

## ABSTRACT

Title of Document:

ASSESSING THE RELATIONSHIPS  
BETWEEN VERTICAL STRUCTURE,  
BIODIVERSITY, AND SUCCESSION IN A  
FOREST ECOSYSTEM USING LIDAR  
REMOTE SENSING

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This thesis used lidar remote sensing to explore the role of vertical structure in forest ecosystem dynamics. In particular, relationship between the vertical distribution, biodiversity, and succession was examined in Hubbard Brook Experimental Forest, NH (HBEF). The first objective was to develop metrics characterizing vertical foliage distribution or canopy layering. Two novel metrics (canopy layer structure categories and number of foliage profile layers) were created, allowing canopy layering to be mapped HBEF. The canopy layer structure metric categorizes areas by comparing the amount of vegetation in under, mid, and overstories. The number of foliage profile layers is related to peaks in the foliage area profile, representing area of dense of “clumped” foliage. Both these metrics varied with canopy height and elevation, areas with taller trees and lower elevations tended to have more foliage profile layers and were classified as categories with a dominant overstory.

The second objective was to examine the relationship between vertical canopy structure and avian species diversity. Multiple vertical structure metrics were derived for 370 bird plots in HBEF. Foliage height diversity (FHD) varied greatly in relation to bird species diversity. Of the foliage distribution metrics, vegetation ratio and number of foliage profile layers explained the most variability in bird species diversity. The lidar metric of height at median return (HOME) had the strongest correlation with bird species diversity ( $r = -0.56$ ). This study showed a moderate correlation between bird species diversity and foliage distribution metrics. It further supports previous studies which question the applicability of FHD.

Finally, change in vertical structure in HBEF was examined using lidar data from 1999 and 2009. Due to significant change in canopy height, canopy cover, vegetation ratio and understory cover during the time period, it was determined that HBEF had not reached steady-state. Recently disturbed areas had significantly higher canopy height growth than undisturbed areas, despite being at higher elevations.

This research presents standardized metrics for the characterization and mapping of canopy foliage distribution. It also provides ecological links between lidar metrics and ecological concepts to enabling these measurements of forest structure to be applied in other areas.

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LIDAR REMOTE SENSING

By

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# Chapter 1: Introduction

## 1.1 Motivation and Background

Forests cover 30% of Earth's terrestrial surface (Zhu & Waller 2003) and support 80% of the global terrestrial biodiversity (World Wildlife Fund 2013). Forests also play a major role in Earth's hydrological and carbon cycles. However, climate change and human influence are affecting forest composition, area, and structure. Degradation and management have led to changes in habitat availability for numerous species (Spies 1998; Eilperin 2009). To protect forest species, the patterns and processes that most impact biodiversity must be better understood. Most habitat and biodiversity studies have characterized forest structure in terms of age, composition, density, and horizontal area characteristics such as cover and proximity to edge (Hinsley et al. 2008; Center for Biological Diversity 2008).

However, forests are 3-dimensional ecosystems, with a vertical component that plays an essential role in ecosystem dynamics (MacArthur & MacArthur 1961; Spies 1998; Latham et al. 1998; Nadkarni et al. 2004; Shaw 2004). Forest vertical structure refers to the spatial arrangement of elements from the ground to the top of the canopy (McElhinny et al. 2005; Bergen et al. 2009). Typical canopy structure characteristics include tree height, canopy height, canopy cover, foliage distribution (also often referred to as "layering"), canopy gap size, leaf area, tree size distribution, biomass, and canopy volume (Spies 1998; McElhinny et al. 2005; Bergen et al. 2009).

The vertical structure of forest canopies directly affects the forest environment (Parker 1995; Nadkarni et al. 2004). The impact on sunlight availability, in particular,

plays a role in both the shaping of the canopy structure as well as the growth and survival of plant species within the forest (Latham et al. 1998; Maguire et al. 1998; Nadkarni et al. 2004). Light levels can vary throughout the forest, depending on the size and frequency of gaps within the canopy as well as with shade from neighboring non-canopy vegetation (Welden et al. 1991). This in turn, impacts the distribution of plant communities within the forest. Species adapted to low light conditions do not respond well in areas with little canopy shading, whereas species adapted to high light conditions (such as canopy trees) grow quickly in areas with less canopy cover, ultimately shading the surrounding vegetation upon reaching adulthood (Welden et al. 1991). Canopy closure also impacts the type and amount of understory vegetation, with noticeable thinning of the understory occurring as the light availability on the forest floor becomes more limited (Franklin et al. 2002; Keller et al. 2003; Nadkarni et al. 2004).

Both forest age (time since disturbance) and environmental variables play a role in determining canopy layering in a forest. As time passes since disturbance, canopy layer structure will change, eventually leading to an “old growth” structure, marked by gaps within the canopy which allow vegetation to flourish at a variety of levels along the vertical column (Spies 1998; Franklin et al. 2002; Keller et al. 2003; Nadkarni et al. 2004; McElhinny et al. 2005). Environmental variables such as slope, aspect, elevation and soil type affect tree growth due to water, light, and nutrient availability, thus affecting vertical canopy structure (Shaw 2004; Thomas & Packham 2007). Studies have shown that tree height and biomass vary along elevation gradients, with areas at higher elevations having shorter trees and less biomass (Whittaker et al. 1974; Hurtt et al. 2004). Forest succession and disturbance are important for forest management in terms of

habitat sustainability, carbon sequestration, and timber harvest (Spies 1998; McElhinny et al. 2005; Falkowski et al. 2009). Differences in vertical structure have been identified between the stages of forest succession (McElhinny et al. 2005; Keller et al. 2003; Franklin et al. 2002). These changes can impact habitat suitability, enabling the availability of species habitat within a forest to change over time (McElhinny et al. 2005). Thus, it is important to understand how aspects of vertical structure change with time.

Many studies have noted the importance of vertical forest structure on faunal biodiversity as well as habitat preference and quality for birds and mammals. MacArthur and MacArthur (1961) provided a seminal study showing that bird species diversity was more strongly related to vertical forest structure than it was to plant species diversity. More recent studies have also shown significant relationships between bird species diversity and metrics which characterize vertical structure within the forest (Clawges et al. 2008; Goetz et al. 2008). Characteristics of vertical structure, particularly canopy height, influence species habitat preference and quality (Hinsley et al. 2002; Hill et al. 2004; Hinsley et al. 2006; Broughton et al. 2006; Hinsley et al. 2008; Smart et al. 2012; Trainor et al. 2013). This important element in habitat preference and quality impacts species in different ways, even within animal guilds. For example, Hinsley et al. (2002) found that the relationship between chick body mass and vegetation height were positive for Blue Tits (*Parus caeruleus*) but were negative for Great Tits (*Parus major L.*).

Advancing beyond simple canopy height, vertical structure within the canopy has been noted as an element in species habitat preference and diversity (MacArthur & MacArthur 1961; Goetz et al. 2010; Swatantran et al. 2012). Structure within the canopy influences bird species feeding patterns, both in terms of food availability/foraging

substrates and actual foraging behavior (Holmes et al. 1979; Robinson & Holmes 1984). Although most of the research linking vertical structure and species habitat has focused on avian species, mammals are also affected by vertical structure. It has been noted that the optimal habitat for the Pacific fisher (*Martes pennanti*) includes areas with dense canopies (Zielinski et al. 2004).

Vertical stratification of the canopy, or canopy layering, has long been used to describe the vertical arrangement of material within the canopy. However, there has been no consensus on how best to define and quantify it (Baker & Wilson, 2000; McElhinny et al. 2005; Parker & Brown 2000; Popma et al. 1988). There is also the issue of examining canopy layering and other attributes of vertical forest structure, at large scales. Previous studies have used hand-drawn canopy profiles or modeling algorithms based on field data to characterize vertical stratification (Paijmans 1970; Sherry 1979; Popma et al. 1988; Aber et al. 1982; Latham et al. 1998; Baker & Wilson 2000). This reliance on field data, which is costly and time-consuming, has limited the applicability of vertical structure (especially canopy layering) as a component of forest management (Weltz et al. 1994; Spies 1998).

Light detection and ranging (lidar) is a form of active remote sensing that provides information on the 3-D structure of forest canopies (Lefsky et al. 2002; Vierling et al. 2008). Both discrete-return and waveform lidar have been used to retrieve many elements of forest structure in many different ecosystems, including canopy height, biomass, and various parameters related the vertical distribution of leaves and branches (e.g. canopy closure, LAI canopy height profile, and vertical foliar diversity) (Dubayah et al. 2000; Lefsky et al. 2002; Hyde et al. 2005; Goetz et al. 2007). Numerous studies have



shown relationships between species habitat preference and biodiversity and lidar metrics that describe various aspects of vertical structure (Goetz et al. 2010; Hill et al. 2004; Hyde et al. 2005; Swatantran et al. 2012). This provides necessary information for forest and species management. For example, lidar has been used to locate areas of potential habitat for the endangered Delmarva Fox Squirrel (Nelson et al. 2005).

Similar to earlier studies of vertical stratification, lidar studies examining canopy layering have not converged on a standard methodology to best characterize this aspect of structure (Zimble et al. 2003; Maltamo et al. 2005; Clawges et al. 2008; Falkowski et al. 2009; Müller et al. 2010). The lack of consistent methods for processing lidar returns and ultimately quantify structure within the forest canopy, such as canopy layering, makes it difficult to apply this information to forest conservation and management. Additionally, many metrics are not directly applicable/translatable to ecological concepts or easily identifiable characteristics within the physical structure of the forest. In order for information on vertical structure (characterization as well as its relationships with species habitat and succession) to be useful for management strategies, it must be understandable to not only the end user (conservationists and foresters) but also applicable to management strategies (Müller et al. 2010).

### 1.2 Dissertation outline

Thus, the ultimate goal of my thesis is to examine the role of vertical structure in forest ecosystem dynamics, specifically relating to biodiversity and succession. To do so, I must assess the utility of full-waveform lidar for forest structure characterization and develop methods that can be used by the research and forest management community for improved characterization, analyses, and monitoring of forest ecosystems. Approaches to

detect and quantify the vertical distribution of foliage within the canopy using lidar data would provide crucial information on forest structure at a landscape scale for forest management and habitat conservation. This would also provide a way of understanding change within forests and their vertical structure as anthropogenic mortality of mature trees increases (Eilperin 2009).

Focusing of the forest ecosystem dynamics of Hubbard Brook Experimental Forest, NH, my thesis is divided into five chapters (introduction, 3 research chapters, and conclusion) (Figure 1.1). The three research chapters address the following objectives:

1. Characterize canopy layering via full-waveform lidar and examine how it varies with environmental variables at the landscape scale (Chapter 2)
2. Determine the relationship between vertical foliage distribution and bird species diversity (Chapter 3)
3. Examine how vertical structure changes over time via lidar-derived metrics (Chapter 4)

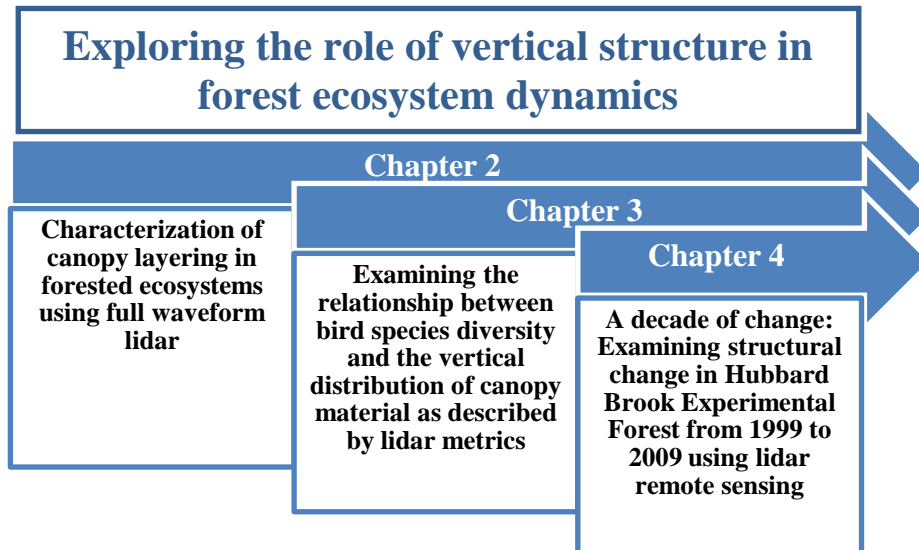


Figure 1.1 Organization of dissertation chapters

Although each chapter addresses a separate research objective, they all tie into the primary goal of exploring the role of vertical structure in forest ecosystem dynamics. In Chapter 2, I address the issue of quantifying canopy layering, which was previously limited due to the lack of data availability. Layering metrics derived from full-waveform lidar enable the variability of this element of vertical structure to be examined, as well as its relationship to landscape scale environmental variables. It has been noted that vertical structure plays a role in forest biodiversity and species habitat preference, especially for avian species. However, the majority of the recent studies comparing lidar-derived vertical structure and species habitat have focused on canopy height. For Chapter 3, I focus on filling the information gap of the relationship between avian species biodiversity and vertical structure, particularly the distribution of foliage within the canopy. The metrics I use in Chapter 3 include the canopy layering metrics developed and examined in Chapter 2, among others. Finally I address questions about forest succession and vertical structure in Chapter 4. Previous research has identified characteristics of vertical structure, which change as a forest moves through successional stages. With the

availability of lidar data from two time periods, the change in vertical structure is quantified and examined based on previous disturbance in HBEF.

### Chapter 2: Characterization of canopy layering in forest ecosystems using full waveform lidar

The goal of Chapter 2 is to characterize the vertical canopy structure in the mixed deciduous forest of Hubbard Brook Experimental Forest (HBEF). Using full-waveform lidar from the Laser Vegetation Imaging Sensor (from NASA Goddard), I examine the vertical distribution of canopy material throughout HBEF. I focus on exploring different methods of mapping the spatial distribution or horizontal variation in vertical canopy layering. Two different methods of characterizing canopy layering were developed from LVIS waveform metrics. Both methods enable the user to examine the variability in vertical structure at the landscape scale. However, they provide different information on foliage distribution throughout the canopy. I examine how both metrics vary across HBEF and how the spatial patterns evident in the vertical structure relate to elevation and canopy height.

### Chapter 3: Examining the relationship between bird species diversity and the vertical distribution of canopy material as described by lidar metrics

In Chapter 3, I build on previous analyses on the relationship between bird species diversity and the vertical distribution of canopy material. Previous studies within HBEF have shown that species richness as well as habitat preference of neotropical migrants are related to vertical canopy structure (Goetz et al. 2007, Goetz et al. 2010, Swatantran et al. 2012). This chapter is structured around three questions:

1. Does the general assumption that bird species diversity increases with foliage height diversity apply to montane forest breeding species in Hubbard Brook Experimental Forest, NH?
2. Out of the different lidar metrics used to describe vertical canopy distribution, which ones have the strongest relationship with and explain the most variability of bird species diversity?
3. How are the results between bird species diversity and the distribution metrics affected when height is accounted for?

Chapter 4: A decade of change: examining structural change in Hubbard Brook Experimental Forest from 1999 to 2009 using lidar remote sensing

Chapter 4 focuses on the change in canopy structure of HBEF from 1999 to 2009.

Using full waveform lidar, I examine how HBEF has changed over the past decade and seek the answer to whether or not HBEF has reached steady-state in terms of vertical structure. First, I examine how the vertical structure in HBEF has changed during the 1999 to 2009 time period, focusing primarily on canopy height, but also including vertical structure variables previously linked to forest succession and species diversity and habitat. Based on the current disturbance regime (1999 – 2009), I determine whether or not HBEF has reached the steady-state based on canopy height and if not, examine if this is due to recent disturbances or recovery from logging in the late 19<sup>th</sup> and 20<sup>th</sup> centuries.

1.3 Summary

Although my thesis focuses on multiple aspects of vertical canopy structure (characterization, relationships with biodiversity and succession), the ultimate purpose is

to increase the understanding of the role of vertical structure in forest ecosystem dynamics, and also provide usable and replicable full-waveform lidar metrics, which describe vertical structure in a way that can be applied for forest conservation and management. By comparing LVIS results to those of past field studies, I draw relationships between lidar-derived metrics and ecological field observations related to forest structure and biodiversity and succession. My hope is that the information gained from this research can be applied to other study areas for a better understanding of the forest structural elements necessary for species diversity and examine how species diversity and habitat would be impacted as forest structure changes (due to anthropogenic or environmental drivers).

## Chapter 2: Characterization of canopy layering in forested ecosystems using full waveform lidar

### 2.1 Introduction

The function and diversity of forest ecosystems are dependent on the physical structure of the vegetation (MacArthur & MacArthur 1961; Spies 1998). Canopy structure, the distribution of plant material within the canopy, can vary as a function of stand age and environmental factors (Latham et al. 1998) and affects species diversity, plant growth, and other aspects of the forest ecosystem (MacArthur & MacArthur 1961; Spies 1998; Latham et al. 1998; Shaw 2004). Ecologists have long noted that vertical structure can account for patterns of animal diversity and richness (MacArthur & MacArthur 1961; DeVries et al. 1997), and have suggested a mechanism of niche partitioning along the vertical axis (e.g., (Kalko & Handley 2001)). Structure and arrangement of canopy layers is also an important component of species habitat suitability, and maps of vertical structure will aid in forest management strategies (Spies 1998). Here, we examine the vertical distribution of material within the canopy and develop methodologies that quantify canopy layering in order to examine how it varies horizontally.

Traditional stratification studies have historically been based on field data, relying on sparse sampling within the forest study area. Hand-drawn canopy profiles are often used to depict vertical stratification (Paijmans 1970; Sherry 1979; Popma et al. 1988), and numerical algorithms have also been used to evaluate layering within field-measured canopy (Aber et al. 1982; Latham et al. 1998; Baker & Wilson 2000).

Both of these analyses are limited to the scale of a sample plot and are subjective in their interpretation. Field-based measurements of vertical forest structure are time-consuming and cannot be practically obtained over large areas, which limit the usefulness of the data when applied to larger areas (Weltz et al. 1994). Moreover, there is no consensus about the best measurement strategy, and a vast range of metrics have been proposed by foresters and researchers for depicting and analyzing the distribution of forest canopy along the vertical axis, especially for canopy layering or vertical stratification (Popma et al. 1988; Baker & Wilson 2000; Parker & Brown 2000; McElhinny et al. 2005). For example, the varying definitions of canopy layering include inconsistent vertical vegetation distribution (Moffett 2000), differing levels of individual tree height (Smith 1973; Hitimana et al. 2004; Maltamo et al. 2005), aggregation of tree species (Smith 1973), and vertical foliage distribution (Parker & Brown 2000). Thus, our ability to both fully understand and compare canopy layering between different forested ecosystems has been limited.

Light detecting and ranging (lidar) remote sensing is an ideal technology to detect layering within the vertical canopy structure. This active form of remote sensing provides information on the 3-D structure of forest canopies by transmitting laser pulses that are then reflected by canopy elements, showing not only height but also the structure within the canopy from the top to the forest floor (Dubayah & Drake 2000; Lefsky et al. 2002; Vierling et al. 2008). Both discrete-return and waveform lidar have been used in many different ecosystems to retrieve elements of forest structure, including canopy height, biomass, and various parameters related to the vertical distribution of leaves and branches (e.g., canopy closure, LAI, canopy height profile, and vertical foliar diversity) (Dubayah



& Drake 2000; Lefsky et al. 2002; Hyde et al. 2005; Goetz et al. 2007; Swatantran et al. 2012).

Numerous lidar-derived products, such as canopy height, canopy cover, canopy complexity, and foliar height diversity, have been shown to accurately depict canopy elements essential for habitat suitability and forest management at the landscape scale (Hill et al. 2004; Hyde et al. 2005; Goetz et al. 2010; Swatantran et al. 2012). Lidar-derived canopy cover is comparable to field-based estimates (Weltz et al. 1994; Means, Acker, Harding, Cohen, et al. 1999; Hyde et al. 2005; Sexton et al. 2009) and has been used as a forest descriptor for research in forest structure and species habitat (Lefsky et al. 2002; Swatantran et al. 2012; Smart et al. 2012; Trainor et al. n.d.). Similarly, the lidar-derived apparent foliage area profile has been used in numerous forest structure studies, providing useful information on forest structure that is comparable to physical measurements (Coops et al. 2007; Jupp et al. 2008).

While some remote sensing studies (usually using discrete return small footprint lidar) have specifically considered vertical stratification, they have not produced a consistent remote-sensing methodology for determining layering within the canopy (Zimble et al. 2003; Maltamo et al. 2005; Clawges et al. 2008; Falkowski et al. 2009; Müller et al. 2010). The number of returns within subjectively determined canopy layers has served as inputs for habitat models (Clawges et al. 2008; Müller et al. 2010). Clawges et al. (2008) suggest that the amount of vegetation within specific layers impacts the habitat suitability for certain avian species. Similarly, Swatantran et al. (2012) suggested stratification in Hubbard Brook Experimental Forest based on bird habitat preferences for canopy cover at different height levels. However, these results have not been translated into ecologically

meaningful terms, such as number of canopy layers or a consistent metric for vertical stratification. Movement towards reconciliation of these new, remotely sensed metrics with more familiar ground measurements provides researchers and forest managers a link by which they can apply landscape scale measurements of vertical structure variability to problems of habitat and forest management that have been severely constrained by lack of data.

Thus, to more fully understand the role of vertical canopy structure in forest dynamics and species habitat, methodologies must be developed that bridge the gap between lidar remote sensing technology and ecological research and conservation application. Basing lidar metrics on variables understood in forestry and ecological research should result in more meaningful information and methodologies that can be applied across ecosystems (Müller et al. 2010). Once this is accomplished, an exploration of factors affecting the spatial variability of vertical canopy structure may lead to important generalizations and insights applicable across ecosystems.

The goal of my research is to characterize the vertical canopy structure in the mixed deciduous forest of Hubbard Brook Experimental Forest (HBEF) and examine the vertical distribution of canopy material using full waveform lidar. In particular, I seek to explore methods for mapping the spatial distribution of vertical canopy layering. First I describe my study area and the lidar data acquisitions over it. Next, I characterize the vertical structure of foliage throughout HBEF. I then outline two methods for depicting vertical structure: the first is based on categorization of structure into nine types, and the second uses the continuous foliage profile to find significant concentrations of vertical canopy material. I apply both methods to produce spatial maps of layering across the

HBEF watershed and explore whether spatial patterns in structure are related to gradients in two factors hypothesized to affect layering, canopy height and terrain elevation, both of which vary greatly within the study area (Figure 2.1). Lastly, I discuss in detail potential sources of variation in our maps and the type of information provided by each layering dataset.

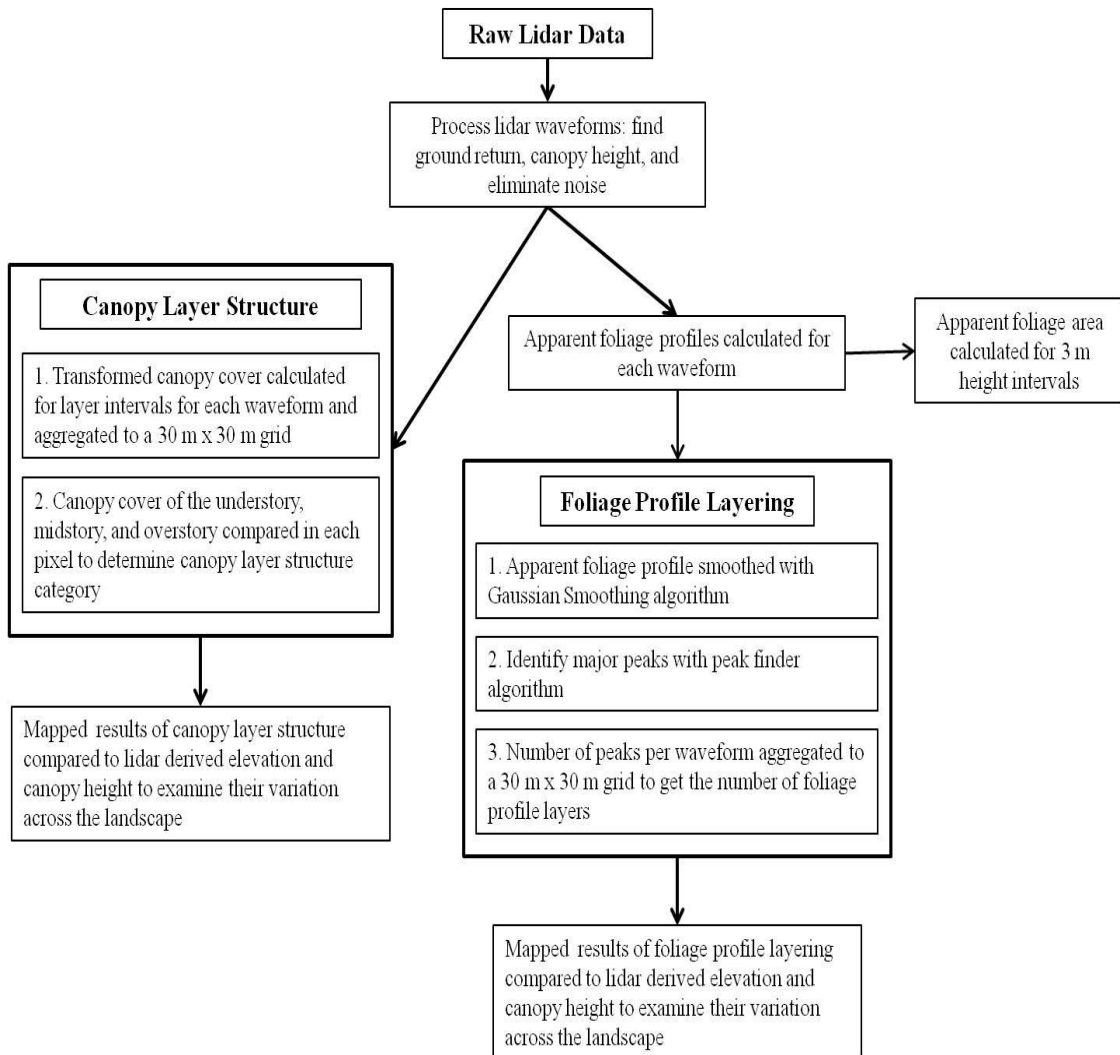


Figure 2.1 Flowchart of lidar processing and analyses

## 2.2. Materials and Methods

### 2.2.1 Study Area

The study area covers 3,185 ha of the White Mountain National Forest, including Hubbard Brook Experimental Forest, and is located in central New Hampshire, USA. The forest resides in an east-west oriented watershed (Figure 2.2). Elevation within HBEF ranges from 220 m to 1,015 m above sea level. The canopy is predominately red spruce (*Picea rubens*), balsam fir (*Abies balsamica*), and birch (*Betula sp.*) at higher elevations and sugar maple (*Acer saccharum*) and beech (*Fagus grandiflora*) at lower elevations (Schwarz et al. 2001).

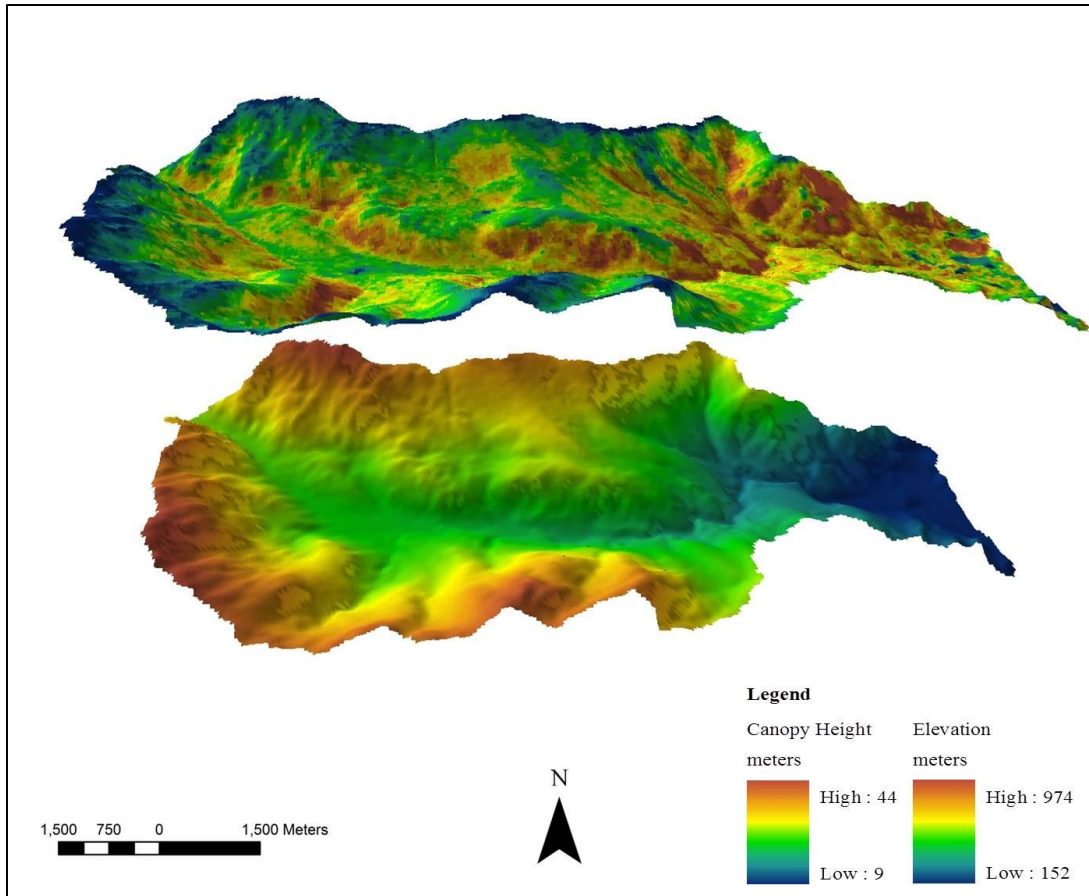


Figure 2.2 Map of Hubbard Brook Experimental Forest. The upper map shows the variation in lidar derived canopy height and the lower map shows the elevation across the study area.

### 2.2.2 Lidar Data

Waveform lidar was acquired over HBEF in the summer of 2009 from the Laser Vegetation Imaging Sensor (LVIS). LVIS is a medium-footprint, full-waveform lidar developed at NASA’s Goddard Space Flight Center (Blair et al. 1999). LVIS records the entire outgoing and return signal to provide waveforms that can be used to map sub-canopy topography, canopy height and vertical foliage profiles. The amplitude of the geolocated waveform at a given height is proportional to the amount of canopy material at that height making it suitable for canopy stratification studies (Hyde et al. 2005). LVIS was flown at an altitude that achieved a nominal 20-m diameter footprint on the ground.

The footprints overlap slightly in the across- and along-track flight direction to achieve approximately contiguous coverage over the entire imaging swath (about 2 km wide for these flights). A detailed description of LVIS waveform processing is available in Hofton et al. (2002) and Dubayah et al. (2010).

High slopes within the study area can sometimes affect the ability of LVIS algorithms to accurately determine ground returns (see Dubayah et al. 2010). While such errors are generally small, they can be as much as a few meters for isolated shots, the effect of which provides an inaccurate estimate of elevation for that observation, and therefore canopy height. Discrete return lidar (DRL) data also were available for HBEF, previous work comparing DRL and LVIS elevations in HBEF found DRL to be more accurate (Swatantran et al. 2012). Therefore, I used the DRL data to correct LVIS ground-finding errors (following Swatantran et al. 2012). However, had there not been a noticeable issue with the LVIS ground returns for this particular set of LVIS data, the DRL measurements would not have been necessary, and the ground and canopy height measurements would have been directly derived from the LVIS data as shown for other LVIS datasets (e.g. Drake et al. 2002; Hyde et al. 2005). DRL measurements were acquired over the area in 2009 with a return density of about 5 shots per square meter. Canopy height was calculated by subtracting average elevation of DRL within an LVIS footprint from the LVIS detected canopy top, which is the lidar return at the top of the waveform greater than the noise threshold (Swatantran et al. 2012) (Figure 2.2).

### 2.2.3 Characterization of vertical canopy structure

#### *Foliage Area Profile*

Lidar-derived apparent foliage profiles portray the vertical distribution of foliage area volume density ( $\text{m}^2/\text{m}^3$ ) (Ni-Meister et al. 2001). These were calculated from the LVIS waveforms based on methods used in Ni-Meister *et al.* (2001) for LVIS lidar data flown over HBEF in 2009. Although it has been noted that in some areas (mainly coniferous forests) the apparent foliage profile can underestimate the foliage area density due to the clumping of needle leaf foliage (Ni-Meister et al. 2001); previous studies have determined that it can still provide useful information on forest structure that is comparable to physical measurements (Coops et al. 2007; Jupp et al. 2008). The apparent foliage area was aggregated into 3-m height bins (from the ground to the top of the canopy) and then averaged over a  $30 \times 30$ -m grid for the entire forest. Due to mixing between the ground and canopy return (Hofton et al. 2002) only the height intervals above 3 m were used because of potential amplification of foliage area near the ground. These profiles were then analyzed for HBEF as a whole, as well as a function of three elevation ranges. Sherry (1979) examined the foliage area of HBEF between 500 and 600 m and I use this as a starting point for our stratification into low, middle, and high elevations. The elevation levels coincide with the terrain features of the forest, with areas of low elevation (< 500 m) occurring around the major rivers and streams in the watershed, middle elevation (500 m to 700 m) occurring in the between the wetland areas and the forest edge, and areas

of high elevation (>700 m) occurring around the edge of the watershed, furthest away from the riverine valleys.

### *Canopy Layer Structure*

Canopy cover in any location is defined as the amount of sky (in percent) obscured by vegetation at nadir. Cumulative canopy cover is the summed canopy cover from the top of the canopy (zero) to the ground (total canopy cover). Lidar derived canopy cover has shown to be comparable to field based estimates (Weltz et al. 1994; Means et al. 1999; Hyde et al. 2005). The high accuracy of lidar derived canopy cover has led it to be used as a forest descriptor for research in forest structure and species habitat (Means et al. 1999; Swatantran et al. 2012). For any particular vertical segment of the canopy, the return waveform energy in that cross-section is divided by the waveform's total return energy, which, after accounting for differences between ground and canopy reflectance, allows for the calculation of cumulative canopy cover.

Cumulative canopy profiles were calculated following methods outlined in Ni-Miester et al. (2001). I further applied the MacArthur-Horn transformation ( $-\ln(1 - \text{cover}(h))$ , where  $h$  refers to height) to account for the extinction of light as it travels through the canopy (MacArthur & Horn 1969; Lefsky et al. 1999a; Lefsky et al. 1999b; Harding et al. 2001). The cumulative profile was used to calculate transformed canopy cover (hereafter “canopy cover” for any given height interval within the canopy (Swatantran et al. 2012)).

We derived canopy cover for three basic canopy layers: understory, midstory, and overstory (Helms 1998; Carey et al. 1999). Similar to MacArthur and MacArthur (MacArthur & MacArthur 1961) the height thresholds defining each of these layers were based on findings of avian species habitat preference in HBEF (Swatantran et al. 2012).



The understory layer is 0 to 5 m, which encompasses shrubs and small saplings (Carey et al. 1999; Globe 2005). The midstory, encompassing larger saplings and intermediate trees (Missouri Department of Conservation n.d.), is 5 to 15 m. The overstory, or upper layer of the canopy (15 m to the top of the canopy), contains more mature seed-bearing trees (Helms 1998).

The waveforms were aggregated into a  $30 \times 30$  m grid and the average transformed canopy cover for each of the 3 layers was calculated for the grid cells. These values were used to determine a canopy layer structure category (defined next) for each grid cell, providing a map of canopy layer structure within HBEF. The canopy layer structure is described by nine canopy configuration categories that are based on the canopy cover relative to the three canopy layers: understory (U), midstory (M), and overstory (O). The canopy cover is compared between the layers, with the overstory compared to the midstory and the midstory compared to the understory. The layers are considered different (either greater or lesser than each other) if there is a difference in the waveform-derived canopy cover greater than 10%. This comparison results in nine configuration categories that can be mapped (Figure 2.3). For example, category 4 (O > M > U) depicts an area where the percent cover in the overstory is greater than the midstory and the midstory cover is greater than that of the understory (in each case by at least 10%). The motivation for such a classification scheme is two-fold. First, it tends to mimic how a field ecologist might describe the canopy from the ground in terms of broad classes. Secondly, it takes a continuous variable (canopy cover), and transforms it into a measure of canopy organization that can be easily mapped and visualized.

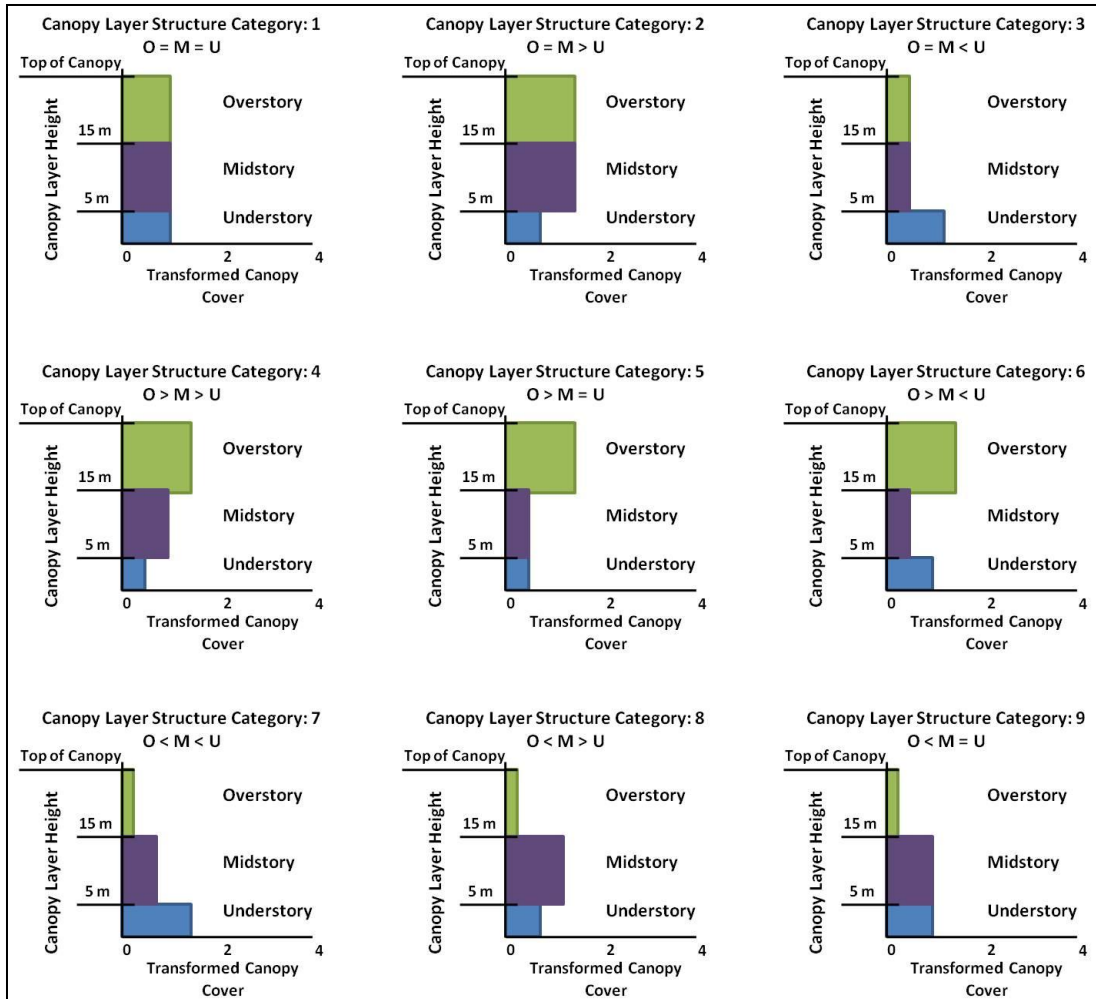


Figure 2.3 Illustrations of the canopy layer structure categories

### *Foliage Profile Layering*

An alternate means of examining the vertical structure of the canopy is to evaluate the continuous profile of the canopy, instead of looking at sections of cumulative measurements (as in canopy layer structure). Peaks and troughs in the apparent foliage profile represent areas of increased and decreased reflection from canopy elements. Assuming that on average the reflectance of the canopy elements do not change much, the peaks of the foliage profile may be inferred to represent major concentrations of

vegetation indicative of canopy layers (Koike et al. 1990; Parker & Brown 2000). To minimize the influence of noise, we first applied a Gaussian smoothing algorithm to the foliage profile, and then found its mode or area with the densest vegetation (Parker & Brown 2000). The other peaks of the smoothed foliage profile were detected using a moving window of five LVIS waveform height bins, which defined a peak at an inflection point in the smoothed foliage profile where afterward the foliage area decreased for five LVIS bins. The peaks were then compared to the mode of the foliage profile to determine if they are large enough to be an area of dense vegetation relative to the mode. I chose a relative difference of 30% as a threshold for determining that a layer occurred at the height; *i.e.*, the peak had to be at least 30% as large as the profile mode. The amount of Gaussian smoothing, moving window size and peak definition parameters were determined by visual analysis.

The output of this algorithm provided the number of peaks for each waveform and the heights at which these peaks occur, which is the mean layer height (Figure 2.4). To minimize the potential for misidentification of canopy layers near the ground due to mixing between the ground and canopy return (Hofton et al. 2002), only peaks occurring 3 m above the ground were selected. The number of apparent foliage area profile peaks was then mapped to depict the canopy layering across the landscape at a 30 m resolution in terms of the number of layers in a location and the height where the layers occur. To do this, a 30 m  $\times$  30 m grid was laid over the study area. The number of layers for each waveform was averaged for the number of waveforms in each grid cell. Then the averaged number of layers was rounded to the nearest whole number to obtain a measure

of layering within each 30 m × 30 m grid cell. The layer heights were also examined to see where layers occurred within the canopy.

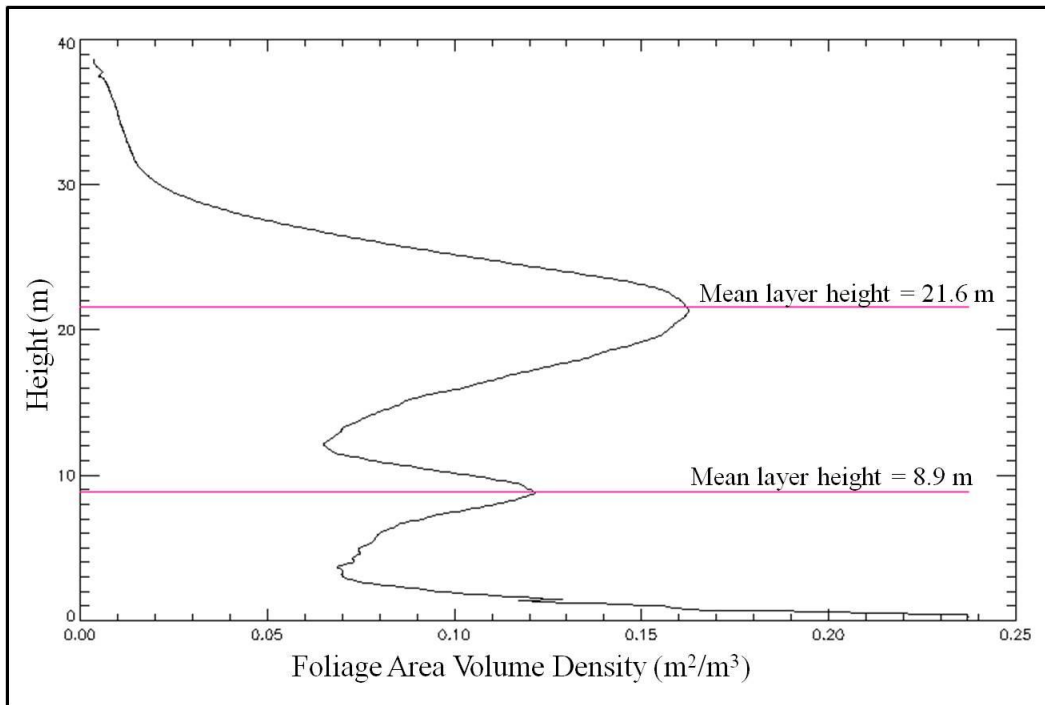


Figure 2.4 Example of layers from foliage profile layering

### 2.2.4 Height and Elevation Analyses

The results of both datasets (canopy layer structure and foliage profile layering) were mapped across HBEF. Boxplots and ANOVAS were used to evaluate how each canopy layering dataset varied with canopy height and elevation.

## 2.3 Results

### 2.3.1 Foliage Area Profile

The majority of the foliage occurred within the middle of the range of canopy heights, between 6 to 15 m (Figure 2.5) with an approximate peak between 9 and 12 m. This result shows that over the entire forest there is less foliage in the upper canopy.

Similarly, foliage area tended to decrease towards the understory. When compared across elevation zones, the height of the peak foliage area changed. The histograms for middle and low elevations have a similar shape to that for HBEF as a whole (dominant midstory), but for high elevations the histogram is markedly different. The foliage area peaked between 6 and 9 m at high elevations but occurred higher in the canopy (between 12 and 19 m) at lower elevations (< 500 m) (Figure 2.5). The low elevations also had the least amount of foliage at the lower part of the canopy (3 to 6 m) when compared to areas of middle and high elevation. At areas of mid elevation (500 to 700 m) the majority of the foliage area occurred between 9 and 16 m within the canopy.

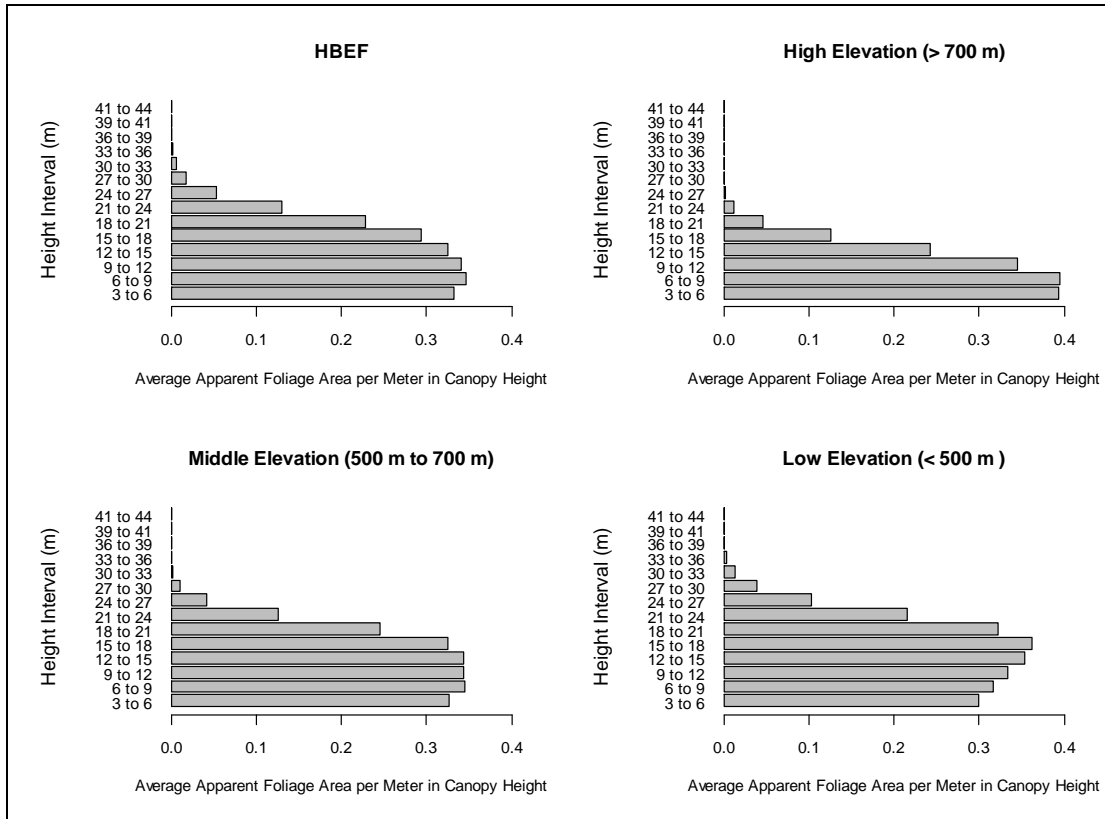


Figure 2.5 The apparent average foliage area profile for HBEF, divided into 3 m height intervals. The top-left graph shows the foliage profile averaged over all of HBEF. The averaged foliage profile for low elevations shows that the amount of foliage peaks between 12 and 19 m in the canopy. This peak in foliage area is lower for canopies at middle (9 to 15m) and low (6 to 9 m) elevations.

### 2.3.2 Canopy Layer Structure

All nine canopy layer structure categories were present in the Hubbard Brook Experimental Forest study area (Figure 2.6). Categories 2 ( $O = M > U$ ) and 4 ( $O > M > U$ ) ( $n = 35975$  and  $6124$  pixels, 10% and 17% respectively) were found mainly in the forest interior, relatively close to rivers. Categories 7 and 9 ( $n = 709$  and  $684$ , 2% and 1.9%) tended to be closer to the edges of the study area. The majority of the forest fell into category 8 ( $O < M > U$ ), which covers almost 2148 ha of forest ( $n = 23925$  pixels, 67%) (Figure 2.7). These areas have a well-developed midstory and

fairly open under- and overstories. The other major categories include categories 4 and 2. These results suggest that the majority of the canopy material within the forest is located in the midstory (5 to 15 m) and that in general HBEF has a fairly open understory.

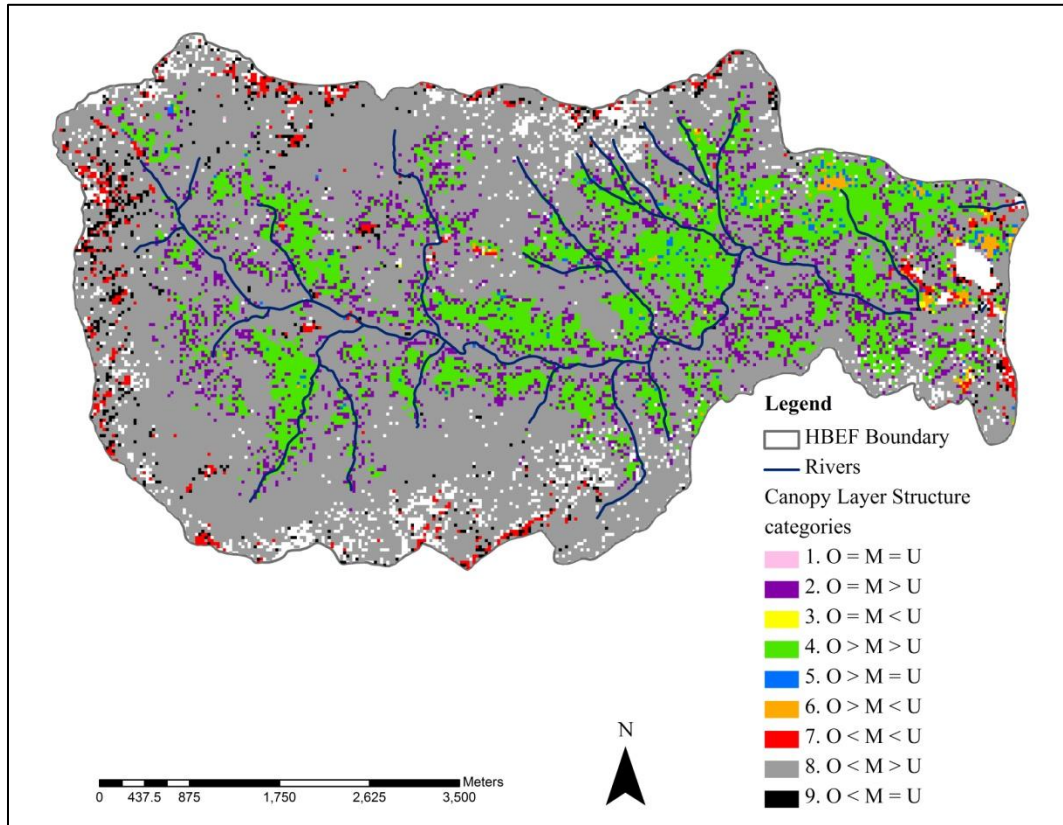


Figure 2.6 Map of canopy layer structure categories in Hubbard Brook. Categories 2 and 4 were mainly found in the forest interior, along rivers. Categories 7 and 9 were predominantly along the ridgeline. Category 8 was found throughout the study area.

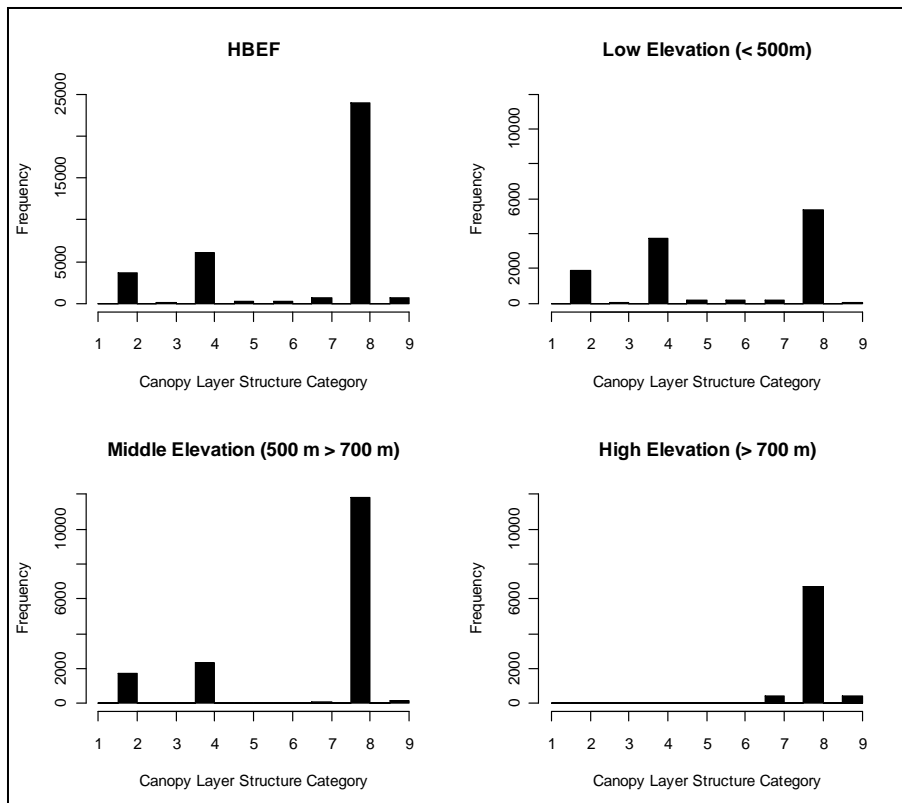


Figure 2.7 Histogram of canopy layer structure categories showing the number of pixels in each canopy layer structure category for all of HBEF (upper left) as well as at the low, middle, and high elevation levels.

The presence of specific canopy layer structure categories was related to overall canopy height and elevation based on the significant difference of median canopy height and elevation for the majority of the categories; that is, some categories were differentiated based on the median canopy height and/or median elevation of that category relative to other categories (Figure 2.8) These results were supported with subsequent ANOVA results ( $p < 0.05$ ) (Figure 2.8). However, there was a wide range both in canopy height and elevation within categories. The categories with higher average canopy heights were categories 4 (30.7 m), 5 (32.7 m) and 6 (32 m), all of which have dominant overstory. Categories 7, 8, and 9, which have an open



overstory, occur at higher elevations, with the average elevation of 646.2 m, 598.1 m, and 706.1 m, respectively.

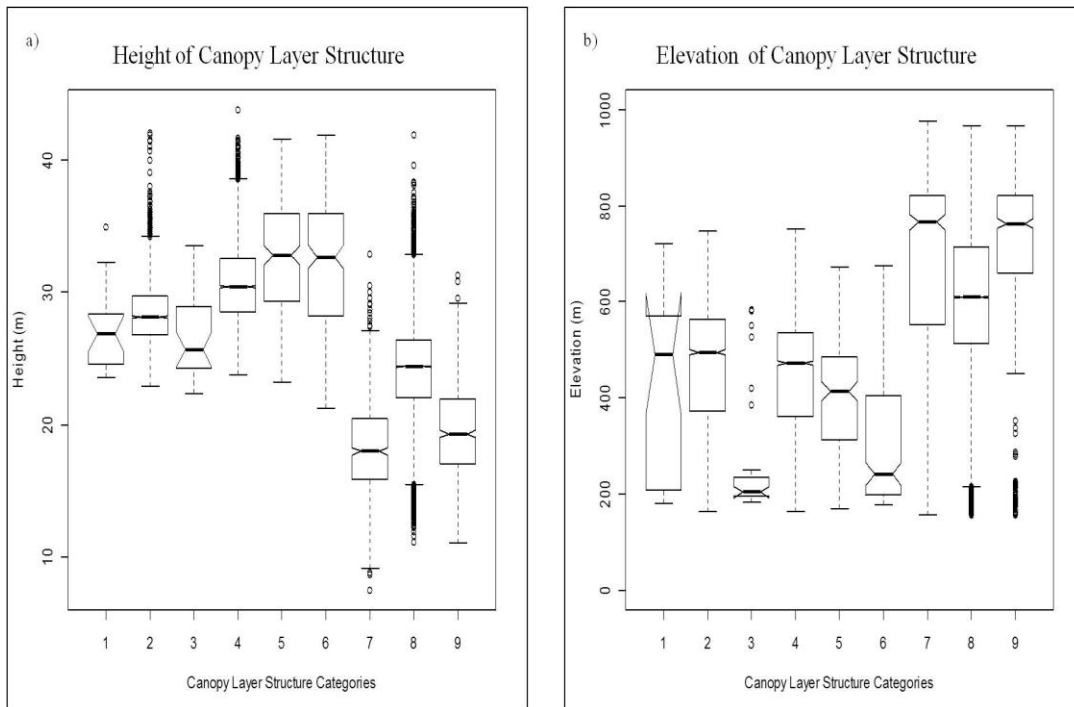


Figure 2.8 Canopy height (a) and elevation (b) distribution for each category of canopy layer structure. Boxes represent the interquartile range, with whiskers defining the range of heights within 1.5 times the upper and lower quartiles. The open circles depict outliers. The median canopy heights differ between most of canopy layer structure categories at roughly the 95% confidence level, as shown by the lack of overlap between notches on the box plots. The small sample size of categories 1, 3, and 6 caused the confidence of the median to be calculated larger than the data range, as depicted by the extended notches on the boxplots.

### 2.3.3 Foliage Profile Layering

The (51%) of the forest study area (1616.3 ha) was comprised of two foliage profile layers (Figure 2.9), and about 40% (1,265 ha) of HBEF had one layer within the canopy. Areas with more than 3 layers accounted for less than 1% of the study area.

Mapped results of the number of foliage profile layers showed that areas with 2 or more foliage profile layers tended to occur in the interior of the forest (Figure 2.10). Areas with one foliage profile layer were found from the edge of the forest to its interior but generally were not found in areas adjacent to rivers. Areas with 0 foliage profile layers (469 pixels in all) were generally located towards the outer edge of HBEF.

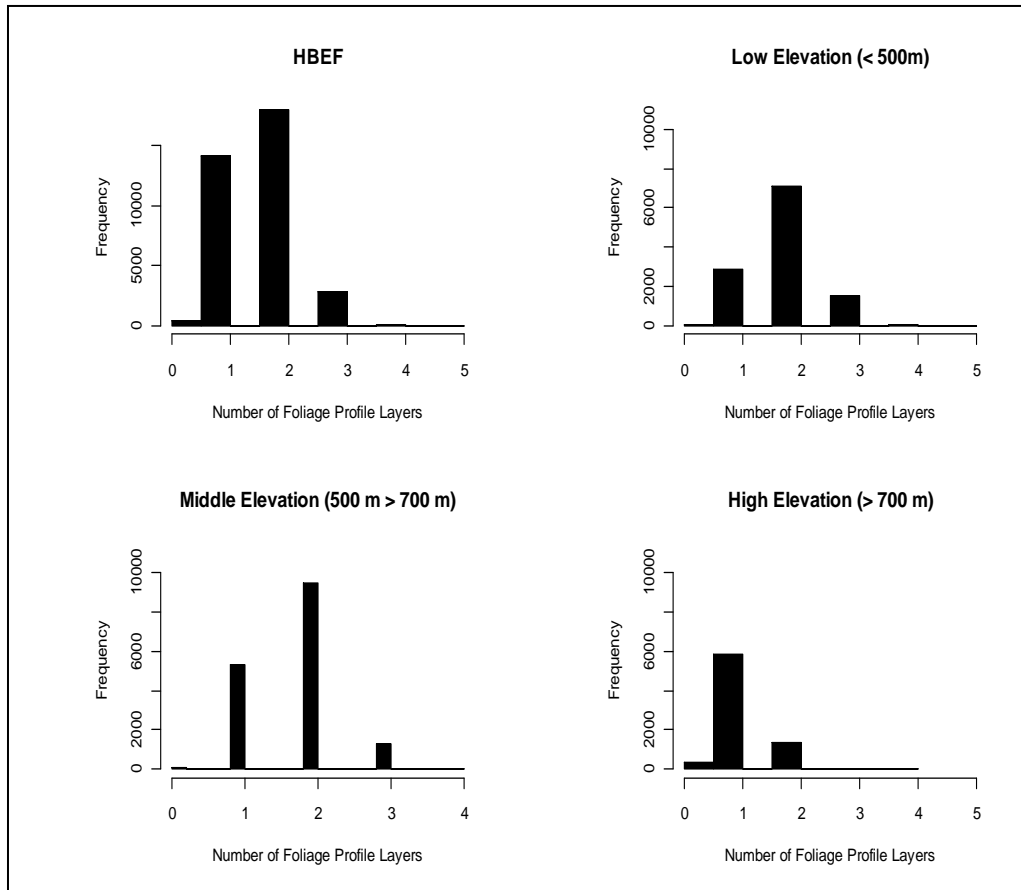


Figure 2.9 Histogram of number of foliage profile layers showing the number of pixels in each group of layers for all of HBEF (upper left) as well as at the low, middle, and high elevation levels.

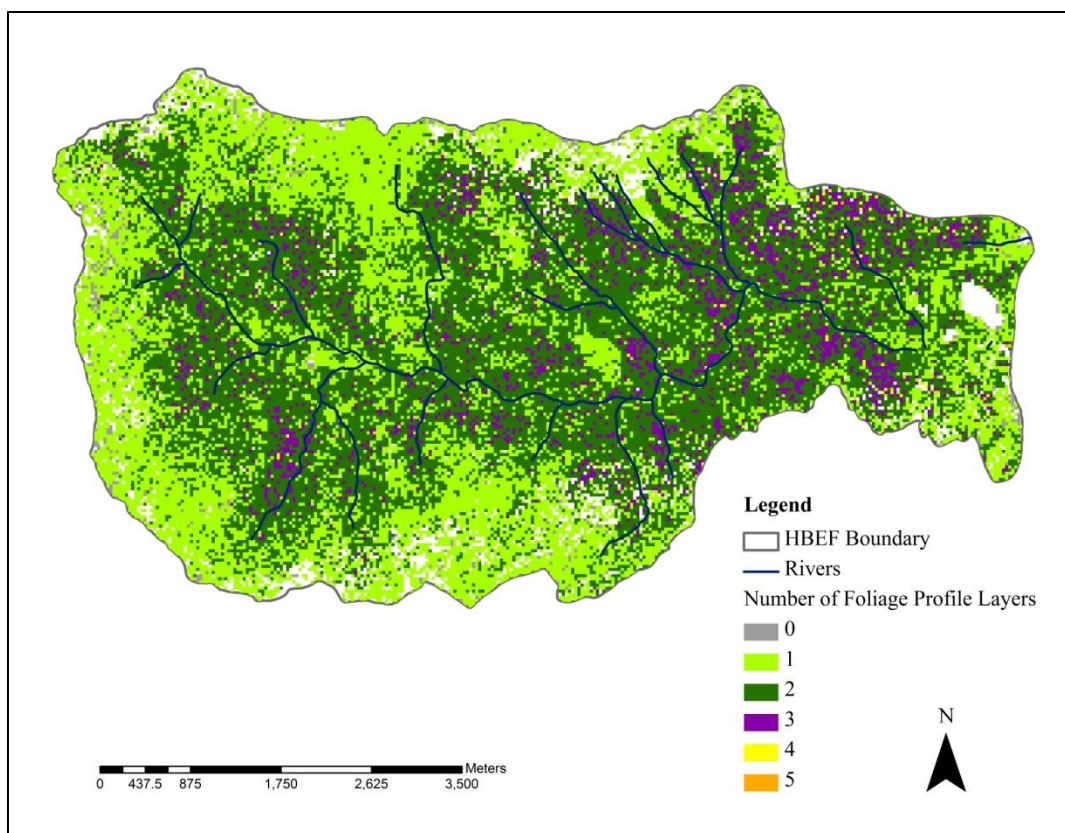


Figure 2.10. Map of number of foliage profile layers across Hubbard Brook Experimental Forest. The areas with more layers (2-5) were predominately in the riverine areas.

The number of foliage profile layers showed a clear, positive relationship with canopy height (Figure 2.11): as canopy height increases, the number of layers increases. Summary boxplots suggest a significant difference in median canopy height between most of the layer groups as well. Single-factor ANOVAs were also run between each number of foliage profile layers, confirming the significant difference ( $p < 0.05$ ) in height between layers.

There was also a large range in elevation for all foliage profile layer groups (Figure 2.11), with the median elevation significantly different between most of the layer groups as seen in the boxplots. The conclusion that the number of layers significantly

varies with elevation was confirmed with ANOVA results ( $p < 0.5$ ). The areas with 0 and 1 layers, which have average elevations of 702.8 m and 627.1 m, occurred at higher elevations than those with 2 to 5 layers (ranging from 516 m to 324.5 m), respectively. There was a strong, negative relationship between numbers of layers and elevation. This is not surprising given the gradient in canopy height that exists at HBEF: trees are shorter as elevation increases.

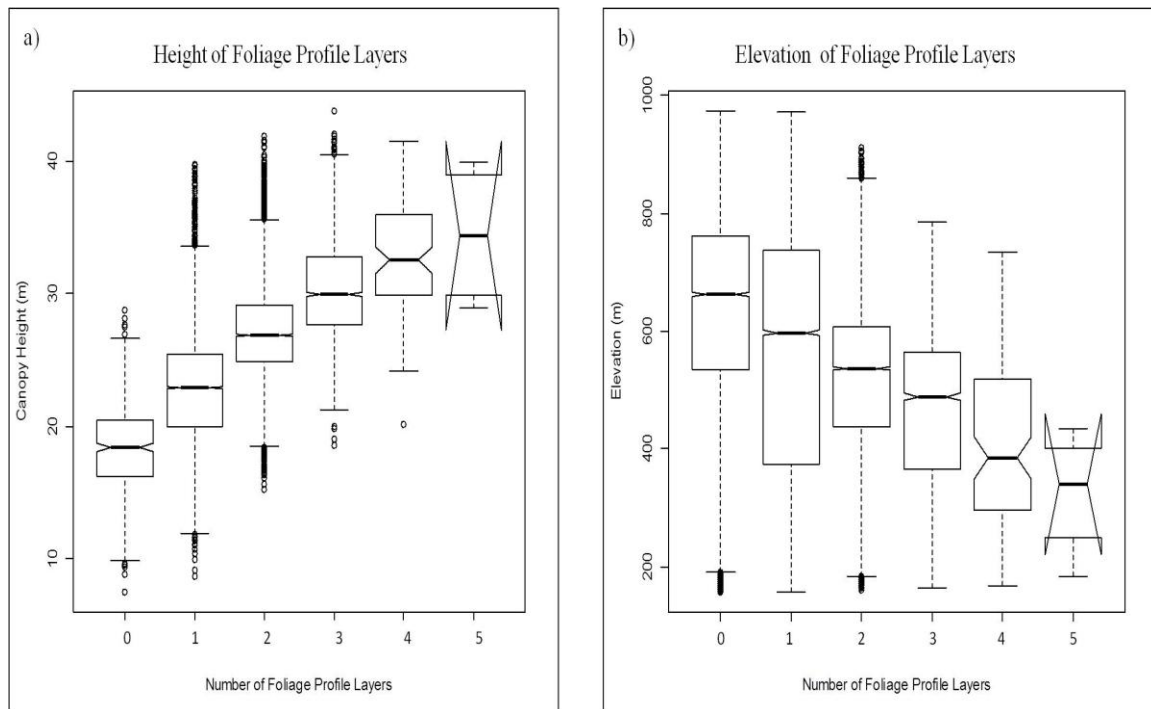


Figure 2.11. Box plots showing the canopy height (a) and elevation (b) distribution for each number of foliage profile layers. The boxes represent the interquartile range, with whiskers defining the range of heights within 1.5 times the upper and lower quartiles. The box plot for 5 layers has calculated notches that extend past the interquartile range, showing that the confidence of the median is wider than the range of the data. This is probably because of the group's small sample size of 4 pixels.

When examined across all multilayer canopies (ranging from 2 to 5 layers), there was a wide range in the height of the top and bottom foliage profile layers (Figure 12).

The median heights were 6.8 m (bottom layer) and 17.5 m (top layer). The height of the top layers varied with the number of layers present in the canopy and tended to increase with the number of layers identified. The lower and middle layers occurred closer together in height relative to the top layer (Figure 2.13).

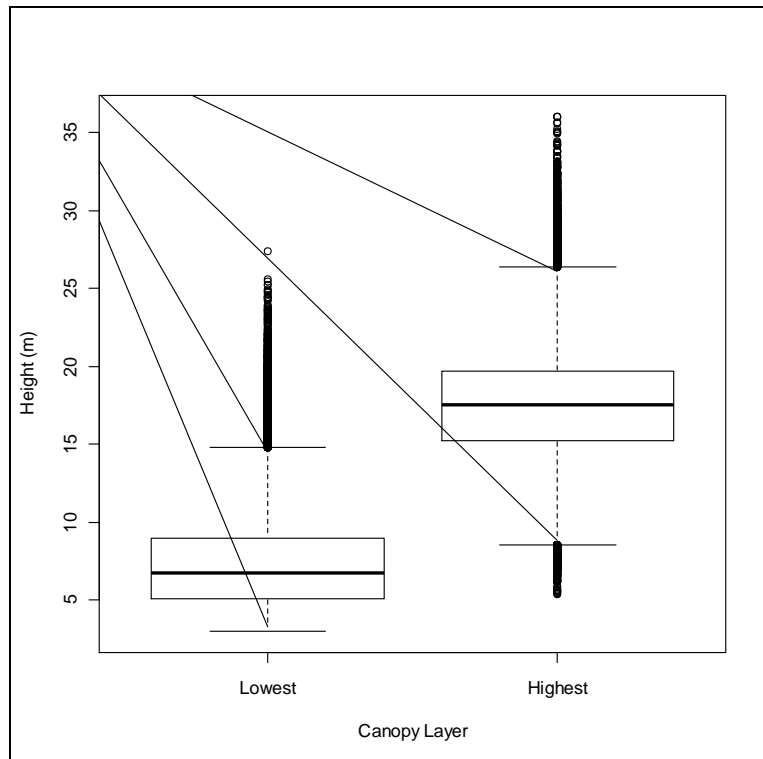


Figure 2.12. Boxplot of the height of the lowest and highest foliage profile layers present in multi-layer systems (2-5) in HBEF.

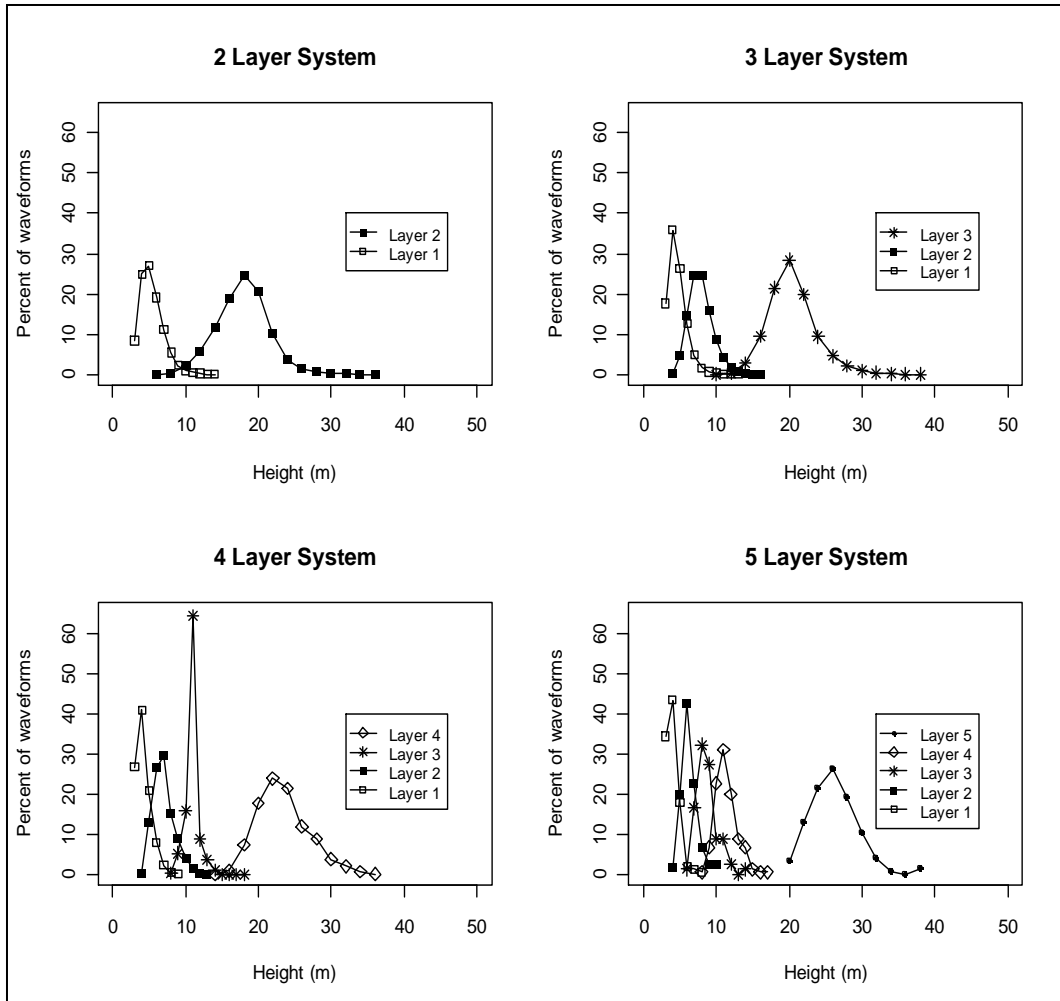


Figure 2.13. Plots of layer heights for all the multi-layer systems in HBEF (2 to 5 layers). The plots show the percent of waveforms at which a layer occurs at a certain height. The height of the top layer tends to be higher in areas with more total layers. Bottom and middle layers are generally closer together in relation to the top layer.

## 2.4 Discussion

I explored how vertical canopy structure varies across HBEF using two metrics to map canopy layering derived from waveform lidar. My results show significant spatial variability in canopy vertical structure, a result which supports previous findings of structural diversity within the forest (Schwarz et al. 2001). Average foliage area profiles

across elevational gradients showed differences in structure at the low, middle, and high elevation levels. Within the foliage profile, the peak in apparent foliage area decreased as elevation increased (from about 13 to 19 m at low elevations to 6 to 9 m at high elevations). Environmental gradients, such as elevation, have been repeatedly shown to have a correlation with plant growth (Austin 1980; Whittaker et al. 1974; Kaufmann & Ryan 1986; Ryan & Yoder 1997; Tardif et al. 2003). These trends have also been examined within HBEF. Whittaker et al. (1974) noted that there were decreasing trends in both tree height and leaf area ratio ( $\text{m}^2/\text{m}^3$ ) with elevation in the forest. These effects could possibly be attributed to the availability of resources (such as water) or changes in climate (such as temperature) that vary along the elevational gradient, affecting tree growth (Austin 1980; Kaufmann & Ryan 1986; Ryan & Yoder 1997; Tardif et al. 2003). In addition, disturbance may play a role. Higher elevations are more prone to the effects of wind throw, ice storms, *etc.*, so that in addition to having slower growth rates, trees are younger at higher elevation because of repeated disturbance (Huang et al. 2009). This finding of structural change along elevational gradients was also seen in the results from both layering data sets.

Sherry (1979) used averaged foliage profiles to describe the vertical structure within a 10-ha plot in HBEF. His results showed the majority of canopy material existing around 20 m and opening dramatically from 15 m to the ground. My results, on the other hand showed the majority of the canopy material existing lower in the canopy, between 6 and 15 m. Due to the contrast in results, we examined the change in vertical structure at differing horizontal scales, including a 9-ha area near the initial Sherry study area. I

found that as the horizontal area increased, a large part of the detail in the vertical structure was lost from the foliage area profile.

Choosing a scale of analysis germane to the research goal is always important—perhaps even more so for canopy structure, as this structure is by its very nature scale-dependent. Because my data had a minimum resolution of about 25 m, I measured canopy structure as opposed to individual tree structure. The power in lidar observations is in providing structure at relatively fine resolutions while at the same time allowing for aggregations to arbitrary but ecologically significant areas. For example, while average structure for the watershed as a whole can be observed, what is more revealing is these average structures within areas where we hypothesize climatic, edaphic, and other factors may play a role in structure and its dynamics, e.g., within elevation zones, or within, say primary *vs.* secondary forests.

My results showed that layering in both datasets is affected by forest growth and its impacting factors, most notably elevation. My results corresponded with previous studies noting the effects of the elevational gradient on forest structure in HBEF (Whittaker et al. 1974). For both datasets, the categories or number of layers associated with lower elevations were also the ones associated with taller canopy heights and vice versa. For the canopy layer structure dataset, these categories were categories 4, 5, and 6, which feature a more dominant overstory. This is possibly a result of tree growth and light competition, with individual canopies expanding as plants increase in height, allowing trees to receive more light for photosynthesis (Ford 1975; Perry 1985; Maguire et al. 1998). Canopy height is expected to decrease with elevation because of constraints on growth by temperature and through increased disturbance (Hurtt et al. 2004; Thomas



et al. 2008). A taller canopy may allow more space for variations in the canopy structure to occur, resulting in more layers, especially since the top layer tends to occur higher in the canopy as the number of layers increases (Figure 2.13).

The foliage profile layering methodology provides a way of assessing the complexity of the canopy without relying on *a priori* height thresholds to determine the vertical distribution of canopy material. However, our analysis did not examine vertical structure of the canopy below 3 m. The 3-m threshold was used to avoid a potential source of error in the foliage profile algorithm caused by the mixing between the waveform ground return and the canopy return, which could inflate foliage area measurements near ground level (Hofton et al. 2002). It is thus possible that areas of dense foliage in the understory were missed in the profile layering analyses.

Given the nature of our three-layer organizational scheme for the canopy layer structure categories, I tested whether the spatially extensive occurrence of categories with a dominant midstory was an artifact of the canopy simply being less than 15 m in height. Recall that my midstory is defined as between 5 and 15 m. If the canopy is less than this height, it would lead to its frequent categorization of dominant midstory because there was no overstory. For the categories where the midstory is greater than the overstory (7, 8, and 9), only 1.4% of pixels (352 out of 25,318) had canopy heights below 15 m. Thus, the layering results are not an artifact of the classification scheme. However, in forests where canopy height is known to be short, considerations should be made when examining canopy layer structure results and care taken to choose more appropriate vertical definitions of under-,

mid- and overstory heights. Indeed, the choice of layer boundary definitions is a critical aspect of the analysis, as illustrated next.

My canopy layer structure methodology relied on literature-based height values to depict the distribution of vegetation within three distinct layers. I used height intervals that coincided with previous observations of avian species preference in HBEF.

However, if the height intervals are changed, the distribution of the nine canopy layer structure categories across the landscape can change dramatically. For example, Figure 2.14 shows how the distribution of categories changes when the midstory height interval is changed from 5 m–15 m to 5 m–10 m. HBEF goes from a forest dominated by midstory vegetation (foliage from larger saplings and the lower portions of mature tree crowns) to a forest dominated by overstory.

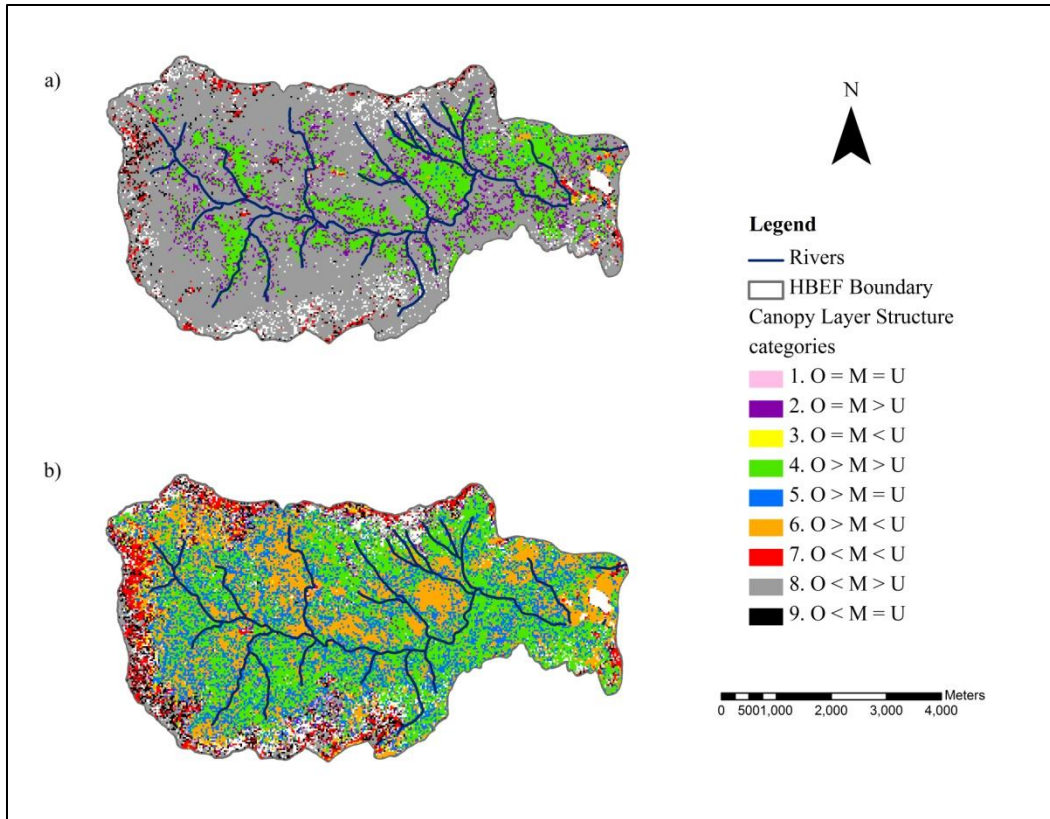


Figure 2.14. Maps of canopy layer structure categories in HBEF using two different height intervals. (a) shows layer heights as 0 to 5 m (understory), 5 to 15 m (midstory) and 15 m to canopy top (overstory). (b) shows layer heights as 0 to 5 m (understory), 5 to 10 m (midstory) and 10 m to canopy top (overstory).

That these results change is not a cause for concern, nor does it suggest a certain arbitrariness that may hinder rational insights and generalizations. Rather it highlights that, just as the choice of spatial scale is important, so too is the choice of a vertical definition. The point of using categories is to generalize structure and organization. In the absence of *a priori* information about logical height intervals, exploratory analyses must be used, conditioned by knowledge of the physical and biological landscape to guide what constitutes “midstory” vs. “overstory”. If extant observations conclude that a particular avian species prefers, say, an open midstory, the definition of “open midstory”

is hopefully available. That it often is not, or varies by researcher, illustrates that the arbitrariness has been the rule in past analyses. I suggest that the methods presented here allow for quantitative assessments, even if definitions may vary. They are still reproducible (knowing the definition) and available at high spatial resolution across entire landscapes.

On the topic of generalization, note also that the full profile data may always be leveraged, to both validate categorizations and even help define them. For example, suppose one did not know how to choose the vertical category cut-offs (*i.e.*, 5–15 m, *etc.*). One could look at the full foliage area profiles to address this issue. Figure 2.15 shows a few foliage area profiles from category 6, which has an open midstory from 5 to 15 m. In these examples, there is more foliage area above 15 m and below 5 m than within the midstory height interval, which supports our choice of layer height intervals. More formally, the class boundaries could be statistically determined based on aspects of the LVIS derived foliage profile. The danger in doing so, however, is the result might be divorced from ecological reality.

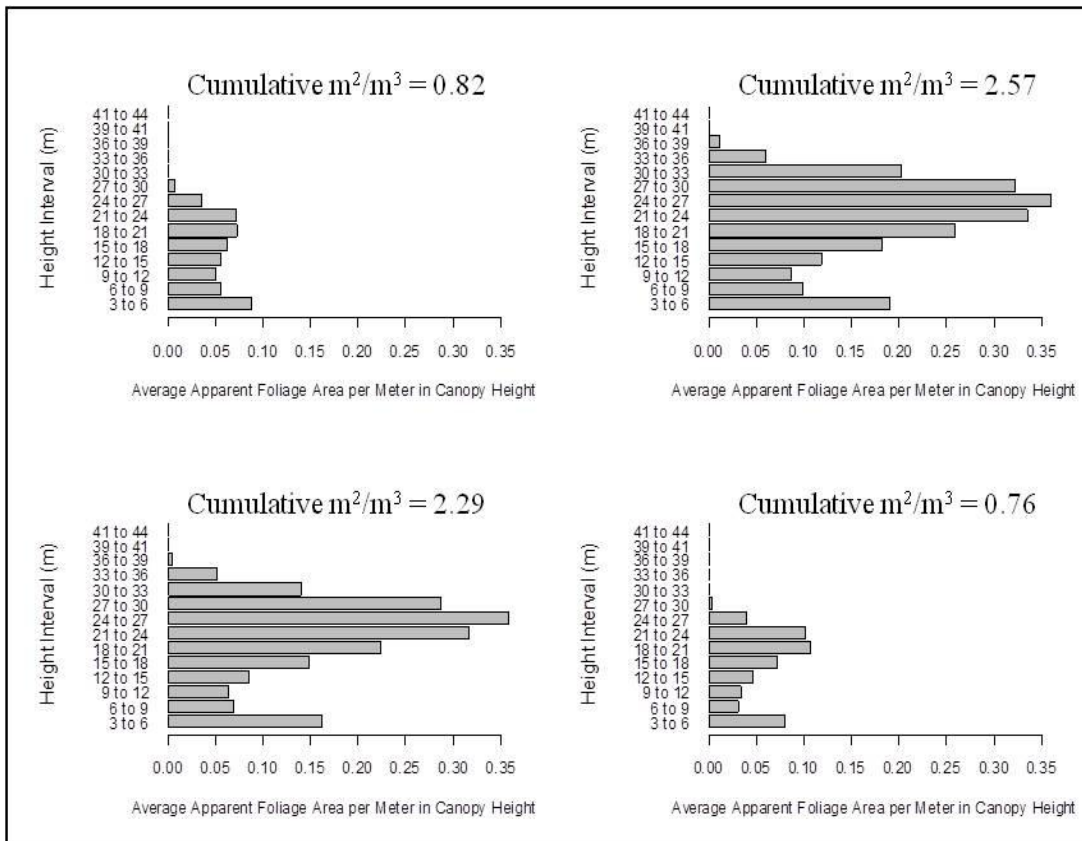


Figure 2.15. The apparent average foliage area profile for sample areas of HBEF that coincide with canopy layer structure category 6, divided into 3 m height intervals. The shape of the profiles shows peaks in the foliage area above 15 m and below 7.5 m. This coincides with the definition of category 6, which has more canopy material in the overstory and understory than the midstory.

## 2.5 Conclusions

I developed two methods to depict the variation of canopy layering across the forested landscape and thus provided a detailed description of the variation of vertical structure of Hubbard Brook Experimental Forest, NH via full-waveform lidar. This type of information can aid in the understanding of forest ecosystem dynamics, habitat suitability, and forest management. My analyses have shown that within Hubbard Brook Experimental Forest the foliage is concentrated in the forest midstory as seen by the peak

in the foliage profiles between 9 and 12 m when examined over the entire forest.

Comparisons of lidar derived foliage profiles to previous descriptions of the forest (e.g., a forest dominated by a dense overstory and open midstory layer (Sherry 1979) led to my determination that horizontal scale greatly influences profile results and detail is lost as profiles (lidar or field-based) are aggregated over larger areas. However, the conclusion that Hubbard Brook has a dominant midstory is supported using the 30 × 30 m canopy layer structure dataset, which categorized 67 % (2148 ha) of the forest as canopy layer structure category 8 (overstory < midstory > understory). Both the canopy layer structure and foliage profile layering datasets show how canopy layering varies along gradients of elevation and canopy height, as seen in previous studies. For example, the dominant overstory categories (categories 2 and 4) and areas containing 2 or more foliage profile layers occurring in the forest interior, in close proximity to rivers (and thus lower elevations), as expected based on the relationship between elevational gradients and tree height and leaf area ratio (Whittaker et al. 1974). However, I will not know the applicability of these datasets and subsequent results until they are developed for other forests. Then the trends in both canopy layer structure and foliage profile layering across Hubbard Brook Experimental Forest can be examined to see if they are a universal component of forest dynamics or an artifact of the study area. Also, each layering dataset presents information on vertical foliage distribution in a different way, with canopy layer structure relying on pre-determined layer heights and foliage profile layering using continuous data to provide a quantitative description of the mid and upper canopy. The usefulness of this type of information on vertical structure needs to be further examined to determine which type of layering information (canopy layer structure or foliage profile

layering) is beneficial for research and management projects, such as habitat modeling, forest succession and management.

## Chapter 3: Examining the relationship between bird species diversity and the vertical distribution of canopy material as described by lidar metrics

### 3.1 Introduction

Beginning with MacArthur and MacArthur (1961), vertical forest structure has been defined as an important element in research involving avian species diversity and habitat preference (Willson 1974; Erdelen 1984; Doran & Holmes 2005; McElhinny et al. 2005). However, many of these early studies were limited in terms of sample size and possibly affected by differences in forest/landcover type. Hence, the exact relationship or the importance of specific vertical structure characteristics (such as foliage height diversity or importance of canopy layers) for bird species diversity is unclear (MacArthur & MacArthur 1961; Willson 1974; Erdelen 1984).

The vertical distribution of canopy material has long been noted as an element of vertical structure that impacts avian species diversity. It has been described in terms of discrete layers or stratification (Robinson & Holmes 1982), as numerous calculations of foliage height diversity (MacArthur & MacArthur 1961; Holmes et al. 1979; Clawges et al. 2008) or as the variation in tree height within a certain area (Seavy et al. 2009).

Despite these various descriptions, the main theory is the same: to maximize species diversity in an area, the canopy must be varied enough to provide ample habitat for numerous species. Holmes et al. (1979) noted that the increased distribution of canopy material provided a wider variety of foraging substrates for bird species in Hubbard Brook Experimental Forest. Similarly, Shaw (2004) noted that the canopy layering



associated with older forests, where the vegetation is predominately in the overstory and understory, will most likely contain the highest avian biodiversity, as this increased complexity of canopy structure has been associated with high levels of species abundance and diversity. This presence of canopy material throughout the vertical column has been seen to increase species richness, an aspect of species diversity, by providing foraging opportunities for species that do not exist when foliage is lost from a certain section of the canopy (Keller et al. 2003).

With the advent of lidar remote sensing, the vertical components of the forest ecosystem can be described at the landscape scale. When applied to habitat and biodiversity studies, lidar metrics have supported findings of field research that the vertical component of the forest ecosystem is important for species habitat suitability and diversity. Numerous studies have focused on canopy height, one of the more basic measures of canopy structure and have found significant relationships between lidar estimated canopy height and bird habitat suitability (Hinsley et al. 2002; Broughton et al. 2006; Hill et al. 2004; Hinsley et al. 2006; Hinsley et al. 2008). However, even though canopy height has been hypothesized to be a possible proxy for other elements of vertical structure (Broughton et al. 2006), studies have noted that lidar is capable of detecting other aspects of vertical structure that contribute to avian habitat selection beyond the more commonly used metrics of canopy height (Goetz et al. 2010; Falkowski et al. 2009; Marinuzzi et al. 2009; Swatantran et al. 2012).

Various lidar metrics have been created to quantify the distribution of canopy material along the vertical column. A few studies have shown that lidar-derived foliage distribution metrics have a significant relationship with bird species diversity and aid in

species diversity models. For example, Clawges et al. (2008) determined that lidar-derived foliage height diversity metrics (based on MacArthur and MacArthur (1961) foliage height diversity calculation) were positively correlated with bird species diversity. Similarly, Goetz et al. (2008) showed that the vertical distribution ratio (a measure of foliage distribution) was an important variable for species richness models. Despite the numerous metrics available for describing the arrangement and distribution of canopy material, researchers have not reached a consensus as to which metric provides the most information about bird species diversity.

My goal for this paper is to further examine the relationship between the vertical distribution of canopy material and bird species diversity in temperate montane forests. To do this, I have structured our methods around three questions. First, does the general assumption that bird species diversity increases with foliage height diversity apply to montane forest breeding species in Hubbard Brook Experimental Forest, NH? Secondly, out of the different lidar metrics used to describe vertical canopy distribution, which ones have the strongest relationship with and explain the most variability of bird species diversity? Height is a measure of vertical structure that has been consistently linked to forest bird richness and species habitat preference and many of the distribution metrics are based off of or related to canopy height. Because of this, my third question is: how are our results between bird species diversity and the distribution metrics affected when height is accounted for?

## 3.2 Materials and Methods

### 3.2.1 Study Area

The study area is located in central New Hampshire, USA, covering 3185 ha of the White Mountain National Forest, including Hubbard Brook Experimental Forest. For more details, see Chapter 2.

### 3.2.2 Bird Data

Routine bird surveys have taken place over 371 survey sites in Hubbard Brook Experimental Forest, NH for 9 years (1999 to 2009, excluding 2005 due to lack of survey site visits) during the breeding season, May-June. The survey plots exist along transects which cross the Hubbard Brook watershed North to South. At each plot, only species within a 50 m radius were counted (Doran & Holmes 2005; Goetz et al. 2010). Only observations of bird species known to breed in HBEF were used to calculate bird species diversity, in order to prevent inflation due to “fly over observations” or migrants. Breeding bird observations were totaled across all 9 years of data for 370 bird plots within HBEF to determine the total abundance of each species. One plot was left out of the analyses due to lack of lidar data. Detection probability was not accounted for since it has been shown that 99.9% of forest species are accounted for using the 10 minute point counts (Betts et al. 2008; Goetz et al. 2010). Also using bird observations over the 9 year time period should increase the probability of detecting the area’s more rare species. Bird species diversity (BSD) was calculated based on the formula provided by MacArthur and MacArthur (1961) (ultimately the Shannon Diversity Index) where  $BSD = - \sum_i p_i \log_e(p_i)$ , in which  $p_i$  is the proportion of individuals in the  $i^{\text{th}}$  species and using the total

abundance values. 52 different species were identified, and the BSD within the plots ranged from 1.47 to 2.75 (Figure 3.1).

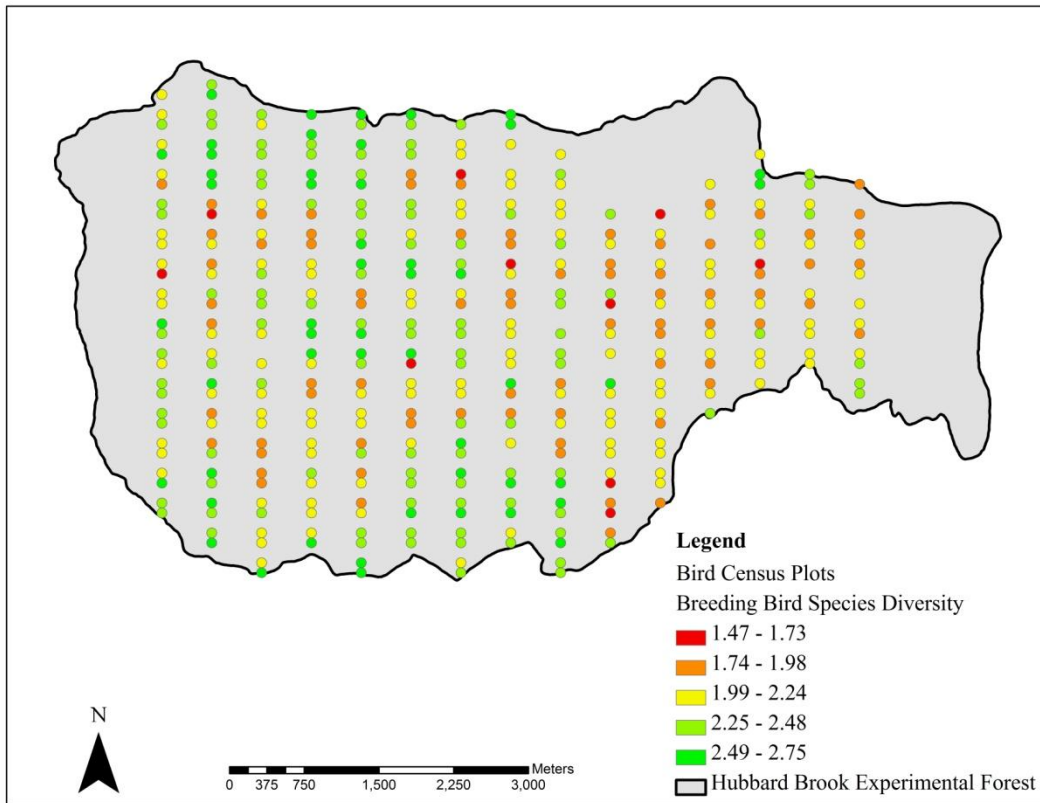


Figure 3.1. Map of Hubbard Brook Experimental Forest, NH indicating the location of the 50 m radius bird plots. The color of the plots represents the calculated bird species diversity index value.

### 3.2.3 Lidar data and calculated metrics

In the summer of 2009, data from NASA Goddard Space Flight Center's Laser Vegetation Imaging Sensor (LVIS) was collected over HBEF. LVIS provides geolocated waveforms that are able to depict vertical foliage profiles and canopy height as well as sub-canopy topography by recording the entire outgoing and return signal (Blair et al. 1999). The amount of canopy material at a particular height is proportional to the amplitude of the LVIS waveform at that height (Hyde et al. 2005). The nominal 20 m LVIS footprints overlap slightly in the across- and along-track flight direction. This

enables approximately contiguous coverage over the entire imaging swath (about 2 km wide for these flights). Hofton et al. (2002) and Dubayah et al. (2010) provide a more detailed description of LVIS data retrieval and waveform processing.

The LVIS shots that fell within the 50 m radius of the HBEF bird survey plots were selected and processed for 370 of the bird plots. The accuracy of elevation determined from LVIS waveforms can sometimes be affected by high slopes (Dubayah et al. 2010). To correct for this, the elevation was determined using discrete return lidar (DRL), which was flown over the area in 2009. The DLR measurements had a return density of around 5 shots per square meter. The LVIS detected canopy top was subtracted from the DRL detected elevation to determine canopy height. The height of median energy was also calculated in this way (Dubayah et al. 2010). Four separate lidar metrics, most of which have been previously used to describe the vertical distribution of forest canopy, were also produced: foliage height diversity (FHD), vertical ratio (VR), canopy layer structure, and the number of foliage profile layers. The information needed for each metric was averaged over the number of LVIS shots that were located in each bird plot.

Foliage height diversity was calculated using the equation as  $FHD = - \sum_i p_i \log_e(p_i)$  (MacArthur & MacArthur 1961), where  $p$  is the proportion of foliage in the  $i^{\text{th}}$  canopy layer. Following MacArthur and MacArthur (1961)'s protocol, three canopy layers were used: layer 1 is 0 to 5 m, layer 2 is 5 to 15 m and layer 3 is 15 m to the top of the canopy. This method of calculating FHD will be referred to as MacArthur's FHD. The layer height demarcations were based on research noting avian species habitat preference with the HBEF study area (Swatantran et al. 2012). Following the example of

Clawges et al. (2008), foliage height diversity was also calculated using varying numbers of layers (4, 5, and 7) and layer height demarcations to evaluate how the relationship between BSD and FHD changes in response to changes in the parameters of the FHD calculation, resulting in 4 different FHD metrics. The layer height demarcations were based on literature (Swatantran et al. 2012) as well as experimental values (Table 3.1).

<b>Metric</b>	<b>Layer 1</b>	<b>Layer 2</b>	<b>Layer 3</b>	<b>Layer 4</b>	<b>Layer 5</b>	<b>Layer 6</b>	<b>Layer 7</b>
MacArthur's FHD	0 to 5	5 to 15	15 +				
FHD 4a	0 to 5	5 to 10	10 to 15	15 +			
FHD 4b	0 to 5	5 to 15	15 to 30	30 +			
FHD 5	0 to 5	5 to 10	10 to 15	15 to 20	20 +		
FHD 7	0 to 5	5 to 10	10 to 15	15 to 20	20 to 25	25 to 30	30 +

Table 3.1. The layer height demarcations in meters above the ground of the 5 calculated foliage height diversity variables.

The vertical ratio (VR) describes the evenness in which canopy elements are distributed. This index (from 0 to 1) is similar to the vertical distribution ratio (VDR), which has been shown to be an important predictor of species richness (Goetz et al. 2007). VR is the ratio of the lidar detected height of median energy (HOME) and canopy height (CH),  $VR = HOME/CH$ . Higher VR values indicate areas where canopy material is more concentrated near the top of the canopy, while lower VR values indicate areas where the canopy material is more concentrated near the ground.

The canopy layer structure metric categorically depicts the distribution of canopy material based on the three pre-defined canopy layers of the understory (0 - 5 m), midstory (5 - 15 m) and overstory (15 m to canopy top) (Whitehurst et al. 2013). The canopy layer structure metric describes how the canopy material is distributed within the canopy and where canopy material is concentrated or lacking. This is accomplished by categorizing areas based on the comparison of the amount of canopy cover between the three layers, resulting in 9 possible categories. To do this, the cumulative or total canopy cover was calculated from the LVIS waveform profiles using the methods of Ni-Meister et al. (2001). For the canopy layer structure categories, the MacArthur-Horn transformation ( $-\ln(1 - \text{cover}(h))$ ), which accounts for the extinction of light as it travels through the canopy, was applied, where  $h$  refers to height), resulting in transformed canopy cover (MacArthur & Horn 1969; Lefsky et al. 1999a; Lefsky et al. 1999b; Harding et al. 2001). The canopy layer structure categories were determined by calculating the MacArthur-Horn transformed canopy cover for the understory (U), midstory (M), and overstory (O) layers of each lidar shot located in the bird plots, based on the methods described in Whitehurst et al. (2013). The lidar-derived transformed canopy cover for each layer height was averaged within the bird plots prior to categorization. The distribution of the canopy layer structure categories across the bird survey plots, revealed that only seven of the categories were represented. Due to low sample size, the plots containing categories 5 (one plot), 6 (one plot), 7 (one plot), and 9 (5 plots) were removed from the analyses. In total only 363 bird plots were used. These plots fell into categories 2 ( $O = M > U$ ,  $n = 38$ ), 4 ( $O > M > U$ ,  $n = 60$ ), and 8 ( $O < M > U$ ,  $n = 264$ ).

The number of foliage profile layers reflects the variation of the amount of canopy material as it is distributed within the vertical column by examining the peaks and troughs in the lidar-derived foliage profile (Whitehurst et al., 2013). This metric is based on the definition of a layer as an area of concentrated vegetation material within the canopy (Koike et al. 1990; Parker & Brown 2000). For foliage profile layering, the number of layers was calculated per waveform and then averaged within each bird plot, as described in Whitehurst et al. (2013). This was used as the general layering scheme for each 50 m radius bird plot. The bird survey plots contained foliage profile layering configurations of 1, 2, and 3 layers. Due to low sample size impacting the robustness of analyses, the plots with 3 layers (8 plots) were removed from the study. The remaining 363 bird plots with one ( $n = 125$ ) and two ( $n = 237$ ) layers were used to compare BSD to the number of foliage profile layers.

#### 3.2.4 Statistical Methods

Linear regression and Pearson's product-moment correlation coefficient were used to examine the relationship between BSD and the continuous lidar metrics (canopy height, VR, MacArthur's FHD and the 4 varying FHD metrics), comparing BSD to a single continuous lidar metric. The relationship between the categorical lidar variables (canopy layer structure categories and number of profile layers) and BSD was examined using ANOVA, Tukey-Kramer post-hoc test, and one-tailed t-test. Omega squared ( $\omega^2$ ) was calculated to determine how much variation in BSD was explained by the different canopy layer structure categories and number of profile layers.

With the continuous metrics (VR, MacArthur's FHD and the 4 varying FHD metrics) height was accounted for by first running linear regression models between BSD



and canopy height. The residuals of those regressions were then used as the dependent variable in regression equations with the continuous canopy distribution metrics. For the categorical metrics (canopy layer structure categories and number of foliage profile layers), canopy height was binned into 5 m intervals. Two-way ANOVAs were run using the height bins and the categorical metrics and the significance of the interaction effect was examined.

### 3.3 Results

#### 3.3.1 BSD versus MacArthur's FHD

There was a significant ( $p < 2.2 \times 10^{-16}$ ) negative correlation between BSD and MacArthur's FHD ( $r = -0.44$ ). This shows that in HBEF, BSD decreases as the foliage becomes more evenly distributed throughout the vertical column. MacArthur's FHD explained 19% of the variation in BSD ( $r^2 = 0.19$ ) (Table 3.2, Figure 3.2).

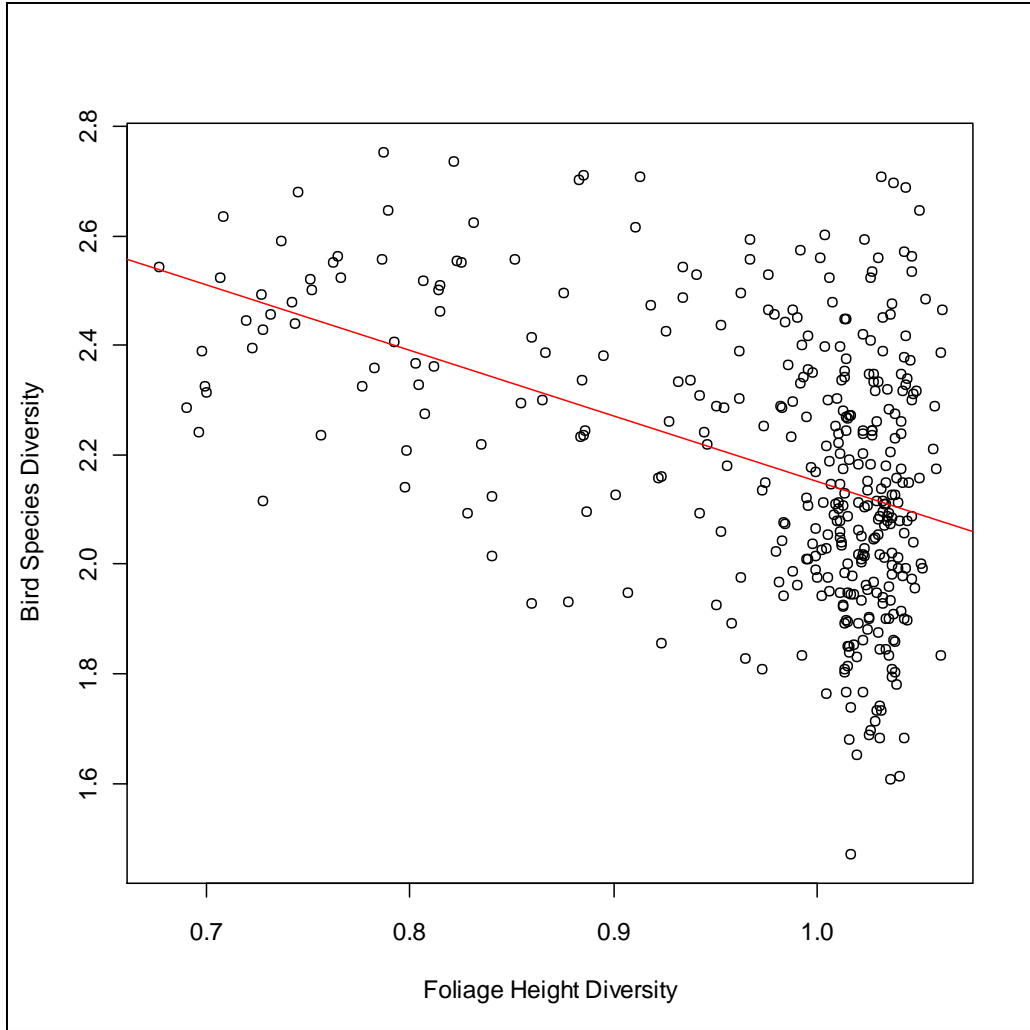


Figure 3.2. Relationship between bird species diversity and MacArthur's foliage height diversity. The red line shows the line of best fit and the negative relationship between the two variables.

<b>Metric</b>	<b>r</b>	<b>r<sup>2</sup></b>
MacArthur's FHD	-0.44	0.19
FHD 4a	-0.20	0.04
FHD 4b	-0.46	0.21
FHD 5	-0.57	0.33
FHD 7	-0.52	0.28
VR	-0.49	0.24
Height	-0.52	0.28

Table 3.2. Pearson's product moment correlation coefficients and  $r^2$  from the linear regressions between the continuous variables (including height) and bird species diversity.

### 3.3.2 BSD versus lidar-derived canopy distribution metrics

The correlations between all the lidar-derived canopy distribution metrics and BSD were significant with  $p < 0.05$  (Table 3.2). The nature of the relationship between BSD and the lidar-derived canopy distribution metrics was negative with the continuous variables, which include VR and all variations of FHD (Figure 3.3). Although not much variation in BSD was explained by the continuous metrics, the FHD metrics calculated using 5 layers and 7 layers (FHD 7 and FHD 5) explained the most BSD variation with

an  $r^2$  of 0.33 and 0.28 respectively. VR explained about 24% of the variation in BSD. The correlation between BSD and the 4 FHD metrics was higher for the FHD metrics calculated with more layers (7 and 5 layers versus 3 and 4 layers). However, FHD 4a (calculated with 4 layers) was less correlated with BSD than the MacArthur's FHD metric (calculated with 3 layers). FHD 4a was the least correlated with BSD out of all the FHD metrics. For FHD 4a, the top layer was lower in the canopy than the other FHD metrics, meaning that the layers were less evenly distributed throughout the canopy.

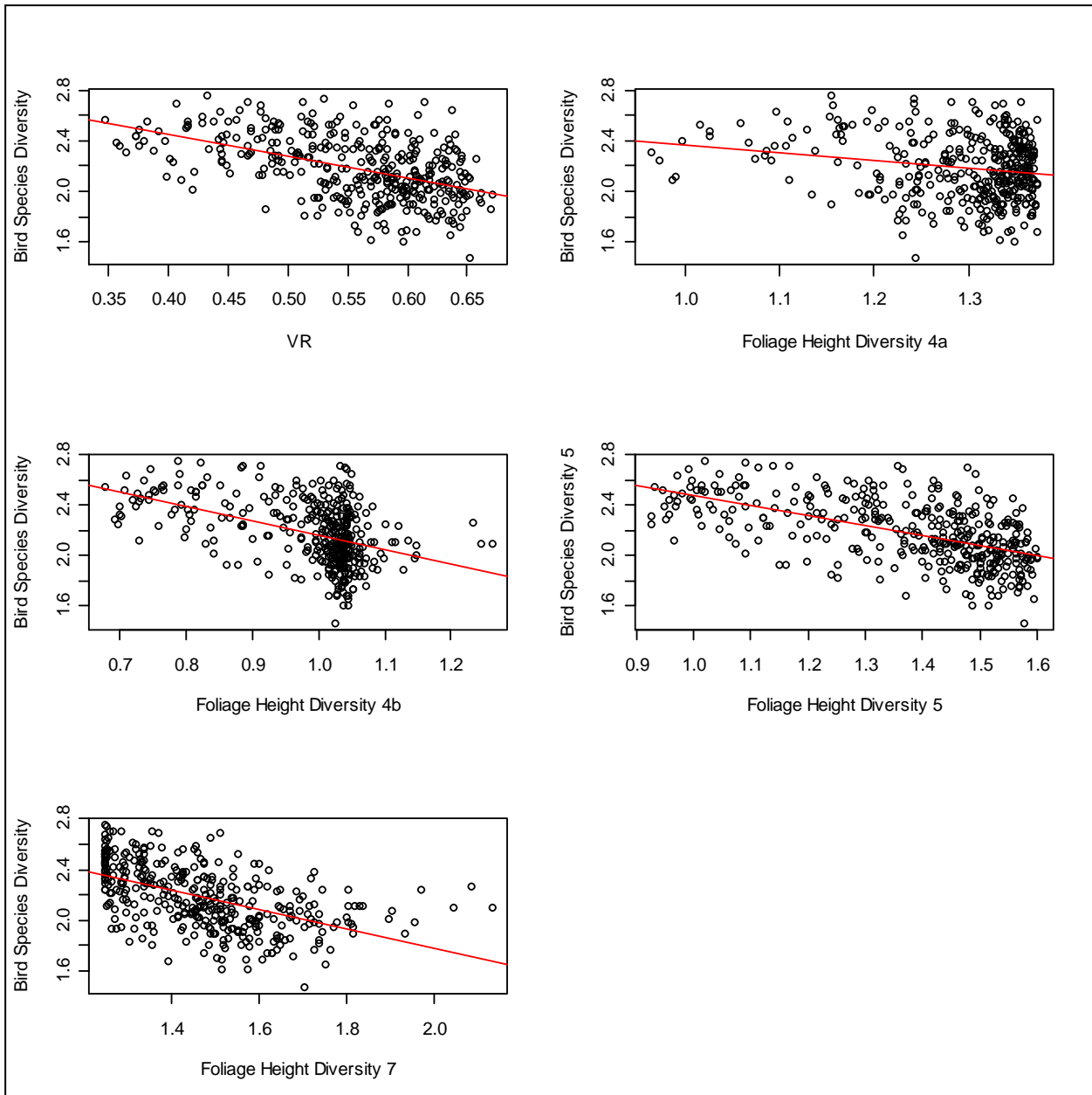


Figure 3.3. Plots of the relationships between bird species diversity and the continuous vertical foliage distribution variables (VR and the 4 additional FHD variables). The red lines show the line of best fit.

ANOVA results showed that there is a significant difference at the 95% confidence level ( $p < 0.05$ ) in the mean BSD between canopy layer structure categories 2, 4, and 8. Tukey-Kramer post-hoc test showed that there was a significant difference in

average BSD between categories 2 and 8 and 4 and 8 at the 95% confidence level. The main difference in these categories is the amount of canopy cover present in the overstory versus the midstory. This is evident because the average BSD of categories 2 and 4 were not significantly different. The difference between these categories is the amount of canopy cover in the overstory versus the midstory, which is greater than the midstory for category 4 and equal to the midstory for category 2. The average BSD of these two categories is significantly different from category 8, where the amount of cover in the overstory is less than the midstory.  $\omega^2$  results showed that 11% of the variation in species richness is accounted for by the different canopy layer structure categories.

The results of the one-tailed t-test showed that the average BSD of plots with one foliage profile layer was significantly greater than that of plots with two foliage profile layers ( $p < 0.05$ ).  $\omega^2$  results showed 27% of the variation in BSD is accounted for by the different number of foliage profile layers.

### 3.3.3 Distribution metrics and BSD after accounting for canopy height

Canopy height had a significant negative correlation with BSD ( $p < 0.01$ ,  $r = -0.52$ ) and explained roughly 28% of the variation in BSD between the bird plots (Figure 3.4). The Pearson's correlation coefficient between canopy height and the other continuous metrics (ranging from 0.43 for FHD4a to 0.93 for FHD7) was significant and greater than the correlation coefficient between the variables and BSD. After accounting for height, only two of the continuous variables were still significant, VR, and FHD 5. FHD 5 was significant ( $p = 0.038$ ). The significance of VR within the regression equation was stronger with a p-value of 0.001. The amount of variation explained by both variables was significantly reduced to about 1.16% for FHD 5 and 2.8% for VR.

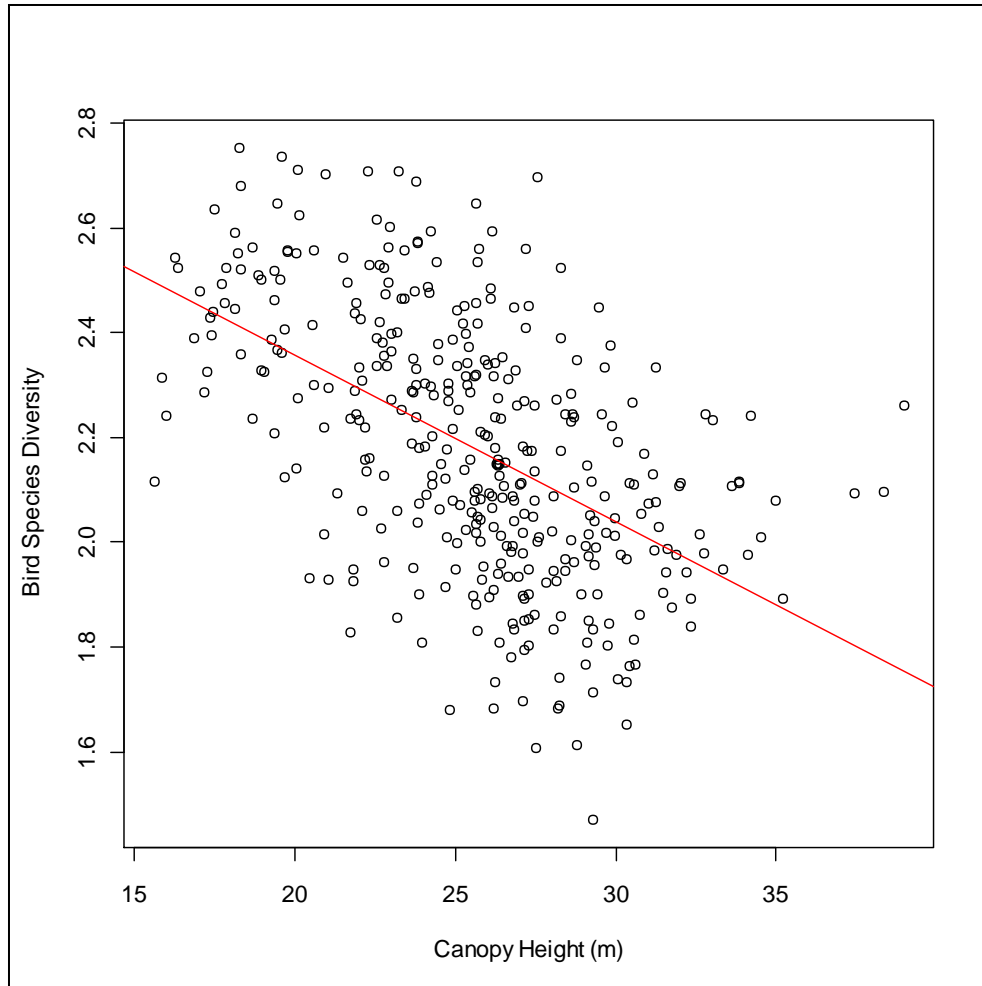


Figure 3.4. Relationship between bird species diversity and canopy height in meters. The red line of best fit indicates the negative relationship between the two.

The significance of the interaction effects for the two-way ANOVA's differed between the two categorical metrics. The significant interaction effect between the height bins and the canopy layer structure categories, show that the impact of the variables on BSD depend on the each other. However, there were no significant interaction effects when the average BSD was examined between height bins and the number of foliage profile layers. Although the number of foliage profile layers does have some relationship to canopy height, it is not enough to impact the outcome in difference of average BSD.

### 3.4 Discussion

Foliage height diversity, as developed by MacArthur and MacArthur (1961) can arguably be labeled as the seminal paper for studies examining avian diversity and forest structure, particularly canopy stratification or layering. However, despite the notoriety of its findings, there has been some debate on the applicability of the results (Karr & Roth 1971; Willson 1974; Pearson 1975; Terborgh 1977; James & Warner 1982; Erdelen 1984). The development of lidar remote sensing has allowed researchers to examine the distribution of canopy material on a larger scale using metrics such as FHD. Thus I am able to expand on and possibly better understand the research of MacArthur and MacArthur (1961). To do this, I examined numerous lidar metrics used to describe the vertical distribution of canopy material, specifically looking at how those metrics relate to bird species diversity. All of the metrics tested had a significant relationship with BSD; however, the nature of that relationship was not necessarily the same as noted in previous studies. My findings show that BSD decreases as foliage material becomes more evenly distributed within the vertical column.

Based on the MacArthur and MacArthur (1961) findings that bird species diversity increases with foliage height diversity, my results are counterintuitive. However, other bird diversity studies have also shown differing results from MacArthur and MacArthur (1961) (Karr and Roth 1971; Willson, 1974 Pearson 1975). Studies by both Willson (1974) and Pearson (1975) found no correlation between FHD and BSD. Karr and Roth (1971) found a positive correlation between BSD and FHD in most but not for all of their study areas. It has also been noted that the BSD/FHD relationship is not applicable when examining landcover types of the same structure (Erdelen 1984). More



recently, the findings of Clawges et al. (2008), found that FHD, as determined from discrete return lidar, was positively correlated with BSD. However, Clawges et al. (2008) found that the correlation did not necessarily increase when FHD has more layers, as predicted by MacArthur and MacArthur (1961). Here, my findings generally agree with the MacArthur and MacArthur (1961) assumption that the correlation between BSD and FHD is stronger as more layers are added and FHD increases (as seen with FHD 5 versus MacArthur's FHD). However, I also found that the placement of layer demarcations impacted the relationship between BSD and FHD, when the number of layers remained the same (as seen with metrics FHD 4a and FHD 4b). Similarly, Clawges et al. (2008) noted that an increase in FHD did not always result in an increase in BSD, but the highest correlations occurred when FHD was divided so that more layers were present in the understory.

The variation in my results compared to previous experiments is not necessarily a reflection on the ability of full waveform lidar metrics to characterize structural variables related to BSD, but more than likely it supports need to focus on more ecologically based variables, as equally noted in the literature (Willson 1974; Erelen 1984; James & Warner 1982; Clawges et al. 2008). Out of all my variables, FHD 5 (which had 5 layers) was the most correlated and explained the most variation in BSD between bird plots. However, the layer demarcations used in the FHD 5 calculation were mainly experimental and do not necessarily reflect foliage layers important for numerous bird species in HBEF. As noted by Erdelen (1984), using the Shannon-diversity index to determine FHD results in the number of layers chosen for the calculation influences the final FHD value.

Histograms of the 5 FHD metrics show not only how FHD increases with the addition of layers, but also how the distribution of FHD values change even though the study area remains the same. The distributions range from highly skewed to the right (MacArthur's FHD and FHD 4a) to a distribution closer to normal (FHD 4b and, FHD 5) and then to a distribution skewed to the left (FHD 7) (Figure 3.5). Hence, the value and distribution of FHD can greatly change with the addition of layers, which ultimately changes the description of the bird plots. Also, the extreme skewedness in the histograms indicates that once the various FHD metrics reach a certain value, the amount of BSD variation explained decreases. Thus, the FHD value may partly be an artifact of how the canopy was analyzed by the researcher instead of a true description of foliage distribution within the canopy (Erdelen 1984).

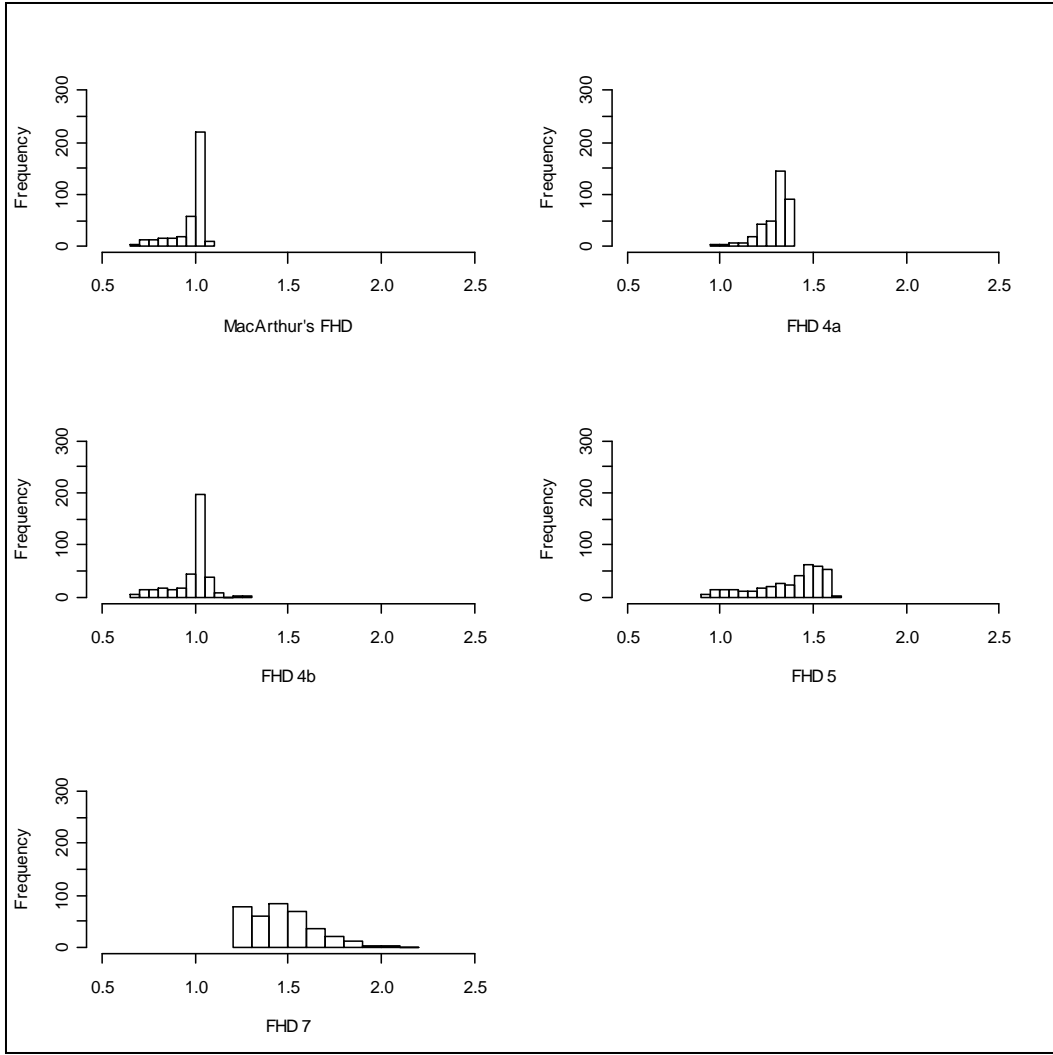


Figure 3.5. Histograms of the FHD metrics showing the distribution of the various FHD values within the 50 m radius bird plots.

The nature of the Shannon diversity index formula also allows for the FHD value to be influenced by the height or depth of the layers. To demonstrate this, I calculated the FHD for the bird plots using 4 layers and varying the layer heights to create 7 new FHD metrics, in addition to FHD 4a and FHD 4b. For example, FHD 4c has layers from 0-5 m, 5-10 m, 10-25 m, and > 25 m, where as FHD 4h has layers from 0-5 m, 5-20 m, 20-30 m, >30 m. The histograms of the FHD values for the 4 layer metrics vary greatly from

metric to metric (Figure 3.6). The shift in the histograms does not seem to be consistent with a variation in layer placement (e.g. larger midstory layers, smaller layers closer to the ground, more layers positioned in the overstory, etc.). Thus, the FHD values assigned to a plot can vary greatly based on layer demarcation, greatly altering the description of the foliage distribution.

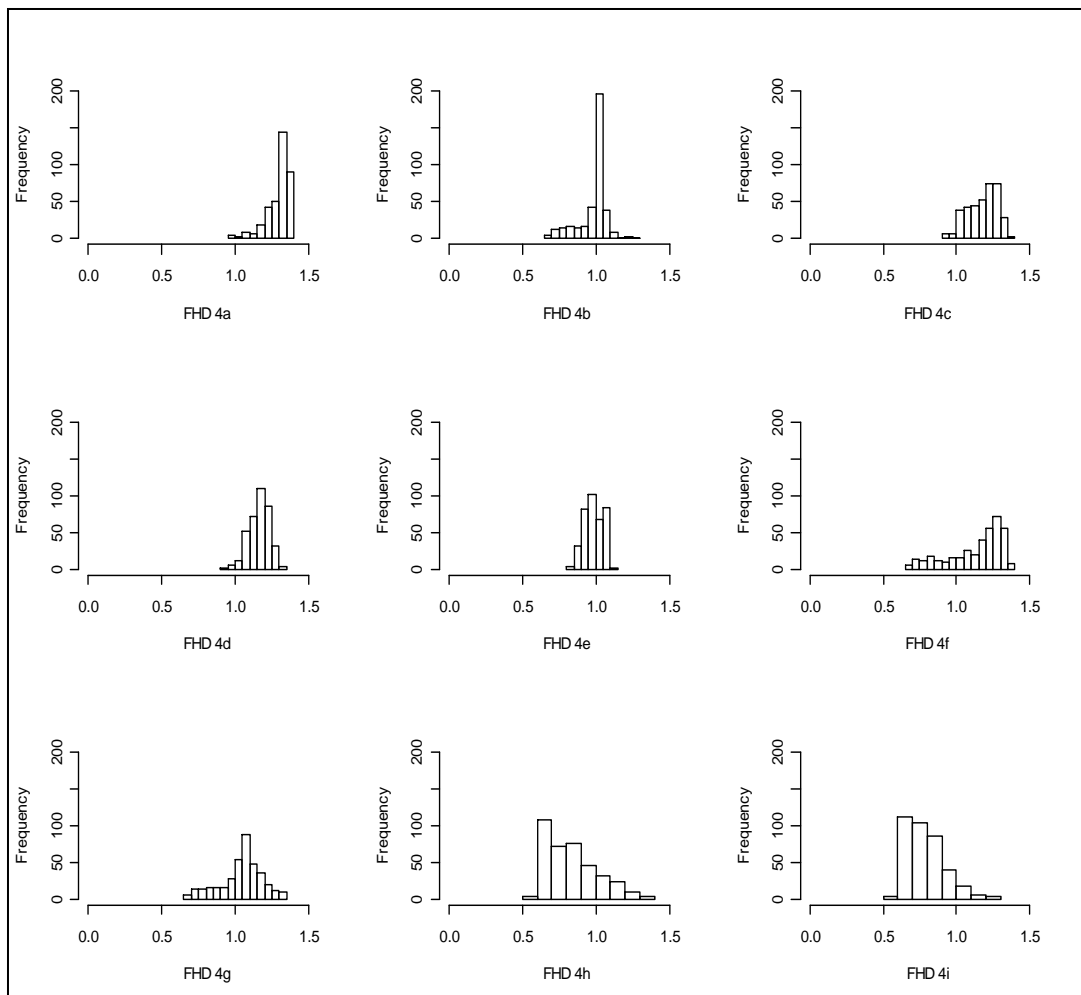


Figure 3.6. Histograms of FHD for 4 layer plots with differing layer heights.

This leads to the question of what information FHD provides about the distribution of foliage. By using the Shannon diversity index, the calculation provides a value describing the proportion of foliage within each layer as compared to the other

layers in the system. Researchers have chosen variations of the FHD calculation based on the highest correlation with BSD, assuming that the high correlation determines the layering arrangement recognized by birds, which is not necessarily a valid assumption (Erdelen 1984). However, FHD only provides information about the layering within an area when the user knows how FHD was calculated (number of layers used and their positions). The actual FHD value itself does not provide much usable information. For example, it is impossible to know based on the FHD value alone, which layer contains the most canopy material. It is also possible to get the same FHD value for two structurally different plots. For example, if one plot has most of the canopy material close to the ground and the other has most of the foliage near the top of the canopy, they could still have the same FHD.

Karr and Roth (1971) noted the problem with structurally different plots having the similar FHD when explaining the difference in the FHD-BSD correlation for their study areas in Panama and the Bahamas. Although the vertical foliage distribution was similar between the two areas, there was a strong positive correlation between BSD and FHD in Panama which was not seen in the Bahamas. The main difference was the volume of vegetation that was higher for the Panama study area, which the authors note as a possible cause for the discrepancy in the BSD-FHD relationship. This, along with the variation in our results as compared to those of other forested ecosystems, further supports the idea that FHD may not be the best metric to uniformly relate to BSD, especially due to the wide variability in its calculation and the lack of information it provides about the actual vertical structure of the forest.

However, this does not show that vertical structure in general does not have/contain valuable information about species biodiversity. Instead, other vertical structure metrics need to be examined for both their relationship to avian species diversity and the type of information they provide about the forested ecosystem. Out of the remaining (non-diversity based metrics) in this study, VR and the number of foliage profile layers, explain the most variation in BSD between bird plots (24% and 27%, respectively).

The negative correlation between BSD and VR shows that clumping near the bottom of the canopy results in increased BSD. Since the waveform amplitude is related to the amount of canopy material, the height at which 50% has been returned (HOME) versus CH (height of 100% return), provides insight as to where areas of canopy material are more dense or clumped. My findings are in contrast to Goetz et al. (2007), where the positive relationship between species richness and VDR  $((CH - HOME)/CH)$  was interpreted as a positive correlation between richness and more evenly distributed foliage. VR and VDR are similar in that they both compare HOME and CH; however, the metrics are inverse, so a positive relationship with VDR would result in a negative relationship with VR. However, Goetz et al. (2007) limited the interpretation of these results to that of the upper canopy.

In actuality, both VR and VDR values denote canopy distribution as clumped in the lower canopy, upper canopy, or evenly distributed within the canopy, based on the relationship between the CH and HOME metrics. For example, in a 50 m height canopy with HOME equaling 10 m, 50% of the waveform energy was reflected back by canopy material spread out over the top 40 m in the canopy. The remaining 50% of the energy

was reflected back from lower 10 m of the canopy, which could also include ground reflectance. For this to happen, the foliage between the top of the canopy and the height of HOME (a distance of 40 m in the vertical column) must be dispersed or open allowing more of the waveform energy to travel through the canopy. The increased distance between CH and HOME (depicted by VDR closer to 1 and VR closer to 0) indicates clumping in the lower part of the canopy, not the even distribution of foliage as interpreted by Goetz et al. (2007).

These findings are further supported by the significant difference in BSD between 1 and 2 foliage profile layer systems. The higher average BSD in areas with one foliage profile layer indicate that one area of denser canopy is more important than areas with more distribution of canopy, as seen in two layer systems, which have two areas with denser canopy material separated by a gap or more open area within the vertical column. The average height of the layers in the 1 layer plots was also not significantly different from the height of HOME for those plots, showing that if there is significant clumping of foliage within one section of the canopy, the height of the peak of the clumping coincides with 50% of the waveform return.

The presence and distribution of foliage within the vertical column provides the multiple canopy niches for different bird species or as noted in Holmes et al. (1979) a distribution of foraging substrates. The presence of canopy material throughout the vertical column would in effect increase the availability of foraging substrates, providing the opportunities for varying species to occupy the same horizontal area. This idea was expanded upon in Robinson and Holmes (1984) where it was noted that the distribution of canopy material related to an increased number of species because it provided more

foraging substrates corresponding to the species' specific morphological adaptations. Also, increase species richness observed in old growth versus closed-canopy mature forests has been attributed to the redistribution of foliage throughout the vertical column in old growth forest stands (Keller et al. 2003).

However, based on the results of this project, it can be considered that although the presence of canopy material is important for BSD, an even distribution of that canopy material may not necessarily provide the foraging niches necessary to support multiple species. Holmes et al. (1979) and Robinson and Holmes (1984) both note that vegetation structure may impact not just the availability of foraging substrates but also how bird species forage. Thus, an uneven distribution of canopy material would enable both species that prefer clumped foliage in the understory, such as the Black-throated Blue Warbler or Red-eyed Vireo (Holmes et al. 1979; Robinson & Holmes 1984) to inhabit the same area as species that require more open areas of the canopy for foraging and traveling. Similarly, Keller et al. (2003) noted that as forest structure changed during succession from clear-cut to more mature areas, the closing canopy reduced the amount of vegetation near the ground. This resulted in a decrease in species richness, particularly in guilds that relied on foraging sites near the ground.

Canopy height is a common metric used to examine bird species habitat preference, suitability and species diversity (Kessler et al. 2001; Hinsley et al. 2002; Hill et al. 2004; Broughton et al. 2006; Hinsley et al. 2006; Hinsley et al. 2008; Goetz et al. 2007). However, considering that all the foliage distribution metrics are related to height (as noted in James & Warner 1982), the question is raised whether or not the foliage distribution metrics provide additional information towards predicting BSD when canopy



height is already being used or are the distribution metrics and height too correlated to be used simultaneously. My results showed a negative correlation between canopy height and BSD in HBEF (Table 3.2). This relationship is different from what was expected based on previous studies, examining forest bird species richness (Kessler et al. 2001). The forest type, age, and other structural components found within the taller forest plots, such as in HBEF could be the reasoning behind this difference in results (Keller et al. 2003). For example, Kessler et al. (2001) found that the strength of correlation between species richness and canopy height was influenced by the range of vegetation structure within the study area.

In general there was a high correlation between canopy height and the vertical distribution metrics. When canopy height is accounted for in the linear model, only the metrics VR and FHD 5 were found to be barely significant. When height was accounted for via two-way ANOVAs with the categorical variables, the number of foliage profile layers did not have a significant interaction with height. Thus, when examining variations in BSD, the impacts of these highly correlated variables need to be taken into account and variables whose relationship with BSD are masked by the use of canopy height (such as COMP, canopy layer structure, and some of the FHD metrics) should not be included. Although it explains the majority of species variability when compared to the other vertical structure metrics, the (although slight) significance of VR and FHD 5 (when height was accounted for) suggests that the relationship between bird species diversity and other aspects of vertical canopy structure should still be examined.

Due to the high correlation between VR and BSD and relationship between the layer height in single layer plots and HOME, we also investigated the relationship

between HOME and BSD (Figure 3.7). The correlation between BSD and HOME was -0.56, and HOME explained 31% of the variation in BSD. Following the trend with the previously discussed metrics, BSD increased as canopy material became concentrated closer to the ground. More surprisingly, the correlation between BSD and HOME was greater than that of BSD and canopy height, albeit slightly. This could be attributed to, as noted previously, that the availability of foliage near the ground provides more foraging substrates for a larger number of species than is provided in the upper parts of the canopy. This coincides with the observations of Keller et al. (2003) that species richness declines in taller mature forests due to loss of vegetation near the ground. So although it is arguably the most popular vertical metric used in avian species diversity and habitat research, canopy height may not be the best or the only vertical structure metric that should be used to better understand forest bird species diversity and habitat.

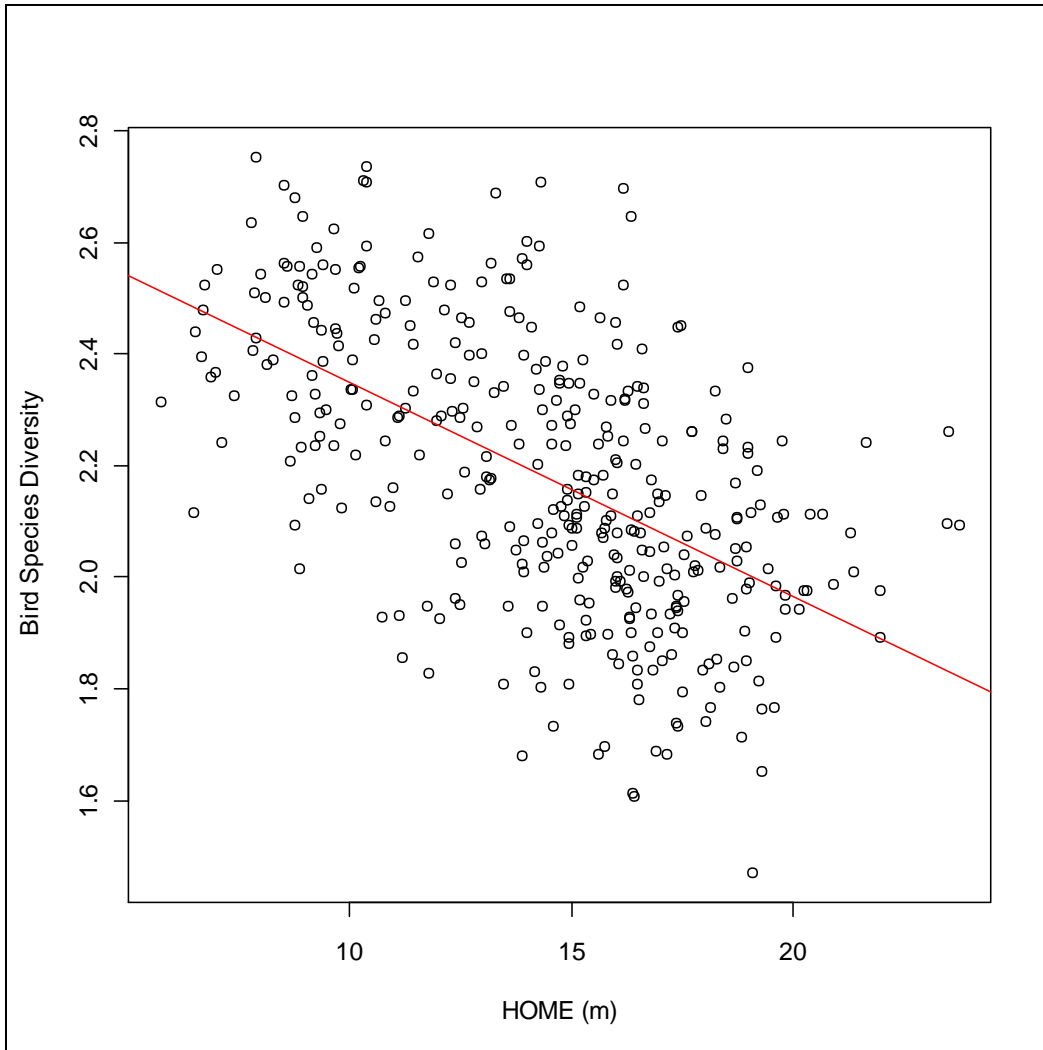


Figure 3.7. Relationship between bird species diversity and HOME in meters. The red line of best fit indicates the negative relationship between the two.

With all the examined variables, the most variation in BSD explained by a single variable was around 30%. This corresponds with previous studies examining species richness and diversity where the amount of variance explained by both a single vertical structure variable and multiple lidar metrics were also low (Goetz et al. 2007; Clawges et al. 2008). The purpose of this project was to determine the relationship between metrics describing the distribution of canopy material and bird species diversity in HBEF and

examine what information these metrics actually provide about forest ecosystem dynamics. Numerous factors impact BSD, including horizontal elements (distance to edge or water), environmental factors (elevation), as well as species interactions (Doran 2003). However, by determining which factors individually have the strongest relationship to species diversity, we gain knowledge about the relationship between avian species and the forest ecosystem and can thus better model and monitor those relationships in the future.

The relationship between avian species and the distribution of canopy material does not end with species diversity or with Hubbard Brook Experimental Forest. As our results showed when compared to previous research, the relationships between BSD and forest structure can vary between forests, potentially due to forest type, age, or avian species present. Similarly, some of the tested metrics in our study have been found to be important for determining habitat preference for a specific species (Goetz et al. 2010). Swatantran et al (2012) also noted the influence of canopy distribution metrics on individual species habitat. Future work needs to be done to determine which of these metrics best relate to certain avian species for improved habitat modeling and ultimately forest management.

### 3.5 Conclusion

Following in the footsteps of MacArthur and MacArthur (1961), I set out to examine the relationships between bird species diversity and the vertical distribution of forest canopy material using lidar metrics. With the numerous available lidar metrics describing vertical foliage distribution, it is important to determine not only which explain the most variation in BSD but also which make the most sense and provide the

most usable ecological information to better understand forest ecosystem dynamics (Müller et al. 2010). My results raise questions noted in previous studies about the applicability of FHD, due to the variability in which it can be calculated and the historical ambiguity of its exact relationship with BSD and the forest ecosystem. Two of my examined variables (VR and the number of foliage profile layers) seem to provide an adequate explanation of BSD variability and corresponding ecological information. The results of VR provide information on where in the canopy the material is distributed, relative to canopy height. The number of foliage profile layers is based on validated measures of foliage area and distribution throughout the canopy (Whitehurst et al. 2013). However, the lidar metric HOME, explained more variation in BSD than any of the distribution metrics as well as the commonly used canopy height metric. To fully understand the relationships between BSD and these variables and how they impact the forest ecosystem as a whole, future research needs to be done examining these relationships in other forests as well as focusing on single species habitat.

# Chapter 4: A decade of change: examining structural change in Hubbard Brook Experimental Forest from 1999 to 2009 using lidar remote sensing

## 4.1 Introduction

Changes to forest composition and structure as a result of disturbance and succession affect a wide range of ecosystem services, including habitat suitability, carbon sequestration, and timber harvest (Spies 1998; McElhinny et al. 2005; Falkowski et al. 2009). Differences in vertical canopy structure have been identified between seral stages of forest succession (e.g., young, intermediate, mature, and old-growth) (Kessler et al. 2001; Keller et al. 2003; Nadkarni et al. 2004; McElhinny et al. 2005). These changes can impact forest-ecosystem attributes that are important for forest ecosystem dynamics, such as biomass accumulation and habitat suitability, and can result in changes in the amount of available habitat for forest fauna (McElhinny et al. 2005; Kessler et al. 2001; Keller et al. 2003; Dubayah et al. 2010).

Hubbard Brook Experimental Forest (HBEF) (New Hampshire, USA) has a complex disturbance history. Since the arrival of Europeans, the amount and degree of large-scale disturbance vastly increased within the forest (Bormann & Likens 1979; Schwarz et al. 2001). The area comprised by the experimental forest was heavily logged in the early 19<sup>th</sup> and 20<sup>th</sup> centuries. Since the creation of HBEF in 1955, large-scale anthropogenic disturbances have been mostly limited to scientific watershed manipulations, which comprise ~5% of the total area (Schwarz et al. 2001). It has been theorized that the scale of natural disturbance in northern hardwood forests, responsible

for their structure and composition, is dominated by small canopy gaps. However, in recent history, HBEF has undergone two notable natural disturbances which resulted in canopy damage, a hurricane in 1938 and an ice storm in 1998, which have been described as infrequent in the region due to their type or severity (Peart et al. 1992; Rhoads et al. 2002). In 1938, a hurricane impacted numerous forested areas in central New England, including HBEF. The exact spatial extent of the effects of the 1998 ice storm are unknown; however, serious damage was noted to occur mainly in older patches of forest, and particularly observed at mid and high elevations (Rhoads 1998; Rhoades et al. 2002). Another, more chronic, natural disturbance has been the invasion of beech bark disease, which recent studies have noted has not resulted in an increase in beech mortality or decrease in growth compared to other tree species within HBEF (Anderson et al. 2006; Siccama et al. 2007).

Comparisons with old-growth northern hardwood forests have suggested that much of the secondary growth forest within HBEF has recovered to a stage where some structural aspects are comparable to those of old-growth forests (Schwarz et al. 2001). However, these same plot-based analyses also noted that HBEF is a structurally diverse forest containing stands at varying states of forest succession. Recent studies (Siccama et al. 2007; van Doorn et al. 2011) have concluded that HBEF is no longer accumulating biomass and have suggested that this forest is closer to reaching the predicted steady-state of old-growth succession, where the total biomass fluctuates locally around a mean. These findings agree with those of Martin and Bailey (1999) who noted that within 100 years after heavy logging, northern hardwood forests could be expected to be comparable to old-growth areas based on basal-area, stem counts, and biomass.

Monitoring of changes to forest stand characteristics within HBEF has primarily focused on demography of individual species (including mortality) and biomass. However, variations in stand characteristics following disturbances, cannot be described solely by variations in species demographics and biomass within the forest ecosystem. Vertical structure, which is related to biomass and plant species diversity and changes with succession, provides further insight into broader dynamics within the forest ecosystem dynamics, notably in relation to wildlife habitat. Numerous studies conducted in HBEF examine the forest's vertical structure and often combine data over many years (e.g. Goetz et al. 2010 and Swatantran et al. 2012, which both compared multiple years of bird survey data and vertical structure for habitat analyses).

The development of lidar remote sensing has allowed forest canopies to be examined from the top of trees to the forest floor (Dubayah & Drake 2000; Lefsky et al. 2002; Vierling et al. 2008). Lidar provides information not only pertaining to canopy height but also information on the horizontal and vertical organization of the canopy (Dubayah et al. 2010; Lefsky et al. 2002; Hyde et al. 2005; Goetz et al. 2007; Swatantran et al. 2012; Whitehurst et al. 2013). Many lidar-derived products, such as canopy height, cover, and biomass, have been shown to accurately depict canopy elements essential for habitat suitability and forest management at the landscape scale (Hill et al. 2004; Hyde et al. 2005; Goetz et al. 2010; Swatantran et al. 2012).

Recently, lidar remote sensing has been used to detect dynamics of forest structure, enabling analyses of structural change over a contiguous study area, where previous studies were limited to plot-scale analyses. These studies have demonstrated that lidar measurements from separate time periods and instruments are comparable (Kellner



et al. 2009; Goetz et al. 2010; Swatantran 2011). Using discrete-return lidar, Kellner et al. (2009) demonstrated that lidar-based measurements of canopy height and dynamics are comparable to field-based measurements. Dubayah et al. (2010) examined change in biomass using change in lidar-derived variables to determine areas of carbon sources and sinks within La Selva, Costa Rica. This study also assessed the sensitivity and accuracy of lidar to detect canopy structure change, showing that with increased sampling, lidar is able to detect very small changes in canopy height across the landscape. Similarly, Swatantran et al. (2011) showed that lidar-derived canopy height change was consistent with land use and its changes detected via optical remote sensing in the Sierra Nevada.

As forests age, changes occur in canopy height, canopy closure, and subcanopy vegetation volume (Spies 1998; Franklin et al. 2002; Nadkarni et al. 2004). Changes in these characteristics have been used to distinguish successional states among forest plots (Schieck et al. 1995; Keller et al. 2003). As stand initiation occurs following a major disturbance event (e.g., harvest) that initiates secondary succession, young forests have relatively short, dense canopies that blend with understory vegetation near the forest floor, (Franklin et al. 2002; Keller et al. 2003; Nadkarni et al. 2004). However, canopy cover increases as succession progresses with tree growth. During the middle stages of succession, the decrease in light availability throughout the vertical column causes the vertical distribution of foliage (including canopy and understory vegetation) to shift upward, away from the ground (Franklin et al. 2002; Keller et al. 2003; Nadkarni et al. 2004). Finally, as the forest enters the old-growth stage of succession, the formation of canopy gaps enables light to reach the understory and the vegetation between the top of

the canopy and the forest floor becomes more evenly distributed (Franklin et al. 2002; Keller et al. 2003; Nadkarni et al. 2004; McElhinny et al. 2005).

Changes in these elements of vertical structure influence other aspects of the forest ecosystem, including floral and faunal species diversity and habitat availability. In particular, relationships between forest structure and avian species have been well documented. Vertical forest structure has been linked to avian species habitat preference, foraging behavior and diversity (Holmes et al. 1979; Robinson & Holmes 1984; Hinsley et al. 2002; Hill et al. 2004; Broughton et al. 2006; Hinsley et al. 2006; Hinsley et al. 2008; Smart et al. 2012). Lidar metrics describing structure within the canopy are related to avian species habitat preference and diversity (Goetz et al. 2007; Goetz et al. 2010; Swatantran et al. 2012). Swatantran et al. (2012) noted that the relationship between species prevalence and canopy cover changed at different height intervals within the forest canopy. Other studies have noted that uneven foliage distribution or “clumping” within the canopy is positively related to bird species diversity (Goetz et al. 2007; Whitehurst et al. n.d.).

Detecting changes within the vertical structure of the canopy across the forested landscape over short time intervals may improve our understanding of forest ecosystem dynamics and thereby aid forest management. The overarching goal of this paper is to examine forest canopy structure dynamics in the temperate montane forests of Hubbard Brook Experimental Forest using full-waveform lidar from 1999 to 2009. In particular, this study addressed the following questions. First, how has canopy height changed in the past 10 years across HBEF? Second, how have other aspects of vertical structure, particularly indicators of forest seral stage and/or faunal species biodiversity, changed

within HBEF from 1999 to 2009? Finally, are observed changes in canopy height consistent with the concept of a forest in steady-state, and if not, can we instead attribute these dynamics to recent episodic disturbances (particularly the 1998 ice storm) or the continuing fingerprint of recovery from logging that occurred in the distant past?

## 4.2 Methods

### 4.2.1 Study Area

Our study area covers 3185 ha of the White Mountain National Forest, including Hubbard Brook Experimental Forest (HBEF). Located in central New Hampshire, USA, the HBEF basin encompasses numerous watersheds and elevation ranges (220 m to 1015 m) (Schwarz et al. 2001). Throughout the entire basin, 10 watersheds have been set aside for experimental forestry research. Five of these watersheds (WS 1, 2, 4, 5, and 101) have undergone specified treatments ranging from timber harvest to the addition of calcium to the soil (Martin 2013). These watersheds were excluded from the study due to the impacts of previous experiments on the natural disturbance regime and forest growth. This allowed our study to focus on the “natural” or non-anthropogenic patterns of forest succession and disturbance within HBEF over the past 10 years.

### 4.2.2 Lidar Data

Lidar data was gathered using the Laser Vegetation and Imaging Sensor (LVIS) developed by NASA Goddard Space Flight Center. This medium-footprint (10 - 25 m), full-waveform lidar records both the outgoing and return signal enabling information about the entire length of the vertical column (from the top of the canopy to the ground) to be gathered for each geolocated waveform (Blair et al. 1999). LVIS was flown over

HBEF in September 1999 (approximately 25 m footprint) as part of the Vegetation Canopy Lidar (VCL) validation mission and then again during August 2009 (approximately 20 m footprint). Both flights occurred during leaf-on conditions, minimizing potential issues in comparing the height or amplitude of return to determine change in foliage volume or amount.

To avoid differential estimates of ground elevation, especially in areas of steep slopes, small-footprint, discrete-return lidar (DRL) acquired in 2009 with a shot density of  $\sim 5/\text{m}^2$ , was used to measure the ground elevation for both the 1999 and 2009 datasets. Assuming no known major shifts in geomorphology occurred from 1999 to 2009, the DRL-based elevation is assumed to be correct for both datasets. The LVIS-measured canopy height was subtracted from the DRL-measured elevation to adjust canopy height for terrain elevation (Swatantran et al. 2012). The Height Of Median Energy (HOME; the height where 50% of the LVIS waveform energy is reflected back to the sensor) was also calculated in this way (Drake et al. 2002; Goetz et al. 2008; Dubayah et al. 2010; Swatantran et al. 2012), as were RH25 and RH75 (the relative height at which 25% and 75% of the LVIS waveform energy is reflected back to the sensor, respectively).

Cumulative canopy cover (hereafter, “canopy cover”) was calculated from the LVIS waveform profiles based on the methods of Ni-Meister et al. (2001). Summed from the top of the canopy to the ground, it is presented as the percent of sky obscured by vegetation. To estimate the amount of canopy cover in the understory, the MacArthur-Horn transformation ( $-\ln(1-\text{cover}(h))$ , where  $h$  equals height) was used in the derivation of cumulative canopy cover from the LVIS waveform profiles. This allowed for the extinction of light as it travels through the canopy to be accounted for (MacArthur &

Horn 1969; Lefsky et al.1999a; Lefsky et al. 1999b; Harding et al. 2001). Although the transformation provides a unit-less result, canopy cover change can still be observed. The amount of understory cover (summed transformed canopy cover from 0 - 5 m) was then converted to a percentage of the cumulative transformed canopy cover for the entire LVIS profile.

Canopy layer structure categories are lidar-derived metrics that categorize the vertical foliage distribution based on the amount of foliage within the understory, midstory, and overstory (Whitehurst et al. 2013). Nine different categories are used to define the differences in canopy material between the three canopy layers, which are distinguished by pre-determined heights within the canopy (understory (0 - 5 m), midstory (5 - 15 m) and overstory (15 m to canopy top)). The amount of foliage within each layer is measured by the cumulative transformed canopy cover, which is calculated for each layer-height bin (Whitehurst et al. 2013).

The vertical ratio (VR) is an index that uses lidar metrics of canopy height and HOME to describe how evenly canopy elements are vertically distributed (Whitehurst et al. n.d.). The calculation,  $VR = HOME/canopy\ height$ , results in values from 0 to 1. VR values close to 1 mean that most of the canopy material is near the top of the canopy, whereas values near 0 indicate that most of the lidar waveform energy was reflected from the lower part of the canopy (Whitehurst et al. n.d.). This metric has been shown to correlate negatively with bird species diversity, supporting previous field and lidar-based studies that noted that clumping of foliage near the ground provides increased foraging substrates for several bird species (Keller et al. 2003).

### 4.2.3 Statistical Analyses

Different flight lines were used in 1999 and 2009, resulting in varying footprint locations across the study area and a limited number of coincident footprint pairs. Although the LVIS waveforms provide information across the entire footprint, the signal is stronger in the middle of the footprint than along the edges, due to the Gaussian nature of the energy distribution (Hyde et al. 2005; O'Dell 2006). This can cause canopy elements on the edges of the waveform to be underestimated. Thus if two waveforms are being compared with little overlap, the change detected may be due to footprint location instead of actual canopy change over time. However, it has been shown that coincident footprints are not necessary for accurate estimates of vertical structure change (Swatantran et al. 2011). Regardless, to ensure that the 1999 and 2009 LVIS shots were describing the same area of vegetation, footprint pairs were selected using 1999 and 2009 footprints that were within 3 meters of each other (Dubayah et al. 2010; Swatantran et al. 2011). This resulted in 15690 pairs located throughout the HBEF study area (Figure 4.1 and Figure 4.2).

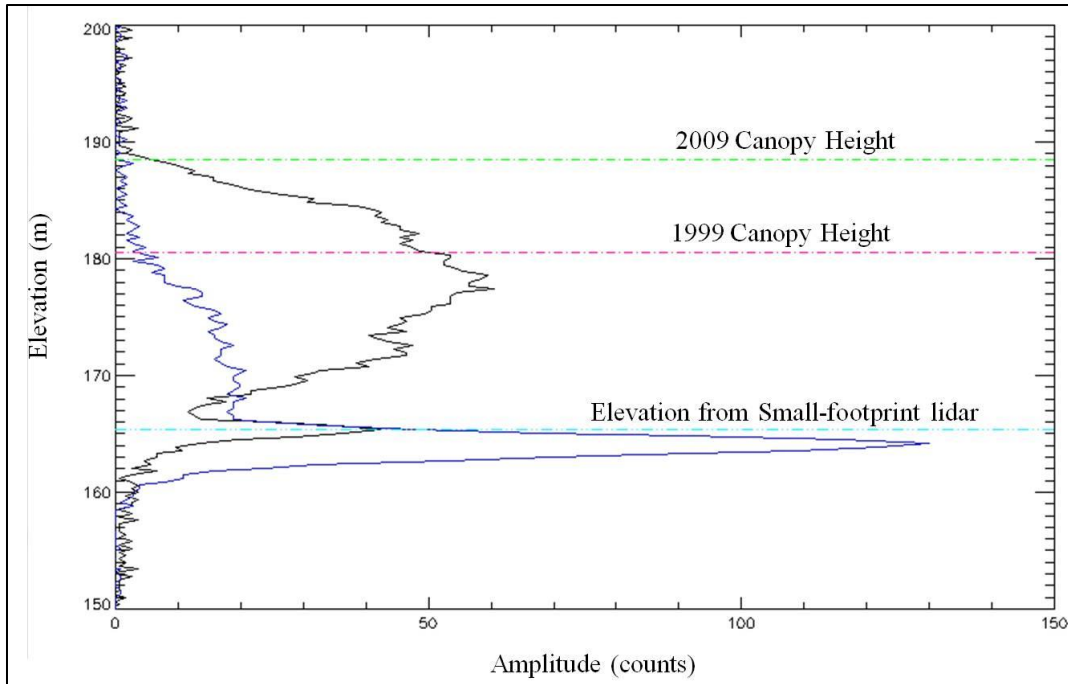


Figure 4.1. Example of LVIS footprint-pair waveforms and comparison of canopy-height metrics. The waveform amplitude is related to the amount of vegetation present in the canopy. Between the two years, waveform-derived canopy cover increased around 60%. The black waveform is from 2009. The purple waveform is from 1999. The difference between the 2009 canopy height (green dashed line) and the 1999 canopy height (dashed pink line) is around 8 m. The cyan line is the elevation derived from small-footprint lidar.

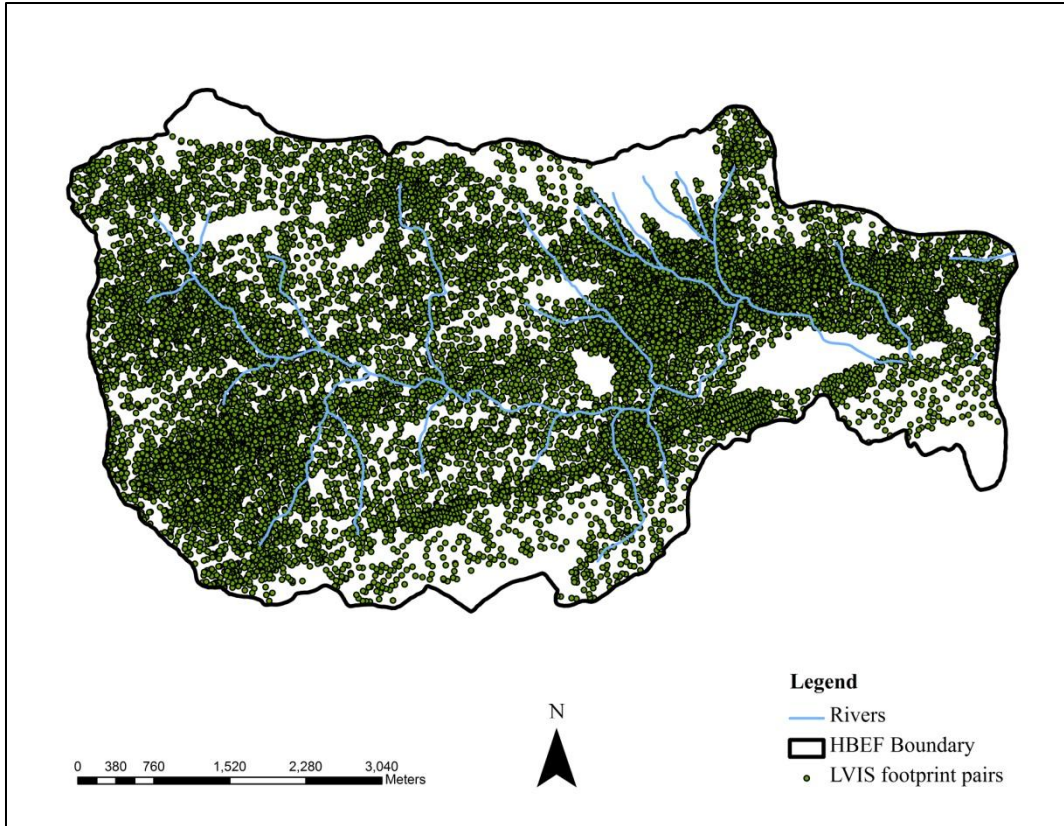


Figure 4.2. Map of footprint pair distribution across HBEF.

Paired t-tests were used to test for significant changes in canopy height, HOME, RH25, RH75, canopy cover, understory cover, and VR between 1999 and 2009. T-tests were also used to determine if there was a difference in canopy-height change between areas impacted by the 1998 ice storm vs. areas that were not.

Markov transition-probability matrices were used to further examine the change in vertical structure. These models have been commonly used to examine vegetation change (Hall et al. 1991; Urban 2005; Biondini & Kandus 2006; Perry & Millington 2008). In order to explore how forest structure was changing in greater detail, transition matrices were used to determine what types of structural changes were occurring for each lidar metric. Each cell of the transition matrix provides the probability that a discrete



height class  $j$  will change to another class  $i$  in a specific time-step  $t$  (Hall et al. 1991; Biondini & Kandus 2006; Perry & Millington 2008). The diagonal cells of the matrix show the retention frequency or the proportion of footprint pairs in each class that remained the same over the decadal span (e.g. height in 1999 = height in 2009). The transition frequency is provided by the off-diagonal cells (e.g. height in 1999 is not equal height in 2009) (Hall et al. 1991). This was applied to all the LVIS metrics: canopy height, HOME, RH25, RH75, canopy cover, understory cover, and VR. The transition classes were set as 5 m intervals for canopy height, HOME, RH25, and RH75.

Assuming constant rates of change, the Markov model projections were used to predict when the steady-state distribution of canopy height might occur (Hall et al. 1991; Stubben & Milligan 2007). Steady-state occurs when gains and losses in each component of the transition probability matrix equalize for a net balance that remains constant over progressive iterations (Stubben & Milligan 2007). The distribution of stage (i.e., height class) was projected through time using the algebraic solution  $n_{t-1} = An_t$ , where  $A$  is the projection matrix,  $n$  is the initial stage, and  $t$  is the time interval (Stubben & Milligan 2007). The time steps at which the probabilities of each element converge provide an estimate of when steady-state will occur, at which point the distributions of each stage are calculated (Stubben & Millington 2007; Perry & Millington 2008).

To better examine the variation of canopy height change across the landscape, 1999 and 2009 LVIS canopy height measurements were mapped at 1 hectare resolution. Aggregating LVIS canopy heights allows the majority of the LVIS data to be utilized (over 100,000 footprints per year). Within each hectare grid cell, changes between the 1999 and 2009 canopy heights were compared using the Wilcoxon-Mann-Whitney rank

sum test. This non-parametric test was used to determine whether or not the difference between canopy heights was significant within a 95% confidence level ( $p < 0.05$ ), since the limited number of LVIS shots in each hectare grid cell (and often unequal number of shots per year) prevented the assumption of a normal distribution. Only grid cells with a significant difference in canopy height were mapped and examined for spatial trends in canopy height change.

### 4.3 Results

#### 4.3.1 Canopy height change

##### *Average Change*

The average difference between canopy heights observed in 2009 and 1999 was 2.23 m, with a standard deviation of 1.94 m. Paired t-tests confirmed significant difference in mean canopy height ( $p < 0.05$ ), with 2009 having the taller canopy. Over half of the footprint pairs changed by at least 2 m in height, and only 8% of the footprint pairs decreased in height from 1999 to 2009.

##### *Transition Matrix*

The probability of gaining in canopy height (moving to a taller height class) was greater than both the probability of remaining in the same height class or moving to a shorter height class (Table 4.1). Shorter canopies were more likely to increase in height, whereas canopies in the taller height classes (25 – 40 m) were more likely to remain in the same class (Figure 4.3). Canopies in the 20 - 25 m height class were equally likely to increase in height or stay the same.

2009	Canopy Height (m)	1999									
		0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	> 40	N
	0-5	-	-	-	-	-	-	-	-	-	-
	5-10	0.5	-	-	-	-	-	-	-	-	1
	10-15	0.5	0.63	0.26	-	-	-	-	-	-	86
	15-20	-	0.25	0.68	0.41	0.01	-	-	-	-	1153
	20-25	-	0.13	0.06	0.54	0.5	0.02	-	-	-	4410
	25-30	-	-	0.01	0.05	0.47	0.68	0.03	-	1	6854
	30-35	-	-	-	-	0.03	0.3	0.70	0.05	-	2658
	35-40	-	-	-	-	-	0.01	0.26	0.75	-	487
	> 40	-	-	-	-	-	-	0.01	0.2	-	41
	N	2	8	290	2227	6285	5501	1245	131	1	15690

Table 4.1. The distribution of canopy-height transition probability. Each cell provides the probability that a discrete class  $j$  will change to another class  $i$  in a specific time-step  $t$ . The diagonal cells (yellow) show the retention frequency or proportion of classes that remained the same.

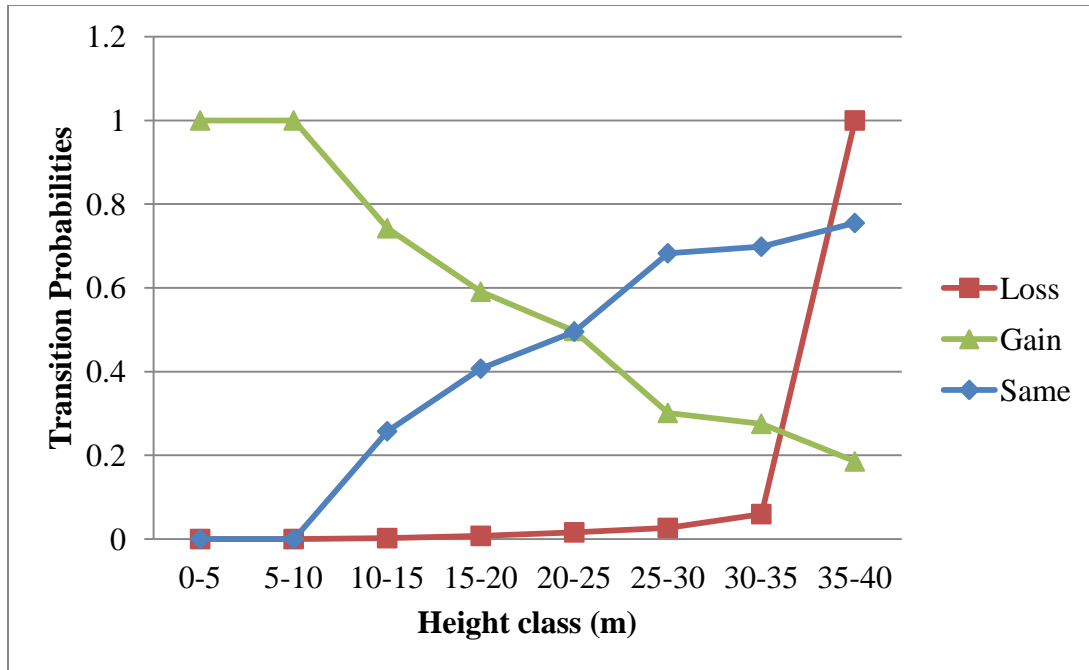


Figure 4.3. Transition probabilities for the LVIS-derived canopy structure metrics of canopy height. These graphs show the probability of transitioning from one class to another from 1999 to 2009. The blue lines indicate probabilities of footprint pairs remaining in the same class from 1999 to 2009. The red line indicates footprint pairs losing value or transitioning to a lower class from 1999 to 2009. The green line shows the probability of footprint pairs gaining in value from 1999 to 2009.

### *Hectare Analysis*

Mapped at 1 ha resolution, the mean change in canopy height from 1999 to 2009 was 2.47 m with a standard deviation of 1.39 m, comparable to the average positive canopy height change observed in the footprint pairs. In 93% of the grid cells the canopy height change was identified as significant at the 95% confidence level by the Wilcoxon-Mann-Whitney test ( $p < 0.05$ ). Only one grid cell significantly decreased in height. When mapped, areas of significant change showed an increase of canopy height up to 5 m throughout the majority of the forest (Figure 4.4). Although scattered throughout the watershed at all elevations, areas with 2 m or less of canopy height increase were more

concentrated at lower elevations. Areas of more intense growth (increases of 5 to 21 m) were few and spatially patchy, occurring at both low and high elevations.

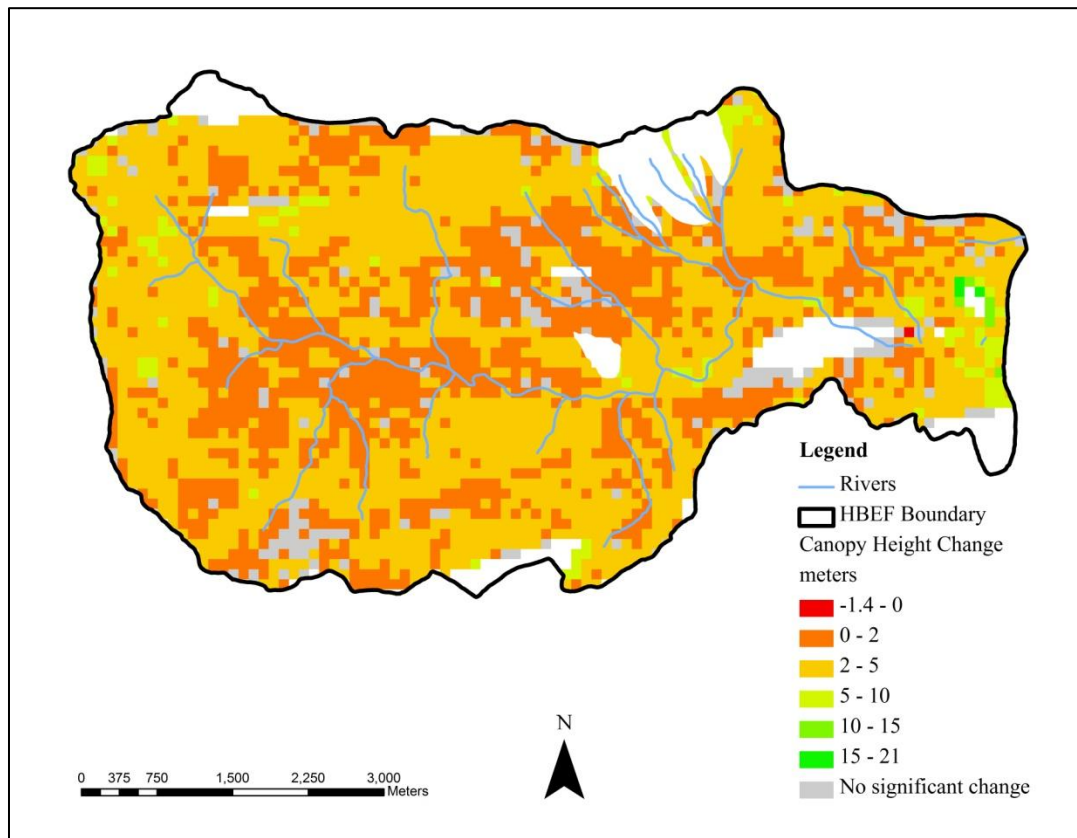


Figure 4.4. Hectare scale map of canopy height change between 1999 and 2009. This map only contains grid cells with significant change at the 95% confidence level as identified by the Wilcoxon-Mann-Whitney test ( $p < 0.05$ ). The gray areas represent areas with no significant change. White areas within HBEF were not included in the analysis, including the experimental watersheds and areas without lidar data.

#### 4.3.2 Changes in lidar metrics previously related to seral stage and biodiversity

##### *Average Change*

Paired T-tests showed that the other structural metrics (HOME, RH25, RH75, VR, canopy cover, and understory cover) also changed significantly over the 10 year period. Understory cover was the only metric with an average significantly less in 2009

than 1999 (Table 4.2). The canopy layer structure categories also changed between the two years. 45% of the footprint pairs transitioned from one category to another.

<b>HBEF Change</b>						
	HOME (m)	VR	Canopy Cover (%)	Understory Cover (%)	RH25 (m)	RH75 (m)
Average	2.55	0.05 6	6.28	-3.97	4.05	1.65
Std Dev	1.95	0.07 2	7.99	8.12	2.50	1.51

Table 4.2. The average change and standard deviation for LVIS structural metrics (2009 – 1999).

### *Transition Matrices*

Changes in HOME were similar to those of canopy height. Areas where 50% of the return occurred lower in the canopy (0 – 15 m) were more likely to increase (Figure 4.5). This trend was also seen in the RH75 metric, which showed a greater likelihood of increase in the lower height classes (RH75 < 15 m) (Figure 4.5). Areas where 75% of the LVIS return occurred at 15 m and above had a higher probability of remaining in the same height class. In 1999, none of the sampled canopies had an RH25 above 20 m (Figure 4.5). This changed over the 10 year time period, so that in 2009, around 4% of the sampled canopies had 25 % of the LVIS return distributed above 15 m. In general, all the RH25 height classes were more likely to increase, with the exception of the 10 -15 m height class, which was more likely to remain the same. The trends of increase within HOME, RH25, and RH75 show that in addition to the overall canopy height of the tallest trees increasing, the height of vegetation within the canopy was also increasing.

a)								
2009	RH 25 (m)	1999						
		<5	5-10	10-15	15-20	20-25	>25	N
	<5	0.32	0.02	0.009	-	-	-	2694
	5-10	0.55	0.32	0.06	-	-	-	6678
	10-15	0.14	0.61	0.57	-	-	-	5691
	15-20	0.003	0.06	0.34	-	-	-	608
	20-25	-	0.001	0.02	1	-	-	18
	>25	-	-	0.002	-	-	-	1
	N	8176	6935	578	1	-	-	15690

b)								
2009	HOME (m)	1999						
		0-5	5-10	10-15	15-20	20-25	25-30	N
	<5	0.17	0.01	0.001	-	-	-	131
	5-10	0.66	0.42	0.02	0.001	-	-	1980
	10-15	0.16	0.52	0.4	0.02	0.003	-	4916
	15-20	0.001	0.05	0.57	0.67	0.07	-	7062
	20-25	-	-	0.01	0.30	0.74	-	1527
	25-30	-	-	-	0.003	0.19	-	74
	N	490	3589	7311	3964	336	-	15690

c)									
2009	RH 75 (m)	1999							
		<5	5-10	10-15	15-20	20-25	25-30	>30	N
	<5	0.22	-	-	-	-	-	-	4
	5-10	0.61	0.37	0.01	-	-	-	-	279
	10-15	0.17	0.59	0.52	0.01	-	-	-	2308
	15-20	-	0.04	0.46	0.61	0.03	-	-	6216
	20-25	-	-	0.01	0.38	0.81	0.09	-	5850
	25-30	-	-	-	-	0.16	0.79	0.33	972
	>30	-	-	-	-	-	0.13	0.67	61
N	18	597	3542	7338	3749	440	6	15690	

Figure 4.5. Transition probability matrices for RH25 (a), HOME (b), and RH75 (c). Each cell provides the probability that a discrete class  $j$  will change to another class  $i$  in a specific time-step  $t$ . The diagonal cells (yellow) show the retention frequency or proportion of classes that remained the same.

For almost all the VR classes, the probability of transitioning to a greater VR class was greater than remaining in the same class or moving to a lower class (Figure 4.6). This indicates that foliage is becoming more dispersed in the vertical column in areas where it was previously clumped lower in the canopy. However, the areas that have

foliage clumping closer to the top of the canopy were more likely to remain so (Figure 4.6). The trend of foliage moving upwards in the canopy is further supported by the high probability of understory cover decrease in the majority of understory cover classes (Figure 4.6). Only areas with very low understory (0 to 2% cover) were more likely to gain foliage or remain the same. Finally, there was an increase in canopy cover across almost all classes. Areas with 80% or more canopy cover were more likely to remain the same or lose canopy cover (Figure 4.6).



a)

2009	VR	1999								
		0-0.1	0.1-0.2	0.2-0.3	0.3-0.4	0.4-0.5	0.5-0.6	0.6-0.7	>0.7	N
	0-0.1	0.24	0.01	-	-	-	-	-	-	16
	0.1-0.2	0.21	0.07	0.02	0.01	-	-	-	-	43
	0.2-0.3	0.24	0.22	0.11	0.04	0.01	-	-	-	184
	0.3-0.4	0.24	0.34	0.34	0.21	0.06	0.01	-	-	808
	0.4-0.5	0.06	0.29	0.4	0.42	0.29	0.05	0.01	-	2420
	0.5-0.6	0.03	0.06	0.12	0.29	0.51	0.41	0.14	0.5	5836
	0.6-0.7	-	0.01	0.01	0.03	0.14	0.51	0.75	0.25	6008
	>0.7	-	-	-	-	-	0.02	0.1	0.25	375
	N	34	143	490	1510	3970	7286	2253	4	15690

b)

2009	% Canopy Cover	1999										
		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	>90	N
	0-0.1	-	-	-	-	-	-	-	-	-	-	-
	0.1-0.2	-	-	-	-	-	-	-	-	-	-	-
	0.2-0.3	-	0.33	0.09	-	-	-	-	-	-	-	-
	0.3-0.4	1	-	0.09	-	0.01	-	-	-	-	-	-
	0.4-0.5	-	-	-	0.06	0.02	-	-	-	-	-	-
	0.5-0.6	-	-	0.36	0.09	0.09	0.03	0.01	-	-	-	56
	0.6-0.7	-	0.33	0.09	0.28	0.14	0.11	0.03	0.02	-	-	172
	0.7-0.8	-	-	0.18	0.38	0.3	0.31	0.19	0.09	0.02	0.01	766
	0.8-0.9	-	0.33	0.09	0.16	0.36	0.44	0.59	0.54	0.28	0.1	4544
	>0.9	-	-	0.09	0.03	0.08	0.11	0.18	0.35	0.69	0.89	10131
	N	1	3	11	32	132	352	926	2576	6948	4709	15690

c)

2009	% Understory Cover	1999										
		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	>90	N
	0-0.1	0.11	0.01	-	-	-	-	-	-	-	-	87
	0.1-0.2	0.7	0.7	0.48	0.22	0.09	0.04	0.02	-	-	-	6935
	0.2-0.3	0.19	0.26	0.44	0.51	0.32	0.19	0.1	0.03	-	-	6025
	0.3-0.4	-	0.02	0.07	0.22	0.4	0.31	0.15	0.08	-	-	1826
	0.4-0.5	-	-	0.01	0.04	0.16	0.32	0.37	0.42	0.21	-	604
	0.5-0.6	-	-	-	-	0.02	0.12	0.24	0.32	0.42	-	154
	0.6-0.7	-	-	-	-	-	0.02	0.09	0.11	0.26	0.14	37
	0.7-0.8	-	-	-	-	-	0.01	0.03	0.05	0.05	0.29	15
	0.8-0.9	-	-	-	-	-	-	-	-	0.05	0.43	6
	>0.9	-	-	-	-	-	-	-	-	-	0.14	1
	N	109	4227	6486	3058	1175	440	131	38	19	7	15690

Figure 4.6. Transition probability matrices for VR (a), canopy cover (b), and understory cover (c). Each cell provides the probability that a discrete class  $j$  will change to another class  $i$  in a specific time-step  $t$ . The diagonal cells (yellow) show the retention frequency or proportion of classes that remained the same.

### 4.3.3 Steady-state analyses and disturbance

The change in the distribution of canopy heights from 1999 to 2009 showed that canopy height in HBEF has yet to reach steady-state (Figure 4.3). Based on the Markov model projections, canopy height could hypothetically reach steady-state in 100 to 150 years under the current disturbance and growth regime. At this point, the majority of the forest would be in the 25 to 40 m height range (Figure 4.7).

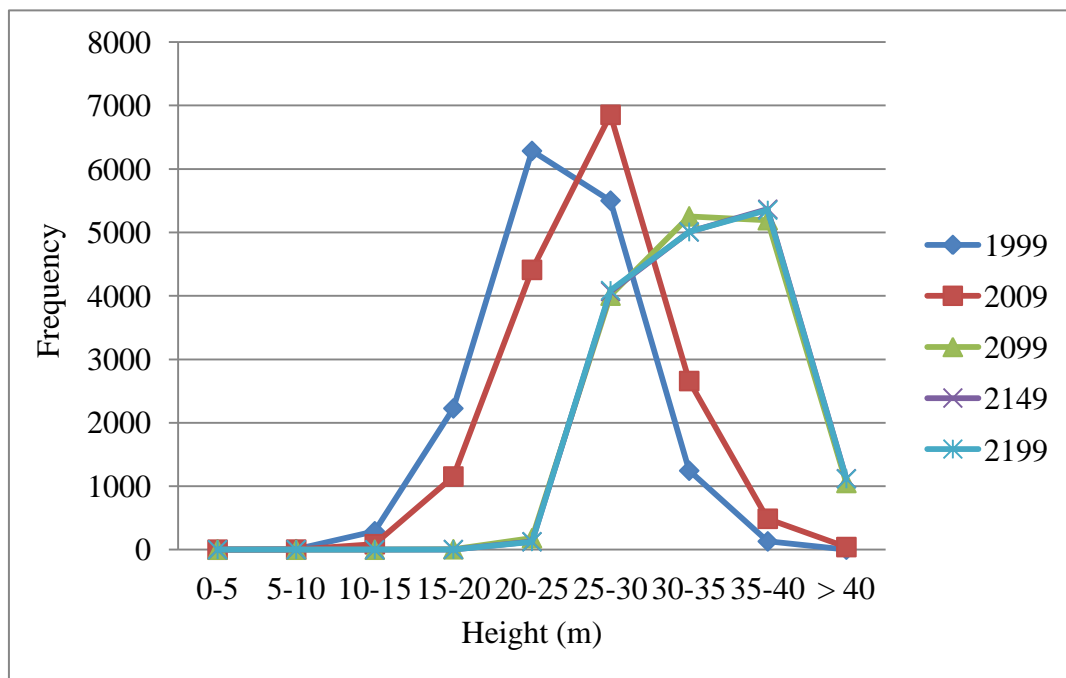


Figure 4.7. Projected canopy height distributions using the transition probability matrix over 200 years using 10 year intervals from 1999 to 2199. Steady-state distribution is hypothetically predicted to occur between 2099 to 2149.

Observing average canopy height changes across the watershed could obscure local impacts of past disturbances. This makes it difficult to determine if the reason canopy height in HBEF has not reached steady-state is due to continuing recovery from

widespread 19<sup>th</sup> century logging or to more recent natural disturbances. In particular, the 1998 ice storm resulted in non-contiguous areas of severe tree damage, mainly in 60 to 120 year old forests at high elevations within HBEF (Rhoades et al. 2002). Rhoads et al. (2002) determined that in Watershed 6, canopies below 624 m in elevation were not damaged by the 1998 ice storm (Figure 4.8). Areas above 624 m in elevation, however, were severely damaged. A two-sample t-test between canopy height change between LVIS footprint pairs at these two elevation levels ( $n = 30$  and  $n = 17$ , respectively) showed that the average change in canopy height was significantly greater above 624 m (mean change = 3.26 m) than below that elevation (mean change = 1.61 m) ( $p = 0.007$ ) (Table 4.3).

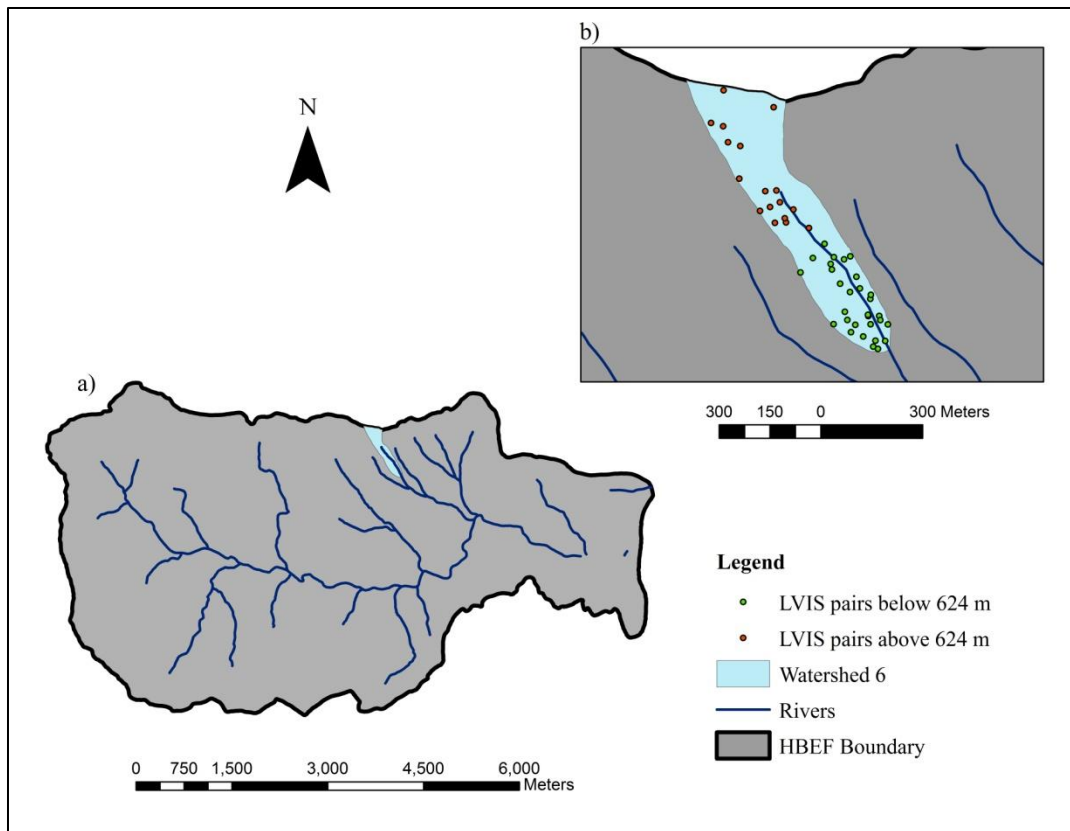


Figure 4.8. (a) Map of HBEF watershed showing Watershed 6 in light blue. (b) Inset map of Watershed 6 showing LVIS footprint pairs in the areas left damaged (orange) and undamaged (green) by the 1998 ice storm.

Elevation (m)	N	Average	p-value
< 624	30	1.61	0.007
> 624	17	3.26	

Table 4.3. T-test results from the 199-2009 canopy height change between damaged (> 624 m) and undamaged (< 624 m) areas of Watershed 6.

Rhoades et al. (2002) noted that, particularly in older sections of forest, the areas most damaged from the 1998 ice storm were located above 600 m in elevation. Based on previous results, noting the increase in canopy height growth between damaged and undamaged areas in Watershed 6, we hypothesized that if the damage from the 1998 ice storm was extensive across HBEF, there should be an observable difference between

1999-2009 canopy height change between damaged and undamaged areas. Based on the observed ice storm damage by Rhoades et al. (2002) the elevation of 600 m was used to divide HBEF into high (> 600 m) and low (< 600 m) elevation bands. T-test showed a significant difference in average canopy height change between the high and low elevation bands (p-value =  $2.49 \times 10^{-7}$ ). The average increase in canopy height was slightly higher in elevations greater than 600 m than in areas at elevations lower than 600 m (Table 4.4).

Elevation (m)	N	Average Change	p-value
< 600	10135	2.18 m	$2.49 \times 10^{-7}$
> 600	5555	2.34 m	

Table 4.4. T-test results between high (> 600 m) and low (< 600 m) elevation bands. The average canopy height change above 600 m was significantly higher than below 600 m.

Finally, to test whether the original results of the steady-state projection that showed HBEF canopy height had not reached steady-state were due to disturbance from the 1998 ice storm, canopy height was examined via a Markov model for elevation less than 600 m (which was relatively undamaged from the 1998 ice storm). There was a high probability of average canopy height increasing, or moving to a higher class (particularly of average canopy heights < 25 m). This was similar to the transition probabilities for HBEF as a whole. The shift in canopy height distributions from 1999 to 2009 shows that canopy height in the undamaged areas of HBEF has yet to reach steady-state (Table 4.4). It would potentially take 100-200 years for the canopy height of this portion of HBEF to reach steady-state (Figure 4.9).

		1999									
		Height class (m)	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	> 40
2009	0-5	-	-	-	-	-	-	-	-	-	-
	5-10	0.5	-	-	-	-	-	-	-	-	1
	10-15	0.5	0.71	0.09	-	-	-	-	-	-	8
	15-20	-	0.14	0.59	0.19	-	-	-	-	-	65
	20-25	-	0.14	0.32	0.67	0.4	0.01	-	-	-	1740
	25-30	-	-	-	0.13	0.5	0.67	0.03	-	1	5308
	30-35	-	-	-	0.01	0.03	0.31	0.70	0.05	-	2492
	35-40	-	-	-	-	-	0.01	0.26	0.75	-	480
	> 40	-	-	-	-	-	-	0.01	0.20	-	41
	N	2	7	22	264	3564	4932	1212	131	1	10135

Table 4.4. Transition probability matrices for canopy height. Each cell provides the probability that a discrete class  $j$  will change to another class  $i$  in a specific time-step  $t$ . The diagonal cells (yellow) show the retention frequency or proportion of classes that remained the same. This shows the probability of transitioning from one class to another from 1999 to 2009.

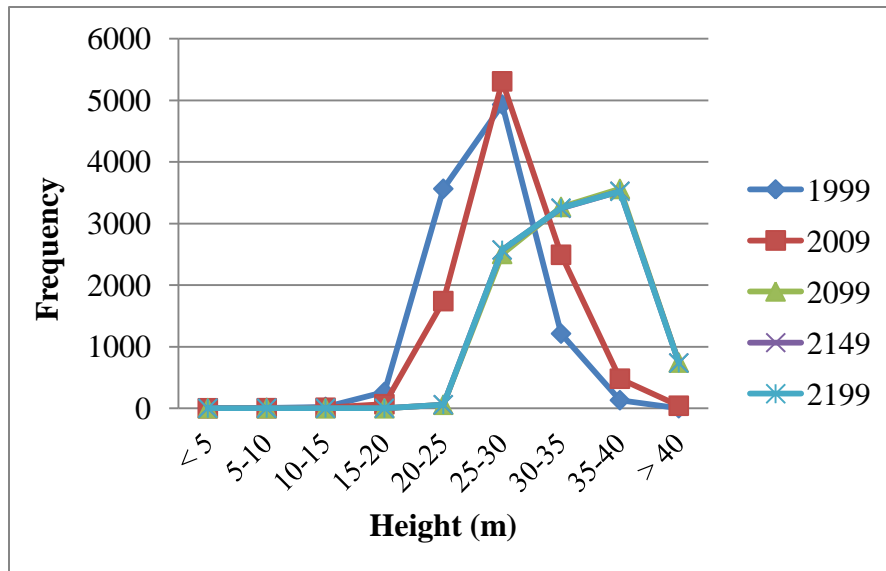


Figure 4.9. Projected canopy height distributions for low elevations of HBEF (< 600 m) using the transition probability matrix over 200 years using 10 year intervals from 1999 to 2199. Steady-state distribution is hypothetically predicted to occur between 2099 to 2199.

#### 4.4 Discussion

Schwarz et al. (2001) noted that HBEF exhibited many characteristics of old-growth northern hardwood forests, despite the existence of numerous stands at different stages of development. Although our study focuses on vertical structure and not biomass or species composition specifically, the results show that significant structural change occurred within HBEF over the 1999 to 2009 time period. We have shown that structural changes within HBEF vary across the watershed and that current structural signs of forest recovery may be more related to recent natural disturbances than historic anthropogenic change.

##### 4.4.1 Canopy height change

Not only did the mean canopy height increase from 1999 to 2009, but the proportions within each canopy height class changed greatly. The increase in canopy

height denotes that HBEF as a whole has yet to reach maximum height, a symptom of the stand maturation stage (Franklin et al. 2002; Nadkarni et al. 2004). This was unexpected, as previous reports have shown that biomass is no longer aggrading within HBEF (Siccama et al. 2007; van Doorn et al. 2011). One reason for this could be large tree mortality prior to 1999 causing the observed canopy height change to be based on saplings that were previously (prior to LVIS data collection) in the subcanopy. If the sapling recruitment was low (as noted in van Doorn et al. 2011), growing saplings would cause the canopy height to increase while not offsetting the loss of biomass due to mortality of large trees. However, more research is needed to fully understand the differences in canopy height change and observed biomass accumulation across HBEF and the impact of recent disturbances on current biomass accumulation.

Spatial analyses at hectare resolution further confirm the net increase in canopy height across the HBEF watershed. In the majority of the watershed, canopy height increased by 5 m or less. Across the watershed, areas with a lesser increase in canopy height were clustered at lower elevations, near rivers—possibly indicative of forests closer to maturity there. Areas of extremely rapid canopy height growth were few and not apparently related to a specific environmental variable (such as elevation) or known disturbance incident.

#### 4.4.2 Changes in lidar metrics related to seral stage and species diversity

The significant changes in the other components of vertical structure (HOME, RH25, RH75, VR, canopy cover, understory cover, and canopy layer structure categories) denote change in the vertical distribution of material *within* the canopy across HBEF. In particular, the increase in canopy cover and the decrease in understory cover are



characteristics of younger, maturing forests. The significant increase in canopy cover and the probability of increasing cover in almost all canopy cover classes from 1999 to 2009 show that HBEF has yet to achieve maximum canopy closure. As forests mature following a disturbance event and after stand initiation, canopy cover increases with stand growth until reaching maximum potential canopy closure. This continues until the forest reaches the old-growth stage where individual tree mortality opens gaps within the canopy (Franklin et al. 2002; McElhinny et al. 2005). However, canopy closure can take decades and in sites with little productivity may never be achieved (Franklin et al. 2002).

This increase in canopy cover results in a decrease in light availability within the vertical column, impacting structure within the canopy. Ultimately this changes the vertical distribution of foliage, reducing the amount of foliage near the ground, as noted by previous studies comparing young, mature, and old-growth stands (Franklin et al. 2002; Keller et al. 2003; Nadkarni et al. 2004). The percentage of cover in the understory (0 - 5 m) decreased for the majority of cover classes from 1999 to 2009. This characteristic decrease in near-ground vegetation has been noted as a result of canopy closure in maturing forests (Franklin et al. 2002; Keller et al. 2003).

VR is a measure of the vertical distribution of canopy material. This shift in the vertical distribution of vegetation, as seen by the decrease in understory cover, is further supported by the significant increase in VR. The vegetation ratio increases as foliage density spreads upward in the vertical column and less of the waveform energy is able to reach the lower parts of the canopy (Whitehurst et al. n.d.). It also indicates that, while canopy cover was increasing across HBEF, the foliage was not filling in evenly throughout the vertical column. If only the VR classes that are greater than 0.5 are

considered (0.6 - 0.7 and > 0.7), the amount of footprints that have a higher foliage density at the top of the canopy increased from 14% in 1999 to 40% in 2009, showing that the vertical distribution is shifting towards a higher foliage density in the upper parts of the canopy. Thus, the upper parts of the canopy were increasing in density while the understory was becoming more open, as also seen by the significant decrease in understory cover and increase in RH25 height.

Along with canopy height and HOME, VR has been related to avian species diversity and habitat preference (Swatantran et al. 2012; Whitehurst et al. n.d.). Changes in these metrics could be indicative of changes in habitat availability and avian biodiversity. The increase in both canopy height and HOME over the past decade is potentially decreasing species habitat within the forest due to the negative relationship between canopy height and HOME and avian species diversity in HBEF (Whitehurst et al. n.d.). Future research is needed to fully understand the dynamics between structural change and flux in biodiversity and habitat availability.

#### 4.4.3 Steady-state analyses and disturbance

Although steady-state models have been criticized for their lack of realism and complexity, they are a useful standard against which to assess observed changes, especially when the data required for more complex models are lacking. To do so, it should be noted that the time to reach steady-state canopy height distribution, as well as the distribution itself, are projections based on the growth and disturbance regime during the 1999 to 2009 time period, as well as the lingering effects of prior disturbances. The matrix models assume that the state of the system at each progressive time step ( $t+1$ ) is only influenced by the previous state ( $t$ ) (Hall et al. 1991; Perry & Millington 2008).

Thus, the result is a hypothetical estimate of equilibrium, which the ecosystem may or may not be able to reach under future environmental conditions or disturbances (Hall et al. 1991; Biondini & Kandus 2006). One cannot assume that the disturbance rate will remain constant over hundreds of years. Additionally, 20<sup>th</sup>-century disturbances, such as the 1938 hurricane and 1998 ice storm, may not result in complete tree-fall, but rather cause damage to tree tops, thereby reducing canopy height within, as opposed to among, individuals. The Markov model based on the lidar data does not take forest age into account when predicting canopy height distribution. Thus the results can be misleading when disturbances do not kill trees, but make them shorter, as the observed growth rate of a small tree is averaged along with the growth rate of an older tree that is the same height due to disturbance.

Future studies should include subsequent lidar acquisitions to include higher-order dynamics such as acceleration or deceleration of growth as time-serial observations (as opposed to the space-for-time substitution by necessity employed here). Further, lack of individual-tree discrimination in 20- to 30-m resolution data, which resulted in a failure to discern cohort establishment versus recovery of damaged individuals, could be ameliorated by repeat lidar measurement at finer horizontal resolution.

Despite their simplicity, 1<sup>st</sup>-order Markov models have been shown to successfully forecast vegetation change over large time scales and can project approximate effects of current management strategies or environmental conditions (Hall et al. 1991; Perry & Milligan 2008). As major disturbances would most likely impede canopy height reaching steady-state in HBEF, our 100-125 year estimate should be considered a naive estimate in the long term. Overall, we have shown that currently the

distribution of canopy height in Hubbard Brook Experimental Forest does not appear to be in steady-state, based on the shift in canopy height distributions between 1999 and 2009, and the vertical canopy structure across the HBEF watershed will continue to change in the near future.

These observed changes in canopy height and the inferred time until steady-state distribution indicate the HBEF is still recovering structurally to past disturbances. To explore whether or not these changes were due to recovery from previous logging or more recent disturbance events, Watershed 6 was examined more closely. Rhoads et al. (2002) noted that areas above 624 m sustained severe damage from the 1998 ice storm while areas below 624 m escaped storm damage, and that species composition was similar between the damaged and undamaged locations. In addition, we observed that canopy height change was significantly greater in the previously damaged area than in the undamaged area.

Repeated disturbance results in younger trees and more open canopies, which allows for more rapid canopy growth (Nadkarni et al. 2004; Huang et al. 2009). Had the recent ice storm damage not affected growth rates, less growth would have been observed in the higher elevations than in the lower elevations. However, in the 2 years after the 1998 ice storm, regrowth—particularly lateral regrowth—was beginning to occur within the damaged sites, and the intensity of the regrowth was related to the severity of the storm damage (Rhoads et al. 2002). The increase in canopy height growth in the damaged areas suggests that much of this growth was due to recovery from recent disturbance rather than from 19<sup>th</sup> and early 20<sup>th</sup> century logging.

Our observations corroborate and extend these findings across the entire experimental forest. Canopy height increases were greater above 600 m than those below 600 m throughout HBEF. Although the exact spatial extent of the 1998 ice storm damage has not been mapped, this significant increase in growth at high elevations indicates that the ice storm damage was spatially extensive at high elevations across the entire HBEF watershed.

This is in contrast to previous studies which have noted a negative relationship between vegetation growth and elevation (Whitaker et al. 1974; Austin 1980; Kaufmann et al. 1986; Ryan & Yoder 1997; Tardif et al. 2003; Schliz 2006; Thomas et al. 2008). To further examine the impacts of recent disturbance on canopy height growth in HBEF, the high elevation band (> 600 m) was divided into mid and high elevations. The mid and high elevation bands were divided along 750 m, as this is where HBEF transitions from hardwood to coniferous forest (Bormann et al. 1970; van Doorn et al. 2011). Average canopy height growth (2.42 m) at mid elevations was the highest for all three elevation bands (Table 4.5). ANOVA shows a significant difference in 1999-2009 canopy height change between all three elevation bands (low: < 600 m, mid: > 600 m to < 750 m, and high: > 750 m). Tukey-Kramer post-hoc test showed that there was a significant difference in average canopy growth between the low and mid elevations as well as the mid and high elevations at the 95% confidence level, although the difference in average canopy height change was slight (Table 4.6). However, there was not a significant difference in average canopy height growth between low and high elevations.

<b>Elevation band</b>	<b>N</b>	<b>Average (m)</b>
Low < 600	10135	2.18
Mid 600-750	3948	2.42
High <750	1607	2.15

Table 4.5. Table 4.5. Average canopy height change from 1999-2009 for low, mid, and high elevation bands.

<b>Elevation band comparisons</b>	<b>Average Difference</b>	<b>Lower CI (m)</b>	<b>Upper CI (m)</b>
Low to Mid	0.24 m	0.15	0.33
Mid to High	0.26 m	0.13	0.4
Low to High	0.02 m	-0.1	0.15

Table 4.6. Tukey-Kramer post-hoc test results for low, mid, and high elevation bands, including the average difference in 1999-2009 canopy height change between elevation bands and upper and lower confidence interval boundaries.

Similar to our earlier results, canopy height growth was significantly higher at mid elevations than low elevations, which is attributed to disturbance from the 1998 ice storm. However, average canopy height increased significantly more at mid elevations than at high elevations. This could be due to change in forest type, as both areas were within the estimated zone of severe ice storm damage. Additionally, environmental variables are more favorable for vegetation growth at lower (in this case, mid) elevations. This also explains the lack of significant difference between average canopy growth at low and high elevations. Although the low elevation canopy is experiencing faster growth rates due to favorable environmental conditions, the climatic and edaphic factors noted to decrease tree growth at high elevations are offset by the increased growth rates due to recent disturbance in those areas (Austin 1980; Kaufmann & Ryan 1986; Ryan & Yoder 1997; Tardif et al. 2003; Schliz 2006; Thomas et al. 2008).

However, we cannot completely rule out continuing recovery from historic logging as a possible source of structural change. Previous studies have shown that although some shifting in canopy height distribution occurs in old-growth areas, the changes are small in magnitude (Kellner et al. 2009). A paired t-test showed significant change occurring in the undamaged area of Watershed 6, with 2009 having the greater canopy height ( $p = 0.0002$ ). This indicates significant canopy height growth occurred in spite of the lack of recent disturbance, which could be due to the fact that it was still recovering from the logging in the 19<sup>th</sup> and 20<sup>th</sup> century. Also, the change in canopy height distributions below 600 m in elevation between 1999 and 2009 indicate that had HBEF not been disturbed by the 1998 ice storm, canopy height would have yet to reach equilibrium in 2009. Markov model projections indicate that it would be between 100 and 200 years before the canopy height of areas not impacted by the ice storm would reach steady-state. This indicates that at least part of the observed changes in canopy structure may be due to historic logging. However, our estimation of the spatial extent 1998 ice storm damage is coarse, and HBEF has undergone other disturbances since the logging in the late 19<sup>th</sup> century. To fully be able to determine whether the structural change observed between 1999 and 2009 was due to historic logging or more recent disturbances, more information is needed on the intensity and spatial distribution of the 1998 ice storm damage and that of the 1938 hurricane.

#### 4.4.4 Change detection using full-waveform lidar

There are two main sources of error associated with lidar-based change detection: ground-finding errors and geolocation errors. The former can occur in areas of varied elevation and steep slopes, as has been the case in HBEF (Dubayah et al. 2010,

Swatantran et al. 2012). To mitigate for this, discrete return lidar was used for the elevation for both the 1999 and 2009 LVIS shots, assuming that no major changes in elevation had occurred during the 10 year time period, and processing of the LVIS height and canopy metrics were adjusted accordingly using the discrete return digital elevation model (Swatantran et al. 2012).

Geolocation errors in either dataset over time can lead to poor co-location between waveform pairs, leading erroneous detection of change. However, random geolocation errors are mitigated by large sample sizes. As demonstrated in Dubayah et al. (2010), the errors in canopy-height change detection are relatively small when averaged over a large dataset. A previous study by Tang & Dubayah (2010) using small-footprint lidar simulated error in 2009 HBEF LVIS canopy height measurements due to geolocation error. Their results indicated that an average error of 1.79 m in canopy height would be expected with a 10 m geolocation error. Assuming that the actual co-location error is 10 m or less between the 1999 and 2009 datasets (including the geolocation error for each dataset and the  $< 3$  m distance between waveform centroids), the average canopy height difference (2.23 m) is less than the average error in canopy height measurement at the 95% confidence interval. Additionally, there is little local variation in terms of canopy structure within HBEF. Variograms of both 1999 and 2009 canopy heights show a range around 285 m and 312 m, respectively. Although there may be some error in the change detected in individual footprint pairs, it should not significantly impact the canopy structure comparisons inferred from such large samples such as used here.

The difference in footprint size between 1999 and 2009 (nominal 25 m and 20 m, respectively) could also be a potential source of error in our change analyses, as



information is being received and compared across different sized areas in each year. However, due to the Gaussian nature of the LVIS pulse, less information is received from the edges of the footprint (Hyde et al. 2005; O'Dell 2006) and the less than 3 m separation between the centroids of footprint pairs means that the majority of the footprints overlap, despite the slight difference in size. The error in vertical structure change due to the variation in footprint size between 1999 and 2009 would be unbiased, which is partially mitigated with large sample size of footprint pairs across HBEF.

#### 4.5 Conclusion

Lidar remote sensing allowed us to examine aspects of vertical forest structure at a scale (both sample size and spatial distribution) that was previously impossible, providing a new aspect of how the Hubbard Brook Experimental Forest ecosystem was changing over time. Changes in the lidar-derived vertical structure metrics showed that vertical structure (specifically aspects related to species diversity and habitat) is changing throughout the HBEF watershed. Watershed-mean canopy height and cover increased from 1999 to 2009, with few locations losing height. The vertical distribution of foliage shifted away from the forest floor, indicating a loss of understory density, toward layers higher in the canopy as well. The canopy height of Hubbard Brook Experimental Forest is not at steady-state. An ice storm in 1998 appears to have heavily damaged areas above 600 m elevation, which exhibited the greatest subsequent increases in canopy height. However, in order to validate these conclusions, improved data on the extent of recent disturbances are necessary. Further, comparisons of vertical structure with subsequent lidar acquisitions are necessary to increase understanding of vertical structure change at longer time scales (e.g. 10, 20, 50 years). Relating change in vertical structure to changes

in biodiversity is an important next step toward improved understanding of how biodiversity and habitat availability are impacted by disturbance and forest succession.

## Chapter 5: Discussion and Conclusion

### 5.1 Conclusion

This dissertation examined the relationships between vertical structure and forest ecosystem dynamics. Using full-waveform lidar, I was able to characterize the structure within the canopy and examine how it is related to biodiversity and forest succession in Hubbard Brook Experimental Forest, NH. In doing so, my goal was to not only examine vertical structure using metrics derived from full-waveform lidar, but also focus on vertical structure metrics that were applicable for future research and forest management.

Chapter 2 focused on the concept of canopy layering, an idea long used in forest ecology. Due to the limitations of previous studies (limited field data, multiple definitions of canopy layering, and few methods of quantifying canopy layering), my first step was to develop a lidar metric that would not only characterize the structure from the top of the canopy to the ground, but would also allow vertical structure to be viewed at the landscape scale. Using LVIS waveform data, specifically transformed canopy cover and the foliage area profile, I was able to create two separate metrics: canopy layer structure categories and number of foliage profile layers. The canopy layer structure categories are determined based on the comparison of canopy cover between the under, mid, and overstory. The number of foliage profile layers is derived from the lidar-derived foliage profile. The number of major peaks (areas of clumping in the vertical column) detected in the foliage profile, denotes the number of layers.

Although both data sets provide different information about vertical canopy structure, they allow the user to see how the vertical structure varies across the landscape. There was a definite relationship with both layering datasets and elevation and canopy

height. Areas with taller trees and lower elevations tended to have more foliage profile layers. These same areas also were generally classified as canopy layer structure categories with a dominant overstory. I also explored how horizontal scale influenced the amount of variability seen in canopy structure. Using the foliage profile, I examined the average foliage area density of the entire HBEF, as well as at low, mid, and high elevations. Aggregating the waveform metrics over the entire forest resulted in a loss of detail as to how the foliage was actually distributed within the canopy. Thus, metrics that can characterize the distribution of foliage within the canopy on a smaller scale (in my case a 30 m resolution) can provide more insight as to the variation of canopy structure throughout the watershed.

For Chapter 3, I explored the relationship between bird species diversity (BSD) and vertical canopy structure, especially the vertical distribution of foliage. Numerous metrics can be derived from full-waveform lidar data. However, I wanted to both examine which metrics had the strongest relationship with bird species diversity and also explore which metrics provided information that was applicable for forest conservation and management.

In my analyses, I included various derivations of MacArthur and MacArthur's (1961) foliage height diversity (FHD), vegetation ratio (VR), canopy layer structure categories, and the number of foliage profile layers. My results supported previous findings that the relationship between FHD and bird species diversity was not necessarily a positive linear relationship as recorded in MacArthur and MacArthur (1961) (Willson 1974; Erdelen 1984). Due to the variability in potential FHD calculations as well as in how it can describe an area, I decided that although some derivations of FHD had a

stronger relationship with bird species diversity than other lidar metrics, it was not the most usable metric for future biodiversity and management studies. VR and the number of foliage profile layers both had a strong relationship with bird species diversity and were still significant (although the amount of explained BSD variability was much reduced) after canopy height was accounted for, unlike most of the FHD metrics. One could argue that for understanding BSD in HBEF, canopy height is the only metric needed, since it is highly correlated with the foliage distribution metrics and explained a comparable amount of variation in BSD. However, I also tested the height of median return from the LVIS waveform (HOME). HOME explained slightly more of the variation in BSD than canopy height. This along with the significance of VR and number of foliage profile layers after height was accounted for, show that we still have more to learn about the relationship of vertical structure and avian species diversity.

Chapter 4 focused on how vertical structure changes with time and relates to forest succession. Using LVIS data from 1999 and 2009, I examined whether or not the vertical structure of HBEF changed significantly over the 10 year time period. I selected the metrics of canopy height, HOME, VR, canopy layer structure categories, canopy cover, and understory cover. Many of these metrics characterize vertical structure in ways that have previously been linked to different stages of forest succession or are linked to species diversity and habitat. The ability to monitor change in vertical structure is essential for forest management and improving the understanding of the process of forest succession.

I found a slight but significant difference in canopy height change from 1999 to 2009 between damaged and undamaged areas from the 1998 ice storm. Areas

experiencing recent disturbances (the ice storm) had a greater increase in canopy height than the undamaged areas despite being at higher elevations. However, based on Markov model projections, the lower elevations in HBEF have yet to reach steady-state. This indicates that the structural dynamics of HBEF may be due to both the effects of recent disturbances and recovery from historic logging.

Lidar remote sensing provides information on the vertical components of the forest ecosystem at scales that were previously impossible. However, the only way this information can truly further the understanding of forest ecosystem dynamics is if it is interpretable over larger knowledge bases. Developing and interpreting metrics and their relationships between aspects of forest ecosystem dynamics was one of the main veins of my thesis. Using previously described definitions of canopy layering or the vertical distribution of foliage, I was able to develop the metrics of canopy layer structure categories and foliage profile layering. Aside from characterizing the vertical distribution of foliage, these metrics had to be fairly easy to interpret. The end user needed to be able to look at a map and see simultaneously how the vertical structure (in this case how the structure varied in the vertical column) varied across the landscape. Similarly, in Chapter 3, I examined species biodiversity using ecological based metrics so that my findings could be applicable to conservation and forest management. Continuing in Chapter 4, I focused not only in using lidar to detect changes in the vertical structure of HBEF, but I also related those changes to the documented ecological characteristics related to forest succession, showing that information from lidar provides more than just change but also can provide insight to forest succession and previous disturbance. Thus, the culmination of the research in my previous chapters not only furthers our knowledge about the role of

vertical structure in northern hardwood forests, but also sets the stage for future research on forest ecosystem dynamics and works to bridge the gap between metrics derived via lidar remote sensing ecological concepts, and the forest management and conservation research community.

### 5.2 Limitations

One limitation common in all my research chapters was the issue of LVIS ground-finding errors in areas with steep slopes (Dubayah et al. 2010; Swatantran et al. 2012). In most cases, the error in LVIS elevation is small; however it can range from being correct to a few meters above or below the actual elevation. While this was corrected by using elevations from discrete return lidar (DRL), this was a correction applied to all waveforms. The small footprint elevation is averaged over the entire area of the LVIS footprint, and although it is generally more accurate than LVIS elevations in high slope areas, it is not foolproof. This shift in elevation, also shifts the height along the waveform that is used for the waveform-derived metrics. In areas where the LVIS elevation is correct or close to the actual elevation, shifting the elevation or stopping point along the waveform for calculating the foliage profile or canopy cover, can impact the results. Elements of the waveform ground-return may be used in the waveform-derived metrics. It is also possible that by adjusting the elevation, sections of the waveform could be missed in the analyses. Ideally, the error in ground elevation could be corrected on a waveform by waveform basis. However, until then, comparisons of waveform-derived metrics using LVIS elevation versus DRL elevations showed that although some change occurred between the metric values, when averaged over the entire study area, there was not a significant difference in the results.

Another area of limitation is field validation for vertical structure metrics. My canopy layering metrics (canopy layer structure categories and number of foliage profile layers) are unable to be validated via field data, due to the limited quantity of field techniques for quantifying canopy layering and variation in the actual definition used for canopy layering between the lidar-derived metrics and previously used field methods. However, both these metrics were created using the lidar-derived canopy cover and foliage area profiles, which have been validated previously in the field (Weltz et al. 1994; Means et al. 1999; Hyde et al. 2005; Coops et al. 2007; Jupp et al. 2008; Sexton et al. 2009).

Finally, there is the issue of geolocation and co-location errors between footprints. This is not a major problem for Chapters 2 and 3, as the lidar waveforms are average over fairly large areas. With the lidar metrics being averaged between multiple shots within each gridcell or bird plot, the effects of a few waveforms being misplaced (either included in the wrong grid cell or excluded from a bird plot, etc.) are minimal. Geolocation errors become more of a problem in Chapter 4, where I compare vertical structure metrics between footprint pairs. Ideally, coincident footprint pairs would be used. However, in order to get a representative sample in both number of shots and distribution across HBEF, footprints in 1999 and 2009 that were less than 3 m apart were used as footprint pairs. Geolocation errors in either year of LVIS data could result in footprint pairs that were more than 3 m apart. However, with nominal 20 and 25 m footprints, a distance of up to 10 m between the footprint centers results in the majority of overlap between the 1999 and 2009 footprints. Thus, the data between the two years is still taken from roughly the same area. The < 3 m separation between pairs was also



chosen because the large number of pairs used (15690 pairs) would mitigate for random geolocation errors. Also, there is little local variation in vertical structure within HBEF, minor alterations in footprint locations would not drastically impact the results of the analyses.

### 5.3 Future Research

One of the next steps for this research is to examine the variation of vertical structure using the foliage distribution metrics in other study areas, including both montane forests similar to HBEF and different forest types such as tropical rain forests or southeastern pine forests. Examining the canopy layering other northeastern forests will help determine whether or not the trends observed between the lidar derived metrics and environmental gradients are actual components of northeastern forest dynamics or an artifact of the HBEF study area. Also applying these metrics to other forest types will improve our understanding of the relationship between vertical structure and forest ecosystem dynamics at a global scale.

The relationship between vertical structure and bird species diversity should also be tested with other avian datasets. Previous research has showed that the relationship between bird species diversity and vertical structure can vary between forests. This is possibly due to other factors such as the variation of avian species in the area, forest age or forest type. Also, while trends in vertical structure (such as lower vegetation ratio or the clumping of foliage closer to the bottom of the vertical column and shorter canopy heights) may be beneficial for overall avian diversity, they may not be beneficial for a specific species. Examining how vertical structure, specifically metrics relating to the distribution of foliage, relates to the habitat preference of specific species would aid

researchers in understanding where species of interest may exist and aid forest managers in determining protocols for preserving and rehabilitating areas specifically for endangered or threatened species. Also, the relationship between vertical structure and biodiversity is not limited to avian species. Exploring the relationship between canopy structure and other forest dwelling species could improve our understanding of species habitat preference and possibly aspects of their behavior.

In Chapter 4, the prediction of steady-state for canopy height was limited by the ten year time period between lidar datasets. While we can get an idea of whether or not canopy height has reached steady-state and gain understanding as to how long it could take to reach that state, the exact time estimate for reaching steady-state is hypothetical. Data from two time points results in a limited view of the natural processes occurring within the forest. Forest succession takes place over hundreds of years, with events impacting the rate of forest change. However, with data from at least 3 different years, acceleration or deceleration in the rate of change can be observed (Whitehurst et al. 2009). Future LVIS missions that coincide with current data (HBEF, Sierra Nevada, CA, La Selva, Costa Rica, etc.) will potentially provide the data necessary to better understand how the rate of forest change changes over time and at different points of forest succession.

Lidar is being increasingly used for other aspects of research, environmental management and urban planning. Strictly using LVIS data would limit future studies based on the previously flown areas (primarily in North America). However, it is possible to derive foliage distribution metrics from small-footprint lidar. Previous studies have used small footprint lidar to examine forest understory and begin examining the vertical

distribution of foliage (such as with foliage height diversity) (Zimble et al. 2003; Clawges et al. 2008; Falkowski et al. 2009). One of the next steps in this research is to examine whether or not the foliage distribution metrics in this study can be replicated using discrete return lidar, comparing the results between the discrete return metrics and environmental gradients to those of the full-waveform metrics from this thesis. The ability to use standard metrics describing the vertical structure within the canopy across lidar platforms would improve the accessibility of information on vertical structure for researchers and ultimately the forest management community.

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