COMPOSITION AND STRUCTURE OF TSUGA CAROLINIANA STANDS IN THE SOUTHERN APPALACHIAN MOUNTAINS

A thesis presented to the faculty of the Graduate School of Western Carolina University in partial fulfillment of the requirements for the degree of Master of Science.

By

Marcus Wind

Director: Dr. Laura E. DeWald
Forestry and Natural Resources

Committee Members: Dr. Tara Keyser, USDA Forest Service
Dr. Beverly Collins, Biology
Dr. Diane Styers, Geosciences and Natural Resources

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ABSTRACT

COMPOSITION AND STRUCTURE OF TSUGA CAROLINIANA STANDS IN THE SOUTHERN APPALACHIAN MOUNTAINS

Marcus Wind, M.S.

Western Carolina University (June 2021)

Director: Dr. Laura E. DeWald

Tsuga caroliniana Engelm. (Carolina hemlock) is a foundation species, so it defines a stand and its specific traits control ecosystem dynamics. This study presents an investigation into the relationships between *Tsuga caroliniana* physiography, population, and community characteristics by describing them across the landscape where it is currently found in North Carolina and Tennessee. The three specific questions asked were: (1) Does the physiography where *Tsuga caroliniana* is found vary? (2) Do community density, size, and diversity of *Tsuga caroliniana* stands vary? (3) Is variation in *Tsuga caroliniana* age, density, and size related to the variation in physiography and/or community density, size, and diversity? To address these questions, twenty 0.05 ha plots were installed in *Tsuga caroliniana* stands at five different sites on National Forest lands in the southern Appalachian Mountains of North Carolina and Tennessee. Sampling included the physiographic variables (aspect, elevation, landform index, and terrain shape index) and community variables (summer and winter canopy density, canopy percentage evergreen, mean diameter at breast height, importance values, species richness, evenness, diversity, percent ground cover of shrubs, and stem density of all trees and snags) which were used to address whether there was variation between the study sites and if they were related to variations in *Tsuga caroliniana* age, density, and size. Variation among the variables were analyzed using ANOVA, the Tukey test was used to separate means for establishing patterns of deviation among sites and species, and regression analyses were used to examine relationships between *Tsuga caroliniana* and stand characteristics. At one site, Dobson's Knob, stands were higher in elevation, faced a different direction, and were in shallower depressions compared to the other sites. Stands at Dobson's Knob also had the lowest summer canopy density and overstory mean diameter, and the highest overstory mean *Tsuga caroliniana* diameter. Another site, Lost Cove, had lower overstory species richness and lower over- and understory diversity, but it had a high percent of older and larger *Tsuga caroliniana* stems. Patterns in variables measured at both the overstory and regeneration level were different. Species richness and diversity varied among sites for the overstory ($p = 0.0054$, and $p = 0.0015$) and regeneration levels ($p = 0.0168$, and $p = 0.0011$), but evenness did not (overstory: $p = 0.1540$; 0.70 ± 0.15, regeneration: $p = 0.5577$; 0.76 ± 0.46). The percentage of the live trees that were *Tsuga caroliniana* varied among sites at the overstory level ($p = 0.0090$), but not at the regeneration layer ($p = 0.1080$; 3.29 ± 5.53). The density of *Acer rubrum* varied from eight other species in the understory ($p \leq 0.0611$), but did not at the overstory level ($p = 0.3690$; 32.5 ± 24.8). With shrubs, species richness varied ($p < 0.0001$), but percentage ground cover did not ($p = 0.7660$, 20.70 ± 25.68). The best sites for the artificial regeneration of *Tsuga caroliniana* occur within an aspect range from north to northwest, an elevation range from 900 m to 950 m, and a TSI range from -0.6 to 0.2, and have Ericaceae shrubs in the understory, a LFI of one, and a summer canopy density around 90 percent. This research suggests that *Tsuga caroliniana* needs a more southerly exposure at higher elevations, and it adds to the body of evidence

confirming the stress tolerant life history strategy of *Tsuga caroliniana* and the suppress effect on establishment of other species by *Rhododendron maximum.*

CHAPTER 1: INTRODUCTION

Once covering much of the northern hemisphere during the prehistoric past, *Tsuga caroliniana* Engelm. (Carolina hemlock) is now only found in small isolated remnant populations. From its official discovery in the mid-nineteenth century to the first extensive studies done on the species in the late twentieth century, it is practically absent from the literature. Since these early studies, the body of knowledge has grown, but it still does not approach the size as that of most other more common species.

Listed as “Near Threatened”, *Tsuga caroliniana* approaches functional extinction from an exotic invasive adelgid from Asia, *Adelges tsugae* (hemlock wooly adelgid). The literature on *Tsuga caroliniana* is not as extensive as what is found for most species that are less isolated and more accessible, so additional contributions to the literature are helpful and necessary for general knowledge and the development of best practices for management of the species. In the field during the data collection portion of this study, all overstory trees had their species, diameter at breast height, mortality status, and positions recorded for future mapping and two cores removed from all live trees for future dendrochronological stand reconstructions. The dendrochronological data will be processed and evaluated for a NCSU doctoral dissertation that will potentially elucidate the stand establishment history of the twenty plots measured in this thesis. Studies, such as mine and the one mentioned at NCSU, on *Tsuga caroliniana* are of interest to the USFS for building on the body of knowledge on management implications for maximizing the chances of success in the preservation and ecological restoration of the species.

This study presents an investigation into the relationships between *Tsuga caroliniana* physiography, population, and community characteristics. Chapter 2 is a review of literature focusing on the geographic range, topography, influence of topography on species distribution, foundation species, shrubs and the exclusion of woody plants, *Tsuga caroliniana* stands, their predicted functional extinction, and disturbance in southern Appalachian forests. Chapter 3 is a manuscript of the thesis project in journal format, and Chapter 4 is the literature cited in this thesis.

CHAPTER 2: LITERATURE REVIEW

Geographic Range

Tsuga caroliniana is a long-lived endemic species, and outside of cultivation is only found in small isolated populations in North and South Carolina, Georgia, Tennessee, and Virginia (Austin et al.2016, Brown 2004, Humphrey 1989, James 1959, Jetton et al. 2008, and Rentch et al. 2000). The species is described as growing at high elevations along dry exposed ridges, ledges, cliffs, and rock outcroppings in the southern Appalachians (Austin et al. 2016, Brown 2004, Humphrey 1989, and Rentch et al. 2000), but it is also found in more mesic sites, in the Piedmont plateau, and as an understory tree on ridge tops (Austin et al. 2016, Brown 2004, Humphrey 1989, and Stevens 1976). The species prefers cool wet summers, and the growth of younger trees are less affected by droughts than mature trees (Austin et al. 2016). *Tsuga caroliniana* can occur in small pure or mixed stands, and some are found growing solitary (Austin et al. 2016, Brown 2004, and Humphrey 1989). The range of the species is thought to be restricted in the north by insufficient summer rain and hardwood competition from fire suppression, and in the south by frequent fires, high summer temperatures, and low availability of exposed rock outcroppings and cliffs (Austin et al. 2016, and Jetton et al. 2008).

Topography

Tsuga caroliniana occurs at elevations reported between 600 m and 1500 m (Austin et al. 2016, Humphrey 1989, and Jetton et al. 2008) and between 700 m to 1,220 m (Brown 2004, and Duncan 1988 cited in Brown 2004); but there are low elevation outliers on the extremity of the range mentioned by Stevens (1976). He found a relic stand between 135 m and 160 m in elevation with a northern aspect in the Piedmont of Virginia, and also reported the northern most population known at 220 m elevation with a northern aspect. These two populations were found on bluffs which contain a variety of relic native plants, had north facing aspects, high diversity of species, and steep rocky terrain. Coker and Totten (1934 cited in Brown 2004) indicated that *Tsuga caroliniana* favors south-facing slopes, while other studies reported the species growing in more westerly aspects such as 255 to 285 degrees (Rentch et al. 2000) and 205 to 247 degrees (Brown 2004), and Humphrey (1989) reported finding the species at northwestern to northeastern aspects.

Influence of Topography on Species Distribution

Topography and soils influence tree species distribution in the southern Appalachians (Copenheaver et al. 2006, Harrison et al. 1989, and McEvoy et al. 1980). Topographical site characteristics, such as slope, slope position, elevation, and aspect, influence other site characteristics, such as light, moisture, soil, and temperature, which in turn affect the establishment, growth and recruitment of vegetation (Copenheaver et al. 2006, and Elliott et al. 1999). Stand age and slope position have been found to be more important than fire history in the explanation of *Pinus strobus* L. invasion into a stand, and while *Quercus montana* Willd. is present at mid-slope, it is more dominant near ridge tops (Copenheaver et al. 2006). Terrain shape, elevation, and soil organic matter were found to explain 50 percent of the variation in species at a study in the Coweeta Basin in western, NC (Copenheaver et al. 2006, and Elliott et al. 1999). Generalist species such as *Acer rubrum* L., *Nyssa sylvatica* Marsh., *Oxydendrum arboreum* (L.) DC., *Quercus montana* (Copenheaver et al. 2006, and Elliott 1999), and *Quercus rubra* L. (Harrison et al.1989) are found in sites with varying geomorphic characteristics. Other species are more site specific such as *Pinus spp.* and Ericaceae shrubs that dominate slopes with southwest aspects and high elevation ridges while mesic species, such as *Liriodendron tulipifera* L., *Prunus serotina* Ehrhart, and *Quercus alba* L., dominated slopes with north-northwest aspects and lower elevations (Copenheaver et al. 2006, and McEvoy et al. 1980).

Foundation Species

A foundation species defines a forest's structure, and its species-specific traits control ecosystem dynamics (Ellison et al. 2005). *Tsuga caroliniana* is considered to be a foundation species (Austin et al. 2016, Ellison et al. 2005, Havill et al. 2008, and Vose et al. 2013) because its overstory creates microclimates in the understory with uniformly low seasonal light level variability and relatively small daily temperature fluctuations (Austin et al. 2016, Rentch et al. 2000, and Jetton et al. 2008). It modifies soil conditions and microclimate by depositing acidic litter and maintaining low light levels in the understory, thus influencing fundamental community and ecosystem characteristics (Austin et al. 2016, and Rentch et al. 2000). *Tsuga caroliniana* provides shelter and food for many wildlife and insect species including *Odocoileus virginianus* (white-tailed deer), *Semiothisa fissinotata* (hemlock angle moths), *Feniseca tarquinius* (harvest butterflies), *Felis rufus* (bobcats), *Clethrionomys gapperi* (red-backed voles), *Sorex palustris* (northern water shrews), and other animals (Brown 2004, Spaulding and Rieske 2010, US Department of the Interior 2000 cited in Brown 2004, and Weckel et al. 2006).

Shrubs and Exclusion of Woody Plants

Nielsen et al. (1999, and 2001) found that *Rhododendron maximum* L. was responsible for reduction in growth of other woody plant species due to production of dense shade and reduction of other resources, and that allelopathy possibly played a role. Ericaceae shrubs found in *Tsuga caroliniana* stands such as *Kalmia latifolia* L. and *Rhododendron catawbiense* Michx., *R. maximum* and *R. minus* Michx., reduced tree species recruitment by shading saplings and reducing soil productivity through its nutrient-poor litter that is slow to decompose (Brown 2004, and Monk et al. 1985). Humphrey (1989), while investigating the findings of Palmer (1987) on the suppression of tree seedling establishment by *Kalmia latifolia* and *Rhododendron catawbiense* and *R. maximum,* found that *Tsuga caroliniana* and *Acer rubrum* were not suppressed while species in the *Quercus* genus were, but others have found *Rhododendron maximum* strongly restricts the survivability of all seedlings thus limiting their ability to transition to sapling size (Beier et al. 2005, Dharmadi et al. 2019, and Hille Ris Lambers and Clark 2013).

Acer rubrum also suppresses other species through high densities of < 15cm tall newly emergent seedlings in the regeneration layer, and Spaulding and Rieske (2010) suggest that this phenomenon is ephemeral. The species rapidly responds to canopy disturbances (Spaulding and Rieske 2010, and Walters and Yawney 1990) due to its high densities and ability to establish itself in shaded understories. In a regeneration layer with more available light, *Betula lenta* L. and *Liriodendron tulipifera* will become more dominant in the canopy than *Acer rubrum* (Beck and Hooper 1986). However, *Acer rubrum* can still replace itself in the canopy, and thus can gradually replace the *Quercus spp.* population in the canopy through greater recruitment (Copenheaver et al. 2006).

Tsuga caroliniana Stands

A late successional forest dominated by *Tsuga caroliniana*, is described by Brown (2004) and Austin et al. (2016), as conditions where the species has high densities, large basal areas, and high importance values. Humphrey (1989) proposed that *Tsuga caroliniana* characteristics (slow growth rate, long life span, shade tolerance, and small evergreen leaves) were compatible with the stress tolerant strategy contained in the three-strategy concept of Grimes (1977, and 1979 cited in Humphrey 1989), and these findings were confirmed by Humphrey's (1989) and Rentch et al's (2000) work. The stress tolerant strategy described by Grime's (1977, and 1979 cited in Humphrey 1989) three-strategy concept involves traits associated with competition and resource exploitation following a disturbance where productivity is chronically low because of limited resources. *Tsuga caroliniana* slowly replaces preestablished species, becoming dominant in later stages of succession where it is difficult for other species to establish (Humphrey 1989). *Quercus alba* and *Q. rubra* also had high importance values and dominant canopy positions in Austin et al.'s (2016) study of late successional *Tsuga caroliniana* stands where these two species along with *Tsuga caroliniana,* accounted for over 95 percent of the trees (Austin et al. 2016).

Predicted Functional Extinction

Currently *Tsuga caroliniana* is a species of concern, being listed as "Near Threatened" on the IUCN Red List, due to its threatened elimination by *Adelges tsugae* Annand (hemlock wooly adelgid), an exotic invasive insect from Japan that is causing mortality throughout *Tsuga caroliniana's* range (Austin et al. 2016, Beane et al. 2010, Brown 2004, Jetton et al. 2008, and Potter et al. 2017). *Tsuga caroliniana* is predicted to be functionally extinct between 2050 and

2063 (Austin et al. 2016, Levy and Walker 2014, and Vose et al. 2013). Spaulding and Rieske (2010) used the Forest Vegetation Simulator (Donnelly et al. 2001 cited in Spaulding and Rieske 2010) to look 20 years into the future at *Tsuga canadensis* (L.) Carr. (eastern hemlock) stands with and without the adelgid, and found complete loss of stands with the exotic invasive adelgid and little change in composition and structure without it. While the relative isolation of *Tsuga caroliniana* makes them more resistant to the transmission of *Adelges tsugae* than *Tsuga canadensis,* when it does arrive the small hemlock populations rapidly collapse (Austin et al. 2016, and Levy and Walker 2014).

With its narrow geographic range and specialized habitat preference, natural populations are predicted to decline rapidly (Austin et al. 2016, and Levy and Walker 2014). Mortality of *Tsuga caroliniana* due to the adelgid allows codominant *Quercus* spp. to occupy the new canopy space, leading to a hardwood forest with an increased density of *Quercus alba* and *Q. rubra, Kalmia latifolia,* and *Rhododendron catawbiense, R. maximum,* and *R. minus* (Austin et al. 2016, Brown 2004, and Monk et al. 1985).

Disturbance in Southern Appalachian Forests

Fire, ice storms, and human manipulation, whether present or absent, are the three primary disturbance agents in the southern Appalachians (Copenheaver et al. 2006). The fire history of the area in general is composed of an era up until the mid-1800s where low intensity ground fire prevailed, then a period until the 1920s where logging and high intensity stand replacing fires were common, and then a final era where fire suppression was practiced (Brose et al. 2001, Copenheaver et al. 2006, and Van Lear and Waldrop 1989). There were also droughts in the 1950s and 1960s in the eastern US that influenced regeneration and growth patterns in the

Appalachians (Copenheaver et al. 2006, Jenkins and Pallardy 1995, McClenahen and Dochinger 1985 cited in Copenheaver et al. 2006, Orwig and Abrams 1997, and Rubino and McCarthy 2000). When fire is absent, *Quercus* spp. are unable to establish in shaded overstory, so shade-tolerant and fire-intolerant species such as *Acer rubrum, Pinus strobus, and Nyssa sylvatica* outcompete and become more dominant than *Quercus spp.* (Abrams 1992, Brose et al. 2001, Christensen 1977, Copenheaver et al. 2006, and Shuler and McClain 2003). When fire is present, it creates even-aged hardwood stands dominated by *Quercus* spp. (Copenheaver et al. 2006).

Ice storms have been shown to produce substantial damage to mid-slopes and ridges due to exposure of these areas to weather (Copenheaver et al. 2006, Lafon et al. 1999, Millward and Kraft 2004, and Warrilow and Mou 1999). Ice storms create canopy gaps from branch damage in the overstory allowing higher rates of shrub and sapling establishment (Copenheaver et al. 2006, and Rebertus et al. 1997). Ice storms in the southern Appalachians have a substantial effect on stand density, regeneration patterns, and understory species composition (Bragg et al. 2003, Copenheaver et al. 2006, Rebertus et al. 1997, and Rhoades 2002).

CHAPTER 3: MANUSCRIPT

Introduction

The geographic range of *Tsuga caroliniana* (Carolina hemlock) once covered much of the Northern hemisphere (Jetton et al. 2008). The species was originally discovered in Pickens County, South Carolina in 1837, and named in 1881 by George Engelmann (Rentch et al. 2000). *Tsuga caroliniana* can achieve heights of 20 m and diameters of 80 cm at breast height (Jetton et al. 2008). It is typically found associated with *Quercus montana* (chestnut oak), *Tsuga canadensis* (eastern hemlock), *Kalmia latifolia* (mountain laurel), *Acer rubrum* (red maple), *Rhododendron* spp. (rhododendron), and *Amelanchier arborea* (Michx. f.) Fern. (serviceberry) (Humphrey 1989, Jetton et al. 2008, and Rentch et al. 2000). The species is shade and drought tolerant and tends to outcompete other species in undisturbed environments where it is found (Jetton et al. 2008).

Tsuga caroliniana is now found only in small isolated populations in Georgia, North Carolina, South Carolina, Tennessee, and Virginia within a roughly 150 km by 450 km area (Jetton et al. 2008; Figure 1). The southern Appalachian Mountains have an annual precipitation range from 1,813 mm to 2,500 mm, and a mean annual temperature of 13 degrees Celsius (Brown 2004). *Tsuga caroliniana* stands are small and isolated even in the densest core of the range (Jetton et al. 2008, Humphrey 1989, and Potter et al. 2017). Their populations at their largest are only moderate in size, and are more commonly found as only a few trees, spread discontinuously across the landscape (Potter et al. 2017). It is considered a rare endemic species that occurs on exposed cliffs, ridges, and slopes at elevations between 600 m and 1,500 m in the southern Appalachian Mountains of western North Carolina and southwestern Virginia (Jetton et al. 2008). Although occurring less often, the species can also be found beside streams in cool moist ravines and in the Piedmont of North Carolina and Virginia at elevations between 100 m and 600 m (Jetton et al. 2008). *Tsuga caroliniana* has been listed as "Near Threatened" because of the predicted decline of its small isolated populations due to *Adelges tsugae* (Austin et al. 2016, Brown 2004, Jetton et al. 2008, Levy and Walker 2014, and Potter et al. 2017). *Quercus* spp. trees and Ericaceae shrubs are predicted to replace *Tsuga caroliniana* in these stands (Austin et al. 2016, and Brown 2004). Physiography is a key element in the demarcation of the range of *Tsuga caroliniana*, and is suspected as a contributing factor in the rate of decline caused by the wooly adelgid because populations in proximity tend to have similar in levels of infestation and condition (Austin et al. 2016, and Levy and Walker 2014). Toward the southern limit of its range, *Tsuga caroliniana* is limited by high temperatures, frequent fires, and a lack of suitable rock outcroppings (Austin et al. 2016, and Jetton et al. 2008). The species range is limited in the north by low precipitation and hardwood competition that is an artifact of low frequency fires (Austin et al. 2016, and Jetton et al. 2008).

The architecture and functional ecology of a foundation species defines a forest's structure, and its species-specific traits control ecosystem dynamics (Ellison et al. 2005). Where it is a foundation species, *Tsuga caroliniana* modifies the light, temperature, and soil pH regimes under its canopy creating a darker more acidic microclimate with lower temperature fluctuations (Austin et al. 2016). Water can be a limiting factor for the species during the growing season with positive, strong, and consistent relationships between radial growth and available moisture (Austin et al. 2016). While its presence on cliffs exposes it to storms that limit chances of older trees reaching larger diameters, these conditions are ideal for establishment due to the exposed nature of the stress prone environment where *Tsuga caroliniana* has a competitive advantage over other species (Austin et al. 2016, and Levy and Walker 2014).

Knowledge of *Tsuga caroliniana* population and community structure is important for understanding population history. However, only a few reports occur in the literature, and the limited results are inconsistent across populations (Levy and Walker 2014). All age classes appear to respond negatively to higher temperatures, but the young trees respond more strongly, thus temperatures predicted for climate change are likely to be detrimental (Austin et al. 2016). Characteristics of some stands indicate gap-phase dynamics associated with loss of species and extreme weather events (Austin et al. 2016), while others appear to display more of an on-going reproduction and recruiting dynamic (Humphrey 1989, Levy and Walker 2014, and Rentch et al. 2000). Before the introduction of the wooly adelgid *Tsuga caroliniana* populations were exhibiting successful regeneration and healthy, densely populated overstories, but they may now be replaced by hardwood trees and some shrub species of the Ericaceae family (Austin et al. 2016).

The purpose of this research was to describe *Tsuga caroliniana* and its community characteristics across the landscape where it is currently found in North Carolina and Tennessee. The three specific questions asked were: (1) Does the physiography where *Tsuga caroliniana* is found vary? (2) Do the community density, size, and diversity of *Tsuga caroliniana* stands vary? (3) Is variation in *Tsuga caroliniana* age, density, and size related to the variation in physiography and/or community density, size, and diversity?

Methods

Site Selection

Occurrence data from the US Forest Service and Camcore at NCSU (K. Frick, US Forest Service, Asheville, NC and W. Whittier, Camcore, Asheville, NC, 2016 unpublished data) were used to locate five *Tsuga caroliniana* sites where stem densities indicated they comprised a major component of the overall stand population. These stands were located in the densest portion of the species' range, within US Forest Service National Forests (Figure 1), because this is one of the most easily estimated indicators of a late successional forest dominated by *Tsuga caroliniana* (Austin et al. 2016, and Brown 2004). Within each site, four study plots were established for a total of 20 plots. At each site, elevations and aspects of the *Tsuga caroliniana* stands were determined. Plot locations were randomly selected to sample the elevation and aspect gradient and to maximize distance between plots within a site. In addition, plots were located to maximize the number of mature *Tsuga caroliniana* individuals (Austin et al. 2016) to capture data from the latest successional stage of *Tsuga caroliniana* stands possible to examine variation at this stage of stand development.

Austin et al.'s (2016) research described composition, structure, and age of *Tsuga caroliniana* stands, so the same size plots and some of the same methods were used in our study so the results of the two studies could be compared. Plots within sites were at least 75 meters apart, and also 0.05 ha (12.62 m radius) in size as per Austin et al. (2016). Subplots, with a 2.5 m radius, were established along the centerline of each plot; at plot-center, 10 m north of plot-center, and 10 m south of plot-center. The subplots were installed for measuring small tree, shrub, and canopy density variables that were impractical for surveying at the whole plot level.

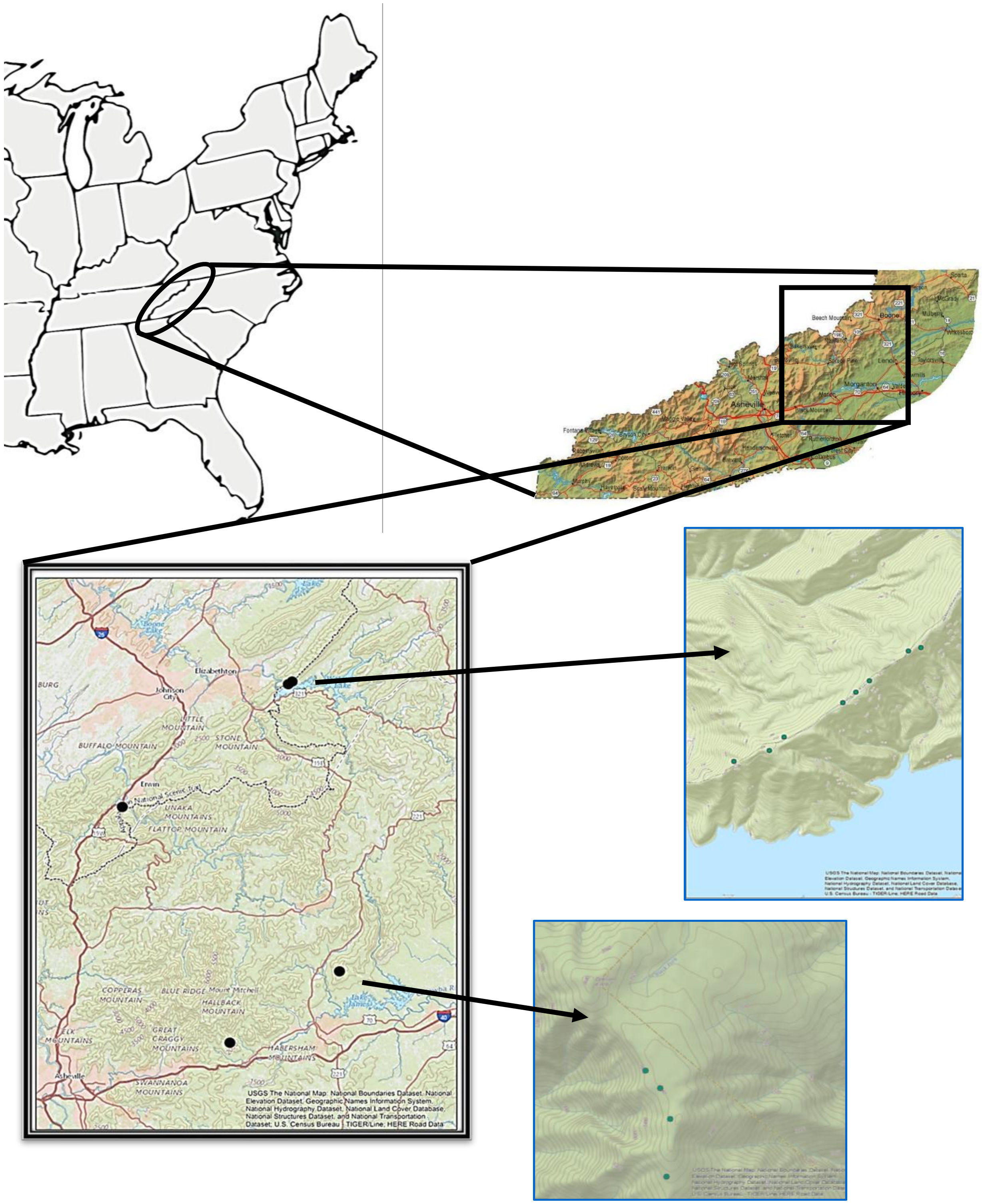


Figure 1. Natural Range of *Tsuga caroliniana* and location of the stands studied

Data Collection and Calculations

Landform and Terrain Shape along with elevation and aspect were physiographic variables used to address whether there was variation between the study sites and if they were related to variations in *Tsuga caroliniana* age, density, and size. Elevation was measured at the plot center using a GPS unit. Aspect was measured with a compass at the plot center. Eight measurements were made to calculate landform index (LFI) and terrain shape index (TSI), starting with the aspect and adding 45 degrees for each additional measurement. A clinometer was used to measure the vertical angle of the inclination to the horizon, due to the variable long distance, for LFI calculations, and a hypsometer was used to measure the vertical angle of the inclination to the boundary of the plot, due to the shorter fixed 12.62m distance, for TSI calculations (McNab 1989, and 1993). LFI and TSI were calculated according to McNab's protocols (1993, and 1989).

Community and individual woody plant variables were used for evaluating variation among sites and their relationship to variations in *Tsuga caroliniana* age, density, and size variables. The variables used were summer and winter canopy density, canopy percentage evergreen, mean diameter at breast height (DBH, 1.4 m above the highest point of ground adjacent to the tree), importance values, species richness, evenness, diversity, percent ground cover of shrubs, and stem density of all trees and snags.

Shade readings for canopy calculations were measured in all four cardinal directions at each of the three nested subplot centers with a convex spherical densiometer, both before and after the growing season (Lemon 1957, and Stickler 1959). Canopy density measurements were calculated from the shade readings at each subplot according to the standard methods outlined by Strickler (1959), and these three subplot measurements were averaged for the associated plot value. Instead of using Lemon's (1957) method that gives artificially high readings and requires individual judgement, I used Strickler's (1959) method where only 17 of the grid line intersections on the face of the instrument opposite the operator are used for each directional reading, and every point of shade measured with the densiometer has a 1.5 percent value when measuring canopy density at the plot level. The winter average canopy density was divided by the summer average canopy density for each plot to establish percent evergreen.

Species, DBH, and live/dead status for all trees greater than or equal to 5.0 cm DBH were measured. The 5.0 cm DBH is the minimum used to distinguish overstory trees from regeneration (Austin et al. 2016, Hart et al. 2012, and Levy and Walker 2014). Regeneration and shrub layer data were collected in the subplots. Trees < 5.0 cm DBH (Hart et al. 2012) were counted for each species and shrubs were inventoried by identifying to at least the Genus taxonomic level, and visually estimating their percent cover to the nearest 5 percent as per Austin et al. (2016). Importance values of overstory trees were calculated using relative tree density, frequency, and dominance of overstory trees. Hill's Diversity Number 0 was chosen as a measure of species richness because of the equivalence of sample size and because the individual species have known proportional abundances (Ludwig and Reynolds 1988). The modified Hill's Ratio, which is relatively uninfluenced by species richness, was chosen as a measure of evenness. Its interpretation is less ambiguous because there is not a requirement to estimate the number of species in the community, and as a single species becomes more dominant, the index approaches zero instead of one (Ludwig and Reynolds 1988). Shannon's Diversity Index, the most common diversity index used in community ecology, was chosen as a measure of diversity (Ludwig and Reynolds 1988). Species richness, evenness, and diversity were calculated according to Ludwig and Reynolds (1988).

Tsuga caroliniana age, density, and size variables were used to determine if relationships existed with community density, size, diversity, and physiography. The density and size variables were measured with the other similar data for the other species of trees. Two cores were extracted using an increment borer from each overstory *Tsuga caroliniana* tree at 0.5 m above the root collar parallel to the slope contour (Austin et al. 2016, Speer 2010, and Stokes and Smiley 1968). *Tsuga caroliniana* cores were processed following standard dendrochronological techniques (Speer 2010, and Stokes and Smiley 1968), and rings were counted to estimate age.

Data Analysis

Of the live trees in the overstory, 15 species (*Acer pensylvanicum* L., *Amelanchier arborea*, *Betula lenta*, *Carya cordiformis* (Wang.) K. Koch and *C. tomentosa* (Poir.) Nutt., *Castanea dentata* (Marsh.) Borkh., *Fagus grandifolia* Ehrh., *Liriodendron tulipifera*, *Magnolia acuminata* L., *Pinus virginiana* Mill., *Prunus serotina, Quercus alba*, *Q. falcata* Michx., and *Q. velutina* Lam., and *Robinia pseudoacacia* L.) were consolidated into an "Other" category for analyses because their importance values were below twelve, and they occurred in two or fewer sites, and seven or fewer plots. The "Other" category of snags was designated for the same reason as live trees and differed from live trees. It included *Acer pensylvanicum*, *Amelanchier arborea*, *Betula lenta*, *Castanea dentata* and *C. pumila* (L.) Miller, *Cornus florida* L., *Liriodendron tulipifera*, *Nyssa sylvatica*, *Oxydendrum arboretum*, *Pinus echinata* Mill. and *P. virginiana*, *Quercus alba*, *Q. coccinea* Muenchh., *Q. rubra*, and *Q. velutina*, *Sassafras albidum* (Nutt.) Nees, snags identified only to the genus level (*Carya* spp., *Pinus* spp., *Quercus* spp.), and snags that could not be identified.

All statistical analyses were done using R (R 2016). Variation among the variables at the site and plot within site levels were analyzed using analysis of variance, where plot nested within site had 15 degrees of freedom. Models including species and site by species interactions as factors had variable degrees of freedom for these factors because the number of species varied among plots. The Tukey test ($p < 0.05$) was used to separate means for establishing patterns of deviation among sites.

Regression analyses were used to examine relationships between *Tsuga caroliniana* and stand characteristics. *Tsuga caroliniana* age, density, and size were separately used as dependent variables in simple univariable linear regressions where the independent variable was one of the physiography and community composition and structure variables analyzed with ANOVA above. Variables in statistically significant simple linear regressions ($p < 0.10$) were combined in multivariable linear regression analyses with the others from the same dependent variable.

Results

The 20 plots ranged in elevation from 618 m to 1,118 m (Table 1) and varied among sites ($p < 0.0001$). Elevation ranges at each site were 618 m – 725 m (Cliff Ridge), 1,091 m – 1,118 m (Dobson's Knob), 932 m – 963 m (Iron Mountain (Top)), 854 m – 920 m (Iron Mountain (Bottom)), and 706 m – 855 m (Lost Cove). Plots faced generally to the northwest and overall site aspect did differ ($p = 0.0751$; Table 1). Three of the four plots at all sites except at Dobson's Knob faced northwest. The plots at Dobson's Knob all faced southwest. The LFI indicated that most plots were in a bowl-type topographical position, but varied among sites ($p = 0.0253$; Table 1) with some sites in deeper depressions than others. The Dobson's Knob site was located in a shallower concavity compared to Cliff Ridge ($p = 0.0703$) and Lost Cove ($p = 0.0370$) that were

Table 1. Variation in abiotic characteristics among five sites containing *Tsuga caroliniana* in the mountains of North Carolina and Tennessee

Variable	**Mean**					**ANOVA**	
	Cliff Ridge	**Dobson's Knob**	**Iron Mountain (Top)**	**Iron Mountain (Bottom)**	**Lost Cove**	**Mean ± Std Dev**	**p-value**
Elevation (m)	665.8	1107.5	946.5	895.3	811.0	885.2 ± 154.3	< 0.0001
Aspect (°)	326.3	228.8	347.5	360.0 (0)	341.3	320.7 ± 75.4	0.0751
Landform Index[1]	0.2	0.1	0.1	0.1	0.2	0.2 ± 0.1	0.0253
Terrain Shape Index[2]	-0.6	0.1	-0.2	0.1	-0.3	-0.2 ± 0.4	0.1030

[1] Topographic index for quantifying slope position and landform (McNab 1992)
[2] Quantitative expression of geometric shape of the land surface (McNab 1989)

in deeper depressions (Table 1). All plots were located mid-slope on sloping terrain with minimal undulations, and TSI did not differ among sites ($p = 0.1030$; Table 1). Most of the stands were dense, with more than 1,100 trees (≥ 5.0 cm DBH) per site (Table 2). *Tsuga caroliniana* had greater stems/ha than any other species (Table 2), and the percentage of *Tsuga caroliniana* trees in the overstory differed significantly ($p = 0.0090$) across sites. It was lowest at Iron Mountain (Top) at 29.6 %, and highest at Lost Cove at 64.7 %. Iron Mountain (Bottom) and Lost Cove had over 50 percent *Tsuga caroliniana* stems which was significantly greater ($p < 0.07$) than most other species' densities (Table 2).

Acer rubrum and *Quercus montana* also had relatively high stem densities at all sites. Stem densities of the "Other" species were variable where Cliff Ridge had four species (mean 65 stems/ha), Dobson's Knob had three (mean 30 stems/ha), Iron Mountain (Top) had ten (mean 260 stems/ha), Iron Mountain (Bottom) had three (mean 65 stems/ha), and Lost Cove had one (mean 5 stems/ha).

The density of trees at the regeneration level did not vary among sites ($p = 0.4590$), but did among species ($p < 0.0001$) where *Acer rubrum* regeneration was significantly greater ($p < 0.06$) than eight other species. The percentage of *Tsuga caroliniana* trees in the regeneration layer was similar among sites ($p = 0.1080$). The percent cover of shrubs did not vary among sites ($p = 0.7660$).

Iron Mountain (Bottom) and Lost Cove had approximately double the mean total number of snags compared to the other sites (Table 3). The majority of snags were *Tsuga caroliniana*, but *Acer rubrum* and *Pinus pungens* Lamb. were also present at higher densities at most sites (Table 3). Overstory snag density did not vary by site ($p = 0.4691$), but did vary at the species level ($p = 0.0004$) with *Acer rubrum* ($p = 0.3750$) and *Pinus strobus* ($p = 0.2620$) being the only

Table 2. Mean density of trees ≥ 5 cm DBH in five sites containing *Tsuga caroliniana* in the mountains of North Carolina and Tennessee

Species	**Mean Number of Trees/Hectare**					**ANOVA**	
	Cliff Ridge	**Dobson's Knob**	**Iron Mountain (Top)**	**Iron Mountain (Bottom)**	**Lost Cove**	**Mean ± Std Dev**	**p-value**
Tsuga caroliniana	515	435	330	875	1095	162.5 ± 110.0	0.0472
Nyssa sylvatica	20	455	5	10	160	32.5 ± 54.6	0.0020
Acer rubrum	140	40	170	135	165	32.5 ± 24.8	0.3690
Quercus montana	105	130	50	155	60	25.0 ± 23.0	0.4680
Pinus strobus	310	5	0	30	0	17.3 ± 38.7	0.0025
Oxydendrum arboreum	65	25	50	115	0	12.8 ± 15.3	0.0639
Quercus rubra	60	10	130	45	5	12.5 ± 16.4	0.0280
Pinus pungens	50	30	0	5	115	10.0 ± 12.2	0.0002
Carya glabra	10	0	125	50	0	9.3 ± 18.3	0.0512
Quercus coccinea	50	110	0	0	10	8.5 ± 14.7	0.0142
Other[1]	65	30	260	65	5	21.3 ± 27.9	0.0009
Total	**1390**	**1270**	**1120**	**1485**	**1615**	47.8 ± 67.6	0.1340

[1] Includes *Acer pensylvanicum*, *Amelanchier arborea*, *Betula lenta*, *Carya cordiformis* and *tomentosa*, *Castanea dentata*, *Fagus grandifolia*, *Liriodendron tulipifera*, *Magnolia acuminata*, *Pinus virginiana*, *Prunus serotina*, *Quercus alba*, *falcata*, and *velutina*, and *Robinia pseudoacacia*

Table 3. Mean density of snags ≥ 5cm DBH in five sites containing *Tsuga caroliniana* in the mountains of North Carolina and Tennessee

Species	**Mean Number of Snags/Hectare**						
	Cliff Ridge	**Dobson's Knob**	**Iron Mountain (Top)**	**Iron Mountain (Bottom)**	**Lost Cove**	**ANOVA**	
						Mean ± Std Dev	**p-value**
Tsuga caroliniana	170	70	120	600	540	75 ± 87.2	0.0609
Pinus pungens	90	110	0	10	60	13.5 ± 16.1	0.0363
Pinus strobus	45	5	0	25	0	5.3 ± 13.8	0.2620
Acer rubrum	5	25	15	40	15	5.0 ± 6.3	0.3750
Quercus montana	0	5	15	30	0	2.5 ± 4.4	0.0600
Other[1]	25	155	105	65	10	18 ± 17.8	0.0068
Total	**335**	**370**	**255**	**770**	**625**	34.1 ± 54.2	0.4691

[1] Includes *Acer pensylvanicum*, *Amelanchier arborea*, *Betula lenta*, *Castanea dentata* and *pumila*, *Cornus florida*, *Liriodendron tulipifera*, *Nyssa sylvatica*, *Oxydendrum arboretum*, *Pinus echinata* and *virginiana*, *Quercus alba*, *coccinea*, *rubra*, and *velutina*, *Sassafras albidum*, snags identified only to the genus level (*Carya* spp., *Pinus* spp., *Quercus* spp.), and snags that could not be identified.

two species whose snag densities did not vary significantly across sites (Table 3). In contrast to the high numbers of live trees (Table 2), *Nyssa sylvatica*, *Oxydendrum arboreum*, *Quercus coccinea* and *Q. rubrum*, and *Carya glabra* (Mill.) Sweet, did not have many snags (Table 3).

Mean diameter of live overstory trees varied among sites ($p < 0.0001$; Table 4) with trees at both Iron Mountain sites being significantly ($p < 0.0008$) larger than at other sites. Trees had overall smaller total mean diameters at Cliff Ridge and Dobson's Knob (Table 4). *Tsuga caroliniana* mean DBH varied among sites ($p < 0.0001$), but the trees were generally smaller than most species, with a mean DBH at least 2 cm less than most other species (Table 4). Cliff Ridge had the smallest average DBH of overstory *Tsuga caroliniana* trees at 12.3cm. Dobson's Knob, at 17.6cm, had the largest average *Tsuga caroliniana* DBH followed by Lost Cove at 16.1cm (Table 4), and both of them were significantly larger ($p < 0.004$) than all other sites. *Acer rubrum* also had relatively small diameters across sites and *Nyssa sylvatica* had the smallest mean diameter across sites while the *Quercus* genus had the largest (Table 4).

Despite having lower biomass than most species, *Tsuga caroliniana* generally had the highest importance value at all sites, with a value of 22.7 more than the next highest species' importance (Table 5; Figure 2). *Quercus montana* and *Q. rubra* and *Acer rubrum* also had relatively higher importance values compared to other species whose importance values ranged from 12.4 to 20.4 (Table 5; Figure 2).

Estimated age of overstory *Tsuga caroliniana* trees varied among sites ($p < 0.0001$). Dobson's Knob had the oldest individual tree at 149 years and Iron Mountain (Top) the youngest at 18. The youngest trees were located at Cliff Ridge (average age = 48.9), while the oldest Carolina hemlock trees were located at Lost Cove (average age = 65.0 years). Lost Cove was significantly older ($p < 0.0001$) than all other sites where average age was within five years of

Table 4. Mean DBH of trees ≥ 5 cm DBH in five sites containing *Tsuga caroliniana* in the mountains of North Carolina and Tennessee

Species	**Mean DBH (cm)**					**ANOVA**	
	Cliff Ridge	**Dobson's Knob**	**Iron Mountain (Top)**	**Iron Mountain (Bottom)**	**Lost Cove**	**Mean ± Std Dev**	**p-value**
Quercus rubra	16.7	18.0	33.4	46.5	16.5	30.8 ± 22.0	0.0071
Quercus montana	18.4	23.7	42.4	32.8	30.5	28.1 ± 15.5	<0.0001
Quercus coccinea	26.0	22.9	n/a[1]	n/a	12.4	23.2 ± 8.9	0.0238
Carya glabra	13.8	n/a	19.5	23.8	n/a	20.3 ± 10.3	0.2381
Pinus pungens	18.2	13.1	n/a	33.3	19.3	18.5 ± 7.4	0.0420
Oxydendrum arboreum	11.4	16.8	15.1	21.5	n/a	17.2 ± 6.8	<0.0001
Pinus strobus	15.9	11.0	n/a	24.0	n/a	16.5 ± 8.4	0.0553
Tsuga caroliniana	12.3	17.6	13.2	13.4	16.1	14.7 ± 7.0	<0.0001
Acer rubrum	12.9	11.9	13.7	18.2	11.1	13.7 ± 8.0	0.0029
Nyssa sylvatica	6.7	10.5	5.0	7.1	10.5	10.3 ± 4.4	0.2550
Other[2]	19.7	10.3	22.5	26.7	31.9	22.0 ± 15.4	0.2041
Total	**15.6**	**15.6**	**20.6**	**24.7**	**18.5**	16.8 ± 10.9	<0.0001

[1] n/a = no trees of this species occurred in the sampled plots on the site
[2] Includes *Acer pensylvanicum*, *Amelanchier arborea*, *Betula lenta*, *Carya cordiformis* and *tomentosa*, *Castanea dentata*, *Fagus grandifolia*, *Liriodendron tulipifera*, *Magnolia acuminata*, *Pinus virginiana*, *Prunus serotina*, *Quercus alba*, *falcata*, and *velutina*, and *Robinia pseudoacacia*

Table 5. Species importance values of trees ≥ 5 cm DBH in five sites containing *Tsuga caroliniana* in the mountains of North Carolina and Tennessee

Species	**Importance Values[1]**						**ANOVA (Basal Area/ha)**	
	Cliff Ridge	**Dobson's Knob**	**Iron Mountain (Top)**	**Iron Mountain (Bottom)**	**Lost Cove**	**Mean**	**Mean ± Std Dev**	**p-value**
Tsuga caroliniana	53.6	59.7	48.2	74.3	94.0	66.0	0.4 ± 0.5	0.0002
Quercus montana	30.5	45.2	56.3	38.2	46.1	43.3	1.6 ± 1.8	0.0033
Quercus rubra	22.3	19.9	51.7	42.6	13.3	30.0	2.0 ± 3.0	0.0229
Acer rubrum	27.2	18.8	34.2	26.6	32.2	27.8	0.4 ± 0.6	0.1045
Nyssa sylvatica	8.7	53.8	4.7	7.8	26.9	20.4	0.2 ± 0.2	0.0563
Pinus pungens	23.4	19.2	0.0	18.9	36.8	19.7	0.5 ± 0.5	0.0466
Quercus coccinea	37.9	38.7	0.0	0.0	14.4	18.2	0.7 ± 0.8	0.0006
Oxydendrum arboreum	17.7	19.5	20.7	27.0	0.0	17.0	0.5 ± 0.4	<0.0001
Pinus strobus	42.3	8.4	0.0	19.7	0.0	14.1	0.5 ± 0.6	0.0167
Carya glabra	10.0	0.0	34.5	17.7	0.0	12.4	0.6 ± 0.8	0.0356
Other[2]	26.5	16.7	49.5	27.1	36.3	31.2	1.1 ± 1.6	0.1990

[1] Combined measure of species relative density, dominance and frequency

[2] Includes *Acer pensylvanicum*, *Amelanchier arborea*, *Betula lenta*, *Carya cordiformis* and *tomentosa*, *Castanea dentata*, *Fagus grandifolia*, *Liriodendron tulipifera*, *Magnolia acuminata*, *Pinus virginiana*, *Prunus serotina*, *Quercus alba*, *falcata*, and *velutina*, and *Robinia pseudoacacia*

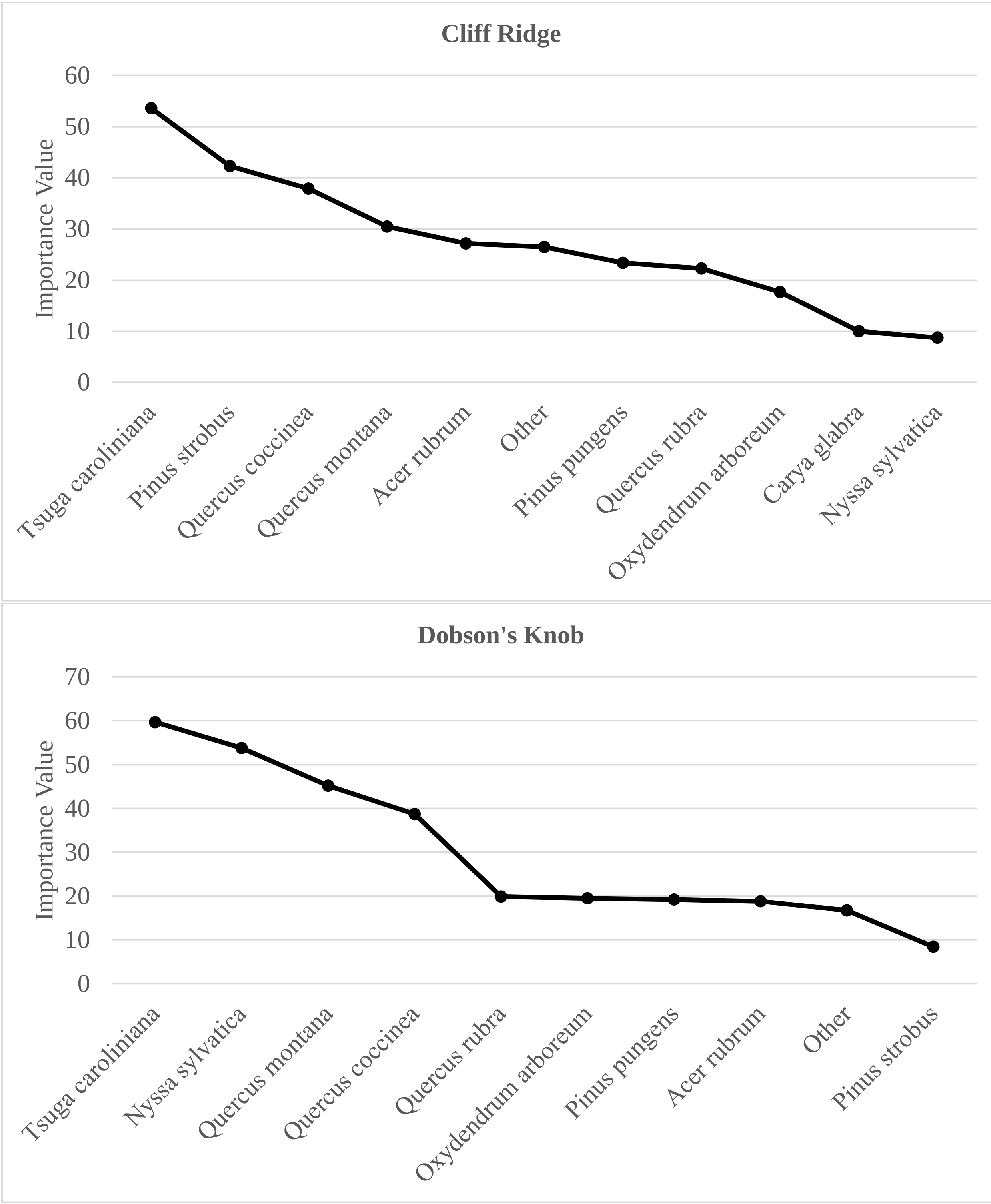
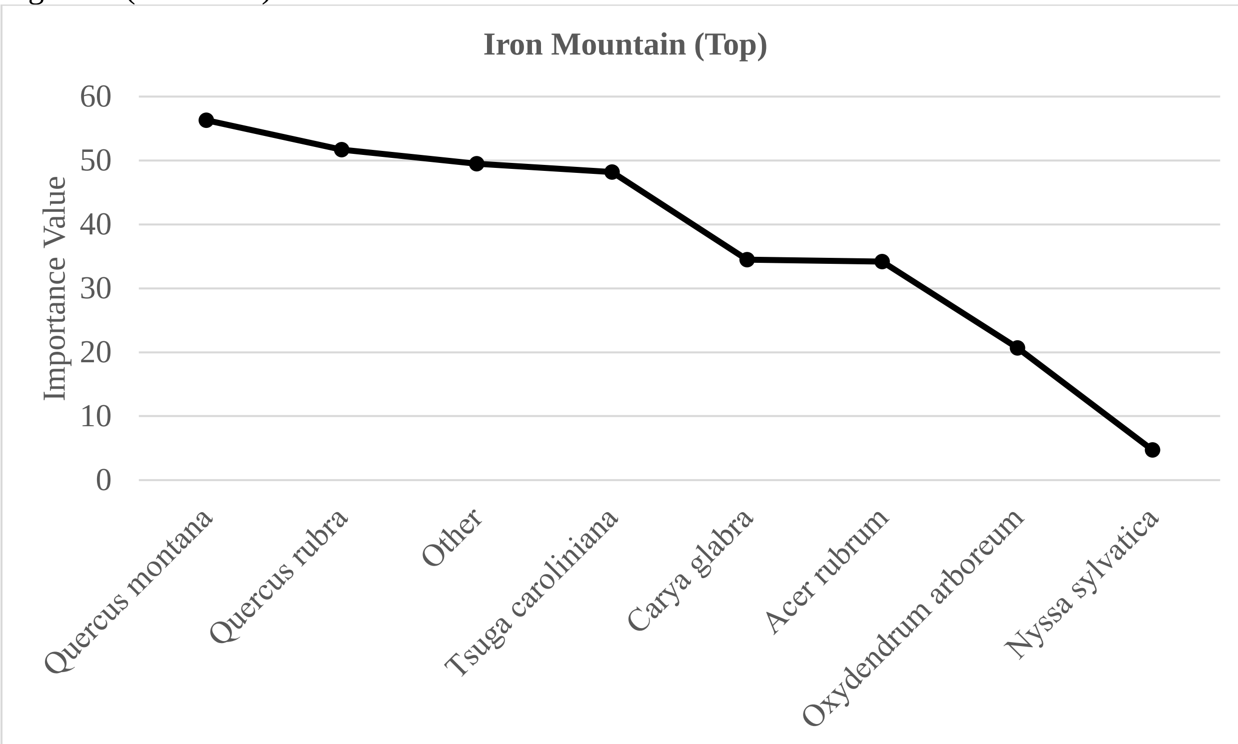


Figure 2. Dominance diversity curves (importance values) of trees ≥ 5 cm DBH for five sites containing Tsuga caroliniana in the mountains of North Carolina and Tennessee

Figure 2. (continued)



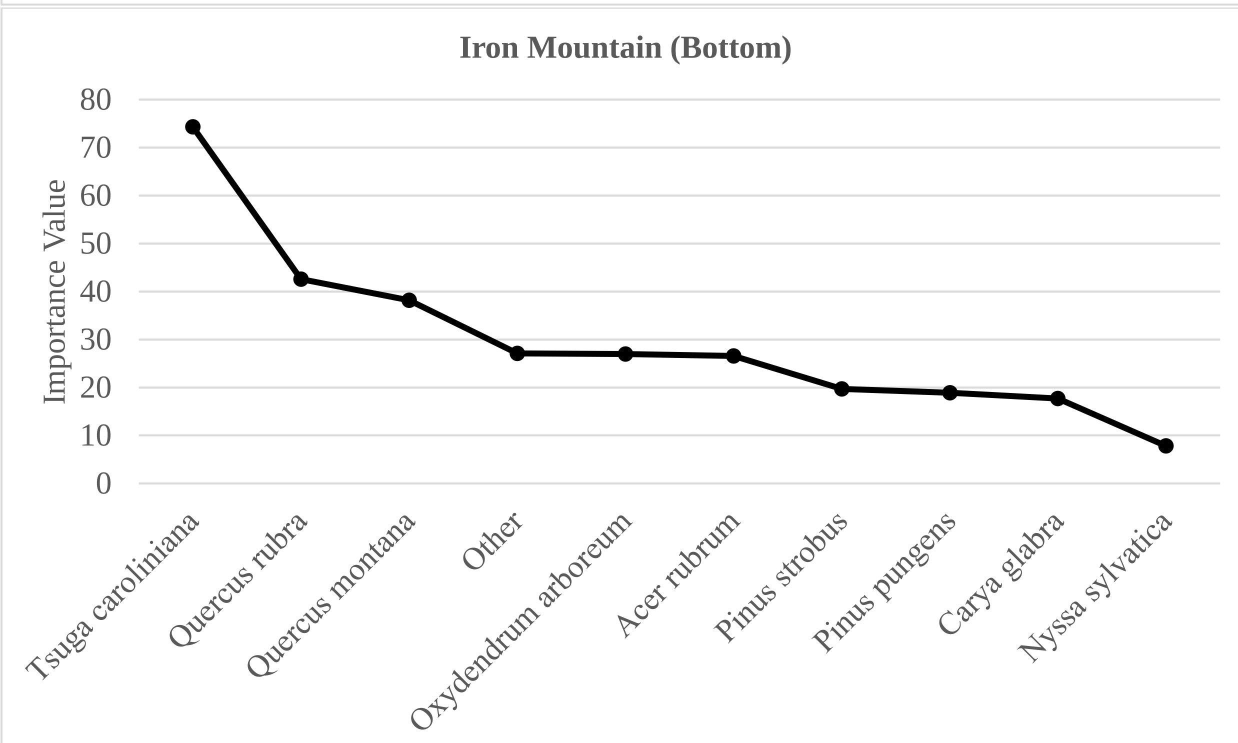
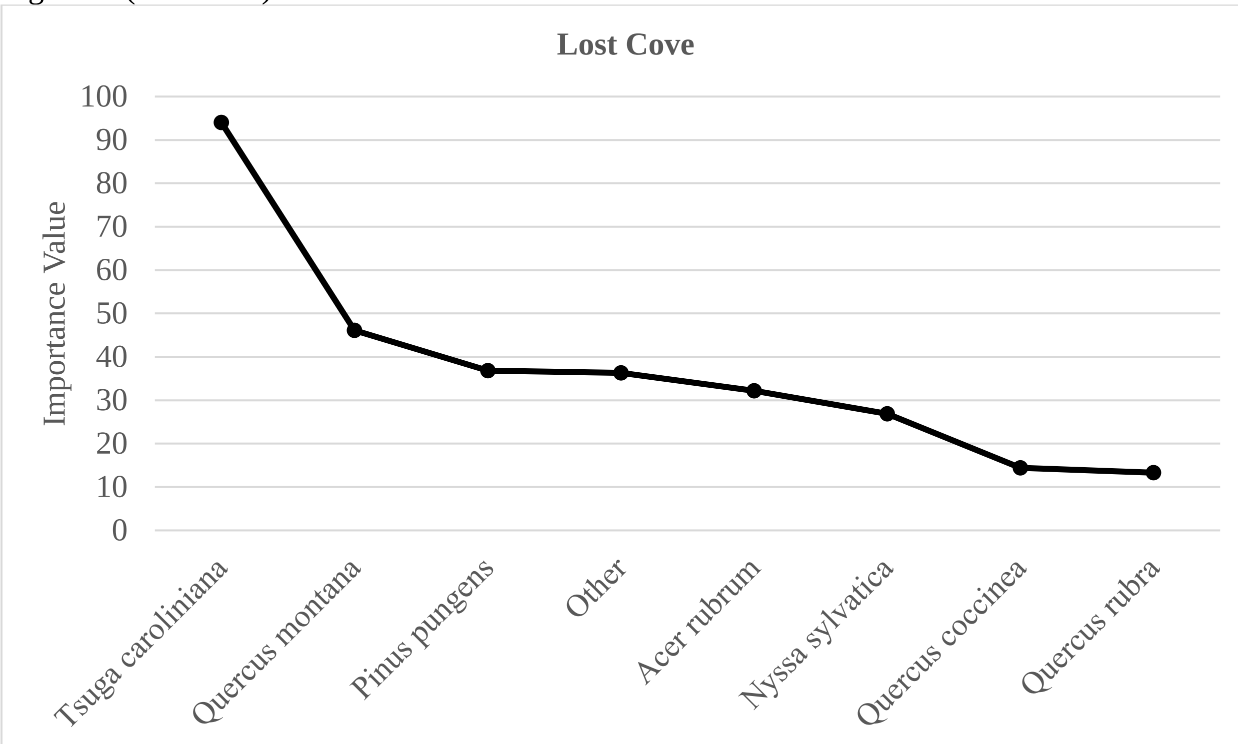


Figure 2. Dominance diversity curves (importance values) of trees ≥ 5 cm DBH for five sites containing Tsuga caroliniana in the mountains of North Carolina and Tennessee

Figure 2. (continued)



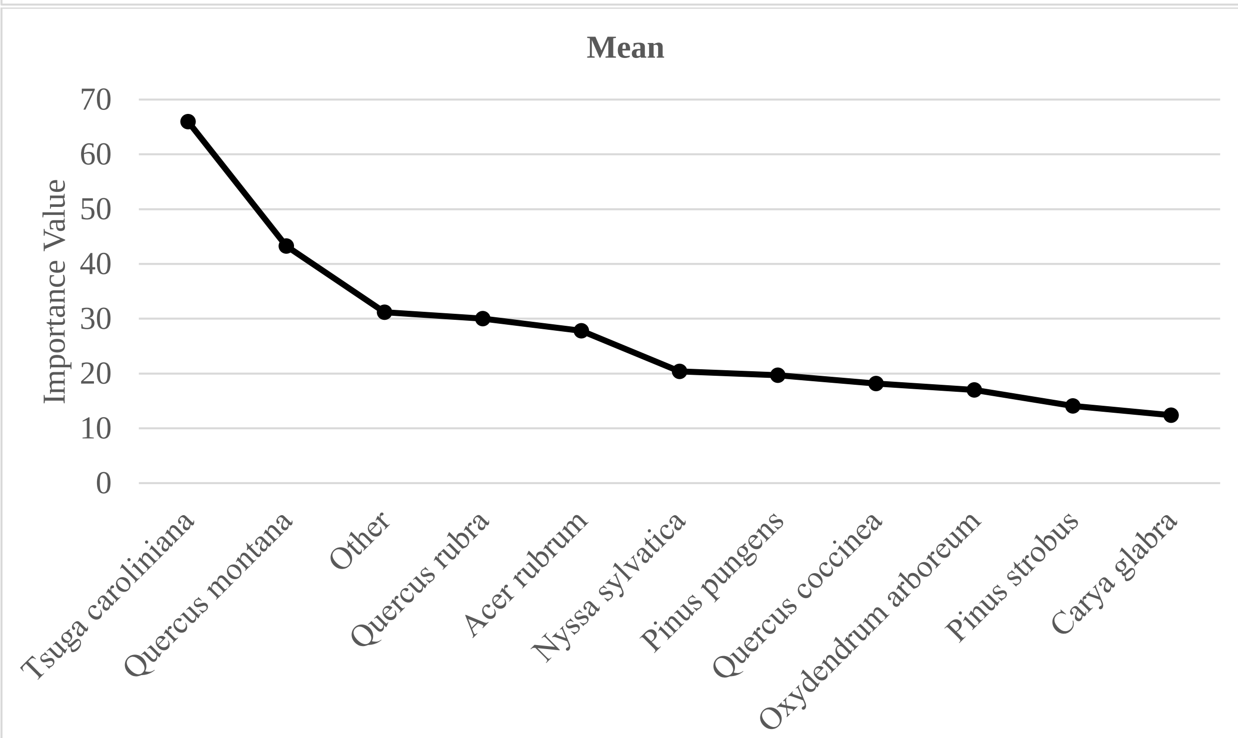


Figure 2. Dominance diversity curves (importance values) of trees ≥ 5 cm DBH for five sites containing Tsuga caroliniana in the mountains of North Carolina and Tennessee

each other.

Overstory species richness varied among sites ($p = 0.0054$; Table 6), with the greatest mean number of species (10.0) occurring at Iron Mountain (Top). Number of species at Lost Cove (5.5) was significantly lower than the other sites ($p < 0.03$) except Dobson's Knob.

Similarly, overstory diversity varied ($p = 0.0168$) among sites (Table 6), with Iron Mountain (Top) having the greatest (2.1) and Lost Cove the lowest (1.1) diversity. Lost Cove had significantly lower diversity than Cliff Ridge ($p = 0.0702$) and Iron Mountain (Top) ($p = 0.0128$). Overstory species evenness ranged from 0.58 to 0.82, and did not vary significantly ($p = 0.1540$) among sites (Table 6).

Species richness in the regeneration layer varied ($p = 0.0015$; Table 6) among sites and was lowest at Lost Cove (2.75) and highest at Iron Mountain (Top) (4.58). Dobson's Knob and Lost Cove had significantly ($p < 0.05$) lower regeneration level species richness compared to Cliff Ridge and Iron Mountain (Top). Species richness of shrubs also varied ($p < 0.0001$; Table 6) among sites, and was significantly ($p < 0.0001$) lower at both Iron Mountain sites ($p < 0.0001$).

Species evenness of the regeneration layer ranged from 0.68 to 0.96, and did not vary significantly ($p = 0.5577$; Table 6). Diversity of the regeneration layer varied significantly among sites ($p = 0.0011$; Table 6) with Cliff Ridge being the most diverse (diversity = 1.0) and Lost Cove being the least diverse (diversity = 0.6). Cliff Ridge varied from Dobson's Knob ($p = 0.0198$) and Lost Cove ($p = 0.0069$), and Lost Cove varied from Cliff Ridge ($p = 0.0069$) and Iron Mountain (Top) ($p = 0.0319$).

Canopy density varied among sites in winter ($p < 0.0001$), summer ($p < 0.0001$), and in percent evergreen ($p < 0.0001$; Table 7). The evergreen component was mainly composed of

Table 6. Variation in diversity among five sites containing *Tsuga caroliniana* in the mountains of North Carolina and Tennessee

Variable	Mean ± Std Dev	p-value
Species Richness of Trees ≥ 5cm DBH (#)	8.1 ± 2.1	0.0054
Species Richness of Trees < 5cm DBH (#)	3.7 ± 1.6	0.0015
Species Richness of Shrubs (#)	1.5 ± 1.3	< 0.0001
Modified Hill's Ratio of Trees ≥ 5cm DBH	0.7 ± 0.2	0.1540
Modified Hill's Ratio of Trees < 5cm DBH	0.8 ± 0.5	0.5577
Shannon's Diversity Index of Trees ≥ 5cm DBH	0.3 ± 0.1	0.0168
Shannon's Diversity Index of Trees < 5cm DBH	0.8 ± 0.4	0.0011

Table 7. Variation in canopy density among five sites containing *Tsuga caroliniana* in the mountains of North Carolina and Tennessee

Canopy Density (%)	Mean					ANOVA	
	Cliff Ridge	Dobson's Knob	Iron Mountain (Top)	Iron Mountain (Bottom)	Lost Cove	Mean ± Std Dev	p-value
Winter	79.8	70.0	56.5	73.5	82.9	72.5 ± 13.3	< 0.0001
Summer	89.3	78.4	86.4	92.4	85.4	86.4 ± 8.8	< 0.0001
Evergreen	89.4	89.3	65.4	79.6	97.1	84.6 ± 15.9	< 0.0001

trees such as *Tsuga caroliniana* and *Pinus* spp. along with *Rhododendron* spp. shrubs with only slightly higher canopy densities in summer than in winter (Table 7). Dobson's Knob differed significantly from all other sites ($p < 0.07$) in having the lowest summer canopy density of 78.4 percent. Iron Mountain (Top) at 56.5 percent differed from all other sites during winter in the same way ($p < 0.07$), and it also had the lowest percentage of evergreen plants at 65.4 percent while Lost Cove had the highest at 97.1 percent (Table 7).

In Summary, Dobson's Knob stands were higher in elevation, faced a different direction, and were in shallower depressions compared to the other sites. Stands at Dobson's Knob also had the lowest summer canopy density and overstory mean diameter, and the highest overstory mean *Tsuga caroliniana* diameter. Lost Cove had lower overstory species richness and lower over- and understory diversity, but it had a high percent of older and larger *Tsuga caroliniana* stems. Patterns in variables measured at both the overstory and regeneration level were different. Species richness and diversity varied among sites for the overstory ($p = 0.0054$, and $p = 0.0015$) and regeneration levels ($p = 0.0168$, and $p = 0.0011$), but evenness did not (overstory: $p = 0.1540$; 0.70 ± 0.15, regeneration: $p = 0.5577$; 0.76 ± 0.46) (Table 6). The percentage of the live trees that were *Tsuga caroliniana* varied among sites at the overstory level ($p = 0.0090$), but not at the regeneration layer ($p = 0.1080$; 3.29 ± 5.53). The density of *Acer rubrum* varied from eight other species in the understory ($p \leq 0.0611$), but did not at the overstory level ($p = 0.3690$; 32.5 ± 24.8; Table 2). With shrubs, species richness varied ($p < 0.0001$), but percentage ground cover did not ($p = 0.7660$, 20.70 ± 25.68; Table 6).

When the statistically significant variables in the simple linear regressions were combined for multivariable analysis, few relationships were found between *Tsuga caroliniana* variables and significant physiographic and community density, size, and diversity variables

(Table 8). Six of the eight *Tsuga caroliniana* dependent variables (overstory age, percentage of overstory and regeneration, overstory DBH, density of live overstory and regeneration) were found to have one ($p < 0.038$) or no ($p > 0.277$) significant independent variables, but they explained less than 45 percent of the variation (adjusted R^2 range of 0.19 to 0.41) in the *Tsuga caroliniana* variables (Table 8). Variation in *Tsuga caroliniana* was generally not strongly explained by multiple linear regression (Table 8). Overstory evenness explained 19 percent of the variation in *Tsuga caroliniana* overstory age, while TSI explained 28 percent of regeneration density (Table 8). Regeneration diversity, species richness, shrub cover, and overstory evenness explained 33 percent of the variation in percentage of overstory *Tsuga caroliniana* trees, and 41 percent of the variation in the percentage of regeneration layer *Tsuga caroliniana* trees was explained by regeneration species richness and physiographic measures. Overstory evenness, snag DBH, and percent ground cover of shrubs accounted for over half (adjusted $R^2 = 0.5149$) the variation of the density of overstory *Tsuga caroliniana* snags (Table 8).

Discussion

The elevation results are consistent with other reports in the literature of where *Tsuga caroliniana* is found in the Appalachian Mountains (Austin et al. 2016, Duncan 1988 cited in Brown 2004, and Rentch et al. 2000). Austin et al. (2016) indicated physiography strongly limited where *Tsuga caroliniana* is found. Yet, despite selecting sites with high densities of *Tsuga caroliniana*, the physiography where the species is found varied in this study. The five sites could be put into three physiographic zones. Cliff Ridge and Lost Cove had the lowest elevation, a northwestern aspect, and are located in the deepest of the topographical landscape concavities. Both Iron Mountain sites, with a elevation level in the middle of the other two physiographic zones, had north-northwestern aspects, and were located in a mid to shallow

Table 8. Relationship between *Tsuga caroliniana* variation and physiography and/or community characteristics among five sites in the mountains of North Carolina and Tennessee.

***Tsuga caroliniana* Variable**	**Independent Variable(s)**	**p-value**	**Adjusted R^2**
Age of overstory trees	Overstory Evenness Index 5	0.0003	0.1864
Percentage of overstory	Regeneration Shannon's Diversity Index	0.1640	0.3315
	Regeneration Species Richness	0.5978	
	Shrub Percent Ground Cover	0.0326	
	Overstory Evenness Index 5	0.2809	
Percentage of regeneration	Elevation	0.2093	0.4128
	Landform Index	0.2737	
	Terrain Shape Index	0.4995	
	Regeneration Species Richness	0.0267	
Overstory DBH	Percentage Evergreen of Canopy Density	0.4086	-0.0624
	Winter Canopy Density	0.8675	
	Live Overstory Stems/ha	0.4296	
	Overstory DBH	0.9010	
Overstory BA/ha	Regeneration Shannon's Diversity Index	0.0330	0.1126
	Summer Canopy Density	0.0563	
Overstory Live #/ha	Aspect	0.0254	0.0498
Regeneration #/ha	Terrain Shape Index	0.0373	0.2773
Snags #/ha	Overstory Evenness Index 5	0.0421	0.5149
	Regeneration Shannon's Diversity Index	0.1417	
	Regeneration Species Richness	0.4936	
	Snags DBH	0.0250	
	Shrub Percent Ground Cover	0.0389	

topographical landscape concavity. Dobson's Knob, had the highest elevation, a southwestern aspect, and the shallowest topographical landscape concavity.

Coker and Totten (1934 cited in Brown 2004) and Brown (2004) describe *Tsuga caroliniana* as favoring south-facing slopes from 205 to 247 degrees, and Rentch et al's (2000) sampling found aspects of 255 to 285 degrees. My results found the average aspect to be to the northwest (321 degrees), with only Dobson's Knob's mean site aspect to the southwest. Humphrey (1989) also found *Tsuga caroliniana* in northerly aspects. The Dobson's Knob site was at the highest elevation and those sites faced southwest similar to Brown (2004), suggesting that *Tsuga caroliniana* needs a more southerly exposure at higher elevations.

Mid-slope positions are stressful due to frequent disturbances caused by drought, ice, and wind (Copenheaver et al. 2006). The fact that *Tsuga caroliniana* is found at these positions suggests it is tolerant to these stresses. Thus, the mid-slope positioning of plots at all sites indicated by the TSI further confirms the stress tolerant life history strategy of *Tsuga caroliniana* (Grimes 1977, 1979 cited in Humphrey 1989, and Rentch et al. 2000).

The species composition of the *Tsuga caroliniana* dominated stands is consistent with the Austin et al. (2016) and Rentch et al. (2000) studies where the most important and dominant (basal area) tree species was *Tsuga caroliniana* followed by *Quercus* spp., and *Acer rubrum*. In addition to these species, Schafale and Weakly (1990) reported *Amelanchier arborea, Tsuga canadensis, Kalmia latifolia*, and *Rhododendron* spp. were also common. The only one of these species not found in my study was *Tsuga canadensis*, but it was present at lower elevations than the *Tsuga caroliniana* stands included in my study. Rentch et al. (2000) found a few *Quercus* spp. in the canopy that were larger diameter than all of the *Tsuga caroliniana,* and the same trend was found in my work. Humphrey (1989) found the same trend in some of his plots. *Quercus* spp. trees are intermediate in shade tolerance, and regeneration is thus not competitive under heavy shade of mature *Tsuga caroliniana* stands (Humphrey 1989, Rentch et al. 2000). The relatively low species diversity found in my study is consistent with Humphrey (1989), Brown (2004), and Rentch et al. (2000) studies. Diversity in plots dominated by *Tsuga caroliniana,* were roughly five times lower than those reported by Elliott et al (1998) in their study on diversity in the Southern Appalachians. Shade, in the understory microclimate created by the *Tsuga caroliniana* overstory, is a likely contributor to this lower diversity due to the exclusion of shade intolerant species in the regeneration layer. The later stage of succession and the associated drop in diversity due to the shaded microclimate is further evidenced by the majority of snag species being either of intermediate, intolerant, or very intolerant of shaded conditions, and the majority of live species being intermediate or fully tolerant to shade.

In the understory Austin et al. (2016) and Humphrey (1989) found *Tsuga caroliniana* to be the most abundant tree species. In contrast, *Acer rubrum* had more than five times as many individuals as the next most abundant species (*Quercus montana*) in my sites. Humphrey (1989) also found *Acer rubrum* and *Quercus* spp. to be abundant in the regeneration layer of *Tsuga caroliniana* stands. The presence of *Acer rubrum* and *Quercus montana*, along with high amounts of *Acer rubrum* indicates a shaded understory where *Acer rubrum* can gradually replace the *Quercus spp.* population in the canopy through greater recruitment (Copenheaver et al. 2006). Austin et al's (2016) and Humphrey's (1989) sites were located in different areas on the same mountain. Austin et al. (2016) did not mention the elevation or aspect of their sites, but they do mention the study area elevation range whose minimum is comparable to my study site maximum. The aspects of Humphrey's (1989) study sites are comparable to my study but elevations are higher suggesting that *Tsuga caroliniana* regeneration increases with elevation, and this suggestion is reinforced by the multivariate results on the percentage of *Tsuga caroliniana* in the regeneration layer being partially explained by elevation.

Rentch et al. (2000) suggests deer herbivory could explain the absence of *Tsuga caroliniana* seedlings, low percent cover of shrubs, and inability of *Acer rubrum* and *pensylvanicum* seedlings to mature, and browsing of *Tsuga canadensis* seedlings and saplings is reported by Weckel et al. (2006). Herbivory could be partially responsible for the low percentage of regeneration and richness found in the understory in my sites.

The Brown (2004), Austin et al. (2016), Humphrey (1989), and Rentch et al. (2000) studies reported two to five species of the Ericaceae family dominated the shrub layer. My study also found the understory was dominated by Ericaceae species, but my species richness was much greater than these other studies. This is probably due to the earlier successional stage of the stands in my study because both the over and understory tree species richness was also much higher than in the other studies. Earlier stages of succession have greater diversity due to the higher levels of light that allow the establishment of shade-intolerant species (Beck and Hooper 1986). Nilsen et al. (1999 and 2001) noted that sites dominated by *Rhododendron maximum* had lower diversity in the shrub and regeneration layers due to the dense shade, reduction in other resources, and possible allelopathy from this species. Our study had a higher species richness overall than the other studies probably because of the larger geographical range covered, but at the site level the species richness was comparable to the other studies. In other words, sites had low diversity, but because the sites contained different species, the entire study had high diversity. Humphrey (1989) found that *Tsuga caroliniana* and *Acer rubrum* were not suppressed while the *Quercus* genus was suppressed by an Ericaceae layer. This combined with the earlier successional stage of the site partly explains why Iron Mountain (Top) has higher species richness and has important implications for the ecological restoration of *Tsuga caroliniana* because it means that these shrubs could control the establishment of other species in the regeneration layer. Elevation, LFI, TSI, and the species richness characteristics are important for describing 41 % of the variation of the regeneration layer made up of *Tsuga caroliniana*.

Lost Cove exhibits indications of being a late successional forest dominated by *Tsuga caroliniana* as described by Brown (2004) and Austin et al. (2016), where the species is the most abundant, and dominant in the stand and thus has the highest ecological importance. It slowly replaces preestablished species, becoming dominant in later stages of succession where it is difficult for other species to establish or survive (Humphrey 1989). *Tsuga caroliniana* at the Lost Cove site was the most abundant (density), most dominant (basal area), and most important (importance value). Lost Cove also had more than twice as many *Tsuga caroliniana* snags as three of the other sites, this is an indicator of later successional stands where slow changes lead to fewer larger stems even after centuries without large-scale disturbances (Runkle 2000). Lost Cove had the lowest and significantly different over- and understory species richness and diversity from the other sites. The late stage of stand development is evidenced by the dominance of shade tolerant species and the high density of *Tsuga caroliniana* in the overstory suggesting it is likely the most mature site.

Iron Mountain (Top) is the youngest of the *Tsuga caroliniana* stands in the study successionally, but it is not at the earliest stage of succession due to the presence of mature *Tsuga caroliniana* in the overstory. It has the highest mean DBH and the lowest importance value for and percentage of *Tsuga caroliniana*. The greater abundance and importance of shade tolerant species in the overstory and shade intolerant species in the regeneration layer at Iron Mountain (Top) displays an earlier successional stage than Lost Cove. It has the highest species richness in both the over- and understory, and the highest overstory and second highest understory diversity which can be contrasted to what Jetton et al. (2008) reported for late successional *Tsuga caroliniana* stands. Iron Mountain (Top) is not an early or late successional stand. The fact that the trees composing the overstory and regeneration layers differ markedly indicates that Iron Mountain (Top) is in the process of successional change (Abrahamson and Gohn 2004).

The stages of stand succession varied within the three physiographic zones. Despite having different physiographic characteristics, the stands at a later stage of succession had higher density, basal area, and importance value of *Tsuga caroliniana,* along with higher snag densities, greater dominance of shade tolerant species, and lower species richness and diversity compared to stands at earlier stages of succession.

The literature and my research suggest two possible explanations for sites with different stages of succession occurring in the same physiographic grouping. The first suggested by the literature (Austin et al. 2016) is temperature fluctuations, where earlier successional stands with more open canopies allow larger temperature fluctuations than the more modified microclimate of later successional stands. The second has to do with the stage of succession at the site when *Tsuga caroliniana* becomes established or the type and scale of disturbance that allowed the egress of said establishment. My results suggest microclimates created by physiography affect light conditions whereby *Tsuga caroliniana* can dominate a more shaded environment faster than it can a less shaded one.

Management Implications

Characteristics of the Lost Cove site would be the ecological trajectory goal for ecological restoration of *Tsuga caroliniana* stands. Artificial regeneration of *Tsuga caroliniana* should occur on sites within an aspect range from north to northwest moving to the southwest at elevations above 1,100 m because this is where *Tsuga caroliniana* has managed to persist historically and this finding is supported by my study. Since the density of the overstory originates in the understory and because it is explained roughly 30 percent by TSI, this regeneration work should be at mid-slope on a terrain within a TSI range from -0.6 to 0.2 to encourage higher overstory density. Importance values should be considered in establishing restoration goals because biomass and basal area per hectare were explained by roughly 10 percent of the low regeneration diversity and high summer canopy density characteristics. A summer canopy density around 90 percent appears important to overstory basal area, possibly due to Ericaceae shrubs lowering regeneration diversity by limiting the seedling establishment of some species and limiting *Acer rubrum's* transition from seedling to overstory tree. In regenerating *Tsuga caroliniana* densities of *Kalmia latifolia* and *Rhododendron* spp. in the shrub layer should be considered due to their shading and ability to suppress seedling establishment of some species and the transition of *Acer rubrum* from seedling to sapling.

To establish new *Tsuga caroliniana* stands, the community composition and structure of the Iron Mountain (Top) site could be a reference site because of its earlier stage of stand succession. Conditions include, an elevation range from 900 to 950 m, LFI of one, and TSI range from -0.6 to 0.2. After establishment, the ecological trajectory would be toward a reference site with a community composition and structure such as Lost Cove; a more mature later successional site.

CHAPTER 4: LITERATURE CITED

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