SPATIAL PATTERN ANALYSIS OF TREE SPECIES DISTRIBUTION IN A CENTRAL APPALACHIAN UPLAND HEATH BARREN

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ABSTRACT

The spatial pattern of plants reflects biotic and abiotic factors, including interactions with surrounding environmental conditions and other plants. Appalachian heath systems are presently understudied regarding spatial point pattern research, despite representing a unique and biologically valuable ecosystem. In this study, we characterized the spatial pattern of three tree species distributions in the upland heath barrens on Cabin Mountain in Canaan Valley, West Virginia through fieldwork, statistical modeling, and the use of geographical information systems (GIS). The research objectives were to: 1) quantify the global and local spatial patterns of trees to infer biotic process, and 2) identify how tree spatial pattern varies with selected biophysical variables, including ground curvature and topographic wetness index, to understand potential relationships between ambient conditions and spatial pattern. The spatial statistics, Ripley's K-function and nearest neighbor analysis, presented a series of different interaction types reflected across size-growth classes and species where the null hypothesis was rejected for some pairs and supported in others. The selected biophysical variables had no significant relationship to spatial pattern at the site. These findings suggest a range of both intraspecific and interspecific interactions are taking place in the heath barrens of Cabin Mountain, where significant levels of facilitation are occurring among encroaching red maple and striped maple, while red spruce is in competition with both species of maple, and that relationships are formed outside the influence of topographic characteristics of the site.

Spatial Pattern Analysis of Tree Species Distribution in a Central Appalachian Upland Heath Barren

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GENERAL AUDIENCE ABSTRACT

The spatial pattern of plants reflects relationships between individual plants or groupings of plants, as well as interactions with surrounding environmental conditions. Appalachian heath barrens are presently understudied in regard to spatial point pattern research, despite representing a unique and biologically valuable ecosystem. In this study, we characterized the spatial pattern of three tree species in the red spruce heath barrens on Cabin Mountain in Canaan Valley, West Virginia through fieldwork, statistical modeling, and the use of geographical information systems (GIS). The research objectives were to: 1) quantify demographics and the spatial pattern of trees to assess for ongoing plant interaction, and 2) understand whether tree spatial pattern is affected by selected biophysical variables, including ground curvature and topographic wetness index, to understand potential relationships between environmental conditions and spatial pattern. The results suggested a range of interactions were occurring across the plot, intraspecies, different species-pairs, and size-growth classes. Most notably, encroaching striped and red maple species had a positive relationship, while red spruce and both maple species had largely competitive relationships. Both topographic wetness index and ground curvature had no significant relationship to spatial pattern at the site. These findings suggest many types of interactions are taking place on Cabin Mountain, both among the trees and the environmental characteristics of the site. This finding indicates that it is possible this historical environment, red spruce heath barren, is being converted into deciduous forest and that interactions are shaping this conversion. a range of both intraspecific and interspecific interactions are taking place in the heath barrens of Cabin Mountain, indicating the possibility of conversion from red spruce heath barrens to deciduous forest, that this pattern is formed outside the influence of topographic characteristics of the site.

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CHAPTER 1: PROBLEM AND INTRODUCTION

Biogeography is a science of synthesis that emphasizes understanding of the spatio-temporal patterns of biodiversity (Ebach and Humphries 2003; Grehan 1993). Knowledge of how abiotic and biotic factors interact to create heterogeneity in spatial patterns of plants and animals is a central theme in the field of biogeography (Cowell and Parker 2004). Landscape ecology in particular, the study of ecological processes over broad spatial scale, has emphasized how ecological and environmental processes work together to produce spatial heterogeneity (Turner 1989).

Spatial pattern analysis examines the physical distribution of individuals in a community, typically represented as points, to uncover the existence and define the nature of its spatial pattern (Haase et al. 1995). A common goal of spatial pattern analysis in ecological research is to elucidate underlying processes that shape distributions (e.g. Wiegand and Moloney 2013). Some patterns exist in response to biological feedback resulting from interactions between the abiotic and biotic elements of a plant's environment, and persist until a specific threshold is surpassed, such as across gradients of abiotic stress (Alados et al. 2017). Pattern-process relationships have been studied in a range of environments, including semi-arid shrubland and marine ecosystems, to high elevation treeline ecotones (Bertness and Callaway 1994; Allen and Walsh 1996; Haase 2001).

Researchers have developed a variety of statistical methods and field techniques to accurately assess process and define pattern. Typically, in spatial pattern analysis, the goal of analysis is to distinguish random from non-random distributions, and to infer the influence of ecological processes on pattern (Haase 1995). One example of a second-order statistical analysis method commonly used by plant ecologists is the Ripley's K-function. Ripley's K-function is a density function, assessing variance between point-to-point distances and interpreting distribution patterns based on random or non-randomness (Haase 1995; Wiegand and Moloney 2013). The location of each plant can be collected manually, through fieldwork, or remotely, using high-resolution satellite imagery. A radius is drawn around an individual tree, and plants within the radius are counted, generating an isotropic cumulative count of the points within the circle from distance 0 to *t* (Fortin et al. 2014). The actual number of plants within the radius is assessed against a simulation of randomly distributed points in a set radius, to derive the function K(r), which represents an expected number of points within a portion of the radius divided by the intensity of the actual pattern (Wiegand and Moloney 2013). The comparison of actual pattern and simulated random pattern is a function frequently utilized in spatial statistics, such as in pair correlation function, O-ring statistic, and nearest neighbor analysis (Wiegand and Moloney 2013).

Statistics such as these have been used in a range of studies, many focusing on relationships between plants in ecosystems in transition. Such transitions can be from natural shifts in environmental conditions, like those found at ecotones, or from environments under a novel pressure, or both (e.g, Harper et al. 2011). For instance, Dearborn and Danby (2020) quantified degrees of tree clustering using a Ripley's K(t) statistic across different elevations, and slope aspects and angles, using satellite imagery of treelines in subarctic Canada. Here, researchers noted that increasing global temperatures are expected to advance treeline position upward and poleward, making spatial analysis of treelines highly relevant to understanding under what conditions these shifts will occur (Dearborn and Danby 2020). Parallels can be found between this work and spatial pattern analysis of rare and vulnerable ecosystems and plants, such as in threatened heathland systems around the world (Ramsay and Fotherby 2007).

Globally, heathland is characterized by ericoid shrubs and sparse low-nutrient, acidic soils, though many different types of heathland exist (Gimingham 1972; Fagúndez 2013). While many types of heathland require human intervention to persist, montane heathland is considered a natural heath in that exposure to high winds and low temperatures prevent tall shrub, and usually, tree growth (Heathland and Moorland). Heathlands are typically populated by specialist species, adapted to a narrow range of environmental conditions, and highly complex interspecific interactions (Fagúndez 2013). In this context, it is important to understand underlying spatial heterogeneity and patterns of plant distribution, for the maintenance of biodiversity and species richness in this vulnerable ecosystem (Mobaied et al. 2016).

The upland heath barrens of Central Appalachia have been shaped by a long land use history (Byers et al. 2010). The presence of heathland in the region emerged as both a natural result of harsh conditions at high elevations and herbivorous mammalian grazing before significant human disturbance on the land, and later as a response to the extensive disturbance caused by European settlement (Allard and Leonard 1952; Weigl and Knowles 1995). Since the 1880s, disturbance from agricultural land use, logging, and fire has intimately shaped the characteristics of these systems (Mueller 1992). Regionally, repeated fires from industrial logging and railway construction beginning in 1884, dramatically altered local soil and species composition (Allard and Leonard 1952; Byers et al. 2010). Prior to the arrival of pulp and paper mills in nearby Davis, WV, and the subsequent construction of the railroad, the region was covered in extensive old-growth spruce forest (Adams and Stephenson 1989). Due to the establishment of industry, fire was able to reach and consume thick layers of biomass, accumulated over thousands of years from the presence of red spruce on the landscape (Byers et al. 2010). The deep layers of humus that once sustained vast coniferous forest were dried out, leaving much of land to erode down to bedrock in the wake of the expansive fires (Allard and Leonard 1952). This era of logging ended by 1924, leaving behind an ecosystem forever altered by the decimation of hundreds of thousands of acres of red spruce forest and the destruction of the high quality soils that characterized the species composition and microclimate of the once old-growth forest (Allard and Leonard 1952; Fortney and Rentch 2003).

Post-disturbance, the land where vast red spruce forests once persisted throughout Canaan Valley was converted to grassland, heath, and deciduous forest (Fortney and Rentch 2003). Red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*), found in the landscape as a remnant of the tundra vegetation that once dominated the area during the Pleistocene glaciation (12,500 y.a.), are slowly re-establishing in the heathland, where the environment is more similar to their historic growing conditions (Allard and Leonard 1952; Byers et al. 2010). In more recent history, heathlands have been susceptible to the effects of climate change, such as rising average temperatures, increased nitrogen deposition, and pollution, (Schirmel et al. 2010; Fagúndez 2013). Additionally, in the Netherlands, England, and Central Appalachia, land-cover change from heath to woody vegetation and scrub has characterized some heathlands, hastening the conversion of high elevation heathland into deciduous forest (Rose et al. 2000; Sowerby et al. 2005; Byers et al. 2010).

The upland heath barrens of central Appalachia are a system of particular interest for studying spatial point-patterns related to biotic interaction due to their unique land-use legacy and environmental characteristics. Patterns of tree establishment and interaction in the heathland of Central Appalachia are especially of interest, given the rarity and vulnerability of these ecosystems, and the rich historical context of red spruce on the landscape.

The purpose of this study is to characterize spatial patterns of tree species distributions in an upland heathland near Canaan Valley, West Virginia, and to elucidate abiotic and biotic processes underlying observed patterns. To accomplish this goal, I used a detailed field survey and remotely sensed spatial imagery. Specifically, our objectives were to:

1. Quantify demographics and spatial pattern of red spruce, red maple, and striped maple in the high elevation heathland barrens of Central Appalachia to infer biotic process through spatial pattern analysis and fieldwork, and;
2. Identify how tree spatial pattern varies with selected biophysical variables, including climatic conditions such as solar radiation, as well as topographic features such as shrub cover and height, ground curvature, to understand potential relationships between ambient conditions and spatial pattern.

Spatial research in the heathland of Central Appalachia would be both a useful and novel contribution to the broader literature focused on global heathland and spatial point pattern analysis. A vast majority of research performed in heathland occur in Europe, with comparatively few studies focused on North American heathland (Fagúndez 2013). This study would be one of the first to utilize point pattern analysis to study tree encroachment in Central Appalachia, laying the groundwork for further research to occur in this understudied system. Furthermore, the methodology of this study will revolve around detailed field collection, including descriptions of species and tree morphology for each tree, that will inform species specific patterns of tree encroachment. Given the unique and changing nature of this ecosystem, it is highly pertinent that research with the potential to envision the future of this system is carried out.

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CHAPTER 2: LITERATURE REVIEW

2.1 Heath Barrens and Land Use

Heathlands are ecosystems dominated by dwarf ericoid species where tree and tall shrub cover are sparse or completely absent (Gimingham 1972). A variety of heath-types occur globally, typically within maritime climatic conditions, but those in Central Appalachia (often referred to as Heath Barrens, e.g. Vanderhorst 2020) are unique in that they occur under various forest types, and under cool, humid conditions at elevations above 1,220m (Whittaker 1963). Heathlands are typically characterized by, though not limited to, species from the family Ericaceae such as mountain laurel (*Kalmia latifolia*), minniebush (*Rhododendron pilosum*), great rhododendron (*Rhododendron maximum*), azaleas (*Rhododendron* spp.), blueberries (*Vaccinium* spp.) and huckleberry (*Gaylussacia* spp.) (Mueller 1992). In Central Appalachia, trees can be found growing among ericaceous shrubbery. Some trees are relicts from previous climatic eras, such as red spruce (*Picea rubens*), while others are resultant from deciduous encroachment upon heathland, such as red maple (*Acer rubrum*) and striped maple (*Acer pennsylvanicum*). Soils are typically thin, sparsely nutritious, and highly acidic podzols (Whittaker 1963).

Heathland can originate by, and be maintained by, both anthropogenic and non-anthropogenic factors, including human-mediated disturbance and management, natural disturbance regimes, and the influence of a range of environmental factors that sometimes prevent canopy vegetation (such as trees) from proliferating (Gimingham 1972; Webb 1998). For heath barrens in Central Appalachia, a combination of natural disturbance, low temperatures, high winds, and high exposure to solar radiation, with anthropogenic disturbance (i.e., livestock, grazing, and fire) has prevented the encroachment of deciduous trees (Byers et al. 2010). Ericaceous shrubs also effectively inhibit tree establishment through the reduction of soil quality, creation of a thick layer of duff that causes seed or seedling desiccation, and blocking of light (Pipkin 2011). When trees do manage to establish in heath barrens, their growth is often stunted by drought stress (Mallik and Kravchenko 2018).

2.2 Tree Encroachment in Appalachian Heathlands

Red spruce is a coniferous tree, remnant from the Wisconsin glaciation of North America. It is found at high elevations in Central and Southern Appalachia, on the ridges and peaks of mountains (Adams et al. 2010). The range of red spruce extends from western North Carolina, USA, northward to central Quebec and New Brunswick, Canada (Adams et al. 2012). Close to the southernmost portion of its range in West and southwestern Virginia, red spruce is found in disjunct populations restricted to elevations above 915m heathland in West Virginia, and 975m in southwestern Virginia (Adams et al. 2010). While red spruce once dominated the landscape at elevations <500m during Wisconsin glaciation (9,500 y.a.), climatic warming restricted its range, allowing deciduous forest to take over where red spruce was lost (Watts 1979). After extensive human disturbance from industrial logging, their range and migration capacity was further reduced, leaving red spruce stands in this region constrained to geographically fractured ‘sky islands’ (White 2019). In the West Virginia highlands, old-growth spruce-fir and hemlock forest once dominated vast swaths of north-west West Virginia as recently as the late 1800s. It was from these mixed conifer forests that deep, moist layers of humus were able to form from the massive accumulation of organic matter, which, once dried, created an ideal fire fuel (Allard and Leonard 1952). Fires ignited by a combination of the railroad activity and mass-logging repeatedly scorched thick, ancient layers of soil for decades, even after logging ended in Canaan Valley in 1924, and led to declines in the remaining red spruce that had not been clear-cut (Fortney and Rentch 2003). Post-disturbance, the land where vast red spruce forests once persisted throughout Canaan Valley was converted to grassland, heath, and deciduous forest (Fortney and Rentch 2003). Hardwoods rapidly replaced spruce-fir cover, and today make it difficult for re-establishment of red spruce in the mid-elevation and lowland regions (Fortney and Rentch 2003).

The encroachment of red spruce into these Central Appalachian heath barrens has significant implications for both the regeneration of red spruce and the continued existence of heathland in this region. For red spruce, rates of seedling germination and survival are dependent upon the vegetation stratum into which tree encroachment occurs, suggesting ericaceous vegetation here impacts recruitment of red spruce (George and Bazzaz 2003). The low quality soils of heathland are typically successful in suppressing the growth of certain deciduous species, but can serve as refugia for this Pleistocene relict (Byers et al. 2010), where competitive stress from deciduous stands is less present (Mobaied et al. 2015 However, as more seed-bearing non-heath species, such as maple (*Acer spp*.), establish in heathland and rates of encroachment subsequently increase, the characteristics that define the heath are subject to intense change that could modify the nature of the ecosystem (Körner et al. 2008; White 2019).

Observations in Canaan Valley suggest a range of tree species have the potential to, and are currently encroaching on heathland, red spruce being among them (Byers et al. 2010; White 2019). Species known to mix with high elevation red spruce forest that border heath in high elevation plateaus of the Allegheny Mountains are yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), black cherry (*Prunus serotina*), and eastern hemlock (*Tsuga canadensis*) (Rentch et al. 2007). Trees documented in the heathland of Cabin Mountain include species of maple (*Acer spp.*), specifically red maple (*Acer rubrum*) and striped maple (*Acer pennsylvanicum*), mountain ash (*Sorbus Americana*), and balsam fir (*Abies balsamea*) (White et al. 2019). Maple species, in particular red maple, are highly adaptive generalists, known to grow in areas with highly acidic soils that have experienced disturbance (Abrams 1998).

2.3 Spatial Pattern and Process

The spatial pattern of an ecological community is understood as the structural placement, distribution, and arrangement of organisms within a given spatial scale (Gustafson et al. 1998). In this context, processes are considered to be the interactions between abiotic and biotic elements in the environment that bear influence over the arrangement of structure. For example, as conditions change along altitudinal gradients in subalpine and alpine plant communities, interactions shift from competition at lower elevations to facilitation at higher elevations (Callaway et al. 2002). Defining connections between scale-informed pattern and ecological process has long been a goal of landscape ecologists and biogeographers, because the spatial distribution of organisms in the landscape can reveal significant information about underlying processes in the system (Turner 1989; Grehan 1993). For example, the spatial distribution of a species may change in response to the invasion of an exotic species, and understanding how certain factors covary with spatial pattern can lead to projections on how the invasive species will move throughout the community (Levine et al. 2000).

Although research on tree pattern in heathlands is scarce, many examples exist whereby researchers have used spatial pattern analysis at other ecotones. Analysis of treeline pattern at alpine treelines, for example, has been particularly useful in understanding shifts in tree distribution at forest-tundra ecotones coinciding with the effects of global change. In such studies, the interplay between site-specific abiotic and biotic factors, climatic trends, and tree pattern was of interest for the purpose of understanding if tree establishment at the boundary reflected an ongoing pattern of encroachment into tundra or vice versa, and the mechanisms behind these patterns (Aune et al. 2011; Harper et al. 2011; Dearborn and Danby 2020). Methodology surrounding spatial point pattern analysis (SPPA) in these studies often involved a combination of field data collection of tree-level characteristics, statistical analyses, and the use of spatial software and imagery (e.g., Aune et al. 2011; Wang et al. 2012; Conway and Danby 2014; Dearborn and Danby 2020). A consistent theme throughout research of tree pattern at ecotones is that local conditions bear a significant influence over heterogeneity of pattern across all sampled plots, suggesting microsite characteristics are vital to telling the spatial story of treeline ecology. For example, Wang et al. (2012) found discrepancies among both the clustering of trees of different life history classes, and clustering of those trees at sites with different microsite availability at the Smith fir treeline on the Tibetan plateau.

There are significant limitations to performing SPPA. Distinguishing between the influence of second-order effects (e.g., plant-plant interaction), and first-order effects (e.g., large-scale environmental heterogeneity) can be challenging, as both may result in a similar emergent pattern and both types of effects typically interact (Wiegand and Moloney 2004; Bolibok 2008).

2.3.1 Biotic Interactions

Plant interactions, which underlie vegetation pattern, are critical in community development and organization, and encompass a range of ecological functions (Brooker et al. 2008). The relationships among plants can be classified as negative (competitive) or positive (facilitative), and then further broken down into direct and indirect interactions. How a relationship is defined depends on a plant's response to other individuals in the community amidst a struggle for resource acquisition and is heavily influenced by the conditions of their environment. Competition describes an interaction in which one individual is disadvantaged by the effects of another (Callaway 1997), while facilitation represents a relationship between plants in which one or both are reaping some benefits from the other individual (Bertness and Callaway 1994). In both interactions, a defining component is whether the ability to acquire certain resources is negatively or positively affected by the characteristics of another plant.

Either of these interactions can be indirect or direct. Direct interactions can be seen when plants, such as the cushion plant of the Patagonian Andes, aid in the generation of habitable microsites for another plant (Cavieres et al. 2002). This can involve the amelioration of temperature, water and nutrient availability, and physical protection from harsh environmental conditions like wind (Cavieres et al. 2002; Resler et al. 2005). An individual can also benefit indirectly from the shade of another plant's leaves, or the dilution of consumer pressure in a dense cluster of other plants (Bertness and Callaway 1994). In vegetated environments, the nature of these interactions plays an important role in structuring ecosystems. Stress can manifest in a number of ways, and the methods by which plants combat this stress can be highly varied. Ultimately, the resulting biotic interaction relies heavily upon the stress tolerance and competitive ability of the species in question (Maestre et al. 2009).

Abiotic conditions and biotic interactions bear dual responsibility for shaping the species composition, biodiversity, and spatial structure of a community. For example, increased nitrogen deposition in the soil can generate a more hospitable environment for competitive plant species, thereby increasing its dominance (Brooker 2006). This dominance from the competitive plant species can, in turn, lead to a decline in biodiversity or the loss of particular species (Brooker 2006). How another member of a community is outcompeted will be specific to both the competitor species and the outcompeted species, as well as the conditions of their environment (Brooks 2003). Interspecific plant interactions also play an important role in altering community response to global change, just as global change plays an important role in altering the nature of interspecific interactions (Brooker 2006). Inversely, conditions amenable to higher levels of facilitation can support the proliferation of exotic species (Llambí et al. 2018).

Multiple theories have arisen in the past 15 years regarding the frequency of varying biotic interactions throughout an ecosystem (Soliveres and Maestre 2015). One hypothesis proposes that biotic interactions trend towards facilitation along a gradient of increasingly “stressful” abiotic conditions, defined as the stress gradient hypothesis (SGH) (Bertness and Callaway 1994; Maestre et al. 2009). This concept is illustrated by broad scale research in montane ecosystems, where the SGH is studied occurring along elevational gradients, with higher levels of facilitation occurring at harsher conditions in higher altitudes (Callaway et al. 2002; Choler et al. 2001). This indicates that plants at lower elevations are mainly limited by resource availability, making competition with other plants a more advantageous response than facilitation. Plants at higher elevations, being more limited by the physical conditions of their environment, then find it advantageous to facilitate the growth of their neighbors as a means to combat the harshness of the environment (Callaway et al. 2002). Interaction shift based on gradient reveals the significance of interdependence; that plants are not always distributed independently of one another, but instead based on their ability to compete and facilitate for their survival and growth under different environmental conditions (Callaway 1997).

The complex gradient concept recognizes vegetation distribution, and thus the spatial pattern of that vegetation, as changing continuously along a spatial environmental gradient throughout the landscape (White 1979). The cumulative effect of abiotic and biotic factors in the environment on species with specific survival strategies and characteristics creates unique spatial signatures on the landscape (Schmidt et al. 2017). Araújo and Rozenfeld (2014) proposed that when the sum of interactions among species trends positive, spatial patterns will emerge independent of scale. Alternatively, competitive interactions tend to be scale-dependent, and more commonly restricted to the local scale (Araújo and Rozenfeld 2014). These interactions can be elucidated using second-order summary statistics to derive a mean number of points within a certain distance from an individual plant that, when compared against a random expected mean, result in a value indicating positive or negative interaction (Velázquez et al. 2016). Point pattern analysis of tree regeneration, with consideration given to underlying microsite topography and shelter features, could expand our understanding of how tree expansion patterns are guided by favorable conditions for expansion in upland heath.

2.3.2 Abiotic Factors

The role of abiotic filtering due to environmental heterogeneity is reflected at broader scales, from the neighborhood to the landscape. Topography, climate, soil quality, and land-use history all have a strong influence in shifting plant interactions and species richness in an area from the generation of abiotic stress (Choler et al. 2001; Callaway et al., 2002; Boyden et al. 2005; Kepfer-Rojas et al. 2015; Llambí et al. 2018). The effects of abiotic factors can extend beyond the resulting net interaction, influencing the type and degree of interaction that occurs (i.e. growth and survival) (Boyden et al. 2005). Land-use legacy can exaggerate these impacts as well. Human disturbance frequently fragments otherwise contiguous plots of forest, reducing potential for plant-plant interaction. These results are seen in high stress heath barrens, where increases in distance between patches of trees due to prior use as pasture can decrease the chances of overall tree seedling colonization from a reduction in facilitative effects (Kepfer-Rojas et al. 2015).

Topographical characteristics, such as ground curvature, can influence pattern through provision of resources, enhancing or minimizing exposure to stressors, and altering how plants interact through physical community structure (Choler et al. 2001). Topography and plant life history may also work in tandem to generate unique mosaics of resource availability (Marfo et al. 2018). For example, microtopographic heterogeneity resulting from soil disturbance can pair poorly with the dispersal mechanisms of plants occupying a space, thereby restricting their establishment and spread throughout a given environment (Rose and Malanson 2012). Soil characteristics, such as acidity and nutritional content, play a large role in defining the spatial distribution of species across ecotones, because soil conditions are often determined by topography, and similarly influence the formation of topographic features on the landscape (Roering et al. 2010). Boulders and surface irregularities can create habitable microsites where low temperatures and high winds are ameliorated, facilitating seedling establishment and thus determining how conifers are distributed above the treeline (Resler et al. 2006; White 2019). Topographic conditions resulting from rock cover at montane microsites can result in a positive sheltering effect, increasing water-holding capacity and stability of the soil, reducing erosion, and shielding plants from harsh winds, allowing trees to establish at sites above a previously established treeline (Resler et al. 2005; White 2019).

Aspect can also modify spatial relationships and vegetation pattern through indirect and direct effects via a similar exposure to environmental stressors. This relationship is seen in a range of abiotically stressful environments, such as heathland (Byers et al. 2010), alpine environments (Choler et al. 2001; Holtmeier and Broll 2005; Resler 2006), and drylands (Haase et al. 2001), where abiotic conditions such as solar radiation, wind flow pattern, length of snow cover, soil moisture, and seasonal temperature variation depend partly on aspect. Northerly aspects, receiving lower exposure to solar radiation and increased wind flow, generate cooler conditions where only cold-adapted, hardy species can flourish and regenerate (Byers et al. 2010).

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CHAPTER 3:

Spatial pattern analysis of tree species distribution in a Central Appalachian upland heath barren

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Spatial Pattern Analysis of Tree Encroachment in a Central Appalachian Upland Heath Barren

The spatial pattern of plants reflects biotic and abiotic factors, including interactions with surrounding environmental conditions and other plants and animals (e.g., herbivory). Appalachian heath systems are presently understudied with respect to spatial point pattern research, despite representing a unique and biologically valuable ecosystem. In this study, we characterized the spatial pattern of three tree species distributions in the upland heath barrens on Cabin Mountain in Canaan Valley, West Virginia through fieldwork, statistical modeling, and the use of geographical information systems (GIS). The research objectives were to: 1) quantify demographics and global and local spatial pattern of trees to infer biotic process, and 2) identify how tree spatial pattern varies with selected biophysical variables, including ground curvature and topographic wetness index, to understand potential relationships between site conditions and spatial pattern. The spatial statistics, Ripley's K-function and nearest neighbor analysis, revealed a predominantly clustered interaction configuration among trees, however, different interaction types were reflected across size-growth classes species pairs. The selected biocorrelates (curvature and TWI) had no significant relationship with spatial pattern at the site. These findings suggest a range of both intraspecific and interspecific interactions are taking place in the heath barrens of Cabin Mountain, where significant levels of facilitation are occurring among encroaching red maple and striped maple, while red spruce is in competition with both species of maple, and that relationships are formed outside the influence of topographic characteristics of the site.

Keywords: Spatial pattern, heath barrens, tree distribution, pattern-process relationships

3.1 Introduction

A heath barren is an ecosystem characterized by ericaceous shrubs, nutrient-poor soils, and tree species typically exhibiting stunted growth (Feldmann 2020). The high elevation heath barrens of Central Appalachia have been shaped by a history of extensive land-use, combined with contemporary disturbances such as climate change, and land use and land cover change (Schirmel et al. 2010). Prior to the arrival of the logging railroads in 1884 to support local pulp and paper mills in Davis, WV, the region was covered in extensive old-growth, relict spruce-fir forests, that were more expansive toward the end of the Pleistocene (~ 12,500 years ago). These forests were characterized by a prehistoric fire regime with a return interval regime of ~ 650 years (Adams and Stephenson 1989; Thomas-Van Gundy et al. 2007). Fires associated with coal-burning logging railroads repeatedly scorched thick layers of soil, which had accumulated over thousands of years, down to bare rock in a span of decades (Byers et al. 2010). By 1924, the era of logging had ended in the region, leaving behind an ecosystem forever altered by the decimation of hundreds of thousands of acres of red spruce (*Picea rubens*) and the destruction of the high-quality soils that supported the native species composition and forest microclimate (Allard and Leonard 1952; Fortney and Rentch 2003).

In the wake of intensive historical land use and fire, ongoing disturbance from agriculture, logging, and invasive species continue to characterize the Allegheny Mountain region of West Virginia (Mueller 1992; Byers et al. 2010). Additionally, tree encroachment aids in the conversion of heathland into deciduous forest (Byers et al. 2010). Red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) were found in the landscape as Pleistocene relicts prior to the emergence of industry in the region, and are slowly re-establishing in the heathland, where the environment is more similar to their historic growing conditions (Byers et al. 2010).

The encroachment of red spruce into Central Appalachian heath barrens has implications for both the regeneration of red spruce and the continued existence of heathland in this region. For red spruce, rates of seedling germination and survival are dependent upon the vegetation stratum into which tree encroachment occurs, suggesting ericaceous vegetation impacts recruitment of red spruce (George and Bazzaz 2003). The low-quality soils of heathland are typically successful in suppressing the growth of certain deciduous species but can serve as refugia for this Pleistocene relict (Byers et al. 2010), where competitive stress from deciduous stands is less present (Mobaied et al. 2015). However, as more seed-bearing non-heath species, such as maple (*Acer* spp.), establish in heathland and rates of encroachment subsequently increase, the characteristics that define the heath are subject to intense change that could modify the nature of the ecosystem (Körner et al. 2008; White 2019).

To fully understand the nature of tree establishment, species-specific information on the spatial patterns of encroaching trees into heath barrens is useful because tree spatial pattern is an outcome of biotic and abiotic processes, that can reveal underlying processes (Soliveres and Maestre 2015). For example, in addition to growth and community-level demographic processes such as establishment and mortality, spatial pattern of trees reflects the nature of interactions among trees (Turner 1989; Grehan 1993; Bertness and Callaway 1994; Levine et al. 2000; Soliveres and Maestre 2015). Concurrently, tree spatial pattern also reflects underlying abiotic factors. Some patterns exist in response to biological feedback resulting from interactions between the abiotic and biotic elements of a plant's environment, and persist until a specific threshold is surpassed, such as across gradients of abiotic stress (Callaway et al. 2002; Alados et al. 2017).

Topographical characteristics, such as ground curvature, can influence pattern through provision of resources, enhancing or minimizing exposure to stressors, and altering how plants interact through physical community structure (Choler et al. 2001; Marfo et al. 2018). Boulders and rock outcrops can create habitable microsites that facilitate seedling establishment where low temperatures, high winds, and moisture stress are ameliorated, thus determining how conifers are distributed (Resler et al. 2005; Resler 2006; White et al. forthcoming). Topographic conditions resulting from rock cover and presence of rocks on exposed sites can result in a positive sheltering effect, generate areas of standing water and increase the water-holding capacity and stability of the soil, reduce erosion, and shield plants from harsh winds, giving tree seedlings an advantage at exposed sites (Resler et al. 2005; White et al. forthcoming). Among trees, particular relevance lies in the presence of colonizer tree species resistant to harsh environmental conditions, which could facilitate the subsequent establishment of other species.

A common goal of spatial pattern analysis in ecological research is to elucidate underlying processes that shape distributions (e.g. Wiegand and Moloney 2013), which is important for understanding and predicting factors that contribute to range shifts (Soliveres and Maestre 2015) and ecosystem recovery. Pattern-process relationships have been studied in a variety of environments, including semi-arid shrubland and marine ecosystems, to high elevation treeline ecotones (Bertness and Callaway 1994; Allen and Walsh 1996; Haase 2001). Typically, the goal of analysis is to distinguish random from non-random distributions, and to infer the influence of ecological processes on pattern (Haase 1995). Researchers have developed a variety of statistical methodology and field techniques to accurately assess process, including Ripley's K-function, kernel density, average nearest neighbor, and the pair correlation function, among others (Wiegand and Moloney 2004).

Here, we examine spatial pattern of trees at Cabin Mountain in Canaan Valley, West

Virginia, USA, considering the influence of biotic interaction and environmental characteristics on resulting tree distributions. Our primary objectives are to: 1) quantify species-specific spatial pattern of trees in the high elevation heathland barrens of Central Appalachia to infer biotic process among species associates through spatial pattern analysis and fieldwork; and 2) identify how tree spatial pattern varies with selected biophysical variables, including solar radiation ground curvature and topographic wetness index (TWI). The goal is to understand potential relationships between ambient conditions and spatial pattern. For objective 1, spatial pattern is tested against the null hypothesis of complete spatial randomness (CSR), which would assume that there is no significant pattern of interaction among trees at our site. For objective 2, it is similarly assumed that tree pattern bears no statistically significant relationship to variations in biophysical factors, and that, regardless of the nature of tree pattern, it emerges outside the influence of selected environmental variables.

Spatial pattern research in the heathland of Central Appalachia would be both a useful and novel contribution to the broader literature focused on global heathland and spatial point pattern analysis. A vast majority of research performed in heathland occur in Europe, with comparatively few studies focused on North American heathland (Fagúndez 2013). This study is one of the first to utilize point pattern analysis to study tree encroachment in Central Appalachian heathlands, thereby establishing a baseline for further research to occur in this understudied system. Furthermore, the methodology of this study will revolve around detailed field collection, including descriptions of species and tree morphology for each tree, that will inform species specific patterns of tree encroachment. Given the unique and changing nature of this ecosystem, it is highly pertinent that research with the potential to envision the future of this system is carried out.

3.2 Methods

3.2.1 Study Area

The study focuses on tree establishment patterns on heath barrens at a study area on Cabin Mountain, located near the southeastern border of Canaan Valley, in Tucker County, West Virginia, (Figure 1). Cabin Mountain runs along the southwest-northeast trending plateau west of the Allegheny plateau, situated at 1170m a.s.l. (Rentch and Fortney 1997). The study area on Cabin Mountain is centered at 39.114° N, 79.346° W on land managed by the Canaan Valley National Wildlife Refuge (CVNWR).

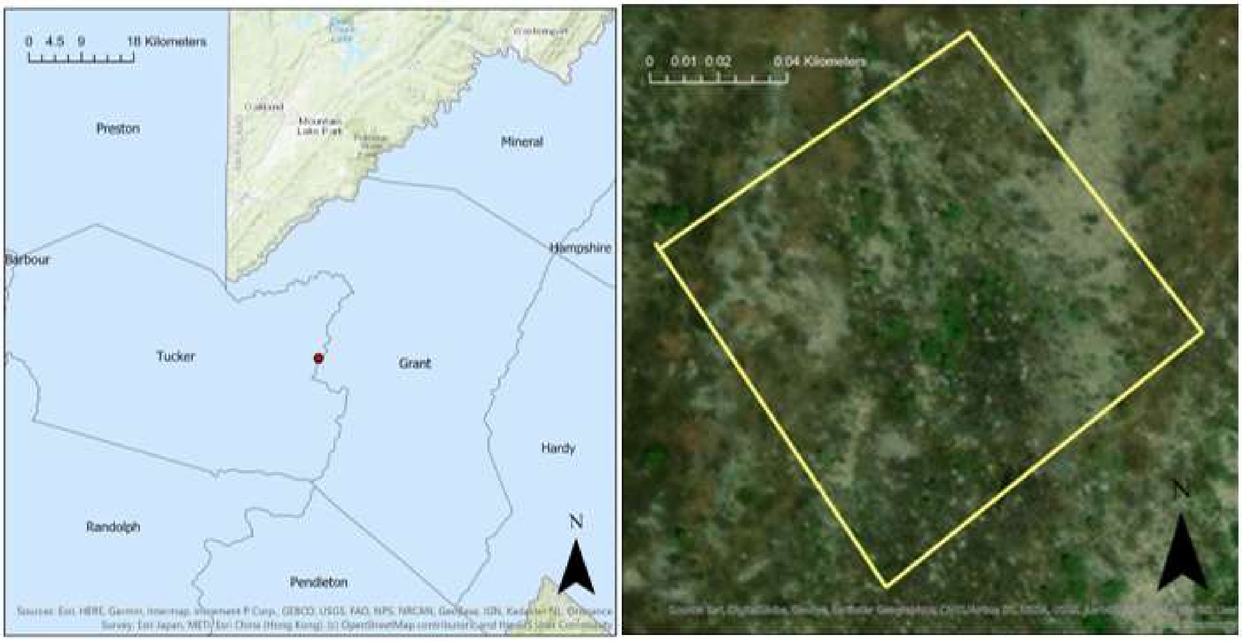


Figure 1. Left: Location of Cabin Mountain site relative to West Virginia counties Tucker, Grant, and others. Right: Rough outline of study area on Cabin Mountain

The upland heath barrens on Cabin Mountain, in particular, and in Central Appalachia, in general, are characterized by acidic soils, ericaceous vegetation cover, and an extensive history of human disturbance across its range (Byers et al. 2010). Conditions in Canaan Valley are favorable to cold-hardy species that are less tolerant of the wider regional climatic regime (Dobrowski 2011). The study area is dominated by Ericaceae, Rosaceae, and Lycopodiaceae families growing as dense, low-lying shrubs with sparse tree cover. Red spruce and balsam fir (*Abies balsamea* (L.) Mill) climax forests were found at lower elevations (<500 m) and were more spatially extensive toward the end of the Pleistocene (Allard & Leonard 1952; Adams et al. 2010). The cool, subalpine climate of this high elevation site, similarly a relict environment from the Pleistocene, allows them to harbor red spruce (*Picea rubens*) at their peaks, though populations have been reduced substantially since the arrival of European logging crews in the mid-1800s (Pauley et al. 2008). Observed tree species here include red spruce (*Picea rubens*), striped maple (*Acer pennsylvanicum*), balsam fir (*Abies balsamea*), mountain ash (*Sorbus americana*), white pine (*Pinus strobus*), and red maple (*Acer rubrum*).

Temperatures in Canaan Valley are generally 5.6-8.3°C cooler than the surrounding lowlands due to its unique elevational position in the landscape, with freezing temperatures occurring at any month of the year and an average summer temperature of 17.7°C (Vogel & Leffler 2015). Winters in this region are moderate to severe, with effects exasperated on the plateau in Cabin Mountain. Freezing to sub-freezing temperatures occur on an average of 160 days, often combined with heavy snowfall, averaging 340 cm from early September to late June. Mean annual precipitation reaches 125 cm per year (Losche and Beverage 1967). Natural disturbance regimes include ice storms, insect damage, and wind disturbance. Wind and ice events comprise the most frequent disturbance at every 100 to 200 years (Thomas-Van Gundy et al. 2007). This subalpine climate shortens average growing season in the Valley to just 89 days, many days shorter than the growing season of areas bordering the Arctic Circle (Vogel and Leffler 2015).

Soils are shallow and highly acidic, truncated by exposed bedrock. Accumulation of organic matter has occurred in some areas in the absence of frequent fires (Byers et al. 2010). The dominant soil types on Cabin Mountain are acidic spodosols and inceptisols, with some ultisols. Spodosols on Cabin Mountain are found on Pottsville sandstone on ridge tops, often having formed under red spruce trees (*Picea rubens* Sarg) or eastern hemlock (*Tsuga canadensis*) (Sencindiver et al. 2015). The spodosols in these sites have low-pH and low fertility, with stony surfaces and high concentrations of rock fragments. Soft, erodible Mauch chunk shale is situated on the side slopes of the Mountain. Here, inceptisols are found with higher silt and lower sand content than spodosols on the ridgetops. Periglacial features remnant from the Wisconsinan Glaciation are also present in the form of exposed rock and blockfields at these high elevation sites (Clark & Ciolkosz 1988). White (2019) reports a relationship between these rocky outcrops and red spruce establishment.

3.2.2 Field Methodology

The methodology for this study included field data collection, and subsequent statistical analysis using both field data and variables derived from geospatial datasets. We obtained point data (coordinates) using a high-resolution (~2-3cm) Trimble Geo7x GNSS for individual trees within a 100x100m quadrat that demarcated sampling boundaries (Figure 1). Terrain was generally even, with fine-scale topographic roughness and a mild, gradual slope across the extent of the plot. Most of the ground cover was heath vegetation, though some large spaces in the plot were rock cover. Quadrat placement at the site was determined by generating a random point coordinate prior to visitation and subsequent field verification. In the field, we used the GPS to navigate to the point, which was designated as the quadrat centroid.

To record pattern among all trees at the site, and delineate potential species-specific and interspecific relationships, we recorded a series of tree-level variables for each tree within the plot. If the tree's bole fell within the boundaries of the quadrat, it was included in sampling. These variables included geo-location of each tree per plot, species, tree height, and diameter at breast height (DBH) or diameter at ground level (DGL). DBH was recorded for trees at or exceeding 1.37m in height, and DGL was measured for those less than 1.37m. Each tree within the plot was recorded individually in a data dictionary as a geoposition with X, Y, and Z coordinates using the Trimble Geo7x GNSS rover. No tree was omitted due to limitations on size or specifications regarding species; each tree in the plot was recorded, provided the tree was visible, at a minimum of 6cm in height. Tree height was measured for all individuals at or above 1.37m using a transect tape and clinometer. Trees below 1.37m were measured with a transect tape or ruler, depending on the height. This tree-level information provided important species-specific and morphological information to inform the point pattern analysis of the plot.

Field-collected data points were partitioned by species and growth class. Since relationships among trees can vary based on age (Larson et al. 2015) and the potential for the sheltering effect of larger trees on smaller trees, these stratifications were important in our analysis. Growth classes were generated based on measurements that aligned with general tree life history measurements (Table 1) (Harcombe 1987; Tree Life History). While we recognize it is likely that growth is affected by the climatically stressful conditions on Cabin Mountain, classification by life history size classes (called growth classes here) provided a standard grouping method upon which we could compare differently sized trees by both height and diameter (Mallik and Kravchenko 2018).

3.2.3 Spatial Analysis and Statistics

To test the null hypothesis of complete spatial randomness (CSR) among all trees, species combinations, and growth history traits, we used a combination of the Ripley's K and nearest neighbor analysis, from which we were able to derive a nearest neighbor index (NNI) and a z-score to test clustering and dispersal of trees. The combination of a first- and second-order spatial statistic provided a supplementary assessment of both global and local data (Perry et al. 2006). On its own, nearest neighbor index is constrained to describing pattern focused on distances at which the nearest neighbor occurs (Perry et al. 2006). Ripley's K extends NNI's inferential reach of pattern up to a range of distances and illustrates the range graphically. However, since Ripley's K is purely inferential, it cannot generate an actual p-value, which is where NNI fills in (Perry et al. 2006).

Nearest neighbor analysis calculated the average distance between the nearest neighbors to each individual within a plot, taking the plot size (100x100m) into consideration. The nearest neighbor index (NNI), the ratio of the observed distance divided by the expected distance, was calculated and served as an indication of clustering or dispersal (How Average Nearest Neighbor Works 2020). Typically, NNI values below 1 indicate a clustered point distribution and values above 1 indicate dispersal, while an NNI at 1 indicates randomness. These results were fortified by the z score, where negative (clustered) and positive (dispersed) values were used to derive a p-value that indicated the statistical significance of impact among the trees versus CSR on pattern. It is important to note that the z-score and NNI reflect the character of pattern at the site, while the p-value suggests the influence of species, species groups, or growth groups on the evidence of pattern (How Average Nearest Neighbor Works). A p-value of $p>0.05$ was considered insignificant, and an indicator of complete spatial randomness on the resulting pattern.

Ripley's K test summarizes cumulative spatial dependence (clustering or dispersion) over distances ranging from 0 to 25% of the maximum extent of the plot boundary (Fortin et al. 2014). For our study, the radius was set at 30 meters, given our plot was 100x100m. The actual number of plants within the radius is assessed against a simulation of randomly distributed points within the same spatial extent. Ripley's K is particularly useful for illustrating point patterns up to these distances in the graph produced in R, where dispersal and clustering were indicated graphically by the 'actual' line falling outside the Monte Carlo simulation envelope, providing further detail to results found from in the first-order analysis (Perry et al. 2006).

The Monte Carlo simulation generated a null distribution given complete spatial randomness out of a series of 999 simulations for both tests. For every simulation, an average nearest neighbor value is generated, and sets the upper and lower boundaries of the simulation envelope. Actual values for nearest neighbor and Ripley's K can then be assessed against these (Velázquez et al. 2016). For NNI, the actual average nearest neighbor is divided by the mean of the Monte Carlo simulated values. For Ripley's K, Monte Carlo values fall along a line, with a surrounding simulation envelope, providing a 'random' reference against which to evaluate the actual pattern (Perry et al. 2006). Spatial statistics were derived using a combination of ArcGISPro and R statistical software, specifically the package 'spatstat' (Baddeley and Turner 2004).

In spatial statistics, the sampling circle can fall outside square or polygon plot, producing a biased estimate of pattern, though this can be fixed with different methods of edge correction

(Wiegand and Moloney 2004). In R, the algorithm computes the maximum radius for which an isotropic edge correction is valid, considering the number of points, the window or boundary around the points, and the corresponding distance value for each point along the radius (Baddeley and Turner 2004). For isotropic edge correction, where the radius falls outside the boundary, points are simulated according to a weight outside the boundary to account for missing data (Ripley 1988).

To fulfill Objective 1 of this study, all trees within the plot were assessed for clustering using both NNI and Ripley's K, and then clustering was assessed across the plot on a species-specific basis. We subsequently analyzed relationships among different species of trees, then relationships among different species of different size-growth classes. Height and DBH/DGL were categorized into growth classes to determine if there was significant non-random pattern among trees at different points in their growth, to assess for underlying relationships (Table 1). Non-random pattern was assessed across spatial scales for all groups, at radius intervals of every 5m, to identify areas of higher spatial heterogeneity, and to identify those where fine-scale processes may be at play (Peters et al. 2007).

Table 1: Size-Growth classes according to tree height and DBH/DGL.

	Small Juvenile (<50cm)	Large Juvenile (50-150cm)	Small Sapling (150-300cm)	Large Sapling (300-500cm)	Pole (>500cm, dbh <10cm)	Adult (>500cm, dbh 10.1-34.99cm)
Picea rubens	34	41	12	21	2	13
Acer rubrum	375	69	10	0	0	0
Acer pennsylvanicum	126	58	0	0	0	0

Using a Monte Carlo simulation combined with both a first-order statistic, nearest neighbor analysis, and a second-order statistic, Ripley's K analysis, to denote pattern across a scale from 0-30 m, point pattern relationships among the following groups were assessed:

1.) All trees within the plot;
2.) Species groups: red maple, striped maple, and red spruce;
3.) Between pairs of species, including groupings of red maple and striped maple, red spruce and striped maple, and red spruce and red maple;
4.) Among morphological groups of each species sorted into size-growth classes, resulting in 36 species-life history combinations (e.g., large sapling red maple and adult red spruce, small juvenile striped maple and small juvenile red spruce, etc.).

3.2.4 Biophysical Correlation Analysis

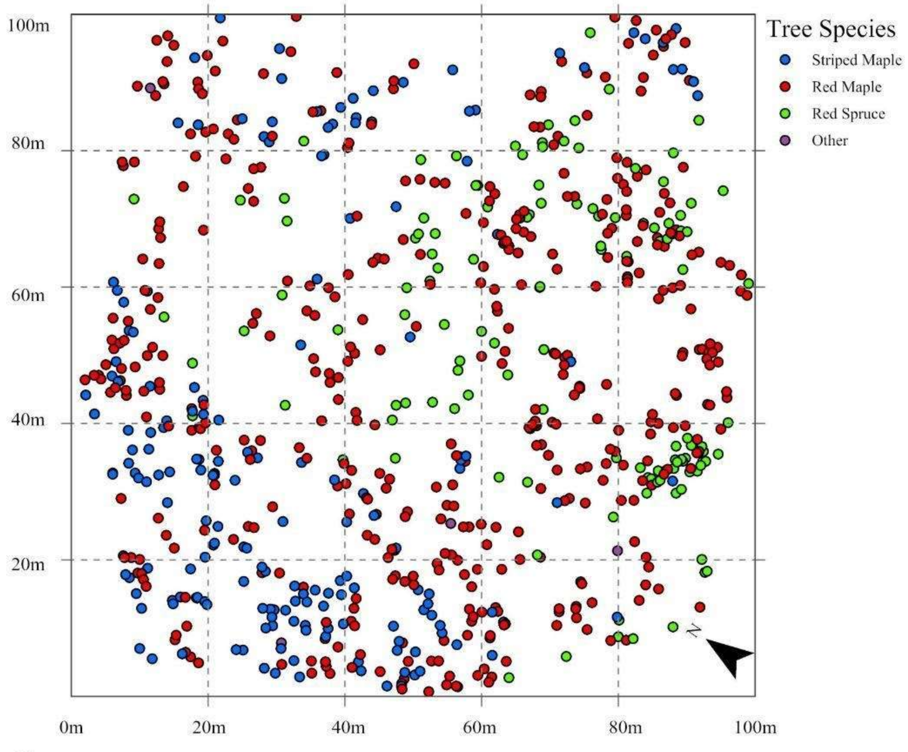
For the purpose of fulfilling Objective 2, we selected two primary biophysical correlates (curvature and a topographic wetness index (TWI) against spatial pattern in order to assess if any of these variables had a significant effect on clustering of trees at the plot. Values for the TWI, curvature, and nearest neighbor distance were assigned to each individual tree point in ArcGIS to create this model. Nearest neighbor distance, representing the closeness in meters of the nearest tree, were obtained for all tree points in the plot and used as a response variable. Nearest neighbor distance served as an indication of the strength of clustering and was regressed against the biophysical predictor variables, TWI and curvature. A correlation analysis model was used to determine the strength of correlation between the selected biophysical variables and nearest neighbor analysis. The biophysical variables served as the predictor variables and average nearest neighbor of each tree was used as a response variable.

All three variables were derived from a USGS-produced 1/9 arc-second (~3 m) resolution digital elevation model (DEM) (U.S. Geological Survey 2012). Using the ArcGIS Analyst toolbox, as well as GRASS GIS raster hydrologic modeling, we derived the curvature raster and a topographic moisture index (TWI) for the plot. TWI is an important modifier of soil moisture, soil pH, and groundwater flow that can function at a fine scale, influencing spatial pattern through the availability of water (Sørensen et al. 2006). Curvature reflects variation in the microtopography of the surface, and has significant implications for soil quality and depth (Wilkinson and Humphreys 2005). In a curvature raster, negative values indicate a surface is upwardly convex with decelerated flow, positive values indicate the surface is upwardly concave with accelerated flow, and a value of 0 indicates the surface is linear.

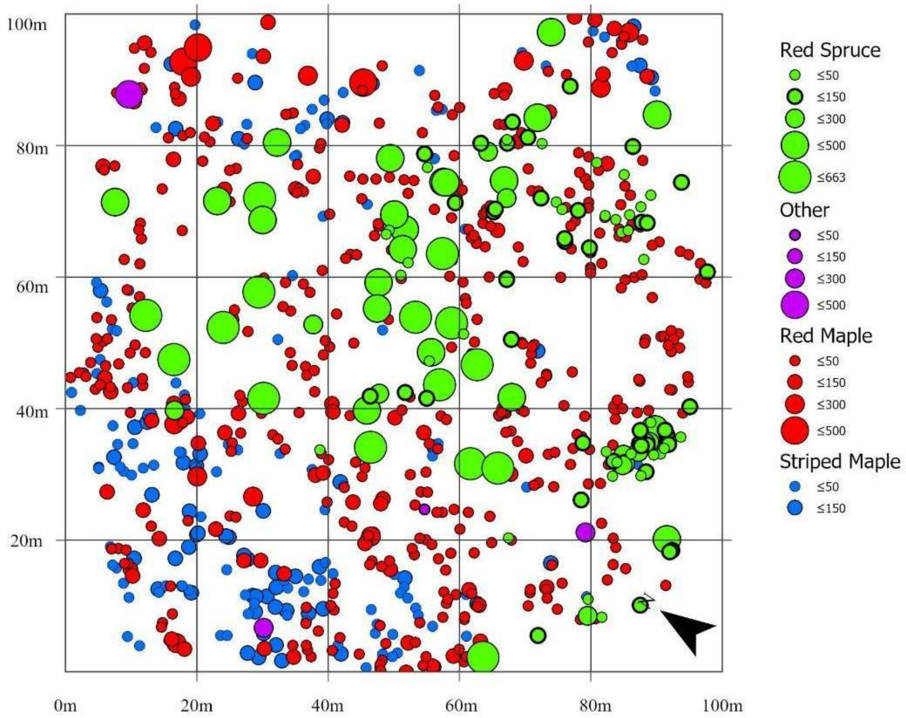
3.3 Results

3.3.1 Summary Statistics

Fieldwork yielded a total of 785 recorded trees in the study plot. Of these trees, 59.6% (*n* = 468) were red maple (*Acer rubrum*), 23.8% (*n* = 187) were striped maple (*Acer pensylvanicum*), 16.1% (*n* = 126) were red spruce (*Picea rubens*), and 0.51% (*n* = 4) were classified as ‘other’ (Table 2 and Figure 1a). Those in the ‘other’ category consisted of one species each of mountain ash (*Sorbus spp.*), white pine (*Pinus strobus*), balsam fir (*Abies balsamea*), and bigtooth aspen (*Populus grandentata)*. Given the low numbers of individuals in the ‘other’ category, spatial analyses focused on the interactions between red maple, red spruce, and striped maple.


100m
80m
60m
40m
20m
0m
20m
40m
60m
80m
100m
N
Tree Species
Striped Maple
Red Maple
Red Spruce
Other

a.



b.

Figure 2. a.) Species distribution map showing striped maple, red maple, red spruce and other species, and b.) Species distribution map showing life history distribution of different species throughout the plot.

Distribution of morphological characteristics varied moderately across species, with an uneven distribution of size-growth classes present in this stand (Figure 2b and Figure 3).

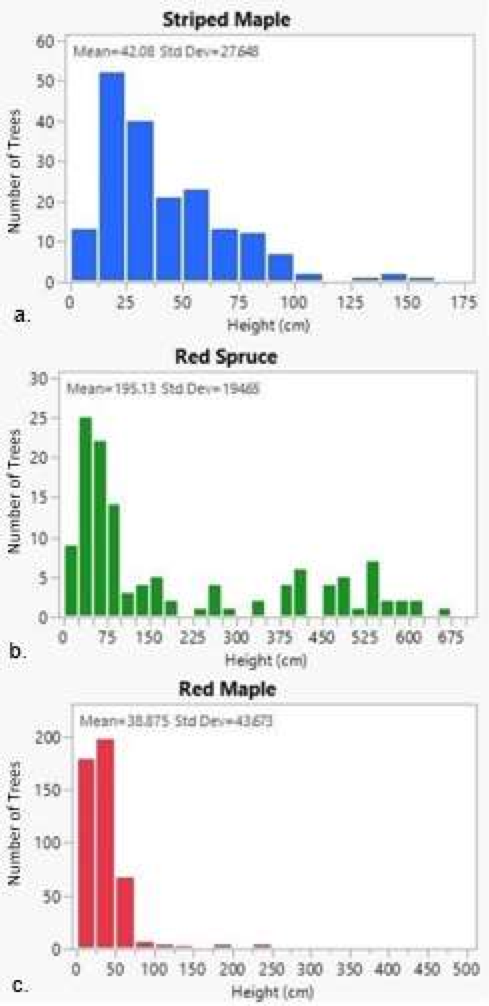


Figure 3: Height distribution of three dominant species a.) striped maple (*Acer pennsylvanicum*), b.) red spruce (*Picea rubens*), and c.) red maple (*Acer rubrum*).

Among all species, juveniles and saplings were more abundant than adults (Figure 3). Red spruce was the only species to have adult individuals in the plot, with the highest average DBH, DGL, and height (Table 2 and Figure 3b). For this study, an individual was considered an adult if they had reached >500cm in height, and a dbh above 10.1cm (Harcombe 1987).

Table 2: Average diameter at breast height (DBH), diameter at ground level (DGL), and height plus the standard error (SE) for red spruce (*Picea rubens*), red maple (*Acer rubrum*), and striped maple (*Acer pensylvanicum*)

Species	N	Mean DBH ± *SE* (cm)	Mean DGL ± *SE* (cm)	Mean Height ± *SE* (cm)
Picea rubens	126	9.78 ± 1.19	1.92 ± 0.156	194 ± 17.3
Acer rubrum	468	2.75 ± 1.02	0.679 ± 0.032	38.9 ± 2.02
Acer pensylvanicum	187	9.76 ± 1.19	0.8 ± 0.065	42.1 ± 2.02

3.3.2 Spatial Point Pattern Analysis

Plot-level results of the nearest neighbor analysis reflected a statistically significant degree of clustering ($p < 0.05$), rejecting the null hypothesis (Table 3). Similar results were seen in individual species groups, where clustering was found within each species group (Table 3). However, when species-pairs were analyzed, relationships between the pairs reflected dispersal and clustering (Table 4). Among size-growth pairs, results of the analyses supported the null hypothesis in some instances (indicating complete spatial randomness and its influence), whereas local clustering and dispersal patterns among differently-sized species was also evident (Table 5).

Pattern among size-growth classes maintained similar patterns to species-pair classes, where red spruce had an either random or dispersed relationship with both maple species, and only striped maple and red maple clustered (Tables 5-7). Among all but one size-growth class (pole), striped maple and red spruce were dispersed (Table 7). Red maple and striped maple had a series of clustered relationships, most notably among small sapling red maple with small juvenile striped maple, and large juvenile red maple, and large juveniles of both species (Table

6). All red spruce and red maple relationships were either dispersed or random in pattern (Table 5).

Table 3: Plot-level spatial statistics reflecting nearest neighbor index (NNI), z score, p-value, and description of pattern

Plot – level statistics	*NNI (Nearest Neighbor Index)*	*Z score*	*p-value*	Description of Pattern
Total trees (all species)	0.75	-13.19	p<0.001	CLUSTERED
Red Spruce	0.73	-6.83	p<0.001	CLUSTERED
Red Maple	0.67	-10.69	p<0.001	CLUSTERED
Striped Maple	0.64	-9.45	p<0.001	CLUSTERED

Table 4: Spatial statistics for species pairs.

Species pairs	*NNI*	*Z score*	*p-value*	Description of Pattern
Red spruce – red maple	1.23	11.53	p<0.001	DISPERSED
Striped maple – red spruce	1.72	30.72	p<0.001	DISPERSED
Red maple – striped maple	0.46	-31.22	p<0.001	CLUSTERED

Table 5: Spatial statistics between red spruce and red maple size-growth classes

Red spruce life history class	Red maple life history class	*NNI*	*Z score*	*p-value*	Description of Pattern
Adult	Small juvenile	0.99	-0.22	0.41	RANDOM
Adult	Large juvenile	1.02	0.35	0.36	RANDOM
Adult	Small sapling	1.11	1.19	0.12	RANDOM
Pole	Small juvenile	1.07	0.49	0.31	RANDOM
Pole	Large juvenile	0.95	-0.45	0.33	RANDOM
Pole	Small sapling	0.84	-1.05	0.15	RANDOM
Large sapling	Small juvenile	1.16	2.39	p<0.01	DISPERSED*
Large sapling	Large juvenile	1.30	5.82	p<0.001	DISPERSED
Large sapling	Small sapling	1.12	1.49	0.07	RANDOM
Small sapling	Small juvenile	0.98	-0.17	0.43	RANDOM
Small sapling	Large juvenile	1.07	1.00	0.16	RANDOM
Small sapling	Small sapling	1.11	1.16	0.12	RANDOM
Large juvenile	Small juvenile	1.47	11.92	p<0.001	DISPERSED*
Large juvenile	Large juvenile	1.50	11.73	p<0.001	DISPERSED
Large juvenile	Small sapling	1.34	11.13	p<0.001	DISPERSED
Small juvenile	Small juvenile	1.49	11.25	p<0.001	DISPERSED*
Small juvenile	Large Juvenile	1.64	14.48	p<0.001	DISPERSED
Small juvenile	Small sapling	1.27	3.68	p<0.001	DISPERSED

*Denotes relationships where results of Ripley's K varied from results of NNI and z-score

Table 6: Spatial statistics between striped maple and red maple size-growth classes.

Striped maple life history class	Red maple life history class	NNI	Z score	*p-value*	Description of Pattern
Small juvenile	Small juvenile	1.13	6.23	p<0.001	DISPERSED
Small juvenile	Large juvenile	0.78	-7.16	p<0.001	CLUSTERED
Small juvenile	Small sapling	0.71	-3.57	p<0.001	CLUSTERED
Large juvenile	Small juvenile	1.36	10.6	p<0.001	DISPERSED
Large juvenile	Large juvenile	0.77	-5.98	p<0.001	CLUSTERED
Large juvenile	Small sapling	0.65	-4.49	p<0.001	CLUSTERED

*Denotes relationships where results of Ripley's K varied from results of NNI and z-score

Table 7: Spatial statistics between striped maple and red spruce size-growth classes.

Striped maple life history class	Red spruce life history class	NNI	Z score	*p-value*	Description of Pattern
Small juvenile	Adult	2.19	1.49	0.07	DISPERSED
Small juvenile	Pole	2.01	-0.89	0.19	DISPERSED*
Small juvenile	Large sapling	1.15	9.94	p<0.001	DISPERSED
Small juvenile	Small sapling	1.56	1.90	p<0.05	DISPERSED
Small juvenile	Large juvenile	1.15	26.88	p<0.001	DISPERSED*
Small juvenile	Small juvenile	1.11	27.99	p<0.001	DISPERSED

Large juvenile	Adult	1.20	2.86	p<0.001	DISPERSED
Large juvenile	Pole	0.86	-1.03	0.15	RANDOM
Large juvenile	Large sapling	1.58	10.88	p<0.001	DISPERSED
Large juvenile	Small sapling	1.23	3.23	p<0.001	DISPERSED
Large juvenile	Large juvenile	1.92	21.95	p<0.001	DISPERSED
Large juvenile	Small juvenile	2.06	22.9	p<0.001	DISPERSED

*Denotes relationships where results of Ripley's K varied from results of NNI and z-score

Results from the Ripley's K test were not always consistent with results of nearest neighbor analysis, given the Ripley's K graph does not reflect the significance of the results. Rather, a Ripley's K graph displays the upper and lower limits of the 999 simulations of the Monte Carlo test and the relationship of the observed values at varying scales' relationship with that line. Results were consistent among the plot-level tree population, where the graph indicated clustering similar to the NNI and z-score. All species-pair groups were clustered, however, these results were inconsistent with results from the nearest neighbor analysis (Figure 4 and Table 3). The Ripley's K test suggested that red spruce and red maple were the only species pair that clustered (Figure 4b), while red spruce and striped maple had a highly dispersed pattern (Figure 4c). Striped maple and red maple fell mostly within the simulation envelope, conforming largely to the null model, with a line slightly above the Monte Carlo random simulation at shorter distances (<15m) and slightly below at a broader scale (>25m) (Figure 4a).

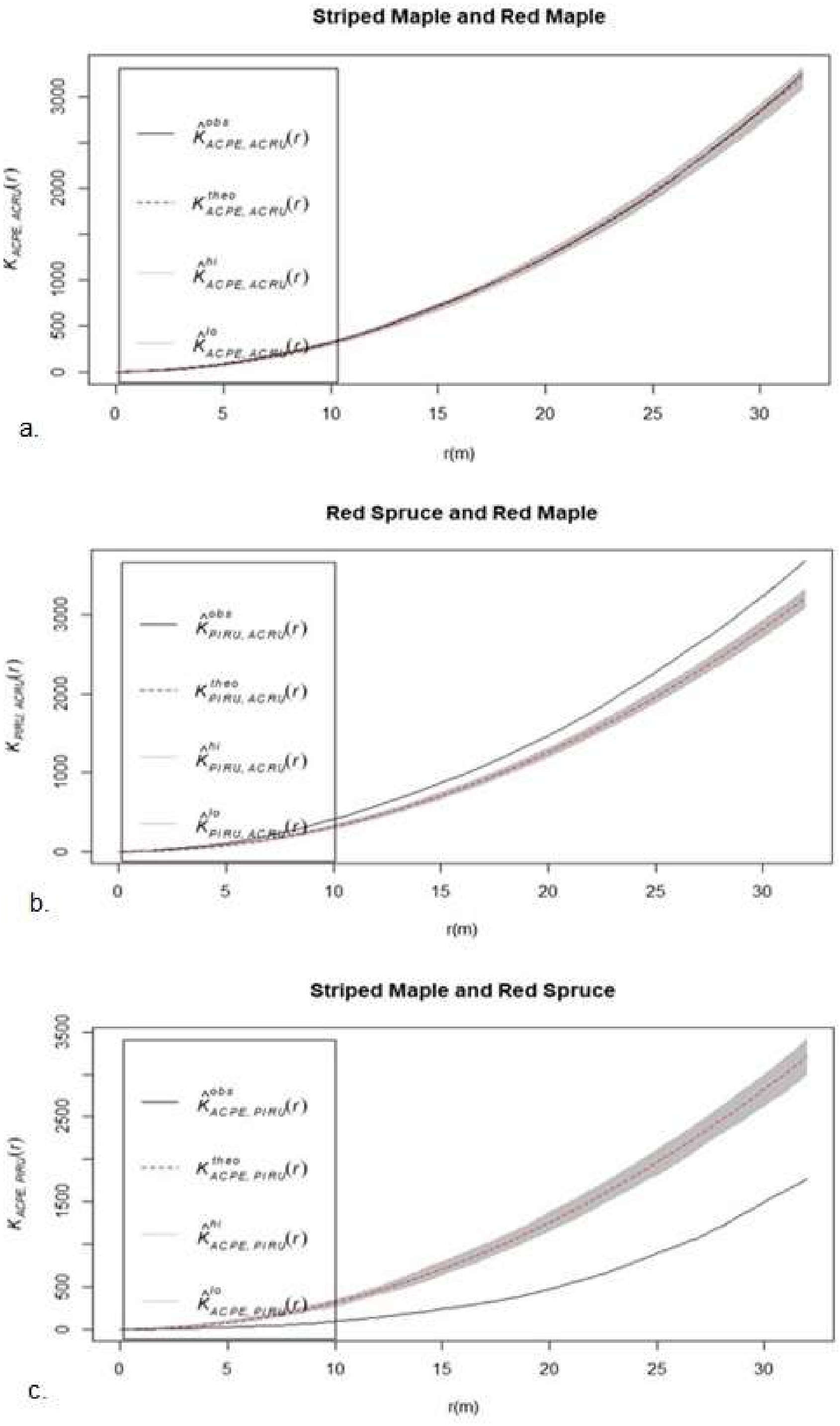


Figure 4: Ripley’s K analysis of intraspecies pattern (black line) with simulation mean (red-dashed line) and confidence envelopes (gray area) using a Monte Carlo simulation with 999 repetitions. From a to c: pattern between species groups red maple and striped maple, red spruce

and red maple, and striped maple and red spruce.

3.3.3 Correlation Analysis of Biophysical Correlates

Overall, the relationship between topography and spatial pattern was found to be insignificant (Table 8). Both TWI and curvature had no significant relationship with spatial pattern at the site (Table 8). Here, spatial statistics showed support for the null hypothesis; that selected biophysical correlates, TWI and ground curvature, had no significant effect on spatial pattern of trees at the site on Cabin Mountain.

Table 8: Statistics for significance of selected biophysical variable on clustering in the plot

Biophysical Variable	Ground Curvature	TWI
R^2	0.002	0.002
F statistic	1.51	1.57
p-value	0.22	0.2107

3.4 Discussion

The purpose of this research was to quantify the spatial pattern of tree encroachment at an upland heath barren on Cabin Mountain, WV, and to infer underlying biotic interactions. The presence of heathland in the region emerged both as a result of the harsh climatic conditions, indigenous burning practices, and herbivorous mammalian grazing before significant human disturbance on the land, and later as a response to the extensive disturbance resulting from European settlement and land use (Allard and Leonard 1952; Weigl and Knowles 1995). Since the 1880s, disturbance from agricultural land use, logging, and fire has intimately shaped the characteristics of these systems, making this analysis unique in the wake of its rich land use history (Mueller 1992).

Specifically, we used nearest neighbor analysis and Ripley's K-function as indicators of positive or negative interactions between individual trees, between pairs of tree species, and according to life history pairs. We also assessed tree pattern in relationship to ground curvature and topographic wetness (TWI), to determine potential underlying relationships between tree patterns and local site conditions.

3.4.1 Plot encroachment characteristics

Within our study plot, red spruce was the only species to have reached maturity (Figure 1b and Table 1), defined by criteria outlined by Harcombe (1987). It is important to note, however, that stunting due to climatically stressful conditions may obscure this interpretation (Mallik and Kravchenko 2018). So, whereas 13 red spruce trees fell into the category of 'adult', it is possible that their age would technically fall into an age category above their classification (Table 1). Among red spruce, there are many more encroaching young spruce than old (Table 1), and an analysis of intraspecies relationships showed evidence for facilitation among all red spruce on the plot (Table 3).

Red maple comprised roughly 60% of the trees in the sample plot (Table 2). A majority of these red maples were small (Figure 1b and Figure 3c), likely representing recent establishment. Red maple is a highly adaptable species, sometimes described as a 'super-generalist' (Abrams 1998). This maple species can grow in highly acidic and disturbed soils (such as those <5.0 pH soils that characterize the study area (Whittaker 1963)) and has a high rate of recruitment, with a range that has been increasing across North America in the past 50 years (Abrams 1998; Fei and Steiner 2007). The encroachment of red maple and striped maple threatens to outcompete North America's most endangered forest types, West Virginian red spruce forest, as deciduous encroachment significantly alters the conditions, such as soil and species composition, that characterize the heath barren and make this habitat suitable for red spruce (Rentch et al. 2007; Körner et al. 2008; White 2019). Both red maple and striped maple have a high tolerance to low temperatures (tolerating absolute minimums of -40°C to -47°C) (Walters and Yawney 1990; Striped Maple 2020), though they fare better and are able to propagate more readily in climates warmer than their lowest tolerance (Walters and Yawney 1990). Red spruce, on the other hand, requires temperatures averaging an annual 2°C to thrive, colder than the preferred temperature of red and striped maple (Walters and Yawney 1990; DeHayes et al. 2001). Although our study did not focus on temperature, it is possible that increases in annual temperature at the study area have ameliorated conditions enough for such a mass establishment, and that maple species may continue to experience regeneration and growth as global temperatures are expected to increase in the coming decade (Abrams 1998; Elsen and Tingley 2015).

3.4.2 Tree Spatial patterns as related to potential underlying processes.

In spatial point pattern analysis, tree pattern is often indicative of underlying ecological processes (Brooker et al. 2008). Competition may be expressed through dispersal, where significant spatial distancing between trees signifies some mechanism preventing growth of trees nearby one another (Callaway 1997). Facilitation may be expressed through clustering, where spatial closeness reflects some mechanism whereby trees are advantaged by growth nearer to one another (Bertness and Callaway 1994). In both interactions, a defining component is whether the ability to acquire certain resources is negatively or positively affected by the characteristics of another plant.

Our results revealed clustering to be the dominant spatial configuration of trees within our study area at the plot level we found that all trees total, and species-specific patterns to be clustered, with significant p-values (Table 3). These patterns could be dependent on plant interactions, perhaps as a result of climate stress following the stress gradient hypothesis, where facilitation increases with abiotic stress (e.g., Bertness and Callaway 1994). This finding is consistent with research at other tree ecotones where spatial clustering or facilitation among trees increased with abiotic extremes (Callaway and Pennings 1998; Camarero et al., 2000; Callaway et al. 2002; Elliott and Kipfmueller 2010). The growing season on Cabin Mountain lasts only 89 days, with lower annual temperatures than the surrounding region and freezes occurring most of the year (Vogel and Leffler 2015). Northwesterly winds here regularly gust between 60-90 mph (Carroll 2020).

It is important to note that other mechanisms may also explain the substantial clustering at this site. For example, some studies interpret clustering as indicative of passive facilitation by fine-scale abiotic factors, such as physical sheltering (e.g., Stine et al. 2010), whereas some suggest life history, such as seed dispersal mechanisms, plays more of a role in clustered pattern than underlying biotic interaction (Plotkin et al. 2002; Harper et al. 2011). One of the biggest challenges with spatial point pattern analysis is distinguishing which process is influencing pattern. For this study, the p-value was intended to help separate pattern by which external, abiotic influence overcame biotic interaction, and those where biotic interaction was a stronger influence on pattern. For instance, NNI and Ripley's K indicated the raw pattern of trees, while the p-value indicated the presence or absence of an underlying relationship (Dixon 2006; Ledo et al. 2014).

Whereas clustering was the dominant spatial configuration, among our results, both species of maple (red maple and striped maple) also had a highly dispersed configuration with red spruce (Table 4). This dispersed configuration suggested that competitive interactions are present among red spruce and other species of maple. There are many fewer red spruce at the site versus striped and red maple, and red spruce preceded maple at the site, possibly lending to their competitive relationship with encroaching deciduous species. On the other hand, red maple and striped maple had a clustered pattern, with a p-value indicating ongoing facilitation (Table 3). There is some evidence to suggest that facilitative interactions could aid in expanding a plants' ecological niche (Choler et al. 2001; Roux et al. 2012). This is a possibility here, where maple trees are expanding beyond their typical niche and into an environment with dissimilar conditions to their typical range (Fei and Steiner et al. 2007).

Red maple and striped maple were the only species-pair to have a significantly clustered relationship, specifically among large juvenile and small sapling red maples, and all juvenile striped maples (Table 6). The spatial aggregation of young striped and red maple supports findings from other studies; that seedlings exhibit higher rates of clustering and spatially homogenize as competition increases with age (Larson et al. 2015; Raventós et al. 2010). Both regularly spaced and random pattern characterized most of the interactions among both maple species and red spruce (Table 5 and Table 7). Regularly spaced pattern, indicating competition, appeared particularly among smaller growth-size classes of both maple species and red spruce, whereas larger red spruce and smaller maple species trended more towards non-interaction, or randomness (Table 5 and Table 7). Similar to findings from species-pairs, it appears that red spruce is competing with encroaching maple, at nearly all size-growth classes.

There are significant limitations to both spatial statistics used in this study. Ripley's K-function, for example, is a cumulative measure of clustering, meaning that estimates of K(r) at each distance synthesizes measurements of clustering at smaller distances up to that distance, versus a measurement of distance at varying rings of distance away from individual trees. Spatial point pattern analysis, in general, is also an inferential tool, meaning that it is not possible based on the test statistics alone to assume the specific processes underlying pattern. Therefore, our interpretation of results is limited to identifying the type and direction of interaction among trees, however, we cannot assume the specific mechanisms behind competition or facilitation nor the pattern. Spatial pattern can also be influenced by seed dispersal mechanisms of individual plants rather than biotic interaction. This can be directly, as determined by the mechanisms of seed dispersal and the range over which they are dispersed, or indirectly through determination of recruitment rates, invasion, range expansion, and gene flow (Ran and Muller-Landau 2000). Ground cover can also influence seed establishment, and thus pattern, through provision of moisture and exclusion of competition, such as in a previous study at Cabin Mountain where rock cover was correlated with red spruce seedling establishment (White et al. forthcoming).

3.4.3 Spatial pattern with respect to local site factors

The results of our correlation analysis of estimated local site conditions indicated that neither curvature nor TWI, both indicators of moisture, had a significant relationship with nearest neighbor distance, an indication of spatial pattern among trees. These results suggest that these soil moisture surrogates have no relation to pattern, as it was measured here. While our plot was relatively large (100x100m), it is possible its singularity and scale contributed to the results. Our selected digital elevation model from which TWI and curvature were extracted was also course relative to the data. Our variables could have been improved had we the time and resources to obtain our own fine-scale DEM of the area, versus a 3 meter DEM taken from

USGS. It is possible topographic features could be functioning on broader scale, but this is unknown given the relatively fine scale of the site. For instance, if we had a wider range of TWI and ground curvature values, as well as a larger tree point dataset, it could be the case that pattern varies significantly with pattern within this larger range (Wilkinson and Humphreys 2005; Sorensen et al. 2006). Other research has also found evidence to suggest that rocky outcrops serving as standing water sources corresponded to red spruce seedling growth at Cabin Mountain, showing there is some correlation among topography and tree growth at the site (White et al. 2019). The failure of biophysical variables, TWI and ground curvature, to have any significant effect on tree pattern simply indicates that these variables are not ecologically significant at the scale of 100x100m on Cabin Mountain. It is likely that a study with either a broader scale and the same scale of DEM, or a finer scale DEM, than what was used here would elucidate at which scale, and to what degree TWI and ground curvature influence pattern. It is well known that both of these environmental factors play a significant role in determining distribution and interaction of plants across multiple ecosystem types (Choler et al. 2001; Holtmeier and Broll 2005; Resler et al. 2005; Roering et al. 2010; Marfo et al. 2018), so it is still highly probable that environmental variation carries some influence on a different scale (White et al. 2019).

3.5 Conclusion

Historically, West Virginia’s upland heath barrens have served as refugia for red spruce (*Picea rubens*), which have been the only species of tree to be able to colonize sites these subalpine high elevation sites, due to harsh climatic conditions, short growing seasons, and low-quality, acidic soils (Byers et al., 2010). However, since 1951, global temperatures have increased 0.6° (IPCC 2014), with effects of warming amplified in montane habitats (Elsen and Tingley 2015). Natural succession of high elevation upland heath, facilitated by increasing global temperatures and atmospheric nitrogen deposition, convert these unique ecosystems and threaten red spruce through changes in species composition (Mobaied et al. 2012; Smith et al. 2016), and soil composition and moisture (Mantilla-Contreras et al. 2012; Serensen et al. 2015). The encroachment of deciduous trees threatens the conservation and status of heathland globally (Kepfer-Rojas et al. 2015). However, Appalachian heathland are underrepresented in the literature. Spatial point pattern analysis is an important tool for detecting ecological process underlying distribution. Biophysical variables can also influence pattern, so it is important to measure correlation for indications of that impact. This study performed spatial point pattern analysis at multiple levels (plot, intraspecies, species-pair, size-growth pairs) and assessed correlation among selected biophysical variables and clustering. Overall, plot-level analysis of both the total plot and individual species indicated clustering and facilitation. Our analysis also suggests that encroaching maple species, striped maple and red maple, have a facilitative relationship, while red spruce has a mostly competitive relationship with maple species. Neither ground curvature nor TWI had any significant impact on measurements of clustering at the site. This study has the potential to expand, both geographically in the understudied heath barrens of Central Appalachia, and methodologically, incorporating more spatial statistics and a more detailed correlation analysis of environmental variables. This study provides an exploratory base upon which further research on spatial point pattern analysis in the heathland of Central Appalachia could be conducted. Further elucidation of underlying mechanisms could look similar to this study, but with a broader scale, potentially synthesizing and highlighting ecosystem change in heath systems across North America. While correlation analysis here was restricted to analysis of the whole plot, future consideration could be taken for analysis of biophysical correlates such as species-level pattern.

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