Biotic and Abiotic Factors of *Picea rubens* (Red Spruce) Seedling Regeneration in Disturbed Heathland Barrens of the Central Appalachians

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ABSTRACT

During the late 19th and early 20th centuries, extensive logging reduced the forests of red spruce (*Picea rubens*) by nearly 99% through portions of West Virginia. In the wake of this disturbance, red spruce has begun regenerating on the ridge and mountaintop areas of Canaan Valley, West Virginia, where heath and grassland communities have both persisted in natural barrens and expanded into formerly forested areas. To understand abiotic and biotic conditions guiding the advance of the red spruce stand, I conducted a broad-scale assessment of thirty-one demographics plots spread across two sites (north Cabin Mountain and Bear Rocks/Dolly Sods), and a more focused assessment of red spruce species associations within thirty-two paired plots at Cabin Mountain. At the 15m x 15m demographics plots, I conducted a count of all *P. rubens* present, measured specimen height, DBH or diameter at ground level (DGL) for specimens < 1.37m tall, and assessed the relative percent cover of rock, shrub, herbaceous, and tree cover. These data, along with additional abiotic components derived from a DEM, formed the basis of my assessment using a generalized linear mixed model (GLMM) to identify the most significant biophysical variables related to *P. rubens* count. In the paired plots, I used the relative interactions index (RII) to compare the total cover of each present non-graminoid vascular species and the grouped cover types Rock, Graminoid, Lichen, Litter, and Moss in one 45cm-radius plot with a < 1.37m *P. rubens* specimen, and one paired 45cm-radius plot in open heath. The significance of differences in total cover were assessed with the Wilcoxon test and Tukey HSD. The GLMM identified percent rock cover and distance from the nearest *P. rubens* stand to be important correlates of *P. rubens* count at the demographic plots. Graminoid cover was found to be higher in *P. rubens* 45cm-radius plots than in paired heath plots, and *Vaccinium angustifolium* cover was found to be concentrated in 45cm radius plots beyond the first 15cm from the *P. rubens* stem. These findings reinforce a complex interplay between both the biotic and abiotic characteristics of a microsite and the successful germination and regeneration of a red spruce seedling in the heathland.

Biotic and Abiotic Factors of *Picea rubens* (Red Spruce) Seedling Regeneration in Disturbed Heathland Barrens of the Central Appalachians

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GENERAL AUDIENCE ABSTRACT

During the late 19th and early 20th centuries, extensive logging reduced the forests of red spruce (*Picea rubens*) by nearly 99% through portions of West Virginia. In the wake of this disturbance, red spruce has begun regenerating on the ridge and mountaintop areas of Canaan Valley, West Virginia, where heath and grassland communities have both persisted in natural barrens and expanded into formerly forested areas. To understand the necessary abiotic and biotic conditions guiding the advance of the red spruce stand, I conducted a broad-scale assessment of thirty-one demographics plots spread across two sites (north Cabin Mountain and Bear Rocks/Dolly Sods), and a more focused assessment of red spruce species associations within thirty-two paired plots at Cabin Mountain. At the 15m x 15m demographics plots, I measured and counted all red spruce present. I collected landscape and community data on each plot using field surveys and a digital elevation model (DEM) to the variables most associated with a higher count of red spruce in each plot. In the 45cm-radius paired plots, I used simple mathematical comparisons to identify positive and negative interactions between red spruce shorter than breast height (1.37m) and different types of cover, including heathland species such as *Vaccinium angustifolium* (lowbush blueberry), rock, graminoid, and moss. Modeling indicated that rock cover, and distance between the plot and the nearest stand of red spruce, were found to be the most significant variable affecting the count of red spruce at each plot, with increased rock cover and shorter stand distance both associated with higher numbers of spruce. In the paired plots, there was slightly higher graminoid cover associated with the tree than with the open heath plot, and *V. angustifolium* was more concentrated beyond 15cm from each red spruce specimen. These findings suggest that rock cover is important for tree regeneration both the biotic and abiotic characteristics of a microsite and the successful germination and regeneration of a tree seedling in heathlands.

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LIST OF FIGURES

LIST OF TABLES

Chapter 1 – Introduction

Biogeography is the subdiscipline of geography concerned with the spatial and temporal distribution of life on Earth. This broad definition encapsulates a research approach that integrates knowledge and methods from a range of allied disciplines to explain biogeographic patterns, and the biotic and abiotic processes that shape these patterns, across geologic and human timescales (Cowell and Parker, 2004). For this reason, it has been described as a science of synthesis (MacDonald, 2003).

The idea that modern biogeographical spatial patterns can be illuminated by their history is explored in the literature as the study of landscape legacy. Landscapes, and the biotic and abiotic elements that comprise them, are influenced by numerous factors acting over the space. These factors include human use (e.g., Foley et al., 2005; Young, 2009; Sitzia and Trentanovi, 2011) and non-anthropogenic processes (Yu et al., 2016; Frey, 1983), such as natural disturbance processes. Together, these factors can profoundly influence the success of biotic communities that depend upon the landscapes in question (Flinn and Vellend, 2005).

Refugia are a type of ecosystem that are shaped by landscape legacy. Broadly speaking, the term *refugia* refers to an area that is disconnected from the physical characteristics of environmental conditions at a higher scale, allowing otherwise restricted biotic communities to persist (Dobrowski, 2011). Pockets of deglaciated terrain in a wider glacial system are an example of such refugia (Dobrowski, 2011). Refugia may be found in localized areas with unique climatic characteristics, distinctive from surrounding landscapes and supporting unique biodiversity assemblages (le Roux and Luoto, 2014). These ‘microrefugia’ may play a key role in facilitating the rapid redistribution of species with certain adaptive characteristics across large areas (Dobrowski, 2011). Therefore, understanding how localized landscape characteristics,

including land-use legacy and biophysical components, relate to the biotic community of a landscape, will further inform understanding of various ecosystem functions at different temporal scales.

Appalachian heathland ecosystems have been profoundly influenced by landscape legacy through intensive land use (Allard and Leonard, 1952; Fortney and Rentch, 2003). The history of West Virginia's uplands is one of drastic landscape change, which has entailed the removal of hundreds of thousands of acres of red spruce forest for timber and agriculture (Allard and Leonard, 1952). Red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) climax forests established in the region during the Pleistocene glaciation, and have remained as refuge communities after the glacial retreat (Allard and Leonard, 1952). Some of the heath barrens and grass bald purportedly have been open since prior to European settlement of West Virginia, but others are the result of historic disturbance to the refuge forest, into which remnants of the refuge community are slowly re-establishing (Allard and Leonard, 1952).

Though much has been written about the heathlands of western Europe (e.g., Feoli, 2010; Ransijn et al., 2015; Mobaied et al., 2016), fewer studies have addressed the Appalachian heathlands, particularly the heath barrens in the Allegheny mountains of West Virginia. Heathland systems of the Central Appalachians are of interest, however, because they have adapted to conditions produced in the wake of dramatic land-use change (Allard and Leonard, 1952), and therefore have wider relevance to the complex discourse on ecosystem resilience and the novel ecosystem (e.g., Holl and Aide, 2011; Murcia et al., 2014; Hobbs, 2016). Even when the heath is considered through a successional lens with climax spruce-fir forest communities (Fortney and Rentch, 2003), research in the heathlands of western Europe have demonstrated a

positive impact of spatial heterogeneity on biodiversity present in the landscape (Mobaied et al., 2015; Mobaied et al., 2016).

The purpose of this study is to characterize vegetation species cover in a heath matrix spatially associated with regeneration of red spruce in the Central Appalachian highlands of Canaan Valley, West Virginia. Heath communities adjoining remaining red spruce stands are present along the surrounding plateaus; I focus on two sites on the eastern edge of the Valley. I assess both heath and trees as an interconnected system whereby understory vegetation may strongly influence tree regeneration dynamics, including the filtering of tree seedling species at early and critical life stages (George and Bazzazz, 2014). By establishing baseline information on interactions between these vegetation communities, with particular attention paid to plants associated with the colonization of tree seedlings in the heath, the goal of this study is to explore how biotic and abiotic processes meaningfully impact the characteristics of a unique, high elevation North American ecosystem, within their historical disturbance context.

Our objectives were threefold:

1. to quantify and characterize through fieldwork the spatial population demographics of red spruce (*Picea rubens*) at two Central Appalachian (Canaan Valley) study sites;
2. to identify the presence of, and subsequently characterize, positive and negative biotic interactions associated with red spruce establishment; and
3. to characterize the biophysical (geomorphological and environmental) correlates of heathland biodiversity and red spruce seedling establishment through geospatial modelling and descriptive statistics

Chapter 2 – Literature Review

2.1. Heathland Vegetation Communities

Heath is an ecosystem type characterized by ericoid dwarf-shrubs with very little tree or tall shrub canopy cover (Gimingham, 1972; Specht, 1979). Here, I use the term 'heathland' to describe the physical landscape across which the heath occurs. Globally, some vegetation communities termed heath may incorporate tree cover in addition to a shrub layer of vegetation associated with heathlands (such as, though not exclusively, Ericaceae), moors, and the *fynbos* of South Africa (Specht, 1979). The heath communities ("heath") of our study area have sparse, if any tree cover, and our area of focus lies in the heathland ecotone immediately adjoining post-disturbance *P. rubens* forest. Heathlands are found globally, in both lowland and subalpine environments, and in both wet and dry forms (Gimingham, 1972). Historically, there have been arguments for both anthropogenic and non-anthropogenic causes of heathland presence and persistence (Gimingham, 1972; Strausbaugh and Core, 1978; Specht, 1979), but overall, both types of heath exist.

The heath families include members of the order Ericales (Vacciniaceae, Diapensiaceae, Ericaceae, Epacridaceae, and Prionotaceae), as well as Grubbiaceae of the order Santalales, and Empetraceae of the order Celastrales (Specht, 1979). Heath vegetation, in general, is commonly sclerophyllous and evergreen, adapted to nutrient-poor, often acidic soils. Similar to the soils of coniferous forests, soil of the heathlands may be subject to podzolization by heath vegetation (Gimingham, 1972).

2.2. Biotic Interactions

Biotic interactions refer collectively to positive and negative exchanges among members of the biotic community (Bertness and Callaway, 1994; Brooker et al., 2008). These interactions

may be direct, such as in the case of nurse-plant and shading effects (Al-Namazi et al., 2017), or indirect, such as in the case of unpalatable cover species shielding more palatable neighbors from herbivory (Callaway et al., 2005). Both are important in shaping community dynamics and biodiversity (Bertness and Callaway, 1994; Callaway, 2007; Brooker et al., 2008; Maestre et al., 2009; Ballantyne and Pickering, 2015).

Facilitation is a positive non-consumer interaction among organisms that contribute to the relative success of at least one other organism (Bertness and Callaway, 1994). Within vegetation communities, a much-studied example is between nurse plants and beneficiaries (Ballantyne and Pickering, 2015; Al-Namazi et al., 2017). Co-development within a vegetation community dependent upon nurse species may cause exotic species to benefit in lesser or otherwise different ways from nurse plant interactions than native species (Llambí et al., 2018). In alpine regions of Australian dwarf shrub and the Andean páramo, facilitative effects of nurse shrub and cushion-type plants were found to increase species diversity within their immediate community (Ballantyne and Pickering, 2015; Hupp et al., 2017).

Competitive processes are also integral to shaping vegetation community structure. Competition is considered a negative interaction between or among organisms, whereby the act of one organism taking in a limited resource can impede the relative ability of another organism to capitalize on the resource (Barbour et al., 1999). Among plants, this interaction may take the form of competition for light (Dohn et al., 2013), for nutrient availability (Mobaied et al., 2015), or for water (e.g., Maestre et al., 2009; Soliveres and Maestre, 2014).

A complex interplay exists between biotic and abiotic stress factors on an ecosystem; interactive characteristics of species emerge under stressful abiotic conditions and exert selective influence within the biotic community, controlling its growth and development. The stress

gradient hypothesis (SGH) posits that as abiotic conditions become more severe, the number of facilitative (positive) plant interactions within a vegetation community will increase, and competitive (negative) interactions will decrease (Bertness and Callaway, 1994). This model has been the subject of discussion as researchers continuously refine the model to more closely examine the interacting forces which that shape vegetation communities (e.g., Bertness and Callaway, 1994; Brooker et al., 2008; Maestre et al., 2009; Soliveres and Maestre, 2014). Research has found that many plant communities, especially in stressful environments such as alpine treelines, do indeed follow the SGH model (Choler et al., 2001; Brooker et al., 2002; Resler et al. 2005; Llambí et al. 2013).

2.3. Red Spruce and its Encroachment in Appalachian Heathlands

Red spruce (*Picea rubens* Sarg.) is an important timber species that previously covered extensive areas around Canaan Valley (Allard and Leonard, 1952). Logging and logging-associated fires cleared most of these red spruce forests in the area of interest, which have subsequently been replaced with heath, bog, and deciduous forest (Fortney and Rentch, 2003). On top of the plateaus along the eastern edge of Canaan Valley, WV, stretches of heathland that established following anthropogenic disturbance in the preceding century can now be found adjoining patches of red spruce forest. Research suggests that the vegetation stratum into which tree encroachment occurs can profoundly and differentially impact tree seedling germination and survival (e.g., George and Bazzazz, 2014) thereby affecting spatial pattern of regeneration, and ultimately recruitment. Thus, interactions between this formerly dominant tree species and the heathlands into which it now encroaches are of interest here.

Red spruce has been described in detail by the US Department of Agriculture (Silvics of North America: Volume 1) (Burns and Honkala, 1990). Red spruce seeds are only statistically

viable for one year, and mature trees may only produce “good” seed crops on a cycle between three and eight years, depending on conditions (Burns and Honkala, 1990). If those seeds do not germinate within a year, it is unlikely they will in the season that follows, and a whole season’s productivity may be impacted by unfavorable germination conditions (Burns and Honkala, 1990). The seedlings that do emerge have short, fragile roots, and can desiccate if they are unable to reach adequately moist soil conditions (Burns and Honkala, 1990). Drought (resulting from this desiccation), crushing, and frost heaving are the highest causes of seedling mortality in the first year, and far more red spruce seedlings tend to regenerate than are successfully recruited (Burns and Honkala, 1990).

Once established, red spruce can persist on areas of poor soil, similar to that found in heathlands. It is a long-lived tree, able to survive for upwards of four centuries, that can survive for extended periods in the shade of the understory at a suppressed growth rate (Burns and Honkala, 1990), and then capitalize on canopy gap openings. This makes them good candidates for timbering that preserves advanced growth, or as a successor to a hardwood forest (Cavallin and Vasseur, 2009).

2.4. Abiotic Factors

Abiotic factors, including geomorphic forms and processes, climatic conditions, and disturbances, affect plant community dynamics. At the broadest scale, macro and mesotopography can alter how a landscape interacts with regional climate, thus create environmental conditions decoupled from regional patterns acting over a broader scale (Dobroski, 2011). This juxtaposition can result in the creation of isolated refugia, where conditions are favorable to species that are less tolerant of the wider regional climatic regime (Dobroski, 2011).

The high-altitude plateaus of Canaan Valley, WV feature an example of one such refuge community, whereby the effects of elevation on temperature allowed boreal species (established when, paradoxically, such species were pushed to warmer climes in the south by Pleistocene glaciation) to remain, following the retreat of the ice sheet and the warming of regions surrounding their mountaintop islands (Allard and Leonard, 1952). Rock outcrops scattered across these mountaintop environments are visually similar to remnants of periglacial process identified in other areas of the Appalachian Highlands (Clark, 1968; Clark and Ciolkosz, 1988). Heath barrens and grass balds may occur in some of these areas today, following disruption of the spruce-fir forests that had previously dominated (Allard and Leonard, 1952).

Aspect can have both a direct and indirect impact on community growth and regeneration. Distinctive mesoclimatic conditions can result from a change in aspect that influence the spatial patterns of vegetation establishment—a pattern especially evident in abiotically stressful environments such as alpine environments, deserts, heathlands, and bogs (e.g., Rose and Malanson, 2012; Holtmeier and Broll, 2005; Resler et al. 2005; Resler 2006; Resler and Stine, 2009). In water-restricted environments, variable depth of snowpack and subsequent water availability on different aspects was shown to influence the relative success of *Tsuga mertensiana* encroaching on heath-shrub meadows in the Cascades (Miller and Halpern, 1998). Aspect also affected timing of snowmelt in Miller and Halpern's findings.

The interplay between snow cover and vegetation, specifically trees, is complex, balancing the potential damage by abrasion (Telewski, 2012) and snow or ice load (Wang et al., 2011) with the insulating effects of deep snow layers to protect against freezing, desiccation, and abrasion (Laybourn-Perry et al., 2012). Artificial lack of snow cover can lead to desiccation of tree seedlings in experimental conditions, and exposure to frost damage (Frey, 1983). In heath

vegetation, early melt has been associated with slowed seasonal growth in *Vaccinium myrtillus* independent of water stress (Gerdol et al., 2013). In Canaan Valley, snow has been recorded at 3,715 feet of elevation, lower than Cabin Mountain and Bear Rocks both, between October and May, with average annual snowfall between the 2001 and 2019 winter seasons at 173 inches (unpublished data, Lesher, 2019).

The impact of wind on tree growth and formation is well-studied (e.g., Wade and Hewson, 1979; Gardiner et al., 2000; Telewski, 2012; Gardiner et al., 2016) and evidence of extreme flagging and deformation associated with wind is visible in exposed red spruce on the mountains surrounding Canaan Valley, where windthrow is the principle form of disturbance in remaining red spruce forest, (Byers et al., 2010). Winds on the exposed plateaus frequently gust in excess of 60mph from the northwest, with gusts of up to 90mph recorded in some cases at Cabin Mountain (unpublished data, Carroll, 2019). Deformation associated with wind includes asymmetry in the crown and occasionally bending of the stem away from the prevailing wind direction (Wade and Hewson, 1979).

2.5. Disturbance Dynamics and Succession in Heathlands

An understanding of present and past disturbance processes is important for explaining the structure and function of vegetation communities. Pickett and White (1985) defined disturbance as, “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment.” (pg. 7) Van der Maarel (1993) states that disturbance must be considered relative to its spatial extent, the frequency or irregularity with which it occurs, and the magnitude of a given event. Ultimately,

disturbances generate spatial heterogeneity in vegetation pattern and biodiversity, resulting in a successional mosaic (van der Maarel, 1993).

For heathlands to persist as heath, there are typically factors acting to suppress the ability of canopy vegetation to succeed (e.g., Gimingham, 1972). Here, I will address the following disturbance factors: 1) history of anthropogenic disturbance in Canaan Valley's forests and subsequent heath communities, 2) the complex role of fire in Canaan Valley and heathlands in general, and 3) succession and encroachment by tree species in heathland.

The recent history of Canaan Valley is characterized by anthropogenic disturbances that were catalyzed by the need for red spruce timber. The old growth red spruce-dominated community was nearly eliminated from the immediate area because of clearcutting practices (Allard and Leonard, 1952). Those conifer forests fostered a deep layer of moist, organic soils, which were, in turn, partially dependent upon the forest community for sheltering from the elements. Once that forest was removed, the moist soils dried out, fueling extensive wildfires that left rock exposed and roots to wither in their wake (Allard and Leonard, 1952). As noted by Burns and Honkala (1990), red spruce is highly intolerant to fire, and those stands not subjected to clearcutting were still at risk. The impressions of those wildfires are still visible in the species composition around the Valley today; for example, Fortney and Rentch (2003) made note of remnant vegetation communities that were likely advantaged by more frequent burns, but predicted this fire-tolerant vegetation would disappear as frequency of burns decreased. Stand-replacing fire disturbances are not common on a large scale in the Central Appalachians, and wind damage events occur more frequently (Byers et al., 2010).

The relationship between heathlands and fire is complex. Fire, along with grazing, has traditionally been the method of management in European heath for thousands of years (Måren et

al., 2010). Globally, many types of heath, such as the Mediterranean heathlands and the *Fynbos* region of South Africa, are expressly fire-adapted (Fagúndez, 2013). Fire can play an important role in initiating germination of certain heath species (Bargmann et al., 2014). In Australian heathlands, a decrease in fire interval can promote a transition from heath to shrubland (Bargmann and Kirkpatrick, 2015), while an increase in the interval of fire, even in fire-adapted heath, may decrease populations of characteristic heath species and prompt a shift to sedges (Bradstock et al., 1997). With the concept of disturbance being relative to the subject, if fire as a disturbance has a more dramatic impact on the encroaching vegetation community than it has on the heath, then fire may be both a disturbance and source of stability in a heathland environment.

Dynamics of heathlands and forests, particularly the colonization of heathlands by woody species, have been the subject of much research, especially in the European Union. This interest is likely to be, in part, based on the addition of heathlands to Annex I of the EC Habitats Directive as "habitats of community interest," (Mobaied et al., 2016). Feoli (2010) found that although encroachment of tree species into a heath would begin slowly, rate of colonization increases gradually. Natural senescence of *Calluna vulgaris* (in Western European heathlands) may affect rates of tree colonization in the absence of management (Feoli 2010; Mobaied et al., 2015). Mobaied et al. (2015) found differences in the rate and distribution of colonization based on other factors, such as low soil quality and competition. The ability of heathlands to succeed on poor soils (Gimingham, 1972) can limit the establishment of certain deciduous species in those areas, whereas coniferous tree species that were outcompeted by deciduous stands may succeed in to areas where soils were too acidic or otherwise poor for deciduous trees to establish (Mobaied et al., 2015). In Denmark, dry heath that had occupied former agricultural land, and been left undisturbed for nearly a century, persisted as heath or transitioned to grassland (Ransijn

et al. 2015). As the number of seed-bearers of non-heath species encroaching into the heath increases, so, too, will the rate at which encroachment continues. Further, with a limited growing season, as found in Canaan Valley's uplands, it is possible the elements of timing and distance from seed source become even more critical. Under experimental conditions, Körner et al. (2008) showed that even a three-week head start for early successional species of herbs, grasses, and legumes can change dominance of the resulting biomass—a finding that highlights the importance of biomass structure for seedling establishment.

Whereas historical disturbance processes in Canaan Valley WV is well documented (e.g., Fortney and Rentch, 2003), literature is lacking on vegetation and successional dynamics in upland heath barrens in light of its intensive land use legacy. Upland heath barrens are generally found on the knobs and plateaus surrounding the Valley and associated vegetation dynamics (Byers et al., 2010). Fortney and Rentch (2003) created successional vegetation models based on a long-term study of the vegetation communities in Canaan Valley that terminated in red spruce-dominated conifer forest as the climax successional community in most cases, including the dry high-elevation heathlands. Through analysis of aerial imagery, they revealed that the total areal extent of heath communities decreased between 1945 and 2000, giving way to hardwood forest in the Valley. However, heathland communities were persisting on the mountain ridges on areas of poor, deleted soils. These observations suggest spatial variation of heath community persistence with respect to disturbance legacy. Such environments are visible today around the well-known Dolly Sods Wilderness area of Monongahela National Forest.

Chapter 3 – Study Area

The heathlands of Appalachia occur in the Allegheny Mountains of West Virginia, and in Great Smoky Mountain National Park (GSMNP), in the southern Appalachians. In GSMNP, these heathlands are described as "heath balds" and are most common in small pockets on west-facing ridges and slopes (Specht, 1979). Though below climatic treeline, upland heathlands persist under harsh climatic conditions, leached or infertile soil conditions, regular fire-disturbance, and windward exposures that slow or preclude substantial conifer incursion, thereby delineating a "localized" treeline (Whittaker, 1956). Above that treeline, heath vegetation persists unsuppressed by canopy development. Whittaker (1956) refers to this idea as a topographic climax—a climax community based upon a local variation rather than a blanket application of successional ideas.

Canaan Valley's heathlands prominently feature Ericaceae, Rosaceae, and Lycopoiaceae families, growing as dense, low-lying shrubs that are subjected to strong and constant westerly winds, relatively low annual temperatures, and relatively high annual rainfall (Strausbaugh and Core, 1978). Remnants of the red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) forest that once constituted 469,000 acres of West Virginia's high elevation evergreen forests can still be seen in Canaan Valley today, and spruce and fir do appear sporadically in the heathland (Strausbaugh and Core, 1978).

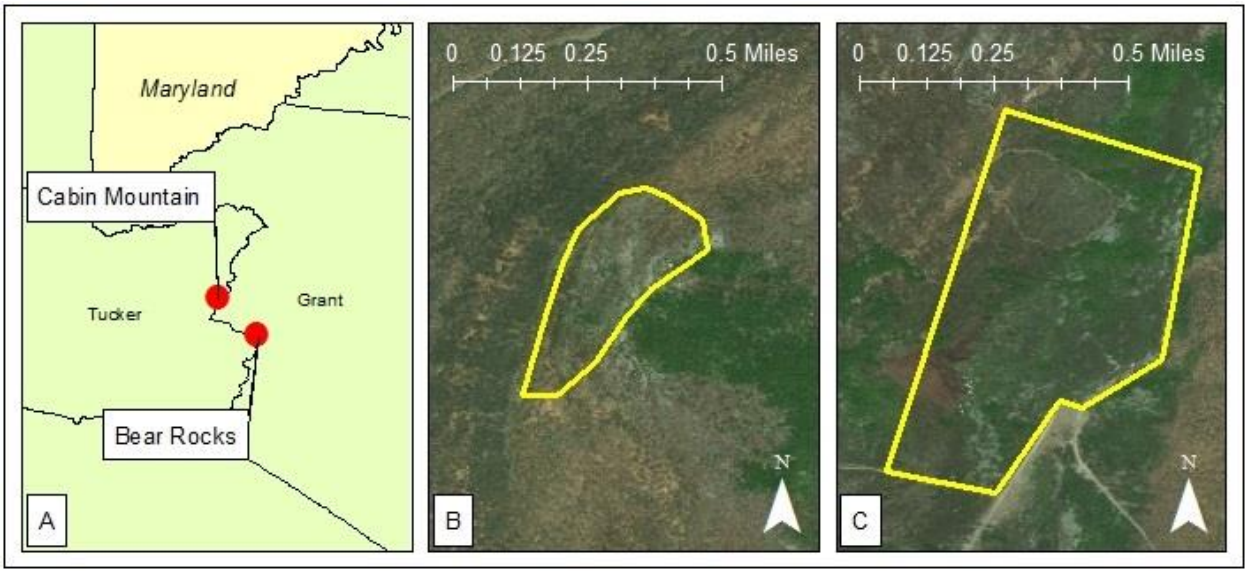

Figure 3.1. Left to right: A) Locations of Cabin Mountain and Bear Rocks sites relative to WV counties Tucker and Grant. B) Rough outline of the Cabin Mountain study area. C) Rough outline of the Bear Rocks study area. Both study area images are at a 1:20,000 scale. Sixteen plots were placed in the Cabin Mountain area, and fifteen at the Bear Rocks site. State and county outlines are 2017 TIGER/Line shapefiles, credited to the U.S. Census Bureau. Basemap layer credits to ESRI, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

The two specific study sites include a National Wildlife Refuge (NWR) managed area of Cabin Mountain, WV, situated along the western edge of the eastward-bounding plateau of the Canaan Valley, and Bear Rocks Preserve (managed by The Nature Conservancy), near Dolly Sods WV, on the eastern edge of the plateau (Fig. 3.1). Cabin Mountain, which runs along the southeastern edge of the valley, rises to roughly 4500 feet a.s.l. (Fortney and Rentch, 2003). Harsh climate conditions in this region substantially truncate the growing season; the frost-free period in Randolph County immediately to the south of Cabin Mountain is 90 days, but frost can occur during any month of the year (Beverage, 1967 cited in Fortney and Rentch, 2003). Oosting and Billings (1951) compared the vegetation demographics in the northern and southern Appalachian red spruce forest communities and found collections of species that were distinct

from one another, and other studies have addressed the vegetation of Canaan Valley proper (e.g., Rentch and Fortney, 1997; Fortney and Rentch, 2003).

Figure 3.2. Multiple periglacial rock pits exposed and interspersed with flagged *P. rubens*, ferns, and heath vegetation. This landscape was photographed at Cabin Mountain.

At Cabin Mountain, micro-scale topographic heterogeneity results in a mixture of dry areas with low shrub and herbaceous cover, saturated shrub bogs with dense moss and fern, and thick heathland with mixtures of reindeer lichen and *Vaccinium angustifolium*. Open pits of frost-shattered rock (e.g., Clark and Ciolkosz, 1988; Fig. 3.2) truncate the landscape and hold moisture and standing water after snowmelt and rain. Large specimens of *Picea rubens* can be seen along

the western edge of the plateau, where dwarf shrub and herbaceous meadows mix. These specimens grow low to the ground in dense mats woven through by deer trails.

At Bear Rocks (at the eastern edge of the plateau), shrub vegetation generally becomes taller and denser descending west and downslope toward the Dolly Sods Wilderness area of Monongahela National Forest. Deer trails and human hiking paths are common at this site. To the northwest, an area of dwarf shrub and heath-bog characterized by patches of heath-type vegetation and saturated "pits" of moss and fern, feature some sub-breast height *P. rubens* specimens scattered on the landscape. Many of these specimens are observed to be slightly yellowed in coloration. Beyond the edge of the study site to the north is a field of intentionally planted *P. rubens* specimens.

Bear Rocks/Dolly Sods is more heavily traversed by hikers and campers. Campsites dot the sides of the road leading up the mountain. The site abuts Monongahela National Forest and the Nature Conservancy property at Bear Rocks includes a parking lot to support visitor traffic.

Chapter 4 – Methodology

4.1. Field Methods

The methodology of this study included field data collection and subsequent statistical analysis using both field data and variables derived from geospatial datasets. Fieldwork occurred between June and early September of 2018 at both study areas. Two sampling procedures were employed in support of our three objectives: large plot sampling (spruce demographics plots) for fulfillment of Objective 1, paired microplot sampling for fulfillment of Objective 2. Both sampling methods supported Objective 3, which was to assess biophysical characteristics of heathland biodiversity and red spruce seedling establishment.

4.1.1. Field Methods: Spruce Demographics Plots

Fifteen plots were established at Bear Rocks, and sixteen plots at Cabin Mountain, for the purpose of sampling red spruce demographics. All demographics plots were 15m by 15m square. Plot placement at each site was determined prior to entering the field by generating random points with a threshold minimum distance of 30 meters between each plot. In the field, I used a Trimble GeoXH GNSS rover to navigate to each point, which became the quadrat centroid. Collection procedures for large plots were based loosely on standards set by the US National Vegetation Classification (Jennings et al., 2004), deviating where necessary to focus on the project's goals. In each spruce demographics plot, I characterized vegetation communities, and collected biophysical information for subsequent statistical analysis following methods similar to those of Byers et al. (2010). Spruce demographic plots were also used to identify appropriate sites for paired microplots, described below, for fulfillment of Objective 2.

Field sampling involved techniques adapted from Byers et al. (2010), with a focus on individual *P. rubens* and landscape characteristics. Plots were positioned in the field with corners

oriented toward each cardinal direction and photographed at each of the cardinal points. Photographs were taken toward the plot center from a camera (angled slightly to the ground) mounted on a monopod from a height of approximately three meters. These photos were documented in the metadata collected for each plot, as well as sampling date, initials of sampling crew members, plot identification information, and GNSS coordinates.

A count of all *P. rubens* specimens present within each spruce demographic plot was recorded. The research team measured height of each *P. rubens* using a transect tape and clinometer. For all individuals at or above 1.37m, the diameter at breast height (DBH) was recorded using a DBH tape, and note was made about the presence or absence of cones. Diameter at ground level (DGL) was recorded for all individuals below 1.37m in height. No other age data were collected for the larger or smaller specimens. A tree was only measured if its stem was at least partially contained within the plot at the base, and not if the stem was outside the area of the plot.

Moisture was assessed visually based on the presence of water at the plot (e.g., saturated soil, standing water; "Hydrology Evidence") and the overall wetness of the plot (e.g., Moist, Somewhat Moist, Dry; "Hydrologic Regime"). The same researchers made assessments for all plots for consistency.

At each large plot, different cover characteristics were assessed in keeping with Objectives 1 and 2. Total exposed rock cover (see Fig. 3.2 for an example) was recorded in the field at each plot, to a minimum of 5% cover. Coverage under 5% of total area were recorded as 0. Other cover groups – herbaceous, subshrub, tall shrub, and tree cover – were estimated using the corner photographs of each plot and were used to label the physiognomic character of each plot. Tall shrub and subshrub were characterized as shrub layer taller than, or up to, one meter in height

respectively. Tree cover was based on vegetation taller than two meters in height, as well as identified tree cover, to include red spruce shorter than two meters. While cover was assessed in these categories, rarely did they overlap; at one Cabin Mountain plot, a stand of *Acer rubrum* formed a canopy over an herbaceous ground layer, with some interspersed shrub cover. Most plots, however, had very little canopy vegetation, and instead were patchworks of fairly discrete, dense cover that precluded other cover types below.

4.1.2. Field Methods: Paired Microplots for Assessing Plant Interactions

In order to assess potential plant interactions associated with spruce regeneration (Objective 2), I established a total of thirty-two pairs of concentric circular plots around *P. rubens* seedlings and saplings to document heath and understory cover associated with spruce regeneration sites. The paired microplots allowed us to assess interactions between the heath community plants, microsite characteristics (such as non-vegetative cover), and *P. rubens* seedlings and saplings using the Relative Interaction Index, as described in detail below. Each pair had one plot centered on a tree and one open heath plot that served as a control. Locations for these paired microplots were based on the abundance of *P. rubens* trees shorter than breast height (1.37m), as determined by the spruce demographics survey. Only specimens shorter than breast height (< 1.37m) were used for this assessment; choosing only specimens shorter than breast height for these microplots served to focus attention on more recent *P. rubens* establishment. I note that some spruce demographic plots had no *P. rubens*, no *P. rubens* shorter than breast height, or only very few applicable *P. rubens* in the area. Four spruce demographic plots were chosen based on the presence of applicable spruce, and eight pairs (sixteen total, eight tree and eight heath) were placed at each location.

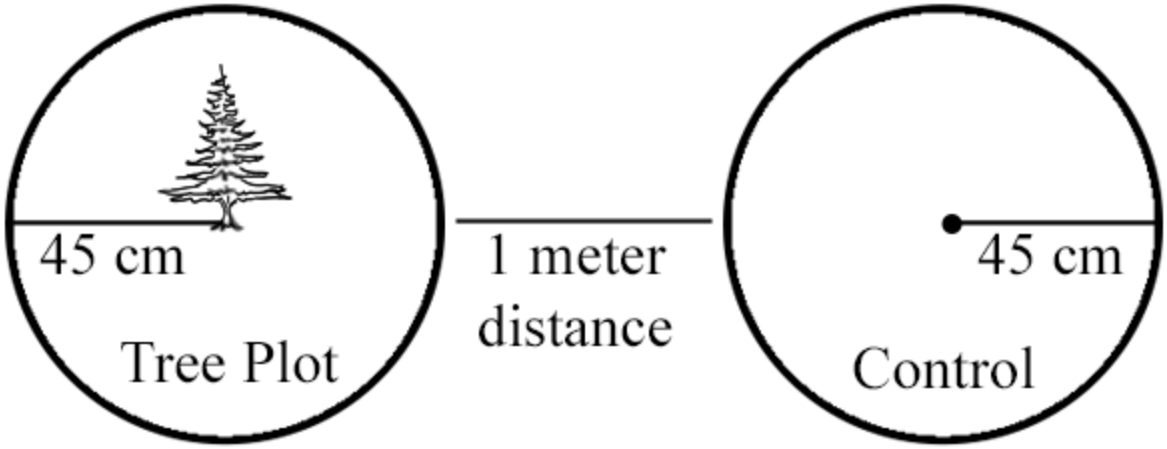

Figure 4.1. Paired plot diagram representing one tree plot (left) and a control plot (right) with one-meter distance separating each edge (not to scale). Control plots were located in a random direction from the associated tree plot.

The primary pair of plots consisted of two plots with 45cm radii. One was centered on a specimen of *P. rubens* (the tree plot), and the other was placed in a random direction from the first plot on vegetation that had no individuals of *P. rubens* contained within it (heath plot, the control). One meter of distance separated the edges of each of these plots. A nested concentric circle contained within the tree plot had a radius of 15cm, also centered on the individual *P. rubens* (Fig. 4.2). The purpose of the concentric 15cm radius plot was to examine the distribution of species and vegetation coverage immediately at the base of the tree, and to qualitatively compare differences between 0 - 15cm and 0 - 45cm cover composition.

Figure 4.2. Nested plot of 15 cm radius, centered on individual *P. rubens*. Each 15 cm radius plot was nested within the original 45 cm tree plots, and the assessment of each was conducted at the same time as the larger tree and control plots.

Within each of these three plots, each vascular plant species was identified and its real coverage within the plot, irrespective of overlap with other vegetation (Jennings et al., 2004), was recorded. Total coverage (%) of graminoids as group, mosses as a group, and lichens as a group were collected in the same way, with note made about the rough number of species within each group. Finally, non-vegetated cover was similarly assessed, and categorized as bare ground, litter, or rock. Assessments of coverage data were made by only two participants in the study in order to maintain a standard of consistency. These coverage data were assessed using the Relative Interactions Index (Armas et al., 2004), allowing us to quantify trends in the relative positive or negative interactions on *P. rubens* (and vice versa), in accordance with Objective 2.

4.2. Statistical Analyses

In support of Objective 3, I used a combination of field methods and a digital elevation model to derive a series of biophysical variables that a review of the literature indicated could impact *P. rubens* regeneration. Variables incorporated into a generalized linear mixed model (GLMM) ultimately included: Site as the random effect, Physiognomic Class (see section 4.2.1),

Rock Cover, Slope, Curvature, Flow Accumulation, and Distance to Stand as independent variables, and *P. rubens* Count as the dependent variable. All thirty-one spruce demographic plots were incorporated into the dataset.

4.2.1. Statistical Analyses: Field-Derived Biophysical Variables

During fieldwork, multiple photographs were taken of each sampling plot for later reference and to characterize each plot qualitatively. Using these photographs, a rough estimate of the area coverage for four physiognomic classes was assessed: Herbaceous Cover (e.g. ferns, graminoids), Subshrub Cover (shrub vegetation up to 1m in height), Tall Shrub Cover (shrub vegetation up to 2m in height), and Tree Cover (*P. rubens* and other tree cover over 2m in height). This assessment was included with the relative cover of exposed rock (Rock Cover) assessed in the field.

For the GLMM, the four vegetation cover types were combined into a categorical variable called Physiognomic Class, which contained three categories based on the dominant vegetation type of the plot, as assessed from the photographs. These categories included: Woodland (Tree Cover dominant), Shrubland (Tall- and Subshrub Cover dominant), and Herbaceous (Herbaceous Cover dominant). The vegetation cover types were condensed to Physiognomic Class categories to reduce artificial correlation between the raw cover percentages (see section 4.2.3). Percent Rock Cover was included separately in its original form.

4.2.2. Statistical Analyses: DEM-Derived Biophysical Variables

Using a clipped 1-meter statewide mosaic digital elevation model (2018) from the West Virginia GIS Technical Center, and basemap imagery provided with ArcGIS Desktop 10.5, I derived additional, terrain-related biophysical variables for inclusion in the GLMM (Table 4.1).

Since segments of the DEM had been resampled from 3m data into 1m imagery, I resampled to a 3m horizontal resolution.

Table 4.1. All Biophysical Variables Derived.

Variable	*Data Source*	*Resolution / Purpose*	*Justification*
Elevation	Digital Elevation Model 1-Meter Statewide Mosaic (2018) - West Virginia GIS Technical Center	Mosaic resampled to 3-meter horizontal resolution for processing at coarsest resolution	Elevation is a topographical element that can impact vegetation communities (e.g. Dobroski, 2011)
Aspect	Geospatial processing conducted on DEM (above) using ESRI's ArcMAP 10.5	Mosaic resampled to 3-meter horizontal resolution for processing at coarsest resolution	Aspect can govern insolation and snowmelt, and slope, curvature, and flow are topographical elements that can impact vegetation communities (e.g. Miller and Halpern, 1998, Rose and Malanson, 2012; Kambo and Danby, 2018)
Slope	Geospatial processing conducted on DEM (above) using ESRI's ArcMAP 10.5	Mosaic resampled to 3-meter horizontal resolution for processing at coarsest resolution	Slope can govern soil moisture dynamics (Kampf et al., 2015)
Curvature	Geospatial processing conducted on DEM (above) using ESRI's ArcMAP 10.5	Mosaic resampled to 3-meter horizontal resolution for processing at coarsest resolution	Describes the complexity of a sloped surface, further impacting landscape-vegetation interaction (Wilkinson and Humphreys, 2005)
Flow Accumulation	Geospatial processing conducted on DEM	Mosaic resampled to 3-meter horizontal	Soil moisture, solifluction, and

	(above) using ESRI's ArcMAP 10.5	resolution for processing at coarsest resolution	fluvial processes have been shown to influence vegetation communities in arctic-alpine environments (le Roux and Luoto, 2014)
Insolation	Geospatial processing conducted on DEM (above) using ESRI's ArcMAP 10.5	Mosaic resampled to 3-meter horizontal resolution for processing at coarsest resolution	Solar radiation is one of the critical factors influencing snowpack (Coughlan and Running, 1997), and snowpack has been shown to influence seedling survival (Gerdol et al., 2013)
Distance to Stand	Measured using linear distance (meters) from center of the plot to the nearest cluster of *P. rubens* identifiable in aerial imagery	Nearest 5m	This represents distance from seed source of the plot center (e.g. Dibble et al., 1999)

Using the center point of each plot as the starting point, I recreated the plots as polygons within ArcMap 10.5. I used these boundaries to create areas for computing Zonal Statistics and generating variables using tools available with ArcGIS. These variables included Elevation, Aspect, Slope, Curvature, Flow Accumulation, and Insolation. Elevation was measured to the center of the plot. All other values were averaged over the whole plot.

Though Elevation, Aspect, and Insolation have been shown in other research (e.g., Coughland and Running, 1997; Wilkinson and Humphreys, 2005; Dowbroski, 2011; Kambo and Danby, 2018) to be useful in assessing vegetation communities (see Table 4.1), they were not included in the final model due to lack of variation in values across the area. The study plots at Bear Rocks and Cabin Mountain were very similar in elevation, varying by only 35m, and

internally was characterized by a range of 18.95 meters at Bear Rocks, 11.22 meters at Cabin Mountain. See Appendix A for the elevation and dominant aspect of each plot (Table 1a, Table 2a).

The final derived variable was Distance to Stand. Using the basemap data provided in ArcMap 10.5, I measured from the center point of each plot to the nearest visible stand in the basemap imagery. Stand was defined as an area identifiable as *P. rubens* forest that was 1) larger than the size of the plot, and 2) dense enough so that other underlying coverages were not visible. These measurements were linear distance made in meters and rounded to the nearest 5m.

4.2.3. Statistical Analyses: Evaluating the Dataset and Conducting the GLMM

A Site identifier (BR / CM) and Count per plot (based on spruce demographic plot data) were added to the field- and DEM-derived biophysical variables in the modeling dataset. Then, using JMP Pro 14, I created a multivariate correlation matrix for all continuous numeric variables to assess artificial correlation. Since percent cover of each vegetation type tended to be highly correlated with one another (as one type increased or decreased, so too did the other types), raw percent cover values were converted to the categorical Physiognomic Class variable (see 4.2.1).

I used a Generalized Linear Mixed-Effect Model (GLMM) using the glmmTMB package in RStudio. The data available and goals of the study drove the choice of the GLMM. The GLMM can be used for descriptive analysis as well as predictive, and this descriptive assessment of the landscape was better in keeping with the objectives. Additionally, though plots were located a minimum distance of 30m apart (and most distance were much greater), the GLMM is equipped to account for potential statistical violations of sampling plot independence (e.g., Hurlbert, 1984). Further, models such as CART, in addition to being primarily predictive, require training data, a need which could not have been met with the small sample size of 31 plots. All candidate

models were run using the glmmTMB package's negative binomial (nbinom2 in the package) log link family structure without zero inflation. Poisson structures were tested but found to be inappropriate due to variances within the data.

4.2.4. Statistical Analyses: Paired Plot Assessment

To support our objective of characterizing biophysical correlates (Objective 3), I derived selected vegetation diversity indicators (e.g., Shannon-Weaver, Simpson's Index, and Beta Diversity) to characterize species composition data in each paired plot. From the paired plots, I assessed biotic and abiotic cover types for the six most populous categories: *Vaccinium angustifolium*, rock, moss, graminoid, lichen, and litter groups (species of moss, graminoid, and lichen were unidentified to the species level). Using JMP Pro 14 statistical software, I calculated variance and performed Shapiro-Wilks tests for normality on datasets for tree and heath plots in each category. The variances for each pair of datasets ranged wildly, and none fitted a normal distribution (from $p < 0.001$ to $p < 0.0447$). Since the data therefore violated the assumptions of the Student's t-test (variance and normality) and the Welch's t-test (normality), a Wilcoxon test was employed instead. The Wilcoxon test was considered valid on the assumption that the cover types within each plot were independent of one another. The null hypothesis is that the cover type for each group will not vary based on whether the cover is in the tree plot or in the heath plot. A Tukey HSD test was also performed on the same datasets, to compare the results to those of the Wilcoxon and assess the method.

I used the Relative Interaction Index (RII) described by Armas et al. (2004) to quantify potential biotic and biophysical associations in the paired microplots (Objective 2). This measure has been used by Llambí et al. (2018) and Hupp et al., (2017) for north Andean paramo

ecosystems to detect the presence and nature of plant interactions. For our purposes, it has the following structure:

$$(N_1 – N_2) / (N_1 + N_2) \qquad \text{Equation 1}$$

RII is arithmetically simple to apply, but competes with and outperforms similar indices for analytical strength and sensitivity, while at the same time measuring both positive and negative interaction symmetrically between -1 and +1 (Armas et al., 2004). As an alternative to removal experiments in this complex habitat, this is a low-impact means of assessing the associations between red spruce and heath vegetation. In this case, N refers to the common measurement variable that is being used to interpret relationships, such as biomass (Armas et al., 2004) or species density (Llambí et al., 2018). For my purposes, N represents real cover.

5.1.1. Population Demographics of Red Spruce in Heath and the Surrounding Environment

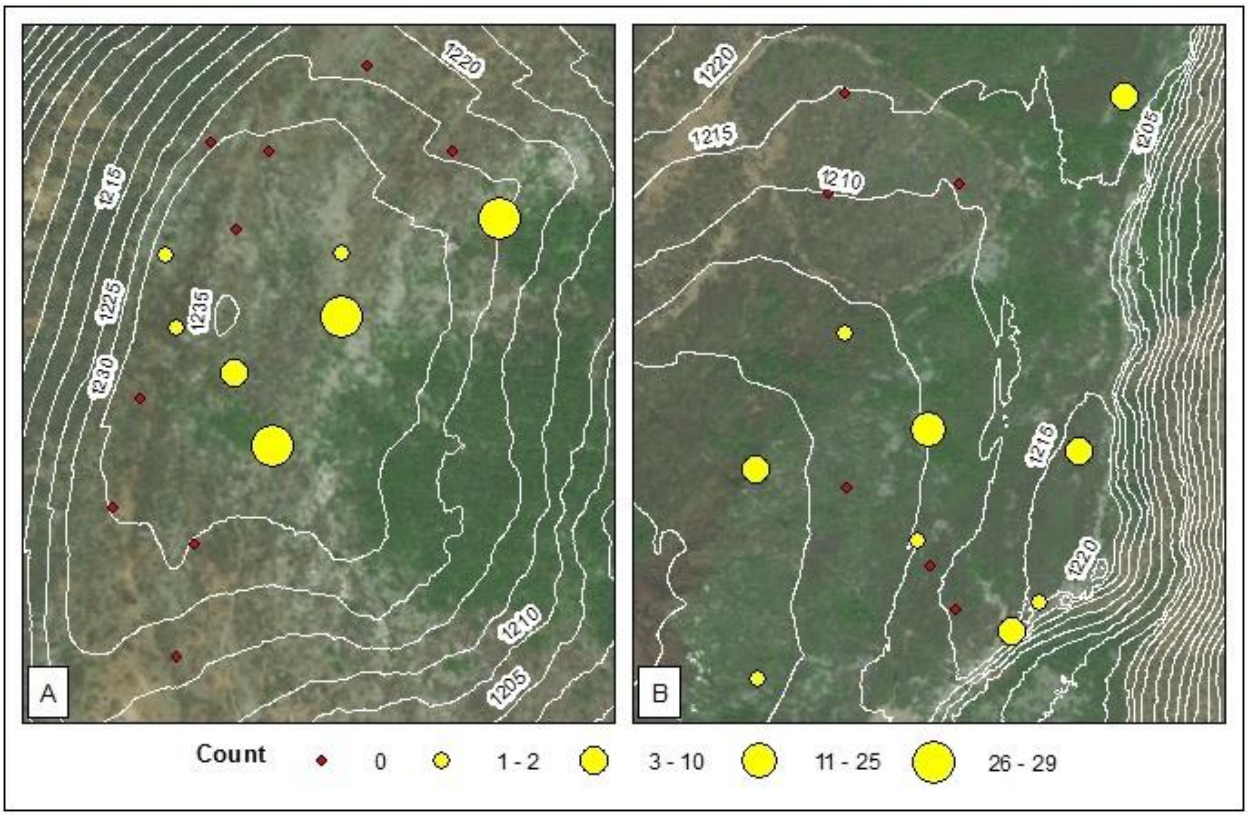

Figure 5.1. Location of census plots present at Cabin Mountain (A) and Bear Rocks (B) sites, with symbols graduated by Count (number of *P. rubens*). Contour lines represent 5m elevation. Basemap layer credits to ESRI, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

I recorded 65 *P. rubens* across all plots in Bear Rocks and 99 at Cabin Mountain, for a total of 164 *P. rubens* trees. Of those, 50 (22 at Bear Rocks, 28 at Cabin Mountain) were taller than breast height (1.37m) and 114 (43 at Bear Rocks, 71 at Cabin Mountain) were shorter than breast height. Overall, trees at the Bear Rocks plots were taller (Table 5.1, Table 5.2). At Cabin Mountain, more specimens of *P. rubens*, particularly saplings and seedlings, were found along a gradient moving toward the dominant *P. rubens* stand (Fig. 5.1). *P. rubens* was the most numerous tree in the heath at both sites. Stunted specimens of *Acer rubrum* were found at Cabin

Mountain, and isolated specimens of *Pinus strubus* (white pine) were identified at both sites. No *Abies balsamea* (balsam fir) were identified at either location.

Table 5.1. Summary statistics for all *P. rubens* individuals > 1.37m.

	Bear Rocks	**Cabin Mountain**	**Combined Sites**
Count	22	28	50
Mean Height (m +/- SD)	5.48 +/- 2.98	3.58 +/- 2.20	4.43 +/- 2.73
Max Height (m)	12.27	9.04	12.27
Min Height (m)	1.45	1.48	1.45
Median Height (m)	5.22	2.56	3.64
Mean DBH (cm +/- SD)	11.01 +/- 8.36	8.06 +/- 7.51	9.38 +/- 7.96
Max DBH (cm)	30.7	27.4	30.7
Min DBH (cm)	0.67	0.65	0.65
Median DBH (cm)	9.95	6	7.5
Number of Cones Observed per Site	8	3	11

Table 5.2 – Summary statistics for all *P. rubens* individuals < 1.37m.

	Bear Rocks	**Cabin Mountain**	**Combined Sites**
Count	43	71	114
Mean Height (cm +/- SD)	66.79 +/- 34.77	41.27 +/- 29.41	50.90 +/- 33.76
Max Height (cm)	131	119	131
Min Height (cm)	12	2	2
Median Height (cm)	66	35	45
Mean DGL (mm +/- SD)	15.66 +/- 9.90	14.24 +/- 11.05	14.77 +/- 10.61
Max DGL (mm)	46.35	49.09	49.09
Min DGL (mm)	3.11	1	1
Median DGL (mm)	14.04	11.82	12.29

Tall shrub cover was limited at both sites, although found more extensively at Bear Rocks. Tree cover includes *P. rubens*, and so plots with a higher *P. rubens* count tend also to have higher tree cover. Statistical descriptions of all cover types were included in Tables 5.3, 5.4, and 5.5, along with stand distance, which is a linear measurement in meters, and density per hectare.

The number of plots containing *P. rubens* was highly variable, and ranged from 1 to 29 trees present per plot at Cabin Mountain and 1 to 25 trees present per plot at Bear Rocks (Table 5.3). Plots without *P. rubens* tended to have slightly higher coverage of subshrub and herbaceous vegetation (Table 5.3). Tree cover was a category of 5% or great coverage in 11 of 31 plots, with a range of 0 to 75% vegetated cover across all 31 plots. The median tree cover was 0, the mean cover was approximately 6%, with 1 SD +/- 14% (Table 5.3).

Table 5.3. *P. rubens* demographics assessment for all plots. Cover values (Rock, Subshrub, Herbaceous, Tall Shrub, and Tree Cover) are all measured in percent of area.

	Plots with no *P. rubens* present	Plots with *P. rubens* present (min 1)	Maximum *P. rubens* count*	Minimum *P. rubens* count^
Number of Plots	15	16	2	4
Max, Min Count	~	~	29	1
Mean Count +/- SD	~	10.25 +/- 10.61	~	~
Median Count	~	7.5	~	~
Range Count	~	28	~	~
Max, Min Count Density (per hectare)	~	~	1288.89	44.44
Mean Count Density (per hectare +/- SD)	~	455.56 +/- 471.56	~	~
Median Count Density (per hectare)	~	333.33	~	~
Range Count Density (per hectare)	~	1244.45	~	~
Max., Min., Range Rock	55%, 0%, 55%	65%, 0%, 65%	35%, 20%, 15%	65%, 0%, 65%
Mean Rock +/- SD	6.4% +/- 14.44%	24.69% +/- 16.34%	27.5% +/- 7.5%	27.5% +/- 23.58%
Median Rock	0%	20%	27.5%	22.5%
Max., Min., Range Subshrub	100%, 20%, 80%	95%, 0%, 95%	35%, 25%, 10%	95%, 0%, 95%
Min. Subshrub	20%	0%	25%	0%
Mean Subshrub +/- SD	64.2% +/ 28.25%	46.25% +/- 27.70%	30% +/- 5%	45% +/- 35.88%
Median Subshrub	75%	35%	30%	42.5%
Max., Min., Range Herbaceous	60%, 0%, 60%	40%, 0%, 40%	25%, 10%, 15%	15%, 0%, 15%
Mean Herbaceous +/- SD	23.4% +/- 22.10%	9.38% +/- 12.23%	17.5% +/- 7.5%	3.75% +/- 6.50%

Median Herbaceous	25%	0%	17.5%	0%
Max., Min., Range Tall Shrub	25%, 0%, 25%	75%, 0%, 75%	10%, 0%, 10%	75%, 0%, 75%
Mean Tall Shrub +/- SD	4% +/- 7.84	13.13% +/- 23.94%	5% +/- 5%	20% +/- 36.74%
Median Tall Shrub	0%	0%	5%	2.5%
Max., Min., Range Tree Cover	70%, 0%, 70%	25%, 0%, 25%	25%, 5%, 20%	5%, 0%, 5%
Mean Tree Cover +/- SD	5.33% +/- 18.07%	5.94% +/- 6.12%	15% +/- 14.14%	3.75% +/- 2.5%
Median Tree Cover	0%	5%	15%	5%
Max., Min., Range Distance (m)	250, 45, 95	145, 5, 140	55, 5, 50	80, 20, 60
Mean Distance (m +/- SD)	120 +/- 66.01	40.63 +/- 39.72	30 +/- 25	51.25 +/- 24.59
Median Distance (m)	95	27.5	30	52.5

* Represents the two plots that had the maximum number of *P. rubens*, 29 specimens.
^ Represents all plots that had the minimum number of *P. rubens*. In this case, there were four plots with only one *P. rubens* present.

Table 5.4. *P. rubens* demographic assessment for Cabin Mountain. Cover values (Rock, Subshrub, Herbaceous, Tall Shrub, and Tree Cover) are all measured in percent of area.

	Plots with no *P. rubens* present	Plots with *P. rubens* present (min 1)	Maximum *P. rubens* count*	Minimum *P. rubens* count^
Number of Plots	9	7	2	1
Max, Min Count	~	~	29	1
Mean Count +/- SD	~	14.14 +/- 12.76	~	~
Median Count	~	8	~	~
Range Count	~	28	~	~
Max, Min Count Density (per hectare)	~	~	1288.89	44.44
Mean Count Density (per hectare +/- SD)	~	628.51 +/- 567.11	~	~
Median Count Density (per hectare)	~	355.56	~	~
Range Count Density (per hectare)	~	1244.45	~	~
Max., Min., Range Rock	55%, 0%, 55%	40%, 15%, 25%	35%, 20%, 15%	20%, 20%, 0%
Mean Rock +/- SD	10.67% +/- 17.37%	27.14% +/- 9.95%	27.5% +/- 7.5%	20%
Median Rock	4%	20%	27.5%	20%
Max., Min., Range Subshrub	75%, 20%, 55%	65%, 25%, 40%	35%, 25%, 10%	60%, 60%, 0%
Mean Subshrub +/- SD	45.33% +/- 19.08	40% +/- 14.64%	30% +/- 5%	60%
Median Subshrub	43%	35%	30%	60%
Max., Min., Range Herbaceous	60%, 21%, 39%	40%, 10%, 30%	15%, 15%, 0%	25%, 10%, 15%

Mean Herbaceous +/- SD	39% +/- 14.34%	21.43% +/- 9.15%	15%	17.5% +/- 7.5%
Median Herbaceous	40%	20%	15%	17.5%
Max., Min., Range Tall Shrub	5%, 0%, 5%	10%, 0%, 10%	10%, 0%, 10%	0%, 0%, 0%
Mean Tall Shrub +/- SD	2.5% +/- 2.5%	1.43% +/- 3.78%	5% +/- 5%	0%
Median Tall Shrub	0%	0%	5%	0%
Max., Min., Range Tree Cover	70%, 0%, 70%	25%, 5%, 20%	25%, 5%, 20%	5%, 5%, 0%
Mean Tree Cover +/- SD	8.89% +/- 23.15%	8.57% +/- 7.48%	15% +/- 14.14%	5%
Median Tree Cover	0%	5%	15%	5%
Max., Min., Range Distance (m)	250, 60, 190	145, 5, 140	55, 5, 50	80, 80, 0
Mean Distance (m +/- SD)	152.22 +/- 63.51	60.71 +/- 48.73	30 +/- 25	80
Median Distance (m)	180	55	30	80

* Represents the two plots that had the maximum number of *P. rubens*, 29 specimens.

^ Represents all plots that had the minimum number of *P. rubens*. In this case, there was one plot with only one *P. rubens* present.

Table 5.5. *P. rubens* demographic assessment for Bear Rocks. Cover values (Rock, Subshrub, Herbaceous, Tall Shrub, and Tree Cover) are all measured in percent of area.

	Plots with no *P. rubens* present	Plots with *P. rubens* present (min 1)	Maximum *P. rubens* count*	Minimum *P. rubens* count^
Number of Plots	6	9	1	3
Max, Min Count	~	~	25	1
Mean Count	~	7.22 +/- 7.25	~	~
Median Count	~	7	~	~
Range Count	~	24	~	~
Max, Min Count Density (per hectare)	~	~	1111.11	44.44
Mean Count Density (per hectare)	~	320.89 +/- 322.22	~	~
Median Count Density (per hectare)	~	311.11	~	~
Range Count Density (per hectare)	~	1066.67	~	~
Max., Min., Range Rock	0%, 0%, 00%	65%, 0%, 65%	20%, 20%, 0%	65%, 0%, 65%
Mean Rock +/- SD	0%	22.78% +/- 19.74%	20%	30% +/- 26.77%
Median Rock	0%	20%	20%	25%
Max., Min., Range Subshrub	100%, 75%, 25%	95%, 0%, 95%	10%, 10%, 0%	95%, 0%, 95%
Mean Subshrub +/- SD	92.5% +/- 10.70%	51.11% +/- 33.81%	10%	40% +/- 40.21%
Median Subshrub	100%	60%	10%	25%
Max., Min., Range Tall Shrub	25%, 0%, 25%	75%, 0%, 75%	60%, 60%, 0%	75%, 0%, 75%
Mean Tall Shrub +/- SD	7.5% +/- 11.73%	22.22% +/- 29.17%	60%	26.67% +/- 41.93%

Median Tall Shrub	0%	5%	60%	5%
Max., Min., Range Tree Cover	0%, 0%, 0%	10%, 0%, 10%	10%, 10%, 0%	5%, 0%, 5%
Mean Tree Cover +/- SD	0%	3.89% +/- 4.17%	10%	3.33% +/- 2.89%
Median Tree Cover	0%	5%	10%	5%
Max., Min., Range Distance (m)	130, 45, 85	70, 5, 65	5, 5, 0	70, 20, 50
Mean Distance (m +/- SD)	71.67 +/- 30.78	25 +/- 20	5	41.67 +/- 20.95
Med. Distance (m)	55	20	5	35

* Represents all plots that had the maximum number of *P. rubens* found at Bear Rocks. One plot had 25 specimens.
^ Represents all plots that had the minimum number of *P. rubens*. In this case, there were three plots with only one *P. rubens* present.

Across all plots (Table 5.3), percent rock cover greater than zero was found more consistently in plots where *P. rubens* are present than plots where they are not. Although range of rock cover is similar (55% in plots with no *P. rubens* plots, and 65% in plots with *P. rubens*), average rock cover in the plots without *P. rubens* is ~6% by comparison to ~25% in plots with *P. rubens*. Of 12 plots with < 5% (reported as 0%) exposed rock coverage, 10 had zero *P. rubens* present. Only 15 plots had zero *P. rubens* present.

Spearman's Rank Correlation was used to compare correlation between one independent and one dependent variable, similar to a logistic regression (MacDonald, 2014). Using Spearman's Rank Correlation on all 31 plots, a Spearman's Rho value of 0.534 (moderate positive correlation, $p < 0.001$) was identified between presence of exposed rock cover and the count of *P. rubens* per plot. Rock was the dominant abiotic cover type, and so comparing the presence of *P. rubens* per plot with the percent of the plot dominated by rock cover contributes to answering Objective 3. Analyzing the same correlation at the site level, correlation between total rock cover

and count at Bear Rocks produced a Spearman's Rho of 0.605 ($p = 0.017$), and for Cabin Mountain, a Spearman's Rho of 0.519 ($p = 0.0395$).

Spearman's Rank Correlation on all 31 plots also uncovered a strong negative correlation (Spearman's Rho value of -0.698, $p < 0.001$) between the distance from the nearest stand and the count of *P. rubens* individuals in the plot. For Bear Rocks alone the Spearman's Rho was a conclusive -0.803 ($p < 0.001$) comparing stand distance and count, and for Cabin Mountain it was -0.701 ($p < 0.0025$). The stand distance measurement represents a gradient outward from a potential seed source. Tables 5.3, 5.4, and 5.5 also support the existence of a correlation between plot distance from the nearest stand and *P. rubens* count.

5.1.2. GLMM

Multiple candidate models were assessed using the biophysical dataset created from field- and DEM-derived variables. The final model revealed rock cover and stand distance to be significant biophysical factors associated with *P. rubens* count at a minimum of 95% confidence (Table 5.6).

Table 5.6. The final GLMM using glmmTMB. Shrubland and Woodland are categories of Physiognomic Class. The third category, Herbaceous, was automatically included as part of the intercept, and values of Shrubland and Woodland were generated relative to Herbaceous cover.

Variable	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	2.333651	0.995237	2.345	0.01904
Shrubland*	0.235273	0.847447	0.278	0.78130
Woodland*	1.376370	1.246687	1.104	0.26958
Rock	**0.061011**	**0.022405**	**2.723**	**0.00647**
Slope	-0.268753	0.160527	-1.674	0.09409
Stand Distance	**-0.033316**	**0.007564**	**-4.404**	**1.06e-05**
Flow Acc.	-0.001992	0.001774	-1.122	0.26172
Curvature	-0.362009	0.374246	-0.967	0.33339

AIC = 132.6, BIC = 147.0. * Categories of Physiognomic Class. The third category, Herbaceous, was automatically included as part of the intercept, and values of Shrubland and Woodland were generated relative to Herbaceous cover.

5.2. Plant Diversity Associated with *P. rubens* Seedlings and Saplings

Sixteen vascular species were identified in the paired plots assessments, excluding *P. rubens*. Although mosses, lichens, and graminoid species were present, they were not identified in at the species level, per plot. The most common identified vascular species by far was *Vaccinium angustifolium*, followed by *Osmunda cinnamomea*. These sixteen species represent seven families, the most common being Ericaceae (4), Rosaceae (4), and Lycopodiaceae (3) (Table 5.7). Mean cover varied widely and standard deviation from the mean was high for all species (Table 5.8).

Table 5.7. Vascular species identified in paired plots, their respective families (Strausbaugh and Core, 1978)

Species	Family	No. Plots (45cm Heath)	No. Plots (45cm Tree)	No. Plots (15cm Tree)
Vaccinium angustifolium	Ericaceae	26	29	20
Vaccinium corymbosum	Ericaceae	2	2	
Kalmia latifolia	Ericaceae	3	2	
Menziesia pilosa	Ericaceae	0	1	
Sorbus americana	Rosaceae	0	1	
Rubus hispidus	Rosaceae	9	9	6
Amelanchier laevis	Rosaceae	1	4	1
Photinia melanocarpa	Rosaceae	0	1	
Lycopodium flabelliforme	Lycopodiaceae	1	0	
Lycopodium obscurum	Lycopodiaceae	9	11	8
Lycopodium clavatum	Lycopodiaceae	2	1	
Pteridium aquilinum	Polypodiaceae	6	4	1
Dennstaedtia punctilobula	Polypodiaceae	4	3	2
Osmunda cinnamomea	Osmundaceae	9	11	4
Acer rubrum	Aceraceae	1	1	1
Oclemena acuinata	Compositae	1	2	1

Table 5.8. Descriptive statistics for 45cm radius paired plot values, heath (H) and tree (T). All values rounded to nearest 5% for cover estimate.

	Max Cover(H)	Mean +/- SD(H)	Max Cover(T)	Mean +/- SD(T)
Vaccinium angustifolium	85	35 +/- 20	70	25 +/- 15
Osmunda cinnamomea	40	30 +/- 20	80	25 +/- 20
Acer rubrum	5	~	5	~
Sorbus americana	~	~	5	~
Pteridium aquilinum	30	20 +/- 10	25	15 +/- 5
Lycopodium flabelliforme	5	~	~	~
Rubus hispidus	30	15 +/- 10	35	15 +/- 10
Lycopodium obscurum	30	10 +/- 5	25	10 +/- 5
Menziesia pilosa	~	~	10	~
Lycopodium clavatum	15	10 +/- 5	5	~
Dennstaedtia punctilobula	20	10 +/- 5	15	5 +/- 5
Amelanchier laevis	5	~	10	5 +/- 0
Oclemena acuinata	5	~	10	10 +/- 5
Vaccinium corymbosum	95	25 +/- 40	20	5 +/- 10
Photinia melanocarpa	~	~	5	~
Kalmia latifolia	80	30 +/- 30	10	5 +/- 5

I performed two assessments to compare significant differences in coverage across different rings of the plot. First, I conducted Wilcoxon tests to compare species and group coverage per plot in all 45cm heath plots and 45cm tree plots, and between 15cm tree plots and 45cm tree plots (Table 5.9). The former was to identify significant differences in vegetation species cover between the tree and heath plots under the same size conditions, and the latter was for assessing close spatial vegetation associations that may be indicative of positive plant interactions important at the seedling and sapling stages. Next, I conducted a Tukey HSD on the same two

datasets, to compare the difference between methods and results. All coverages represent areal percent, allowing for comparison between different sizes of the same plot type.

Table 5.9. Comparison of the Wilcoxon 2-Sample Normal Approximation values for each cover category. 45-cm radius heath and tree plots are compared (Heath-Tree Pairs, 45cm), and then 15-cm and 45-cm overlapping tree plots are compared (Tree-Tree Pairs, 45cm and 15cm).

Cover Type	Heath-Tree Pairs, 45cm – Wilcoxon Tests		Tree-Tree Pairs, 45cm and 15cm Wilcoxon Tests	
	Z	Prob > |Z|	Z	Prob > |Z|
Rock	1.0778	0.2811	**2.4594**	**0.0139***
Moss	1.0336	0.3013	-0.3265	0.7441
Lichen	0.8726	0.3829	1.0702	0.2845
Litter	-1.0689	0.2851	-0.5788	0.5627
Graminoid	**2.0256**	**0.0428***	**2.1610**	**0.0307***
Vaccinium angustifolium	-0.4455	0.6560	**3.0795**	**0.0021***

Based on a 2-Sample Test, normal approximation, for the tree-heath 45cm radius pairs, only the graminoid coverage group rejected the null hypothesis at 95% confidence (Table 5.9). The mean of graminoid group coverage was higher in the tree plots than the heath plots. Of the tree-tree pairs, the groups rock and graminoid both reject the null hypothesis at 95% confidence; the means of both groups were higher in the 45cm radius plot than the 15cm radius plot, suggesting less concentration of these coverages at the immediate base (15cm radius) of the tree.

When the same dataset was evaluated using a Tukey HSD comparison of means, there were small differences in the results. Graminoid cover differed between the heath and tree plots at 90% confidence instead of 95%, and was not significant between 45cm and 15cm radius tree pairs. Instead, rock cover between the 45cm and 15cm pairs differed significantly ($p = 0.033$) and was more expansive across the 45cm radius plot than within the 15cm subplot. This suggests

that rock cover across the 45cm radius tree plots was uneven at the base of the tree when analyzed with Tukey HSD. Mean *V. angustifolium* cover also differed with significance at the base of the tree, consistent with the Wilcoxon test values.

Table 5.10. Comparison of the Tukey HSD values for each cover category. 45cm radius heath and tree plots are compared (Heath-Tree Pairs, 45cm), and then 15cm and 45cm overlapping tree plots are compared (Tree-Tree Pairs, 45cm and 15cm). One standard deviation of difference is reported for each.

Cover Type	Heath-Tree Pairs, 45cm – Tukey HSD			Tree-Tree Pairs, 45cm and 15cm Tukey HSD		
	Difference	St. D	p-Value	Difference	St. D	p-Value
Rock	2.938	6.219	0.638	**11.406**	**5.225**	**0.033***
Moss	1.875	5.468	0.733	4.844	5.978	0.421
Lichen	2.188	4.169	0.602	3.094	4.186	0.463
Litter	8.031	5.720	0.165	5.937	5.537	0.288
Graminoid	4.375	2.333	0.066	3.969	2.568	0.127
Vaccinium angustifolium	4.406	5.175	0.398	**10.813**	**4.215**	**0.013***

5.2.1. RII

The community heterogeneity across the Cabin Mountain site presented a challenge for comparing vegetation types using the RII at this sample size, as the species present in each plot varied considerably over the study area (Table 5.7). The most consistently identified vascular species in the paired heath/tree plots was *V. angustifolium*.

Not all vascular species were present in all pairs. The RII was originally designed to compare a single common trait (Armas et al., 2004). Many pairs existed where the cover group of the test (e.g. *V. angustifolium*, rock cover, moss cover) was not present in both plots. Two categories were generated: Total RII, which included all pairs, including those in which a given group was

present in only one plot of the pair; and Adjusted RII, which only included pairs in which the group was present in both plots. The RII was conducted on both datasets (Total and Adjusted) to compare the difference, and results for each group were included in Table 5.11.

Table 5.11. The five cover groups and the most populous vascular plant, *Vaccinium angustifolium*.

Group	Total Pairs	Adj. Pairs	Total RII	Adj. RII
Moss	28	19	0.064 +/- 0.667	0.042 +/- 0.414
Graminoid	25	12	0.368 +/- 0.671	0.016 +/- 0.328
Rock	27	16	0.150 +/- 0.680	0.004 +/- 0.384
Lichen	30	23	0.079 +/- 0.596	-0.028 +/- 0.398
Litter	24	15	-0.078 +/- 0.696	-0.057 +/- 0.400
Vaccinium angustifolium	30	25	0.002 +/- 0.568	-0.117 +/- 0.409

All RII values in Table 5.11 are mean values with one standard deviation. RII has a range of -1 to +1, negative values conveying a negative interaction/association and positive values conveying a positive association. This positive association could suggest a facilitative relationship between the subject and the red spruce. Adjusted RII values were all close to zero at this sample size, using this method. There was a wide range for all values (Fig. 5.2).

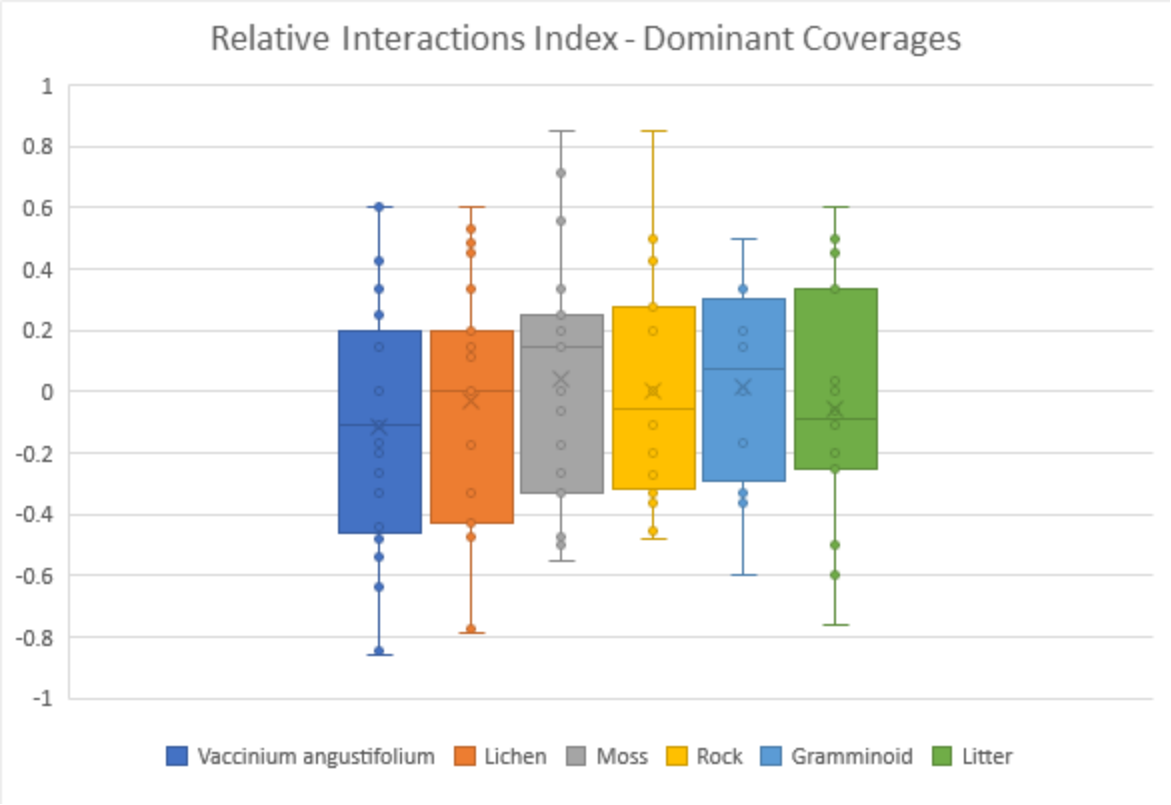

Figure 5.2. The adjusted RII of the five cover groups plus *V. angustifolium*. A positive value (between 0 and +1) suggests a positive interaction between the subject and the spruce, a negative value (between 0 and -1) suggests a negative association between the subject and the spruce.

5.2.2. Biodiversity

I calculated the Shannon-Weaver index and the Simpson's Diversity index for each 45cm tree and heath plot, and for all 15cm tree plots. *P. rubens* was not included in any diversity and richness assessments. The Shannon-Weaver and Simpson's Diversity index are alpha diversity measures that record species diversity within single plots. They can be compared among plots on the condition that measurement techniques were identical in all cases (McCune and Grace, 2002). Although often used to assess diversity of species abundance, in this study these indices were used to assess diversity of species cover. Cover was measured per the methods, with cover of each group estimated independently of other cover types. Diversity of cover is valid within our interpretation because the cover characteristics of the plots where *P. rubens* individuals are

or are not present is of interest, more so than the relative abundance of species. Only identified vascular plants were included in each calculation, excluding graminoids (which were not identified) and all bryophytes. As a result, some plots were unsuited for either of these indices, calculating either zero or one accordingly.

Table 5.12. Comparison of the Wilcoxon 2-Sample Test, Normal Approximation for the Simpson's and Shannon-Weaver alpha diversity metrics for the 45cm radius Heath-Tree pairs and the overlapping 15 and 45cm radius Tree-Tree pairs. For the Shannon-Weaver Index, higher values convey greater richness and evenness of a community. For the Simpon's Index, values range between 0 and 1, with 0 and 1 conveying a perfectly homogenous and a perfectly heterogeneous community respectively.

	Heath-Tree Pairs, 45cm – Wilcoxon Tests		Tree-Tree Pairs, 45 and 15cm Wilcoxon Tests	
	Z	Prob > |Z|	Z	Prob > |Z|
Simpson's Index	0.4585	0.6466	-0.4284	0.6683
Shannon-Weaver	0.9676	0.3332	3.5530	0.0004

A Wilcoxon test was also used to assess statistical difference between diversity of each tree and heath pair in thirty-two plots, and each pair of 15cm and 45cm tree plots. The difference between means of the Shannon-Weaver values were significant at 99% confidence between the 15cm and 45cm ring pairs, but the Simpson's values based on the same test, and means compared between the heath and tree pairs, were not reported as significant (Table 5.12).

For the 45cm paired heath and tree plots, I calculated beta diversity without a gradient (see McCune and Grace, page 31, citing Whittaker, 1972). Beta diversity metrics measure the diversity across a landscape. Graminoids were excluded, but all other vascular plants except *P. rubens* were incorporated.

$$(\beta_w) = (S_c / S) - 1 \qquad \text{Equation 2}$$

The average species cover richness for the heath plots was 2.5 (+/- 1.2 SD) compared to 2.7 (+/- 1.2) for tree plots. The beta diversity for each group was also similar at 4.3 (heath) and 4.6 (tree) respectively, and 5.2 when repeated for the entire dataset.

Chapter 6 – Discussion

6.1. Red Spruce Demographics at Cabin Mountain and Bear Rocks.

Several demographic differences existed between the two study sites. The *P. rubens* specimens identified at Bear Rocks were consistently taller and had larger DBH than the ones found at Cabin Mountain (Tables 5.1, 5.2). Heavy flagging was noted consistently at both sites and was most extreme in mature specimens nearest the sloping edge of the site (to the west at Cabin Mountain (Fig. 6.1), and to the east at Dolly Sods Wilderness area).

The Department of Geography at Virginia Tech, in collaboration with Canaan Valley National Wildlife Refuge, maintains and operates a weather station at the Cabin Mountain study site, which has reported dominant northwesterly winds and regular gusts between 60 and 90mph (unpublished data, Carroll, 2019). Flagging and deformation of trees has been examined as an indicator of wind direction and severity (Wade and Hewson, 1979). In *Picea abies* at alpine treelines, greater intensity of wind speeds has been shown to decrease biomass (Kăspar, 2017). Most plots at Bear Rocks were downslope of the edge (Fig. 5.1), in locations which may have provided shelter from the strongest winds. The plots at Cabin Mountain, however, were situated on the ridge top of the ridge and more exposed to high winds. Field observers at Cabin Mountain and near the eastern edge of Bear Rocks also noted long, trailing leaders on the red spruce, running low to the ground and occasionally through other vegetation or around large rocks. These are also growth forms consistent with wind stress (Telewski, 2012; Gardiner et al., 2016).

Snow data are unavailable at the Cabin Mountain site; however, over fifteen years of snow records from lower elevations in Canaan Valley indicate consistent annual winter snow values of at least 100 inches, with an average of 173 between 2001 and 2018 (unpublished data, Lesher, 2019). Anecdotal reports of drifting at Cabin Mountain and the Bear Rocks/Dolly Sods area

report massive drifts persisting into the summer months, but also that the last few decades have seen changes in drifting patterns correlated with changes in vegetation. Living snow fences are a snow management technique practiced to control drifting using live vegetation (Heavey and Volk, 2014), and both trees and shrubs may be incorporated into living fences (Laybourn-Perry, 2012). Differences in the heath community, such as the development of a taller shrub layer as found at Bear Rocks (Table 5.5) could potentially alter the landscape's relationship with snow insulation and snowmelt. The potential for a feedback between changes in the vegetation community and changes in the pattern of snow deposition and drifting on a landscape, particularly as it may relate to red spruce, is a matter worthy of further study.

Figure 6.1. Flagged red spruce on the edge of the west-facing slope on Cabin Mountain. Photo taken in April, 2018, before the start of fieldwork.

6.2. Biotic and Abiotic Interactions with Regenerating *P. rubens*

The existence of both facilitative and competitive interactions among plants is well-studied (e.g., Bertness and Callaway, 1994; Callaway, 2007; Brooker et al., 2008; Maestre et al., 2009; Ballantyne and Pickering, 2015), and studies on the relative increase in facilitative interactions with increasing abiotic stress, the stress gradient hypothesis, similarly has been a subject of intense research and debate (e.g., Brooker et al., 2002; Maestre et al., 2009; Michaelet et al., 2014). Facilitative affects may be species-specific, or may represent a more general relationship between specimens based on the ways they alter the site conditions in their immediate vicinities, such as any larger plant being able to provide shade or a windbreak (Callaway, 1998). Further, inanimate objects, such as rocks, have also been shown to be spatially associated with tree seedlings (Resler et al., 2005).

In this study, I used the Relative Interactions Index to identify associations between types of cover (e.g., rock, graminoid, *V. angustifolium*) and *P. rubens* of < 1.37m in height. The RII was chosen because it is a straightforward metric to apply and has been used successfully in assessing spatial associations from both field and experimental conditions (e.g., Taboada et al., 2017; Zhou et al, 2018; Gao et al., 2018). At the sampling resolution used in this study (32 pairs of 45cm radius plots 1m in distance apart), the RII values recorded no strong positive or negative associations between cover types and *P. rubens* (Table 5.11). A Wilcoxon test and a Tukey HSD were used to evaluate the significance of mean differences in cover. With the Wilcoxon, only graminoid cover varied significantly between heath and tree plots at a 45cm radius (Table 5.9), being more extensive in cover in tree plots than the open heath plot. This was not the case with the Tukey HSD, which did not find graminoid cover to be significant at 95% confidence. It is likely that given the resolution of the plots there are no overriding biotic (e.g., vascular plots,

bryophytes) or abiotic (e.g., rock) cover types that vary to a statistically significant degree ($p < 0.05$) between the heath and tree plots.

A slight negative (nonsignificant) association was uncovered between *P. rubens* and *V. angustifolium* (RII = -0.117 +/- 0.409). The Wilcoxon and Tukey HSD tests found no significant difference ($p > 0.05$) between *Vaccinium* coverage in tree and open heath plots at 45cm; however, field observations revealed almost no *P. rubens* specimens regenerating directly under or within dense *Vaccinium* vegetation. These observations of *P. rubens* occupying breaks in the shrub layer were corroborated by both the Wilcoxon and Tukey HSD tests comparing *Vaccinium* coverage between 45m and 15cm tree plots ($p < 0.05$, Table 5.9 and Table 5.10), which indicate that *Vaccinium* coverage within 45cm of the tree is concentrated beyond the first 15cm from the stem. Thick mats of *Vaccinium* are not conducive to successful germination by *P. rubens*. Plot species diversity, measured with the Simpson's Index and Shannon-Weaver Index, did not vary significantly among heath and tree plots (Table 5.12).

Figure 6.2. A specimen of *P. rubens* grows from between two boulders at Cabin Mountain. Other instances of this were catalogued while traversing both sites, particularly at the Dolly Sods Wilderness Area.

Though the RII did not uncover a strong positive or negative association between rock cover and *P. rubens* seedlings (RII = 0.004 +/- 0.384), general observations support the potential presence of nurse effects by boulders (e.g., Pérez, 2017; Bürzle et al., 2018; Fig. 6.2) and other vegetation (e.g., Carlsson and Callaghan, 1991; Llambí et al, 2018; Fig. 6.3). The significance of rock the role of rock cover as shelter and its benefits to subalpine vegetation communities is discussed in greater detail in section 6.3.1. As an alternative to conducting comparisons of cover in *P. rubens* and open plots, future work applying the RII in the field could focus on *P. rubens* alone, comparing specimens of *P. rubens* sampled haphazardly instead of randomly that are and are not associated with a specific feature of interest (i.e., *P. rubens* in the proximity of rock cover

by comparison to *P. rubens* that are some distance away from rock cover). This is similar to the method used by Taboada et al. (2017) in studying *Pinus pinaster* recovery after fire regimes.

Figure 6.3. (Left) A specimen of *P. rubens* is sheltered under a specimen of *Acer* spp., and another (right) performs the same service. These specimens were located on the northern edge of the Cabin Mountain site.

6.3.1. Biophysical Correlates of Red Spruce Establishment: Rock Cover and Spruce Count

Rock cover was found to be the most significant cover type related to *P. rubens* count in the red spruce demographic plots based on the GLMM. This finding is supported particularly in literature relating to tree regeneration in alpine ecotones (e.g., Resler et al., 2005; Resler, 2006; Pérez, 2009). Cabin Mountain demographic plots where red spruce was present featured an average of ~27% rock cover, as opposed to ~11% rock cover in the Cabin Mountain plots that had no red spruce (Table 5.4). At Bear Rocks, the six plots with no red spruce present each also

had no rock cover, by comparison to a mean of ~23% in plots with *P. rubens* presence (Table 5.5).

That rock cover was found to be associated with *P. rubens* counts at a broader (15m x 15m) resolution, but not at the finer resolution of the paired RII plots, was unexpected, but likely indicates that the scale-dependent nature at which rock cover is related to the presence of *P. rubens*, and calls for additional research. Nonetheless, rock cover is likely to provide some site improvements that benefit conifer seedlings at early life stages in harsh environments, as has been documented in literature from other locations. For example, rock cover has been associated with increased moisture availability for plants beneath boulders or in blocky soil (e.g., Pérez, 1991; Pérez, 2009), temperature regulation in alpine treelines (Greenwood et al., 2015), slope stabilization for vegetation (Pérez, 2017), and nurse cover features for seedlings after fire events (Coop and Schoettle, 2009). Fire events have been found to expose rock cover by burning away organic matter and litter (Stine and Butler, 2015), and rock features that retain moisture can support regeneration where more desiccated post-fire soils cannot. Periglacial blockfields present on both Cabin Mountain and at Bear Rocks were observed to retain water, to the benefit of surrounding vegetation (Fig. 6.4).

The benefits posed to seedlings by sheltering features, such as rock cover, must still be balanced with other needs of the seedling that those features could impede. Because of the shallow root system of *P. rubens* seedlings (e.g., Burns and Honkala, 2010; Walter et al., 2017) access to sufficient soil for germination could override the importance of other needs met by rock cover, increasing the distance between regenerating seedlings and sheltering rock features. Bürzle et al. (2017) found the common sheltering distances of *Rhododendron*, *Betula*, and *Abies* species to vary between one another and in different habitats along a forest-alpine treeline

ecotone, all the minimum distance in all cases was greater than 15cm, the minimum distance in our study. Thus, this research draws the important distinction between the point of germination for a seed relying on rock cover (as one might expect for concentrations within 15cm), and the presence of rock cover in the near vicinity of regenerating or long-established *P. rubens.* Additional research could endeavor to identify whether there exists a preferred distance from exposed rock, blockfields, or any sheltering features for *P. rubens* seedlings and saplings to regenerate successfully.

Figure 6.4. Photo taken in April, 2018, at Cabin Mountain shows a small, yellowed *P. rubens* specimen growing directly from a shallow soil bed amidst a suspected periglacial rock deposit that has retained meltwater from a prior snow.

6.3.2. Biophysical Correlates of Red Spruce Establishment: Stand Distance and Count

Distance from stand was found to be associated with the count of *P. rubens* specimens at each study area. This factor likely relates to gradient of seedling establishment from the stand edge, based on dispersal characteristics. There are two components of stand distance relevant to this discussion: the presence of seeds in a given location, and the ability of the seed to germinate and regenerate at the location where the seed is trapped. Using count as a measurement of *P. rubens* focuses on the second of those components, the distribution of regeneration instead of the distribution of seeds.

Shorter distances from a seed source (e.g., Dibble et al., 1999; Cavallin and Vasseur, 2009) and the prevalence of mature, seed-producing specimens already present in a location (Feoli, 2010) have both been shown to result in higher rates of establishment by vegetation, including *P. rubens*. Across all demographics plots, the median distance from stand at plots with no *P. rubens* present was 95m (mean 120 +/- ~66, see Table 5.3), and to plots with *P. rubens* the median distance was 27.5 (mean 40 +/- ~40, see Table 5.3). These numbers roughly correspond with research that has identified an approximate dispersal range of roughly 100 meters from the parent tree for *P. rubens*, with successful dispersal to greater distances being unlikely (e.g., Hughes and Betchel, 1997; Dumais and Prévost, 2007; Walter et al., 2017).

P. rubens seeds are wind-dispersed (Burns and Honkala, 1990), and the typical wind speed, consistency, and direction at each study site would therefore be relevant to understanding the distribution of spruce seeds beyond the stand and into the heath. Distribution of seeds can also depend on other landscape features in addition to distance from source, such as the shape of underlying surface features at seed trap locations (Reichman, 1984), and the size of soil and other “capture” particles relative to the diaspore (such as a *P. rubens* seed) (Chambers et al.,

1991). Though this study focused on the presence or absence of regenerating seedlings in the heath, future work could examine whether red spruce seeds are even present in the soil beneath dense *Vaccinium* mats. In the course of this research, almost no *P. rubens* seedlings were found to have germinated under heath vegetation.

Though research specifically examining the expansion of red spruce into upland heath is limited due to the novel nature of this ecosystem, we can look for roughly analogous research in the way that red spruce expands into clearcuts. Hughes and Betchel (1997) reported that while density of seed dispersal into montane and lowland clearcuts in Canadian spruce/fir forests decreased at distances greater than 30m, there was no discernable pattern in how distance impacted *P. rubens* regeneration in the clearcut. However, they proposed that the disconnect in their study between seed dispersal density and seedling establishment density in spruce could be a function of year-to-year variation in local conditions (weather events, wind patterns, other disturbance). Patterns of seed dispersal and regeneration could vary significantly across a regenerating gradient in any given season, confounding a short field season's capacity to capture a conclusive picture of regeneration patterns.

The successful dispersal of a seed does not necessarily ensure its germination, regeneration, or recruitment to a stand; *P. rubens* establishment may be limited by abiotic and biotic interactions, such as competition with shrubs, and site conditions where seeds fall. Byers et al. (2010) documented likelihood of spruce competition with *Rhododendron* spp, and this study. Further, several studies note that leaf litter may preclude seedling germination (e.g. Moore, 1917; Westveld, 1926, 1930, as cited in Baldwin, 1934; Burns and Honkala, 1990). Stine et al. (2011) found in the *P. rubens*-dominated cranberry bogs of Central Appalachia that the predominance of tree islands in the meadow-forest ecotone existed on hummocks, as opposed to hollows. By

contrast, some site factors can enhance the likelihood of red spruce regeneration. For example, shelter features, such as deadwood (e.g., Dumais and Prévost, 2007; Bürzle et al., 2018) and rock cover (Bürzle et al., 2018), can favor regeneration of seedlings that might otherwise desiccate or freeze when trapped in organic litter from the heath matrix on the open plateau. Work with tree islands and microtopographic features at alpine treeline ecotones (e.g., Marr, 1977; Holtmeier and Broll, 1992; Resler et al., 2005; Resler, 2006) has described the development of vegetation islands growing under abiotically stressful conditions, such as for lack of moisture and prevalence of damaging winds.

The advancement of the *P. rubens* stand must be studied with respect to the natural temporal resolution of both *P. rubens* itself and the biotic and abiotic factors constricting and facilitating its expansion. *P. rubens* seed crops are abundant and scarce based on a three- to eight-year cycle (Burns and Honkala, 1990), but other natural cycles may stifle advancement even in those high-seed years. This study found lower concentrations of *Vaccinium* cover within 15cm of *P. rubens* seedling stems (Table 5.9), suggesting higher seedling regeneration in gaps in the heath. Gaps in European heathlands are dependent upon natural senescence of the heath vegetation, and so the age of the heath can control the pace that colonizing species find success regenerating in these openings (Feoli, 2010; Mobaied et al., 2015). Once a gap in the heath appears, though, the order in which different colonizing species arrive to establish the new community has been shown to impact the success of late-comers to the gap (Körner et al., 2008), thus making the success of red spruce seedlings advancing into the heath a matter of precise timing. Further, the needs of a specimen change over its life cycle from seed to seedling to sapling and tree (Kambo and Danby, 2018); a microsite conducive to the germination of a seed may not meet the longer-term needs of a larger seedling or sapling (Fig. 6.5). Long-term point pattern analysis of regenerating *P.*

rubens, with consideration given to underlying microsite topography and shelter features, could expand on our understanding of how limited stands of *P. rubens* are guided by favorable conditions for expansion in upland heath.

Figure 6.5. A *P. rubens* specimen growing from an accumulation of sediment and suspected biocrust in a rock crevice.

6.4. Successional Trends in Central Appalachian Upland Heath Barrens

The stable persistence of heath ecosystems is dependent upon processes that facilitate the heath matrix while suppressing encroaching vegetation (Gimingham, 1972). Heath communities in parts of Europe are under active management to prevent woody encroachment and reforestation, including grazing and fire management (e.g., Mobaied et al., 2011; Mobaied et al., 2015). The physical legacy of heavy past use (Kepfer-Rojas et al., 2014, 2015, 2017), routine

disturbance such as fire (Bargmann et al., 2014), windthrow (Byers et al., 2010), biotic disruption (Canals and Sebastià, 2002), or natural limiting factors (Whittaker, 1956) are necessary to keep a heathland open and prevent tree canopy closure (Gimingham, 1972). If natural senescence of the heath over time results in gaps in cover upon which *P. rubens* can capitalize in the long term, the slow march of the stand across both Bear Rocks and Cabin Mountain is possible. This trajectory is presumed by Fortney and Rentch (2003).

It is likely that the return of the red spruce stand would have a significant impact on the community assemblage of the understory, and might displace the heath entirely. In the field, little vegetation grew at the base of *P. rubens*, particularly where tree cover was dense, movement through the stand was difficult, and light penetration was low. Studies of *Tsuga canadensis* found its presence to limit both diversity and productivity in its understory across an abiotic gradient by comparison to a control, suggesting it exerts a foundational influence on the biota of its immediate community (Martin and Goebel, 2013). Similarly, in studying understory communities of *P. rubens* forests, Dibble et al. (1999) proposed that the *P. rubens* more likely imposed control over the species in its understory, rather than the other way around.

The different ways in which climate change will impact ecosystems are variable and complex. Research into how best to model these impacts is continuously evolving (e.g., Feoli, 2010; Sormunen et al., 2011; Kongstad et al., 2012; Wylie et al., 2014). Holtmeier and Broll (2005) discuss the subsequent impacts on the treeline ecotone, which has been cited as a bellwether for climate change's impact on altitude (e.g., Smith et al., 2009), and advise that to think about how climate change will affect vegetation communities at altitude, we must also think about how they are impacted now. Treelines at an altitude that are dependent upon climate will still experience delay before shifting, based on the life cycle of the vegetation communities

involved (Holtmeier and Broll, 2005). If those treelines are not dependent upon climate, however, changes may be unpredictable, if they occur at all.

The ecotone separating the stand of *P. rubens* from the heath barrens at Cabin Mountain and Bear Rocks is not a climatic treeline, and exists within the context of a complex history (e.g., Allard and Leonard, 1952; Quenzel, 1965; Rentch and Fortney, 1997; Fortney and Rentch, 2003) and uncertain future. Moving forward, the scale of time over which climate change acts and the ecosystem responds will determine whether or not the red spruce and balsam fir forests of the pre-logging period will return. Because of the slow rate of *P. rubens* encroachment into the heath observed in the field, I propose that the more frequent disturbance regimes associated with the Anthropocene (Loudemilk et al, 2012; Asselin et al., 2006) – particularly fire disturbance, potentially increased drought – will prevent a full return to the former climax community. Ultimately, isolated populations of *P. rubens* that remain on mountaintops such as on Cabin Mountain will likely be replaced with a novel, more disturbance-tolerant community. Heath communities have been shown in some models to be resistant to temperature fluctuations, changes in atmospheric CO_2, and changes in water regimes (Kongstad et al., 2012); if these findings are also true for our study areas, heath is poised to persist on both plateaus.

6.5. Future Research

The work described in this report serves as a baseline for future research into the landscape interactions that are the context for regenerating red spruce stands in Canaan Valley's upland heaths. Many areas for future investigation have already been identified, both based on the results of analysis conducted here and field observations of patterns in the landscape. Additionally, there remain multiple biophysical and bioclimatic variables that warrant further research. These topics include:

- A study of soil depth, penetrability, and moisture along gradients from the edge of Cabin Mountain east to the *P. rubens* stand.
- An analysis of snow drift formation, lifespan, and spatial pattern around both study sites.
- A transect survey of vegetation ascending Cabin Mountain's west-facing slope to examine the impacts shaping the vegetation community as elevation increases.
- A transect survey of how flagging patterns change with distance across each study site.

Chapter 7 – Conclusion

Heaths represent a widely diverse biotic community that occupies a landscape niche, appearing under conditions of frequent natural disturbance (Canals and Sebastià, 2002; Måren et al., 2010; Fagúndez, 2013; Bargmann et al., 2014; Bargmann and Kirkpatrick, 2015), intensive historical disturbance (Kepfer-Rojas et al., 2014, 2015, 2017), or climatic conditions that limit the success of canopy closure (Whittaker, 1956; Gimingham, 1972). They also represent areas of recognized global biodiversity (Mobaied et al., 2016), and some examples of heath communities have been shown to be well-situated to succeed in the face of global climate change (Kongstad et al., 2012). The mountaintop balds and heath barrens of Central Appalachia occupy places both historically open and forested (Allard and Leonard, 1952), a condition that has been shown in boreal forests to indicate unstable and stable states controlled by local disturbance regimes (Asselin et al., 2006) Windthrow is the most common form of disturbance in this area (Byers et al., 2010), and strong winds were noted based on the patterns of flagging present at both sites (Wade and Hewson, 1979).

In examining the encroachment or return of *P. rubens* to these heathlands following historical overuse, I have identified that distance from stand and relative surrounding coverage of rock (periglacial blockfields) were associated with a higher count of red spruce in a given plot. I did not identify strong facilitative or competitive effects occurring between *P. rubens* seedlings and specific nearby vascular species, or other biotic or abiotic cover types within 45cm, but noted that seedling *P. rubens* very rarely were present under areas of dense Ericaceae cover. I posit that at the forest-heath ecotone, the rate of *P. rubens* advance into the heath is slow and tenuous, and that the time it would take for it to expand fully into these open landscapes is by no means guaranteed in the face of a globally changing climate.

Chapter 8 – Citations

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Appendix A

Table 1a. Summary of Cabin Mountain Plot Characteristics.

Plot	Vegetation Type	Hydrology	Disturbance	Count	Elevation (m)	Dominant Aspect
CM02	Herbaceous	Dry	Deer trails	0	1222.33	Southeast
CM04	Herbaceous	Dry	Deer scat	0	1230.2	Southwest
CM05	Dwarf shrub	Dry	Deer trails, scat, insects	0	1229.55	Southeast
CM06	Herbaceous	Somewhat Moist	Deer trails, scat, insects	28	1232.78	Southwest
CM08	Woodland	Dry		0	1231.88	South
CM13	Dwarf shrub	Somewhat Moist	Deer trails, wind	1	1232.08	Southwest
CM14	Dwarf shrub	Saturated	Deer trails	8	1233.25	Southwest
CM16	Dwarf shrub	Somewhat Moist		29	1233.55	Southwest
CM17	Dwarf shrub	Dry		2	1231.9	West
CM18	Herbaceous	Dry	Deer trails, wind	0	1233.31	Northwest
CM20	Dwarf shrub	Somewhat Moist		2	1233.19	South
CM22	Woodland	Somewhat Moist	Deer trails	29	1225.71	Southeast
CM23	Herbaceous	Dry	Deer trails	0	1229.46	Northwest
CM24	Dwarf shrub	Dry		0	1231.31	Northwest
CM26	Dwarf shrub	Somewhat Moist	Deer trails	0	1224.43	Northeast
CM29	Dwarf shrub	Somewhat Moist	Deer trails, scat	0	1223.69	North

Table 2a. Summary of Bear Rocks Plot Characteristics.

Plot	Vegetation Type	Hydrology	Disturbances	Count	Elevation (m)	Dominant Aspect
BR01	Dwarf shrub	Dry	Trails/roads	2	1215.1	South
BR02	Dwarf shrub	Somewhat Moist	Trails/roads	10	1214.24	Southwest
BR03	Shrubland	Somewhat Moist	Deer trails	0	1210.87	West
BR04	Shrubland	Somewhat Moist	Deer trails	0	1208.31	West
BR05	Shrubland	Somewhat Moist	Deer trails, scat, human trash	1	1206.48	West
BR06	Shrubland	Somewhat Moist	Trails/roads, deer trails	9	1198.01	West
BR07	Shrubland	Somewhat Moist	Deer trails, scat	9	1216.17	Northwest
BR08	Shrubland	Somewhat Moist		1	1198.7	West
BR09	Shrubland	Dry		7	1216.96	South
BR10	Dwarf shrub	Moist	Deer trails	1	1203.25	West
BR11	Dwarf shrub	Moist	Deer trails, insects	0	1214.73	South
BR12	Dwarf shrub	Saturated	Deer trails, scat	0	1210	South
BR13	Dwarf shrub	Dry	Deer trails	0	1200.73	Southwest
BR14	Dwarf shrub	Moist		0	1210.72	Southwest
BR15	Shrubland	Somewhat Moist		25	1205.67	West

Appendix B

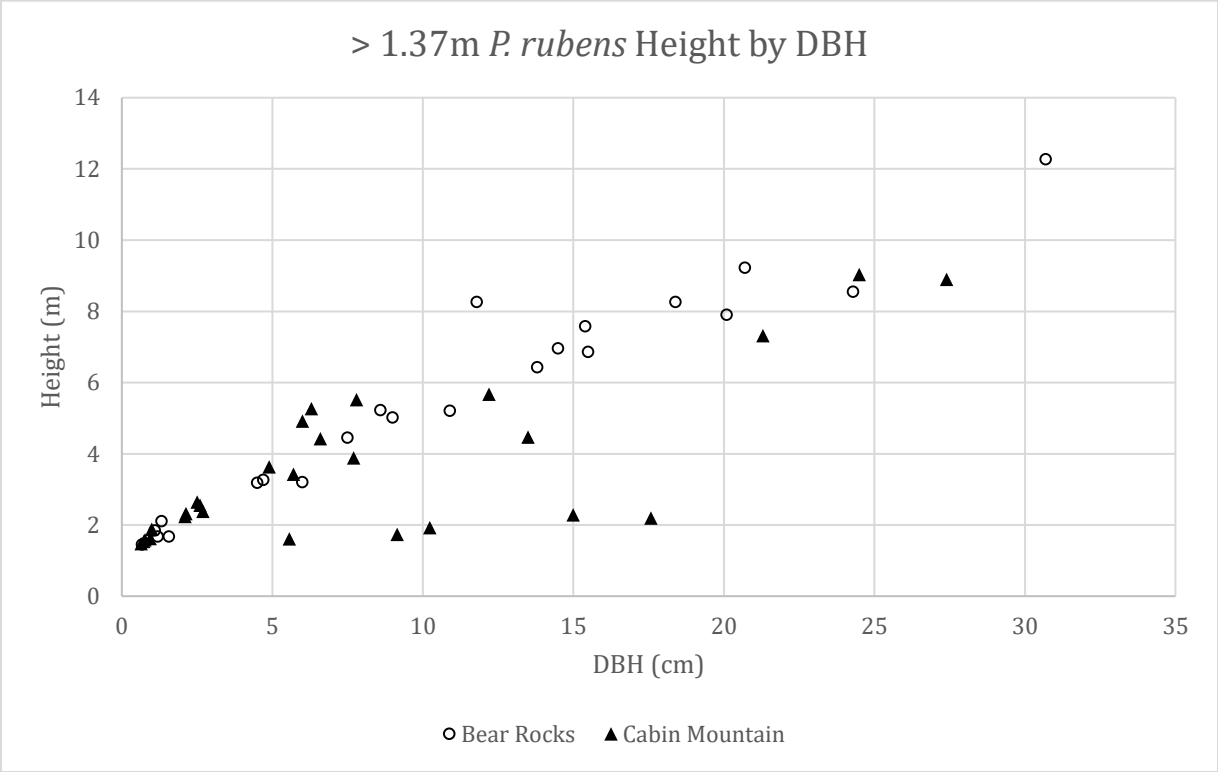

Figure 1b. Comparative height (m) and diameter at breast height (DBH, cm) of all *P. rubens* specimens of greater than 1.37m tall at both sites.

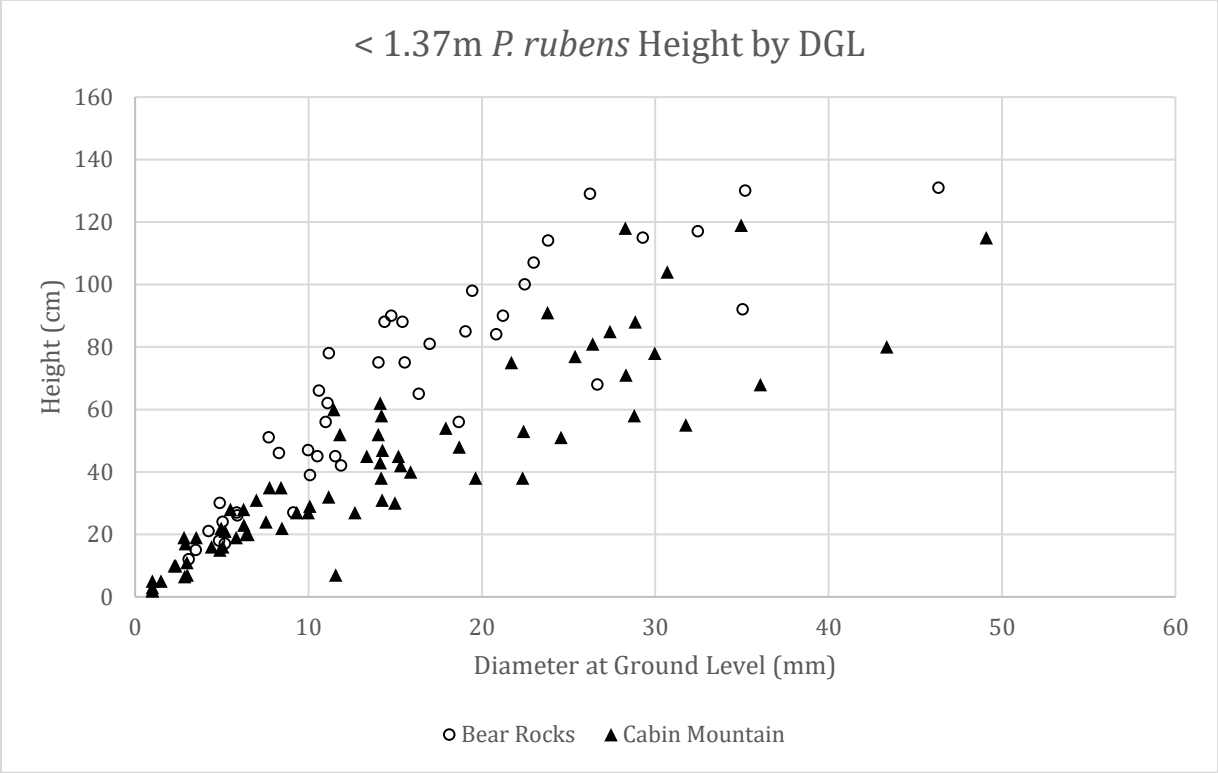

Figure 2b. Comparative height (cm) and diameter at ground level (DGL, mm) of all *P. rubens* specimens at both sites that were shorter than 1.37m high.