SPRUCE-FIR FORESTS

Concept: Spruce-Fir Forests are communities of the highest elevations in North Carolina, naturally dominated or codominated by *Picea rubens* or *Abies fraseri*.

Distinguishing Features: Spruce-Fir Forests are distinguished from all other natural communities by the present or former dominance or codominance of *Picea rubens, Abies fraseri*, or occasionally by *Sorbus americana* at high elevations. Severely disturbed examples may be dominated by *Rubus canadensis*, residual *Betula alleghaniensis*, or by a variety of shrub species. A few of examples of Mountain Bogs and Fens may be dominated or codominated by *Picea rubens*, but will have saturated soils associated with *Sphagnum* spp. and other wetland species.

The Fraser Fir Forest type is distinguished by dominance by *Abies fraseri* at the highest elevations, great than 67% before balsam woolly adelgid-caused mortality. Examples dominated by *Picea rubens* alone or in combination with the other species represent the Red Spruce—Fraser Fir Forest type.

Sites: Spruce-Fir forests occupy all topographic settings, other than seepage-fed wetlands, at high elevations, extending to the highest peaks. The lower elevation for continuous spruce-fir forest mosaics is around 5500 feet, but some subtypes extend in patches down to 4500 feet or even 4000 feet.

Soils: Generally Inceptisols (Humadepts) of the Burton, Craggey, and Wayah series. In ecological literature on spruce-fir forests, soils are generally described as organic rich and extremely rocky, often as consisting of nothing but organic matter over rock. However, many sites can be observed to have loamy soil which, though rocky, is fairly deep. It has been noted in West Virginia that spruce forests generally have Spodosols, in contrast to other kinds of soils under hardwoods, with the belief that the acidic litter of spruce or hemlock is responsible for creation of the spodic horizon (Mathias, et al. 2015 [**or find paper in Science Advances 2017**] This does not appear to be the case in North Carolina. Soils here are very heterogeneous, and spodic horizons may be present locally but not widely.

Hydrology: Mesic to wet due to high rainfall, long periods bathed in fog, low temperatures, and high water-holding capacity in the organic-rich soil. Several high mountain ranges have measured average annual rainfall of 70-80 inches, and studies have found a comparable amount of additional water input through dripping of fog moisture. Rime ice is also common in winter. Although not commonly considered wetlands, many sites may be saturated for long periods in the growing season.

Vegetation: Communities of this theme are naturally closed forests where not recently disturbed. *Picea rubens* and *Abies fraseri* codominates in most of the elevational range, *Abies* becomes dominant at the highest elevations. *Betula alleghaniensis* codominates at lower elevations, and is present as a minor component at most elevations. *Sorbus americana* may occasionally dominate or codominate locally. Lower strata vary among communities, but most examples contain members of a suite of characteristic species that seldom found in lower elevation communities. These include *Oxalis montana, Dryopteris campyloptera, Clintonia borealis, Sambucus racemosa*

var. *pubens*, *Vaccinium erythrocarpum*, and a number of bryophytes such as *Hycomium splendens*. A large suite of rare plant and animal species also occur primarily in Spruce-Fir Forests.

Canopy composition has been drastically altered by the introduction of the balsam woolly adelgid, which killed all adult firs in the 1960s-1970s. Since that time, some stands have increased in cover of *Picea*, *Sorbus*, and *Betula*, others have also had significant spruce mortality and now are nearly treeless, and in others, young *Abies* have grown into dense stands of young canopy trees. Old-growth stands before the adelgid were notable for their large basal areas, and some remain so (?? Smith and Nichols 1999, 39.6 sq. m/ha. Rose and Nicholas 2008).

Dynamics: These communities in the natural state are uneven-aged, with abundant large, old trees. Work on population dynamics has found formation of small gaps by the death of one or several trees to be the most common mode of natural disturbance and gap phase regeneration the typical mode of tree reproduction (Busing 1985; White, MacKenzie, and Busing 1985). Natural fire is essentially absent in these communities, and the large blowdowns that are known are generally associated with artificial openings. Observations in the 1980s-2000s suggest that both ice and wind storms are significant factors creating small to medium size gaps.

Both spruce and fir produce abundant seedlings which persist beneath closed canopy until a gap is produced. However, this advanced regeneration can be observed to be extremely variable and patchy. Spruce is among the most shade-tolerant of trees, able to achieve up to 82% of its maximum photosynthesis at light levels found in sun flecks beneath a canopy (Alexander et al. 1995). Rentch, et al. (2016), in West Virginia, found understory spruce individuals 20-70 years old. Conversely, high light levels, especially when they appear suddenly, have been observed to harm spruce. Fox (1977) suggested a reciprocal replacement pattern between spruce and fir, with each tending to invade gaps left by the other. However, Busing (1985) found that fir was more likely to capture gaps made by all species. Spruce retained dominance or codominance despite its lower probability of gap capture because of its much greater longevity (300-400 years vs. 70-100 for fir). Yellow birch captured enough gaps to remain a permanent minor part of the community. Logging of spruce-fir forests without slash fires, as happened on Roan Mountain, could lead to nearly pure stands of fir.

Spruce-fir forests are especially vulnerable to human-caused disturbances such as logging and associated fire, as was widespread in the early 1900s. When the canopy was removed, the soil organic layer was able to dry and carry fire. Logging slash fires were described as consuming the organic soil itself as well as the seedling bank. The dominant trees, particularly spruce, were often unable to reestablish in cleared and burned areas (Korstian 1937, Saunders 1979, Pyle and Schafale 1985, 1988), and many burned areas have not reestablished full forest cover after more than a century. Though the failure of regeneration was sometimes attributed to the loss of organic soils, a similar failure is apparent on many deep mineral soils. However, Brown (1941) noted that spruce and fir were able to invade Grassy Balds and Heath Balds on Roan Mountain.

All Red Spruce--Fraser Fir Forests which escaped logging have been disturbed in recent years by the balsam woolly adelgid (*Adelges piceae*), an introduced insect pest which spread through the region in the 1960s. The adelgid kills essentially all adult firs, but is not able to infest young firs that have smooth bark. Degree of disturbance depends on the amount of Abies fraseri initially

present. Short term changes resulting from fir death included an increase in *Rubus canadensis* and various shrubs, and a decrease in moss and forest herbs (Boner 1979; DeSelm and Boner 1984). Jenkins (2003) noted a decline in *Oxalis montana* and *Clintonia borealis*, an increase in *Dryopteris campyloptera*, and a drastic increase in R*ubus*. Boner (1979) found that seedlings of fir increased with time since adelgid attack. Witter and Ragenovich (1986) suggested that fir seedlings present at the time of attack would be able to mature and reproduce before succumbing to the adelgid, but noted that if this failed to occur, *Abies fraseri* will cease to be a significant part of these high elevation southern Appalachian communities, since there is no seed bank in the soil. My observations suggest longer term results have been quite variable. Young firs have matured into well-developed canopies in many areas in all mountain ranges, but substantial areas have remained with broken canopies or remain treeless *Rubus* thickets. Balsam woolly adelgids are much less abundant than when they were spreading through large populations of susceptible trees, but they reappear in some patches and kill the newly mature trees.

In addition to the effects of the Balsam Woolly Adelgid, there has been widespread concern about declines in growth rates and unhealthy conditions of spruce through the 1980s and 1990s. These phenomena are believed to be similar to more severe declines observed in Europe and in the northeastern United States, hypothesized to be the result of air pollution. Extensive research appeared inconclusive on the subject of spruce decline and, although Dull, et al. (1988) reported that spruce-fir mortality patterns could be largely explained by balsam woolly adelgid effects, concern remains about potential effects of air pollutants. Mathis et al. ((2015) noted that tree growth rates increased dramatically at the time the Clean Air Act revisions greatly reduced acid deposition; Soule (2011) noted a similar pattern, though he noted that increased growth also corresponded with increased warmer climatic conditions.
It is widely accepted that during the colder climate of the Pleistocene, alpine tundra occurred at the highest elevations, and that spruce-fir forests in general migrated to lower elevations. It has been noted that spruce and fir are absent from several mountain ranges that reach elevations where they occur in other ranges. This is attributed to a period of warmer climate after the glaciation, the Hypsithermal, when spruce-fir forests may have been unable to persist at these elevations.

It is often said that spruce and fir have limited dispersal ability, and this is supported by the limited return to areas where they were removed by slash fires, and by their failure to return over thousands of years to ranges that apparently lost them during the Hypsithermal period. However, one range where they are absent, the Craggy Mountains, has a high elevation connection to spruce-fir forests of the Black Mountains, and spruce and fir can be seen spreading in small numbers across this connection at present. In ranges with spruce-fir forest, spruce trees can be seen in lower elevation communities and several miles from their optimal habitat, suggesting at least occasional seed dispersal to greater distances.

Though not noted in literature to my knowledge, these species may have been kept confined to their high elevation habitat by fire as much as by climate.

Comments: Ecological interest in spruce-fir forests has been intense, and there is extensive literature on them extending back to the early 1900s and continuing at present (Schafale – bibliography).

The Southern Appalachian spruce-fir forests are often named to indicate a relationship to the boreal forests of Canada. They share a number of species with the northern forests, but also contain a number of Southern Appalachian endemic species which set them apart. These include *Abies fraseri* itself. **[add other endemics]**

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