carolina.
159. Weigl, P.D. 1978. Resource overlap, interspecific interactions, and the distribution of the flying squirrels, *Glaucomys volans* and *G. sabrinus*. *American Midland Naturalist* 100(1): 83-96. Summarized literature on southern and northern flying squirrel habitat selection, nesting sites, and diet items. Designed an experiment using large outdoor cages to determine competition and habitat use. Found no evidence of interspecific nest sharing. Observed that southern flying squirrels was more aggressive than northern flying squirrels when defending a home range. Southern flying squirrels preferred hardwood habitat, whereas northern flying squirrels did not show a preference. Distribution of both species may be correlated with resource requirements and interspecific interactions.
160. Weigl, P.D. 2007. The northern flying squirrel (*Glaucomys sabrinus*): A conservation challenge. *Journal of Mammalogy* 88(4): 897-907. Reviewed literature of northern flying squirrels to determine what factors may influence conservation of this species. Found the major problem with conserving this species is understanding its complex ecological role with it associated forest communities and determining how anthropogenic activities influence this species. Listed considerations when attempting to conserve this species in various regions throughout its extensive range.
161. 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 North Carolina Department of Transportation and U.S. Fish and Wildlife Service. Wake Forest University, Winston-Salem, NC. Assessed trapping success, population parameters, nighttime activity, movement patterns, home range size, den sites, habitat analysis, predation, and effects of a scenic highway on Carolina northern flying squirrels in an atypical northern hardwood-hemlock forest at the southernmost extent of its range in the Appalachian Mountains. Found that no radio-collared individuals crossed the Cherohala Skyway during the study and may be an absolute barrier to flying squirrel movement, further fragmenting this isolate and small population. Flying squirrels have unusually larger home ranges, live in discrete areas, are genetically depauperate, and have low levels of *Strongyloides robustus* in this atypical habitat.
162. Weigl, P.D., T.W. Knowles, and A.C. Boynton. 1992. The distribution and ecology of the northern flying squirrel, *Glaucomys sabrinus coloratus*, in the southern Appalachians. North Carolina Wildlife Resources Commission Publication, Raleigh, NC. Five-year study determining distribution and ecology of Carolina northern flying squirrels in western North Carolina and eastern Tennessee. Describes population characteristics (e.g., sex ratio, body size, reproduction, social behavior), climatic factors, habitat, food habits, home range size, movements, nest use, social interactions, interspecific interactions, and potential threats. Seminal work for this subspecies.

163. Wells-Gosling, N. 1985. **Flying squirrels: Gliders in the dark.** Smithsonian Institution Press, Washington D.C. Observational book on life history, behavior, and development of captive and wild northern and southern flying squirrels.
164. Wells-Gosling, N., and L.R. Heaney. 1984. ***Glaucomys sabrinus*.** *Mammalian Species* 229: 1-8. Synthesized species account of northern flying squirrels using peer-reviewed literature. Reviews literature on taxonomy, subspecies, distribution, species diagnosis, general characteristics, distribution, fossil record, form and function, ontogeny and reproduction, ecology, behavior, and genetics.
165. Wetzel, E.J., and P.D. Weigl. 1994. **Ecological implications for flying squirrels (*Glaucomys* spp.) of effects of temperature on the in vitro development and behavior of *Strongyloides robustus*.** *American Midland Naturalist* 131(1): 43-54. Studied effects of temperature on *Strongyloides robustus* egg-hatching success, juvenile survival, and behavior with implications for North American flying squirrels. Egg hatching and larval development declined with decreasing temperatures. Larva did not survive freezing, although eggs showed a low resistance to freezing temperature. Prevalence and intensity of infection rates between Southern and northern flying squirrels are partly due to environmental differences between habitats, with lower rates in northern flying squirrels. Overlaps in the nest use of these species may help facilitate transmission of this parasite between flying squirrel species.
166. Wilson, J.A., D.A. Kelt, and D.H. Van Vuren. 2008. **Home range and activity of northern flying squirrels (*Glaucomys sabrinus*) in the Sierra Nevada.** *Southwestern Naturalist* 53(1): 21-28. Calculated home ranges, nest tree, and distance to nest trees during night activity for northern flying squirrels in California. Juvenile males had smaller home ranges than adult males, but there were no significant differences in home range size between genders or between forest stand types. Majority of cavities were in live trees and snags, although use of drey nests were observed. Average distance of nightly activity from nearest nest tree did not vary during the course of the night, although females had a tendency to travel further from nest trees.
167. Witt, J.W. 1991. **Fluctuations in the weight and trap response for *Glaucomys sabrinus* in western Oregon.** *Journal of Mammalogy* 72(3): 612-615. Studied capture success and mean weight of northern flying squirrels. Found spring and autumn had the most consistent and highest average trapping success, while fluctuations in weight observed in the late autumn-early winter may be related to abundance of food resources.
168. Witt, J.W. 1992. **Home range and density estimates for the northern flying squirrel, *Glaucomys sabrinus*, in western Oregon.** *Journal of Mammalogy* 73(4): 921-929. Used live-trapping and radio-telemetry to estimate home range size and population densities of northern flying squirrels. Home ranges were estimated using two techniques: inclusive boundary strip method and minimum-convex-polygon technique. Found flying squirrel densities were higher in old-growth forest stand versus a second-growth forest stand.
169. Zabel, C.J., and J.R. Waters. 1997. **Food preferences of captive northern flying squirrels from the Lassen National Forest in northeastern California.** *Northwest Science* 71(2): 103-107. Studied food preferences of northern flying squirrels using cafeteria-

style feeding trials using hypogeous fungi, epigeous fungi, and lichens. Observed northern flying squirrels preferentially selected hypogeous fungi to other types of naturally occurring foods, although that partiality varied among truffles of different species. Forest management practices and natural disturbances may influence the availability of foods favored by flying squirrels.

APPALACHIAN SPRUCE-FIR PAPERS

1. **Adams, H.S., and S.L. Stephenson. 1989. Old-growth red spruce communities in the mid-Appalachians. *Vegetatio* 85(1): 45-56.** Through the 1980s, annual growth in overstory red spruce in 3 Allegheny (West Virginia) and one Ridge and Valley (Virginia) old-growth patches was slow. Mid-story response to canopy gaps also was limited. However, understory red spruce seem to shown positive growth patterns and expansion. Climate change and acid deposition were hypothesized as factors influencing red spruce forest growth.
2. **Adams, H.S., and S.L. Stephenson. 1991. High elevation coniferous forests in Virginia. *Virginia Journal of Science* 42(4): 391-399.** Red spruce occurs sporadically in western Virginia in two areas in the Blue Ridge: Mt. Rogers-area (Grayson-Smyth) counties as a red spruce-Fraser fir community and the Limberlost Area as eastern hemlock-red spruce bog in Shenandoah National Park (Madison County). Sizable patches of upland Ridge and Valley red spruce occur in Highland County along the West Virginia line and on Beartown and Clinch Mountain WMA in Russell County. Small patches of occur in bogs in the Mountain Lake area of Giles County and as upland stands in Rockingham County on Shenandoah Mountain and above Burke's Garden in Tazewell County.
3. **Adams, H.S., and S.L. Stephenson. 2010. Twenty-five years of succession in the spruce-fir forests on Mt. Rogers in Southwestern Virginia. *Castanea* 75(2): 205-210.** Despite widespread Fraser fir mortality following balsam woolly adelgid infestation and loss of most older overstory trees, Fraser fir, yellow birch, and mountain ash increased (in canopy gaps) whereas red spruce decreased in all stratum from the 1980s to 2007 at Mt. Rogers and bryophytes replaced some of the herbaceous flora. Still, overall community composition was generally similar between the time periods.
4. **Adams, H.S., S.L. Stephenson, T.J. Blasing, and D.N. Duvick. 1985. Growth-trend declines of spruce and fir in mid-Appalachian subalpine forests. *Environmental and Experimental Biology* 25(4): 315-325.** Red spruce and fir (Fraser and balsam) growth declines in West Virginia and Virginia associated with drought conditions in the 1960s were not reversed by subsequent moist periods in the 1970s and early 1980s. Speculated that atmospheric deposition may have been a contributing factor to slowed growth trends.
5. **Adams, H.S., S.L. Stephenson, A.W. Rollins, and M.B. Adams. 2010. The isolated red spruce communities of Virginia and West Virginia. Pp. 1-12 in *Proceedings from the conference on the ecology and management of high-elevation forests in the central and southern Appalachian Mountains*. Eds. Rentch, J.S., and T.M. Schuler. General**

Technical Report NRS-P-64. Northern Research Station, Forest Service, U.S. Department of Agriculture, Newtown Square, PA. Considerable floristic differences occurred between forests containing red spruce among Blue Ridge, Ridge and Valley and Appalachian Plateau sites and between those stands that were upland versus bog communities. Data contain in this paper are intended to serve as baseline community conditions to be used to assess forest change over time.

6. **Amman, G.D. 1966. Some new infestations of the balsam woolly aphid in North Carolina, with possible modes of dispersal. *Journal of Economic Entomology* 59(3): 508-511.** Discusses the infestation of balsam woolly adelgid in North Carolina, from the first occurrence in nursery between Mt. Mitchell and Grandfather Mountain to other locations in the state, including Roan Mountain and Mt. Sterling. Predicts year of adelgid infestation by totals the number of tree deaths and examining trees for red wood, which occurs as a result of adelgid feeding. Concludes that the dispersal agent between sites is probably wind.
7. **Amman, G.D., and C.F. Speers. 1965. Balsam woolly aphid in the southern Appalachians. *Journal of Forestry* 63: 18-20.** Briefly described balsam woolly adelgid infestation in North Carolina, the adelgid's life history, and how fir trees are injured by infestation. Using hydraulic-spray application of 12.5% benzene hexachloride water emulsion will provide aphid control for 2 years. Introductions of biological control agents for the adelgid were brought from Europe in 1959 and certain species were shown to reduce adelgid numbers in caged experiments.
8. **Andersen, C.P., and S.B. McLaughlin. 1991. Seasonal changes in shoot water relations of *Picea rubens* at two high elevation sites in the Smoky Mountains. *Tree Physiology* 8: 11-21.** Assessed seasonal changes in water relations of current-year shoots of red spruce at two elevations on Clingman's Dome. Concluded that water stress is not the dominant stress influencing growth patterns. Dry periods at higher elevations may cause greater water stress on trees than at lower elevations due to a more open canopy via Fraser fir death and shallower soils profiles. Patterns of cold hardiness development were observed in red spruce at both sites in late fall and trees were probably not experiencing winter desiccation stress even when soil temperatures were near freezing.
9. **Aneja, V.P., W.P. Robarge, C.S. Claiborn, A. Murthy, D. Soo-Kim, and Z. Li. 1992. Chemical climatology of high elevation spruce-fir forests in the southern Appalachian mountains. *Environmental Pollution* 75: 89-96.** A meteorological tower established at Mt. Mitchell State Park in the late 1980s showed that foggy conditions prevailed 20-40% of the time. Precipitating clouds were less acidic than non-precipitating clouds. Clouds from westerly winds were more acidic than those from easterly or southern winds. Approximately half of acidic deposition was from cloud contact. Ozone occurred at levels known to produce foliar damage.
10. **Arthur, F.H., and F.P. Hain. 1984. Seasonal history of the balsam woolly adegid (*Homoptera: Adelgidae*) in natural stands and plantations of Fraser fir. *Journal of Economic Entomology* 77(5): 1154-1158.** Emergence time of balsam woolly populations differs by elevation, with earlier emergence occurring at plantations at lower elevations versus natural stands at higher elevations. Two generations typically occurred in 1983, with additional generations occurring at lower elevations.

11. **Bailey, C.M., and S. Ware. 1990. Red spruce forests of Highland County, Virginia: biogeographical considerations. *Castanea* 55(4): 245-258.** Upland and riparian red spruce in the portion of Highland County that is west of the Allegheny Front appears to be stable and similar in distribution prior to human disturbance from the late 1800s to present. Upland sites contained black cherry and black birch as associates whereas lowland, swamp stands contained Eastern hemlock and red maple as associates.
12. **Baker, M., H.V. 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.** Uptake and retention of nitrogen in high elevation red spruce-Fraser fir forests are highly variable depending more on stand condition and less on elevation or aspect. Only a fraction of nitrogen is sequestered in wood and foliar increment, with most returning to the forest floor in litterfall.
13. **Banks, S.A. 2013. Forest response to the U.S. 1990 Clean Air Act: The southern spruce-fir ecosystem. M.S. thesis. North Carolina State University, Raleigh, NC.** A survey of high elevation forest plots in the Black Mountains from 1985 – 2012 showed that acidic atmospheric deposition peaked in 1998 and had declined significantly by 2012. Fraser fir regeneration following widespread mortality from balsam woolly adelgid was abundant. After showing tremendous increase in stem density, fir stands began entering the stem exclusion phase of development by 2012. Red spruce mortality occurred and there was an overall decrease in the number of stems over time, however, there was an overall increase in live basal area of red spruce.
14. **Bardhan, S., Jose, S., Jenkins, M. A., Webster, C. R., Udawatta, R. P., & Stehn, S. E. 2012. Microbial community diversity and composition across a gradient of soil acidity in spruce–fir forests of the southern Appalachian Mountains. *Applied Soil Ecology*, 61: 60-68.** Dominance of acidophilic bacteria suggest that the acid-saturated, poorly buffered soils in the southern Appalachians indicates that reductions in atmospheric acid deposition still have not had an impact on the microbial community.
15. **Bataineh, M., L. Kenefic, A. Weiskittel, R. Wagner, and J. Brissette. 2013. Influence of partial harvesting and site factors on the abundance and composition of natural regeneration in the Acadian Forest of Maine, USA. *Forest Ecology and Management* 306: 96-106.** Overstory composition and understory advance regeneration influence post-harvest response in mixed northern hardwoods-red spruce-balsam fir that soil and site class conditions in Maine.
16. **Battles, J.J., and T.J. Fahey. 2000. Gap dynamics following forest decline: A case study of red spruce forests. *Ecological Applications* 10(3): 760-774.** Red spruce canopy gaps formed by standing dead trees will be captured by advance regeneration rather than new seedlings if forest floor disturbance is limited. Balsam fir has or will capture many gaps in the Northeast following red spruce dieback. Yellow birch seedlings will outgrow balsam fir seedlings which will outgrow red spruce seedlings when present in a gap.
17. **Battles, J.J., T.J. Fahey, and E.M.B. Harney. 1995. Spatial patterning in the canopy gap regime of a subalpine *Abies-Picea* forest in the northeastern United States.**

Journal of Vegetation Science 6(6): 807-814. Forest canopy gaps in Northeastern red spruce-balsam fir forests were more abundant at or near ridgelines and along streams than sideslopes and backslopes. Steeper slopes tended to have more canopy gaps than less steep slopes.

18. **Beane, N.R. 2010. Using environmental and site-specific variables to model current and future distribution to red spruce (*Picea rubens* Sarg.) forest habitat in West Virginia. Ph.D. Dissertation. West Virginia University, Morgantown, WV.** Maxent modeling suggests by 2080, under various climate change scenarios, little to no red spruce-dominated forest will remain in the Appalachian Plateau of West Virginia. Models may not have fully accounted for past distribution however, and therefore possibly underestimated red spruce climatic tolerances.
19. **Beane, N.R., Rentch, J.S., and Schuler, T.M. 2013. Using maximum entropy modeling to identify and prioritize red spruce forest habitat in West Virginia. Research Paper NRS-23. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station.** Maxent modeling was used to assess the low, medium and high probability of potential red spruce occurrence in West Virginia. Elevations of above 2950 ft and those with mean summer temperatures no greater than 20°C were identified as current or potentially suitable for red spruce. Areas of high probability should be targeted for restoration or stand enhancement because they will have the greatest resistance to future climate change and/or represent areas that could benefit species such as the Virginia northern flying squirrel the most as well as provide good landscape connectivity.
20. **Berry, Z.C., and W.K. Smith. 2012. Cloud pattern and water relations in *Picea rubens* and *Abies fraseri* southern Appalachian Mountains, USA. Agricultural and Forest Meteorology 162: 27-34.** Decreases in the frequency of low cloud immersion in the Southern Appalachian red spruce-Fraser fir zone may be detrimental to the ecophysiology of red spruce and Fraser fir causing longer stomatal closure that may limit growth potential and survivability in seedlings and small trees.
21. **Bessey, C.E. 1899. Botanical notes: Spruce and pine forests of West Virginia. Science 10(241): 188-190.** Using 2400 foot as the lower elevational limit for red spruce in the Allegheny Mountains, it is possible that approximately 2,000,000 acre of conifer-dominated or mixed conifer-hardwood forest occurred in West Virginia prior to exploitative logging and subsequent burning.
22. **Bintz, W.W., and D.J. Butcher. 2007. Characterization of the health of southern Appalachian red spruce (*Picea rubens*) through determination of calcium, magnesium, and aluminum concentrations in foliage and soil. Microchemical Journal 87: 170-174.** Ratios for calcium/aluminum have improved from the 1980s through the 2000s in high elevation red spruce forests along the Blue Ridge Parkway and Great Smoky Mountains National Park. Although many sampled sites were still considered “at risk”, overall forest health has improved.
23. **Bogle, M.A., and R.R. Turner. 1984. Lead in vegetation, forest floor material, and soils of the spruce-fir zone, GSMNP. Pp. 211-224 in The southern Appalachian spruce-fir ecosystem: Its biology and threats. Eds. P.S. White. Research/Resources**

Management Report SER-71. Great Smoky Mountains National Park, National Park Service, U.S. Department of Interior, Gatlinburg, TN, USA. Studied lead concentrations in the red spruce- Fraser fir ecosystem and found that levels were not exceptionally high, contrary to previous studies. Although lower levels were found compared to other studies, low concentrations may still possess an ecological threat to this fragile ecosystem.

24. **Bruck, R.I., and W.P. Robarge. 1988. Change in forest structure in the boreal montane ecosystem of Mt. Mitchell, North Carolina. European Journal of Forest Pathology 18: 357-366.** 1984-1987 was a period of extreme overstory mortality for red spruce and Fraser fir trees monitoring at a series of sites along elevational and aspect gradients at Mt. Mitchell. Causation was speculative but included: balsam woolly adelgid attack, atmospheric acid deposition, wind/ice damage, and warmer temperatures.
25. **Bruck, R.I., W.P. Robarge, and A. McDaniel. 1989. Forest decline in the boreal montane ecosystems of the Southern Appalachian Mountains. Water, Air, and Soil Pollution 48: 161-180.** Acid cloud immersion alters waxy cuticles on red spruce needles causing waxy plugs in stomata in the Mt. Mitchell area. These plugs probably disrupt transpiration and photosynthetic efficiency leading to slow or reduced growth. Unlike balsam woolly adelgid infestation in Fraser fir, no evidence of insect infestation was found in red spruce in the area.
26. **Bunn, W.A., M.A. Jenkins, C.B. Brown, and N.J. Sanders. 2010. Change within and among forest communities: The influence of historic disturbance, environmental gradients, and community attributes. Ecography 33: 425-434.** Forest plots established in 1978 and resurveyed in 2007 in the Great Smoky Mountains National Park showed that plots subjected to logging lost species or shifted species during the survey period more than compared to those that were never logged. However, environmental and physical factors shaped community composition more so than one-time disturbance from logging.
27. **Busing, R.T. 2004. Red spruce dynamics in an old southern Appalachian forest. Journal of the Torrey Botanical Society 131(4): 337-342.** Following Fraser fir mortality from balsam woolly adelgid, canopy red spruce mortality from exposure and windthrow events was elevated in an old-growth stand in the Great Smoky Mountains National Park. However, many red spruce residuals displayed elevated diameter growth. Overall basal area has been reduced by half. Overstory red spruce mortality will continue to be high until the understory stratum reaches the overstory and stands are once again fully stocked.
28. **Busing, R.T., and E.E.C. Clebsch. 1988. Fraser fir mortality and the dynamics of a Great Smoky Mountains fir-spruce stand. Castanea 53(3): 177-182.** Through the 1980s, Fraser fir basal area had been reduced by half on Clingman's Dome in the Great Smoky Mountains National Park. Minor increases and release of other species such as red spruce also occurred.
29. **Busing, R.T., E.E.C. Clebsch, C.C. Eager, and E.F. Pauley. 1988. Two decades of change in a Great Smoky Mountains spruce-fir forest. Journal of the Torrey Botanical Society 115(1): 25-31.** Two high elevation forest plots surveyed in the 1960s and revisited in the 1980s in the Great Smoky Mountains National Park showed little change other than the loss of overstory Fraser fir from balsam woolly adelgid.

30. **Busing, R.T., and E.F. Pauley. 1994. Mortality trends in a southern Appalachian red spruce population. *Forest Ecology and Management* 64: 41-45.** Red spruce mortality increased from windthrow following Fraser fir mortality from balsam woolly adelgid in the Great Smoky Mountains National Park.
31. **Busing, R.T., P.S. White, and M.D. MacKenzie. 1993. Gradient analysis of old-spruce-fir forests of the Great Smoky Mountains circa 1935. *Canadian Journal of Botany* 71: 951-958.** Analyzed survey plots containing red spruce or Fraser fir with no past logging or burning history from 1930s plot data. Found that stand basal area and stem density were positively correlated with increased elevation and higher on south-facing slopes versus other aspects. Fraser fir was had the dominant basal area in stands above 5900 ft, while red spruce dominated stands between 3608 – 6230 ft. Yellow birch was dominant on mesic slopes between 4100 – 4760 ft, especially in coves. Elevation was the only environmental factor influencing ecotone position between spruce-fir forests and northern hardwoods.
32. **Busing, R.T., and X. Wu. 1990. Size-specific mortality, growth, and structure of a Great Smoky Mountains red spruce population. *Canadian Journal of Forest Research* 20: 206-210.** Examined red spruce population dynamics in an old growth spruce-fir stand. Found that a large proportion of the population was less than 100 years old, although the population contained trees of all ages, exhibiting a similar diameter distribution pattern to other old-growth forests. Intermediate size trees had lower mortality rates and higher radial growth rates versus smaller (<11.8 in dbh) or larger (>23.6 in dbh) trees. Canopy trees exhibited standing death at a greater rate than death by windfall.
33. **Byers, E.A., J.P. Vanderhorst, and B.P. Streets. 2010. Classification and conservation assessment of upland red spruce communities in West Virginia. *Wildlife Resources Section, West Virginia Division of Natural Resources, Elkins, WV.*** Classification of red spruce-dominated forests in West Virginia yielded 5 distinct communities: red spruce-southern mountain cranberry, red spruce-yellow birch, red spruce-great rhododendron, red spruce-eastern hemlock-American beech and red spruce heath rocky woodland. Associations with Eastern hemlock, American beech and great rhododendron occurred at middle and lower elevations, particularly in sheltered landforms. Yellow birch associations were found on good sites at higher elevations. Southern mountain cranberry associations occurred at the highest elevations whereas the heath rocky woodland associations an edaphic community found primarily on high-elevation, xeric portions of the Allegheny Front/Ridge and Valley interface. Predictions of red spruce decline from climate change may be overestimated.
34. **Ciesla, W.M., H.L. Lambert and R.T. Franklin. 1965. Status of the balsam woolly aphid in North Carolina and Tennessee - 1964. *Forest Service Report 65-1-1, U.S. Department of Agriculture.*** Conducted aerial and ground surveys to determine balsam woolly adelgid infestation. New locations on Roan Mountain, Grandfather Mountain, and Cataloochee Knob were found. Infestation in new locations were close to previous known infestations on Roan Mountain and Mt. Sterling. An infestation in a Fraser fir plantation in Blowing Rock, NC was also detected.

35. **Cogbill, C.V., and P.S. White. 1991. The latitude-elevation relationship for spruce-fir forest and treeline along the Appalachian Mountain chain. *Vegetatio* 94(2): 153-175.** Appalachian red spruce-fir forests differ from boreal communities by the presence of Fraser fir and disturbance regimes based on wind rather than fire. South to north elevational decreases in hardwood/red spruce-fir ecotones occur where the mean July temperature is 62.6°F. Elevation-latitude relationships are similar to those seen in eastern Asia.
36. **Cogbill, C.V., P.S. White, and S.K. Wisser. 1997. Predicting treeline elevation in the southern Appalachians. *Castanea* 62(3): 137-146.** The hypothetical treeline at 36 degrees North latitude in the southern Appalachians was computed to be approximately 7930 ft based on modeling and comparisons to similar landforms in temperate Asia.
37. **Collins, B., T.M. Schuler, W.M. Ford, and D. Hawkins. 2010. Stand dynamics of relict red spruce in the Alarka Creek headwaters, North Carolina. Pp. 22-27 in *Proceedings from the conference on the ecology and management of high-elevation forests in the central and southern Appalachian Mountains*. Eds. Rentch, J.S., and T.M. Schuler. General Technical Report NRS-P-64. Northern Research Station, Forest Service, U.S. Department of Agriculture, Newtown Square, PA.** A relict mixed stand containing red spruce in a bog at the headwaters of Alarka Creek in Swain County, North Carolina showed evidence of continued red spruce growth and recruitment. Dendrochronologic analyses showed a decline in growth in the 1930s consistent with regional trends and some impact from a recent infestation of southern pine beetle was evident. The sheltered site partially buffers red spruce from otherwise unfavorable climatic conditions at such a low latitude and low elevation.
38. **Crandall, D.L. 1958. Ground vegetation patterns of the spruce-fir area of the Great Smoky Mountains National Park. *Ecological Monographs* 28(4): 337-360.** Variations in understory communities of Southern Appalachian red spruce-Fraser fir forest contain admixtures of 1) *Oxalis-Hylocomium*, 2) *Oxalis-Dryopteris*, 3) *Viburnum-Vaccinium-Lycopodium*, 4) *Senecio*, 5) *Rhododendron* along elevational and aspect gradient (exposed/xeric to sheltered/moist). Soils show evidence of pozolization. Wind is the most common natural disturbance, particular for Fraser fir stands at the highest elevations and most exposed locations. This type is slow or unable to recover from fire after several decades.
39. **Davis, J.H. 1930. Vegetation of the Black Mountains of North Carolina: An ecological study. *Journal of the Elisha Mitchell Society* 45: 291-318.** A detailed examination of the forest communities and their distributions by elevation, aspect and topographic position in the Black Mountains with variants and sub-types of the red spruce- Fraser fir community, northern hardwoods and Appalachian hardwoods (cove hardwoods, oak-chestnut, etc.) is provided. This paper provides some early distinct descriptions of beech gaps and hardwood “cloud” forests. Areas logged and subsequent burned in the red spruce-Fraser fir zone experienced significant erosion and typically regenerated to fire cherry and yellow birch, though evidence conifer seeding establishment throughout the denuded areas was occurring.
40. **Delcourt, H.A., and P.A. Delcourt. 1984. Late-quatarnary history of the spruce-fir ecosystem in the southern Appalachian Mountain region. Pp 22-35 in *The southern Appalachian spruce-fir ecosystem: Its biology and threats*. Eds. P.S. White. Research/Resources Management Report SER-71. Great Smoky Mountains National**

Park, National Park Service, U.S. Department of Interior, Gatlinburg, TN, USA.

Discussed the extent and composition of spruce-fir communities in the southern Appalachian Mountains from 18,000 years ago during the Pleistocene period to the present day. Conclude that spruce-fir in the southern Appalachians are the only true relict ecosystem of this forest type in the post-glacial period, although extent and floristic composition has changed over that time. Red spruce-Fraser fir ecosystems were expanding in the late Holocene, but that expansion has been interrupted due to anthropogenic activities, such as industrial logging and climate change.

41. **Dey, J.P. 1978. Fruticose and Foliose lichens of the high-mountain areas of the southern Appalachians 81(1): 1-93.** Approximately 16 species of lichens are indicative of the red spruce-Fraser fir forests in the southern Appalachians, though most species are not exclusively tied to a particular community type. Because of its flaking bark, fewer species of lichens occur on red spruce than Fraser fir.
42. **Duchesne, L., and M. Prévost. 2013. Canopy disturbance and intertree competition: implications for tree growth and recruitment in two yellow birch–conifer stands in Quebec, Canada. Journal of Forest Research18: 168-178.** Red spruce and balsam fir can recruit under their own species' canopy cover were as at least 25% of the overstory must be disturbed for red maple and yellow birch advance regeneration to be established. Partial cutting practices to harvest red spruce can ensure successful red spruce regeneration and continued capture of a forest site.
43. **Dull, C.W., J.D. Ward, H.D. Brown, G.W. Ryan, W.H. Clerke, and R.J. Uhler. 1988. Evaluation of spruce and fir mortality in the southern Appalachian Mountains. R-8-PR13, Southern Region, Forest Service, U.S. Department of Agriculture, Atlanta, GA.** Used aerial photography and ground plots to determine mortality of red spruce and Fraser fir in southwestern Virginia, western North Carolina, and eastern Tennessee. Found the spruce-fir forest type occurs over 65,752 acres in six major geographic areas, with the majority occurring on Great Smoky Mountains National Park (74%). Severe mortality increased with increasing elevation and was tied to Fraser fir mortality, which was correlated with elevation. However, red spruce mortality was not above expected natural mortality in a high-elevation forest, where volume of dead trees was variable by elevation.
44. **Eager, C. 1978. Distribution and characteristics of balsam woolly aphid infestations in the Great Smoky Mountains. M.S. thesis. University of Tennessee, Knoxville, TN.** Conducted surveys to determine history, current distribution, and level of infection of balsam woolly adelgid within the Great Smoky Mountains National Park. The adelgid arrived in the park in 1960 with initial infestation on Mt. Sterling. The adelgid was found throughout the entire spruce-fir ecosystem within the park, although infestation was greater in stands on the eastern portion of the park versus the western portion. Higher levels of infestation were common in mixed, mature, uneven-aged stands versus dense, young, even-aged stands of Fraser fir.
45. **Eager, C. 1984. Review of the biology and ecology of the balsam woolly aphid in southern Appalachian spruce-fir forests. Pp. 36-50 in The southern Appalachian spruce-fir ecosystem: Its biology and threats. Eds. P.S. White. Research/Resources Management Report SER-71. Great Smoky Mountains National Park, National Park**

Service, U.S. Department of Interior, Gatlinburg, TN, USA. Discusses introduction and spread of balsam woolly adelgid in the southern Appalachians, where it was first detected on Mt. Mitchell in 1957. The biology and ecology of the balsam woolly aphid is discussed, including dispersal and interactions with the host tree species in the southern Appalachians, Fraser fir. Highlights current status of this forest insect in the southern Appalachians at time of publication.

46. **Eager, C., and M.B. Adams (eds). 1992. Ecology and decline of red spruce in the eastern United States. Springer-Verlag.** Accumulation of research on red spruce, including forest characteristics, forest health, growth trends, and air pollution effects. Also synthesized the current knowledge of red spruce decline at high elevation sites, concluding that air pollution has played a significant role in the regional decline of red spruce.
47. **Eager, C., H. Van Miegroet, S.B. McLaughlin, and N.S. Nicholas. 1996. Evaluation of effects of acidic deposition to terrestrial ecosystems in Class I areas of the southern Appalachians. Report to the Southern Appalachian Mountains Initiative.** Long-term annual red spruce mortality in the southern Appalachians has been stable at about 1%, but has remained > 4% for Fraser fir. Dry deposition rates are greater in the red spruce-Fraser fir high elevation zone than elsewhere in the southern Appalachians. High elevation soils are naturally low in base saturation so the ability to absorb and buffer acidic additions is limited. Above 5000 ft., tree growth may be reduced. Throughout, nitrogen saturation and leaching patterns are influenced by stand condition.
48. **Elias, P.E., J.A. Burger, and M.B. Adams. 2009. Acid deposition effects on forest composition and growth on the Monongahela National Forest, West Virginia. Forest Ecology and Management 258: 2175-2182.** High levels of atmospheric deposition may have contributed to slower than expected growth increments in FIA plots sampled 1989-2001 in the central Appalachians of West Virginia. Positive growth in trees was correlated with concentrations of calcium and potassium in the surface horizon whereas concentrations of aluminum in the subsurface horizon were negatively correlated with growth. Evidence of "fertilization" from nitrogen deposition was not clearly shown. Cause and effect impacts of atmospheric deposition on forest health in the region will require additional experimentation, including better controls and the ability to provide nutrient additions.
49. **Feldman, S.B., L.W., Zelazny, and J.C. Baker. 1991. High-elevation forest soils of the southern Appalachians: I. Distribution of parent materials and soil-landscape relationships. Soil Science Society of America Journal 55(6): 1782-1791.** Assessed soils of red spruce-Fraser fir forests in the southern Appalachians. Soils did not differ in physical and morphological properties, despite differences in parent material and local geography. However, soils did exhibit differing chemical and mineralogical properties depending on parent material type.
50. **Feldman, S.B., L.W. Zelazny, and J.C. Baker. 1991. High-elevation forest soils of the southern Appalachians: II. Geomorphology, pedogenesis, and clay mineralogy. Soil Science Society of America Journal 55: 1782-1791.** Soils in red spruce-Fraser fir forests in the southern Appalachians are more similar to Spodosols found in low elevation northern Appalachian spruce-fir forests versus adjacent low elevation soils in the southern Appalachians.

51. Fraver, S., and A.S. White. 2005. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. *Journal of Vegetation Science* 16: 597-610. Red spruce can persist for many decades as suppressed advance regeneration that will respond to release, i.e., canopy gap. Overstory trees can achieve considerable longevity. These two factors allow red spruce communities to maintain and perpetuate themselves in absence of large stand-replacing disturbances which could allow a community shift.
52. Garten, C.T., W.M. Post, P.J. Hanson, and L.W. Cooper. 1999. Forest soil carbon inventories and dynamics along an elevation gradient in the Southern Appalachian Mountains. *Biogeochemistry* 45(2): 115-145. Soil organic carbon stocks and turnover time were higher in the red spruce-Fraser fir zone (>5250 ft) than at lower elevations and/or hardwood forests in the southern Appalachians. A 7.2°F increase in mean annual temperature could reduce soil organic carbon by >45%
53. Goelz, J.C.G., T.E. Burke, and S.M. Zedaker. 1999. Long-term growth trends of red spruce and Fraser fir at Mt. Rogers, Virginia, and Mt. Mitchell, North Carolina. *Forest Ecology and Management* 115: 49-59. In contrast with other studies, results showing a decline in red spruce and Fraser fir growth in the 20th Century in the Mt. Rogers and Mt. Mitchell areas were equivocal. Tree to tree variation and yearly fluctuation was evident. Declines or suppressed growth was only clearly identified for suppressed or dying stems.
54. Griscom, B., H.Griscom, and S. Deacon. 2011. Species-specific barriers to tree regeneration in high elevation habitats of West Virginia. *Restoration Ecology* 19(5): 660-670. Red spruce seedlings planted in high elevation field and forest sites in West Virginia showed greater annual survival than did planted hardwood seedlings. Impacts from white-tailed deer herbivory were minimal on red spruce, however, competition from herbaceous and graminoid flora did affect growth and survival.
55. Harmon, M.E., S.P. Bratton, and P.S. White. 1983. Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. *Vegetatio* 55: 129-139. Since the 1940s, virtually no natural ignition or man-caused fires have occurred in the red spruce-Fraser fir zone of the Great Smoky Mountains National Park. That along with long post-fire litter depth recovery times (>60 years) and relatively low number of woody species capable of stump-sprouting suggests this community is not fire-adapted and probably had a very long natural fire return interval. Full impact of the balsam woolly adelgid on Fraser fir populations is unknown but two scenarios are possible: functional extirpation or a shifting mosaic of diseased, mid-aged to older stands and younger, healthy stands not yet affected by the insect.
56. Hay, R.L., C.C. Eager, and K.D. Johnson. 1978. Fraser fir in the Great Smoky Mountains National Park: its demise by the balsam woolly aphid (*Adelges piceae* Ratz.). U.S. Dept. of Interior, National Park Service, Southeast Region, Contract Report. Report on the biology, distribution, and impact of the balsam woolly adelgid on Fraser fir in the Great Smoky Mountains National Park.

57. Hayes, M., A. Moody, P.S. White, and J.L. Costanza. 2006. **The influence of logging and topography on the distribution of spruce-fir forests near their southern limits in Great Smoky Mountains National Park, USA. *Plant Ecology* 189: 59-70.** In the Great Smoky Mountains National Park, on north-facing slopes presence or reestablishment of red spruce-Fraser fir was independent of logging history. However, on south-facing, warmer slopes, regeneration of red spruce-Fraser fir following logging was affected as the community type occurred >100 m higher in elevation in logged stands than unlogged stands at the same aspect or degree of insolation.
58. Hoffman, R.L. 1950. **Records of *Picea* in Virginia. *Castanea* 15(1): 55-58.** Red spruce occurs in scattered patches in western Virginia in Giles, Grayson, Highland, Rockingham, Smyth, Tazewell and Washington counties. Limited site descriptions are provided.
59. Hollingsworth, R.G., and F.P. Hain. 1991. **Balsam woolly adelgid (*Homoptera: Adelgidae*) and spruce-fir decline in the southern Appalachians: Assessing pest relevance in a damaged ecosystem. *Florida Entomologist* 74(2): 179-187.** Infestation of Fraser fir by balsam woolly adelgid interferes with sap flow and increases proportion of heartwood relative to sapwood. The mortality of trees may be increased by synergistic effects from atmospheric deposition and other factors.
60. Hopkins, A.D. 1891. **Black spruce. Pp 93-102 in Preliminary Report, Bulletin No. 17, West Virginia Agricultural Experiment Station, Morgantown, WV.** The distribution and acreage of red spruce forests in West Virginia were investigated in the 1880s just prior to the start of the industrial logging era. Surveys suggested >500,000 acres of relatively pure red spruce forest in the High Allegheny Mountains. At that time, large areas of dead and dying timber due to an infestation of Scolytid beetles was occurring.
61. Hornbeck, J.W., and J.N. Kochenderfer. 1998. **Growth trends and management implications for West Virginia's red spruce forests. *Northern Journal of Applied Forestry* 15(4): 197-202.** Declines in red spruce growth in both natural stands and plantation from the 1940s – 1990s was attributed to overstocking and competition. Overall growth rates and stand basal areas suggest that stands in the region are healthy and productive. Growth trends could be reversed by thinning or other harvests that would encourage regeneration.
62. Houle, D., P.J. Richard, S.O., Ndzangou, and M. Richer-Lafleche. 2012. **Compositional vegetation changes and increased red spruce abundance during the Little Ice Age in a sugar maple forest of north-eastern North America. *Plant Ecology* 213(6): 1027-1035.** Red spruce increased in abundance from the 12th through late 19th Century in eastern North America, coinciding with the climatic phenomenon known as the “Little Ice Age”. Decline in the distribution and condition of red spruce may be more a result of a past normal warming trend more so than atmospheric deposition, although this (deposition) could have served as an aggravating factor.
63. Jenkins, D.H., J. Sullivan, G.S. Amacher, N.S. Nicholas, and D.W. Reaves. 2002. **Valuing high altitude spruce-fir forest improvements: importance of forest condition and recreation activity. *Journal of Forest Economics* 8: 77-99.** Assessed willingness-to-pay surveys for changing forest conditions in red spruce-Fraser fir forests (i.e., insect

infestation, air pollution) to evaluate benefits from forest protection. Found consumptive forest users (i.e., hunters, anglers) had forest values that were sensitive to changes in forest condition, were as nonconsumptive forest users (i.e., hikers, campers) had values insensitive to forest change. Additionally, consumptive forest users have lower values for forest protection than nonconsumptive users, highlighting variations in public value for forest protection.

64. **Jenkins, M.A. 2003. Impact of the balsam wooly adelgid (*Adelges piceae* Ratz.) on an *Abies fraseri* (Pursh) Poir. Dominated stand near the summit of Mount LeConte, Tennessee. *Castanea* 68(2): 109-118.** Fraser fir stands assessed in 1979 in the Mt. LeConte area in 2001. Overstory basal area and density decreased. Although variable and dependent on how much advance regeneration was present prior to adelgid attack, understory basal area and density of Fraser fir increased. Fire cherry and mountain ash also responded to overstory mortality of Fraser fir. Blackberry increased in some plots. Sampled stands were in various states of transition and flux. The long-term status of Fraser fir is still unknown and will depend upon the ability of current regeneration to produce seed prior to expected insect-caused mortality as trees mature.
65. **Jenkins, M.A. 2007. Vegetation communities of Great Smoky Mountains National Park. *Southeastern Naturalist* 6: 35-56.** Discusses vegetation communities, included spruce-fir forests, of the Great Smoky Mountains National Park. Spruce-fir forests occur over 15,500 acres of the park (8% of the total area).
66. **Johnson, A.H., E.R. Cook, and T.G. Siccama. 1988. Climate and red spruce growth and decline in the northern Appalachians. *Proceedings of the National Academy of Science* 85: 5369-5373.** From the 1960s through the 1980s, mortality and widespread dieback of red spruce was observed throughout New York and New England. The 1960s were a period of abnormally cold winters and winter damage perhaps linked to elevated ozone levels was speculated as one explanation, along with region-wide drought, wind storms and outbreaks of spruce budworm.
67. **Johnson, D.W., H. Van Miegroet, S.E. Lindberg, D.E. Todd, and R.B. Harrison. 1991. Nutrient cycling in red spruce forest of the Great Smoky Mountains. *Canadian Journal of Forest Research* 21: 769-787.** Soils in the Clingman's Dome area of the Great Smoky Mountains National Park showed high levels of nitrogen leaching/export and accumulation of aluminum at or near levels where trees would be considered stressed in the 1980s. Nonetheless, visible impact to red spruce was not evident.
68. **Johnson, D.M., and W.K. Smith. 2006. Low clouds and cloud immersion enhance photosynthesis in understory species of a southern Appalachian spruce-fir forest (USA). *American Journal of Botany* 93(11): 1625-1632.** Photosynthetically active radiation at Mt. Mitchell and Roan Mountain, North Carolina was higher on clear days than cloud-immersed days. Carbon gains were higher in open forest stands on clear days. However, carbon gains were 22% greater for Fraser fir seedling under closed canopies during periods of cloud immersion where diffuse light penetration was more constant and uniform in these micro-sites. Climate changes that alter cloud height and immersion days could be ecologically significant to high elevation red spruce-Fraser fir communities, although the direction of change and impact is unknown at present.

69. **Johnson, K.D. 1977. Balsam woolly aphid infestation of Fraser fir in the Great Smoky Mountains. M.S. thesis. University of Tennessee, Knoxville, TN.** Ascertained relationship between levels of balsam woolly adelgid infestation and tree characteristics, such as size, crown position, and bark characteristics. Tree size was most significant determining adelgid populations on a tree and damage sustained: smaller trees sustained more damage, but larger trees supported the heaviest adelgid populations.
70. **Koo, K., B.C. Patten, and R.O. Teskey. 2011. Assessing environmental factors in red spruce (*Picea rubens* Sarg.) growth in the Great Smoky Mountains National Park: From conceptual model, envirogram, to simulation model. *Ecological Modelling* 222: 824-834.** Simulation models were developed that explain annual radial increment of red spruce growth in the Great Smoky Mountains suggest a complicated array of direct and indirect effects are operating locally. Model factors were assembled using an envirogram approach to elucidate how direct and indirect factors interact, i.e., climate dictates whether red spruce can occur in the region, however, indirect topographic factors such as aspect and sheltering are stronger modifiers. Model performance coarsely tracked observed values in some years.
71. **Korstian, C.F. 1937. Perpetuation of spruce on cut-over and burned lands in the higher Southern Appalachian Mountains. *Ecological Monographs* 7(1): 125-167.** Surveys of red spruce-dominated forests in North Carolina, Tennessee, West Virginia and Virginia in the early 1930s showed about 50,000 acres remaining after exploitative logging and widespread fire from an original 1,000,000 acres. Regeneration of red spruce or Fraser fir occurred best on sites that were not burned and had less of an original hardwood component. Fire kills seedlings and reduces or eliminates seed sources from residual conifers, allowing hardwoods such as fire cherry, black cherry and yellow birch to capture the stand and subsequent growing space. Red spruce seedling growth is slow relative to that of hardwood species. Native red spruce and Fraser fir perform better in post-fire plantings than a host of exotics. To be successful, plantings must occur immediately post-disturbance even on rocky, thin soils. Care must be taken when harvesting red spruce and diameter limit/partial cutting systems that retain much of the overstory are believed preferable to clearcutting. Efforts to preferentially remove hardwoods from mature mixed stands will benefit red spruce by creating growing space for residuals and limiting future hardwood seed sources.
72. **Krustchinsky, A.R. 2007. Post-fire recovery and successional dynamics of an old-growth red spruce forest in the Southern Appalachian Mountains. M.S. Thesis. Texas A&M University, College Station, Texas.** A dendrochronologic analysis of red spruce on Whitetop Mountain, Virginia showed that red spruce radial growth was correlated with precipitation and minimum temperatures of the previous year. Hardwoods, particularly yellow birch, increased in relative importance following a series of fires and logging that occurred in the early 20th Century. However, it is believed fires were light surface fires because many overstory stems predated the disturbance. Some red spruce were released by increase in growing space/light availability following partial cutting at that time. Red spruce continues to occupy all strata and surveyed plots showed evidence of advance regeneration.

73. Lawrence, G.B., W.C. Shortle, M.B. David, K.T. Smith, R.A.F. Warby, and A.G. Lapenis. 2012. Early indications of soil recovery from acidic deposition in US red spruce forests. *Soil Science Society of America Journal* 76(4): 1407-1417. Soil pH has increased and the concentration of available aluminum has decreased in soils where red spruce forests occur in the Northeast from the 1980s to present concomitant with a decline in deposition of SO_4^{2-} (a.k.a. sulfate). Soil recovery has had a vegetative process component as lower soil aluminum is a result of lower concentrations in litterfall, organic layers and fine roots.
74. LeBlanc, D.C., N.S. Nicholas, and S.M. Zedaker. 1992. Prevalence of individual-tree growth decline in red spruce populations of the Southern Appalachian Mountains. *Canadian Journal of Forest Research* 22: 905-914. Growth declines in red spruce in the southern Appalachians from the 1960s through 1980s was most apparent above 1980 m in elevation. Below that, no decline beyond historic ranges were noted. Possible explanatory mechanisms include reduced winter tolerance at elevations where acid cloud immersion and colder weather are more prevalent and exposure damage in stands that had high levels of Fraser fir mortality.
75. Lovett, G.M., and J.D. Kinsman. 1990. Atmospheric pollutant deposition to high-elevation ecosystems. *Atmospheric Environment* 24 (11): 2767-2786. Review of deposition of atmospheric pollutants with focus on mountains in eastern North America. High-elevation sites receive higher amounts of sulfate, nitrate, hydrogen, lead, and ozone deposition, although rates of pollutants deposition in mountain areas is highly variable due to topographic, vegetative, and meteorological conditions influencing cloud water deposition as well as wet and dry deposition.
76. Mazzeo, P.M. 1966. Notes on the conifers of Shenandoah National Park. *Castanea* 31(3): 240-247. Discusses the occurrence of conifer species, including red spruce and balsam fir, in Shenandoah National Park. Red spruce occurs on Hawksbill, Stony Man Mountain, and damp places of Limberlost, some transplants by Civilian Conservation Corps (CCC) exist in other areas. Balsam fir occurs natively on Hawksbill, Stony Man Mountain, and Crescent Rocks, other areas were transplanted by CCC projects.
77. McLaughlin, S.B., C.P. Andersen, P.J. Hanson, M.G. Tjoelker, and W.K. Roy. 1991. Increased dark respiration and calcium deficiency of red spruce in relation to acidic deposition at high-elevation southern Appalachian Mountains sites. *Canadian Journal of Forestry* 21: 1234-1244. Higher elevation red spruce-Fraser fir stands have increased dark respiration, because calcium tends to be deficient at these sites versus lower elevation sites. Acidic deposition may be a contributing factor influencing decreased calcium levels at high elevation sites, which are lower than low elevation sites due to naturally high leaching rates.
78. McLaughlin, S.B., D.J. Downing, T.J. Blasting, E.R. Cook, and H.S. Adams. 1987. An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the Eastern United States. *Oecologia* 72(4): 487-501. Decreases in radial growth in southern Appalachian red spruce occurred at higher elevations whereas red spruce at lower elevations did not display reduced growth. Sites were not considered overstocked, so competition was not believed to be a contributing factor.

79. McNab, W.H., J.H. Holbrook, and T.M. Oprean. 2010. Species composition and stand structure of a large red spruce planting 67 years after its establishment in western North Carolina. Pp. 126-133 *in* Proceedings from the conference on the ecology and management of high-elevation forests in the central and southern Appalachian Mountains. Eds. Rentch, J.S., and T.M. Schuler. General Technical Report NRS-P-64. Northern Research Station, Forest Service, U.S. Department of Agriculture, Newtown Square, PA. A red spruce plantation established at 5580 ft in the Balsam Mountains of North Carolina showed that red spruce growth was moderately correlated with terrain shape index and aspect. Yellow birch was the only other significant woody component in the stand.
80. Minckler, L.S. 1940. Early planting experiments in the spruce-fir type of the southern Appalachians. *Journal of Forestry* 38: 651-654. Trial plantings of various conifer species at 5600 feet on east and south aspects following the exploitative logging and subsequent fires in the Southern Appalachian red spruce-Fraser fir zone, showed that native Fraser fir and red spruce and non-native Norway spruce and red pine had the best rates of growth and survival. Red pine grew equally well on both aspects. However, growth was better on east aspects for the other three species as they were less adapted to xeric conditions than red pine.
81. Minckler, L.S. 1945. Reforestation in the spruce type in the Southern Appalachian. *Journal of Forestry* 43(5): 349-356. Test plantings of red spruce and red pine on sites with herbaceous cover, sites with undesirable hardwood or brush regeneration and sites with abundant rocks, thin or no soil and sparse vegetation were conducted in 1940 on the Pisgah National Forest in North Carolina and the Monongahela National Forest in West Virginia. Plantings varied by quality of seedling stock, site preparation, and planting technique. Plantings where herbaceous or competing woody vegetation was not controlled were less successful than sites site prepped with a cool fire and/or subjected to livestock grazing following planting.
82. Moore, P. T., R.J. DeRose, J.N. Long, and H. van Miegroet. 2012. Using silviculture to influence carbon sequestration in southern Appalachian spruce-fir forests. *Forests*, 3(2): 300-316. Simulations in Forest Vegetation Simulator of red spruce-Fraser fir stands in the Noland Divide Watershed portion of the Great Smoky Mountains suggest that even-aged harvests and regeneration over 100-year rotations sequestered more carbon (depending on fate of harvest wood) that did no action or uneven-aged harvest scenarios.
83. Moore, P.T., H. Van Miegroet, and N.S. Nicholas. 2007. Relative role of understory and overstory in carbon and nitrogen cycling in a southern Appalachian spruce-fir forest. *Canadian Journal of Forest Research* 37: 2689 – 2700. Measurement of aboveground pools and fluxes of biomass, carbon and nitrogen in the overstory and understory of red spruce stands in the Noland Divide Watershed of the Great Smoky Mountains indicate that lower elevation stands largely have recovered from balsam woolly adelgid infestation on Fraser fir and windthrow/exposure mortality of red spruce. Recovery has been slower at higher elevations but is occurring. Although herbaceous plants account for only 1% of the forest biomass, this portion of the community is responsible for uptake of approximately 50% of the available nitrogen input.

84. Moore, P.T., H. Van Miegroet, and N.S. Nicholas. 2008. Examination of forest recovery scenarios in a Southern Appalachian *Picea-Abies* forest. *Forestry* 81(2): 183-194. Examination of plot data from the Noland Divide Watershed in the Great Smoky Mountains National Park from 1993-2008 suggests that yellow birch has not responded noticeably to earlier overstory mortality of Fraser fir and red spruce. There is limited to equivocal evidence of red spruce spread. Biomass of Fraser fir has increased and concerns that Fraser fir will be locally extirpated are unfounded.
85. Morin, R.S., and R.H. Widmann. 2010. A comparison of the status of spruce in high-elevation forests on public and private land in the southern and central Appalachian Mountains. Pp. 134-139 *in* Proceedings from the conference on the ecology and management of high-elevation forests in the central and southern Appalachian Mountains. Eds. Rentch, J.S., and T.M. Schuler. General Technical Report NRS-P-64. Northern Research Station, Forest Service, U.S. Department of Agriculture, Newtown Square, PA. Analysis of Forestry Inventory Analysis data from Pennsylvania, West Virginia, Virginia, North Carolina and Tennessee show that approximately 90% of the red spruce forest type is on public land, though only 72% of red spruce trees tallied were on public land. Red spruce regeneration in extant stands is abundance suggesting the type will maintain itself. One-third of plots in the maple-beech-birch forest type (northern hardwoods) contained a large red spruce component as regeneration indicating that the red spruce type increase and expand its importance and extent in future forests.
86. Nicholas, N.S., and S.M. Zedaker. 1992. Expected stand behavior: site quality estimation for southern Appalachian red spruce. *Forest Ecology and Management* 47: 39-50. Produced site index curves for red spruce in the southern Appalachians to provide an indicator of site productivity and quality. Found that average site index decreases as elevation increases. Site index is also higher in pure spruce stands and decreases with increasing yellow birch or Fraser fir components in the stand.
87. Nicholas, N.S., S.M. Zedaker, and C. Eager. 1992. A comparison of overstory community structure in three Southern Appalachian spruce-fir forests. *Bulletin of the Torrey Botanical Club* 119(3): 316-332. Surveyed red spruce-Fraser fir forest stands at Mt. Rogers, Black Mountains, and Great Smoky Mountains to determine stand structure and compare current status of each forest stand to previous studies. The majority of Great Smoky Mountains sites were old-growth, while Mt. Rogers and Black Mountains had variable disturbance histories resulting in second-growth stands. Diameter distributions are skewed to smaller trees (<17.7 in dbh) at Mt. Rogers and Black Mountains, but skewed towards larger trees (> 17.7 in dbh) at Great Smoky Mountains. Black Mountains and Great Smoky Mountains show a shift from red spruce to Fraser fir due to balsam woolly adelgid infestations, but the trend is opposite at Mt. Rogers suggesting adelgid infestations may not have been as devastating in these stands.
88. Nicholas, N.S., S.M. Zedaker, C. Eager, 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(3): 289-299. Assessed seedfall and seedling recruitment in red spruce-Fraser fir in the Great Smoky Mountains over a 5 year period. Red spruce seed viability and densities of germinants and seedlings decreased with increasing elevation,

whereas Fraser fir germinant densities were higher with increases in elevation. Establishment of understory spruce and fir is influenced by intermittent seed production, adequate seed viability which may not be concurrent with high production years, germination rates, and survivorship of germinants and seedlings.

89. **Nodvin, S.C., H. Van Miegroet, S.E. Lindberg, N.S. Nicholas, and D.W. Johnson. 1995. Acidic deposition, ecosystem processes, and nitrogen saturation in a high elevation southern Appalachians watershed. *Water, Air, and Soil Pollution* 85: 1647-1652.** Used a watershed scale study to monitor precipitation, throughfall, stream hydrology, and stream chemistry in a red spruce-Fraser fir forest in the Great Smoky Mountains. Found the system was highly nitrogen saturated, thereby promoting chronic and episodic stream acidification.
90. **Noss, R.F., E.T. LaRoe, and J.M. Scott. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. *Biological Report* 28. U.S. National Biological Service, Washington, D.C.** Determined high-elevation red spruce-Fraser fir in the southern Appalachian Mountains to be one of the most critically endangered forest ecosystems in the United States. Found decreases of 35-57% in the southern Appalachians and 88-90% in the central Appalachians due to industrial logging activities and subsequent fires at the turn of the 20th century. Indicated 100% of southern Appalachian spruce-fir forests are seriously affected by balsam wooly adelgid and air pollution.
91. **Nowacki, G., R. Carr, and M. Van Dyck. 2010. The current status of red spruce in the Eastern United States: Distribution, population trends, and environmental drivers. Pp. 140-162 in *Proceedings from the conference on the ecology and management of high-elevation forests in the central and southern Appalachian Mountains*. Eds. Rentch, J.S., and T.M. Schuler. General Technical Report NRS-P-64. Northern Research Station, Forest Service, U.S. Department of Agriculture, Newtown Square, PA.** Determined red spruce forests in the southern Appalachians have higher red spruce densities, basal area, and overall importance versus red spruce forests in other regions. Red spruce populations are increasing due to increased regeneration and recruitment, reflecting the natural recovery of red spruce after industrial logging at the turn of the 20th century. Elevation and snowfall are strong predictors of spruce in the southern Appalachians, whereas temperature is the predictor in the Northeast.
92. **Oosting, H.J., and W.D. Billings. 1951. A comparison of virgin spruce-fir forest in the northern and southern Appalachian system. *Ecology* 32(1): 84-103.** Recorded the composition and structure of virgin red spruce-fir stands in the Appalachian Mountain and compare virgin stands between the southern and northern Appalachians. Stands at higher elevations in the Great Smoky Mountains are comparable to northern stands found in the White Mountains, although lower temperature extremes and snow precipitation, and greater rates of humidity and rain precipitation are associated with the southern Appalachians. Soils in both regions are podzols, although organics layers are thicker and more distinct in the northern Appalachians. A high proportion of species are consistent between northern and southern forests, although both areas have certain endemic species. Southern forests have higher herb and bryophyte cover, and average tree height is greater versus northern forests, indicating that growing conditions for spruce and fir is more favorable in the south.

93. Petersen, R.H. 1984. Comments on the fungi of the spruce-fir forest of the southern Appalachian mountains. Pp. 151-154 *in* The southern Appalachian spruce-fir ecosystem: Its biology and threats. Eds. P.S. White. Research/Resources Management Report SER-71. Great Smoky Mountains National Park, National Park Service, U.S. Department of Interior, Gatlinburg, TN, USA. Highlighted the lack of knowledge of fungi associated with high-elevation red spruce-Fraser fir forests in the southern Appalachians. Touches on lack of information and field work conducted on mycorrhizal fungi, which produce fruiting bodies called truffles and are an important diet of northern flying squirrels.
94. Petty, W.H., and S.E. Linberg. 1990. An intensive 1-month investigation of trace metal deposition and throughfall at a mountain spruce forest. *Water, Air, and Soil Pollution* 53: 213-226. Measured levels of lead, cadmium, zinc, and magnesium in a spruce forest for the month of July in 1986. Found that dry deposition of heavy metals, such as lead, influence total metal fluxes, especially during dry periods. Their research also confirms decreased levels of lead concentrations in the Great Smoky Mountains over the last decade.
95. Pier, P.A., F.C. Thornton, C. McDuffie, and P.J. Hanson. 1992. CO₂ exchange rates of red spruce during the second season of exposure to ozone and acidic cloud deposition. *Environmental and Experimental Botany* 32(2): 115-124. Conducted field experiments on red spruce seedlings in exclusion chambers that influenced ambient ozone and clouds levels. Found that ozone and acidic cloud water caused an increase in respiration of seedlings.
96. Pitekla, L.F., and D.J. Raynal. 1989. Forest decline and acidic deposition. *Ecology* 70(1): 2-10. Reviews forest decline due to acid rain in Europe and North America. Evaluates red spruce decline in the eastern United States and discussed current hypothesis for the decline. Concludes that little evidence exists that forest declines are caused solely by acidic deposition.
97. Pittillo, J.D. 1984. Regional differences of spruce-fir forests of the southern Blue Ridge south of Virginia. Pp 70-86 *in* The southern Appalachian spruce-fir ecosystem: Its biology and threats. Eds. P.S. White. Research/Resources Management Report SER-71. Great Smoky Mountains National Park, National Park Service, U.S. Department of Interior, Gatlinburg, TN, USA. Examines current knowledge of isolated sky islands of spruce-fir forests south of Virginia, focusing on differences between different islands and suggestions for future research needs.
98. Pyle, C. 1984. Pre-disturbance in the spruce-fir forests of Great Smoky Mountains National Park. Pp. 115-130 *in* The southern Appalachian spruce-fir ecosystem: Its biology and threats. Eds. P.S. White. Research/Resources Management Report SER-71. Great Smoky Mountains National Park, National Park Service, U.S. Department of Interior, Gatlinburg, TN, USA. Reviewed estimates of pre-logging and post-logging red spruce-Fraser fir in the southern Appalachians, including Great Smoky Mountains National Park, where industrial logging and subsequent fires were major disturbances prior to the designation of the park. Variation in estimates of pre-logging spruce is due to various definitions of red spruce forest and the red spruce-hardwood

ecotone. Determined the extent of red spruce-Fraser fir within the park and found 60% of this forest type is on the Raven Fork, Middle Prong, and West Prong watersheds.

99. Pyle, C. 1985. **Vegetation disturbance history of Great Smoky Mountains National Park: an analysis of archival maps and records. Research/Resources Management Report SER-77. Southeast Regional Office, U.S. Department of the Interior, National Park Service, Atlanta, GA.** Mapped major pre-park human disturbances for the Great Smoky Mountains National Park. Disturbance types included concentrated settlements, corporate logging, diffuse disturbance, livestock grazing, and fire. Also mapped virgin forest types within the park that received little or no disturbance prior to the park establishment.
100. Pyle, C. 1988. **The type and extent of anthropogenic vegetation disturbance in the Great Smoky Mountains before National Park Service acquisition. Castanea 53 (3): 183-196.** Determined type and extent of disturbances in Great Smoky Mountains National Park prior to establishment. Corporate logging and diffuse disturbance were the disturbance types with the largest extent within the park. Approximately 20% of the park had little or no record of disturbance and despite balsam woolly adelgid infestation and loss of the American chestnut, 6 of 28 major watersheds represent the best benchmarks for natural conditions within the park.
101. Pyle, C., and M.P. Schafale. 1988. **Land use history of three spruce-fir forest sites in Southern Appalachia. Forest and Conservation History 32(1): 4-21.** Described the historical anthropogenic disturbance of red spruce-Fraser fir forests of Mt. Rogers, Black Mountains, and the Great Smoky Mountains. Gives an account of past logging, burning, grazing, other human activities (e.g., tourism) and stochastic events (e.g., windthrows, ice storms) at each site.
102. Ramseur, G.S. 1960. **The vascular flora of high mountain communities of the southern Appalachians. Journal of Elisha Mitchell Science Society 76: 82-112.** A study on 1) the taxonomic study of the southern Appalachians red spruce-Fraser fir ecosystem, 2) comparison of flora of isolated sky islands, 3) successional stages leading to the red spruce-Fraser fir forest type, and 4) the geographic range the red spruce and Fraser fir dominance.
103. Reed, J.E., and W.K. Smith. 2012. **Stomatal frequency, distribution, and needle hydrophobicity in cloud forest spruce and fir, southern Appalachian Mountains. Review of Undergraduate Research in Agricultural and Life Sciences 7(1): 3-11.** Investigated leaf surface stomatal frequency and hydrophobicity of red spruce and Fraser fir near Mt. Mitchell in Pisgah National Forest. Stomatal frequency was similar between high and low elevation sites for both species. Stomatal patterns were non-random in both species. Leaf morphology and epicuticular wax formation may be influenced by atmospheric temperature and carbon dioxide levels, which could affect respiration rates in both of these high elevation species.
104. Rentch, J.S., T.M. Schuler, W.M. Ford, and G.J. Nowacki. 2007. **Red spruce stand dynamics, simulations, and restoration opportunities in the central Appalachians. Restoration Ecology 15(3): 440-452.** Assessed prospects for red spruce restoration in the central Appalachians. Use modeling in the Forest Vegetation Simulator to demonstrate the ability for silviculture to be used for restoration.

105. **Rentch, J.S., T.M. Schuler, G.J. Nowacki, N.R. Beane, and W.M. Ford. 2010. Canopy gap dynamics of second-growth red spruce-northern hardwood stands in West Virginia. *Forest Ecology and Management* 260: 1921-1929.** In second-growth forests influenced by clearcut logging practices during the turn of the 20th century, canopy gaps tend to be small, with a mean canopy gap size of 574.8 ft². Yearly canopy turnover rate is 1.4%. The most frequent gap maker was American beech, due to presence of beech-bark disease at study site. Most average size gaps close prior to red spruce ascension to the overstory, requiring additional overhead releases for understory red spruce to be recruited to the overstory canopy. Gap creation or overhead thinning via selection harvest could be an appropriate method for red spruce restoration.
106. **Rheinhardt, R.D. 1984. Comparative study of composition and distribution patterns of subalpine forests in the Balsam Mountains of southwest Virginia and the Great Smoky Mountains. *Bulletin of the Torrey Botanical Club* 111(4): 489-493.** Examined differences between spruce-fir communities on Mt. Rogers and Whitetop Mountains in Virginia and the Great Smoky Mountains. Composition between red spruce-Fraser fir forests on Mt. Rogers is similar to stands in the Smokies at similar elevations, whereas Whitetop lacks Fraser fir although elevations are suitable for this species. In Virginia, red spruce should cover slopes between 3900-5000 feet and lack of spruce forests below 4700 feet may be a result of anthropogenic disturbance.
107. **Rheinhardt, R.D., and S.A. Ware. 1984. Vegetation of the Balsam Mountains of southwestern Virginia: A phytosociological study. *Bulletin of the Torrey Botanical Club* 111(3): 287-300.** Describes vegetation communities of Balsam Mountains in Virginia and compares them with other high-elevation sites in the southern Appalachians. Mt. Rogers harbors the most northern extent of Fraser fir in southern Appalachians. Approximately 70% of Balsam Mountains are old-growth forests, with most undisturbed forests above 3773 ft in elevation, including boreal forests on Mt. Rogers and Whitetop which are believed to have never been logged. Separated vegetation into 9 different community types, including red spruce and red spruce-Fraser fir. Red spruce can extend down to 4692 ft at this site. High elevation sites on Whitetop should be environmentally capable of supporting spruce-fir forests, but only spruce occurs. Prior to industrial logging operations, slopes below 4920 ft may have been dominated by red spruce.
108. **Richardson, A.D., E.G. Denny, T.G. Siccamo, and X. Lee. 2003. Potential effects of a rising cloud ceiling on high elevation forests in eastern North America. *American Meteorological Society* 16: 2093-2098.** Assessed climate change effects on cloud-ceiling height in the Appalachian Mountains. Found rate of rising cloud-ceiling is positively related to higher latitudes. A rising cloud ceiling could cause community shifts, especially between deciduous and red spruce-Fraser fir forests, due to changes in moisture and cloud emersion at high elevation sites.
109. **Robinson, J.F., and E. Thor. 1969. Natural variation in *Abies* of the southern Appalachians. *Forest Science* 15: 238-245.** Determined variation in Fraser, intermediate, and balsam fir species in the southern, central, and northern Appalachians, respectively. Determined intermediate fir (occurring in West Virginia and northwestern Virginia) is

probably not of hybrid origin. Disjunct subpopulations of fir (i.e., intermediate fir from balsam fir) are relicts of a contiguous fir population.

110. **Rollins, A.W., H.S. Adams, and S.L. Stephenson. 2010. Changes in forest composition and structure across the red spruce-hardwood ecotone in the central Appalachians. *Castanea* 75(3): 303-314.** Examined changes in red spruce-northern hardwood ecotone forests over a 10-year period in eastern West Virginia and southwestern Virginia. Found the red spruce maintained its ecological importance or increased in number in all size classes. Expansions into northern hardwood forests were noted at some site, indicating that the red spruce forest type is stable and expanding in the central Appalachians.
111. **Rose, A.K., and N.S. Nicholas. 2008. Coarse woody debris in a southern Appalachian spruce-fir forest of the Great Smoky Mountains National Park. *Natural Areas Journal* 28(4): 342-355.** Measured volume, mass, changes in density, and changes in carbon and nitrogen concentration during decomposition in an old-growth red spruce-Fraser fir forest with balsam woolly adelgid infestation. Volume of coarse woody debris (CWD) was compared to other spruce-fir forests infested by the adelgid. Balsam woolly adelgid has impacted this ecosystem by increasing the amount of CWD.
112. **Rustad, L.E., and J.L. Campbell. 2012. A novel ice storm manipulation experiment in a northern hardwood forest. *Canadian Journal of Forest Research* 42(10): 1810-1818.** Measured canopy damage caused by an experimental ice glaze event on a northern hardwood dominant stand at Hubbard Brook, New Hampshire. Applied ice between 0.28 – 0.47 in of radial thickness, which is below the minimum cutoff for ice storm warnings by the US National Weather Service. Nevertheless, the ice glaze treatment resulted in significant canopy damage increasing the amount of fine and coarse woody debris on the forest floor, leaf-on canopy openness, and qualitative damage assessments. This disturbance type has a strong potential to shape the future structure and function of northern hardwood forests.
113. **Saunders, P.R. 1984. Recreational impacts in the southern Appalachian spruce-fir ecosystem. Pp. 100-114 in *The southern Appalachian spruce-fir ecosystem: Its biology and threats*. Eds. P.S. White. *Research/Resources Management Report SER-71. Great Smoky Mountains National Park, National Park Service, U.S. Department of Interior, Gatlinburg, TN, USA.*** Discussed how recreation influences red spruce-Fraser fir forests, especially when interacting with natural disturbances such as windthrow dynamics. Also notes the extent of red spruce and red spruce-Fraser fir forest types at different sites prior to and after industrial logging.
114. **Saunders, P.R., G.A. Smathers, and G.S. Ramseur. 1983. Succession of a spruce-fir burn in the Plott Balsam Mountains, North Carolina. *Castanea* 48(1): 41-47.** Assessed one hectare fire caused by a campfire in 1955 near Waterrock Knob in the Plott Balsam Mountains. The tree species composition was similar to logged red spruce-Fraser fir stands which were logged 30-50 years ago. Burned soils and erosions from severe fire caused a dense shrub layer may reduce tree regeneration.
115. **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.** Quantified and compared stand characteristics of

second-growth and old-growth red spruce forest communities. Snag basal area, height of dominant and co-dominant spruce, and maximum diameter were less in second-growth forests. Second-growth forests are overstocked and thinning small diameter trees may accelerate growth rates for individual trees and create certain old-growth attributes on a shorter time scale.

116. Sheppard, L.J., R.I. Smith, and M.G.R. Cannell. 1989. Frost hardiness of *Picea rubens* growing in spruce decline regions of the Appalachians. *Tree Physiology* 5: 25-37. Determined if pollutants predispose red spruce to frost damage by freeze-testing spruce shoots. Concluded that pollutant-induced susceptibility to damage from freezing is inadequate to explain spruce decline in the Appalachian Mountains.
117. Silver, W.L., T.G. Siccama, C. Johnson, and A.H. Johnson. 1991. Changes in red spruce population in montane forests of the Appalachians, 1982-1987. *American Midland Naturalist* 125(2): 340-347. Conducted a study to determine red spruce decline in the Appalachian Mountains. Found a substantial increase in the amount of standing dead canopy size red spruce at three sites in the northern Appalachians, with mortality occurring at the majority of sites higher than 2950 ft in elevation. In the southern Appalachians, there was no change in dead red spruce or crown vigor except the Mt. Mitchell and Roan Mountain sites, although changes were somewhat associated with ice storm damage. Results indicate that red spruce health and vigor may be decreasing at northern sites, but not southern sites.
118. Smith, G.F., and N.S. Nicholas. 1998. Patterns of overstory composition in the fir and fir-spruce forests of the Great Smoky Mountains after balsam woolly adelgid infestation. *American Midland Naturalist* 139(2): 340-352. Assessed declines in Fraser fir from balsam woolly adelgid infestation at 5 sites in the Great Smoky Mountains. Approximately 70% mortality was observed for standing fir basal area. Fir on Mt. Collins declined four years prior to the study, resulting in the highest mortality (91%) among the sites. Over the short-term, live Fraser fir density or mortality, treefall rates, and recruitment was associated with time since major mortality event. Predicted standing dead fir would increase 5-8 years after a major mortality event, but then decrease as snags fall and young Fraser fir fill the overstory.
119. Smith, G.F., and N.S. Nicholas. 1999. Post-disturbance spruce-fir forest stand dynamics at seven disjunct sites. *Castanea* 64(2): 175-186. Quantified the structure and dynamics of logged and old-growth red spruce-Fraser fir stands. Logged sites had higher recruitment rates, red spruce distributions skewed towards younger trees, and larger mean annual diameter growth increments. Logged stands had higher amounts of deciduous trees and lower abundance of spruce compared to old-growth sites, indicating that recovery from logging occurs over a lengthy period and it may be decades before previously logged sites begin to resemble old-growth forest communities.
120. Soule, P.T. 2011. Changing climate, atmospheric composition, and radial tree growth in a spruce-fir ecosystem on Grandfather Mountain, North Carolina. *Natural Areas Journal* 31(1): 65-74. Used dendrochronology to determine changes in radial growth rates of red spruce on Grandfather Mountain. Found radial growth rates trended positively through time and were associated with higher temperatures, lower amounts of precipitation, higher

atmospheric carbon, and lower amounts of sulfur dioxide and nitrogen dioxide. Found an increase of mean summer temperatures at Grandfather Mountain has increased more than 2.5°F over a 51 year period. Concluded that even though red spruce trees responded positively to increased temperatures and decreased precipitation, this may be a response to changes in climate that may still result in local extirpation of this species if temperatures continue to increase beyond a positive threshold.

121. **Springer, M.E. 1984. Soils in the spruce-fir region of the Great Smoky Mountains. Pp. 201-210 in The southern Appalachian spruce-fir ecosystem: Its biology and threats. Eds. P.S. White. Research/Resources Management Report SER-71. Great Smoky Mountains National Park, National Park Service, U.S. Department of Interior, Gatlinburg, TN, USA.** Soil types found under stands of red spruce-Fraser fir are extremely acidic and low in base saturation. Red spruce-Fraser fir forests have thicker organic horizons than northern hardwood forests. Variation in soil type is related to parent material, aspect, elevation, and vegetation communities. Predicted Spodosols or Inceptisols under variations of red spruce-Fraser fir vegetation types.
122. **Stehn, S.E., M.A. Jenkins, C.R. Webster, and S. Jose. 2013. Regeneration responses to exogenous disturbance gradients in southern Appalachian *Picea-Abies* forests. *Forest Ecology and Management* 289: 98-105.** Determined forest regeneration patterns in red spruce-Fraser fir forests with overstory mortality from the balsam woolly adelgid and acid deposition. Density of Fraser fir was associated with time since initial adelgid infestation. Fraser fir regeneration was influenced by elevation, blackberry cover, and soil concentrations of N, CA, and AL. Nitrogen deposition in the soil may influence the distribution of blackberry cover, which may negatively influence fir regeneration.
123. **Stephenson, S.L., and H.S. Adams. 1984. The spruce-fir forest on the summit of Mount Rogers in southwestern Virginia. *Bulletin of the Torrey Botanical Club* 111(1): 69-75.** Northern most extent of red spruce-Fraser fir forest type in at Mt. Rogers. Obtained quantitative data on vegetation structure and composition, as well as soil characteristics, and compared them with other red spruce-Fraser fir communities in the southern Appalachians. Fir and mountain ash had the highest importance values on ridgetops. Proportion of fir dominance in the overstory increases with elevation. Yellow birch had a relatively low importance value, most likely due to elevation. Fraser fir and red spruce were represented in all size classes. Red spruce-fir forests at Mt. Rogers are ecological similar to other stands in the southern Appalachians.
124. **Stephenson, S.L., and H.S. Adams. 1986. An ecological study of balsam fir communities in West Virginia. *Bulletin of the Torrey Botanical Club* 113(4): 372-381.** Measured the composition and structure of stands containing balsam fir at Canaan Valley, Blister Swamp, and Blister Run in West Virginia. Balsam fir was probably a minor component in pre-industrial logged forests and restricted to wet area above 3200 ft in elevation. Balsam fir was dominate at Blister Swamp and Blister Run, but red spruce and eastern hemlock were dominant at Canaan Valley. Blister Run has the most stable fir community compared to the other two sites. Balsam fir dominated stands were ecological similar to red spruce dominated stands, although there are some compositional and structural differences between the two forest types.

125. Stephenson, S.L., and J.F. Clovis. 1983. **Spruce forests of Allegheny Mountains in central West Virginia. *Castanea* 48(1): 1-12.** Provide quantitative descriptions of red spruce forests in the Allegheny Mountains of West Virginia and compare to spruce-fir forests in the northern and southern Appalachian Mountains. The majority of taxa occurring in spruce-fir forests of the northern and southern Appalachians are also present in the central Appalachians, with nearly equal numbers of taxa present from the northern and southern Appalachians. With exception of the absence of balsam fir in the majority of spruce forests in West Virginia, these stands are not different in composition from northern or southern spruce stands.
126. Tewksbury, C.E., and H. Van Miegroet. 2007. **Soil organic carbon dynamics along a climatic gradient in a southern Appalachian spruce-fir forest. *Canadian Journal of Forest Research* 37: 1161-1172.** Assessed the effects of temperature on soil carbon storage and dynamics in a red spruce-Fraser fir forest. Average annual soil temperature and days above 41°F were negatively correlated with increasing elevation. Forest floor carbon accumulation decreased significantly with elevation, but total soil carbon showed no trend. Cooler, higher elevations showed the lowest carbon turnover rates due to low decomposition rates. Soils with lower annual soil temperatures had lower mean annual CO₂ efflux.
127. Thomas-Van Gundy, M., M. Strager, and J. Rentch. 2012. **Site characteristics of red spruce witness tree locations in the uplands of West Virginia, USA. *The Journal of the Torrey Botanical Society*, 139(4): 391-405.** To increase understanding of historical red spruce-dominated forests in West Virginia, analyzed witness tree data from land deeds ranging from 1752 – 1899. Found that red spruce witness trees were found at higher elevations than non-spruce witness trees throughout the study area, but red spruce witness trees in the western Allegheny Mountains were found at lower elevations than non-spruce witness trees. Red spruce witness trees were associated with northeastern aspects on acidic and frigid soils.
128. Van Deusen, P.C (eds.). 1988. **Analyses of Great Smoky Mountain red spruce tree ring data. General Technical Report SO-69, Southern Forest Experiment Station, Forest Service, U.S. Department of Agriculture, New Orleans, LA.** Discussed multiple methods of tree ring analysis for red spruce, including time series models and fractal analysis.
129. Van Miegroet, H., P.T. Moore, C.E. Tewksbury, and N.S. Nicholas. 2007. **Carbon sources and sinks in high-elevation spruce-fir forests of the Southeastern US. *Forest Ecology and Management* 238: 249-260.** Investigates carbon pools, fluxes, and net ecosystem balance for red spruce-Fraser fir forests in the Great Smoky Mountains. On average, the forest contained 179 tons C acre⁻¹ with approximately half of the carbon stored below ground. Live trees represented a large, but variable, carbon pool. Dead wood contained up to 15% of total ecosystem carbon. The mean carbon sequestration over a 10 year period was 1204 tons C acre⁻¹ year⁻¹, but increased from 972 tons C acre⁻¹ year⁻¹ to 1387 tons C acre⁻¹ year⁻¹ during the latter part of the study. This trend was found especially at higher elevations, although increases in dead wood during that period may account for the increase.

130. **Wahlenberg, W.G. 1951. Planting in the Appalachian spruce-fir type. *Journal of Forestry* 49: 569-571.** Discussed planting of red spruce and Fraser fir in cut-over and burned areas in the southern Appalachians as a means to accelerate the establishment of this forest type.
131. **Webster, K.L., I.F. Creed, N.S. Nicholas, and H. Van Miegroet. 2004. Exploring interactions between pollutant emissions and climatic variability in growth of red spruce in the Great Smoky Mountains National Park. *Water, Air, and Soil Pollution* 159: 225-248.** Analyzed dendrochronology to determine changes in radial growth in red spruce. Found radial growth declines from 1940s-1970s and increases in the 1970s. Trees on ridges showed earlier, faster, and more homogenous declines than trees on sheltered landforms. Impact of atmospheric deposition may be more immediate for spruce on ridges versus sheltered landforms.
132. **White, P.B., P. Soulé, and S. van de Gevel. 2013. Impacts of human disturbance on the temporal stability of climate-growth relationships in a red spruce forest, southern Appalachian Mountains, USA. *Dendrochronologia*. 32(1): 71-77.** Used dendrochronology to investigate the temporal stability of a heavily disturbed second-growth red spruce-Fraser fir forest on Roan Mountain. Spruce temperature sensitivity occurred after clearcut harvesting, where canopy removal likely accentuated growth effects linked to temperature. Warmer summer temperatures result in reduced growth rates the following growing season by premature consumption of nutrient reserves. Results indicate how past disturbances can effect high-elevation tree response to climatic events.
133. **White, P.B., S.L. van de Gevel, and P.T. Soule. 2012. Succession and disturbance in an endangered red spruce-Fraser fir forest in the Southern Appalachian Mountains, North Carolina, USA. *Endangered Species Research* 18: 17-25.** Studied successional status and radial growth patterns in a heavily disturbed red spruce-Fraser fir forest on Roan Mountain. Changes in forest structure and species richness occurred with industrial logging and balsam woolly adelgid infestations. Although red spruce and fir were co-dominant prior to logging, increases in even-aged fir-dominate stands over spruce after disturbance is attributed to the rapid regeneration of fir over the shade-tolerant spruce.
134. **White, P.S. 1984. The southern Appalachian spruce-fir ecosystem: An introduction. Pp. 1-21 in *The southern Appalachian spruce-fir ecosystem: Its biology and threats*. Eds. P.S. White. *Research/Resources Management Report SER-71*. Great Smoky Mountains National Park, National Park Service, U.S. Department of Interior, Gatlinburg, TN, USA.** Defined the red spruce-Fraser fir forests of the southern Appalachians, southernmost extent of this forest type in eastern North America, as a distinct variant from other red spruce-Fraser fir forests on the continent due to isolation and small extent. Discusses threats, such as balsam woolly adelgid, and conservation status of this ecosystem. Highlights research within the Great Smoky Mountains National Park during time of publication.
135. **White, P.S., M.D. MacKenzie, and R.T. Busing. 1985. Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. *Canadian Journal of Forest Research* 15: 233-240.** Quantified natural disturbance regimes of old-growth forests and described community response to small treefall gaps. Found that gap frequencies in

southern Appalachian red spruce-Fraser fir forests occurred over similar proportion of the landscape as fire disturbance frequencies in northern latitude boreal forests, although patch size was considerably small for the former. Small-scale gap disturbance is the main disturbance type in southern Appalachian red spruce-Fraser fir forests and determines canopy composition.

136. **White, P.S., and L.A. Renfro. 1984. Appendix I. Vascular plants of the southern Appalachian spruce-fir: Annotated checklists arranged by geography, habitat, and growth form. Pp. 235-246 in The southern Appalachian spruce-fir ecosystem: Its biology and threats. Eds. P.S. White. Research/Resources Management Report SER-71. Great Smoky Mountains National Park, National Park Service, U.S. Department of Interior, Gatlinburg, TN, USA.** List of woody and herbaceous plant species found in red spruce-Fraser fir ecosystems of the southern Appalachians.
137. **Zedaker, S.M., D.M. Hyink, and D.W. Smith. 1987. Growth declines in red spruce: Are they natural or anthropogenic? Journal of Forestry 85: 34-36.** Demonstrated that radial incremental growth patterns of red spruce decrease as a stand ages, perplexing interpretations of atmospheric deposition's influence on tree growth. Natural stand dynamics, especially related to site index, stand density, land-use history, etc., must be taken in account to be able to correctly determine if anthropogenic stressors are influencing growth patterns.