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FINDING OLD FORESTS: THE STRUCTURAL PATTERNS &
DISTRIBUTION OF VERMONT'S OLD GROWTH

A Final Project Presented

by

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Finding Old Forests: The Structural Patterns & Distribution of Vermont's Old Growth

**A UVM FIELD NATURALIST PROJECT PRESENTED BY:
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Wilderness Trust

In Collaboration With: Future Forests – Future Streams, P.I. WS Keeton

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Chapter I: The Importance of Old Forests in Vermont & The Predictive Potential of Maximum Entropy Modeling

Introduction

Old and mature forests are highly valued ecosystems for their rich biodiversity, unique habitat, carbon sequestration abilities, hydrologic function, and aesthetic value (Gray et al., 2023). The ecosystem services old forests offer carry implications related to global climate change mitigation and adaptation (Pelz et al., 2023). Despite their significance, there is a considerable gap in our understanding of old-growth forest distribution within the United States. As noted by Gray et al. (2023), there is a lack of clarity on how to define and locate these complex forest ecosystems; it has repeatedly been described as a “wicked” problem. To address this knowledge gap, President Biden’s Executive Order 14072 (2022) directed the USDA Forest Service and USDI Bureau of Land Management to define, identify, and inventory old-growth and mature forests on Federal lands with the aim to conserve and restore them. Despite no longer being an active executive order, it brought renewed attention to old forest ecosystems at the national level.

While old forests are recognized as important at a national level, inventorying them at that scale is challenging due to the regional differences among forest types and land use history (Pelz et al., 2023). This gives credence to assessing the quantity and distribution of old and mature forests at a smaller state or regional scale.

Vermont’s history of agriculture and deforestation strongly influenced present-day forest structure, age, and distribution across the state (Cogbill, 2000). Deforestation for agriculture purposes reached its peak in central New England between 1820 and 1880 when over 80% of the land was clear. Subsequent reforestation of abandoned fields, starting around 1850, contributed to the gradual resurgence of forest cover (Foster, 1992), yet, at present old forests remain rare within a matrix of secondary forests. It’s estimated that as of 1996 only 0.4% of forests in the East were old-growth, compared to >75% of pre-settlement forest (Davis, 1996). Despite the scarcity in Vermont as at the national level, the precise quantity and spatial distribution of old forest stands are poorly understood.

Before European settlement, Vermont's landscape was dominated by old, mature forests, characterized by structurally complex stands that included canopy gaps, areas of natural disturbance, and occasional wetlands or rocky outcrops. The native flora and fauna of Vermont are adapted to this type of variable forest structure which is absent or less common in younger secondary forests (Zaino et al., 2018). This underscores the ecological, cultural, and climatic importance of identifying and conserving old-growth forests, both nationally and at a state level within Vermont. Furthermore, this literature review aims to synthesize key research on old forests and modeling techniques, providing a foundation for understanding how predictive modeling can aid in identifying these ecosystems for conservation and management efforts.

Definitions and Characteristics of Old Forests

Defining old or old-growth forests is a persistent challenge in forest ecology. Although old and young forests often differ in structural characteristics and developmental trajectories, defining what constitutes an “old” forest is difficult because old forest structures can emerge through multiple developmental pathways, shaped by diverse site histories and disturbance regimes. These differing developmental pathways can lead to structural variability across forest stands. Therefore, structural attributes like coarse woody debris volume, or tip-up mounds are not always reliable indicators of stand age. This variability makes it difficult to draw clear boundaries between old and non-old forests. The process of defining old-growth frequently necessitates researchers to make subjective decisions, such as setting thresholds based on factors like stand age, tree density exceeding a specific diameter, or other non-structural attributes of forests (Gray et al., 2023).

Multiple definitions for old-growth have been proposed in the literature. Fowells (1965) and McGee et al. (1999) define old-growth stands as those containing trees at least one-half of their species’ maximum life expectancy. Dunwiddie and Leverett (1996) utilized that same definition and set additional criteria requiring old-growth stands to cover a minimum of 3 hectares, show minimal human disturbance, and demonstrate evidence of regeneration—particularly of late-successional species. Other studies have relied on the age of dominant canopy trees as a distinguishing factor, categorizing forests as old-growth when tree age exceeds 150 years and as mature when they range between 80 and 150 years (Keeton et al., 2007).

Given the varying definitions of old old-growth forest presented in literature and this studies aim to build on existing Vermont Agency of Natural Resources research, inventories, and methodologies, the definition of old forests provided in the *Vermont Conservation Design: Part 2: Natural Communities and Habitats Technical Report* will be used.

Old forests are biologically mature forests, often having escaped stand-replacing disturbance for more than 100 years and exhibiting minimal evidence of human-caused disturbance as well as continuity of process, senescence of trees, and regeneration response. In addition, these forests may exhibit many of the following associated characteristics: 1) some trees exceeding 150 years in age for most forest types (100 years for balsam fir, 200 years for eastern hemlock); 2) native tree species characteristic of the forest type present in multiple ages; and 3) complex stand structures that include a broad distribution of tree diameters, multiple vertical vegetative layers, natural canopy gaps, abundant coarse woody material (reflecting the diameters of the standing trees) in all stages of decay and numerous large standing dead trees. It is expected that old forests operate under natural disturbance regimes and may include small areas of regenerating forest as a result of these disturbances. (Zaino et al., 2018)

The process of forest aging leads old forests to have distinctive structural attributes that set them apart from younger stands. One defining characteristic is the presence of large, mature trees, which results in higher basal areas and greater densities of large-diameter individuals (McGee et al., 1999). These trees develop unique morphological features over time, including bark balding,

reduced taper in the trunk, large twisted upper limbs, and a lower leaf area to trunk volume ratio (Pederson, 2010). Such traits are identifying features and contribute to the overall complexity of old-growth ecosystems.

The structural complexity of old-growth forests is evident in both vertical and horizontal dimensions and may vary considerably between sites (Keeton et al., 2007). Vertically, trees occupy multiple canopy strata, reflecting the presence of multiple age classes and contributing to a layered, diverse structure. Horizontally, old forests exhibit a patchy, heterogeneous structure characterized by canopy gaps and clusters of regenerating vegetation. Horizontal diversification depends on gap-forming disturbances and is often the latest structural feature to develop (Franklin et al., 2002). The structural differences between young and old forests are shaped by distinct tree mortality processes. In younger stands, mortality is largely driven by competition for light and resources, whereas in older forests, trees are more likely to die due to agents such as insect infestations, disease, or wind disturbances (Franklin & Van Pelt, 2004).

Tree mortality plays a critical role in shaping old forests by creating gaps in the canopy and contributing to the accumulation of large volumes of deadwood, particularly in the form of fallen logs (Harmon et al., 1986). The death of overstory trees leads to the formation of canopy openings, which tend to be larger in old-growth forests due to the greater size of individual trees. When these large trees fall, they often cause additional collateral damage, further expanding gaps and influencing forest regeneration dynamics (Barton & Keeton, 2018).

Ecological & Functional Significance of Old-Growth Forests

Eastern North American old-growth forests have accumulated genetic diversity since the last glaciation, fostering complex ecological interactions, serving as critical reservoirs of biodiversity, and providing niche habitats for a diverse range of species. Their structural complexity, including features such as large snags, decomposing logs, and ancient live trees, creates a mosaic of microhabitats that support a variety of organisms (McGee, 2018). The presence of large coarse woody debris (CWD) and tip-up mounds, for example, provides crucial microhabitats for species such as red-backed salamanders (Pough et al., 1987). Additionally, canopy-dominant trees in old-growth stands develop expansive, twisting upper branches that host substrate used by arboreal organisms (Pederson, 2010). While few Eastern species are true old-growth obligates, many such as the red-backed salamander rely on microhabitats that are more abundant in old-growth forests, where their fitness and relative abundance are likely to be higher.

Bryophytes are especially abundant in old-growth stands, where they contribute to unique species assemblages and enhance overall biodiversity. Research conducted in western Massachusetts found that bryophyte species diversity was twice as high in old-growth forests compared to secondary forests, and that sugar maple (*Acer saccharum*) trees in old-growth stands supported more bryophyte species than similarly sized trees in younger forests (Cooper-Ellis, 1998). McGee and Kimmerer (2002) similarly observed in the Adirondacks that although the total bryophyte cover remained consistent across forest age classes, the composition of bryophyte communities

varied. Old-growth stands tended to support a higher diversity of calcicoles and mesophytic bryophyte species (*Brachythecium oxycladon*, *Anomodon rugelii*, *Porella platyphylloidea*, *Anomodon attenuatus*, *Leucodon brachypus*, and *Neckera pennata*). In contrast, secondary forests were more commonly dominated by xerophytic bryophytes (*Platygyrium repens*, *Frullania eboracensis*, *Hypnum pallescens*, *Brachythecium reflexum*, and *Ulota crispa*). This differentiation in species composition underscores the influence of forest age and structural complexity on bryophyte community assemblages.

Beyond biodiversity, old-growth forests provide essential ecosystem functions, including carbon storage and climate regulation. Studies have shown that eastern old-growth forests contain higher biomass and carbon density when compared to young and mature forests, underscoring their role in long-term carbon sequestration (Keeton et al., 2011; McGarvey et al., 2015). Although not all old-growth forests function as net carbon sinks, the majority of late-successional forests worldwide continue to sequester carbon as they age, playing a critical removal role in global carbon cycling (Luyssaert et al., 2008).

In addition to their ecological significance, old-growth forests offer cultural and psychological benefits. Many individuals derive aesthetic, recreational, and spiritual fulfillment from these ancient landscapes. The largely undisturbed nature of old-growth forests provides a rare opportunity to experience ecosystems that have persisted for centuries, fostering connection to the natural world (Moore, 2007).

Ecological Applications for Maximum Entropy Modeling

Maximum entropy modeling (MaxEnt) has become a widely used tool in ecological research, particularly for species distribution modeling. MaxEnt is a presence-only model that uses known occurrence locations and environmental predictors to estimate a species' niche and geographic distribution (West et al., 2016). Unlike traditional modeling approaches that require both presence and absence data, MaxEnt's reliance on presence-only data makes it particularly valuable in ecological studies, where true absence records are often unavailable or unreliable. By analyzing environmental variables associated with known occurrences, MaxEnt produces a continuous habitat suitability map, with values ranging from 0 to 1, indicating the relative likelihood of a species' presence in different areas.

In addition to species distribution, MaxEnt has been widely applied to habitat suitability modeling. It has proven especially useful for identifying suitable habitats for species of conservation concern, where occurrence data may be sparse. For example, Perkins-Taylor and Frey (2020) compared MaxEnt to a traditional occupancy model for a rare chipmunk species (*Neotamias quadrivittatus oscuraensis*) in New Mexico and found that MaxEnt effectively captured known environmental requirements, such as elevation, vegetation, and terrain features. Similarly, Rebelo and Jones (2010) used MaxEnt to predict the distribution of an endangered bat (*Barbastella barbastellus*), identifying 15 new suitable habitat locations and extending its known range by 100 km to the south

in Portugal. These studies demonstrate the utility of MaxEnt in guiding conservation actions, including field surveys and protected area designation.

Beyond species distribution, MaxEnt has also been applied to predict the spread of invasive species, aiding in containment and removal efforts. For example, West et al. (2016) developed a MaxEnt model to assess habitat suitability for an invasive grass (*Bromus tectorum*) in Rocky Mountain National Park. When tested against independent presence/absence data collected in subsequent years, the model successfully predicted newly invaded sites, demonstrating MaxEnt's potential for proactive conservation planning.

Although MaxEnt has primarily been used for single-species distribution modeling, its application in predicting ecological community types remains relatively unexplored. One such study by Pfennigwerth et al. (2019) successfully used MaxEnt to model wetland plant community distributions in Great Smoky Mountains National Park. Their model identified 359 previously undocumented wetland occurrences, allowing land managers to inventory 93 high-elevation wetland sites in three field seasons—twice the efficiency of previous methods. This research suggests that MaxEnt can be a powerful tool for modeling the distribution of entire plant communities, providing an opportunity to enhance conservation planning at broader ecological scales.

MaxEnt not only outperforms other common distribution algorithms across sample size classes (Wisz et al., 2008), but it also generates useful predictions from limited data sets, making it particularly well-suited for studies with sparse occurrence records (Elith & Graham, 2009). However, despite these advantages, the reliance on presence-only data introduces potential biases. For instance, if occurrence data are geographically skewed, such as being clustered near roads or populated areas, MaxEnt may reflect sampling bias rather than true habitat suitability. Furthermore, because MaxEnt outputs a relative suitability index rather than a direct probability of presence, careful calibration is required to ensure accurate ecological interpretation (Elith & Graham, 2009).

Model evaluation and validation are critical components of MaxEnt applications. The most common performance metric used is the area under the receiver operating characteristic (ROC) curve (AUC), which measures how well the model distinguishes presence locations from background points (Elith et al., 2006). While MaxEnt models often yield high AUC values, these should be interpreted cautiously, as AUC can be influenced by the spatial extent of background data (West et al., 2016). Complementary validation approaches, such as independent field data collection or threshold-dependent measures like sensitivity and specificity, help ensure robust predictions. Sensitivity measures the percentage of correctly classified presences, while specificity measures the percentage of correctly classified absences, offering additional insight into model performance. A highly sensitive model is optimal for studies where maximum potential distribution is valued, such as predicting invasive species distribution. Conversely, a highly specific model is useful for studies identifying rare occurrences, where resources want to be channeled towards finding more presence locations. Ideally, MaxEnt models should be validated

using independent occurrence records collected after model development or from different regions to assess true predictive power (West et al., 2016). Despite field sampling being a strong validation strategy, studies involving ground truthing like Rebelo & Jones (2010) and Pfennigwerth et al. (2019) are still uncommon.

MaxEnt's flexibility, strong predictive performance, and ability to operate with limited data have made it a cornerstone of species and habitat distribution modeling. When applied carefully, with attention to bias correction, validation, and ecological interpretation, MaxEnt has potential as a valuable tool for conservation planning and ecological research related to old-growth forest distribution.

Conclusion

Old-growth forests play a crucial ecological role, serving as biodiversity hotspots, carbon sinks, and contributors to ecosystem resilience (Keeton et al., 2011; Gray et al., 2023). Despite their importance, their identification and conservation remain challenging due to inconsistent definitions, historical land use impacts, and the difficulty of conducting large-scale inventories (Gray et al., 2023; Pelz et al., 2023). In Vermont, as in other regions, understanding the distribution and structural characteristics of old-growth forests is essential for effective conservation planning and land management strategies.

Predictive modeling, particularly MaxEnt, offers a promising approach for addressing gaps in old-growth forest identification. While traditionally used for species distribution modeling, MaxEnt has shown success in predicting ecological communities and habitat suitability with limited presence-only data (Pfennigwerth et al., 2019; Elith & Graham, 2009). Its application to old-growth forest distribution is a novel but logical extension, building on its demonstrated effectiveness in single-species and wetland community modeling. However, MaxEnt's reliance on presence-only data introduces potential biases, underscoring the need for careful model calibration and complementary field validation to ensure accuracy and reliability.

Ultimately, the conservation of old-growth forests is vital for maintaining biodiversity, sustaining ecosystem services, and mitigating climate change impacts (Pelz et al., 2023). Predictive modeling, when used in conjunction with field validation, can serve as a powerful tool for guiding conservation efforts. This research highlights the potential of MaxEnt in identifying and preserving Vermont's remaining old forests, contributing to broader sustainable forest management and environmental policy initiatives.

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Chapter II: Patterns and Sources of Variability Across Natural Community Types in Late-Successional & Old-Growth Forests

Abstract

Old forests are ecologically significant yet increasingly rare across the eastern United States. In Vermont, widespread historical land use has obscured their distribution, leaving many stands undocumented. This study investigates the structural characteristics and spatial patterns of late-successional and old-growth forests in Vermont, with a focus on assessing the utility of the Vermont Old Forest Prediction Model, a MaxEnt-based tool designed to identify likely old forest locations. Thirty-three forest sites were sampled using a stratified random approach informed by the model's suitability scores. Forest structure was measured using standardized inventory methods, and natural community classifications were assigned in the field. Results revealed that dominant tree age was positively correlated with key structural attributes such as large tree density, large tree basal area, and aboveground biomass. No significant structural variation was detected among natural community types. Multivariate analyses showed partial clustering by seral stage but weak overall separation. The prediction model's suitability scores were significantly correlated with dominant tree age, supporting its value for guiding surveys. Five previously undocumented old forests were identified, highlighting the model's application as a conservation planning tool. This research contributes to a better understanding of old forest structure in Vermont and demonstrates how predictive modeling and field surveys can be integrated to support inventory efforts and conservation strategies.

Introduction

Old forests, characterized broadly by structural complexity and minimal recent anthropogenic disturbance, play a critical ecological role in forested landscapes. These ecosystems support rich biodiversity, offer unique habitat niches, and act as long-term carbon sinks. The presence of ancient trees, large standing snags, decomposing logs, and diverse canopy layers creates microhabitats that support a high diversity of organisms (McGee, 2018). In the eastern United States old-growth forests are exceedingly rare, comprising less than 1% of forest cover in 1996 (Davis, 1996).

In Vermont, the rarity of old forests is a direct consequence of land-use history. By the mid-1800s, more than 80% of the region had been cleared for agriculture (Foster, 1992). Since widespread farm abandonment in the late 19th century, forests have regenerated naturally across much of the state. Yet most are still under 150 years old and lack the structural features that define mature or old growth conditions. Although the Vermont Agency of Natural Resources maintains a partial inventory of known old forest stands, it is believed that there are still unknown stands to identify within the state, particularly on private and federal land.

The conservation of mature and old forests is critical for long-term ecosystem function. These forests support higher beta biodiversity, including richer bryophyte communities (Cooper-Ellis, 1998; McGee and Kimmerer, 2002), and provide essential structural features, such as coarse woody debris (CWD) and large snags that serve as habitat for species like red-backed salamanders and Northern spotted owls (Pough et al., 1987; Spies & Duncan, 2009). Additionally, they store significantly more carbon than younger forests, contributing to climate mitigation as a natural climate solution (Keeton et al., 2011; McGarvey et al., 2015). The Vermont Conservation Design identifies mature and old forests as vital for biodiversity and ecological resilience, making the expansion of old forest cover a top conservation priority (Zaino et al., 2018).

Despite their importance, no widely available method exists to delineate mature and old-growth forests with high spatial accuracy (Gray et al., 2023). To address this gap, this study leverages the Vermont Old Forest Prediction Model (Vanko, 2024)—a MaxEnt-based spatial model that predicts areas of potential old forest based on satellite derived environmental variables and known presence points. MaxEnt predictive modeling offers an efficient way to guide field sampling and identify candidate sites for conservation, building on previous applications in wetland and rare community mapping in the Great Smoky Mountains National Park (Pfennigwerth et al., 2019).

This research is guided by two key questions: What are the patterns and sources of variability in late-successional and old-growth forest structure across different natural community types in Vermont? And what insights can a stratified random study provide regarding the efficacy of the Vermont Old Forest Prediction Model? It is hypothesized that structural attributes associated with old-growth are positively correlated with dominant tree age across a range of natural community types, and that significant structural differences exist among late-successional and old-growth forests across these different communities. To address these questions, this study classifies forests by seral stage and natural community type using forest inventory data and assesses the effectiveness of the Vermont Old Forest Prediction Model in guiding the identification of old forest locations.

Methods

Study Area

The study area primarily spans the Northern and Southern Green Mountain Biophysical regions of Vermont, USA (Thompson et al., 2019). Three sites outside these regions were sampled opportunistically. Limited to areas below 762 meters (2,500 ft) elevation, the study area encompasses private, federal, state, and municipal land.

The Northern and Southern Green Mountain regions are part of the Appalachian Mountain chain that extends along the eastern seaboard of North America from Alabama to Québec. The Green Mountain's geology is characterized by acidic bedrock consisting of non-calcareous schists, phyllites, gneisses, and granofels (Thompson et al., 2019). Vermont's decadal mean temperatures were 19 °C in summer and -6.3 °C in winter, and the mean annual precipitation was 109 cm from 2011 to 2020 (Galford et al., 2021).

A stratified random sampling approach based on the Vermont Old Forest Prediction Model (Vanko, 2024) was employed to identify sampling sites. To be considered a potential sampling site, a forest patch had to meet the following criteria: (1) be at least 3 ha of contiguous forest (verified using GIS), (2) have at least 68% of a 150 m × 150 m pixel classified as suitable old forest habitat by the Vermont Old Forest Prediction Model, (3) not already be identified as old forest in the VT Natural Community Inventory (Vermont Fish & Wildlife Department, 2024), (4) not be classified as "No" old forest in the VT Natural Community Inventory. In addition to sites meeting these criteria, four random sites classified as old forest in the VT Natural Community Inventory were also sampled. Forested areas that met all listed criteria were stratified by biophysical region and by the pixel's mean old forest suitability percentile. Stratifying in this manner ensured that sampling was geographically dispersed across the Green Mountain region of Vermont and that all percentile classes of suitable old forest habitat were represented. Sampling strategy did not use a priori knowledge to control for forest type, or natural community. Figure 1 shows the locations sampled as part of this study.

Old Forest Sampling Locations

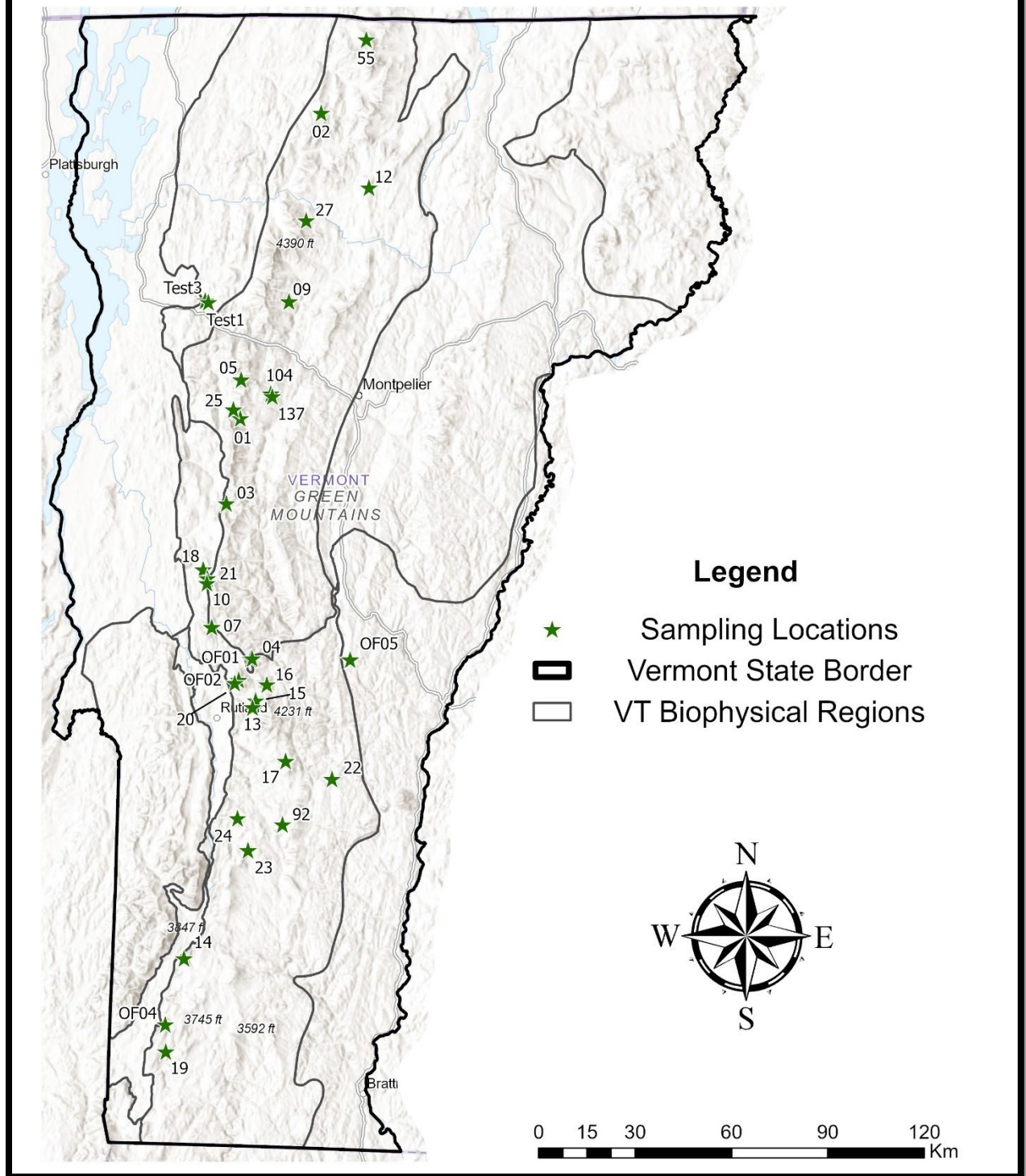
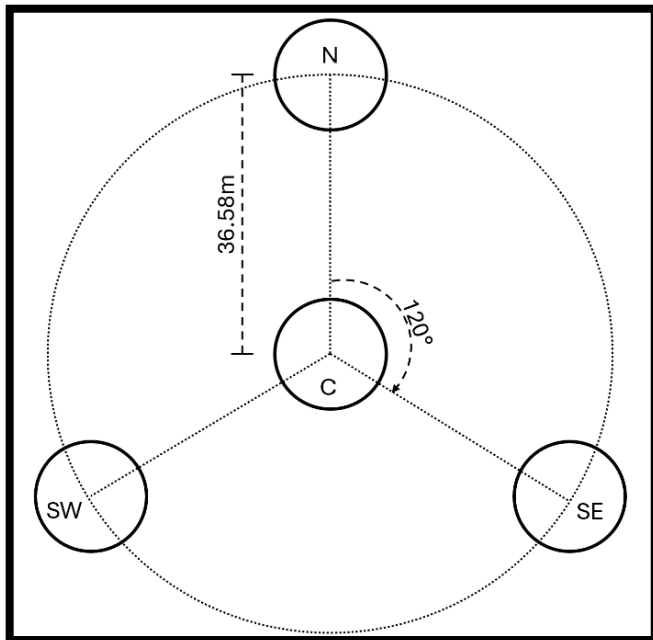


Figure 1: Map of forest sampling sites. Each sampling site is represented with a green star and labeled with the site's unique identifier.

An equal number of sampling site coordinates were generated across strata using the Create Random Points tool in ArcGIS Pro. To prevent spatial autocorrelation, sampling sites were placed at least 500 m apart. For sampling sites on private property, land access permission was attempted; if not granted, a replacement sampling site was randomly generated. In total, 33 sites were sampled, consisting of 11 high-, 9 medium-, and 11 low-suitability old forest sites. Classes were determined by using the quantile break method in ArcGIS Pro to classify suitability scores (averaged to 150m X 150m pixels) into 3 classes with equal frequencies of pixels in each class. Suitability classes represent the following scores: high-suitability is 0.573 to 0.96, medium-suitability is .458 to 0.573, and low-suitability is 0.276 to 0.458. Additionally, two sites considered unsuitable old forest habitat by the Vermont Old Forest Prediction Model were sampled opportunistically. While the suitability classes are being called low, medium, and high it should be noted that all sampling locations needed to meet a minimum suitability threshold of 0.234¹, which represents an AUC of 0.910, and are considered “likely” locations of old forest.

Field Methods

At each site, sampling plots were established following the Forest Inventory and Analysis (FIA) plot cluster design (Forest Service & U.S. Department of Agriculture, 2023). Plot clusters consisted of four plots, except in cases where safety or time constraints limited the number of plots sampled. Each plot cluster was assigned a numerical identifier, and individual plots were named using a combination of the cluster number and a letter representing their geographic position: Center (C), North (N), Southeast (SE), and Southwest (SW). Figure 2 shows the plot cluster schematic used.



For each plot cluster, plot “C”’s center coordinates were randomly generated in ArcGIS Pro and located in the field using an iPhone 11 (± 3 m accuracy) equipped with Field Maps (ESRI). From the center of the center plot three additional plots within each cluster were established using a compass and meter tape at azimuths of 0° (N), 120° (SE), and 240° (SW), with plot centers spaced 36.58 m apart. If terrain features, such as steep drop-offs prevented precise subplot placement, the center was relocated in 10 m increments along the designated azimuth until an appropriate plot center was placed. If a safe location did

Figure 2: Forest inventory plot cluster schematic.

¹ 0.234 threshold was established through model testing by model developer Alex Vanko

not exist within 30m of the original plot center the plot was not sampled.

At each plot center two types of forest inventory plots were established. A variable radius plot was used to sample standing trees ≥ 5 cm diameter at breast height (DBH), species composition, and dominant tree age; and an 8 m radius (0.02 ha) fixed-area plot was used for coarse woody debris (CWD) sampling. The sample of standing trees included in each variable radius plot was identified using a 10 basal area factor (BAF) prism.

Tree measurements included DBH, species identification, and tree status based on Maser (1979). Heights were measured for standing dead trees and trees selected for coring using a Trupulse 200 laser rangefinder (Laser Technology, Centennial, Colorado). Tree age was estimated from increment cores collected at breast height (1.37m) from one dominant canopy tree per plot following McGee et al. (1999). The selection of trees for coring was guided by morphological indicators of age, including bark characteristics, low trunk taper, large twisted upper limbs, and a low leaf area to trunk volume ratio (Pederson, 2010). Cores were initially examined in the field for ring counts, with a subset (30%) mounted later and recounted under a dissecting microscope. Cores from species including eastern hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*) tended to crumble, making it logistically challenging to preserve and mount cores. Therefore, lab recounts were limited to the following species: red spruce (*Picea rubens*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), paper birch (*Betula papyrifera*), and American beech (*Fagus grandifolia*). Coring was not permitted at five sampling sites; at one site (OF05), dominant tree age estimates were obtained from literature (Cogbill & Engstrom, 2005).

Downed wood particles qualified as CWD if they were ≥ 10 cm in diameter, ≥ 1 m in length, and leaning more than 45° . Species, decay class (Woodall et al., 2005), log length, and diameters at each end were recorded.

In addition to structural measurements, site-level environmental variables were assessed, including slope (measured with a clinometer), aspect (measured with a compass), and landscape form (concave, convex, or flat) determined through field interpretation. Each site was assigned a natural community classification following Thompson et al. (2019).

A qualitative assessment of old forest characteristics was conducted using a ranked system of common, uncommon, or absent. The evaluation included the presence of multiple vertical vegetative layers, broad DBH distributions, presence of natural canopy gaps, large standing dead trees (≥ 30 cm DBH), CWD in all stages of decay, CWD representative of living tree size classes, epiphytes associated with old trees (*Lobaria pulmonaria*, *Porella platyphylla*, and *Neckera pennata*) (G. G. McGee & Kimmerer, 2002), pit and mound topography, and visible logging stumps. Responses were recorded independently by three field team members before discussion to minimize observer bias.

All forest metrics were recorded using a custom designed [ESRI Survey123 form](#). For details on this survey and to see a paper data sheet version reference Appendix B: Field Survey Form.

Data Analysis

A quality assurance and control process was applied to screen the inventory data for and to eliminate transcription errors. I used the Northeast Management Decision Model (NED-2; Twery et al. 2005) to calculate forest structure metrics related to standing trees. CWD volume was calculated using the equation for a frustum: $Volume = \frac{1}{3} \pi l(r^2 + R^2 + rR)$ where r = small radius (cm), R = large radius (cm), l = length (cm). CWD volume was converted to biomass estimates using species and decay class specific densities reported in M. E. Harmon et al. (2008). The average dominant tree age by site was estimated from tree ring counts. This is likely a conservative method of tree age estimation because cores were obtained at breast height, meaning that the years it took a sapling to reach breast height are unaccounted for. When only partial cores existed due to heartwood rot the average increments from outer, sound, core sections were extrapolated to inner, decayed sections (McGee et al., 1999).

Forest structural patterns were analyzed both categorically, by age class, and continuously, using average dominant tree age. Sites were classified as either "old", "late successional", or "young to early mature". Classification as old required that sites meet the definition of old forest from Zaino et al. (2018). In line with this definition, the qualitative assessment of old forest characteristics informed the classification in conjunction with the average dominant tree age. For sites where tree coring was not possible, or where other researchers estimated tree ages, those external age estimates were considered when determining whether a site qualified as old forest (Cogbill & Engstrom, 2005; Vermont Fish & Wildlife Department, 2024). Late successional sites were defined as sites with an average dominant tree age greater than 100 years (Whitman & Hagan, 2007), and young to early mature sites had an average dominant tree age below 100 years.

Pearson's correlation coefficient tests were conducted to evaluate if there is a positive correlation between dominant tree age and forest structural characteristics associated with old growth forests across a range of natural community types (Table 1). This test measured the strength and direction of linear relationships between variables, and statistical significance was determined using an $\alpha = 0.05$. All available continuous structural metrics were tested. Additionally, Pearson's correlation coefficient testing was used to identify significant relationships between structural variables and the site's Vermont Old Forest Prediction Model score (averaged to a 150 X 150 m cell).

To test if forest structural characteristics vary significantly among late successional/old growth (LS/OG) forests across the natural community types a Kuskal-Wallis test was used. This a nonparametric method used to compare three or more groups. Additionally, a post hoc exploration of differences in forest structure between specific natural community pairs was done using Dunn's test which is a nonparametric test appropriate for multigroup comparisons (Dinno, 2015). Dunn's test is typically done only if a Kruskal-Wallis test produces a significant result, but it was done on all structural attributes to understand if there were any natural community comparisons worth exploring further, even if results didn't meet the $\alpha = 0.05$ threshold. P-values produced by Dunn's test were adjusted using the Bonferroni method to reduce the risk of type I error.

To evaluate forest homogeneity an F-test was used to compare the variances of structural characteristics between old forests compared to the other age categories of late successional and young to early mature.

Pearson's correlation coefficient results informed the data reduction process. Only structural variables with statistically significant correlations ($p < 0.05$) were retained for further multivariate analysis. In cases where multiple variables were significantly correlated with each other—indicating collinearity—only the variable with the lower p-value was retained to reduce redundancy.

Following data reduction, significant structural variables were analyzed using two multivariate techniques: non-metric multidimensional scaling (NMDS) and hierarchical cluster analysis. NMDS was chosen because it is a robust, non-parametric ordination method well suited for ecological data. It does not assume linear relationships among variables, can accommodate any distance measure, and uses ranked distances to reduce the distortion often introduced by zero-heavy datasets. NMDS was performed using a Bray–Curtis distance matrix to explore compositional dissimilarities in forest structure across sites.

Hierarchical cluster analysis was also used to assess structural similarity among sites. This method groups samples using an agglomerative approach. Ward's method was selected because it minimizes within-cluster variance, and Euclidean distance was used to preserve true spatial distances in the structural dataset. Together, these approaches were used to explore patterns of structural similarity among sites and to evaluate whether age categories or natural community types clustered distinctly in multivariate space.

Mapping

Mapping natural communities of interest, particularly old forest, was a key component of this project. All areas identified as old forest were mapped using ArcGIS Pro. For any field sampling location not already included in the Vermont Natural Community Inventory, a natural community assessment was conducted in the field and subsequently mapped, regardless of forest age. Additional mapping details are provided in each site's natural community survey form, available as supplemental material (Appendix A: List of Supplementary Material).

Sites that were heavily disturbed and did not meet criteria for natural communities were excluded from both community assessment and boundary mapping. For example, Site 13 is a Norway spruce (*Picea abies*) plantation composed of even-aged trees, and Site 22 was actively being logged during the sampling period.

Natural community boundaries were mapped conservatively. Due to logistical constraints, on-foot delineation of community edges was not feasible. Instead, basemap satellite imagery (ESRI) and lidar data (Vermont Center for Geographic Information et al., 2018) were used to estimate boundaries where possible. Most mapped natural communities were located within large, matrix

forests. As mapping 100+ acre communities was beyond the scope of this study, small polygons were delineated to represent only the portions of the community directly surveyed on foot.

As a secondary check of old forest classification, historic aerial imagery from 1942 (Vermont Center for Geographic Information, 2019b) was used to confirm that forest cover existed at that time. Since this imagery is not georeferenced, available tiles were manually georeferenced in ArcGIS Pro using long-standing landscape features such as roads, and bridges. While generally effective, this process was challenging in areas with wall-to-wall forest canopy because there were no discernable permanent landscape features. 1942 historic imagery is not available statewide, so old forest areas without 1942 imagery were validated using 1962 imagery (VT Center for Geographic Information, 2019a). The 1942 imagery was also used on a subset of the young to mature forests to determine if sparse, or no tree coverage could be seen there. It was possible to discern sparse tree cover from fully forested areas.

Results

Exploration of Forest Structure

The results revealed broadly positive relationships between forest age and structural complexity, despite considerable variability across sites. As dominant tree age increased, several indicators of structural development, particularly those associated with biomass accumulation and large tree presence, showed statistically significant positive correlations.

The results of the Pearson's correlation coefficient tests showed that dominant tree age was positively correlated with several measures of aboveground biomass (AGB): total AGB ($r = 0.515$, $p = 0.004$), tree AGB ($r = 0.496$, $p = 0.005$), and live tree AGB ($r = 0.476$, $p = 0.008$).

Among basal area metrics, only basal area of large trees showed a significant positive correlation with dominant tree age ($r = 0.598$, $p = 0.0005$). No significant relationships were found for total basal area, live basal area, or standing dead basal area.

Tree density metrics yielded mixed results. Total tree density ($r = -0.384$, $p = 0.036$) and standing dead tree density ($r = -0.388$, $p = 0.034$) both decreased as dominant tree age increased, while large tree density, which includes living and dead $> 50\text{cm}$ DBH trees, showed the inverse trend. As dominant tree age increased so did large tree density ($r = 0.513$, $p = 0.004$). Live tree density did not exhibit a statistically significant correlation.

In addition to structural metrics, slope was also positively correlated with dominant tree age ($r = 0.430$, $p = 0.018$).

Additional metrics that showed no statistically significant correlations include CWD biomass and quadratic mean DBH.

Table 1: Pearson’s correlation coefficient results for forest structure attributes compared to dominant average tree age

Attribute	P Value	R Value	R Squared
Above Ground Biomass (Mg/ha)			
Total	0.004	0.515	0.265
Tree	0.005	0.496	0.246
Live Tree	0.008	0.476	0.226
Standing Dead	0.233	0.224	0.050
CWD Biomass (Mg/ha)	0.054	0.355	0.126
Basal Area (m ² /ha)			
Total	0.646	-0.087	0.008
Live Tree	0.732	-0.065	0.004
Standing Dead	0.664	-0.083	0.007
Large Tree*	0.0005	0.598	0.357
Tree Quadratic Mean DBH (cm)	0.304	0.194	0.038
Tree Density (no/ha)			
Total	0.036	-0.384	0.147
Live Tree	0.066	-0.340	0.115
Standing Dead	0.034	-0.388	0.151
Large Tree *	0.004	0.513	0.263
Slope	0.018	0.430	0.180

Note: Significant results are given in boldface based on $\alpha = 0.05$. * > 50 cm

Structural characteristics associated with late successional and old-growth forests (LS/OG) were generally consistent across natural community types. To evaluate this, forest structure metrics were compared across natural community types using a Kruskal-Wallis test. Testing was limited to natural community types with at least three LS/OG replicates. With an $\alpha = 0.05$ no significant differences between forest structure metrics were detected across natural community types (Table 2). However, large tree density is approaching significance with a p-value of 0.07. Despite there being no significant differences in structure metrics across natural community types a Dunn’s test was done to complete pairwise comparisons of each natural community type. Due to the iterative nature of multiple pairwise comparisons, a Bonferroni-adjusted p -value was applied to reduce the risk of type I error. After this correction, Dunn’s test revealed no statistically significant differences in forest structure metrics among natural community types.

Table 2: Comparing forest structural characteristics among late successional/old growth (LS/OG) forests across natural community types using Kruskal-Wallis tests

Attribute	P Value
Above Ground Biomass (Mg/ha)	
Total	0.407
Tree	0.272
Live Tree	0.140
Standing Dead	0.980
CWD Biomass (Mg/ha)	0.890
Basal Area (m ² /ha)	
Total	0.373
Live Tree	0.432
Standing Dead	0.942
Large Tree *	0.088
Tree Quadratic Mean DBH (cm)	0.159
Tree Density (no/ha)	
Total	0.126
Live Tree	0.188
Standing Dead	0.579
Large Tree *	0.070
Dominant Average Tree Age	0.941

Note: Significant results are given in boldface based on $\alpha = 0.05$. * > 50 cm. Natural community types included in test were limited to those with at least 3 replicates LS/OG. Natural Communities Tested: Northern Hardwood Forest, Rich Northern Hardwood Forest, Montane Yellow Birch-Red Spruce Forest, and Hemlock-Northern Hardwood Forest.

To examine patterns of forest homogeneity, structural attribute variances were compared using an F-test. Tested attributes include total basal area, total tree density, large tree density, and tree quadratic mean DBH. Results indicate that of the tested attributes, only large tree density showed a significant difference in variance between forest age classes, with old forests exhibiting significantly higher and more consistent variability compared to young and early mature, and late successional forest (F-test, $p = 0.021$). This pattern is illustrated in Figure 3.

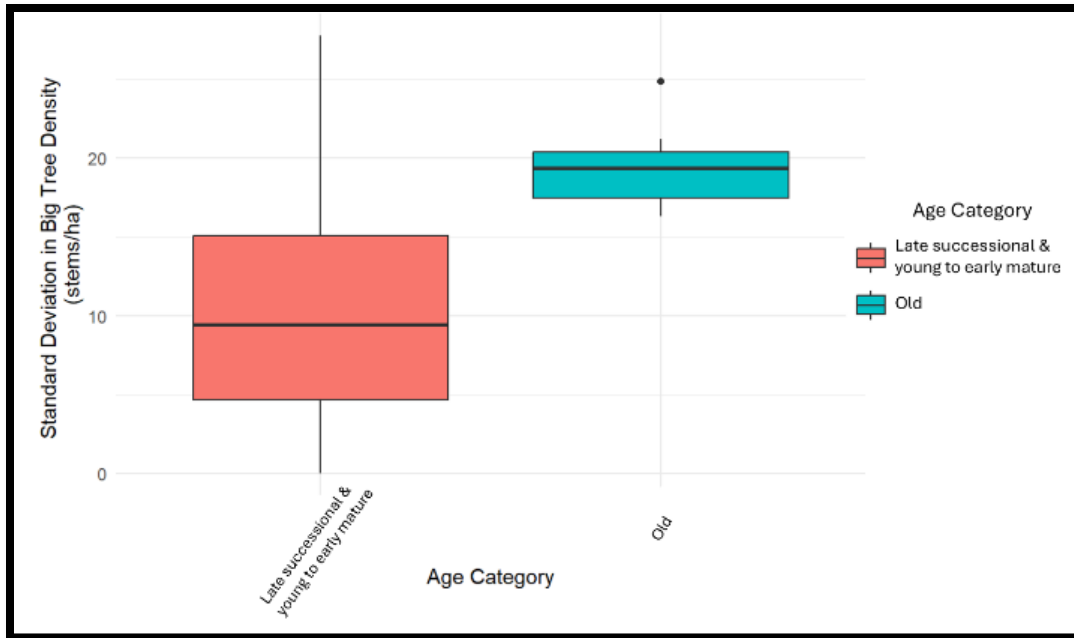


Figure 3: Boxplot of standard deviation in large tree density (stems/ha) across seral stages. The central line represents the median, the box bounds the interquartile range (IQR), and the whiskers extend to $1.5 \times$ IQR. Points beyond the whiskers represent outliers.

Multivariate Approach

Multivariate ordination revealed structural gradients associated with forest age, particularly in relation to biomass and tree density. To examine patterns in forest structure across seral stages, a Non-Metric Multidimensional Scaling (NMDS) analysis was performed using structural variables: total AGB, large tree basal area, average dominant tree age, and tree density. The final two-dimensional solution had a stress value of 0.183, a moderate but acceptable fit for ecological data (Clarke, 1993). The NMDS plot (Figure 4) illustrates the ordination of all sampling sites, color-coded by dominant tree age and shaped by age category (young, early mature, and late successional as circles; old forest as triangles). Structural gradients were evident, with tree density primarily associated with NMDS1, while large tree basal area and total AGB aligned more closely with NMDS2. Sites with older trees tended to cluster toward higher values of AGB and large tree basal area, whereas younger sites were associated with higher tree density.

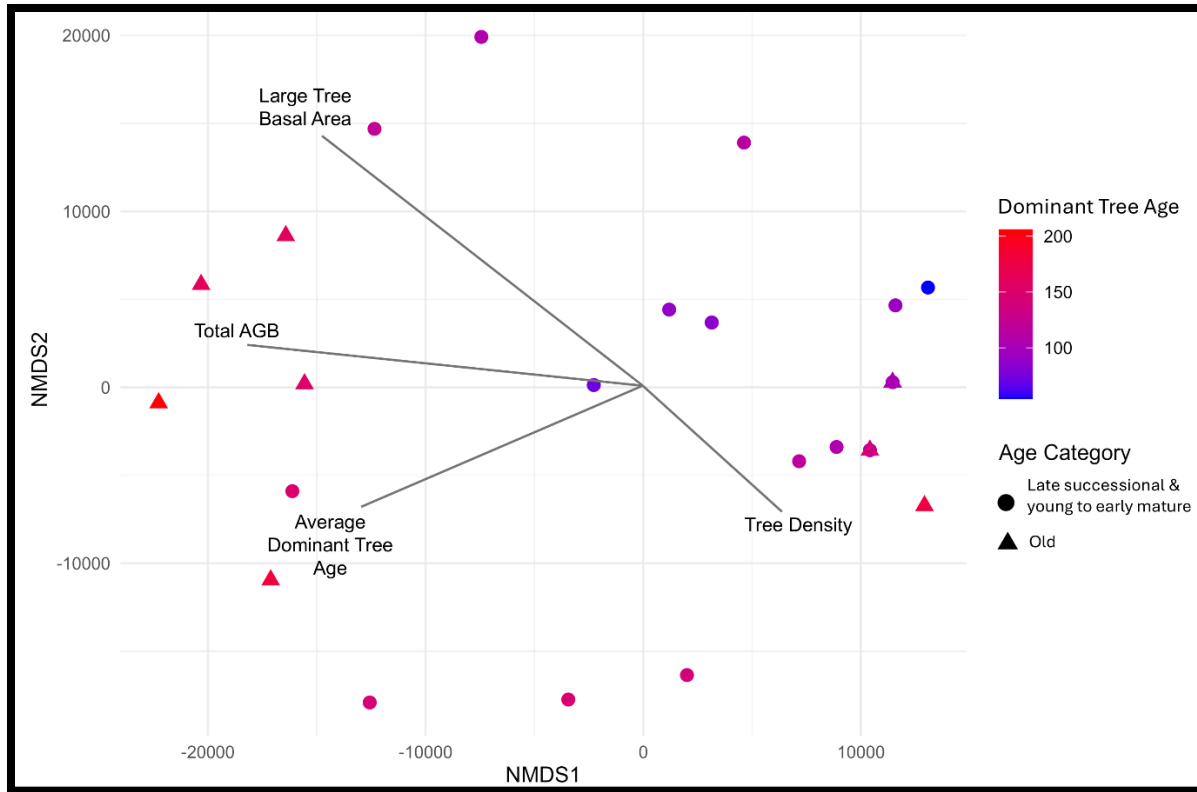


Figure 4: Non-metric multidimensional scaling (NMDS) ordination of forest sampling sites based on structural attributes. 2D solution, stress = 0.183. Structural attributes used: total AGB (Mg/ha), average dominant tree age (years), large tree basal area (>50cm, m²/ha), total tree density (no./ha).

To further understand if old growth forest characteristics vary significantly across natural community types I tested for distinct clustering in multivariate space using hierarchical clustering. The cluster analysis was performed using Ward's linkage method and a Euclidean distance matrix. The analysis included four structural variables: dominant tree age, total AGB, basal area of large trees, and tree density. The resulting clusters were visualized with a dendrogram, delineating three primary clusters (Figure 5). To determine if the clusters were well-separated and cohesive a silhouette score was generated (Rousseeuw, 1987). The average silhouette width was 0.294, suggesting that although clusters are present, the separation between groups is weak and should be interpreted with caution.

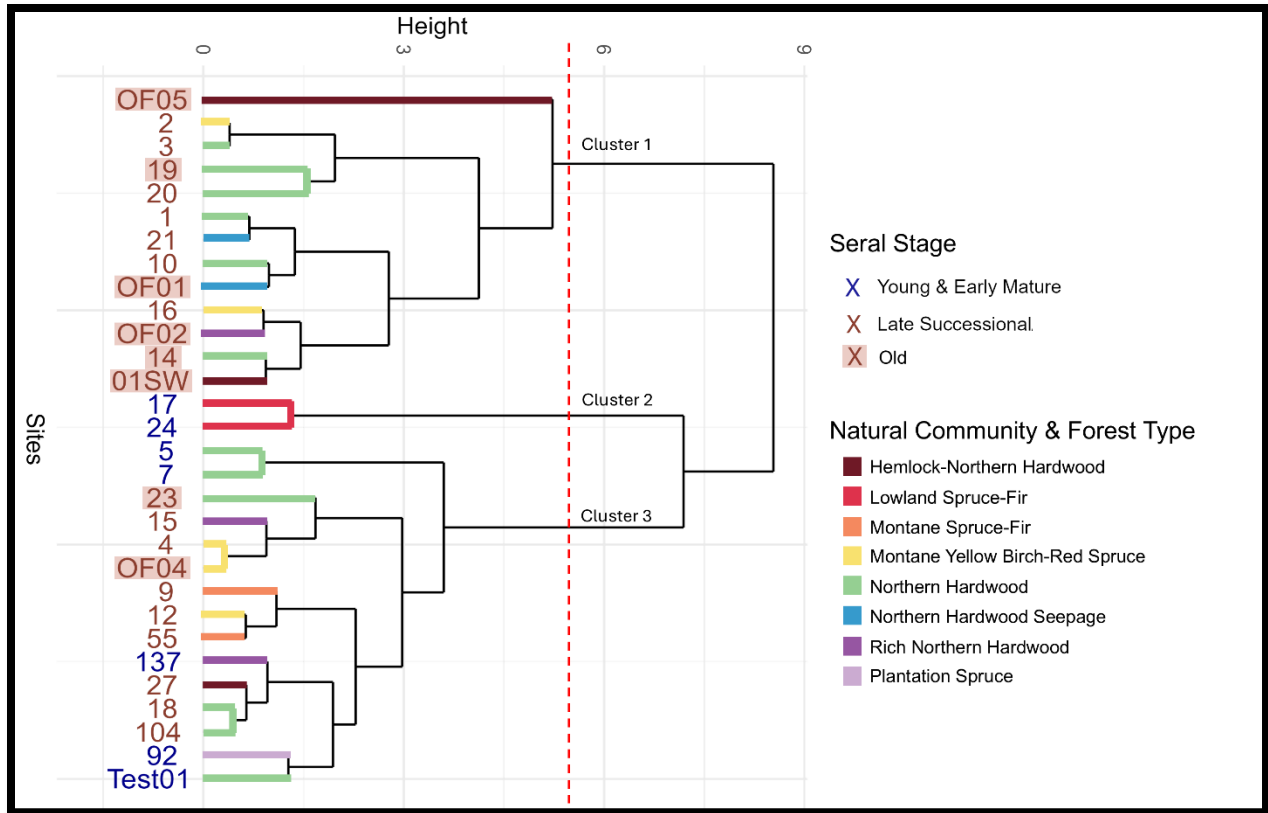


Figure 5: Dendrogram showing hierarchical cluster analysis results. Clustering performed using a Euclidean distance matrix and Ward's linkage method. Variable included: dominant tree age, total AGB, basal area of large trees, and tree density. The red dashed line indicates the cluster cut height (5.5). Site text labels are color-coded by seral stage where young and early mature is blue, late successional is brown, and old is brown and highlighted. Natural community or forest type is denoted through color coded branches.

While an average silhouette width of 0.294 indicates weak clustering there are still some patterns worth noting. No young and early mature sites are part of cluster one, and cluster one includes six out of the eight old forest sites suggesting some clustering by seral stage. Additionally, the only Lowland Spruce-Fir Forest sites group together, alone, in cluster number two, suggesting that they are structurally unique from the other natural community types.

Vermont Old Forest Prediction Model

Pearson’s correlation coefficients were calculated to compare the MaxEnt suitability scores produced by the Vermont Old Forest Prediction Model (Vanko, 2024) with available forest structure metrics. Among the metrics tested, suitability scores showed no significant correlation with any structural features except dominant tree age (Table 3).

Table 3: Pearson’s correlation coefficient results for forest structure attributes compared to MaxEnt suitability score.

Attribute	P Value	R Value	R Squared
Above Ground Biomass (Mg/ha)			
Total	0.719	0.066	0.004
Tree	0.655	0.082	0.007
Live Tree	0.475	0.131	0.017
Standing Dead	0.680	-0.076	0.006
CWD Biomass (Mg/ha)	0.557	-0.108	0.012
Basal Area (m ² /ha)			
Total	0.286	-0.194	0.038
Live Tree	0.470	-0.132	0.018
Standing Dead	0.256	-0.207	0.043
Large Tree *	0.087	0.308	0.095
Tree Quadratic Mean DBH (cm)	0.338	0.175	0.031
Tree Density (no/ha)			
Total	0.150	-0.261	0.068
Live Tree	0.270	-0.201	0.040
Standing Dead	0.104	-0.293	0.086
Large Tree *	0.126	0.276	0.076
Dominant Average Tree Age	0.018	0.435	0.189

Note: Significant results are given in boldface based on $\alpha = 0.05$. * > 50 cm

The old forest suitability score and dominant tree age relationship yielded a p-value of 0.018, and an R^2 value of 0.19 indicating a significant positive correlation at the $\alpha = 0.05$ level. As illustrated in Figure 6, there is a lot of noise in the data, but sites with older dominant tree cohorts tended to receive higher suitability scores.

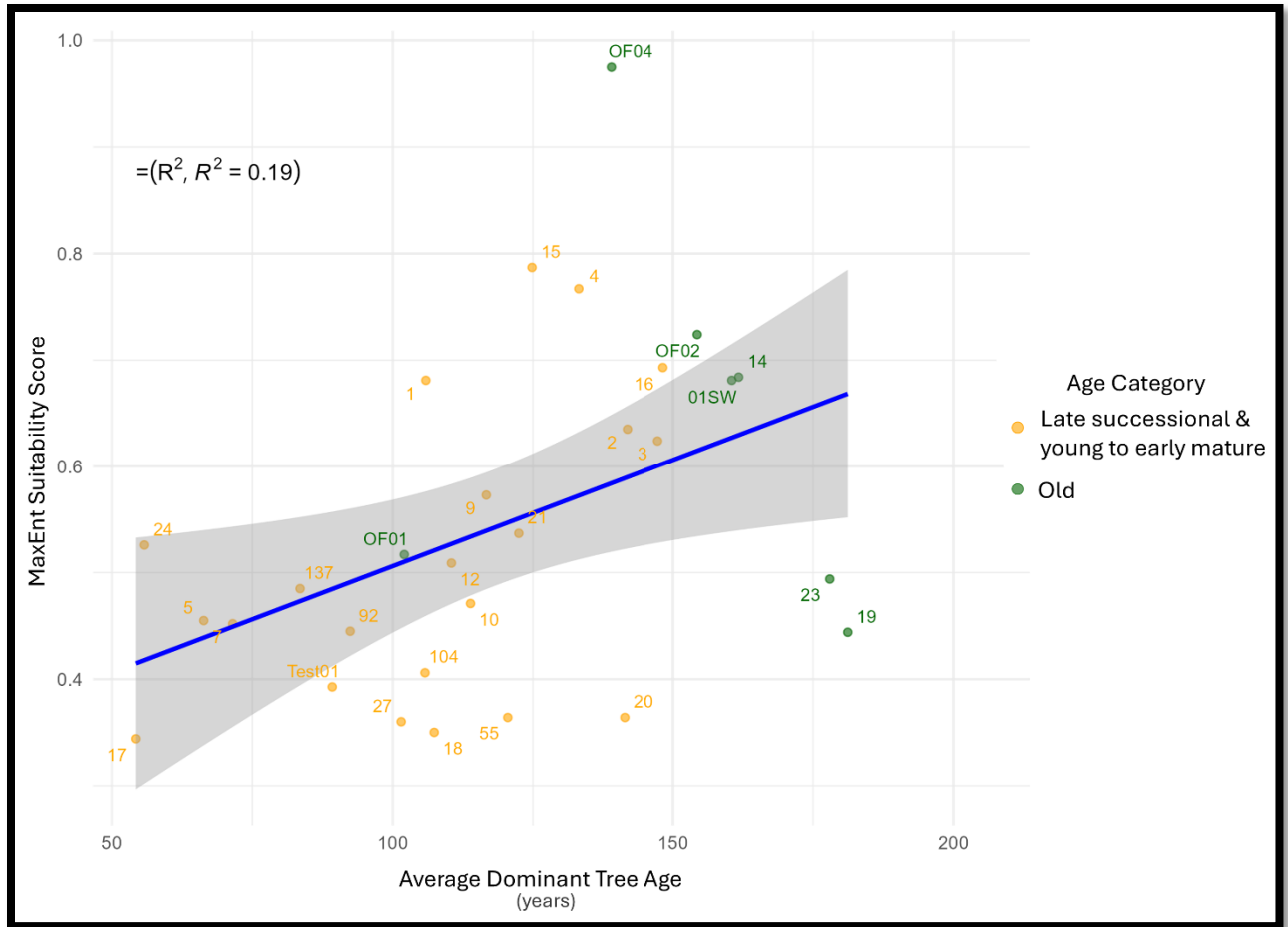


Figure 6: Scatter plot of average dominant tree ages on the X-axis and Vermont Old Forest (MaxEnt) suitability scores on the Y-axis. Each plotted point represents a sampling location. Coloration of points represents the age category of the site’s canopy dominant trees. A Pearson’s correlation coefficient results in a p-value of 0.018 representing a statistically significant ($\alpha < 0.05$) correlation.

Spatial Distribution of Identified Old Forest

Assessing the plot sampling locations for natural community type and determining whether they qualified as old forest was a key component of both the fieldwork and data analysis process. Through this study, five locations were identified as old forest, despite not being previously recognized as such in the Vermont Natural Community Inventory. See Figure 7 for a map of these locations.

Four of the five sites were directly sampled through plot placement. The fifth was identified during fieldwork, even though no plot was established at that exact location. Of the five old forests, three are Northern Hardwood Forests, one is a Montane Yellow Birch–Red Spruce Forest, and one is a Hemlock–Northern Hardwood Forest.

Site 01, shown in the top middle panel of Figure 7, is a narrow 0.4-hectare patch of Hemlock–Northern Hardwood Forest (Image 1) located in Fayston, VT. The narrowness of this stand means that only the southwest sampling plot was situated within the old forest. While this patch is already mapped in the Vermont Natural Community Inventory, it was not previously known to be old. The patch is small and confined to the steep, bouldery banks of a small gorge. Despite its size, it contains large yellow birch (*Betula alleghaniensis*) and hemlock (*Tsuga canadensis*) trees over 200 years old. However, the patch’s limited extent restricts its ability to function fully as an old forest; large standing and down deadwood is uncommon. It is believed that past human disturbance in the area excluded this patch due to its difficult terrain.



Image 1: Site 01's South West Subplot in Fayston, VT

Another location, shown in the top right panel of Figure 7, is a stand of Montane Yellow Birch–Red Spruce Forest located south of Site 16 (Deer Leap Mountain). It was first identified as an area of interest during field sampling at Site 16. After completing plot sampling, the site was revisited to assess whether any surrounding forest could qualify as old. The region was explored on foot, with attention to old-growth characteristics, signs of past human disturbance, and additional tree aging. The forest immediately surrounding the plot cluster was determined to be mature rather than old because it exhibited signs of historical logging, including old stumps. Additionally, tree cores collected during the initial sampling and follow-up visit did not indicate the presence of live trees older than 150 years.

However, a nearby forest patch south of the sampling location was identified as old forest. This spot was not sampled through a formal plot but was assessed using visual interpretation and tree coring. It exhibited structural indicators of old growth, including large CWD, large living and standing dead trees, the presence of lungwort (*Lobaria pulmonaria*), and at least one red spruce (*Picea rubens*) with 240 extremely tight growth rings at breast height.

The remaining three old forest locations shown in Figure 7 are stands of Northern Hardwood Forest located within Green Mountain National Forest. All three sites have canopy-dominant trees that are at least 150 years old. Sites 14 and 23 occur on steep, rocky terrain, whereas Site 19 is situated on a more gradual slope. Further information on these sites—including species lists, soil series, bedrock data, images, and descriptive summaries—can be found in their respective natural community survey forms and in the "Suggested Natural Communities" feature class, both included as supplementary materials with this report (Appendix A: List of Supplementary Material).

Discussion

This study demonstrates that forest structural features associated with old age, such as increased aboveground biomass, and large tree density, develop consistently across a variety of natural community types in Vermont and are aligned with research conducted in Adirondack old-growth forests (McGee et al., 1999; Keeton et al., 2007). While some structural metrics followed expected patterns there was a high level of structural variability across sites. Natural community type was not shown to be the source of this variability.

The Vermont Old Forest Prediction Model showed promise as a tool for identifying likely old forest sites, particularly through its correlation with dominant tree age. Most individual structural metrics were not significantly correlated with model suitability scores, suggesting the model's ability to effectively integrate multiple inputs to reflect cumulative indicators of forest maturity. This reinforces its potential utility for guiding conservation fieldwork, especially when paired with on-the-ground assessment and supplemental resources such as historical imagery and local ecological knowledge.

Forest Structure

The first hypothesis, that dominant tree age would be positively correlated with structural features indicative of old forest conditions across natural community types, was supported by the results. The results showed significant positive correlations between age and AGB (total, tree, & live tree), large tree basal area, and large tree density. Trends consistent with previous research in Northern Hardwood and Riparian Forests in the Adirondacks (McGee et al., 1999; Keeton et al., 2007). A negative correlation between total tree density and stand age was also observed, a pattern supported by some studies (McGee et al., 1999; Ziegler, 2000), though not universally (Keeton et al., 2007).

Notably, no significant relationship was found between dominant tree age and CWD biomass. This differs from some prior research that shows CWD accumulation as a structural component of old-growth forests (M. Harmon et al., 1986; Keeton et al., 2007). However, findings align with McGee (1998), who found that CWD biomass was only significantly related to stand age when CWD was larger than 50 cm in diameter, while small to mid-size CWD (<25 cm) did not vary substantially between stands of different ages. One explanation might be that standing and downed wood biomass is influenced by stem density, which was negatively correlated with age in this study. Younger forests, with higher stem densities, have more trees available to contribute to the deadwood pool through density-dependent mortality (Oliver & Larson, 1996). Additionally, this study's CWD analysis did not differentiate size classes beyond the ≥ 10 cm threshold. Applying a higher minimum diameter threshold, such as 25 cm, might have excluded small to mid-size diameter logs and yielded different results.

Old forests exhibited both a higher mean and significantly greater variability in large tree density compared to young to early mature, and late successional forests (F-test, $p = 0.021$). This suggests that old forests are not only characterized by greater large-tree abundance, but also by greater structural heterogeneity in large trees, likely reflecting complex and site-specific disturbance legacies (Barton & Keeton, 2018). In contrast, when late successional and old forests were grouped

together and compared to young to early mature forests, this pattern did not hold—suggesting that variability in large tree density is a distinguishing feature of old forests, rather than a characteristic shared with late successional stands.

The second hypothesis predicted significant variation in forest structure among late-successional and old-growth forests across different natural communities. This hypothesis was not supported. Kruskal-Wallis tests and post hoc Dunn's tests found no significant differences in structure among community types. These results, coupled with the Pearson's correlation coefficients, suggest that successional trends such as increasing AGB, large tree basal area, and decreasing stem density with age align with existing literature regardless of natural community type. This indicates that structural development over time follows consistent trajectories across a variety of natural community types.

Extrapolation of these results is limited by relatively small sample size and the specific types of natural communities included within the study scope. Stratifying by natural community was not feasible because sampling intentionally included areas that had not been previously classified in the VT Natural Community Inventory. As a result, natural community representation is uneven, with 38% of sampling sites classified as Northern Hardwood Forest and 58% within the broader Northern Hardwood Formation. Expanding future sampling to include more community types and increasing replicates within and across sites could improve the resolution of comparisons.

One outlier, Site OF01—an old Northern Hardwood Seepage Forest—stood out structurally. It has the lowest total stem density across all sites but maintains a relatively high large tree density (ranked 7 out of 34 for large tree density). Additionally, it had the second lowest CWD biomass compared to other old forest sites. Due to less than 3 replicates existing within the Northern Hardwood Seepage Forest designation it was not one of the natural community types included in the Kruskal-Wallis or Dunn's testing. Although significant structural variation was not detected among tested LS/OG forests, the distinct characteristics of Site OF01 suggest that some community types—especially those with naturally low stem densities or glade-like structures—may express old-growth attributes differently. Future research into the late-seral structure of Seepage Forests is warranted to better understand how old-growth characteristics manifest in these systems and if it differs from other forest types.

To evaluate whether forest structure varied by seral stage or natural community type, multivariate analyses were used to test for distinct clustering patterns among sites. NMDS ordination revealed gradients driven by variables such as total AGB and large tree basal area, which tended to separate old forests from younger stands. Hierarchical cluster analysis showed that six of the eight old forest sites grouped within the same cluster, yet the low silhouette score (0.294) indicates weak overall clustering (Rousseeuw, 1987). These results suggest that while old forests exhibit distinct structural tendencies, variability across sites and community types can obscure clean separation in multivariate space. This heterogeneity likely reflects complex combinations of disturbance legacies, site specific conditions, and stand history.

Vermont Old Forest Prediction Model

To address the question of what insights a stratified random study can provide regarding the efficacy of the Vermont Old Forest Prediction Model, this study evaluated whether the model's suitability scores were correlated with structural indicators of old forest. Correlations between structural attributes and suitability score were for the most part not observed. The one significant relationship found was between suitability score and dominant tree age. AGB and basal area were not significantly correlated with model output, despite satellite derived estimates of those metrics informing the model. This disconnect suggests that, although these structural attributes are inputs, the suitability score reflects a complex and successful integration of all variables rather than a direct influence from any single one. An exploration of how on-the-ground measurements compare to satellite-derived datasets is a worthwhile next step to fine tune which datasets are used as model inputs. The Vermont Old Forest Prediction Model's output scores correlating with forest age is a promising indicator of its intended function—to identify areas with high likelihood of harboring old forests.

Exploring the inclusion of a slope dataset as a model parameter is recommended next step. A significant positive correlation was found between field-measured slope and dominant tree age, suggesting that steeper areas may be more likely to harbor old forests. Given Vermont's history of widespread forest clearing, remaining old forests are likely to persist in areas that were historically less accessible, such as steep or rugged terrain.

The evaluation of the model's performance was limited to areas below 762 meters (2,500 feet) in elevation. While this study focused exclusively on lower elevation forests, the model predicts a substantial portion of old forest distribution above this 762m threshold. Additional field validation in montane forest settings would be needed to understand the model's accuracy across Vermont's full elevational range.

Old Forest Detection Implications

An exciting outcome of this research was the identification of five previously undocumented old forest patches, four of which are located on federal land within the Green Mountain National Forest (Figure 7). These findings highlight the value of using the Vermont Old Forest Prediction Model to guide fieldwork. Sites were sampled across the full range of suitability scores and without prior knowledge of forest condition or land use history, providing an unbiased test of the model's utility. The identification of old forest stands under these conditions suggests that targeting high suitability scores is an effective strategy for efficiently locating old forests, as higher scores are associated with older dominant tree cohorts and, consequently, a greater likelihood of encountering old forest.

The prediction model's utility may be further enhanced when paired with a priori information, such as VT Natural Community Inventory notes, historical observations, and local forest expertise. Notably, two of the five sites identified as old were located in areas where nearby element occurrences had previously suggested the potential for old forest—a fact only discovered after field sampling was completed. Another useful methodological step for targeting old forest sites is reviewing historical aerial imagery prior to fieldwork. Although aerial imagery from 1942 and

1962 (VT Center for Geographic Information, 2019a, 2019b) was not reviewed for every sampling location, it was examined for all old forest sites, and a subset of younger sites to estimate the time of last disturbance. If this exploration of imagery had been conducted prior to fieldwork, at least four—and potentially more—sites could have been excluded based on evidence of minimal or no forest cover. While this step was not taken before fieldwork due to the study's intentionally randomized sampling design, historical imagery proves to be a valuable tool for preemptively excluding sites unlikely to contain old forest.

Study Limitations and Potential Sources of Error

Two sources of potential error warrant discussion. The first pertains to tree age estimation. Age estimates follow established methods described by McGee (1998) and used by Keeton et al. (2007), in which increment cores are collected at breast height (1.37 m), and any missing rings due to heartwood rot are estimated by extrapolating ring frequency from the intact portion of the core. This approach includes four primary limitations: (1) excluding the number of years it took for a sapling to reach breast height, (2) assuming consistent radial growth throughout the tree's life, (3) assuming the pith is centered in the trunk, and (4) potential inaccuracies in ring counts due to human error. Tree age estimates in this study are considered conservative, particularly for shade-tolerant species, which grow slowly during canopy suppression. As a result, rings missing due to heartwood rot likely occur at a higher frequency (rings/cm) than in the extrapolated section. Additionally, the years it took a sapling to reach breast height are not included in age estimates. To estimate human error, 30% of collected cores were dried, mounted, and recounted under a dissecting microscope, resulting in a mean absolute error of 13.86 rings and a mean percentage error of 11.41%.

The second potential source of error is sampling bias related to site accessibility and landowner permission. Although sampling was randomized across the full range of suitability scores, practical constraints meant that only sites with landowner access and physical feasibility could be included. Two sites had to be randomly regenerated while actively in the field due to inability to reach the originally generated plot centers, one site was not sampled at all due to remoteness, and one site was replaced due to placement on a greater than 50 degree slope. This may have led to the exclusion of more remote or inaccessible forest areas, potentially underrepresenting some structural or ecological conditions. While efforts were made to reduce bias, future studies could improve representation by integrating sampling in remote locations where back country camping may be required.

Conclusion

This study investigated the structural characteristics and distribution of late-successional and old-growth forests in Vermont through field sampling informed by the Vermont Old Forest Prediction Model. Field-based assessments confirmed the presence of old forest stands in five predicted locations across multiple natural community types. These old forest stands were characterized by large-diameter trees, lower overall stem densities, and high quantities of AGB when compared to younger stands. These structural attributes did not differ across included community types, suggesting that the attributes long associated with Eastern old-growth are consistent in Vermont.

The Vermont Old Forest Prediction Model, a MaxEnt-based tool, was used to guide field sampling and identify likely locations of old forest. Several previously undocumented old forest sites were confirmed through this approach, supporting the model's utility as a complementary tool for identifying candidate areas for investigation. However, the model's predictive accuracy remains limited, and its output should not be used in isolation to define old forest presence. Instead, the model shows promise as one of multiple tools for guiding survey efforts, particularly in regions where existing field-based inventories are sparse.

The results of this study contribute to a growing understanding of the structural attributes that define old forests in Vermont and demonstrate the value of pairing predictive modeling with ground-based assessments. These findings lay the groundwork for future efforts to improve inventory methods and support the delineation of Vermont's remaining old forests.

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APPENDICES

Appendix A: List of Supplementary Material

The following is a list of supplementary materials that support the findings reported in this document and have been shared with the Vermont Agency of Natural Resources, The Wildlands Network, and Northeast Wilderness Trust, and additional relevant parties in separate files.

1. Completed Natural Community Survey Forms

- a. Shared as individual word documents.
- b. Include site descriptions and all other relevant natural community information.

2. Site Location Imagery

- a. Shared as image files organized in labeled folders. Images accompany the natural community surveys.

3. Geospatial Files

- a. Shared as a zipped geodatabase.
- b. Includes suggested natural community polygons to accompany natural community surveys, and plot sampling locations.

4. Data Tables

- a. Shared as Excel files with accompanying “read me” files to explain all sheets, tables, and formulas.

Appendix B: Field Survey Form

[Survey 123 Link](#)

All data was collected through a Survey123 data form, link provided above. Below is a printable data collection form that includes the same fields as the Survey123 form. The survey 123 form has additional reference images for standing and downed wood decay classes.

Plot Cluster:	Sub Plot:
Date Measured:	Scribe Name:
X Coordinate:	Y Coordinate:
Old Forest: Yes No	Natural Community Type:
Aspect / Bearing:	Slope:
Landform:	Evidence of Human Land Use:
Evidence of Natural Disturbance:	Additional Notes:

Plot Structure	Common	Uncommon	Absent
Multiple vertical vegetative layers	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Trees with a broad distribution of DBHs	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Natural canopy gaps visible from plot center	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Large standing dead trees (standing dead >30cm DBH)	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Coarse downed wood in all stages of decay	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Coarse downed wood representative of living tree size classes	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Presence of epiphytes associated with old trees (Lobaria pulmonaria, Porella platyphylla, or Neckera pennata)	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Pit and mound topography	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Logging stumps visible from plot center	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>

Plot Description/Notes:

