Competitive status of red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*) at ecotonal transitions in southern Appalachian sky islands

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ABSTRACT

Southern Appalachian spruce-fir sky islands are globally threatened, boreal relict forests where red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*) are dominant. Fraser fir dominates at the highest elevations with spruce-fir and spruce-dominated stands at middle elevations and hardwoods associating at lower elevations. A primary concern is encroachment of hardwoods upslope as climate change-driven milder temperatures and high precipitation confine spruce-fir forests to even higher elevations. We performed a dendrochronological analysis of growth rates in red spruce, Fraser fir, and competing hardwoods between cover types and slope aspects at six sky islands. We created linear models to test effects of aspect, cover type, and year on basal area growth measurements of red spruce, Fraser fir, and hardwoods to assess effects of competition. Growth rates were significantly affected by species, aspect, cover type, and year, and generally increased over time. Red spruce growth rates varied by combination of aspect and cover type but were greater than those of hardwoods on northern and southern aspects. Fraser fir growth rates were negative on southern-facing fir-dominated stands but increased in all other stands with the highest growth rates found in fir-dominated stands. The differences we report by cover type and aspect could help conservation practitioners prioritize treatment locations to improve climate resiliency.

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GENERAL AUDIENCE ABSTRACT

Spruce-fir sky islands are globally threatened forests left over from the last ice age and are mainly composed of red spruce and Fraser fir. Fraser fir is found at higher elevations, surrounded by red spruce, with deciduous trees at low elevations. There is concern that deciduous trees could take over current spruce-fir forests when temperatures increase and precipitation changes due to climate change. We measured tree rings and compared growth trends of red spruce, Fraser fir, and deciduous trees at six sky islands by species composition and slope direction. Each of these factors influenced growth over time, which was generally increasing. Red spruce growth depended on the combination of forest type and slope direction but increased more than that of deciduous trees on north- and south-facing slopes. Fraser fir growth decreased on south-facing slopes in forest patches primarily composed of fir. In all other combinations of slope direction and forest type, Fraser fir growth increased, with greater increases in patches mainly composed of Fraser fir. These positive growth trends suggest that these forests may be more resilient to competition than expected. Conservation professionals could use these differences in growth trends to decide where resources can be used most efficiently to expand and protect sky islands from climate-driven decline.

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Introduction

Montane ecosystems worldwide sustain unique and often species-rich community assemblages, (La Sorte & Jetz 2010), making them a globally important source of biodiversity and a conservation priority. Many of these systems have been altered by anthropogenic disturbances, and today, they are at risk of declining further as climate change progresses (Christmann & Menor 2021). Some high-elevation ecosystems have climatic, topographical, and ecological conditions so distinct from surrounding ecosystems that they can be considered biogeographical 'islands' (MacArthur & Wilson 2001). Such biogeographical islands can be found at high elevations in the southeastern United States, where cold temperatures and high precipitation relative to lower elevations sustain glacial relict forests dominated by red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*).

Coniferous forests containing red spruce and Fraser fir were widespread in the southeastern United States during Pleistocene glaciation (Watts 1980). Today, in the post-glacial Holocene, spruce-fir forests are confined to high-elevation mountain peaks as boreal relict ecosystems termed 'sky islands' (Berry & Smith 2012). Sky island forests are composed of almost pure stands of Fraser fir at the highest elevations (> 1,890 m), ringed by red spruce at mid-elevations (1,620 – 1,890 m) and mixed northern hardwood forest at lower elevations (< 1,620 m; White et al. 1984, Cogbill & White 1991). Red spruce and Fraser fir are conifers adapted to mild summers and a high amount of precipitation, particularly in the winter (Andrews et al. 2022). After the range of southeastern spruce-fir forests contracted due to climatic warming following the Pleistocene glaciation, it decreased further due to anthropogenic disturbances (Nowacki et al. 2010). In the late nineteenth and early twentieth centuries, red spruce was considered a desirable pulpwood and timber species in the Appalachian Mountains and was widely overharvested without plans to regenerate forests (White et al. 2012). Slash fires, which can kill regenerating and mature remnant spruce and fir, often ignited

following logging, killing remnant spruce and fir trees and seed and exposing the substrate to significant erosion following rain events (Rollins et al. 2010, Nowacki et al. 2010).

Human communities value southeastern Appalachian spruce-fir sky islands for their unique species assemblages and for social values they can provide, namely ecotourism (Swanson 2012). The loss of these unique forests would also result in the loss of essential habitat for a diversity of understory plants, wildlife, bryophytes, and insects, including eight endemic species of lichen, numerous threatened stream insects, the northern saw-whet owl (*Aegolius acadicus*), the green salamander (*Aneides aeneus*), and the Carolina northern flying squirrel (*Glaucomys sabrinus coloratus*). Today, there is concern that changes in temperature and precipitation regimes, accelerated by climate change, may continue to limit to even higher elevations the climatic conditions that sustain sky island ecosystems (Delcourt & Delcourt 1998). Spruce-fir forests are at risk of further population fragmentation, loss of habitat to encroaching hardwoods, and increased infestations of both native and invasive pest insects (Iverson et al. 2017, Hain 1988).

Dendrochronological studies can provide information about tree responses to climate changes and other disturbances and allow us to assess changes in growth over time (Sheppard 2010). Continued study of recent trends in growth and competition is necessary to evaluate the resiliency of spruce-fir forests to anthropogenic disturbances, including climate change, in relatively understudied southern Appalachian sky islands. In this study, we compare growth rates across species, aspects, elevation, and cover types at six southern Appalachian sky islands with the following objectives: a) develop a comparison of the growth rates of red spruce, Fraser fir, and common northern hardwood competitors at the edges of spruce-fir sky islands; b) measure the composition of the regeneration layer along the transition zone of sky islands; and c) compare growth rates and regeneration of red spruce, Fraser fir, and their hardwood competitors along aspects. We hypothesized that a) Fraser fir would have the highest growth rates and regeneration within the fir-

dominated cover type, red spruce would have the highest growth rates and regeneration within the spruce-dominated cover type, and hardwoods would have the highest growth rates and regeneration of any species within the spruce-hardwood cover type; b) Growth rates and regeneration of red spruce and Fraser fir would increase with increasing elevation, while growth rates and regeneration of hardwoods would decrease; and c) All species would have the greatest growth and regeneration on northerly aspects.

Justification

Southern Appalachian spruce-fir forests are a conservation priority due to their fragmented range and concern that shifting temperature and precipitation regimes due to climate change will drive further loss of these forests as suitable environmental conditions are confined farther upslope. However, limited literature on spruce-fir community dynamics is available for several sky islands, with most studies focusing on the low-elevation spruce-fir forests of the central Appalachian Mountains or high elevation sites in the Great Smoky Mountains. In this study, we seek to expand knowledge of growth rates and regeneration in red spruce and Fraser fir forests in the southern Appalachian Mountains by comparing growth rates of red spruce and Fraser fir between elevation, slope aspects, and forest composition. Furthermore, we perform a novel comparison of growth rates of red spruce to those of northern hardwoods to gauge possible impacts of competition on red spruce growth and inform management decisions.

Literature Review

Montane habitats harbor a large portion of the world's biodiversity but are exceptionally sensitive to degradation from climate change and other anthropogenic disturbances (Christmann & Menor 2021, McCain & Colwell 2011). Humans have directly altered montane ecosystems for

centuries through natural resource exploitation, urban and agricultural development, and pollution (Huntley 1991). Today, the rate of global habitat declines and biodiversity loss is hastened by climate change (Willis & Bhagwat 2009). Stress resulting from global climate change can be compounded for organisms that rely on geographically constrained montane habitats, especially those previously damaged or fragmented by human activities (Chakraborty et al. 2018, Collingham & Huntley 2000). Based on evidence from past periods of climatic change, many organisms, including trees, are expected to migrate to areas with the climatic, geological and topographical factors that fit their ecological niches (Huntley 1991). Migrating cold-adapted conifers, such as those found in southern Appalachian sky islands, are expected to face the additional pressure of competition with hardwood species, which may expand upslope as mountainous climates become warmer and drier than historically (Andrews et al. 2022, Iverson et al. 2008, Walter et al. 2016).

Southern Appalachian sky islands are isolated, high-elevation montane forests dominated by red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*). Red spruce is a long-lived, shade-tolerant species, with individuals able to survive up to 400 years and suppressed trees able to persist in the understory for long periods of time (Yetter et al. 2021, USDA 1990). Fraser fir can live for approximately 150 years and is endemic to the southern Appalachian Mountains (USDA 1990, Frank 1990, Busing & Clebsch 1988). Red spruce is found between sea level and 1,370 m in elevation in Maine, Vermont, and New Hampshire and much of New Brunswick, Nova Scotia, and New York (USDA 1990). The ecotonal transition between spruce-fir forest and deciduous forest tends to occur at approximately 1,680 m in its southern range around latitude 35°N, but red spruce is found at only 150 m near 49°N (Cogbill & White 1991). Appalachian spruce-fir forests are considered relicts of boreal coniferous forests that were widespread on mountain peaks and at the southern edge of glacial extent during the Pleistocene, with Fraser fir further limited to higher

elevations during the hypsithermal period of warming which lasted from approximately 8,700 to 5,000 years ago (Potter et al. 2008, Guilday 1982).

Today, red spruce and Fraser fir in the southern Appalachians are confined by temperature and precipitation to small, disjunct sky islands (USDA 2023). White et al. (1984) applied the theory of island biogeography to southern Appalachian peaks with elevation over 1,680 m, the point at which mixed northern hardwoods tend to transition into red spruce- and Fraser fir-dominated forest. Southern Appalachian spruce-fir forests have a severely limited extent compared to their historical range in southeastern North America (Delcourt and Delcourt 1998). The contemporary range of red spruce spans from southern New Brunswick and Nova Scotia as far south as North Carolina and Tennessee (Little 1971). Present-day southern Appalachian spruce-fir forests occupy between 10 and 50 percent of their historical range (Nicholas et al. 1992). Isolated sky islands are found at altitudes above 1,500m in the southern Appalachian Mountains of North Carolina and Tennessee and above 1,110 in Virginia (Diggins & Ford 2022, Eagar & Adams 1992, Adams & Stephenson 1989).

Forests of co-dominant red spruce and Fraser fir are found at high altitudes where summer temperatures are milder than at low altitudes and cloud immersion provides a major water source (Berry et al. 2014). On mountains south of approximately 36˚N latitude, red spruce dominates middle elevations (1,400 – 1,800 m) and may associate with Fraser fir between 1,750 and 1,890 m, whereas Fraser fir begins to dominate m and can form pure stands at 1,890 (Kaylor et al. 2017, Busing et al. 1988). Spruce-fir forests are sustained by the mild summer temperatures and high frequency of cloud immersion at high elevations and, though they can persist on several soil types (primarily spodosols, histosols, and inceptisols) spruce and fir have a competitive advantage over hardwoods on well-drained or more acidic soil (Walter et al. 2016, Berry et al. 2014, Eagar & Adams 1992).

Fraser fir, a major component of spruce-fir forests, is threatened by the invasive balsam woolly adelgid (*Adelges piceae*). The balsam woolly adelgid is native to central Europe and was introduced accidentally to North America, where it decimates Fraser fir populations by causing crown dieback, reduced fluid transfer, and often mortality (Hollingsworth & Hain 1991). The impacts of the balsam woolly adelgid are expected to increase with increasing temperatures, and there is some concern that population declines could result from mortality of fir before they reproduce (McManamay 2011, Hain 1988).

At most uncut/unburned and some replanted sites in the southern Appalachian Mountains, red spruce-mixed hardwood forest occurs between 1,370 and 1,580 m, shifting to spruce-fir above this elevation (Groton & Eagar 1988). The mixed northern hardwood forests surrounding spruce-fir sky islands at low elevations are often composed of birches (*Betula spp.*), maples (*Acer spp.*), and American beech (*Fagus grandifolia*), and sometimes include eastern hemlock (*Tsuga canadensis)*, northern red oak (*Quercus rubra*) and serviceberry (*Amelanchier spp.*; Eagar & Adams 1992, Cogbill & White 1991). In the southern Appalachian Mountains, main hardwood competitors at more exposed, xeric sites tend to be northern red oak (*Quercus rubra*) and beech, whereas yellow birch and serviceberry (*Amelanchier* spp.) occur at more mesic or sheltered sites (Odom & McNab 2000). Efforts to conserve and restore southern Appalachian spruce-fir sky islands are motivated in part by the concern that with increasing temperatures and shifts in precipitation, these hardwoods may encroach upon the limited habitat suitable for spruce-fir forests.

Several rare and threatened understory plant and wildlife species are dependent on spruce-fir forests. Fauna endemic to spruce-fir sky islands include the spruce-fir moss spider (*Microhexura montivaga*), and Carolina northern flying squirrel (*G. s. coloratus*) (Diggins et al. 2017, Seaborn & Catley 2016). The spruce-fir moss spider is found only in six spruce-fir sky islands in the southern Appalachian Mountains and lives in bryophyte mats sustained by the high moisture in sky islands

and sheltered from desiccation by canopies of red spruce and Fraser fir (Diggins & Ford 2021). The spruce-fir moss spider is a federally endangered species. The Carolina northern flying squirrel, also a federally endangered species, is thought to be a montane conifer forest associate which dens primarily in red spruce (Diggins et al. 2016). The Appalachian Mountains may lose these threatened animals if spruce-fir forests are further fragmented or completely lost.

Sky islands are also havens for unique plants found nowhere else in the southern Appalachians. White et al. (1984) observed high rare plant richness generally correlated with large sky islands containing 5-20 peaks, which tend to include higher maximum elevations (1954 – 2037 m) than smaller sky islands and included a range of elevations from 1683 – 1916 m. Two plant species designated nationally rare, *Cacalia rugelia* and *Nemopanthus collinus*, are found on high peaks in the southern Appalachian Mountains (White et al. 1984). Lichen diversity is also high in the southern Appalachians, with at least eight endemic species and 18 species only found in the United States in the southern Appalachians (Hodkinson 2010, Dey 1978). Rare insects in the southern Appalachians include over 70 benthic macroinvertebrates (Orders Ephemeroptera, Plecoptera, and Trichoptera) in streams ecosystems and 27 ground beetles (Order Coleoptera: Family Carabidae) in spruce-fir forests (Browne et al. 2014, Morse et al. 1993).

To preserve southern Appalachian spruce-fir forests and the biodiversity they sustain, restoration practitioners are focused on mitigating the consequences of climate change and encouraging recruitment of additional age classes where populations are single-aged (Rentch et al. 2016). At sites where spruce-fir forests were clearcut or clearcut-and-burned in the early twentieth century, resulting in single-aged populations, restoration activities focus on the release of suppressed red spruce into the overstory by cutting small canopy gaps (SASRI Fall Meeting 2022). In the central Appalachians, red spruce has responded with increased basal area and height growth to small gap release from competing hardwoods (Rentch et al. 2016, Hornbeck and Kochenderfer 1998).

Similarly, Fraser fir is shade-tolerant and its advance regeneration can grow rapidly and be recruited to the overstory when canopy gaps are created (Busing & Clebsch 1988). Recruiting suppressed red spruce and Fraser fir into the overstory is essential to the continued survival of these forests because continued regeneration will require additional nearby seed sources as mature overstory red spruce die. Restoring or even expanding Appalachian spruce-fir forests, while mitigating encroachment of hardwoods into these systems, may increase their resilience to climate change.

Land use history

Spruce-fir forests may have been a sustainably used cultural resource for Indigenous peoples including the Cherokee, Tutelo, and Monacan, but following European settlement, spruce-fir forests were heavily disturbed by exploitative logging practices (Native Land Digital 2024, Pyle & Schafale 1988). Prior to the early 1700s, Indigenous tribes in the southern Appalachians entered the montane forests of the Blue Ridge to hunt, fish, and gather, cleared low-elevation hardwood forests for agriculture, and established today's montane grassy balds by repeatedly burning forest to improve grazing and hunt deer and elk (Wilhelm 1968). By the early nineteenth century, some logging of spruce-dominated forests was conducted by European settlers moving westward through New York and Pennsylvania, but the largest removal of these forests in the central and southern Appalachians occurred between 1880 and 1920, after the advent of the steam engine (Adams et al. 2010, Nowacki et al. 2010). Red spruce, especially when immature, is vulnerable to fire due to its high resin production, retention of low branches, shallow root system, and thin, slow-growing bark which offers little protection from flames (Murphy 1917). Fires that resulted after heavy logging also limited red spruce and Fraser fir regeneration by burning through the organic horizon, causing the substrate to erode to mineral soil and eventually to the bedrock, destroying spruce-fir seed and regeneration (McManamay et al. 2011, Rollins et al. 2010). In locations where elevation and

topography allowed for conversion to grazing land, many late-successional red spruce stands have been replaced by northern hardwoods and fast-growing mesic species (Mayfield & Hicks 2010).

Exploitative logging of spruce-fir forests was motivated by the demand for wood products without consideration to forest regeneration. Red spruce was the main source of paper pulp in eastern North America during the early twentieth century and was an important lumber source across its range (White et al. 2012, Korstian 1937). This innovation allowed raw forest products to be transported long distances via railroads, and the subsequent development of steam-powered skidders and sawmills increased the scale of logging ventures (Nowacki et al. 2010). By the end of the early twentieth century, much of Virginia's, North Carolina's and Tennessee's spruce-fir forests were clearcut or selectively cut (White et al. 2012). In the early twentieth century, spruce pulpwood was transported via steam- or animal-powered skidders (Korstian 1937).

Native peoples primarily impacted downslope northern hardwoods forests and used high elevations for hunting, gathering, and fishing, though some montane stands were burned to form clearings to encourage ungulate grazing. Southern Appalachian spruce-fir forests were significantly disturbed by humans in the late nineteenth and early twentieth centuries primarily through intensive logging and the slash fires that followed. Intensive logging in the late nineteenth and early twentieth century was often performed without ensuring future regeneration or seed sources, and soils and the regeneration layer were degraded in subsequent ignitions of slash. Red spruce was a major timber and pulpwood species in the southern Appalachians during this time, and was overharvested after the inventions of steam engines and subsequently steam-powered skidders and sawmills. Virginia's Mount Rogers and North Carolina's Black Mountains were major sources of red spruce logs, which were transported out of both regions by rail.

Current and future threats

Today, most sky islands are protected from exploitative logging through public ownership as state parks or the US Forest Service, but these forests will continue to experience anthropogenically driven disturbances as climate change progresses. As climate change causes suitable habitat for red spruce to shrink and shift to higher elevations, red spruce populations are expected to decline and may experience local extirpation (Mayfield & Hicks 2010). Hardwoods currently found competing with red spruce below 1,400 m are expected to respond differently as temperature and precipitation shifts due to climate change, with some species expanding upslope into spruce-fir forests and others decreasing in abundance (Iverson & Prasad 2001). Moreover, several species associated with spruce-fir forests, including American beech, eastern hemlock, and Fraser fir, are experiencing mortality driven by invasive pest insects and emergent diseases (McIntire 2023, Paradis et al. 2007, McManamay et al. 2011). Other insects native to North America, namely the spruce beetle, southern pine beetle, and spruce budworm, may also pose an increasing threat to spruce-fir forests as increasing temperatures cause greater overwinter survival and range expansions (Cudmore et al. 2010, Collins et al. 2010, Silver et al. 1991). In a study where future importance values (calculated using plot stem counts and basal area) were modeled under various climate change scenarios, red spruce was predicted to decline in forests where it is currently of high importance, with high or complete loss of suitable habitat under the most extreme greenhouse gas emissions scenarios (Iverson et al. 2008). Fraser fir, a species with an already limited natural range, likewise faces severe threats to its survival. Listed as critically imperiled in Virginia and significantly rare in North Carolina, Fraser fir is designated a federal species of concern and a globally imperiled species vulnerable to extinction (Virginia Department of Conservation and Recreation 2021, McManamay et al. 2011). High-elevation montane animals and trees such as red spruce and Fraser fir may also face

decreasing genetic diversity and genetic exchange between populations as their ranges shrink and fragment (Potter et al. 2010).

The effects of climate change-driven seasonal temperature and precipitation shifts on hardwoods at the red spruce-northern hardwoods ecotonal transition are expected to vary by species. Yellow birch (*Betula alleghaniensis*), sweet birch (*Betula lenta*), and northern red oak (*Quercus rubra*) are the most likely to increase in abundance in Appalachian red spruce communities, whereas American beech and sugar maple (*Acer saccarum*) may decline under pressures including insect outbreaks, emergent diseases, and loss of suitable habitat. Yellow and sweet birch are abundant in southern Appalachian Forest Inventory and Analysis (FIA) plots, and in a study comparing seedling density and biomass by latitude in eastern U.S. FIA plots, yellow birch and northern red oak were among the species with the most significant observed northward shifts, suggesting that in the southern Appalachians, these species could undergo shifts in elevation similar to red spruce and Fraser fir with upslope restriction of suitable climatic conditions (Nowacki et al. 2011, Woodall et al. 2009). Modeling of future forest composition using FIA data also indicates widespread projected increases in red maple abundance, with the greatest increases in the western part of its natural range (Matthews & Iverson 2017, Fei & Steiner 2007). Suitable habitat for sugar maple is predicted to decline across its range, with the greatest loss in the southern extent of its range, which includes the southern Appalachians, where, when not limited by soil acidity, sugar maple may advance upslope with shifting cold temperatures (Matthews & Iverson 2016, Houle et al. 2007).

American beech is an important associate in southern Appalachian transitional ecotones which forms a unique southeastern ecosystem, but the species is threatened by two emerging diseases. Primarily within the Great Smokey Mountains National Park, American beech forms pure or almost-pure stands above 1,400 m termed 'beech gaps', which are considered a rare montane ecosystem (Poteat & Vandermast 2010). The mechanics by which red spruce and Fraser fir are

excluded in beech gaps are not fully understood, but because all three species can grow on soils with similar pH ranges, spruce and fir could instead be excluded due to the allelopathic compounds leached into soil from beech litter (Poteat & Vandermast 2010). Expansion of American beech has been associated with increasing temperatures, especially higher growing season temperatures (Bose et al. 2017). However, despite its historical competitiveness in high-elevation forests, American beech may become a less viable competitor in the future due to its susceptibility to two diseases, beach leaf disease and beech bark disease. Beech leaf disease is thought to be caused by the foliar parasitic nematode *Litylenchus crenatae*, and symptoms include gall formation between leaf veins, deformation, shrinkage, and thickening of leaves, and in severe cases, loss of buds and an asynchrony or lack of spring leaf flush (McIntire 2023). Beech bark disease occurs when fungal pathogens (genus *Neonectria*) enter the phloem or cambium via the tiny wounds caused by the feeding of the invasive *Cryptococcus fagisuga* (Burke et al. 2020). In the northeastern United States where the disease dynamic has been on the landscape longer, beech bark disease has resulted in the development of beech thickets following mortality-driven stump sprouting (McIntire 2023). Beech leaf disease is expected to cause further forest compositional and structural changes by compromising tree gas exchange and carbon assimilation capabilities (McIntire 2023).

Eastern hemlock, which can be found in low-elevation spruce-fir forests, is facing decline due to outbreaks of an invasive insect, the hemlock woolly adelgid (*Adelges tsugae*). Encroachment of eastern hemlock into spruce-fir dominated systems is unlikely to increase as it is limited by soils and topography and because it is susceptible to mortality driven by outbreaks of hemlock woolly adelgid, which is projected to expand to areas where it was previously excluded by cold winter temperatures (Saladyga & Maxwell 2015, Paradis et al. 2007). Loss of eastern hemlock has been correlated with forest changes including increased invasive species populations and conversion to hardwood-

dominated composition (Saladyga & Maxwell 2015), but gaps opened by falling hemlocks might also hasten recruitment of additional red spruce age classes into the overstory.

Insect outbreaks may also pose an increasing threat to red spruce and Fraser fir as climate change progresses. Most southeastern spruce-fir forests have experienced periodic infestations of balsam woolly adelgid (*Adelges piceae*) since the mid-twentieth century (White et al. 2012). The balsam woolly adelgid, an insect native to central European forests dominated by *Abies alba* can cause crown dieback, mortality, and decreased reproductive success in Fraser and balsam fir (*Abies balsamea*; Eagar & Adams 1992, Hain 1988). Balsam woolly adelgid was first observed on Fraser fir in the central and southern Appalachians in 1955, but the adelgid is thought to have originally been introduced to North America accidentally through nursery stock in Maine and Nova Scotia (Nicholas et al. 1992). Crown infestations tend to manifest as excessive drooping of new shoots and swelling of nodes and buds with decreased growth, while infestations on the stem consist of distinctive fluffy white masses (Hain 1988). Mortality typically occurs between two and six years, and is thought to be caused by abnormal wood development and damage to sapwood, which inhibits fluid transfer (Hollingsworth & Hain 1991). Balsam woolly adelgid infestations can occur on trees with diameter at breast height (DBH) greater than four centimeters, but Fraser fir does not reproduce until 15-17 cm DBH (McManamay et al. 2011). Although some evidence of continued Fraser fir regeneration and fluctuations in balsam woolly adelgid populations have been reported, there is concern that Fraser fir populations will slowly dwindle if more individuals are killed before they can reproduce in turn (McManamay et al. 2011, Potter et al. 2005).

The invasive balsam woolly adelgid and the spruce budworm (*Choristoneura fumiferana*) pose a significant threat to the survival of Fraser fir, and other insect pests including southern pine beetle (*Dendroctonus frontalis*) and the spruce beetle (*Dendroctonus rufipennis*) may threaten the integrity of spruce-fir forests further as temperature increases increase overwinter survival and range expansions

(Lumley et al. 2020, Cudmore et al. 2010). In a dendroecological study of red spruce in the Alarka Creek watershed (North Carolina), Collins et al. (2010) observed rapid recovery after a southern pine beetle outbreak in the 1990s and noted that only 20% of red spruce surveyed exhibited symptoms of southern pine beetle damage. The native range of the spruce beetle encompasses much of Canada and Alaska with pockets in the Rocky Mountains and Appalachian Mountains (Holsten et al. 1989). Mortality driven by spruce beetle infestation has been reported in New Hampshire (Silver et al. 1991), but few serious infestations have been reported in the southern Appalachian Mountains. While more readily observed in the large, contiguous spruce-dominated forests of central and southern Canada, spruce budworm persists in small, scattered subpopulations in the Appalachians, where it feeds on red spruce and balsam fir (*Abies balsamea*) in the central Appalachians (Lumley et al. 2020). In spruce-fir forests, the loss of Fraser fir can increase the risk of wind and ice storm damage to surviving trees, especially those on exposed ridgetops (Busing 2004, Cook & Zedaker 1992).

Hardwood species that are currently of high importance at middle elevations in the southern Appalachians are expected to respond differently to climate change, with yellow birch, sweet birch, and northern red oak most likely to move upslope into spruce-fir forests and American beech and sugar maple expected to decline (McIntire 2023, Matthews & Iverson 2016, Nowacki et al. 2011, Woodall 2009). Sugar maple may lose suitable habitat in the northeastern U.S. as temperature regimes shift, but could expand upslope in the southern Appalachians. Increasing losses of eastern hemlock and American beech are expected due to presence of the invasive hemlock woolly adelgid and two emergent diseases in American beech. Fraser fir is an important component of spruce-fir forests over 1,580 m, but its populations have already been subject to significant damage from the invasive balsam woolly adelgid. Several insect pests, including the southern pine beetle, spruce

beetle, and spruce budworm could cause increasing loss of red spruce and Fraser fir as more frequent mild winter temperatures increase overwinter survival rates.

Summary

Globally, montane habitats sustain unique ecological communities and provide ecosystem services to human populations worldwide, but they are particularly vulnerable to the consequences of climate change. Southeastern spruce-fir forests have been heavily impacted by early twentieth-century logging and slash fires and are still imperiled by climate change-exacerbated factors including increasing insect outbreaks and loss of suitable habitat. These sky islands are a conservation and restoration priority due to their status as a threatened forest type that provides habitat for several at-risk wildlife and understory plant species. In the southern Appalachian Mountains, spruce-fir forests are surrounded by mixed northern hardwoods, some of which are expected to encroach on spruce-fir forest habitat and others to decline due to invasive insects and emergent diseases. The primary restoration activity currently performed in southern Appalachian sky islands is the creation of small canopy gaps to release suppressed understory red spruce and hasten the development of multi-aged stands. Some current research on Fraser fir focuses on understanding resistance to balsam woolly adelgid and preventing future outbreaks. The changes in forest composition and pest dynamics projected as climate change progresses necessitate study of the current state of southern Appalachian spruce-fir and spruce-hardwood forests. Therefore, we performed a study of growth rates and competition in southern Appalachian sky islands to a) develop a comparison of the growth rates of red spruce, Fraser fir, and common northern hardwood competitors at the edges of spruce-fir sky islands; b) measure the composition of the regeneration layer along the transition zone of sky islands; and c) compare growth rates and regeneration of red spruce, Fraser fir, and their hardwood competitors along aspects.

Materials and Methods

Site Descriptions

Our study was conducted at five sites with spruce-fir forests: Mount Rogers in Virginia; Little Sam Knob, Grandfather Mountain, Black Balsam Knob, and Mount Mitchell in North Carolina; and Roan Mountain on the Tennessee-North Carolina border (Fig. 1, Table 1).

Fig. 1: Map of study areas encompassing spruce-fir (*Picea-Abies*) forests and the spruce-hardwoods ecotonal transition in Virginia, North Carolina, and Tennessee, 2023.

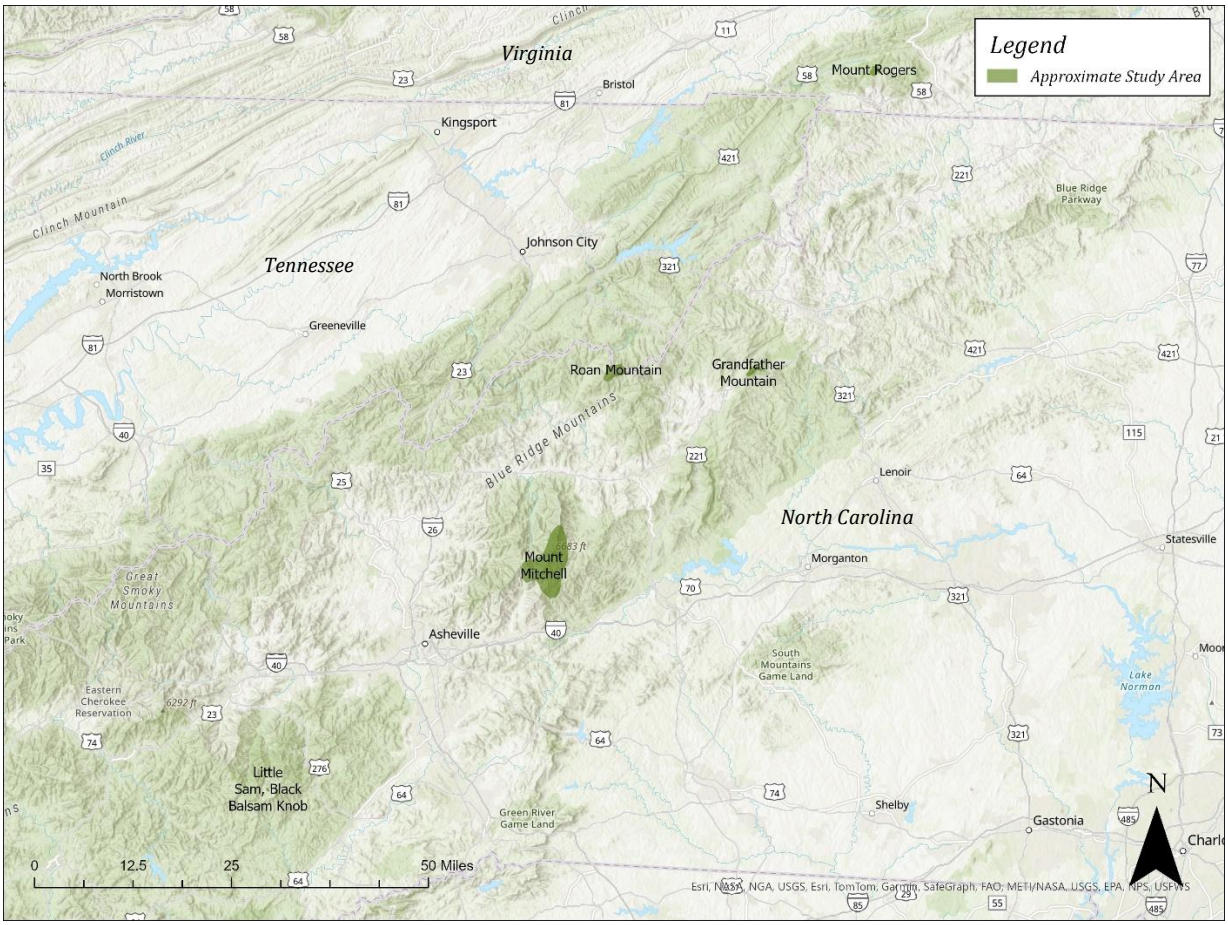

Table 1. Peak coordinates, total area coverage of spruce-fir (*Abies-Picea*) forest, annual mean precipitation, seasonal precipitation range, annual temperature range, and year of most recent recorded infestation of balsam woolly adelgid (*Adelges piceae*) for Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA), 2023, listed in ascending order by peak elevation.

Site	Peak Elevation	Lat. Long.	Total Area Coverage of Spruce-fir	Mean Monthly Precipitation (min., cm – max., cm)	Mean Annual Temperature Range	First recorded adelgid presence
Mount Rogers	1746 m	81˚32'50" W, 36˚39'26" N	4.19 km²	7.8 cm (Oct.) – 13.6 cm (July)	-3.9 ˚C – 28.7 ˚C	1979
Little Sam Knob	1786 m	82˚53'48" W, 35˚19'17" N	0.27 km²	33.7 cm (June) – 44.5 cm (Sept.)	14.8 ˚C – 26.3 ˚C	NA
Grandfather Mountain	1812 m	81˚49'16" W, 36˚6'11" N	3.8 km²	8.5 cm (Jan.) – 18.1 cm (Sept.)	-3.9 ˚C – 27.1 ˚C	1963
Black Balsam Knob	1894 m	82˚52'32" W, 35˚19'51" N	0.81 km²	33.7 cm (June) – 44.5 cm (Sept.)	14.8 ˚C – 26.3 ˚C	NA
Roan Mountain	1916 m	82˚8'8" W, 36˚6'11" N	8.62 km²	8.4 cm (Nov.) – 17.4 cm (July)	-3.5 ˚C –26.2 ˚C	1962
Mount Mitchell	2037 m	82˚15'55" W, 35˚45'55" N	24.46 km²	31.3 cm (Feb.) – 61.2 cm (July)	-6.8 ˚C – 18.7 ˚C	1957

Mount Rogers is located within the Mount Rogers National Recreation Area in the Jefferson National Forest. Collectively, Mount Rogers and nearby Whitetop Mountain are termed the Balsam Mountains of Virginia. Mount Rogers, the highest peak in Virginia at 1,746 m in elevation, is situated in the Blue Ridge physiographic province (National Parks Service 2023). Annual mean precipitation is estimated to be over 150 cm near the summit of Mount Rogers (Stephenson & Adams 1984). The soils in our Mount Rogers study area are predominantly Blackarn-Bloodyhorse Complex, which is classified as a well-drained, moderately to extremely acidic, and rocky inceptisol series developed from weathered metamorphic and igneous parent material (California Soil Resources Lab 2024). Presence of spruce-fir forest on Mount Rogers varies by elevation depending on aspect, with spruce-fir forest found above 1,500 m on the northern slope, above 1,600 m to the northwest, west, and south, and above 1,700 to the southwest (Stephenson & Adams 1984). The spruce-fir forest at Mount Rogers is dominated by Fraser fir with a major red spruce component and smaller populations of mountain ash (*Sorbus americana*) and yellow birch (Stephenson & Adams 1984). In their study of forest composition at Mount Rogers, the Black Mountains, and the Great Smoky Mountains, Nicholas and Zedaker (1992) reported a relative lack of balsam woolly adelgid damage to Fraser fir in comparison with more widespread mortality on other mountains. Although smaller or mixed red spruce stands occur from Whitetop Mountain and Bills Ridge in the west as far east as the Little Wilson Creek National Forest Wilderness Area, our Mount Rogers study area focused on the spruce-fir-dominated sky island at Mount Rogers (Diggins 2023; personal correspondence).

Little Sam Knob and Black Balsam Knob are located in the Nantahala National Forest, just southwest of Asheville, North Carolina. Little Sam Knob has a maximum elevation of 1,786 m and 0.27 km^2 of spruce-fir forest interspersed with hardwoods. The nearby Black Balsam Knob is slightly higher with a maximum elevation of 1,894 m and 0.84 km^2 of spruce-fir cover. The mean annual precipitation recorded since 2004 at the closest weather station, near the Cradle of Forestry in

America, is approximately 39.2 cm (National Weather Service 2024). Soils at Little Sam Knob are classified as Tanasee-Balsam complex, well-drained inceptisols formed from the weathering of igneous and metamorphic rocks (California Soil Resources Lab 2024). At Black Balsam Knob, most soil is Wayah series, with some Tanasee-Balsam and some stony, loamy unclassified floodplain inceptisol soils to the west (California Soil Resources Lab 2024).

Roan Mountain is situated within the Pisgah National Forest in North Carolina and the Cherokee National Forest in Tennessee. Roan Mountain is approximately 19 km^2 in area with a peak elevation of 1,916 m at Roan High Knob. Roan Mountain lies within the Blue Ridge physiographic province (US EPA 2022). Mean annual precipitation at Roan Mountain is estimated to be approximately 141 cm (White et al. 2014). The soils at Roan High Knob and extending along the ridge to the east and west are predominantly classified under the Wayah-Burton Complex and are considered course-loamy, well-drained inceptisols developed from the weathering of igneous and metamorphic parent materials, with high organic material content near the surface (California Soil Resources Lab 2024). The southern aspect soils are also largely classified as Wayah-Burton Complex. To the north of Roan High Knob, soils are Burton-Craggey Complex, with similar characteristics to the Wayah-Burton Complex but sometimes classified as somewhat excessively drained (California Soil Resources Lab 2024). Prior to logging in the 1930s, the hardwood component at Roan Mountain was reported to contain yellow birch, *Acer spicatum*, American beech, mountain ash, *Aesculus octandra*, and *Prunus pensylvanica* (White et al. 2014). A more recent survey of forest composition found Fraser fir dominating above 1800 m, with red spruce at the second highest importance (White et al. 2012). Our study focused on the sky island that encompasses the Roan High Bluff Trailhead parking lot and the Rhododendron Gardens area in Pisgah National Forest, extending past the Carver's Gap Trailhead in the east and to Feeding Ridge in the southwest (Diggins 2023; personal correspondence).

Historically, Grandfather Mountain was a privately-owned tourist destination (Swanson 2012). Grandfather Mountain is situated within the Blue Ridge physiographical province (National Parks Service 2023) and today is preserved by the Grandfather Mountain Stewardship Foundation, the Grandfather Mountain State Park, and conservation easements held by The Conservation Fund and The Nature Conservancy (Soulé 2011). The summit of Grandfather Mountain at Calloway Peak is 1,812 m in elevation. Annual mean precipitation is approximately 115 cm at the Mile High Swinging Bridge southwest of Calloway Peak (Grandfather Mountain Stewardship Foundation 2024). The soils at Calloway Peak are primarily classified as Clingman-Craggey-Rock Outcrop Complex, which includes Clingman well-drained, strongly to extremely acidic histosols and somewhat excessively drained Craggey inceptisols, rocky soils resulting from the weathering of metamorphic rocks (California Soil Resources Lab 2024). Downslope from Calloway Peak, soils are composed mainly of well-drained, highly weathered Balsam inceptisols, with small proportions classified as rock outcrop and rubble land. Clingman-Craggey-Rock Outcrop Complex soils compose most of the ridge leading southwest from Calloway Peak to the Mile-High Swinging Bridge at Grandfather Mountain Stewardship Foundation. Red spruce has been found at Grandfather Mountain between 1,340 and 1,784 m in elevation (Soulé 2011). The westernmost extent of the sky island is near the Grandfather Mountain Peak at 1,614 m and stretches almost to the Spice Bottom Trail and just across the Blue Ridge Parkway in the east (Diggins 2023; personal correspondence). Red spruce at Grandfather Mountain is associated with Fraser fir and mixed northern hardwoods (Grandfather Mountain Stewardship Foundation 2023, Ramseur 1960).

With a summit elevation of 2,037 m, Mount Mitchell is the highest peak in the Appalachian Mountains. The sky island following the ridge of Mount Mitchell is encompassed by Mount Mitchell State Park and Blue Ridge Parkway National Park. Patchy, mixed stands of red spruce extend from the sky island northward to Rogers Mountain, eastward to Pinnacle Mountain, northward along

Maple Camp Ridge and toward the South Toe River from Little Mountain to the Blue Ridge Parkway (Diggins 2023; personal correspondence). Southwestern North Carolina, where Mount Mitchell is located, can receive over 200 cm of precipitation annually (NOAA Water Information Center 1974). Soils along the ridge of Mount Mitchell are mostly composed of the Burton-Craggey complex of very strongly acidic inceptisols, with varying proportions of rock outcrop on the eastern and western slopes. The Black Mountains, which include Mount Mitchell, historically supported one of the largest areas of spruce-fir forest in the southern Appalachian Mountains, but have experienced balsam woolly adelgid infestation since 1957, leading to fir mortality between 83 and 98 percent, depending on stand composition (Lusk et al. 2010). In a survey of Mount Mitchell forest composition since balsam woolly adelgid infestation, Lusk et al. (2010) found that mountain ash and yellow birch were the main hardwoods associating with red spruce and Fraser fir in these forest types, comprising between 77 and 93 percent of total hardwoods across the surveyed forest types. Nicholas and Zedaker (1992) found that spruce-fir forest composition in the Black Mountains was consistent with the tendency of spruce-fir forests to shift from spruce-dominated to fir-dominated with increasing elevation, but also that increasing mortality due to balsam woolly adelgid infestations caused dead firs to outnumber live firs.

Data Collection

We systematically sampled the canopy and regeneration layer at each site by selecting survey points at the ecotonal transition between spruce-dominated forest and mixed hardwood forest (classified "spruce-hardwood"), within the spruce-dominated forest, at the ecotonal transition between spruce-dominated and fir-dominated forest ("spruce-fir"), and within the fir-dominated forest on each cardinal aspect (north, south, east, west) and one at the summit (Fig. 1). We used Google Earth (Google: Mountain View, CA, USA) and ArcGIS (ESRI: Redlands, CA, USA) to establish the first four points at each site in the spruce-hardwood ecotonal transition, with one on

each cardinal aspect in the spruce-hardwood ecotonal transition. Once each point was located in the field, a visual stem count was used to determine cover type, with approximately 50% red spruce/50% mixed northern hardwoods classified as "spruce-hardwood", >60% red spruce classified as "spruce-dominated", >20% red spruce and >20% Fraser fir classified as "spruce-fir", and >60% Fraser fir classified as "fir-dominated" (Fig. 1). Stands containing any red spruce and Fraser fir with >20% hardwoods were classified "spruce-fir-hardwood." If the point originally selected using Google Earth/ArcGIS was classified as "spruce-hardwood", we advanced upslope, using established trails whenever possible and stopping as soon as the cover type began transitioning to sample the next transitional ecotone. If the pre-selected point was classified as a different cover type, we proceeded downslope until we reached the approximate transition from hardwood-dominated to spruce-hardwoods.

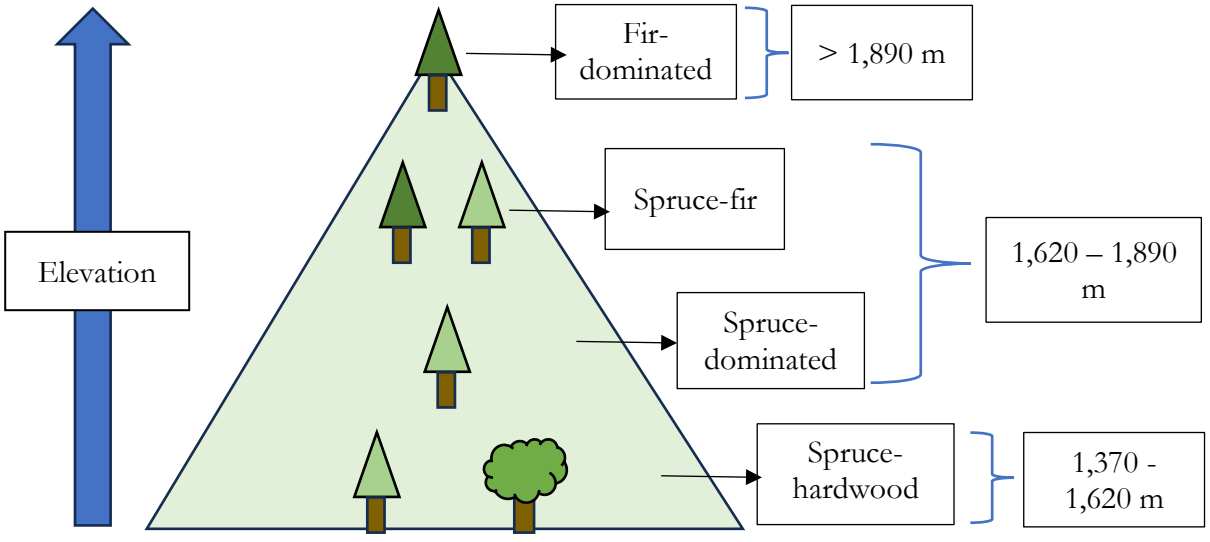

Fig. 2: Graphic representation of expected arrangement of fir (*Abies*)-dominated, spruce-fir (*Picea-Abies*), spruce-dominated, and spruce-hardwood cover types in southern Appalachian sky islands, (North Carolina, Tennessee, and Virginia, USA), 2023. Elevation increases from bottom to top of figure.

At each plot, we selected the five dominant/co-dominant red spruce, Fraser fir, and/or hardwoods, depending on cover type classification, nearest to our randomized survey point in horizontal distance (Fig. 2). After measuring diameter at breast height (1.37 m above the ground), a 5 mm increment core was extracted at breast height from each selected tree. Each cored tree was marked as a waypoint on both a Garmin Montana (Garmin: Olathe, KS, USA) and a Geode GPS (Juniper Systems: Logan, UT, USA) to have backup data in case either device failed. The elevation displayed on the Geode GPS when held up to the tree at breast height was recorded. One 0.25 m^2 PVC quadrat plot was placed at the survey point, and we tallied every stem shorter than 1.37 m by species, measured the tallest stem and recorded its species (Fig. 2). We then measured 6 m from the first quadrat, walking in a straight line north of the point using a compass (Fig. 2). At 6 m, we placed the quadrat again and repeated the tally (Fig. 2). We walked an additional 6 m from this point, and repeated this transect to the east, south, and west of the first quadrat (Fig. 2).

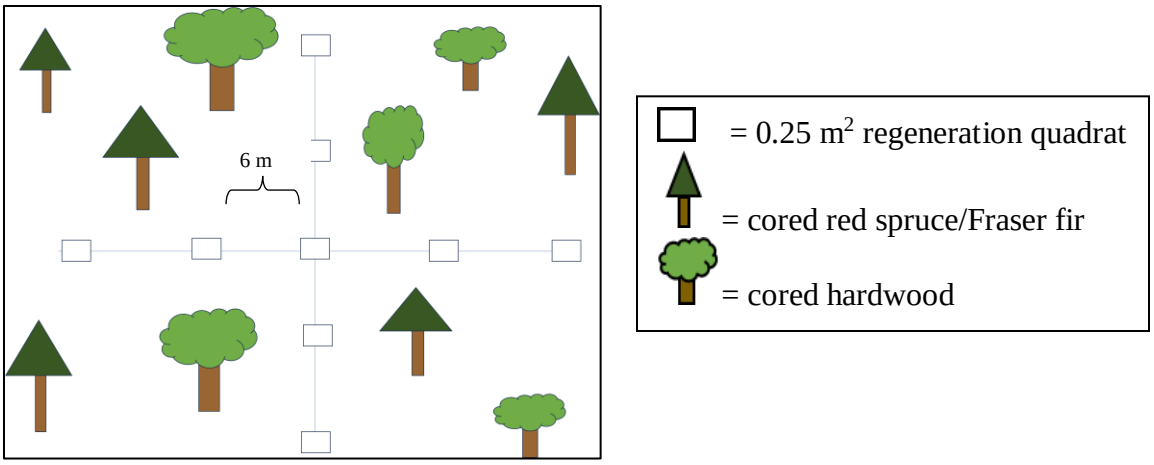

Fig. 3: Graphic representation of field survey protocol in southern Appalachian sky islands (North Carolina, Tennessee, and Virginia, USA), 2023. The regeneration quadrat at the center of the cross shape of quadrats represents the preselected survey point. Dark green trees represent cored red spruce (*Picea rubens*) and/or Fraser fir (*Abies fraseri*), and lighter green trees represent hardwoods.

Lab Analysis

Increment cores from red spruce, Fraser fir, and competing hardwoods were secured on grooved lath holders using wood glue, then sanded with progressively finer sandpaper grits (Stokes & Smiley 1996). Growth rings were counted and assigned calendar years beginning with the outermost ring following the cross-dating procedure outlined by Yamaguchi (1990). Annual growth rings for all species were measured to the nearest 0.002 mm with a TA Unislide Measurement System (Velmex, Inc., Bloomfield, NY). Millimeter ring width measurements were converted into basal area increment values in R (R Core Team 2024) using the *bai.in* function in Package *DplR,* which converts ring width measurements, measured in millimeters, into area values, accounting for the distance between the pith and the measured ring (Bunn et al. 2023).

Data Analysis

Statistical analysis was conducted in R (R Core Team 2024). We ran a repeated-measures analysis of variance (ANOVA) on basal area increment (henceforth BAI; cm^2 $year^{-1}$), with species, aspect, year, cover type (i.e. spruce-hardwood, spruce-dominated, spruce-fir, and fir-dominated) as predictor values, site as a random effect and unique core identifier as the grouping variable and an α of 0.05 using package *lme4* (Bates et al. 2015). Slopes of BAI for each combination of species, cover type and aspect over time were calculated using *lstrends*. To detect differences in BAI over time among aspect, cover type, and species, we performed pairwise comparisons of the slopes using the pairs function (Bates et al. 2015). Fraser fir was found in the following cover types: fir-dominated, spruce-fir, fir-hardwood, and spruce-fir-hardwood. However, the spruce-fir-hardwood and fir-hardwood cover types were not widely observed across aspects or sites, so we excluded these cover types from analysis. Similarly, red spruce was most frequently found in spruce-dominated, spruce-hardwood, and spruce-fir stands, so red spruce in spruce-fir-hardwood cover types were excluded. We visually displayed BAI over time using *ggplot2* (Wickham 2016). With *ggplot2*, we added linear

regression equations to each plot using subsets by species (combining red spruce and hardwoods to assess competition). We also ran a mixed-effects ANOVA on mean BAI from 1964–2022 (cm^2) with elevation, species, and their interaction as predictor variables and site as a random effect. We calculated slope coefficients using *lstrends* and performed pairwise contrasts with the *pairs* function (Bates et al. 2015). Mean BAI was calculated for each increment core by averaging BAI values between 1964-2022, as cross-dating of cores showed that the majority of sampled trees had reached 1.37 m (the height at which cores were taken and therefore the origin of each core) by 1964. To visualize these trends, we created a scatterplot of mean BAI between 1964-2022 by elevation and calculated linear regression equations and R^2 values using *ggplot2* (Wickham 2016).

Results

Across sites, BAI changed significantly over time, often increasing (Table 2; Fig. 2). Annual BAI values varied by species, cover type, aspect, and all interactions between these terms (Table 2; Fig. 2).

Table 2. Analysis of variance (α= 0.05) results for effects of species, cover type, aspect, and year on basal area increment (cm^2yr^{-1}) of red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods in spruce-hardwood, spruce-dominated, spruce-fir, and fir-dominated cover types at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA), 2023. [1]Reference condition.

Term	Estimate	Standard Error	DF	p-value
Intercept:	9.17e2	1.23e02	8.64e3	<0.0001
Fraser fir	-2.78e3	1.57e2	9.18e3	<0.0001
Red spruce	-1.08e3	9.90e1	8.99e3	<0.0001
Cover type:				
Spruce-dominated	-8.65e2	1.41e2	8.39e3	<0.0001
Spruce-fir	4.36e1	7.72e1	7.77e3	0.58
Spruce-hardwood	-1.08e3	1.20e2	8.63e3	<0.0001
Fir-dominated[1]	-	-	-	-
Aspect				
North	-1.09e3	1.10e2	7.83e3	<0.0001

East[1]	-	-	-	-
South	-9.36e2	2.06e2	9.07e3	<0.0001
Summit	1.64e3	1.01e2	3.80e3	<0.0001
West	-1.45e3	1.89e2	4.50e3	<0.0001
Year				
Cover type * Aspect				
North * spruce-dominated	1.14e3	1.36e2	1.76e3	<0.0001
South * spruce-dominated	8.14e2	2.23e2	3.65e3	0.0003
West * spruce-dominated	1.26e3	2.05e2	3.64e3	<0.0001
East * spruce-dominated[1]	-	-	-	-
North * spruce-fir	1.21e3	1.17e2	2.26e3	<0.0001
South * spruce-fir	1.22e3	2.14e2	4.09e3	<0.0001
North * spruce-hardwood	1.19e3	1.05e2	2.08e3	<0.0001
South * spruce-hardwood	7.82e2	2.07e2	4.37e3	0.0002
West * spruce-hardwood	1.44e3	1.91e2	4.18e3	<0.0001
Cover type * Year				
Spruce-dominated * Year	4.44e-1	7.04e-2	9.12e3	<0.0001
Spruce-fir * Year	-2.19e-2	3.86e-2	8.21e3	0.57
Spruce-hardwood * Year	5.53e-1	5.98e-2	9.59e3	<0.0001
Fir-dominated * Year[1]	-	-	-	-
Cover type * Species				
Fraser fir * spruce-dominated	2.14e3	1.82e2	2.45e3	<0.0001
Fraser fir * fir-dominated[1]	-	-	-	-
Red spruce * spruce-dominated	7.17e2	1.23e2	1.62e3	<0.0001
Fraser fir * spruce-fir	1.70e3	1.29e2	2.78e3	<0.0001
Fraser fir * spruce-hardwood	4.87e2	1.29e2	3.17e3	0.0002
Red spruce * spruce-hardwood	1.10e3	9.24e1	1.81e3	<0.0001
Hardwoods * spruce-hardwood[1]	-	-	-	-
Species * Year				
Fraser fir * Year	1.40e0	7.83e-2	8.22e3	<0.0001
Red spruce * Year	5.54e-1	4.94e-3	7.37e3	<0.0001
Hardwoods * Year[1]	-	-	-	-
Species * Aspect				
Fraser fir * North	2.13e3	1.61e2	3.12e3	<0.0001
Red spruce * North	-2.91e2	4.62e1	1.47e3	<0.0001
Hardwoods * North	-	-	-	-
Fraser fir * South	2.85e3	2.36e2	4.15e3	<0.0001
Red spruce * South	-2.81e2	5.99e1	1.29e3	<0.0001
Hardwoods * South	-	-	-	-
Fraser fir * West	1.75e3	2.56e2	5.25e3	<0.0001
Red spruce * West	-1.82e2	5.86e1	1.26e3	0.002
Hardwoods * West	-	-	-	-
Fraser fir * East	-	-	-	-
Red spruce * East	-	-	-	-
Hardwoods * East	-	-	-	-
Aspect * Year * Species				
Fraser fir * North * Year	1.08e0	8.03e-2	8.03e3	<0.0001

Red spruce * North * Year	1.45e-1	2.30e-2	5.79e3	<0.0001
Hardwoods * North * Year	-	-	-	-
Fraser fir * South * Year	-1.43e0	1.18e-1	7.91e3	<0.0001
Red spruce * South * Year	1.37e-1	2.99e-2	4.86e3	<0.0001
Hardwoods * South * Year	-	-	-	-
Fraser fir * West * Year	-8.86e-1	1.27e-1	8.27e3	<0.0001
Red spruce * West * Year	8.99e-2	2.92e-2	5.32e3	0.002
Hardwoods * West * Year	-	-	-	-
Fraser fir * East * Year[1]	-	-	-	-
Red spruce * East * Year[1]	-	-	-	-
Hardwoods * East * Year[1]	-	-	-	-
Cover type * Year * Species				
Fraser fir * spruce-dominated * Year	-1.08e0	9.05e-2	7.62e3	<0.0001
Red spruce * spruce-dominated * Year	-3.69e-1	6.12e-2	6.90e3	<0.0001
Fraser fir * spruce-fir * Year	-8.50e-1	6.42e-2	6.22e3	<0.0001
Fraser fir * spruce-hardwood * Year	-2.47e-1	6.44e-2	4.69e3	0.0001
Red spruce * spruce-hardwood * Year	-5.61e-1	4.61e-2	6.49e3	<0.0001
Hardwoods * Spruce-hardwood * Year[1]	-	-	-	-
Cover type * Aspect * Year				
North * spruce-dominated * Year	-5.83e-1	6.81e-2	8.85e3	<0.0001
South * spruce-dominated * Year	-4.18e-1	1.11e-1	8.62e3	0.0002
West * spruce-dominated * Year	-6.43e-1	1.02e-1	8.55e3	<0.0001
East * spruce-dominated * Year[1]	-	-	-	-
North * spruce-fir * Year	-6.18e-1	5.83e-2	9.08e3	<0.0001
South * spruce-fir * Year	-6.15e-1	1.07e-1	8.48e3	<0.0001
East * spruce-fir * Year[1]	-	-	-	-
North * spruce-hardwood * Year	-6.08e-1	5.23e-2	9.62e3	<0.0001
South * spruce-hardwood * Year	-4.00e-1	1.03e-1	8.77e3	0.0001
West * spruce-hardwood * Year	-7.30e-1	9.53e-2	8.78e3	<0.0001
East * spruce-hardwood * Year[1]	-	-	-	-
Cover type * Aspect * Species * Year				<0.0001
Red spruce * North * Spruce-dominated * Year	-2.73e1	9.79e1	1.27e3	0.78
Red spruce * East * Spruce-dominated * Year	-	-	-	-
Red spruce * South * Spruce-dominated * Year	4.91e2	1.13e2	1.26e3	<0.0001
Fraser fir * West * Spruce-dominated * Year	-1.17e3	3.00e2	4.36e3	<0.0001
Red spruce * West * Spruce-dominated * Year	6.47e2	1.04e2	1.34e3	<0.0001
Red spruce * East * Spruce-dominated * Year[1]	-	-	-	-

Fraser fir * North * Spruce-fir * Year	-2.65e3	1.75e2	2.92e3	<0.0001
Fraser fir * South * Spruce-fir * Year	-3.39e3	2.50e2	3.59e3	<0.0001
Fraser fir * East * Spruce-fir * Year[1]	-	-	-	-
Hardwoods * North * Spruce-hardwood * Year[1]	-	-	-	-
Hardwoods * East * Spruce-hardwood * Year[1]	-	-	-	-
Hardwoods * South * Spruce-hardwood * Year[1]	-	-	-	-
Hardwoods * West * Spruce-hardwood * Year[1]	-	-	-	-

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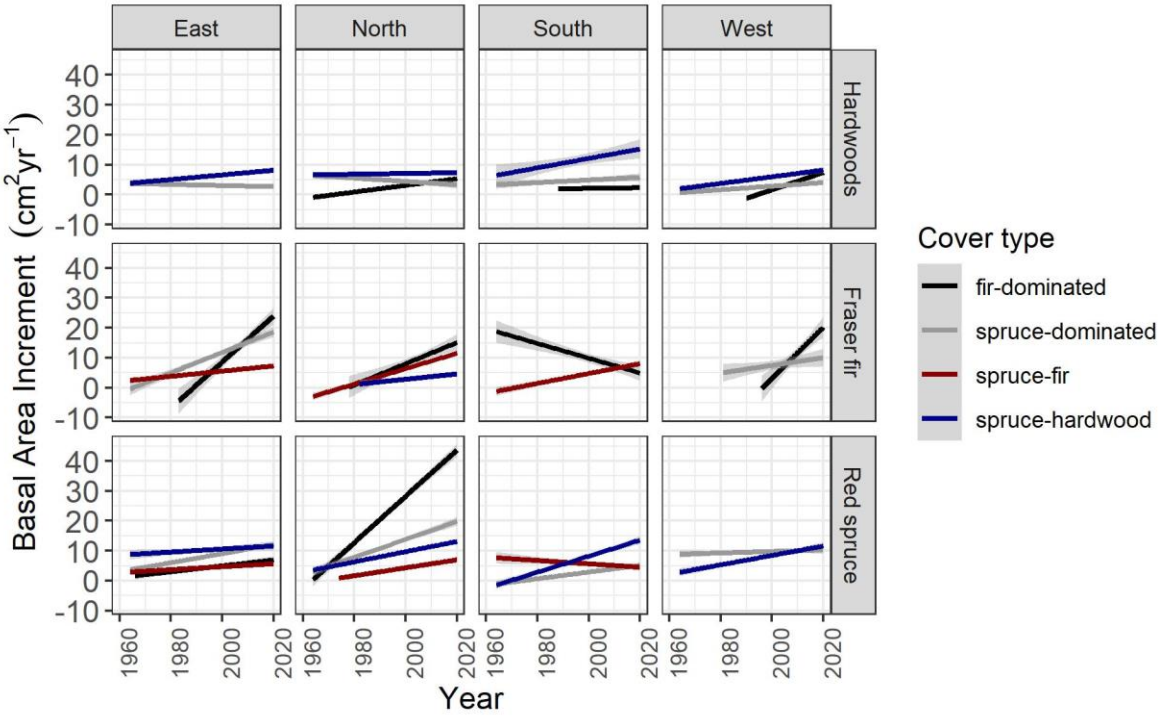

Fig. 4. Linear trends of basal area increment by year (cm^2yr^{-1}) for red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA) by aspect and cover type.

Growth rates of Fraser fir

Fraser fir BAI in fir-dominated stands increased over time on all aspects except the south, with the greatest growth rates on the eastern aspect (Table 3–4, Fig. 4). In fir-dominated stands,

Fraser fir growth rates were significantly greater on northern, eastern, and western aspects than on summits (Table 3, Fig. 4). Growth rates in fir-dominated stands on western aspects were also significantly greater than on northern and southern aspects, with the highest growth rates on eastern aspects (Table 3–4, Fig. 4). In fir-dominated stands, growth rates varied across aspects but were generally increasing except on the southern aspect (Table 4).

Table 3. Differences in slope coefficients with standard error and p-values ($\alpha = 0.05$) of basal area increment over time for Fraser fir (*Abies fraseri*) growing in fir-dominated stands at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA).

Contrast	Estimate	Standard Error (SE)	p-value
North – summit	0.30	0.04	<0.0001
North – west	-0.37	0.09	<0.0001
East – summit	0.81	0.06	<0.0001
South – west	-0.81	0.09	<0.0001
Summit – west	-0.67	0.08	<0.0001

Table 4. Slope coefficients for linear model of basal area increment values over time (cm^2yr^{-1}) for Fraser fir (*Abies fraseri*) growing in fir-dominated and spruce-fir (*Picea-Abies*) cover types on each aspect where the cover type was observed at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA).

Cover type	Aspect	Slope	Standard Error
Fir-dominated	North	0.41	0.04
	East	0.93	0.05
	South	-0.03	0.04
	West	0.78	0.08
	Summit	0.11	0.01
Spruce-fir	North	0.26	0.03
	East	0.06	0.02
	South	0.19	0.03

The only significant differences in growth rates between fir-dominated and spruce-fir cover types were on eastern aspects, where growth rates were greater in fir-dominated stands, and on southern aspects, where growth rates were greater in spruce-fir stands (Fig. 3, Table 5). The spruce-

fir cover type was only represented on northern, eastern, and southern aspects. Fraser fir growth rates were significantly greater in fir-dominated stands than in spruce-fir stands on eastern aspects (Fig. 3, Table 5). On southern aspects, Fraser fir growth rates were higher in spruce-fir stands than in fir-dominated stands, where BAI values decreased over time (Fig. 3, Table 5). In spruce-fir stands, Fraser fir growth rates were significantly greater on northern and southern aspects than on eastern aspects (Fig. 3, Table 5). No contrasts between red spruce and Fraser fir growing in spruce-fir stands on the same aspects were statistically significant (Table 6). Although spruce-fir stands were underrepresented on some aspects, growth rates of Fraser fir were lower in spruce-fir stands than in fir-dominated stands on eastern aspects, lower in fir-dominated stands than spruce-fir on southern aspects, and greatest on northern aspects in spruce-fir stands (Fig. 3, Table 5).

Table 5. Differences in slope coefficients with standard error and p-values ($\alpha = 0.05$) of basal area increment over time for Fraser fir (*Abies fraseri*) growing in fir-dominated and spruce-fir (*Abies-Picea*) cover types on each aspect where cover type was observed at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA).

Contrast	Estimate	Standard Error (SE)	p-value
Fir-dominated (east) – spruce-fir (east)	0.87	0.06	<0.0001
Spruce-fir (south) – fir-dominated (south)	-0.23	0.04	0.0003
Spruce-fir (east) – spruce-fir (south)	-0.13	0.03	0.03
Spruce-fir (east) – spruce-fir (north)	-0.20	0.03	<0.0001

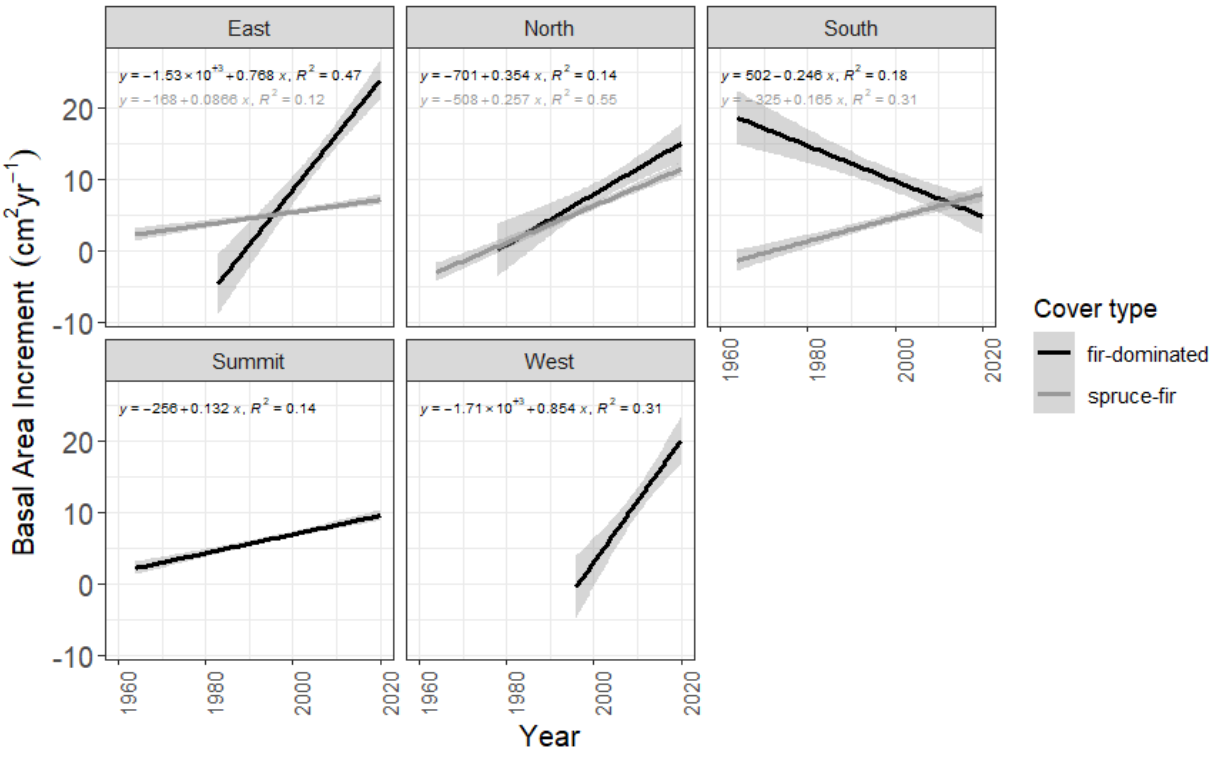

Fig. 5: Linear trends of basal area increment by year (cm^2yr^{-1}) for Fraser fir (*Abies fraseri*) at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA) by aspect and cover type. Spruce-fir (*Abies-Picea*) cover type was not located in the field on western aspects or summits.

Table 6. Differences in slope coefficients with standard error and p-values ($\alpha = 0.05$) of basal area increment over time for red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*) in spruce-fir stands at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA). Spruce-fir cover type was underrepresented on western aspects, so contrast was inestimable.

Contrast	Estimate	Standard Error (SE)	p-value
Fraser fir, spruce-fir (east) – Red spruce, spruce-fir (east)	-0.0002	0.02	1.00
Fraser fir, spruce-fir (north) – Red spruce, spruce-fir (north)	0.11	0.04	0.75
Fraser fir, spruce-fir (south) – red spruce, spruce-fir (south)	1.35	0.04	0.08
Fraser fir, spruce-fir (west) – red spruce, spruce-fir (west)	NA	NA	NA

Growth rates of red spruce and northern hardwoods

Differences in red spruce growth rates were dependent on aspect and cover type (Table 7). Growth rates were greater in spruce-dominated stands than spruce-fir stands on northern and eastern aspects and greater in spruce-hardwood stands than spruce-fir stands on southern aspects (Table 7-8, Fig. 5). On northern and eastern aspects, red spruce growth rates were significantly greater in spruce-dominated stands than in spruce-fir stands (Table 7-8, Fig. 5). On southern aspects, growth rates were greater in spruce-hardwood stands than spruce-fir stands (Table 7-8, Fig. 5). Growth rates in spruce-fir stands were greater on northern aspects than eastern aspects and southern aspects (Table 7-8, Fig. 5). Red spruce had greater growth rates in spruce-dominated than spruce-fir stands on northern and eastern aspects, while growth rates were greater in spruce-hardwood stands than spruce-fir stands on southern aspects, greatest in spruce-dominated and spruce-fir stands on northern aspects, and greatest in spruce-hardwood stands on southern aspects (Table 7-8, Fig. 5).

Table 7: Differences in slope coefficients with standard error and p-values ($\alpha = 0.05$) of basal area increment over time for red spruce (*Picea rubens*) in spruce-hardwood, spruce-dominated, and spruce-fir (*Abies-Picea*) cover types at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA), 2023.

Contrast	Estimate	Standard Error	p-value
Spruce-dominated (north) – spruce-fir (north)	0.15	0.03	0.007
Spruce-dominated (east) – spruce-fir (east)	0.10	0.02	0.0005
Spruce-fir (south) – spruce-hardwood (south)	-0.23	0.03	<0.0001
Spruce-dominated (north) – spruce-hardwood (north)	0.13	0.02	<0.0001
Spruce-dominated (west) – spruce-hardwood (west)	-0.15	0.02	<0.0001
Spruce-dominated (south) – spruce-hardwood (south)	-1.79	0.03	<0.0001
Spruce-hardwood (east) – spruce-hardwood (north)	-0.10	0.02	<0.0001

Spruce-hardwood (east) – spruce-hardwood (south)	-0.22	0.02	<0.0001
Spruce-hardwood (east) – spruce-hardwood (west)	-0.09	0.02	0.0002
Spruce-hardwood (north) – spruce-hardwood (south)	-0.12	0.02	<0.0001
Spruce-hardwood (south) – spruce-hardwood (west)	0.12	0.02	0.0001

Table 8: Slope coefficients for each cover type – aspect combination with significantly different trends in basal area increment over time (cm^2yr^{-1}) for red spruce (*Picea rubens*) at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA).

Cover type	Aspect	Slope coefficient	Standard Error (SE)
Spruce-dominated	North	0.30	0.01
	East	0.16	0.01
	South	0.11	0.02
	West	0.02	0.01
Spruce-hardwood	North	0.17	0.01
	East	0.08	0.01
	South	0.29	0.02
	West	0.17	0.01
Spruce-fir	North	0.15	0.03
	East	0.06	0.01
	South	0.06	0.02

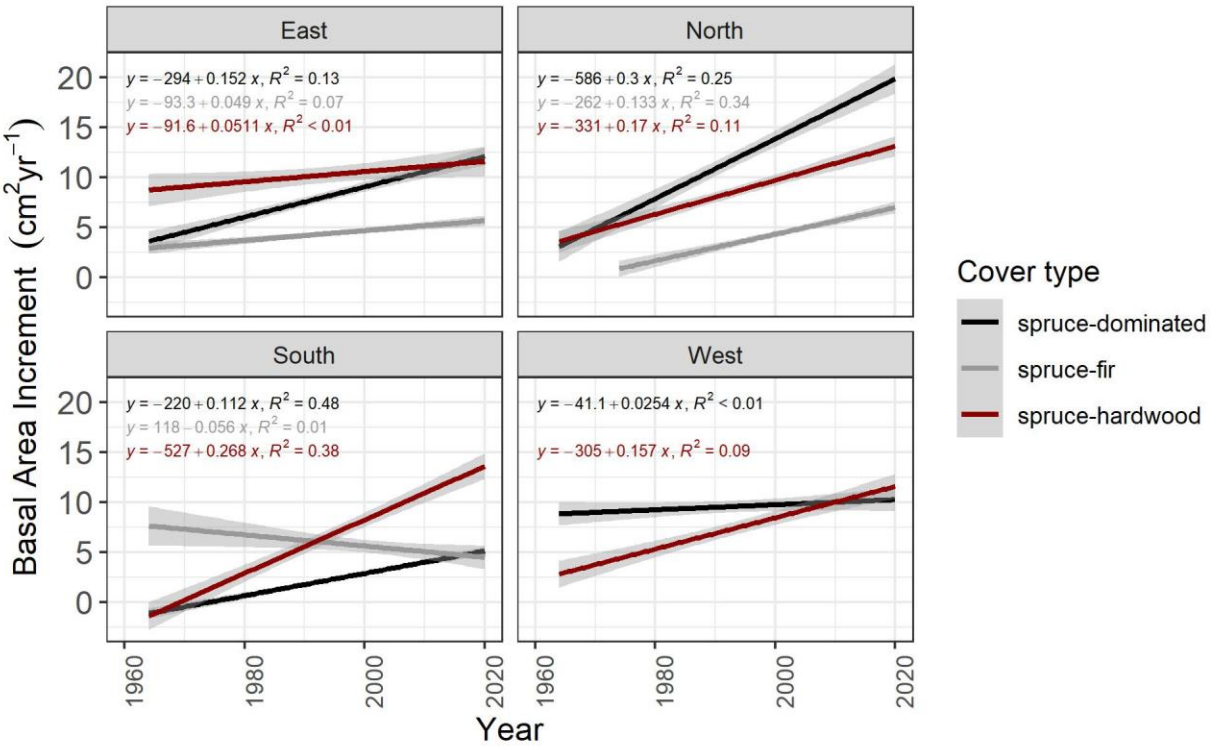

Fig. 6: Linear trends of basal area increment by year (cm^2yr^{-1}) for red spruce (*Picea rubens*) in spruce-dominated, spruce-fir (*Abies-Picea*) and spruce-hardwood cover types at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA) by aspect and cover type. Spruce-fir cover type was not located in the field on western aspects.

Red spruce had greater growth rates in spruce-hardwood stands than in spruce-dominated and spruce-fir stands on western and southern aspects and had the greatest growth rates on southern aspects and least on eastern aspects, while hardwoods had greater growth rates on northern aspects than southern aspects (Fig. 5, Table 9-10). Red spruce on northern aspects had significantly greater growth rates in spruce-dominated stands than spruce-hardwood stands (Table 7-8, Fig. 5). On western aspects, red spruce growth rates were greater in spruce-hardwood stands than spruce-dominated stands (Table 7-8, Fig. 5). Spruce-hardwood stands on southern aspects also had greater growth rates than spruce-dominated stands on the same aspect (Table 7-8, Fig. 5). In spruce-hardwood stands, red spruce growth rates were significantly lower on eastern aspects than on all

other aspects (Table 7-8, Fig. 5). Growth rates of red spruce in spruce-hardwood stands on southern aspects were also significantly greater than those on northern and western aspects (Table 7-8, Fig. 5). In spruce-hardwood stands, red spruce growth rates were greater than those of hardwoods on northern and southern aspects (Table 9). The growth rates of hardwoods in spruce-hardwood stands on northern aspects were also less than the growth rates of hardwoods on southern aspects (Table 9-10). Red spruce had greater growth rates in spruce-hardwood stands than spruce-dominated stands on western and southern aspects and greater growth rates in spruce-dominated stands on northern aspects, with significantly greater growth rates in red spruce than hardwoods in spruce-hardwood stands on northern and southern aspects (Table 7-9, Fig. 5).

Table 9: Differences in slope coefficients with standard error and p-values (α= 0.05) of basal area increment over time (cm^2yr^{-1}) for red spruce (*Picea rubens*) and hardwoods in spruce-hardwood stands at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA).

Contrast	Estimate	Standard Error (SE)	p-value
Hardwoods (north) – red spruce (north)	-0.14	0.02	<0.0001
Hardwoods (south) – red spruce (south)	-0.13	0.03	0.002
Hardwoods (north) – hardwoods (south)	-0.13	0.02	<0.0001

Table 10: Slope coefficients for hardwoods on each aspect in spruce (*Picea*)-hardwood cover types with significantly different trends in basal area increment over time at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA), 2023.

Cover type	Aspect	Slope	Standard Error (SE)
Spruce-hardwood	North	0.03	0.01
	South	0.16	0.02

Elevation:

Elevation alone was not a strong predictor for mean BAI, but its effect on the linear trend of mean BAI varied by species, with mean BAI of hardwoods decreasing as elevation increased and

that of red spruce and Fraser fir increasing as elevation increased (Table 11, Fig. 6). Mean BAI values were not significantly affected by elevation but were significantly affected by species and the interaction between species and elevation (Table 11). Fraser fir did not have a significantly different trend in mean BAI by elevation from that of red spruce or hardwoods, but hardwoods and red spruce had significantly different trendlines (Table 12, Fig. 6). Mean BAI values of red spruce and Fraser fir had a weak positive relationship with elevation, while hardwoods had a weak negative relationship (Fig. 6). Although mean BAI was not significantly affected by elevation, the linear trends of mean BAI by elevation were significantly different for hardwoods and red spruce, with a negative relationship in hardwoods and a positive relationship in red spruce (Table 11-12).

Table 11: Terms and p-values for analysis of variance ($\alpha = 0.05$) of the effects of species, elevation, and their interaction on mean basal area increment (cm^2) from 1964-2022 for red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods in spruce-hardwood, spruce-dominated, and spruce-fir, fir-dominated cover types at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA).
[1]Reference condition.

Term	Estimate	Standard Error	D.F.	p-value
Species				
Intercept	33.75	10.19	207.22	0.001
Fraser fir	-28.92	15.80	267.18	0.07
Red spruce	-28.92	10.65	264.17	0.007
Hardwoods[1]	-	-	-	-
Elevation	-0.02	0.006	224.27	0.007
Species*Elevation				
Fraser fir * Elevation	0.02	0.009	266.73	0.03
Red spruce * Elevation	0.02	0.006	264.25	0.002
Hardwoods * Elevation[1]	-	-	-	-

Table 12: Differences in slope coefficients with standard error and p-values (alpha-level = 0.05) of mean basal area increment by elevation for red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods in spruce-hardwood, spruce-dominated, spruce-fir, and fir-dominated cover types at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA).

Species	Estimate	Standard Error (SE)	p-value
Hardwoods – Fraser fir	-0.02	0.009	0.08 (NS)
Hardwoods – Red spruce	-0.02	0.006	0.007
Fraser fir – Red spruce	-0.0003	0.008	1.0 (NS)

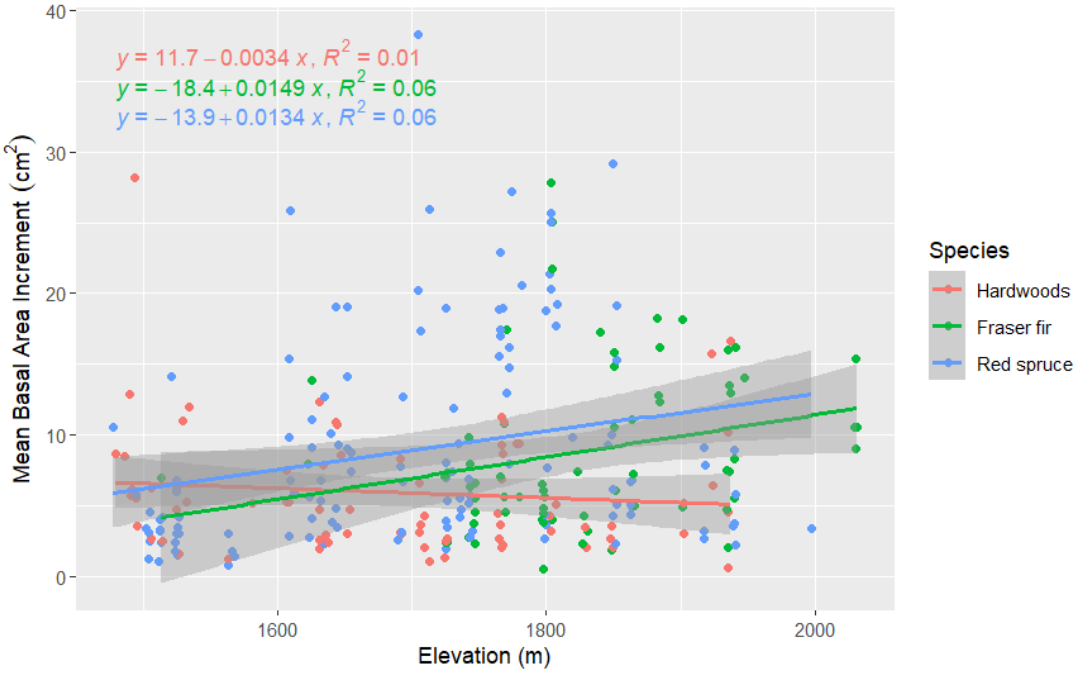

Fig. 7: Mean basal area increment (cm^2) from 1964-2022 of each sampled tree plotted by elevation at 1.37 m above the ground for red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods in spruce-hardwood, spruce-dominated, spruce-fir, and fir-dominated cover types at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA).

Regeneration

Insufficient stems were present in our regeneration samples to permit testing of differences in regeneration by overstory cover type, elevation, and aspect. Seedlings and saplings observed were predominantly Fraser fir followed by red spruce (see Appendix 2). Other species observed in the

regeneration layer were red maple, American beech, striped maple (*Acer pensylvanicum*), and birch species. During field sampling, we often observed dense Fraser fir regeneration at high elevations and sometimes observed dense red spruce regeneration.

Discussion

Basal area increment (BAI) values generally increased over time, with red spruce tending to grow faster than its hardwood competitors and Fraser fir tending to grow faster than red spruce, its common competitor for growing space at the fir-dominated to spruce-fir ecotonal transition. Growth trends varied by species, cover type, aspect, and all their interactions but generally held over most aspects and cover types across sites. The general lack of regeneration prevented statistical analysis of this facet of competitive status among species, but the majority of seedlings and saplings were Fraser fir, followed by red spruce, with low counts of hardwood seedlings/saplings. Our observed presence of red spruce regeneration is consistent with other reports of red spruce in the understory in the central Appalachians and in southwestern North Carolina (Collins et al. 2011, Rollins et al. 2010). The regenerating stems counted were primarily Fraser fir and red spruce, suggesting the need for restoration treatments which encourage recruitment of these species into the overstory to accelerate range expansions and increase resiliency to stressors and disturbance agents in these systems.

Fraser fir BAI increased over time in spruce-fir stands on all aspects where they were found and in fir-dominated stands on all aspects except the south. The greater growth rates of Fraser fir in fir-dominated stands as compared to spruce-fir stands on eastern aspects were consistent with our hypotheses, but the opposite trend we observed on southern aspects was more unexpected. The greater growth rates of Fraser fir in spruce-fir stands on northern aspects were also consistent with our hypotheses, but in fir-dominated stands, we unexpectedly saw greater growth rates on eastern

aspects, which might correspond to areas of high adelgid mortality where young fir were released from mature competitors. Notably, in fir-dominated stands on eastern and western aspects, where growth rates were the highest in this cover type, no sampled fir had an estimated age at DBH prior to 1982, which is after the first recorded balsam woolly adelgid infestation at all sites. White et al. (2012) noted that Fraser fir sampled above 1800 m at Roan Mountain exhibited irregular early growth following establishment after the conclusion of intensive logging in 1937. Irregular early growth in young trees established in canopy openings created by balsam woolly adelgid-driven mortality could have contributed to the relatively dramatic increases in growth rates on eastern and western aspects.

We also saw increasing mean BAI values of Fraser fir with increasing elevation, which was consistent with our hypotheses. Similarly, the greater growth rates of Fraser fir in fir-dominated than spruce-fir stands and the greater Fraser fir mean BAI with increasing elevation agree with the high mean diameter increment at high elevations observed in the southern Appalachians by Smith & Nicholas (1999), which they attributed to Fraser fir's adaptation to high elevation conditions and to stand thinning following balsam woolly adelgid-driven mortality. Conversely, the lower mean BAI values we observed in this species at low elevations could support concerns that Fraser fir may decline at low elevations as climate change progresses. For example, Kaylor et al. (2017), who modeled future Fraser fir seedling densities and overstory populations in the Great Smoky Mountains, predicted a population decline at their lowest-elevation site due to rising summer temperatures and increasing survival and expansion of pest insects such as the balsam woolly adelgid. In addition, western aspects may be more exposed to prevailing winds with eastern aspects being more protected, such as at Mount Rogers and Mount Mitchell (Goelz et al. 1998). Wind stress could also be a factor in the greatest increases in Fraser fir BAI values being found on exposed western aspects as stem diameter increases have been observed in Fraser fir subjected to mechanical-

and wind-driven flexure changes in both laboratory and field trials (Telewski & Jaffe 1986). Conversely, fir on more protected eastern aspects might allocate more resources to height growth.

Consistent with our hypotheses, growth rates of red spruce were greater in spruce-dominated stands than spruce-fir stands on northern and eastern aspects and greater on northern aspects in spruce-dominated and spruce-fir stands. Contrary to our hypotheses, growth rates were greater in spruce-hardwood stands than in spruce-dominated stands on southern and western aspects. We also saw greater growth rates in red spruce than in hardwoods in spruce-hardwood stands on northern and southern aspects. This finding contradicts our hypothesis of greater growth rates in hardwoods than in red spruce but is consistent with Smith and Nicholas' (1999) finding of greater mean annual diameter increment values in red spruce compared to hardwoods in logged stands at middle elevations and in unlogged stands at low- and middle-elevations. Our results highlight the need to increase understanding of the mechanisms of competition and resources in this forest type. The greater growth rates we observed in red spruce in spruce-hardwood stands compared to spruce-dominated stands, which are often at higher elevations, could be due in part to decreasing site quality, shorter growing seasons, and lower temperatures with increasing elevation, as suggested by Nicholas and Zedaker (1992). Recent studies have found pools and fluxes of several soil nutrients (i.e. nitrogen and soil organic carbon) to be more often influenced by topography than elevation (Tewksbury & Van Miegroet 2007, Garten 2000), and we did not sample soils, so further studies of competition dynamics in these systems would benefit from analyses of soils and topography effects.

We also observed greater growth rates of red spruce on north and east aspects in spruce-dominated stands, which could be a result of the tendency of these slopes to maintain cooler temperatures due to less direct sunlight, which may offer a competitive advantage to cold-adapted red spruce (Mayfield & Hicks 2010). Although red spruce is better-adapted to cold, wet high-

elevation conditions because they can photosynthesize prior to leaf-out in hardwoods, photosynthesis rates are still limited by low winter temperatures (Schaberg et al. 1998). Similarly, the greater growth rates of red spruce in spruce-dominated stands compared to spruce-fir stands on northern and eastern aspects could indicate a threshold in its adaptation to these conditions (Smith & Nicholas 1999), especially when competing with Fraser fir. The decreasing Fraser fir growth rates and relatively low red spruce growth rates we observed on southern aspects must be taken with caution due to low sample sizes on the southern aspect in each main cover type, but may indicate negative effects of warmer, drier conditions on these cold-adapted conifers (Berry & Smith 2012, Collins et al. 2011). The variable growth rates we observed by aspect could help restoration practitioners prioritize planting and enhancement projects for spruce-fir forests, but our results also highlight the need for further study on the effects of topography (i.e. sheltering and cold air drainages), soils, stand dynamics, and competition on southern Appalachian sky islands.

Our results suggest greater resiliency of spruce-fir sky islands and lower competitive pressure between red spruce and northern hardwoods than expected. Red spruce growth rates outpaced those of hardwoods on two aspects across sites, suggesting that red spruce can sometimes outcompete hardwoods at the spruce-hardwood ecotonal transition. The generally increasing growth rates in red spruce and Fraser fir indicate the ability of these forests to persist in current conditions. We also saw weak positive relationships between elevation and mean BAI values in red spruce and Fraser fir and a weak negative relationship in hardwoods, which is consistent with the understanding that red spruce and Fraser fir require relatively low summer temperatures and high precipitation, which increase as elevation increases in the southern Appalachians. This study captures broad trends in basal area growth of red spruce, Fraser fir, and northern hardwoods, and highlights the need for further research on the effects of changing precipitation and temperature regimes, competition dynamics, and pest infestations on montane southern Appalachian forest systems.

Conclusion

Basal area increment (BAI) values of red spruce, Fraser fir, and hardwoods increased over time except on southern aspects, suggesting that generally, southern Appalachian spruce-fir forests may be able to persist, even where competition with hardwoods is a factor. On southern aspects, growth rates of Fraser fir decreased in fir-dominated stands, which could support concerns that Fraser fir may decline in warmer, drier conditions due to climate change, but we caution extrapolation based on this aspect because of low sample size. However, red spruce had greater growth rates in spruce-dominated stands than in spruce-fir stands on cooler, moister northern and eastern aspects, perhaps highlighting a threshold in its adaptation to these conditions, especially when competing with Fraser fir. Red spruce had greater growth rates in spruce-hardwood stands than in spruce-dominated stands on southern and western aspects, which is unexpected on these warmer, drier aspects and may suggest greater resiliency to climatic and competition factors than previously thought, but merits additional study. In spruce-hardwood stands on northern and southern aspects, hardwood growth rates were significantly lower than those of red spruce, which also supports better resiliency of red spruce to competition with hardwoods than we had hypothesized. The generally increasing growth rates of red spruce and Fraser fir holds promising implications for the survival and expansion of spruce-fir forests. Furthermore, the greater growth rates in red spruce compared to hardwoods in northern- and southern-facing spruce-hardwood stands suggests that competitive pressure from hardwoods is not currently intense enough to cause red spruce growth rates to decline. Anecdotally, we observed more Fraser fir and red spruce regenerating stems than hardwood stems, suggesting that red spruce and Fraser fir could also be outpacing hardwoods in this important facet of competition, but deer browse pressure could also have influenced our low number of observed hardwood regeneration.

In spruce-fir and spruce-dominated stands, the growth rates of red spruce were greatest on northern aspects, whereas growth rates were the greatest on southern aspects for hardwoods and for red spruce growing in spruce-hardwood stands. Managers hoping to maximize spruce-fir forest restoration success could therefore focus on northern aspects, where competing hardwoods had low growth rates, red spruce had high growth rates in spruce-dominated and spruce-hardwood stands, and growth rates of Fraser fir in spruce-fir stands were the highest. In fir-dominated stands, the highest growth rates of Fraser fir were on eastern aspects, so these areas could be prioritized in pest-infestation prevention measures to protect hardier trees with a greater chance of survival. The trends of mean BAI relative to elevation were significantly different between hardwoods and red spruce, with a negative relationship between elevation and mean BAI for hardwoods and positive relationships for red spruce and Fraser fir. Comparing the increasing mean BAI of red spruce and Fraser fir to the decreasing mean BAI in hardwoods with increasing elevation highlights the greater tolerance of these species to the low temperatures, high precipitation, and rocky soils that tend to be found at higher elevations, so to maximize efficacy of resources, managers could focus on enhancing stand composition and resiliency in existing high-elevation spruce-fir stands.

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Appendix 1:

Growth rates by site:

Basal area increment (BAI) was significantly affected by site, species, year, and all two- and three-way interactions between these terms (Table 13). Trends in BAI over time at each study site are described below.

Table 12. Analysis of variance results ($\alpha = 0.05$) for effects of site, species, year, and their interactions on basal area increment (cm^2yr^{-1}) of red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods in spruce-hardwood, spruce-dominated, and spruce-fir, and fir-dominated cover types at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA), 2023. [1]Reference condition.

Term	Estimate	Standard Error	p-value
Site			
Intercept	-2.94e2	5.79e1	<0.0001
Grandfather Mountain	9.55e1	6.56e1	0.15
Little Sam Knob	1.02e2	7.00e1	0.15
Mount Mitchell	1.39e2	7.01e1	0.05
Mount Rogers	2.69e2	7.10e1	0.0002
Roan Mountain	3.62e2	6.78e1	<0.0001
Black Balsam Knob[1]	-	-	-
Species			
Red spruce	-1.33e2	6.57e1	0.04
Fraser fir	-9.42e2	9.86e1	<0.0001
Hardwoods[1]	-	-	-
Year	1.49e-1	2.89e-2	<0.0001
Site * Species			<0.0001
Grandfather Mountain * Fraser fir	9.30e2	1.10e2	<0.0001
Little Sam Knob * Fraser fir	NA	NA	NA
Mount Mitchell * Fraser fir	6.05e2	1.17e2	<0.0001
Mount Rogers * Fraser fir	9.47e2	1.20e2	<0.0001
Black Balsam Knob * Fraser fir[1]	-	-	-
Grandfather Mountain * Red spruce	1.35e2	8.24e1	0.0001
Little Sam Knob * Red spruce	-3.16e2	8.24e1	0.07
Mount Mitchell * Red spruce	-8.20	8.23e1	0.92
Mount Rogers * Red spruce	-2.17e2	8.51e1	0.01
Roan Mountain * Red spruce	-1.32e2	7.83e1	0.09
Black Balsam Knob * Red spruce[1]	-	-	-
Grandfather Mountain * Hardwoods[1]			
Little Sam Knob * Hardwoods[1]			
Mount Mitchell * Hardwoods[1]	-4.68e-1	3.28e-2	0.16

Mount Rogers * Hardwoods[1]	-5.06e-2	3.50e-2	0.15
Black Balsam Knob * Hardwoods[1]	-6.76e-2	3.50e-2	0.05
Site * Year			
Grandfather Mountain * Year	-4.61e-2	3.28e-2	0.16
Little Sam Knob * Year	-5.06e-2	3.50e-2	0.15
Mount Mitchell * Year	-6.76e-2	3.50e-2	0.05
Mount Rogers * Year	-1.32e-1	3.55e-2	0.0002
Roan Mountain * Year	-1.80e-1	3.39e-2	<0.0001
Black Balsam Knob * Year[1]	-	-	-
Species * Year			
Fraser fir * Year	4.73e-1	4.92e-2	<0.0001
Red spruce * Year	7.31e-2	3.28e-2	0.03
Hardwoods * Year[1]	-	-	-
Site * Species * Year			
Grandfather Mountain * Fraser fir * Year	-4.68e-1	5.48e-2	<0.0001
Little Sam Knob * Fraser fir * Year	NA	NA	NA
Mount Mitchell * Fraser fir * Year	-3.04e-1	5.86e-2	<0.0001
Mount Rogers * Fraser fir * Year	-4.78e-1	5.97e-2	<0.0001
Roan Mountain * Fraser fir * Year	-3.08e-1	5.47e-2	<0.0001
Black Balsam Knob * Fraser fir * Year[1]	-	-	-
Little Sam Knob * Red spruce * Year	1.57e-1	4.12e-2	0.0001
Grandfather Mountain * Red spruce *	-7.53e-2	3.78e-2	0.05
Mount Mitchell * Red spruce * Year	-4.27e-4	4.11e-2	0.99
Mount Rogers * Red spruce * Year	1.02e-1	4.26e-2	0.02
Roan Mouuntain * Red spruce * Year	5.98e-2	3.91e-2	0.13
Black Balsam Knob * Red spruce * Year[1]	-	-	-
Grandfather Mountain * Hardwoods * Year[1]	-	-	-
Little Sam Knob * Hardwoods * Year[1]	-	-	-
Mount Mitchell * Hardwoods * Year[1]	-	-	-
Mount Rogers * Hardwoods * Year[1]	-	-	-
Roan Mountain * Hardwoods * Year[1]	-	-	-
Black Balsam Knob * Hardwoods * Year[1]	-	-	-

Mount Rogers:

Our survey of cover types at Mount Rogers was incomplete, so cover type was excluded from this analysis, but BAI at Mount Rogers changed significantly over time and was significantly affected by species, aspect, and all their interactions (Table 13). Our sample size from Mount Rogers was too small to run a *post-hoc* analysis on these factors, but a visual inspection of linear growth trends shows that annual BAI of red spruce in spruce-hardwood cover types increased on all aspects at Mount Rogers (Fig. 7). The highest growth rates were on the eastern aspect, but it is important to

note that all sampled trees on this aspect had estimated initiation dates after 2000 (Fig. 7). Red spruce growth rates were higher than those of hardwoods on the southern and western aspects. Due to low sample size, results from Fraser fir growing at the Mount Rogers summit should be taken with caution, but these trees appear to have a slowly increasing trend in BAI over time (Fig. 7).

Table 13: Analysis of variance results ($\alpha = 0.05$) for effects of species, aspect, year, and all two- and three-way interactions on basal area increment (cm^2yr^{-1}) of red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods at Mount Rogers, Virginia, USA.

Term	p-value
Species	<0.0001
Aspect	<0.0001
Year	<0.0001
Species * Aspect	<0.0001
Species * Year	<0.0001
Aspect * Year	<0.0001
Species * Aspect * Year	<0.0001

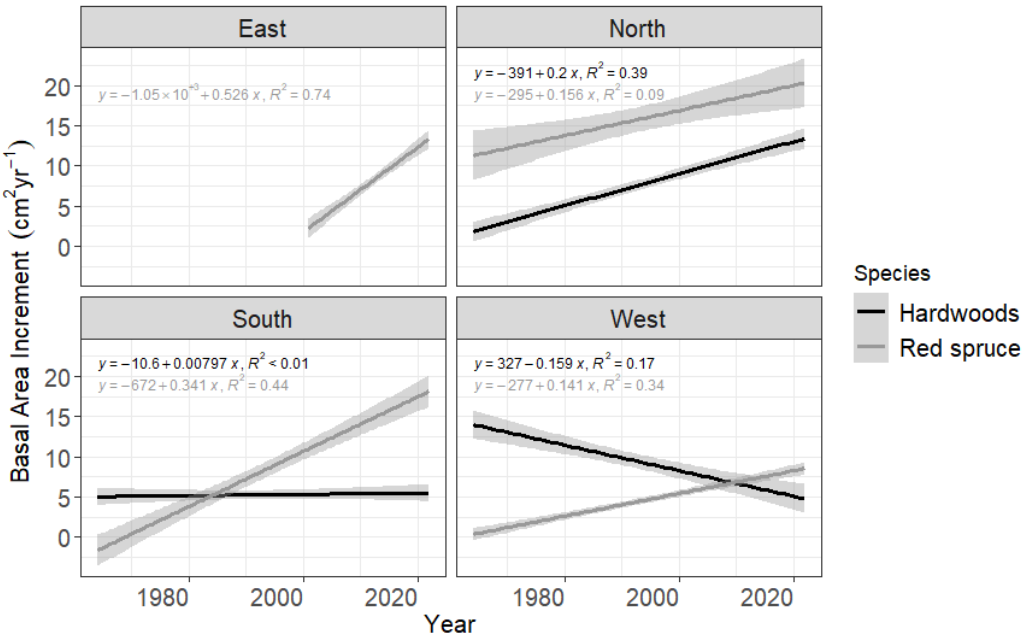

Fig. 7. Linear model of basal area increment over time (cm^2yr^{-1}) by aspect for red spruce (*Picea rubens*) and hardwoods growing in hardwood-dominated and spruce-hardwood stands at Mount Rogers, Virginia, USA.

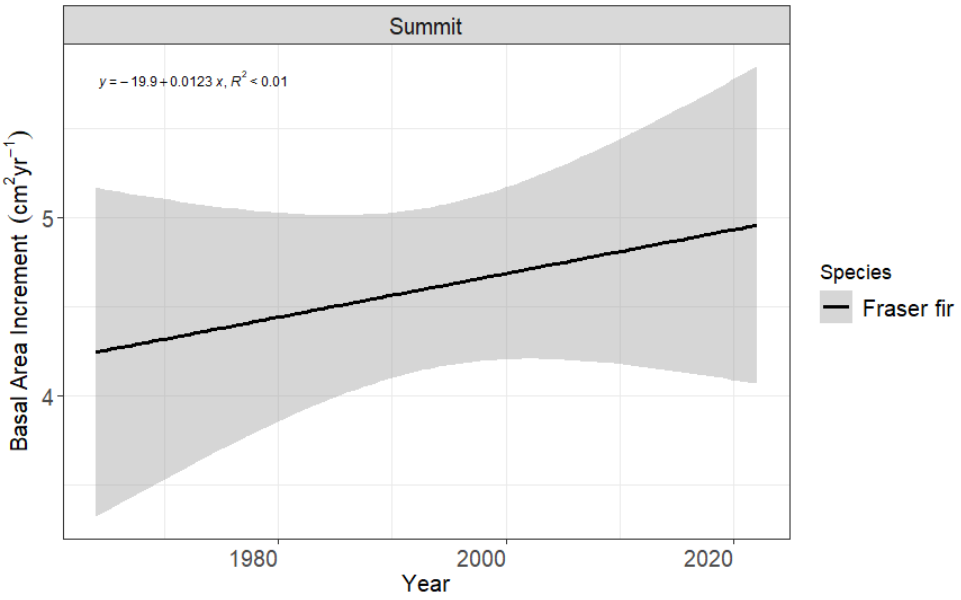

Fig. 8. Linear model of basal area increment over time (cm^2yr^{-1}) by aspect for Fraser fir (*Abies fraseri*) growing at Mount Rogers, Virginia, USA.

Little Sam Knob:

BAI values from Little Sam Knob were significantly affected by species, cover type, year, and several interactions, but were not significantly affected by aspect (Table 14). The fir-dominated cover type was not represented at Little Sam Knob and Fraser fir were excluded from this site-specific analysis due to low sample size. Low overall sample size also prevented a *post-hoc* analysis, but a visual analysis of BAI over time suggests that growth rates of red spruce were greater than those of hardwoods in all cover types at Little Sam Knob, with the greatest growth rates of red spruce in spruce-fir-hardwood stands and the greatest growth rate of hardwoods in spruce-hardwood stands (Fig. 9).

Table 14: Analysis of variance results for effects of species, cover type, aspect, year, and all two- and three-way interactions on basal area increment (cm^2yr^{-1}) of red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods at Little Sam Knob, North Carolina, USA.

Term	p-value
Species	<0.0001
Cover type	<0.0001
Aspect	0.97
Year	<0.0001
Species * Cover type	<0.0001
Species * Aspect	0.03
Cover type * Year	<0.0001
Species * Year	<0.0001
Aspect * Year	0.99
Species * Cover type * Year	<0.0001
Species * Aspect * Year	0.03

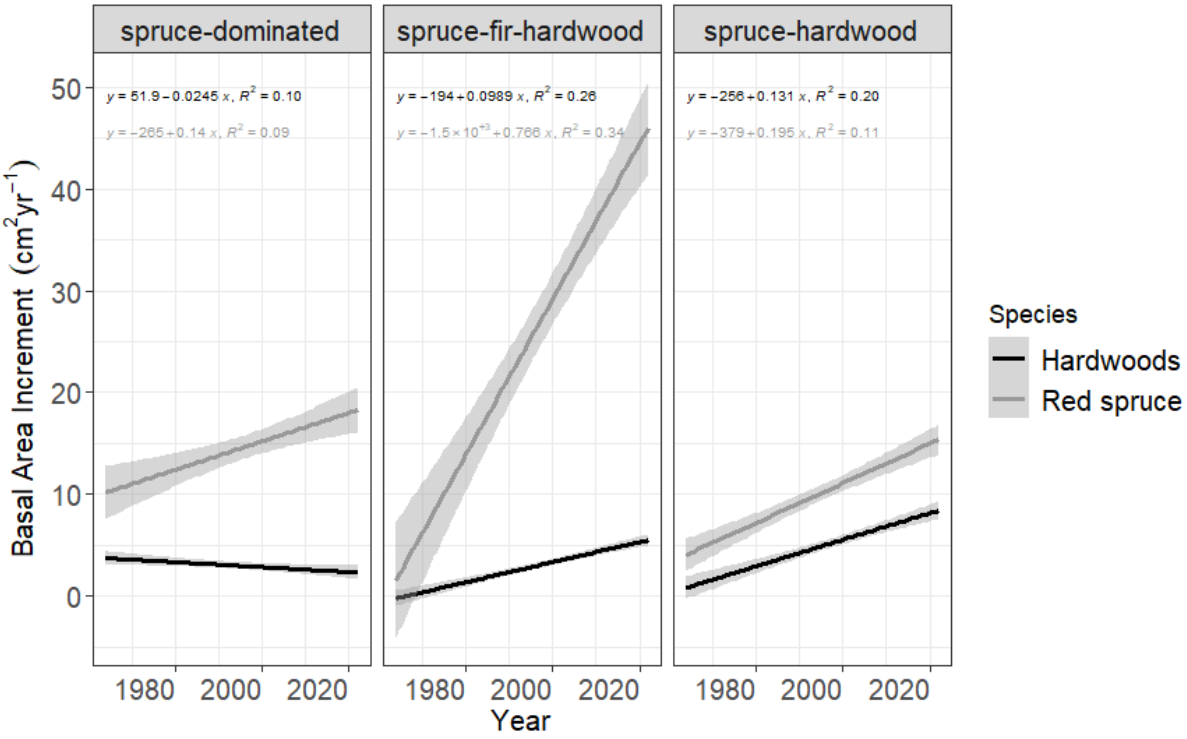

Fig. 9: Linear model of basal area increment over time (cm^2yr^{-1}) by aspect for red spruce (*Picea rubens*) and hardwoods by cover type at Little Sam Knob, North Carolina, USA.

Grandfather Mountain:

At Grandfather Mountain, BAI changed significantly over time and was significantly affected by species, cover type, aspect, and all two- and three-way interactions between these factors (Table 15). On the eastern aspect of Grandfather Mountain, red spruce had significantly greater growth rates in spruce-dominated stands than in spruce-fir and spruce-hardwood stands (Table 16, Fig. 10). Red spruce in eastern spruce-dominated stands also had greater growth rates than those on the southern and western aspects (Table 16, Fig. 10). In spruce-hardwood stands, red spruce had significantly greater growth rates on the northern and southern aspects than the eastern aspect (Table 16, Fig. 10). In spruce-hardwood stands on the northern aspect, growth rates were significantly greater in red spruce than in hardwoods (Table 16, Fig. 10). Hardwoods growing in spruce-hardwood stands had significantly greater growth rates on the southern aspect than on the northern and western aspects (Table 16, Fig. 10).

Table 15: Analysis of variance results (α= 0.05) for effects of species, cover type, year, and their interactions on basal area increment (cm^2yr^{-1}) of red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods at Grandfather Mountain, North Carolina, USA.

Term	p-value
Species	<0.0001
Cover type	<0.0001
Aspect	<0.0001
Year	<0.0001
Species * Cover type	0.004
Species * Aspect	<0.0001
Cover type * Aspect	<0.0001
Species * Year	<0.0001
Cover type * Year	<0.0001
Aspect * Year	0.0001
Species * Cover type * Aspect	0.05
Species * Cover type * Year	0.004
Species * Aspect * Year	<0.0001
Cover type * Aspect * Year	<0.0001
Species * Aspect * Cover type * Year	0.045

Table 16: P-values, estimates, and standard error for significantly different cover-type and aspect contrasts for red spruce (*Picea rubens*), hardwoods, and Fraser fir (*Abies fraseri*) at Grandfather Mountain, North Carolina, USA.

Contrast	Estimate ± Standard Error (SE)	p-value
Red spruce, spruce-dominated (east) – red spruce, spruce-fir (east)	0.15 ± 0.02	<0.0001
Red spruce, spruce-dominated (east) – red spruce, spruce-hardwood (east)	0.11 ± 0.02	<0.0001
Red spruce, spruce-dominated (east) – red spruce, spruce-dominated (south)	0.08 ± 0.02	0.02
Red spruce, spruce-dominated (east) – red spruce, spruce-dominated (west)	0.17 ± 0.02	<0.0001
Red spruce, spruce-hardwood (east) – red spruce, spruce-hardwood (north)	-0.10 ± 0.02	<0.0001
Red spruce, spruce-hardwood (east) – red spruce, spruce-hardwood (south)	-0.10 ± 0.03	0.02
Hardwoods, spruce-hardwood (north) – Red spruce, spruce-hardwood (north)	-0.11 ± 0.02	<0.0001
Hardwoods, spruce-hardwood (north) – Hardwoods, spruce-hardwood (south)	-0.10 ± 0.02	0.003
Hardwoods, spruce-hardwood (south) – Hardwoods, spruce-hardwood (west)	0.13 ± 0.03	0.006

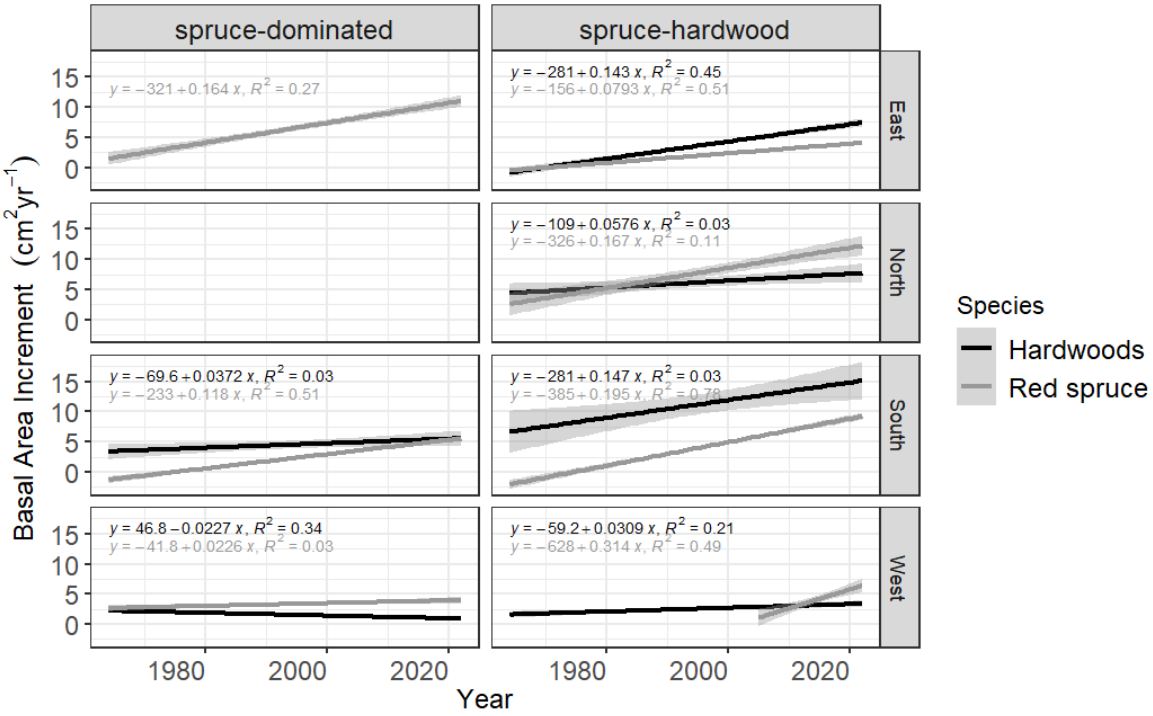

Fig. 10: Linear models of basal area increment over time (cm^2yr^{-1}) for red spruce (*Picea rubens*) and hardwoods in spruce-dominated and spruce-hardwood cover types at Grandfather Mountain, North Carolina, USA by aspect and cover type. Spruce-dominated cover type was not located in the field on the northern aspect.

Black Balsam Knob:

Black Balsam Knob BAI values were significantly affected by species, cover type, aspect, year, and several of their interactions (Table 17). The sample size from Black Balsam Knob was too small to permit *post-hoc* testing, and cover types were not well-represented across aspects. However, a visual inspection of trends in BAI over time by aspect shows that red spruce had the greatest growth rates on the northern and eastern aspects, while Fraser fir had the greatest growth rates on the southern aspect (Fig. 17). Growth rates were low in both hardwoods and red spruce on the western aspect, but hardwoods had slightly greater growth rates (Fig. 17).

Table 16. Analysis of variance results ($\alpha = 0.05$) for effects of species, cover type, year, and their significant interactions on basal area increment (cm^2yr^{-1}) of red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods at Black Balsam Knob, North Carolina, USA (alpha level = 0.05).

Term	p-value
Species	<0.0001
Cover type	<0.0001
Aspect	<0.0001
Year	<0.0001
Species * Cover type	<0.0001
Species * Year	<0.0001
Cover type * Year	<0.0001
Aspect * Year	<0.0001
Species * Cover type * Year	<0.0001

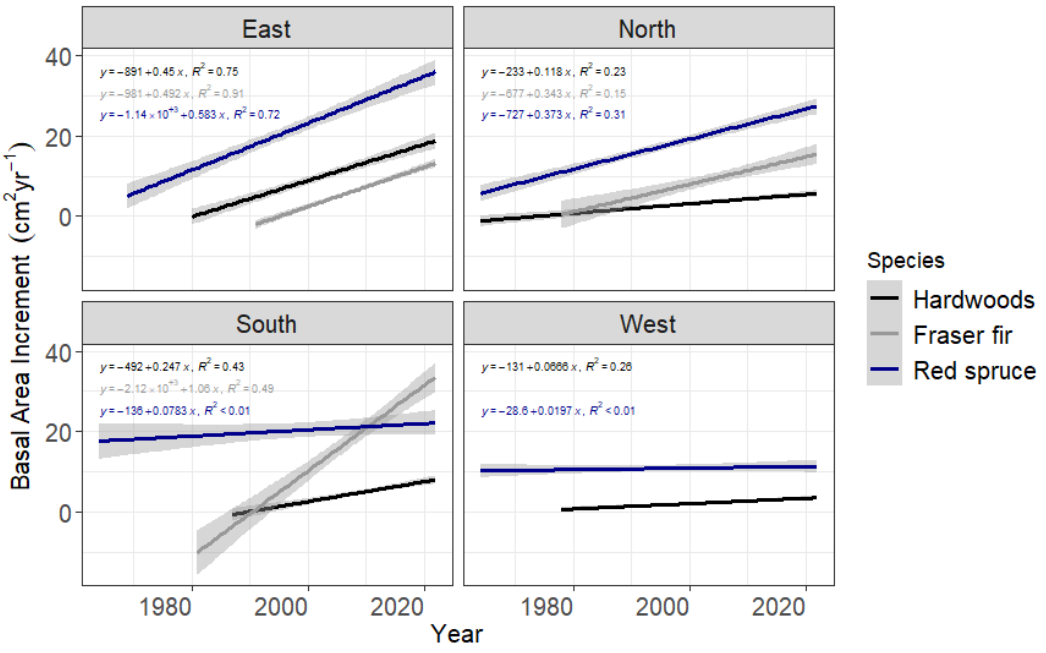

Fig. 11. Linear models of basal area increment over time (cm^2yr^{-1}) for red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*) and hardwoods in spruce-dominated and spruce-hardwood cover types at Black Balsam Knob, North Carolina, USA by aspect.

Roan Mountain:

At Roan Mountain, BAI values changed over time and were significantly affected by species, cover type, and aspect, and several two- and three-way interactions (Table 17). In fir-dominated stands, Fraser fir had significantly greater growth rates on the eastern aspect than the southern aspect (Table 18, Fig. 12). On the southern aspect, Fraser fir had significantly greater growth rates in spruce-fir stands than fir-dominated stands (Table 18, Fig. 12). Fraser fir in the southern spruce-fir stand also had greater growth rates than the red spruce in that stand (Table 18, Fig. 12). Fraser fir in this stand also had significantly greater growth rates than Fraser fir in the southwestern spruce-fir stand (Table 18, Fig. 12). Red spruce growing in spruce-dominated stands had significantly greater growth rates on the northern aspect than the eastern aspect (Table 18,

Fig. 12). On several aspects, the spruce-hardwood cover type was not located or inaccessible in the field, so hardwoods were sampled in the spruce-dominated cover type where present. However, in the spruce-hardwood stand on the northern aspect, red spruce had significantly greater growth rates than hardwoods (Table 18). In addition, the western aspect was inaccessible due to topography, so we sampled the southwestern aspect instead. In the spruce-fir cover type, Fraser fir had significantly greater growth rates on the northern aspect than the southwestern (Table 18, Fig. 12).

Table 17: Analysis of variance results ($\alpha = 0.05$) for effects of species, cover type, year, and their interactions on basal area increment (cm^2yr^{-1}) of red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods at Roan Mountain, North Carolina/Tennessee, USA (alpha level = 0.05).

Term	p-value
Species	<0.0001
Cover type	<0.0001
Aspect	<0.0001
Year	<0.0001
Species * Cover type	<0.0001
Cover type * Year	<0.0001
Aspect * Year	<0.0001
Species * Cover type * Year	<0.0001

Table 18: P-values, estimates, and standard error for significantly different cover-type and aspect contrasts ($\alpha = 0.05$) for red spruce (*Picea rubens*), hardwoods, and Fraser fir (*Abies fraseri*) at Roan Mountain, North Carolina/Tennessee, USA (alpha level = 0.05).

Term	Estimate ± Standard Error (SE)	p-value
Fraser fir, fir-dominated (east) – Fraser fir, fir-dominated (south)	0.95 ± 0.06	<0.0001
Red spruce, spruce-dominated (east) – Red spruce, spruce-dominated (north)	-0.20 ± 0.03	<0.0001
Fraser fir, spruce-fir (north) – Fraser fir, spruce-fir (southwest)	0.06 ± 0.03	<0.0001
Hardwoods, spruce-hardwood (north) – Red spruce, spruce-hardwood (north)	-0.26 ± 0.03	<0.0001
Fraser fir, fir-dominated (south) – Fraser fir, spruce-fir (south)	-0.21 ± 0.04	<0.0001
Fraser fir, spruce-fir (south) – Red spruce, spruce-fir (south)	0.15 ± 0.03	0.003
Fraser fir, spruce-fir (south) – Fraser fir, spruce-fir (southwest)	0.10 ± 0.03	0.03

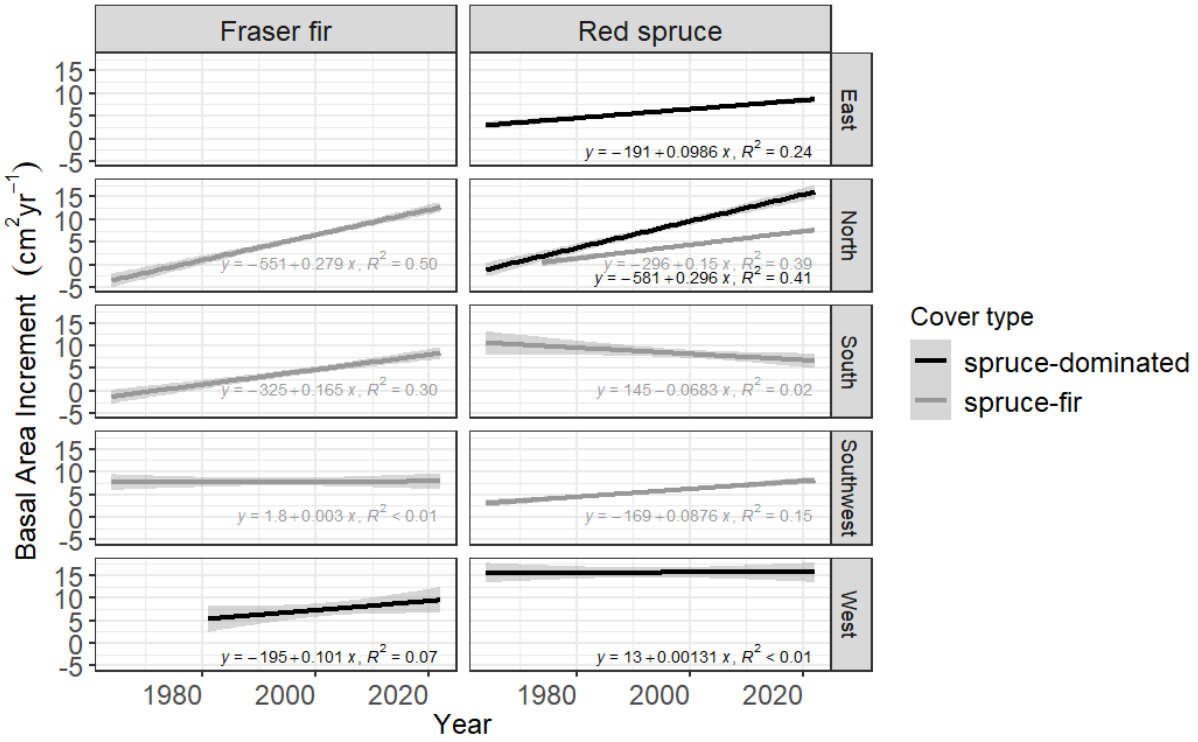

Fig. 12. Linear models of basal area increment over time (cm^2yr^{-1}) for red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*) by aspect at Roan Mountain, North Carolina/Tennessee, USA.

Mount Mitchell:

BAI values from Mount Mitchell were significantly affected by species, cover type, aspect, year, and several of their interactions (Table 19). Sample size was insufficient to perform *post-hoc* testing and cover types were not evenly distributed by aspect, but a visual inspection of the trends by cover type indicates that red spruce and Fraser fir had positive growth rates in fir-dominated, spruce-fir-hardwood, and spruce-hardwood cover types, while hardwoods had declining growth in the spruce-hardwood cover type (Fig. 13). Red spruce had the greatest growth rate in spruce-fir-hardwood stands, while Fraser fir and hardwoods had the greatest growth in fir-dominated stands (Fig. 13). However, it is important to be cautious when generalizing from these results, due to our

low sample size and the highly disturbed stand sampled on the western aspect due to the low and middle slopes of the aspect being inaccessible private property.

Table 19. Analysis of variance results ($\alpha = 0.05$) for effects of species, cover type, year, and their interactions on basal area increment (cm^2yr^{-1}) of red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods at Mount Mitchell, North Carolina, USA.

Term	p-value
Species	<0.0001
Cover type	<0.0001
Aspect	<0.0001
Year	<0.0001
Species * Cover type	<0.0001
Species * Year	<0.0001
Cover type * Year	<0.0001
Species * Year	<0.0001
Aspect * Year	<0.0001
Species * Cover type * Year	<0.0001

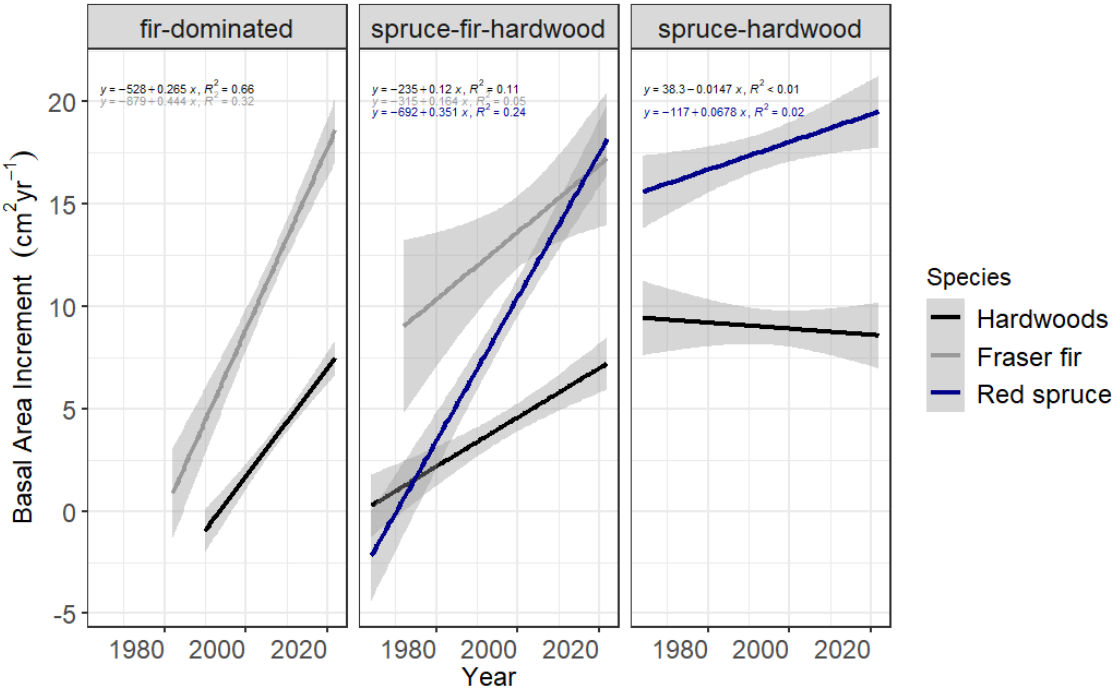

Fig. 13. Linear models of basal area increment by year (cm^2yr^{-1}) for red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*) by aspect at Mount Mitchell, North Carolina, USA.

Appendix 2:

Regeneration and age data:

Table 20. Distribution and mean estimated initiation year of overstory for red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*) for all expected cover types at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA), 2023, with additional observed cover types included. Mean estimated overstory initiation was averaged from all cores at each cover type/aspect combination with estimable pith dates.

	Cover type	Aspect	Species	Mean Estimated Overstory Initiation (± 10 yrs)	Located in field? (Y/N)
Mount Rogers	Spruce-hardwood	North	Red spruce	1925	Yes
			Hardwoods	No data	
		East	Red spruce	2001	Yes
			Hardwoods	No data	
		South	Red spruce	1906	Yes
			Hardwoods	1884	
		West	Red spruce	1884	Yes
			Hardwoods	No data	
	Spruce-dominated	North	Red spruce	No data	No
		East	Red spruce	No data	No
		South	Red spruce	No data	No
		West	Red spruce	No data	No
	Spruce-fir	North	Fraser fir	No data	No
			Red spruce	No data	
		East	Fraser fir	No data	No
			Red spruce	No data	
		South	Fraser fir	No data	No
			Red spruce	No data	
		West	Fraser fir	No data	No
			Red spruce	No data	
	Fir-dominated	Summit	Fraser fir	1949	Yes
Little Sam's Knob	Spruce-hardwood	North	Red spruce	1959	Yes
			Hardwoods	1969	
		East	Red spruce	1949	Yes
		South	Red spruce	No data	No
			Hardwoods	No data	
		West	Red spruce	1956	Yes
			Hardwoods	1960	
		North	Red spruce	No data	No

	Spruce-dominated	East	Red spruce	1955	No
		South	Red spruce	No data	No
		West	Red spruce	No data	No
	Spruce-fir-hardwood	South	Red spruce	1966	Yes
			Fraser fir	No data	No
			Hardwoods	1970	Yes
	Spruce-fir	North	Red spruce	No data	No
			Fraser fir	No data	
		East	Red spruce	No data	No
			Fraser fir	No data	
		South	Red spruce	No data	No
			Fraser fir	No data	
		West	Red spruce	No data	No
			Fraser fir	No data	
	Fir-dominated	Summit	Fraser fir	No data	No
Grandfather Mountain	Spruce-hardwood	North	Hardwoods	1960	Yes
			Red spruce	1949	
		East	Red spruce	1914	Yes
			Hardwoods	1966	
		South	Red spruce	1959	Yes
			Hardwoods	1961	
		West	Red spruce	2005	Yes
			Hardwoods	1935	
	Spruce-dominated	North	Red spruce	1879	Yes
		East	Red spruce	1926	Yes
		South	Red spruce	No data	Yes
			Hardwoods	1951	
		West	Red spruce	1870	Yes
			Hardwoods	1906	
	Spruce-fir	North	Red spruce	No data	No
			Fraser fir	No data	
		East	Fraser fir	1956	Yes
			Red spruce	1953	
		South	Red spruce	1984	Yes
			Fraser fir	1995	
		West	Red spruce	No data	No
			Fraser fir	No data	
	Fir-dominated	Summit	Fraser fir	1965	Yes
Black Balsam Knob	Spruce-hardwood	North	Red spruce	No data	No
			Hardwoods	No data	
		East	Red spruce	No data	No
			Hardwoods	No data	
		South	Red spruce	No data	No
			Hardwoods	No data	
		West	Red spruce	No data	No

			Hardwoods	No data	
	Spruce-dominated	North	Red spruce	1955	Yes
		East	Red spruce	No data	No
		South	Red spruce	No data	No
		West	Red spruce	1957	Yes
			Hardwoods	1981	
	Spruce-fir	North	Red spruce	No data	No
			Fraser fir	No data	
		East	Red spruce	No data	No
			Fraser fir	No data	
		South	Red spruce	No data	No
			Fraser fir	No data	
		West	Red spruce	No data	No
			Fraser fir	No data	
	Fir-dominated	Summit	Fraser fir	No data	No
		North	Fraser fir	1983	Yes
			Hardwoods	1973	
	Fir-hardwood	North	Red spruce	1983	Yes
			Fraser fir	1983	
		East	Red spruce	1956	Yes
			Fraser fir	No data	
			Hardwoods	1980	
	Spruce-fir-hardwood	South	Fraser fir	1987	Yes
			Red spruce	1935	
			Hardwoods	1995	
Roan Mountain	Spruce-hardwood	North	Red spruce	1956	Yes
			Hardwoods	1922	
		East	Red spruce	No data	No
			Hardwoods	No data	
		South	Red spruce	No data	No
			Hardwoods	No data	
		West	Red spruce	1970	No
			Hardwoods	No data	
	Spruce-dominated	North	Red spruce	1932	Yes
			Hardwoods	1810	
		East	Red spruce	1963	Yes
		South	Fraser fir	1980	Yes
			Red spruce	1942	
		West	Fraser fir	1980	Yes
			Hardwoods	1971	
			Red spruce	1939	
	Spruce-fir	North	Fraser fir	1975	Yes
			Red spruce	1979	
		East	Fraser fir	No data	Yes
			Red spruce	1930	

		South	Fraser fir	1970	Yes
			Red spruce	1976	
		Southwest	Fraser fir	1944	Yes
			Red spruce	1933	
		West	Fraser fir	No data	No
			Red spruce	No data	
		Summit	Fraser fir	1931	Yes
	Fir-dominated	Summit	Fraser fir	No data	No
		East	Fraser fir	1991	Yes
		Southwest	Fraser fir	1939	Yes
		North	Fraser fir	2007	Yes
			Red spruce	1965	
		East	Fraser fir	1986	Yes
		South	Fraser fir	1974	Yes
			Hardwoods	1986	
	Fir-hardwood	Summit	Hardwood	1974	Yes
			Fraser fir	1938	
Mount Mitchell	Spruce-hardwood	North	Red spruce	No data	No
			Fraser fir	No data	
		East	Red spruce	1950	Yes
			Hardwoods	1959	
		South	Red spruce	No data	No
			Hardwoods	No data	
		West	Red spruce	No data	No
			Hardwoods	No data	
	Spruce-dominated	North	Red spruce	No data	No
		East	Red spruce	No data	No
		South	Red spruce	No data	No
		West	Red spruce	No data	No
	Spruce-fir	North	Fraser fir	No data	No
			Red spruce	No data	
		East	Fraser fir	1975	Yes
			Red spruce	1975	
		South	Fraser fir	No data	No
			Red spruce	No data	
		West	Fraser fir	1995	Yes
			Red spruce	No data	
	Fir-dominated	Summit	Fraser fir	1979	Yes
		North	Fraser fir	No data	No
		West	Fraser fir	1995	Yes
			Hardwoods	1997	
	Fir-hardwood	North	Fraser fir	1981	Yes
			Hardwoods	1990	
	Spruce-fir-hardwood	East	Red spruce	1968	Yes
		South	Fraser fir	1980	Yes

			Red spruce	1960	
			Hardwoods	1966	

Table 8: Count of regenerating stems of red spruce (*Picea rubens*), Fraser fir (*Abies fraseri*), and hardwoods by overstory plot aspect and cover type at Mt. Rogers, Little Sam Knob, Grandfather Mountain, Black Balsam Knob, Roan Mountain, and Mt. Mitchell (North Carolina, Tennessee, and Virginia, USA), 2023.

	Cover type	Aspect	Species	Number of seedlings/saplings
Mount Rogers	Spruce-hardwood	North	Red spruce	0
			Hardwoods	6
		East	Red spruce	0
			Hardwoods	0
		South	Red spruce	0
			Hardwoods	0
		West	Red spruce	0
			Hardwoods	4
	Spruce-dominated	North	Red spruce	0
		East	Red spruce	0
		South	Red spruce	0
		West	Red spruce	0
	Spruce-fir	North	Fraser fir	0
			Red spruce	0
		East	Fraser fir	0
			Red spruce	0
		South	Fraser fir	0
			Red spruce	0
		West	Fraser fir	0
			Red spruce	0
	Fir-dominated	Summit	Fraser fir	1
			Red spruce	8
		South	Fraser fir	0
			Red spruce	6
Little Sam's Knob	Spruce-hardwood	North	Red spruce	0
			Hardwoods	0
		East	Red spruce	5
			Hardwoods	0
		South	Red spruce	0
			Hardwoods	0
		West	Red spruce	0
			Hardwoods	0
	Spruce-dominated	North	Red spruce	0
		East	Red spruce	0
		South	Red spruce	0

		West	Red spruce	0
	Spruce-fir-hardwood	South	Red spruce	5
			Fraser fir	2
			Hardwoods	0
	Spruce-fir	North	Red spruce	0
			Fraser fir	0
		East	Red spruce	0
			Fraser fir	0
		South	Red spruce	0
			Fraser fir	0
		West	Red spruce	0
			Fraser fir	0
	Fir-dominated	Summit	Fraser fir	0
Grandfather Mountain	Spruce-hardwood	North	Hardwoods	0
			Red spruce	0
			Fraser fir	30
		East	Red spruce	0
			Hardwoods	0
		South	Red spruce	0
			Hardwoods	0
		West	Red spruce	0
			Hardwoods	0
	Spruce-dominated	North	Red spruce	0
			Fraser fir	0
		East	Red spruce	2
			Fraser fir	4
		South	Red spruce	5
		West	Red spruce	0
	Spruce-fir	North	Fraser fir	0
			Red spruce	0
		East	Fraser fir	61
			Red spruce	2
		South	Red spruce	5
			Fraser fir	0
		West	Red spruce	0
			Fraser fir	0
	Fir-dominated	Summit	Fraser fir	5
Black Balsam Knob	Spruce-hardwood	North	Red spruce	0
			Hardwoods	0
		East	Red spruce	0
			Hardwoods	0
		South	Red spruce	0
			Hardwoods	0
		West	Red spruce	0
			Hardwoods	0

	Spruce-dominated	North	Red spruce	0
		East	Red spruce	0
		South	Red spruce	0
		West	Red spruce	6
			Hardwoods	0
	Spruce-fir	North	Red spruce	0
			Fraser fir	0
		East	Red spruce	0
			Fraser fir	0
		South	Red spruce	0
			Fraser fir	0
		West	Red spruce	0
			Fraser fir	0
	Fir-dominated	Summit	Fraser fir	0
		North	Fraser fir	0
	Fir-hardwood	North	Fraser fir	0
			Hardwoods	0
		East	Fraser fir	0
			Hardwoods	0
	Spruce-fir-hardwood	South	Fraser fir	2
			Red spruce	5
			Hardwoods	0
Roan Mountain	Spruce-hardwood	North	Red spruce	0
			Hardwoods	0
		East	Red spruce	0
			Hardwoods	0
		South	Red spruce	0
			Hardwoods	0
		West	Red spruce	0
			Hardwoods	0
	Spruce-dominated	North	Red spruce	2
		East	Red spruce	0
		South	Red spruce	0
		West	Fraser fir	14
			Red spruce	3
	Spruce-fir	North	Fraser fir	1
			Red spruce	3
		East	Fraser fir	0
			Red spruce	0
		South	Fraser fir	123
			Red spruce	4
		Southwest	Fraser fir	11
			Red spruce	0
		West	Fraser fir	0
			Red spruce	0

		Summit	Fraser fir	0
			Red spruce	0
	Fir-dominated	Summit	Fraser fir	37
		East	Fraser fir	2
			Red spruce	12
		Southwest	Fraser fir	0
		North	Fraser fir	0
			Red spruce	0
		East	Fraser fir	0
		South	Fraser fir	0
			Hardwoods	0
	Fir-hardwood	Summit	Hardwood	0
			Fraser fir	0
Mount Mitchell	Spruce-hardwood	North	Red spruce	0
			Hardwoods	0
		East	Red spruce	0
			Hardwoods	0
		South	Red spruce	0
			Hardwoods	0
		West	Red spruce	0
			Hardwoods	0
	Spruce-dominated	North	Red spruce	0
		East	Red spruce	0
		South	Red spruce	0
		West	Red spruce	0
	Spruce-fir	North	Fraser fir	0
			Red spruce	0
		East	Fraser fir	14
			Red spruce	8
		South	Fraser fir	0
			Red spruce	0
		West	Fraser fir	1
			Red spruce	0
	Fir-dominated	Summit	Fraser fir	27
		North	Fraser fir	160
		West	Fraser fir	0
	Fir-hardwood	North	Fraser fir	6
			Hardwoods	0
			Red spruce	2
	Spruce-fir-hardwood	East	Fraser fir	0
			Red spruce	0
			Hardwoods	0
		South	Fraser fir	0
			Red spruce	0
			Hardwoods	0