SPRUCE–FIR FORESTS

Contents

SPRUCE–FIR FORESTS THEME

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* in upland sites at elevations above 5000 feet. 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 these will have saturated soils and wetland species such as *Sphagnum spp*. at least in substantial portions.

Within the theme, Fraser Fir Forests are distinguished by dominance by *Abies fraseri* at the highest elevations, great than 67% before balsam woolly adelgid-caused mortality. The Red Spruce–Fraser Fir Forest type has a canopy naturally dominated or codominated by *Picea rubens*, often in combination with *Abies fraseri* or *Betula lenta*.

Sites: Spruce–Fir forests occupy almost all landforms at the highest elevations. Other than seepage-fed wetlands and rock outcrops, they cover the high 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. A pattern of inverted elevation zones is sometimes observed, where Spruce–Fir Forests occur below other communities such as Northern Hardwood Forests or Mountain Oak Forests in sheltered coves and areas with cold air drainage.

Soils: Spruce-Fir Forests are generally mapped as Inceptisols (Humadepts) of the Burton, Craggey, and Wayah series, but those in the Great Smoky Mountains are more recently mapped as Clingman (Lithic Udifolist). 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, and many sites have extremely heterogenous soils. 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 (Nauman et al. 2015). This has been used to identify sites for restoration of spruce forest. Spodosols have not been identified in North Carolina, but may yet be found, at least as one component of a heterogeneous soil mix.

Hydrology: Spruce–Fir Forests are mesic to wet due to high rainfall, long periods bathed in fog, low temperatures, and, usually, high water-holding capacity in the organic-rich soil. Several high mountain ranges have had 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 with small canopy gaps, where not recently disturbed. *Picea rubens* and *Abies fraseri* codominate in most of the elevational range,

while *Abies* becomes dominant at the highest elevations. *Picea* may dominate at the lowest elevations, but more often codominates with *Betula alleghaniensis*. *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 are 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 *Hylcomium 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, which may be numerous after major storms.

Both spruce and fir produce abundant seedlings that are shade-tolerant and persist beneath the 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, can lead to nearly pure stands of fir at elevations that would otherwise have mixed canopies.

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 that escaped logging have been disturbed in recent years by the balsam woolly adelgid (*Adelges piceae*), an introduced insect pest that 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. The 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 fails to occur in most places, *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. The author's observations suggest longer term results have been quite variable. Young firs have matured into well-developed canopies in many areas in all mountain ranges where they occur, but substantial areas still have 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 was regarded as 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 remained about potential effects of air pollutants. Mathis et al. (2015) and others have noted that tree growth rates increased dramatically around the same time that Clean Air Act revisions greatly reduced acid deposition, suggesting air pollution was important. 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, drier 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 some longer distance seed dispersal.

Though not apparently noted in literature, it is quite possible that the lower elevation limits of spruce, and perhaps of fir and associated species, is determined not by warmer climate, per se, but by the past occurrence of fire. Spruce populations persist at lower elevations in wetlands and in a couple of valley settings, including a couple south of the range of Spruce-Fir Forest communities on the mountain tops.

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 (literature reviewed in Schafale 1987).

The Southern Appalachian spruce-fir forests are sometimes called boreal forests 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 that set them apart. These include *Abies fraseri* itself.

References:

Alexander, J.D., J.R. Donnelly, and J.B. Shane.1995. Photosynthetic and transpirational responses of red spruce understory trees to light and temperature. Tree Physiology 15:393-398.

Boner, R.R. 1979. Effects of Fraser Fir Death on Population Dynamics in Southern Appalachian Boreal Ecosystems. M.S. Thesis, University of Tennessee, Knoxville.

Brown, D.M. 1941. Vegetation of Roan Mountain: a phytogeographical and successional study. Ecological Monographs 11:61-97.

Busing, R.T. 1985. Gap and Stand Dynamics of a Southern Appalachian Spruce-Fir Forest. Ph.D. Dissertation, University of Tennessee, Knoxville.

Cain, S.A. 1931. Ecological studies of the vegetation of the Great Smoky Mountains of North Carolina and Tennessee. Botanical Gazette 91:22-41.

Crandall, D.L 1958. Ground vegetation patterns of the spruce-fir areas of the Smoky Mountains. Ecological Monographs 28:337-360

Davis, J.H. 1930. Vegetation of the Black Mountains of North Carolina: an ecological study. Journal of the Elisha Mitchell Scientific Society 45:291-318.

DeSelm, H.R. and R.R. Boner. 1984. Understory changes in spruce-fir during the first 16-20 years following the death of fir. In: P.S. White (ed.): The Southern Appalachian Spruce-Fir Ecosystem: Its Biology and Threats. National Park Service Research/Resources Management Rept. SER-71.

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. Protection Report R8-PR, U.S. Forest Service, Southern Region, U.S. Dept. of Agriculture.

Eagar, C. 1984. Review of the biology and ecology of the balsam woolly aphid in southern Appalachian spruce-fir forest. In: P.S. White (ed.): The Southern Appalachian spruce-fir ecosystem: its biology and threats. National Park Service Research/Resources Management Rept. SER-71.

Fox, J.F. 1977. Alternation and coexistence of tree species. American Naturalist 111:69-89.

Jenkins, M.A. 2003. Impact of the balsam woolly adelgid (Adelges piceae Ratz.) on an Abies fraseri-dominated stand near the summit of Mount LeConte, Tennessee. Castanea 68:109-118.

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

Mathias, J.M., L.A. Scholtz, B.T.Russell, and R.B. Thomas. 2015. Using tree rings of red spruce in the Central Appalachian Mountains to explore growth trends before and after the Clean Air Act. Abstract for Ecological Society of America Annual Meeting. Baltimore, MD.

Nauman, T.W., J.A. Thompsons, S.J. Teets, T.A. Dilliplane, J.W. Bell, S.J. Connolly, H.J. Liebermann, and K.M. Yoast. 2015. Ghosts of the forest: Mapping pedomemory to guide forest restoration. Geoderma http://dx.doi.org/10.1016/j.geoderma.2015.02.002. Elsevier B.V. 0016-7061.

Pittillo, J.D. 1984. Regional differences of spruce-fir forests of the southern Blue Ridge south of Virginia. In: P.S. White (ed.) The Southern Appalachian spruce-fir ecosystem: its biology and threats. National Park Service Research/Resources Management Rept. SER-71.

Pyle, C. 1984. Pre-park disturbance in the spruce-fir forests of Great Smoky Mountains National Park. In: P.S. White (ed.). The Southern Appalachian spruce-fir ecosystem: its biology and threats. National Park Service Research/Resources Management Rept. SER-71.

Pyle, C. and M.P. Schafale. 1985. History of disturbance in spruce-fir forest of the SARRMC intensive study sites -- Mt. Rogers National Recreation Area, Black Mountains, and Great Smoky Mountains. Report to Southern Appalachian Spruce-Fir Ecosystem Assessment Program.

Pyle, C. and M.P. Schafale. 1988. Land use history of three southern Appalachian spruce-fir forest study sties. Journal of Forest History 32:4-21.

Rentch, J.S., W.M. Ford, T.S. Schuler, J.Palmer, and C.A. Diggins. 2016. Release of suppressed red spruce using canopy gap creation – ecological restoration in the Central Appalachians. Natural Areas Journal 36:29-37.

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 Torrey Botanical Club 111:489-493.

Rose, A.K. and N.S. Nicholas. 2008. Coarse woody debris in a Southern Appalachian spruce-fir forest in the Great Smoky Mountains National Park. Natural Areas Journal 28:342-355.

Saunders, P.R. 1979. The vegetational impact of human disturbance on the spruce-fir forests of the Southern Appalachian Mountains. Ph.D. Dissertation, Duke University, Durham, NC.

Schafale, M.P. 1987. Indexed Bibliography of Southern Appalachian Spruce-Fir Forests. Report to SARRMC

Smith, G.F. and N.S. Nicholas. 1999. Post-disturbance spruce-fir forest stand dynamics at seven disjunct sites. Castanea 64:176-186.

Schofield, W.B. 1960. The ecotone between spruce-fir and deciduous forest in the Great Smoky Mountains. Ph.D. Dissertation, Duke University, Durham, NC.

Schwartzkopf, S.K. 1974. Comparative vegetation analysis of five spruce- fir areas in the Southern Appalachians. Unpublished research report, Furman University.

Soule, P.T. 2011. Changing climate, atmospheric composition, and radial tree growth in a spruce-fir ecosystem on Grandfather Mountain, NC Natural Areas Journal 31:65-74 .

Watson-Cook, E.L. 2017. Characteristics and classification of southern Appalachian spruce-fir forests. M.S. Thesis, University of North Carolina, Chapel Hill.

Weaver, G.T. 1972. Dry matter and nutrient dynamics in red spruce-Fraser fir and yellow birch ecosystems in the Balsam Mountains, western North Carolina. Ph.D. Dissertation, University of Tennessee, Knoxville.

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 Resources 15:233-240.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1-80.

Witter, J.A. and I. Ragenovich. 1986. Regeneration of Fraser fir at Mount Mitchell, North Carolina after depredations by the balsam woolly adelgid. Forest Science 32:585-594.

KEY TO SPRUCE—FIR FORESTS

1. Highest elevation sites, generally above 6200 feet (but may be lower on sites with extreme weather such as Grandfather Mountain). Canopy tending to dominance by *Abies fraseri* (Historically dominated by *Abies*. At present, may have young *Abies* stands, sparse *Abies* along with sparse *Picea, Sorbus americana*, or *Betula alleghaniensis;* or may be dominated by *Rubus canadensis* or other shrubs and have dense snags or fallen logs of a former *Abies* stand. Note that less extreme sites may become dominated by *Abies* if logged and not burned, as at Roan Mountain, but these are better regarded as Red Spruce—Fraser Fir Forests.).
    2. Forest with a dense shrub layer of evergreen ericaceous shrubs, generally with *Rhododendron catawbiense* dominant. Occurring in small patches on sharp, exposed topography or on shallow soil **..... Fraser Fir Forest (Rhododendron Subtype)**
    2. Forest without a dense evergreen shrub layer; ground cover of mosses, ferns, other herbs, or deciduous shrubs, sometimes with little ground cover in dense young stands. Occurring in fairly large patches on deep soils in a variety of topography ..... **Fraser Fir Forest (Herb Subtype)**

1. Mid to relatively lower elevation sites, generally 4500-6200 feet. Canopy dominated by *Picea rubens*, or codominated by *Picea* with *Abies fraseri*, *Sorbus americana*, or *Betula alleghaniensis*.
    3. Sites boulderfields, with complete cover of large rocks with open space beneath them. Most vegetation growing on rock surfaces or in organic accumulations on and between rocks……. .....**Red Spruce–Fraser Fir Forest (Boulderfield Subtype)**
    3. Sites not boulderfields; plants rooted in deep or shallow, relatively continuous soil.
        4. Mid elevation sites, generally 5500-6200 feet. Canopy generally dominated by *Picea rubens*, potentially along with *Abies fraseri* or occasionally *Sorbus americana*; *Betula alleghaniensis* is present only in small numbers, not codominant.
            5. Forest with a dense shrub layer of evergreen ericaceous shrubs, generally with *Rhododendron catawbiense* or *Rhododendron maximum* dominant. Occurring in small patches on sharp, exposed topography or on shallow soil .... **Red Spruce–Fraser Fir Forest (Rhododendron Subtype**)
            5. Forest without a dense evergreen shrub layer; ground cover of mosses, ferns, other herbs, or deciduous shrubs, sometimes with little ground cover in dense young stands. Occurring on deep soils in a variety of topography, often in large patches .... **Red Spruce–Fraser Fir Forest (Herb Subtype)**
        4. Lower elevation sites, generally below 5500 feet, in mosaics with hardwood forests. Canopy codominated by *Picea rubens* and *Betula alleghaniensis*, or occasionally by *Picea rubens* with *Tsuga canadensis, Quercus rubra*, or without codominants.
            6. Forest with a dense shrub layer of evergreen ericaceous shrubs, generally with *Rhododendron catawbiense, Rhododendron maximum,* or *Kalmia latifolia* dominant.
                7. Occurring in small patches on sharp, exposed topography or on shallow soil. Shrub layer may include *Kalmia latifolia, Rhododendron catawbiense,* or other species of drier sites ..... **Red Spruce–Fraser Fir Forest (Birch Transition Shrub Subtype)**
                7. Occurring in small patches in sheltered ravines. *Tsuga canadensis* sometimes codominates. Shrub layer usually *Rhododendron maximum* .... **Red Spruce–Fraser Fir Forest (Low Rhododendron Subtype)**
            6. Forest without a dense evergreen shrub layer; ground cover of mosses, ferns, other herbs, or deciduous shrubs, sometimes with little ground cover in dense young stands. Occurring on deep soils in a variety of topography, often in large patches .... **Red Spruce–Fraser Fir Forest (Birch Transition Herb Subtype)**

FRASER FIR FOREST (HERB SUBTYPE)

Concept: Fraser Fir Forests are the highest mountain forests, in which *Abies fraseri* naturally dominates and the few other tree species are distinctly subordinate under natural conditions. Widespread mortality caused by balsam woolly adelgid has left many areas devoid of canopy at present. The Herb Subtype encompasses those examples without a substantial evergreen heath layer, which generally have deciduous shrubs and well-developed herb layers. Forests where *Abies fraseri* formerly dominated and has not regenerated may be regarded as degraded examples of this subtype or may be classified as successional communities. Forests where *Abies fraseri* canopies died and regenerated as very dense stands that have no shrub or herb layer are included in this subtype. A few natural forests dominated by *Sorbus americana* along with *Abies fraseri* are also included here. This community is a higher elevation analogue of Red Spruce–Fraser Fir Forest (Herb Subtype).

Distinguishing Features: Fraser Fir Forest is theoretically distinguished from Red Spruce–Fraser Fir Forest and all other natural communities by having present or recent past natural dominance by *Abies fraseri*, making up 67% or more of the canopy cover. The Herb Subtype is distinguished from the Rhododendron Subtype by dominance of the lower strata by herbs or deciduous shrubs, rather than *Rhododendron* or other evergreen heaths.

Because of widespread destruction of fir canopy by the balsam woolly adelgid, examples are now dominated by young fir trees or by successional vegetation of *Rubus allegheniensis* or other species. The presence of large numbers of dead conifer stems at very high elevation, combined with absence or scarcity of other mature trees, is generally sufficient to distinguish a damaged Fraser Fir Forest from other high elevation community types. Some Red Spruce–Fraser Fir Forests became dominated by *Abies fraseri* after logging in the early part of the century, since Fraser fir more readily establishes in gaps than red spruce. These can be difficult to distinguish without historical data but can be expected to gradually succeed to greater spruce dominance.

Synonyms: Synonyms: *Abies fraseri / Viburnum lantanoides / Dryopteris campyloptera - Oxalis montana / Hylocomium splendens* Forest (CEGL006049).
Ecological Systems: Central and Southern Appalachian Spruce-Fir Forest (CES202.028).

Sites: Fraser Fir Forest occurs on ridge tops and slopes at the highest elevations, generally above 6200 feet, though lower in the extreme climate of Grandfather Mountain.

Soils: Most examples are mapped as Burton (Typic Humadept) or Craggey (Lithic Humadept). However, areas in the Great Smoky Mountains are more recently mapped as Clingman (Lithic Udifolist). Discussion among soil scientists suggests that soils in spruce-fir communities are extremely heterogeneous and that Spodosols are also possible.

Hydrology: These are likely the wettest of the spruce-fir forests, occurring where fog is most common and rainfall is high. Some soils may be shallow and rocky, but thick litter and moss cover retain moisture.

Vegetation: In undisturbed condition, the Herb Subtype exists as a closed forest, broken by small to medium size gaps. *Abies fraseri* makes up more than 75% of the canopy in natural undisturbed condition. Occasionally *Sorbus americana* codominates. Smaller amounts of *Picea rubens* and generally even less *Betula alleghaniensis* are usually present. Occasional *Prunus pensylvanica* and *Acer spicatum* may be the only other trees. The shrub layer may be moderate in density to nearly absent. Saplings of *Abies* and *Picea* may dominate, or combinations of *Viburnum lantanoides*, *Vaccinium erythrocarpum*, *Vaccinium simulatum*, *Vaccinium corymbosum*, and *Sambucus racemosa* var. *pubens* may predominate. The herb layer is dense in mature stands, though it may be sparse under dense young canopies. Species characteristic of most spruce-fir forests predominate, including *Dryopteris campyloptera*, *Athyrium asplenioides, Oxalis montana, Carex intumescens, Carex brunnescens, Oclemena acuminata, Clintonia borealis, Solidago glomerata*, and *Chelone lyonia*. Other species noted by Crandall (1958) in the Smokies, before widespread fir mortality, include *Monotropa uniflora, Impatiens pallida, Houstonia serpyllifolia*, and *Streptopus roseus*. Mosses often cover the ground, alone or under the herbs. *Hylacomium splendens* is most often dominant, but *Hypnum crista-castrensis*, *Rhytidiadelphus triquinatus*, *Polytrichum* spp., and other species may be abundant. Mature forests also often have dense cover of mosses and liverworts on the trunks of fir trees, whose smooth bark is particularly hospitable for epiphytes.

After universal destruction of the fir canopies by balsam woolly adelgid, canopies in these communities now range from sparse to dense young or maturing *Abies* or are replaced by successional *Rubus canadensis* or shrub stands. Young-mature forests often have little shrub, herb, or moss layer beneath a dense canopy, and the young tree trunks have not yet developed the characteristic epiphytic cover.

Range and Abundance: Ranked G1. This subtype is confined to just a few mountain ranges: the Black Mountains, Smokies, Richland Balsam, and Grandfather Mountain. It is present on Mount LeConte and Clingmans Dome in Tennesssee but is otherwise endemic to North Carolina.

Associations and Patterns: The Herb Subtype grades to Fraser Fir Forest (Rhododendron Subtype) on more exposed sites. It grades to Red Spruce–Fraser Fir Forest, especially the Herb Subtype, at lower elevations.

Variation: Watson-Cook (2017) recognized two minor variants as well as the classic version of this community. Both of the variants are in lower mountain ranges in places that were logged; they thus appear to be fir-dominated successional versions of Red Spruce–Fraser Fir Forest rather than places that have all the characteristics of Fraser Fir Forest. Crandall (1958) recognized four site types within the range of variation covered by this subtype: Oxalis-Hylacomium, Oxalis-Dryopteris, Viburnum-Vaccinium-Dryopteris, and Senecio (i.e., *Rugelia nudicaulis*). These do not seem to be distinguishable in the broader range of this community. Given the extreme changes all examples have undergone, much greater variation in disturbance response now masks any such variation. Many examples that remain now show none of these undergrowth types. *Rugelia nudicaulis* is confined to the Smoky Mountains and could be recognized as a variant, but the occurrence of this species too has been heavily altered by the universal disturbance.

Dynamics: Dynamics are generally similar to those throughout the Spruce–Fir Forests theme. However, the extreme high elevation and exposure of this subtype may subject it to more frequent

or extreme disturbance by wind and ice. The dominance of fir without codominant spruce on the highest peaks has been noted in ecological literature for decades (e.g., Whittaker 1956). Some spruce, and even birch, is generally present to the highest elevations, showing the change in communities does not indicate a limit of physiological tolerance of the high elevation but only a shift in dominance. Busing (1985) and White et al. (1985) found that fir captured canopy gaps at several times the rate the spruce did. The two coexisted in typical Red Spruce–Fraser Fir Forests because this was balanced by the much shorter life span of fir. This dynamic may be shifted at the highest elevations, with more frequent natural disturbance reducing the advantage of spruce's potential life span.

The anomalous natural occurrence of Fraser Fir Forest at lower elevation on Grandfather Mountain likely is caused by greater wind disturbance in the more extreme weather there. The shift to fir dominance after logging (without slash fires), as at Roan Mountain, also results from the ability of fir to capture gaps. Those logged stands can be expected to shift back to spruce dominance over time.

In northern Appalachian forests of *Abies balsamea*, there is a well-studied phenomenon of "fir waves" — migrating elongate canopy gaps. A progression of tree ages on one side shows how the gap has moved in the direction of prevailing winds. The mechanism is increased harshness of the environment at the downwind edge of a gap, which makes older trees more likely to die. On the upwind side, young trees that established on the more sheltered side of the gap are less susceptible to wind. The result is a set of periodic wave-live gradients in tree age. A similar pattern reportedly could be observed in fir forests in Japan. Shortly before the last fir stands died, a pattern of linear gaps was visible on the flank of Mount Mitchell. It is possible that this phenomenon occurred there as well, but the evidence is now lost. Once the structured age pattern is eliminated, it may not easily reform.

Comments: A successional association, *Rubus canadensis* - (*Rubus idaeus ssp. strigosus*) / *Athyrium filix-femina* - *Solidago glomerata* Shrubland (CEGL003893), has been defined to cover examples of fir forests where canopy trees have died and not regenerated.

The distinction between Red Spruce–Fraser Fir Forest and Fraser Fir Forest has been blurred by the widespread death of firs and may become lost as the climate becomes warmer. However, it appears worth keeping recognition of these community types for the present. After 50 years since the first widespread death of fir, spruce has not come to dominate the highest peaks.

Rare species:

References:

Busing, R.T. 1985. Gap and Stand Dynamics of a Southern Appalachian Spruce-Fir Forest. Ph.D. Dissertation, University of Tennessee, Knoxville.

Crandall, D.L 1958. Ground vegetation patterns of the spruce-fir areas of the Smoky Mountains. Ecological Monographs 28:337-360

Watson-Cook, E.L. 2017. Characteristics and classification of southern Appalachian spruce-fir forests. M.S. Thesis, University of North Carolina, Chapel Hill.

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 Resources 15:233-240.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1-80.

FRASER FIR FOREST (RHODODENDRON SUBTYPE)

Concept: Fraser Fir Forests are the highest mountain forests, in which *Abies fraseri* naturally dominates and the few other tree species are distinctly subordinate under natural conditions. Widespread mortality caused by balsam woolly adelgid has left many areas devoid of canopy at present. The Rhododendron Subtype covers those examples with canopies dominated by *Abies fraseri* and with a substantial evergreen heath layer, usually *Rhododendron catawbiense*. These are generally associated with more exposed topography, such as sharp ridge tops, and areas with shallow soil near rock outcrops.

Distinguishing Features: Fraser Fir Forest is theoretically distinguished from Red Spruce–Fraser Fir Forest and all other natural communities by having present or recent past natural dominance by *Abies fraseri*, making up 67 percent or more of the canopy cover. The Rhododendron Subtype is distinguished from the Herb Subtype by having a well-developed shrub layer dominated by *Rhododendron* or other evergreen heaths in places with exposed topography. Exposed very high elevation sites with large numbers of dead trees and dominance by *Rhododendron* can be assumed to be degraded examples of this subtype.

Synonyms: *Abies fraseri / (Rhododendron catawbiense, Rhododendron carolinianum*) Forest (CEGL006308).
Ecological Systems: Central and Southern Appalachian Spruce-Fir Forest (CES202.028).

Sites: Fraser Fir Forest occurs on ridge tops and slopes at the highest elevations, generally above 6200 feet, though lower in the extreme climate of Grandfather Mountain. The Rhododendron Subtype occurs on sharp ridge tops, south-facing slopes, and areas with shallow soils.

Soils: This subtype occurs in association with rock outcrops and in other areas that appear to have shallow soil. They generally are not specifically distinguished in soil mapping but are likely as heterogeneous as other spruce-fir soils.

Hydrology: As with other Spruce–Fir Forests, this community is generally wet to mesic, sometimes saturated for long periods. However, the shallow soil is more prone to becoming dry in periods without rain or fog.

Vegetation: The Rhododendron Subtype has a closed to open tree canopy dominated by *Abies fraseri*, sometimes with small numbers of *Picea rubens*, *Sorbus americana*, *Betula alleghaniensis*, or *Prunus pensylvanica*. The canopy trees may be small and stunted. There generally are no other understory species, though *Acer spicatum*, *Amelanchier arborea*, or other understory species of other subtypes might be present. There is a dense shrub layer, generally dominated by *Rhododendron catawbiense* or *Rhododendron carolinianum*. Other shrubs may include *Rhododendron (Menziesia) pilosum* or *Diervilla sessilifolia.* Herbs are sparse, sometimes completely absent except on small rock outcrops within the community. However, bryophytes may be abundant in some places, with *Hylocomium splendens*, *Sphagnum* spp., and *Polytrichum ohioense* being noted by Crandall (1958).

Range and Abundance: Ranked G1. This subtype is one of the rarest of Spruce–Fir Forests, occurring only as small patches within a matrix of the Herb Subtype. It is confined to just a few mountain ranges: the Black Mountains, Smokies, Richland Balsam, and Grandfather Mountain. It is present on Mount LeConte and Clingmans Dome in Tennessee but is otherwise endemic to North Carolina.

Associations and Patterns: The Rhododendron Subtype is associated with the Herb Subtype, and often grades to High Elevation Rocky Summit.

Variation: Examples may be heterogeneous over very fine scales, with the transition to adjacent communities or with occurrence of small rock outcrops within them.

Dynamics: All aspects of general Spruce-Fir Forest dynamics are expected to be similar in this subtype, except that the more extreme sites may have more frequent natural disturbance and slower tree regeneration.

Comments: This subtype appears to be very rare and is often absent even on exposed ridge tops. Some literature suggests it is part of a regularly occurring community pattern, but this is not the case in the author's experience.

Rare species:

References:

Crandall, D.L 1958. Ground vegetation patterns of the spruce-fir areas of the Smoky Mountains. Ecological Monographs 28:337-360

RED SPRUCE–FRASER FIR FOREST (HERB SUBTYPE)

Concept: Red Spruce–Fraser Forests are high mountain forests in which *Picea rubens* (or occasionally *Sorbus americana*), with or without *Abies fraseri* or hardwoods, are naturally dominant. The Herb Subtype covers the most common examples with canopies of primarily *Picea rubens*, generally with *Abies fraseri*, only minor amounts of other trees, and lower strata consisting of deciduous shrubs, herbs, and mosses.

Distinguishing Features: Red Spruce–Fraser Fir Forests are distinguished by canopy dominance of *Picea rubens* alone or with *Abies fraseri*, *Betula alleghaniensis, Sorbus americana*, or occasionally other hardwoods, in a high elevation upland setting. The Herb Subtype is distinguished from the Rhododendron Subtype and Low Rhododendron Subtype by dominance of the lower strata by herbs or deciduous shrubs, rather than by *Rhododendron* spp. It is distinguished from the Birch Transition Herb Subtype and Birch Transition Shrub Subtype by having less than 33% cover of *Betula alleghaniensis* or other hardwoods (other than *Sorbus americana)* in the canopy, counting gaps recently occupied by now-dead *Abies fraseri*. The Herb Subtype is distinguished from the Boulderfield Subtype, which also has a deciduous shrub, herb, and moss undergrowth, by having boulder cover less than 90 percent, having a richer herb layer, and having *Ribes* spp., *Polypodium appalachianum*, and other boulderfield species present in no more than small numbers.

Synonyms: Synonyms: *Picea rubens - (Abies fraseri) / Vaccinium erythrocarpum / Oxalis montana - Dryopteris campyloptera / Hylocomium splendens* Forest (CEGL007131).
Ecological Systems: Central and Southern Appalachian Spruce-Fir Forest (CES202.028).
SAF 34: Red Spruce-Fraser Fir (in part).

Sites: The Herb Subtype occurs on ridge tops and slopes at high elevations, generally 5500-6200 feet.

Soils: Any of the soils typical of high mountains may support this community. See the discussion of soils for the Spruce-Fir Forests theme as a whole.

Hydrology: Red Spruce-Fraser Fir Forests are mesic to wet due to high rainfall, long periods bathed in fog, low temperatures, and, usually, high water-holding capacity in the organic-rich soil.

Vegetation: In a natural state, the Herb Subtype is a closed forest, except for small to medium canopy gaps. It is dominated by *Picea rubens* with varying amounts of *Abies fraseri* and limited amounts of *Betula alleghaniensis* and *Sorbus americana*. *Betula cordifolia* and other tree species may be present only in small numbers. *Betula alleghaniensis* is usually present but comprises less than 33% of the canopy in unaltered stands. *Abies* is usually present but may be absent. Watson-Cook (2017) found an average of 25-50% cover each of *Picea* and *Abies* in the cluster of typical plots of this community. *Betula alleghaniensis* averaged 10-25% cover; *Sorbus* average cover was very low.

The understory is sparse to moderate except in canopy gaps. All three main canopy dominants may be fairly abundant in the understory. Other species may include *Acer spicatum*, *Acer rubrum*, *Acer*

pensylvanicum, *Fagus grandifolia*, and *Amelanchier arborea*. The shrub layer may be sparse to dense. Sometimes saplings of spruce or fir dominate it. *Vaccinium erythrocarpum*, *Vaccinium corymbosum*, *Vaccinium simulatum*, *Viburnum lantanoides*, *Viburnum cassinoides*, and *Sambucus racemosa* var. *pubens* are reported as relatively frequent and abundant in most site descriptions. *Rubus canadensis* has become frequent and often abundant after widespread canopy opening from a variety of causes. However, Watson-Cook (2017), analyzing plot data generally from the 1990s-2000s, found *Rhododendron maximum* to be the most constant shrub species, and the most abundant on average. The other shrub species were less constant and had lower average abundance. The herb layer may range from nearly absent to a lush cover of ferns or forbs over a thick bed of moss. Most often dominant species are *Dryopteris campyloptera, Dryopteris intermedia, Athyrium asplenioides, Dennstaedtia punctilobula*, *Oclemena acuminata, Oxalis montana*, *Ageratina altissima* var. *roanensis* and, in the Smokies, *Rugelia nudicaulis*. Other frequent and abundant herbs include *Carex intumescens*, *Circaea alpine*, *Chelone glabra*, *Eurybia chlorolepis*, *Glyceria melicaria*, *Clintonia borealis*, *Viola blanda*, *Tiarella cordifolia*, *Huperzia lucidula*, *Solidago glomerata,* and *Dryopteris intermedia* (Watson-Cook 2017; Crandall 1958; Whittaker 1956; Pittillo 1984. Bryophytes are usually particularly prominent in these communities. *Hylocomium splendens*, *Ptilimnium crista-castrensis*, *Polytrichum* spp., and *Atrichum* spp. may form dense beds, alone or beneath fern or forb cover. Epiphytic mosses and liverworts are also characteristic, with several species specialized for bark of mature fir trees. This lush, bryophyte-rich herb layer is now uncommon but was common in older stands with intact canopy in the author's experience in the 1980s. It is emphasized by almost all earlier literature.

Range and Abundance: Ranked G2. This appears to be the most widespread of the spruce-fir communities, probably because it is more broadly defined than most, but it is still extremely limited by the scarcity of land area at high elevation and by losses in the early 1900s. The bulk of the global range of this community and corresponding NVC association is in North Carolina; it extends into Tennessee and Virginia. The southern limit is Richland Balsam and the central Smoky Mountains; the northern limit is Mt. Rogers in Virginia, but some disjunct stands farther north are also attributed to the association. Spruce-fir forests of all subtypes are absent from several mountain ranges within their geographic and elevation range, such as the Craggy Mountains and Elk Knob.

Associations and Patterns: The Herb Subtype is usually associated with other subtypes of Red Spruce-Fraser Fir Forest, grading to the Rhododendron Subtype around rock outcrops, to the Birch Transition Herb and Birch Transition Shrub Subtypes at lower elevation. It grades to Fraser Fir Forest at higher elevations. Northern Hardwood Forest (Beech Gap Subtype) may occur in the same elevational range, on upper south-facing concave slopes.

Variation: This is the most broadly defined of the spruce-fir subtypes, representing the most common version in the middle range of its environment. As such, there is substantial variation in vegetation, especially in the lower strata. Variation is now confused because of widespread alteration caused by balsam woolly adelgid, and variable recovery since that time. There are floristic and vegetational differences among Red Spruce–Fraser Fir Forest in different mountain ranges (Pittillo 1984; Schwartzkopf 1974), but most such differences are much less than the variation within single stands. Crandall (1958), working in old-growth forests of the Smokies before balsam woolly adelgid disturbance, described five undergrowth types in spruce-fir forests

of the Smokies, three of which would fall within this subtype. Her *Oxalis-Hylacomium* and *Viburnum-Vaccinium-Dryopteris*, said to be associated with different elevational ranges, do not seem to be readily distinguishable throughout the range of the community. Her third, *Cacalia rugelia* (=*Rugelia nudicaulis*) type is distinctive for biogeographic reasons, because the species is limited to the Great Smoky Mountains. Watson-Cook (2017), analyzing CVS data representing most sites other than the Smokies, post-adelgid, found four floristic clusters within this subtype that she chose to recognize. One is transitional to the Birch Transition Herb Subtype, one is transitional to the Rhododendron Subtype, and one represents a more herbaceous/less shrubby set, relative to the fourth, classic version. The numbers of plots representing those clusters other than the classic is small, generally three, and the level of difference seems too small to recognize as variants, though further consideration is warranted.

Thus, two variants are recognized:
1. Typic Variant has variable deciduous shrub, forb, fern, and moss dominance in the lower strata. It remains heterogeneous, and study of occurrences if they stabilize and recover from recent disturbances may lead to confirmation of the Crandall (1958) subtypes or recognition of other subtypes.
2. Ragwort Variant is a biogeographic variant having *Rugelia nudicaulis* as the predominant herb. This species occurs only in the Great Smoky Mountains, where it often dominates the herb layer. This variant co-occurs with the Typic Variant in the Smokies, and occurs nowhere else.

Dynamics: All of the dynamics discussed in the theme description apply to this subtype.

Comments: Most of the extensive study of Spruce-Fir Forests in general has been carried out in examples of this subtype.

Rare species:
Vascular plants: *Abies fraseri, Betula papyrifera var. cordifolia, Botrychium oneidense, Rugelia nudicaulis, Calamagrostis canadensis, Cardamine clematitis, Carex projecta, Cinna latifolia, Geum geniculatum, Glyceria nubigena, Phegopteris connectilis, Poa palustris, Rhododendron vaseyi, Stachys clingmanii, Streptopus amplexifolius,* and *Streptopus roseus* var. *roseus.*
Nonvascular plants: *Bazzania nudicaulis, Brachydontium trichodes, Frullania oakesiana, Harpanthus drummondii, Leptodontium excelsum, Leptoscyphus cuneifolius, Lophozia attenuata, Metzgeria temperata, Nardia scalaris, Plagiochila corniculata,* and *Sphenolobopsis pearsonii.*
Vertebrate animals: *Aegolius acadicus, Catharus guttatus, Corvus corax, Desmognathus wrightii, Glaucomys sabrinus coloratus, Parus atricapillus,* and *Sylvilagus transitionalis*.
Invertebrate animals: *Microhexura montivaga*.

References:
Brown, D.M. 1941. Vegetation of Roan Mountain: a phytogeographical and successional study. Ecological Monographs 11:61-97.

Cain, S.A. 1931. Ecological studies of the vegetation of the Great Smoky Mountains of North Carolina and Tennessee. Botanical Gazette 91:22-41.

Crandall, D.L 1958. Ground vegetation patterns of the spruce-fir areas of the Smoky Mountains. Ecological Monographs 28:337-360

Davis, J.H. 1930. Vegetation of the Black Mountains of North Carolina: an ecological study. J. Elisha Mitchell Sci. Soc. 45:291-318.

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

Pittillo, J.D. 1984. Regional differences of spruce-fir forests of the southern Blue Ridge south of Virginia. In: P.S. White (ed.) The Southern Appalachian spruce-fir ecosystem: its biology and threats. National Park Service Research/Resources Management Rept. SER-71.

Pyle, C. 1984. Pre-park disturbance in the spruce-fir forests of Great Smoky Mountains National Park. In: P.S. White (ed.). The Southern Appalachian spruce-fir ecosystem: its biology and threats. National Park Service Research/Resources Management Rept. SER-71.

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 Torrey Botanical Club 111:489-493.

Schofield, W.B. 1960. The ecotone between spruce-fir and deciduous forest in the Great Smoky Mountains. Ph.D. Dissertation, Duke University, Durham, NC.

Schwartzkopf, S.K. 1974. Comparative vegetation analysis of five spruce- fir areas in the Southern Appalachians. Unpublished research report, Furman University.

Soule, P.T. 2011. Changing climate, atmospheric composition, and radial tree growth in a spruce-fir ecosystem on Grandfather Mountain, NC. Natural Areas Journal 31:65-74 .

Watson-Cook, E.L. 2017. Characteristics and classification of southern Appalachian spruce-fir forests. M.S. Thesis, University of North Carolina, Chapel Hill.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1-80.

RED SPRUCE–FRASER FIR FOREST (RHODODENDRON SUBTYPE)

Concept: Red Spruce–Fraser Forests are high mountain forests in which *Picea rubens* (or occasionally *Sorbus americana*), with or without *Abies fraseri* or hardwoods, are naturally dominant. The Rhododendron Subtype covers those examples with a substantial evergreen heath shrub layer, generally associated with exposed topography and shallow soils.

Distinguishing Features: Red Spruce–Fraser Fir Forests are distinguished by canopy dominance of *Picea rubens* alone or with *Abies fraseri*, *Betula alleghaniensis, Sorbus americana*, or occasionally other hardwoods, in a high elevation upland setting. The Rhododendron Subtype is distinguished from the Low Rhododendron Subtype by occurrence at higher elevations, in topographically exposed sites, and generally by having substantial *Rhododendron catawbiense* or *Rhododendron carolinianum* rather than strong dominance by *Rhododendron maximum*. It is distinguished from the Herb Subtype and Boulderfield Subtype by its well-developed evergreen shrub layer. It is distinguished from the Birch Transition Subtypes by having less than 33% cover of *Betula* in the canopy. This subtype may be transitional to Heath Bald, but can be distinguished by a well-developed, though sometimes open, tree canopy.

Synonyms: *Picea rubens* - (*Abies fraseri*) / (*Rhododendron catawbiense, Rhododendron maximum*) Forest (CEGL007130).
Ecological Systems: Central and Southern Appalachian Spruce-Fir Forest (CES202.028).

Sites: The Rhododendron Subtype occurs on sharp ridge tops and convex slopes, generally 5500-6200 feet, generally with shallow soils or associated with rock outcrops.

Soils: This subtype occurs in association with rock outcrops and in other areas that appear to have shallow soil. Soils are mapped similarly to other Spruce-Fir Forests, but may represent inclusions.

Hydrology: As with other Spruce-Fir Forests, the Rhododendron Subtype is generally wet to mesic, sometimes saturated for long periods. However, the shallow soil is more prone to becoming dry in periods without rain or fog.

Vegetation: The Shrub Subtype has a closed to open tree canopy dominated by *Picea rubens*, with varying amounts of *Abies fraseri*, *Betula alleghaniensis*, and *Sorbus americana*. While the canopy may be open due to fir mortality, it may also be open due to the presence of rock outcrops and possibly due to greater canopy mortality related to shallow soils. Watson-Cook (2017) reported an average of 25-50% spruce cover, with other species much less abundant. The understory, if present, consists primarily of the canopy species. *Amelanchier laevis* is the only other understory species noted. There is a dense shrub layer dominated by *Rhododendron catawbiense* and *Rhododendron maximum*. Other shrubs reported as abundant in some places are *Viburnum cassinoides*, *Vaccinium simulatum*, *Viburnum lantanoides*, *Diervilla sessiliflora*, *Pieris floribunda*, *Aronia melanocarpa*, *Vaccinium stamineum*, and *Vaccinium pallidum* (Watson-Cook 2017; Crandall 1958). The latter species is uncertain; it might possibly represent *Vaccinium altomontanum*. Herbs are generally sparse and consist of the same species as in the Herb Subtype. *Dryopteris campyloptera* and *Carex brunnescens* are among the species noted in studies, though Watson-Cook (2017) had a number of other species in plots that were transitional to the Herb

Subtype. The CVS data set analyzed by Watson-Cook appears to under-represent this subtype, with only a few plots from a very limited number of sites. This is to be expected given the frequent steepness and difficulty of working in this community. Older qualitative site descriptions usually don't distinguish this subtype from other subtypes, making it difficult to characterize this subtype.

Range and Abundance: Ranked G1. This subtype is much less extensive than the Herb Subtype. Even in areas with extensive spruce-fir forest, such as the central Smokies, it is limited to small patches. It appears to be present in fewer sites, but this is uncertain given that it is not distinguished in many site descriptions.

Associations and Patterns: The Rhododendron Subtype generally grades to the Herb Subtype, but it may grade to any other subtype, to Fraser Fir Forest, Heath Bald, or High Elevation Rocky Summit.

Variation: Examples are often heterogeneous over very fine scales, with the transition to adjacent communities or with occurrence of small rock outcrops within them. Crandall (1958) loosely recognized a rhododendron-viburnum type, codominated by *Viburnum lantanoides*. Watson-Cook (2017) recognized a variant cluster transitional to a community resembling the Herb Subtype and also recognized within the Herb Subtype a more shrubby version transitional to the Rhododendron Subtype. In both cases, I regard these as ecotonal and not distinct enough to recognize as formal variants. More distinctive variants might be found amid the variations in shrub composition among ranges, such as the abundance of *Pieris floribunda* in examples at Shining Rock, but these need further study before recognizing.

Dynamics: All aspects of general Spruce-Fir Forest dynamics are expected to be similar in this subtype, except that the more extreme sites may have more frequent natural disturbance and slower tree regeneration. Though not well known, it appears that landslides, abundant in some mountain ranges, may create habitat for this subtype.

Comments: As with the Rhododendron Subtype of Fraser Fir Forest, this subtype appears to be very rare and is often absent even on exposed ridge tops. Some literature suggests it is part of a regularly occurring community pattern, but this is not the case in the author's experience.

Rare species:
Vascular plants: *Betula cordifolia, Geum geniculatum, Glyceria nubigena Phegopteris connectilis, Rhododendron vaseyi, Rubus strigosus,* and *Solidago spithamaea*.
Nonvascular plants: *Gymnoderma lineare*.
Vertebrate animals: *Aegolius acadicus, Catharus guttatus, Desmognathus wrightii, Glaucomys sabrinus coloratus,* and *Sylvilagus transitionalis.*
Invertebrate animals: *Microhexura montivaga*.

References:
Crandall, D.L 1958. Ground vegetation patterns of the spruce-fir areas of the Smoky Mountains. Ecological Monographs 28:337-360

Watson-Cook, E.L. 2017. Characteristics and classification of southern Appalachian spruce-fir forests. M.S. Thesis, University of North Carolina, Chapel Hill.

RED SPRUCE–FRASER FIR FOREST (BOULDERFIELD SUBTYPE)

Concept: Red Spruce–Fraser Forests are high mountain forests in which *Picea rubens* (or occasionally *Sorbus americana*), with or without *Abies fraseri* or hardwoods, are naturally dominant. The Boulderfield Subtype covers *Picea*-dominated boulderfields. Plants capable of rooting in moss mats or shallow soil make up most of the community. This subtype is transitional to the High Elevation Birch Boulderfield Forest type of lower elevations, but it is more similar to other spruce-fir forests than lower elevation boulderfields are to Northern Hardwood Forests.

Distinguishing Features: Red Spruce–Fraser Fir Forests are distinguished by canopy dominance of *Picea rubens* alone or with other species, in a high elevation upland setting. The Boulderfield Subtype is distinguished from all other subtypes by occurring on a well-developed boulderfield. It has near 100% ground cover of large rocks, with open spaces beneath the boulders, and with soil present only as small pockets on top of rock. The herb layer consists primarily of species that can root on moss mats or small soil pockets, such as *Polypodium appalachianum* and mosses. While many spruce-fir forests of all subtypes are rocky and have shallow soil, this subtype is reserved for the rare extreme setting of well-developed boulderfields.

Synonyms: *Picea rubens / Ribes glandulosum* Forest (CEGL007128).
Ecological Systems: Central and Southern Appalachian Spruce-Fir Forest (CES202.028).

Sites: The Boulderfield Subtype occurs on steep high elevation slopes. Boulderfields are either talus beneath large outcrops or colluvial deposits, apparently the result of periglacial processes during the Pleistocene.

Soils: Soils probably represent an unnamed series. Boulders, often up to several meters across, cover all of the surface, and generally are piled several deep. There are voids between the boulders below the surface. Soil is limited to shallow accumulations of organic matter on top of rocks or small accumulations at contacts between them.

Hydrology: The general setting is mesic to wet due to high rainfall, long periods bathed in fog, and low temperatures; however, water-holding capacity is low in the small soil pockets and drainage is rapid through the large voids. Conditions may become dry in even short periods of drought.

Vegetation: The Boulderfield Subtype has a closed or somewhat open canopy dominated by *Picea rubens* and *Betula alleghaniensis*, sometimes with small numbers of *Abies fraseri* or *Tsuga canadensis*. The understory is dominated by *Acer spicatum*, with *Sorbus americana* the only other likely species other than canopy species. There may be a very open shrub layer, with *Viburnum lantanoides* the most constant and abundant species. Other shrubs sparsely present may include *Vaccinium erythrocarpum*, *Rhododendron catawbiense*, and *Ribes cynosbati* or *Ribes glandulosum*. The herb layer consists primarily of species able to live on bare rock. There is often extensive moss cover. *Polypodium appalachiana* is extensive in most places. Other herbs typical of spruce-fir forests are present in favorable soil pockets, including *Dryopteris campyloptera*, *Dryopteris intermedia*, *Oxalis montana,* and *Huperzia lucidula*.

Range and Abundance: Ranked G1. This may be the rarest of Spruce–Fir Forest subtypes. Extensive examples are known only from Grandfather Mountain, but it apparently is present in the Smokies and possibly on Roan Mountain. It is either endemic to North Carolina or has a small occurrence in Tennessee.

Associations and Patterns: The Boulderfield Subtype grades to other subtypes of Red Spruce–Fraser Fir Forest.

Variation: Examples vary with the transition to adjacent communities.

Dynamics: Dynamics are presumably similar to the Spruce–Fir Forests theme in general, but canopy gaps can be expected to persist longer because of the difficulty of tree establishment. The extent of the ground surface where tree seedlings can establish is limited, though it is sufficient to lead to a full forest canopy. The boulderfields seem to be stable but shifting or falling of rocks may occur occasionally and lead to local disturbance.

Comments: This is one of the least studied spruce-fir subtypes. It is not mentioned in any of the earlier published literature. It has been observed by the author, several CVS plots document it, and it was recognized in Watson-Cook (2017) based on these plots.

Recognition of well-developed boulderfields is easy in person, where the near total cover of moss- and fern-covered rocks is very distinctive and the near impossibility of walking is obvious. They can be difficult to recognize in both qualitative descriptions and plot data, since many spruce-fir sites have abundant boulders and since boulderfield communities can have many species of deeper soils present in small numbers.

Though *Ribes* was mentioned in earlier drafts of the 4th approximation and is included in the NVC association name, no species of *Ribes* is abundant in any of the plots or in known examples of this community.

Rare species: Though not well studied, this subtype presumably may harbor rare small mammals characteristic of other boulderfields.

References:

Watson-Cook, E.L. 2017. Characteristics and classification of southern Appalachian spruce-fir forests. M.S. Thesis, University of North Carolina, Chapel Hill.

RED SPRUCE–FRASER FIR FOREST (BIRCH TRANSITION HERB SUBTYPE)

Concept: Red Spruce–Fraser Forests are high mountain forests in which *Picea rubens* (or occasionally *Sorbus americana*), with or without *Abies fraseri* or hardwoods, are naturally dominant. The Birch Transition Herb Subtype covers forests in the broad transition zone on open slopes, where Red Spruce–Fraser Fir Forest grades to Northern Hardwood Forest with a fairly even mix of *Betula alleghaniensis* and *Picea rubens*, and where a dense ericaceous shrub layer is absent. This is the lower elevation equivalent of the Herb Subtype.

Distinguishing Features: The Birch Transition Herb Subtype is distinguished from most other subtypes by canopy composition, which naturally includes more than 33% cover of *Betula alleghaniensis* and more than 33% cover of *Picea rubens* in a well-developed, undisturbed canopy. It is distinguished from the Birch Transition Shrub Subtype, which has a similar canopy, by having lower strata of deciduous shrubs and herbs, instead of evergreen shrubs. It is distinguished from the Boulderfield Subtype by having less than 90 percent boulder cover and having only small amounts of characteristic boulderfield species.

Synonyms: *Picea rubens - (Betula alleghaniensis, Aesculus flava) / Viburnum lantanoides / Oxalis montana - Solidago glomerata* Forest (CEGL006256).
Ecological Systems: Central and Southern Appalachian Spruce-Fir Forest (CES202.028).

Sites: The Birch Transition Herb Subtype occurs on open slopes and upper valleys in the lower elevational range of spruce-fir forests, generally 4500-5500 feet elevation.

Soils: It is unclear how much the discussion of soils for the Spruce-Fir Forests theme applies to the Birch Transition Herb Subtype. Soils likely are similar to those of other spruce-fir forests but may be deeper and better developed in the somewhat lower elevation and warmer climate.

Hydrology: Moisture levels are high, as in other spruce-fir forests, but warmer temperatures and occurrence below the zone of maximum fog likely makes this community less wet.

Vegetation: The Birch Transition Herb Subtype forest canopy is closed except for recent gaps. The canopy is codominated by a combination of *Picea rubens* and *Betula alleghaniensis*. *Abies fraseri* may occasionally be present, and a variety of lower elevation trees may occur in smaller numbers, including *Aesculus flava, Acer rubrum*, *Acer saccharum*, *Betula lenta*, *Fagus grandifolia*, and *Quercus rubra*. Watson-Cook (2017) described this community in detail, based on CVS plot data. The understory is generally dominated by *Acer pensylvanicum*, *Acer spicatum*, or some of the canopy species. Deciduous shrubs may be of moderate density, with *Vaccinium erythrocarpum*, *Viburnum lantanoides*, and *Ilex montana* often abundant. *Rhododendron catawbiense* and *Rhododendron maximum* may be present in small amounts. The herb layer is well developed, and is dominated by vascular plants rather than bryophytes. The most frequent and abundant species are *Maianthemum canadense, Oclemena acuminata, Oxalis montana, Huperzia lucidula, Dryopteris intermedia*, *Clintonia borealis*, *Dryopteris intermedia*, and *Carex pensylvanica.* A number of shrub and herb species shared with lower elevation communities may be present, including *Eurybia chlorolepis*, *Maianthemum racemosum*, *Medeola virginica*, *Parathelypteris noveboracensis*, *Smilax herbacea*, *Viola pallens*, *Trillium erectum*, and

Hamamelis virginiana. Other species of high elevations, such as *Dryopteris campyloptera*, may also be present. Crandall (1958) also noted *Rudbeckia laciniata, Nabalus altissima, Polygonatum pubescens, Hydrangea arborescens, Viburnum cassinoides, Solidago curtissii, Laportea canadensis* and a variety of additional herbaceous species in this community in the Smokies.

Range and Abundance: Ranked G2. The equivalent NVC association is attributed only to North Carolina and Tennessee, though comparable communities may exist in Virginia. It is one the most common subtypes but is nevertheless of very limited extent.

Associations and Patterns: The Birch Transition Herb Subtype is intermediate between the Herb Subtype and Northern Hardwood Forest, and grades to both. It may be associated with the Birch Transition Shrub Subtype or Low Rhododendron Subtype locally. Its pattern of occurrence on the landscape appears to be patchy and irregular, with the communities that are ostensibly of higher and lower elevations often interspersed within the same elevation. This is often attributed to the effects of logging, with an assumption that spruce was once present in areas that now appear to be Northern Hardwood Forest, or that the mixed canopy indicates a loss of spruce. This may sometimes be true but cannot be assumed to be true. A similar patchwork pattern is visible in the unlogged forests of the Great Smoky Mountains. This pattern needs further investigation.

Variation: Examples vary with the transition to adjacent communities. Watson-Cook (2017) identified several groupings within the CVS data. Two she recommended as new associations and two as more minor variations that appear to be related to the transition to adjacent communities. These are not adopted as new subtypes at this time but are recognized as variants. They should be investigated for consistent occurrence and may warrant recognition as subtypes in the future. Crandall (1958) recognized two groupings within the range covered by the subtype. One she called a *Viburnum* type, which had high cover of deciduous shrubs. The other, called *Aster* type, had a diversity of forbs.

There are thus three variants recognized:
1. Typic Variant fits the general description of the subtype
2. Rich Variant contains a higher diversity of species in all strata and contains species suggestive of richer soil, such as *Laportea canadensis* and *Brachyelytrum erectum*. Four plots were identified as this group that represents this variant, all in the Balsam Mountains near Shining Rock, and all substantially altered by logging and slash fires. Crandall's *Aster* type may have affinities to this as well, as it contains *Laportea*. This variant is almost well enough marked to be treated as a subtype. Further investigation may find it so, especially if it is found in other mountain ranges where conditions would seem to be appropriate for it, such as Roan Mountain and the Black Mountains.
3. Heartleaf Birch Variant contains an appreciable component of *Betula cordifoilia* along with the typical dominants. Two plots were identified as this group, both in the Black Mountains, the only range where the species occurs in North Carolina.

Dynamics: The dynamics of this subtype have not been specifically addressed as distinct from the widely studied higher elevation Herb Subtype. They likely are similar, but the warmer, less exposed environment allows greater competitiveness of *Betula* and allows a number of additional species to persist. These lower elevation sites are closer to areas that naturally burned regularly, but they are still generally separated from more fire-adapted communities by a zone of the less

flammable Northern Hardwood Forest. The abundance of fire-intolerant spruce suggests fire is not a significant influence.

Because this subtype has little or no fir, it has not been devastated by balsam woolly adelgid the way higher elevation subtypes have. It apparently was still affected by the slowing of growth that was believed to be caused by air pollution and acid deposition.

Logging and slash fires in the early 1900s affected this subtype to varying degrees. Because of the higher concentration of spruce at higher elevation, logging railroads were built above it and logging reached it with varying levels of intensity. Slash fires, too, may have halted or lost intensity before reaching it. In some places, there are remnant patches of this subtype where the other subtypes uphill were devastated by logging and fires. In other places, forests are in a young or successional state across this zone, making it difficult to tell the natural proportions of trees and thus difficult to distinguish the communities.

Because the patchy distribution of this subtype relative to other Red Spruce–Fraser Fir Forests and Northern Hardwood Forests occurs in areas that were never logged, it, as with the mixed canopy, cannot be assumed to be a result of past logging. The natural drivers that lead to this patchiness are not known and need investigation.

Comments: This subtype is intermediate between Red Spruce–Fraser Fir Forest and Northern Hardwood Forest. It could perhaps be placed as easily in either type. It is clearly ecotonal, being intermediate between more typical spruce-fir and northern hardwoods. Its recognition as a distinct community is justified by its ability to occupy extensive areas. It appears to be optimal habitat for *Glaucomys sabrinus coloratus*, which uses a mix of spruce and birch.

Ulrey's (2002) analysis of 1273 mountain forest plots found a yellow birch-spruce community, which was included in the group of northern hardwood forests rather than the spruce-fir group. It seems to include both the Birch Transition Herb and Birch Transition Shrub subtypes. However, Rhododendron maximum had high 81% constancy among the 16 yellow birch-spruce plots. The only species with high constancy in Ulrey (2002) (combined herb and shrub subtypes) is *Ilex montana.*

There has been substantial concern, more so in the Central Appalachians, that forests of mixed spruce and birch represent formerly spruce-dominated forests that were altered by logging. There are many places where spruce forests that were logged and burned did not recover to spruce dominance; some now are closed forests with mixed canopies but more lack a full forest canopy altogether. Mixed forests are naturally extensive in the lower elevational range of spruce, including in areas never logged. Mixed forests cannot be assumed to be products of alteration. In much of the elevational range of this subtype, natural hardwood forests are also present. Hardwood forests also cannot be assumed to represent former spruce or mixed forests without evidence of past composition.

Rare species:
Vertebrate animals: *Aegolius acadicus* and *Glaucomys sabrinus coloratus*.

References:

Crandall, D.L 1958. Ground vegetation patterns of the spruce-fir areas of the Smoky Mountains. Ecological Monographs 28:337-360

Ulrey, C.J. 2002. The relationship between soil fertility and the forests of the Southern Appalachian region. PhD dissertation, North Carolina State University, Raleigh.

Watson-Cook, E.L. 2017. Characteristics and classification of southern Appalachian spruce-fir forests. M.S. Thesis, University of North Carolina, Chapel Hill.

RED SPRUCE–FRASER FIR FOREST (BIRCH TRANSITION SHRUB SUBTYPE)

Concept: Red Spruce–Fraser Forests are high mountain forests in which *Picea rubens* (or occasionally *Sorbus americana*), with or without *Abies fraseri* or hardwoods, are naturally dominant. The Birch Transition Shrub Subtype covers forests in the broad transition zone on open slopes, where Red Spruce–Fraser Fir Forest grades to Northern Hardwood Forest with a fairly even mix of *Betula alleghaniensis* and *Picea rubens*, and where a dense evergreen shrub layer is present. It is a lower elevation analogue of the Rhododendron Subtype. The shrub layer is usually *Rhododendron catawbiense* or *Rhododendron maximum*, but in the Smokies, *Leucothoe fontanesiana* may dominate.

Distinguishing Features: The Birch Transition Shrub Subtype is distinguished from most other subtypes by canopy composition, which naturally includes more than 33% cover of *Betula alleghaniensis* and more than 33% cover of *Picea rubens* in a well-developed, undisturbed canopy. It is distinguished from the Birch Transition Herb Subtype by having a dense evergreen shrub layer rather than deciduous shrubs and herbs.

Synonyms: Synonyms: *Picea rubens - (Betula alleghaniensis, Aesculus flava) / Rhododendron (maximum, catawbiense)* Forest (CEGL004983).
Ecological Systems: Central and Southern Appalachian Spruce-Fir Forest (CES202.028).

Sites: The Birch Transition Shrub Subtype occurs on sharp ridge tops and convex slopes, generally at 4500-5500 feet elevation, generally with shallow soils or associated with rock outcrops.

Soils: Soils are usually mapped as Inceptisols (Humadepts) of the Burton, Craggey, and Wayah series, but may represent inclusions of a shallower series.

Hydrology: As with other Spruce-Fir Forests, the Birch Transition Shrub Subtype is generally wet to mesic, sometimes saturated for long periods. However, the shallow soil is more prone to becoming dry in periods without rain or fog. Warmer temperatures and occurrence below the zone of maximum fog likely makes this community less wet than higher elevation subtypes.

Vegetation: The Birch Transition Shrub Subtype has a closed to open tree canopy codominated by *Picea rubens* and *Betula alleghaniensis*. Other trees may include *Quercus rubra*, *Tsuga canadensis*, *Fagus grandifolia*, and *Acer rubrum*. The understory may also include *Amelanchier laevis*, *Acer spicatum*, and *Acer pensylvanicum*. The dense shrub layer is usually dominated by *Rhododendron maximum*, with *Rhododendron catawbiense* much less frequent. Deciduous shrubs such as *Viburnum lantanoides, Vaccinium erythrocarpum*, and *Ilex montana* may be present in small amounts. The herb layer is sparse. Species are those typical of other spruce-fir forests, such as *Dryopteris campyloptera, Dryopteris intermedia,* and *Oclemena acuminata*. *Polypodium appalachianum* may be abundant where rock cover is high (Watson-Cook 2017; Crandall 1958).

Range and Abundance: Ranked G1?. This subtype was once thought confined to the Smokies, but it appears to be present in several other ranges. The association ranges into adjacent Tennessee and southern Virginia.

Associations and Patterns: The Birch Transition Shrub Subtype grades to the Birch Transition Herb Subtype on deeper soils and less exposed topography. It may grade to other subtypes or to Northern Hardwood Forest.

Variation: No variants are recognized.

Dynamics: The dynamics of this subtype have not been specifically addressed as distinct from the widely studied higher elevation Herb Subtype. They likely are similar, but the warmer, less exposed environment allows greater competitiveness of *Betula*. These lower elevation sites are closer to areas that naturally burned regularly, but they are still generally separated from more fire-adapted communities by a zone of the less flammable Northern Hardwood Forest. The abundance of fire-intolerant spruce suggests fire is not a significant influence. However, the ridge top locations may make them more susceptible to lightning.

Comments: The association corresponding to this subtype was created for vegetation in the Great Smoky Mountains. It is unclear if it occurs in any other parts of North Carolina. It may only questionably be distinct from the Low Rhododendron Subtype.

Rare species:

References:

Crandall, D.L 1958. Ground vegetation patterns of the spruce-fir areas of the Smoky Mountains. Ecological Monographs 28:337-360

Watson-Cook, E.L. 2017. Characteristics and classification of southern Appalachian spruce-fir forests. M.S. Thesis, University of North Carolina, Chapel Hill.

RED SPRUCE–FRASER FIR FOREST (LOW RHODODENDRON SUBTYPE)

Concept: Red Spruce–Fraser Forests are high mountain forests in which *Picea rubens* (or occasionally *Sorbus americana*), with or without *Abies fraseri* or hardwoods, are naturally dominant. The Low Rhododendron Subtype covers the lowest elevation examples of Red Spruce–Fraser Forest Forests, in moist, topographically sheltered sites. This subtype is transitional from spruce-fir forest to Acidic Cove Forest. *Picea rubens* dominates or codominates with other mesophytic trees and there is an evergreen shrub layer.

Distinguishing Features: Red Spruce–Fraser Fir Forests are distinguished by canopy dominance of *Picea rubens* alone or with *Abies fraseri*, *Betula alleghaniensis, Sorbus americana*, or occasionally other hardwoods, in a high elevation upland setting. The Low Rhododendron Subtype is distinguished from other lower elevation Red Spruce–Fraser Fir Forests subtypes by the combination of sheltered concave topography with a dense shrub layer of *Rhododendron maximum*. If other tree species are present, they often are species of lower elevation mesic sites, such as *Tsuga canadensis* but may include *Betula alleghaniensis*. It often represents a situation of inverted zonation, occurring downhill of Northern Hardwood Forest or Mountain Oak Forest. The Birch Transition Shrub Subtype and Rhododendron Subtype may also have abundant *Rhododendron maximum* but occur on convex topography such as ridges and have associated species of drier sites.

Synonyms: *Picea rubens - (Tsuga canadensis) / Rhododendron maximum* Forest (CEGL006152).
Red Spruce Forest (Protected Slope Subtype) (NVC).
Ecological Systems: Central and Southern Appalachian Spruce-Fir Forest (CES202.028).

Sites: The Low Rhododendron Subtype occurs on north-facing slopes, sheltered slopes, valley heads, and ravines, generally at lower elevations than other subtypes. The full elevational range is not well known, but examples are known down to near 4000 feet. Some examples occur as downward extensions of spruce from extensive spruce-fir forests into upper valleys, while a few are anomalous occurrences in high valleys distant from other spruce-fir forests. Cold air drainage may be important for their occurrence at these low elevations.

Soils: Soils are not well known for this subtype.

Hydrology: Conditions are mesic due to topographic sheltering, but this subtype occurs below the elevation of frequent fog and high rainfall, and its water input may be much lower than higher elevation subtypes. Some occurrences are associated with Swamp Forest–Bog Complex, where wetter conditions may be present.

Vegetation: The Low Rhododendron Subtype has a closed to open tree canopy dominated by *Picea rubens*, sometimes codominated by *Tsuga canadensis* or *Betula alleghaniensis*. Other trees may include *Acer rubrum*, *Sorbus americana*, and in the understory, *Acer spicatum,* or *Amelanchier laevis*. There is a dense shrub layer dominated by *Rhododendron maximum*. *Kalmia latifolia* may be fairly abundant, and though not reported, it is possible that *Leucothoe fontanesiana* could dominate. Other shrubs include those typical of other spruce-fir forests, such as *Viburnum*

lantanoides, *Vaccinium erythrocarpum*, and *Vaccinium simulatum*, and sometimes species shared with nearby wetlands, such as *Viburnum cassinoides* and *Sorbus melanocarpa*.

Range and Abundance: Ranked G2? This subtype is often not mentioned or described well enough to be recognized in past reports, making its abundance difficult to know. The corresponding NVC association is broadly defined, and is considered to range northward to West Virginia, as well as into Tennessee.

Associations and Patterns: Most examples of the Low Rhododendron Subtype occur as part of a mosaic of spruce–fir forests in the highest mountain ranges. However, unusual examples of this subtype occur without other spruce-fir forests in lower elevation sites at Alarka Laurel and Long Hope Valley. In other sites, the Birch Transition Shrub or Birch Transition Herb Subtype may be present uphill, but this subtype often extends below the elevational range of other spruce-fir forests, so that it is surrounded by Northern Hardwood Forest on adjacent ridges. Downhill may be Acidic Cove Forest. A couple unusual examples are associated with Swamp Forest–Bog Complex (Spruce Subtype).

Variation: Variation is not well known, other than that *Tsuga canadensis* may or may not codominate. No formal variants are recognized.

Dynamics: The dynamics of this unusual subtype are virtually unknown and may be different from the rest of the Spruce-Fir Forests theme.

Comments: The corresponding NVC association may be more broadly defined than this subtype. Its description mentions occurrence on ridges as well as in valleys in parts of the range and mentions *Rhododendron catawbiense* sometimes mixed in the shrub layer. This would appear to overlap the concept of the Birch Transition Shrub Subtype and its equivalent association, and it is unclear how they would be distinguished in such vegetation. This may represent variation in states farther north, where the Birch Transition Shrub Subtype or Rhododendron Subtype are not recognized.

Early versions of the 4th approximation recognized a Hemlock Subtype at lower elevations. This has been lumped into this subtype. The NVC association corresponding to it, *Picea rubens* - *Tsuga canadensis / Rhododendron maximum* Forest (CEGL006272), has also been lumped.

Rare species:

References: