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Analyzing spatial variation and change in the structure of boreal old-growth forests

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Academic dissertation

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Global environmental change and other anthropogenic changes, such as changes in disturbance regimes alter the structure and dynamics of boreal old-growth forests (boreal forests with negligible human impact, henceforth natural boreal forests). Changes in these forests greatly influence key ecosystem properties such as biodiversity and carbon cycle. Hence, understanding the development of the remaining natural boreal forests is particularly important.

This thesis examines how boreal forest structure varies in space and changes over time. Forest structure was examined in three natural boreal forest landscapes (2 km × 2 km each) in northern Fennoscandia and two landscapes in eastern North America. Canopy cover that was visually interpreted from stereopairs of aerial photographs taken between the years 1959 and 2011 was used as a surrogate measure of forest structure to quantify and examine spatial variation and/or temporal change, and Bayesian inference was used to separate credible ecological phenomena from the noise caused by visual interpretation error.

This thesis presents and applies a novel methodology to study changes in forest structure. We calibrated visual canopy cover interpretations made from time series of aerial photographs with canopy cover reconstructions that were based on field- and tree-ring measurements. We successfully identified credible changes in forest structure in each studied landscape, but also noted that the visual interpretation of canopy cover was prone to systematic and random error that depended on, e.g., aerial photo quality. Due to this error, changes that occurred at the level of an individual tree could not be credibly discerned. Still, the methodology can be used to detect both abrupt and slow continuous changes in forest ecosystems. The methodology was extended to examine spatial variation in forest structure. The results revealed variation in forest structure at multiple spatial scales which showed similarities despite the differences in dominant tree species and disturbance regimes between the studied landscapes. The variability was connected with scale-dependent driving processes that also showed similarities among the landscapes. Last, the methodology was applied to study how varying scale of observation influences how changes in forest structure are perceived over different periods of time. This multi-scale change analysis revealed a synchronous and prevalent cover increase at large spatial scales in the majority of the studied landscapes, and canopy cover decrease and increase in areas that were subjects to disturbances. Changes of variable direction and magnitude were detected at smaller spatial scales in each studied landscape.

The results indicated that historical aerial photographs are a valuable resource in studying how forest ecosystems develop, but the notable errors in their visual interpretation need to be taken into account in analysis of change. The results aligned with the hierarchy theory and the hierarchical patch dynamics concept by showing that the structure of natural boreal forests vary and change at discernible spatial scales, and showed that these scales can be identified and quantified objectively. While gap- and patch-scale changes were important, the most notable changes occurred at large spatial scales, contradicting the conventional view that changes in the structure of natural boreal forests are mostly due to gap dynamics. This suggests that the studied forests are currently responding to large scale drivers that cause trend-like increase in their canopy cover and consequently in biomass.

Keywords: forest dynamics, canopy cover, aerial photography, dendrochronology, Bayesian inference, scale dependency

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LIST OF ORIGINAL ARTICLES

This thesis is based on the following chapters, which are referred to in the text by their Roman numerals. Chapter II is reprinted with the kind permission of Springer. Article III is an author version of a manuscript submitted for peer-review.

I Kulha N., Pasanen L., Aakala T. (2018). How to calibrate historical aerial photographs: A change analysis of naturally dynamic boreal forest landscapes. Forests 9(10), 631. https://doi.org/10.3390/f9100631

II Kulha N., Pasanen L., Holmström L., De Grandpré L., Kuuluvainen T., Aakala T. (2019a). At what scales and why does forest structure vary in naturally dynamic boreal forests? An analysis of forest landscapes on two continents. Ecosystems 22(4): 709–724. https://doi.org/10.1007/s10021-018-0297-2

III Kulha N., Pasanen L., Holmström L., De Grandpré L., Gauthier S., Kuuluvainen T., Aakala T. (2019b). Decadal-scale analysis reveals structural changes at multiple spatial scales in boreal old-growth forests. Submitted manuscript.

AUTHOR CONTRIBUTION

Niko Kulha (NK) is responsible for the summary of this thesis, and contributed to the chapters within the thesis as follows:

NK interpreted the aerial photographs, and conducted the data analyses in **I**–**III** with Leena Pasanen. NK wrote the first manuscript version in **I** and **III**, and with Leena Pasanen and Tuomas Aakala in **II**. NK led the writing of the last manuscript version in **I**–**III**, and the revision process in **I**–**III**.

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INTRODUCTION

Natural boreal forests

Extensive areas of boreal forests are still outside of direct human influence and can be considered to display their natural structure and dynamics (Gauthier et al. 2015; Watson et al. 2018). These natural boreal forests are vital for biodiversity conservation (Andrew et al. 2014), carbon sequestration and storage (Bradshaw and Warkentin 2015), and for water (Steffen et al. 2015) and nutrient cycling (Wickland and Neff 2008). They greatly influence energy fluxes by altering land surface albedo (Steffen et al. 2015) and significantly contribute to the maintenance of indigenous cultures and human health (Watson et al. 2018). Monitoring the state of these forests and understanding their development is needed if we are to preserve these ecosystems and the manifold ecosystem properties they provide (Gauthier et al. 2015).

Many of the key ecosystem properties that natural boreal forests provide are closely linked with structural dynamics and complexity (e.g., variation in tree age structure, variation in tree species composition, variation in the availability of dead wood of different size and in different stage of decay, complexity in canopy structure) in these forests (Angelstam and Kuuluvainen 2004; Hardiman et al. 2013). For example, natural boreal forests are valuable from biodiversity conservation perspective because their high structural variability provides a wide array of habitats which in turn sustain a diverse biota (Bergeron and Fenton 2012). Similarly, the multilayered and structurally complex canopies in natural boreal forests enable more efficient use of available sunlight. Consequently, these forests have high carbon storage capacity (Hardiman et al. 2013). The structural complexity of natural boreal forests is also linked to the high resilience of these forests (Kuuluvainen et al. 2014; Johnstone et al. 2016), meaning that these forests have high capability to recover their essential structure and function after a perturbation (Wu 2013).

Because the value that natural boreal forests provide is linked to their structure and structural dynamics, it is vital to understand how the structure of natural boreal forests varies in space and changes over time. Improving the understanding of natural boreal forest dynamics would further help to improve and diversify forest management practices that aim to increase structural diversity in managed boreal forests by emulating natural forest dynamics. Currently, the dominant forest management practice in the boreal region (i.e. clear-cut) contradicts the variable and complex forest dynamics observed in the naturally dynamic forests of the region (Kuuluvainen 2009; Kuuluvainen et al. 2014), with negative influence for, e.g., biodiversity conservation (Bergeron and Fenton 2012).

Forest structure changes at different temporal scales

The processes that influence forest dynamics in natural boreal forests occur over different periods of time. Consequently, the structure of natural boreal forests changes variably at different temporal scales. For example, while tree growth is generally slow in the boreal region, it changes forest structure gradually over the whole biome (Luo et al. 2019a). Because of the slowness of tree growth, boreal forests typically respond slowly to processes that influence tree growth, such as changes in climate (Luo et al. 2019b; Ols et al. 2019). On the contrary, disturbances may kill trees and change forest structure abruptly (De Grandpré et al. 2000). However, because disturbances initiate succession, they also have a prolonged effect on how forest structure develops (Gauthier et al. 2010). For example, in natural boreal forests a stand-replacing fire may continue to influence forest structure for centuries (Aakala 2018). The changes in forest structure that occur at different temporal scales, and the slow responses to environmental changes indicate that long-term studies are needed to understand how boreal forest structure develops in time.

The changes in forest structure that occur at different temporal scales set methodological challenges for forest change analysis. Several approaches have been developed to meet these challenges. In the boreal region, the commonly used approaches include permanent plot measurements and tree-ring reconstructions (Marchand et al. 2018). In permanent plot measurements, the same forest stand is repeatedly measured to form a picture of how forest changes over time (e.g., Hofgaard 1993). In tree-ring reconstructions, the annual growth information stored in tree rings is used to analyze forest dynamics over time (e.g., Fraver et al. 2008). However, practical problems limit the use of these approaches in large-scale forest change analyses. Permanent plots are usually rather small and few of those that currently exist are located in natural boreal forests (but see, e.g., Fraver et al. 2014; Young et al. 2017; Luo et al. 2019a). Similarly, the amount of work required for tree-ring reconstructions has limited its use to small spatial scales, typically that of a forest stand (Kuuluvainen and Aakala 2011). Due to uncertainties that are related to upscaling, the results of these stand-scale observations are difficult to generalize for larger spatial scales (Scholes 2017; Luo et al. 2019b). This means that long-term analysis of boreal forest dynamics over large spatial scales requires the development of novel approaches that capture both slow and abrupt changes in forest structure, and that can be used to examine changes that occur over extensive areas.

Various remote sensors enable the examination of forest dynamics over large spatial scales and in remote locations (e.g., Ju and Masek 2016; Lydersen and Collins 2018; Senf et al. 2018). Because most of the sensors have become operational only recently, their observations cover relatively short periods of time. From the space-borne sensors, the few exceptions are data from the Landsat program (active from the early 1970s on), and from various old intelligence satellites such as Corona (active from late 1950s to early 1970s; Song et al. 2015). Especially Landsat imagery have widely been used to study forest dynamics over time (e.g., Ju and Masek 2016; Senf et al. 2018; Sulla-Menashe et al. 2018). However, the moderate resolution of early Landsat imagery (60 m × 60 m in Landsat 1–5) prevents stand-scale analysis of forest dynamics using these images. The use of the imagery from old intelligence satellites is constrained by their limited spatial coverage and temporal resolution, and short time span.

Among remotely sensed records, aerial photographs span the longest period of time (available from the early 20th century on and widespread following the WWII; Morgan et al. 2010). Due to their wide availability and high resolution, aerial photographs have been commonly applied to study spatial (Nakashizuka et al. 1995) and temporal (Gauthier et al. 2010) forest dynamics, even at an individual tree level (Korpela 2004), as well as for forest management planning purposes (Morgan and Gergel 2013). In forest dynamics research, aerial photographs have been especially useful in analyzing how disturbances shape forest structure (Beaty and Taylor 2001; D’Aoust et al. 2004). However, their usage in detecting other types of changes (e.g., slow continuous change due to tree growth) has been limited (Morgan and Gergel 2013; Lydersen and Collins 2018), with the exception of studies of tree range shifts (e.g., Danby and Hik 2007; Franco and Morgan 2007). A major reason for this limitation is the lack of ground-truth values especially for the historical aerial photographs (Browning et al. 2009). This means that the uncertainty that is ubiquitous in measurements derived from aerial photographs of varying quality cannot be accounted for (Morgan and

Gergel 2013) and is typically neglected (Lechner et al. 2012). Consequently, changes that occur in forest ecosystems cannot be reliably assessed.

Previous studies of vegetation dynamics have used tree-ring measurements to complement aerial photo analyses (e.g., Beaty and Taylor 2001; Franco and Morgan 2007). However, such studies have typically focused only on the detection and analysis of abrupt changes due to, for example, fire or insect disturbance (Stephens et al. 2003; Bouchard and Pothier 2010). Tree-ring increment expresses yearly tree growth. Hence, tree-ring width measurements can be used to calculate tree diameter at a particular time point during the life span of a tree. This suggests that tree-ring measurements could be used to produce ground truth values for aerial photographs retrospectively by reconstructing tree sizes at the year the analyzed aerial photograph was taken. Given the decadal time span of aerial photographs, this further suggests that also the slow continuous changes in forest structure could be studied combining aerial photo and tree-ring analyses, while accounting for the uncertainty that is related to the aerial photo analysis. The first aim of this dissertation was to develop such a methodology, and apply it to study changes in natural boreal forest structure.

Forest structure changes at different spatial scales

In addition to various temporal scales, the multiple processes that influence boreal forest structure also occur at various spatial scales. This means that forest structure varies and changes at multiple spatial scales, and that forest dynamics is scale-dependent (Kotliar and Wiens 1990; Elkie and Rempel 2001). As an example of these scale-dependent processes, tree-tree competition for light, water and/or nutrients changes forest structure at small, within-stand scales (Aakala et al. 2016), whereas changes in climate may influence how forest structure changes at large spatial scales (Hofgaard et al. 2018). Some processes that drive changes in forest structure, such as disturbances, operate on multiple spatial scales. For example, wind disturbances typically influence forest structure at stand or patch-scale (Kuuluvainen and Aakala 2011; Girard et al. 2014), while fire may alter forest structure at the scale of a forest landscape (Zackrisson 1977; De Grandpré et al. 2000). Because the processes that drive changes in forest structure occur at different spatial scales, the magnitude and even the direction of how forest structure changes can differ depending on the spatial scale of observation. This indicates that changes in forest structure need to be examined at multiple spatial scales.

The processes that alter the structure of natural boreal forests can be roughly categorized based on their turnover time (Carpenter and Turner 2001). Here, the term turnover time does not refer only to the mean time between successive events such as disturbances (Pickett and White 1985), but generally to factors that change in a manner that also changes ecosystem structure (Carpenter and Turner 2001). Some processes have moderately (e.g., changes in climate) or extremely slow (e.g., weathering, changes in topography) turnover times. These processes may change forest structure over decades, centuries or millennia. Other processes have more rapid turnover times, and their influence to forest structure can be examined at annual time scales (e.g., disturbances; De Grandpré et al. 2000; St-Denis et al. 2010). Due to their long turnover time, the extremely slow processes can be considered as constant parameters which change forest structure over long time intervals. Consequently, their influence cannot necessarily be revealed by studying how forest structure changes over time. Instead, how these constants influence forest structure can be studied by analyzing how forest structure varies in space. This suggests that augmenting temporal change analysis with the examination of spatial variability could enhance the understanding of forest dynamics and the processes that influence it.

The prevailing theory in landscape ecology assumes that spatial patterns within a landscape are related to a driving process in a scale-dependent manner (Wu 2013). This means that landscape patterns at a particular scale are indicative of driving processes, and suggests that these patterns could be used to examine the development of the landscape at this scale. In forest dynamics research context, this implies that the processes that drive changes in forest structure could be examined by analyzing the change patterns at different spatial scales (Elkie and Rempel 2001). Similarly, the scale-dependent spatial variability in forest structure is indicative of the effect that the constants (i.e. processes with long turnover times) have on forest structure, and this effect could be analyzed by examining how forest structure varies at different spatial scales. However, also the fast processes induce spatial variation in forest structure (Kuuluvainen et al. 2014). Hence, discerning the influence of a particular driver based on the landscape pattern is difficult (Emmett et al. 2019). While identifying the drivers of change requires careful consideration, the landscape patterns are still effective in analyzing how forest structure varies in space and changes in time.

The hierarchy theory suggests that complex systems such as forest ecosystems are often hierarchically organized (O'Neill et al. 1986), meaning that these systems consist of nested components with different spatial scales. This assumption is shared by hierarchical patch dynamics concept, which views ecosystem dynamics as a composite of patch changes in time and space (Wu and Loucks 1995). The hierarchy theory further suggests that because the interactions are weaker between than within the components, these components with different scales are loosely coupled (Simon 1962; O'Neill et al. 1986). The loose coupling refers to a central quality of hierarchical systems that is their near-decomposability, which further implies that the components which from a hierarchical system can be decomposed and examined separately. This procedure is referred to as off-scaling (Simon 1962). Off-scaling allows for parsimonious examination of a component with a specific spatial scale and produces a greater simplification and better understanding of the examined system (Simon 1962). In forest dynamics research context, hierarchy theory provides a theoretical background for analyzing scale-dependent patterns in forest structure. The idea that the structure of boreal old-growth forests varies and changes at various spatial scales that are discernible sets the theoretical premise for the chapters that examine forest structure at multiple scales (**II**–**III**).

In light of the hierarchy theory and the hierarchical patch dynamic concept, the hierarchical scales at which forest structure develops could be examined by identifying the salient scales at which the development occurs (O'Neill et al. 1986; Wu and Loucks 1995). In earlier literature, such scales are referred to as, e.g., the characteristic scales (Wu 1999). Specifically, the characteristic scale refers to the scale at which organisms interact with their environment. After the identification and separation of the characteristic scales, scale-dependent forest dynamics could then be analyzed by studying the landscape patterns at these specific scales. Analyzing the spatial patterns of variability (**II**) and temporal change (**III**) at multiple spatial scales are the second and third aim of this thesis.

The multiscale analysis of forest dynamics requires that the characteristic scales are somehow identified. In the boreal region, conventional theory of forest dynamics recognizes two distinct disturbance regime types with alternative spatial scales: small-scale gap dynamics (e.g., Pham et al. 2004; St-Denis et al. 2010) and dynamics driven by stand-replacing disturbances at large spatial scales (e.g., Zackrisson 1977; De Grandpré et al. 2000; Bouchard et al. 2008). Gap dynamics refers to changes that occur at scales ranging from individual tree level up to forest stand scale (Kuuluvainen 1994). This type of dynamics typically prevails in late-successional boreal forests as tree age-related mortality due to, e.g., fungi, insects and physical forces increases (Kuuluvainen et al. 2014). Stand-replacing changes result from catastrophic physical processes such as severe fire events or storms which may occur independent of forest age (e.g., Zackrisson 1977; Shorohova et al. 2011; Wallenius 2011). Stand-replacing disturbances may alter forest structure over large spatial scales (De Grandpré et al. 2000), and initiate secondary succession that potentially leads to even-aged stand development (Sirén 1955). Besides the changes that occur at these distinct scales, more recent evidence suggests that boreal forest dynamics occurs at levels beyond this gap-landscape – dichotomy. More specifically, the role of complex partial and patchy disturbances and associated forest dynamics have recently been emphasized in the boreal region (Kuuluvainen and Aakala 2011; Bergeron and Fenton 2012; Kuuluvainen et al. 2014).

The characteristic scales at which ecological processes occur do not necessarily overlap with predetermined scales of observation (Lechner et al. 2012). In forest dynamics research context this means that forest dynamics may occur at scales other than those examined, or at other than the scales at which forest dynamics is commonly thought to occur. In natural boreal forests, the scales at which forest dynamics occur may differ between forest landscapes depending on, e.g., dominant tree species or tree age structure (Kuuluvainen 1994; Aakala and Kuuluvainen 2011). This suggests that for comprehensive analysis on how forest structure varies or changes, the scales at which patterns in forest structure are analyzed should not necessarily be selected *a priori*. Instead, the characteristic scales at which the most salient ecological processes in the studied forest ecosystem occur could be objectively identified from the analyzed data (Hay et al. 2002). The identification of such scales enables the analysis of the most relevant ecological patterns and promotes comprehensive understanding of how forest ecosystems develop (Scholes 2017).

AIMS AND STRUCTURE OF THIS DISSERTATION

This dissertation examines how the structure of natural boreal forests varies in space and changes over time. Forest structure was studied in two distinct geographical regions, and at multiple spatial scales using time series of aerial photographs together with field- and tree-ring measurements. Specifically, the aims of this dissertation were to:

1) Develop and apply a novel methodology to study forest ecosystem change using time series of aerial photographs, while accounting for the uncertainty that is related to the use of these photographs.

2) Identify spatial scales at which the structure of natural boreal forests varies, and analyze the variation at these scales.

3) Identify the factors that cause spatial variation in the structure of natural boreal forests at multiple spatial scales

4) Analyze how natural boreal forest structure changes over decades, and at multiple spatial scales.

The three research papers (hereafter chapters) in this dissertation address these objectives. In chapter **I**, a methodology for quantification of the uncertainty in the visual interpretation of aerial photographs of varying quality using tree-ring and field measurements is presented and applied. Chapter **II** extends the methodology to analyze scale-dependent variation in the landscape structure of natural boreal forest, and the factors and processes influencing this variation. Chapter **III** investigates trends and spatial scale dependencies in how the structure of natural boreal forest changes over time, using and extending the methodology presented in **I**.

MATERIALS AND METHODS

Study areas

Geography, climate and soils

The studies were conducted in the same five natural boreal forest landscapes in two distinct geographic regions: northeastern Finland and the North Shore region in Quebec, eastern Canada (Fig. 1). In Quebec, two landscapes were studied, hereafter denoted Lac Dionne and Pistuacanis (Fig. 1B). The three landscapes studied in Finland are hereafter denoted Hirvaskangas, Pommituskukkulat and Hongikkovaara (Fig. 1C). Of these landscapes, Hirvaskangas and Pommituskukkulat are located in Värriö Strict Nature Reserve (established in 1981), and Hongikkovaara in Maltio Strict Nature Reserve (established in 1956). Each studied landscape have an area of 4 km^2 (2 km × 2 km). The studied landscapes have never been commercially logged. However, the Finnish landscapes are influenced by reindeer herding, in connection to which light selection felling has taken place.

Humid subarctic climate characterizes both studied regions (class Dfc according to Köppen climate classification system). The mean annual temperature in the Finnish study region is -1 °C. The mean temperatures for the coldest (January) and warmest (July) months are -13 °C and +13 °C, respectively. The average annual precipitation sum is 570 mm. The mean annual temperature in the Quebecois study region is 0 °C. The mean t emperatures for the coldest (January) and warmest (July) months are -18 °C and +14 °C, respectively. Average annual precipitation is 1100 mm (All climate data are averages from years 1970–2000; Fick and Hijmans 2017).

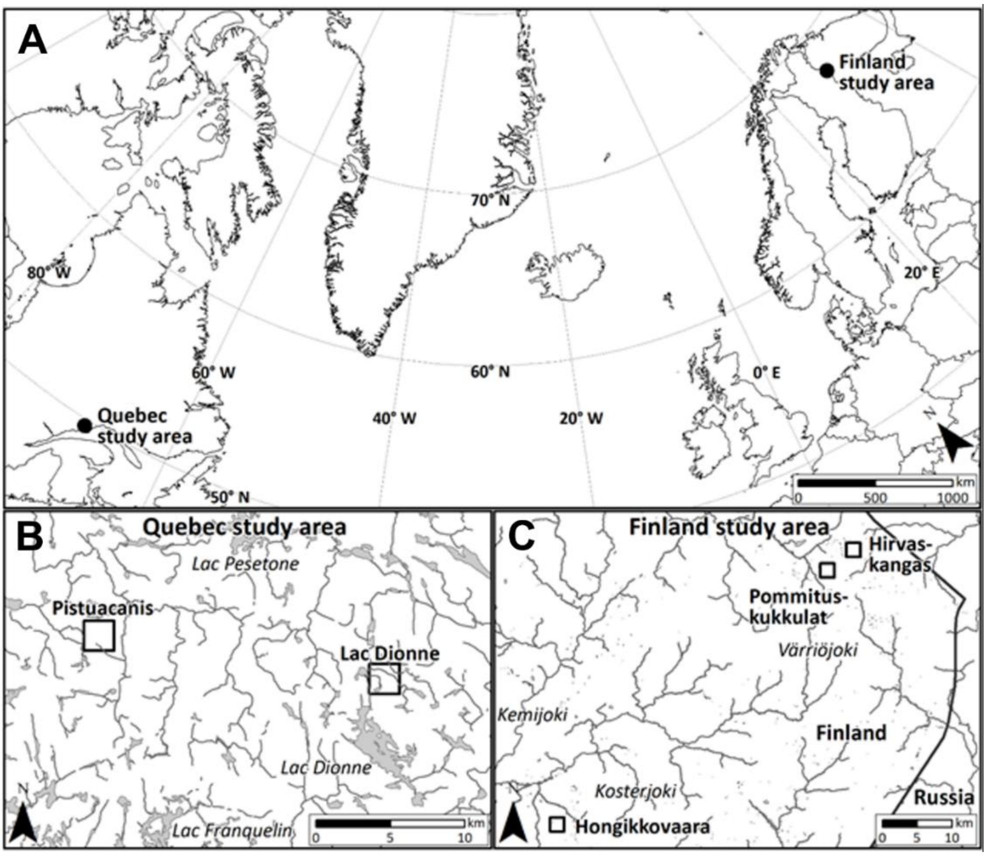

Figure 1. The location of the studied regions (A), and the studied landscapes within the Quebecois (B) and Finnish (C) study regions.

Both studied regions are characterized by mosaics of forests on mineral soil, waterbodies, and forested and open peatlands. Soils are quaternary glacial deposits. In Finland, undifferentiated tills are the most prevalent soil type. Other common soil types include sorted glacial formations, organic soils and rocky outcrops. The Fennoscandian Shield underlies the glacial deposits. The topography is characterized by low mountain fells with gently rolling slopes, and depressions between the fells. The fells typically have treeless upper slopes with rocky outcrops or thin soils. In the studied landscapes, the elevation ranges between 200 and 500 m above sea level (asl).

In the North Shore region, slopes vary from low to moderate. Layers of undifferentiated glacial tills are common on the gentle slopes and depressions, as are glaciofluvial sand deposits in floors of larger valleys and rocky outcrops on moderate slopes and summits. The bedrock of the studied region is part of the Canadian Shield. Generally, the North Shore region has rugged terrain. The elevation ranges from 300 to 500 m asl in the studied landscapes.

Dominant tree species, succession and disturbance history

The studied landscapes were initially selected with the following criteria: (in order of importance) 1) the forests in the landscape are naturally dynamic, 2) the landscape is accessible by boat or by foot, and 3) the landscape contains as much forest as possible, given the landscape mosaics. In addition to these criteria, landscapes dominated by different tree species were selected to be able to analyze forest structure in various boreal landscapes. Of the studied landscapes, Hirvaskangas is mostly formed of pure *Pinus sylverstris* (L.) stands (proportion of *P. sylverstris* >75 %). *Picea abies* (L.) Karst and *Betula pubescens* (Ehrh.) dominate in Pommituskukkulat. Stands of *P. sylvestris*, of mixed *P. sylvestris/P. abies*, and of mixed *P. abies/B. pubescens* are common in Hongikkovaara. *Picea mariana* (Mill.) is the most common tree species in Lac Dionne landscape, while some parts of the landscape are dominated by *Abies balsamea* (L.). Pistuacanis is dominated by *A. balsamea*, with *P. mariana* occurrence in limited parts of the landscape.

The relative dominance of tree species is reflective of site productivity and long-term disturbance history in both studied regions (e.g., Sirén 1955; Engelmark et al. 1998; Gauthier et al. 2010). In Finland, the shade-intolerant *P. sylvestris* typically dominates on the low-productivity xeric sites throughout the successional development (*sensu* Cajander 1949). The more productive mesic sites are usually dominated by *Betula* spp. in the early and by *P. abies* in the late-successional stage (Sirén 1955). In the absence of stand-replacing disturbance, sub-xeric sites often undergo a gradual shift from *P. sylvestris* to *P. abies* dominance (Engelmark et al. 1998). In Quebec, *P. mariana* often forms nearly pure stands on sites with low productivity, while *A. balsamea* may occur as a co-dominant in the more productive sites, or may form monospecific stands (De Grandpré et al. 2000). In mixed stands the relative dominance of *A. balsamea* typically increases with stand age, but *P. mariana* is seldom fully outcompeted (Gauthier et al. 2010). Due to partial disturbances, other tree species such as *Picea glauca* (Moench) Voss and *Betula papyrifera* (Marsh). can persist in the canopy dominated by *P. mariana* or *A. balsamea*, even when fire return intervals are long (Bergeron 2000; Gauthier et al. 2010).

Differences in disturbance regime and disturbance history can be expected to cause differences in how forest structure varies in space and changes in time. Hence, two regions that differ markedly in their disturbance regimes were analyzed. Of the disturbance regimes in the studied landscapes, forest fires were common in the Finnish study region prior to the 20th century, especially surface fires in the xeric *P. sylvestris*-dominated forests, as typical for northern European boreal forests in general (Kuuluvainen and Aakala 2011; Aakala 2018). In 1831, most of Hirvaskangas and roughly 30% of the nearby Pommituskukkulat landscape burned. These, and previous fires have influenced the tree age structure in the *P. sylvestris*-dominated areas, and explain the high proportion of the post-fire *B. pubescens* in the mesic parts of the landscapes (e.g., in the middle of the Pommituskukkulat landscape; Aakala 2018, **II**). In Hongikkovaara landscape, the influence of the last larger fire in 1777 is still visible in the tree age structure of the landscape (Aakala 2018). In the absence of fire, small-scale mortality events of individual trees or groups of few trees (i.e. gap dynamics) drive stand dynamics in the Finnish study landscapes (Kuuluvainen and Aakala 2011). Storms of moderate severity occur infrequently but may fell trees over large areas, especially if the trees are weakened by, e.g., fungal infection prior the storm (Fraver et al. 2008). In addition to natural disturbances, reindeer herding influences the studied Finnish landscapes, most notably in the Pommituskukkulat landscape. Connected with reindeer herding, selection felling of individual trees has occurred in Hirvaskangas and Pommituskukkulat.

In Quebec, the recurrent spruce budworm, *Choristoneura fumiferana* (Clemens), outbreaks are a major disturbance factor (Bouchard and Pothier 2010). Of the dominant tree species, *A. balsamea* is highly susceptible to spruce budworm defoliation. *P. mariana* is also defoliated by spruce budworm, but to a lesser degree compared to *A. balsamea* (Hennigar et al. 2008). In 2019, there was an ongoing outbreak in the North Shore region that began in ca. 2006 (Bognounou et al. 2017). The previous severe outbreak occurred from the 1970s to the mid-1980s (Bouchard and Pothier 2010). Gap dynamics due to, for example, partial windthrow drive the old-growth stands between the outbreaks and in the absence of stand-replacing disturbances such as large-scale fire events (Pham et al. 2004; St-Denis et al. 2010; Girard et al. 2014). Fire maps by Bouchard et al. (2008) indicate that Lac Dionne burnt in 1810, while Pistuacanis seems to have avoided fires during the last 200 years.

What can be considered as old-growth forest is a matter of how the term old-growth is defined. Traditionally, tree age has been an important concept in the definition of a boreal old-growth forest (Hilbert and Wiensczyk 2007). More recent attempts to define old-growth have pointed out that due to the dynamic nature of forests, a definition that is based solely on a static variable can be problematic (Kneeshaw and Gauthier 2003; Hilbert and Wiensczyk 2007). As an example of a more dynamic definition for old-growth, Kneeshaw and Gauthier (2003) define that the onset of old-growth stage is reached when at a landscape scale the post-disturbance cohort begins to be replaced by trees recruitment from lower canopy layers. In this dissertation, the abovementioned definition by Kneeshaw and Gauthier (2003) is followed, with the augmentation that no management practices have taken place in the forests.

The field data used in this dissertation indicates that the fires that occurred in the Finnish landscapes during the late 18th or early 19th century were non-stand-replacing (Aakala 2018). Hence, and because of the known lack of forest management practices, these landscapes and Pistuacanis landscape where stand-replacing fires have not occurred for the last 200 years can be defined as old-growth landscapes. However, Lac Dionne landscape in Quebec experienced a major fire in 1810 (Bouchard et al. 2008), and the majority of the trees in the landscape have originated after the fire event. The longevity of *P. mariana* that dominates in Lac Dionne landscape is generally below 150 years (Gauthier et al. 2010). This means that the time interval between the last fire event and the onset of studies in this dissertation (1965) exceeds the general longevity of *P. mariana.* Hence, also Lac Dionne is considered old-growth landscape.

Aerial photographs, their orientation and visual canopy cover interpretation

Aerial photographs

The chapters in this dissertation use visually interpreted canopy cover as a surrogate measure for forest structure to quantify how forest structure varies in space (**II**) and changes in time (**I**, **III**). The retrieval of the canopy cover values from the time series of aerial photographs was reported in detail in **I**, and the same canopy cover values were used in **III**. In chapter **II**, a subset of the canopy cover values were used (i.e. not the whole time series). Briefly, canopy cover information was obtained by visually interpreting stereopairs of aerial photographs from three time points (Table 1). Henceforth, the aerial photographs from the three time points are denoted as the newest, middlemost and oldest photograph, and the time interval between the newest and the oldest photograph as the whole study interval, the time interval between the middlemost and the oldest photograph as the first study interval, and the time interval between the newest and the middlemost photograph as the second time interval. A specific combination of a landscape and an aerial photograph is (e.g., the middlemost photograph in Lac Dionne) is denoted scene. In chapter **II**, visual interpretation of canopy cover made from the newest aerial photographs was used in detailed analysis of how natural boreal forest structure varies in space. Here, total canopy cover and the proportion of various tree species, as well as the number of standing and fallen dead trees were interpreted using the newest high quality aerial photographs. In the interpretation, conifers were identified to species level, but deciduous trees were not separated.

Because the availability of suitable photographs depended on the studied landscape, the exact period of time covered in chapters **I** and **III** differed between the landscapes (Table 1). For the same reason, the photo years also varied for the newest photographs used in chapter **II** (Table 1). For the oldest photographs, the oldest photographs available for each landscape were selected. For the middlemost photographs, several alternatives were available for certain landscapes. Here, the ones with the best quality and stereo-cover over the landscape were chosen. For the newest photographs, the most recent photographs available at the time of the fieldwork were chosen. The oldest photographs were panchromatic, the others false-color.

Table 1. The aerial photographs used in the studies of this dissertation. The Finnish photographs are from the National Land Survey Finland, except for the 1972 photo in Hongikkovaara and 1991 photo in Hirvaskangas which are from the Finnish Defence Forces, and the middlemost photos in Pommituskukkulat and Hongikkovaara which are from Blom Geomatics AS. The newest Quebecois photographs are from Ministère des Forêts, de la Faune et des Parcs du Québec, and the older photographs from Geomatheque Ltd., QC, Canada.

	Oldest photographs			**Middlemost photographs**			**Newest photographs**		
	Year	**Scale**	**Pixel size (m)**	**Year**	**Scale**	**Pixel size (m)**	**Year**	**Scale**	**Pixel size (m)**
Hirvaskangas	1959	1:30000	0.6	1991	1:31000	0.4	2011	1:20000	0.5
Pommituskukkulat	1959	1:30000	0.9	1988	1:30000	0.4	2011	1:20000	0.5
Hongikkovaara	1972	1:60000	0.9	1988	1:30000	0.4	2010	1:20000	0.5
Lac Dionne	1965	1:16000	0.2	1987	1:15000	0.2	2011	1:11000	0.3
Pistuacanis	1965	1:16000	0.2	1987	1:15000	0.2	2011	1:11000	0.3

Aerial photo orientation

Accurate orientation of aerial photographs in a coordinate system that remains constant over time is required for precise retrospective photogrammetric measurements (Korpela 2004). Hence, the aerial photographs needed to be accurately oriented prior the visual canopy cover interpretation. The exterior orientation of the photographs was done using aerial triangulation, which normally relies on ground control points. Here, such ground control points were lacking. This shortage was compensated by using the direct sensor orientation to solve the exterior orientation of the newest photographs that was delivered with this exterior orientation data, and multitemporal tie points to bring the historical photographs to the same coordinate system with the newest photographs Korpela (2006).

The newest photographs for all landscapes, the oldest photographs for Quebec, and the middlemost photographs for Pistuacanis were all accompanied by exterior orientation parameters (projection center coordinates x, y, z, and the three camera rotation angles ω, ϕ, and κ). For the middlemost photographs in Pommituskukkulat and Hongikkovaara, camera calibration certificates were available, and contained information of the focal length and/or principal distance of the used camera, of the location of the principal point in the fiducial coordinate system, and of lens distortions. For the middlemost photographs in Hirvaskangas and Lac Dionne, and the oldest photographs in all the Finnish landscapes, only the calibrated camera constant was available. For those, the standard values for the camera type were used for the fiducial mark coordinates and the fiducial center position. Lens distortions were considered to be minor and were not corrected.

Due to the lack of ground-control points, the orientation of the historical photographs reported in chapter **I** was begun by measuring the coordinates for objects visible in the accurately oriented new photographs, and on the historical photo to be oriented. Such objects included large rocks, building corners, and bases of solitary trees. The z coordinate (elevation) for these points was derived from the digital elevation models (National Land Survey Finland, Ministère des Forêts, de la Faune et des Parcs du Québec). The photographs were oriented using the experimental software by Korpela (2006), and ESPA software (ESPA Systems Ltd., Espoo, Finland).

Visual canopy cover interpretation

After the orientation, stereopairs of aerial photographs were visually interpreted using an interpretation grid of 0.1 ha cells (31.62 m × 31.62 m, 4096 cells per grid). The grid was constructed with the Fishnet-tool in ArcGIS Desktop 9.3 (Environmental Systems Research Institute, Redlands, CA, USA). The elevation information needed for the nodes of the stereointerpretation grid was derived from a digital elevation model with 10 m horizontal resolution in Finland (National Land Survey Finland) and 20 m in Quebec (Ministère des Forêts, de la Faune et des Parcs du Québec).

Canopy cover was interpreted for each interpretation grid cell as the proportion of the forest floor covered by the vertical projection of tree crowns that reach within the cell. If a cell was not completely in a forested area (e.g., waterbody, open peatland) at the time of one of the used photographs, the cell was regarded as non-forested and was excluded from further analyses in chapters **I** and **III**. In chapter **II**, only the cells that were considered non-forested at the time of the newest photographs were excluded from further analyses.

Subjectivity of the visual aerial photo interpretation can cause bias in the interpretation results (Morgan and Gergel 2013). To reduce bias due to improving interpretation skill, the interpretation grids were divided into sixteen parts (256 cells each). Using these sub-grids, the newest photographs for each landscape were interpreted first in randomized order, and then the other photographs in randomized order. From the newest photographs, also the proportion of various tree species of the total canopy cover, and the number of standing and fallen dead were recorded. Conifers were identified to species level, but the deciduous trees were not separated. The tree species proportions were used in calibration model selection (**I**), and to explain the spatial variability patterns in forest structure together with the dead wood interpretations (**II**). EspaCity software (version 11.0.15306.1; ESPA Systems Ltd., Espoo, Finland) and a passive 3D monitor were used in the interpretation.

Field data for the calibration of visual interpretation

To reduce systematic error (henceforth bias) from the visual canopy cover interpretation, to quantify the random error associated with the interpretation, and to produce canopy cover posterior distributions, the interpretation was calibrated using canopy cover derived from field measurements as ground truth values. The field measurements were done in summer 2012 in Finland and 2013 in Quebec. Consequently, the aerial photographs were taken 1–53 years earlier than the field measurements were done. To obtain ground truth values at the year corresponding to the year when the aerial photographs were taken, canopy cover was reconstructed for a random sample of the grid cells to correspond to the aerial photo years. These reconstructions were used as ground truth values for the visual interpretation. The results of all the visual canopy cover interpretations used in this dissertation, as well as their error distribution quantifications are presented in chapter **I**. The error distributions were used to assess the uncertainty of the identified patterns of how forest structure changes in time (**I**, **III**), and varies in space (**II**). The basis of the field sampling and tree crown size reconstruction are only briefly explained here.

To select a random sample of the grid cells for field sampling, the interpretation grids were first divided into quadrants (Aakala et al. 2016). Then, 4 cells in each quadrant were randomly selected (16 cells per landscape). The division was made to ensure that cells were selected from different parts of the landscape, as interpretation error might differ in different parts of the aerial photographs (for example, trees appear larger when further away from the aerial photo nadir; Korpela 2004). All the selected 48 cells were sampled in the Finnish landscapes. However, for logistic constraints, only 2–3 cells per quadrant were sampled in Quebec (9 cells per landscape). Except for the two pilot-phase cells in Pommituskukkulat landscape, only cells located at a minimum distance of 100 m from the previously selected cells were selected.

In the field, all trees with a minimum diameter of 10 cm at 1.3-m height and whose crown reached within the selected cell were mapped using a FieldMap measuring system (IFER Ltd., Jílové u Prahy, Czech Republic; see Aakala et al. 2016 for full details on the field sampling). The utilized measuring system combines an electronic compass and a laser rangefinder to the FieldMap LT mapping software on a handheld computer. In each sampled cell and for all trees, species, diameter at 1.3 m height, and tree height were recorded. Further, an increment core was extracted from each tree at approximately 1 m height using a standard 5.15 mm borer. Coordinates of each stem center on the plot were measured using an arbitrary Cartesian coordinate system with origin in the southwest corner of the cell. To obtain the crown sizes for the live trees, crown projections were mapped by measuring 4–8 points along the crown dripline on different sides of the crown, the total number of points depending on the crown irregularity. The more irregular the crown, the more points were mapped.

Dead trees within the cell selected for field sampling were mapped and recorded similarly, and classified into six decay classes following Aakala (2010). Stem base centers were used for the location of each tree. If a dead tree had stem base outside but close to the cell border, a subjective estimation of whether the crown reached the cell while the tree was alive was done based on the crowns of nearby live trees of the same species and corresponding size. An increment core similar to live trees was extracted. In cases of advanced decay, a partial disk was cut using a chainsaw.

Canopy cover reconstruction from the field data

In **I**–**III**, the field-measured canopy covers and tree-ring measurements were used to reconstruct canopy cover in the sampled cells to correspond to the years the aerial photographs used in the particular study were taken. For the canopy cover reconstruction, the full radial growth histories of the field-sampled trees presented in Aakala et al. (2018) were utilized. In the reconstruction, the field-measured tree canopy size was set as a starting point. Then, tree canopy sizes were back-calculated based on their growth histories (Fig 2, see **I** for full details on the procedure). If a trees shrank below the 10 cm at 1.3-m height sampling threshold it was removed from the reconstruction. When the aerial photo year was reached, the relationship between tree diameter and crown area was used to convert the change in tree size to change in crown size (Fig. A1 in **I**). In the back-calculation, dead trees were resurrected at their cross-dated year of death. After resurrection their diameter and canopy size change was quantified similar to live trees, but assuming circular crown shape. Last, the overlapping crown areas were removed, and the proportional canopy cover for the field-sampled cells at the aerial photo years was calculated as the sum of non-overlapping crown areas within a cell divided by the cell area.

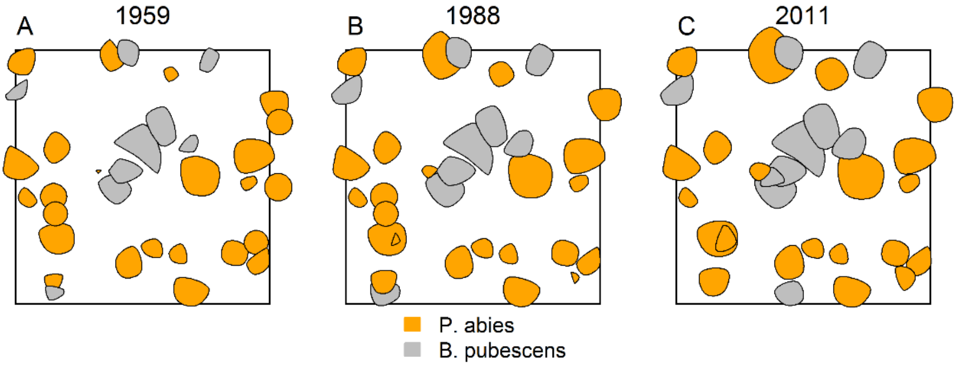

Figure 2. An example of the results of a canopy cover reconstruction in one of the field sites located in Pommituskukkulat landscape. The panels are canopy maps where a polygon represents an individual tree canopy. The maps show the reconstructed canopy cover at the time of the oldest (A), middlemost (B) and newest (C) aerial photograph in the particular landscape. The colors represent the tree species in the site. N.B. the overlapping canopies and the canopies that exceed the site area have not been removed from this example.

Bias and error in the visual canopy cover interpretation

Separating credible canopy cover variation or change from visual interpretation error was essential in all the chapters within this dissertation. Hence, the influence of bias needed to be minimized and the amount random error quantified. For this, regression models between the reconstructed and interpreted canopy cover were used to explore the sources of bias and error in the interpretation (**I**). Henceforth these regression models are denoted calibration models. In calibration model selection, the pairwise interactions between the interpreted canopy cover, interpreted landscape and the year the aerial photograph was taken (surrogate measure for photo quality) were tested with ANCOVA (Table A1 in **I**).

The accuracy of the interpretation depended on the interpreted landscape and on aerial photo quality. Hence, individual calibration models for the oldest, middlemost and newest aerial photographs were used when calibrating the visual interpretation (**I**, **III**). Due to the dependency between interpretation success and the interpreted landscape, the same calibration models could not be used in each landscape. Instead, the largest coefficients of determination (R^2) and smallest residual standard errors were obtained when Hirvaskangas and Pommituskukkulat, and Lac Dionne and Pistuacanis were calibrated with their own models and Hongikkovaara with its individual model when calibrating the interpretations made from the oldest and middlemost photographs (**I**). For the newest photographs the use of separate calibration models did not increase calibration success. Hence, all Finnish landscapes were calibrated in the same model, and the Quebecois landscapes in the same model when calibrating the interpretations made from the newest photographs (**I**–**III**). However, the calibration model for the newest photographs in the Finnish landscapes improved when the proportion of P. abies in the cell was included as a predictor (Table A2 in **I**). Hence, the proportion of P. abies was included in this calibration model. The calibration model residuals were used to further explore the sources of bias and error in the visual interpretation (**I**), and the posterior predictive distributions for canopy cover that were developed based on the calibration models were used in to examine the credibility of the results.

The calibrated canopy cover values were compiled into raster maps. In chapters **I** and **III,** temporal changes in canopy cover were analyzed. Hence, the sequential canopy cover maps were subtracted to produce maps of canopy cover change. These maps depict changes in canopy cover during the first, the second and the whole time interval. For each map of canopy cover change, the annual canopy cover change rate was further quantified by dividing the canopy cover change in each cell during a time interval by the length of the particular interval (**III**).

Due to their high quality, the newest aerial photographs enabled a more detailed analysis of forest structure compared to the older aerial photographs (**II**). For example, tree species composition (proportion of canopy cover) and the amount of dead wood (number of snags and logs) were interpretable using the newest photographs. Hence, the canopy cover interpretation made using the newest photographs was used to study spatial variation in forest structure in detail, and the interpretations of tree species composition and amount of dead wood were used to explain the variation in canopy cover (**II**). The dead wood interpretation and the interpretation of tree species composition were calibrated in a process similar to the calibration of canopy cover interpretation (**II**).

Spatial scales and patterns of canopy cover variation (II) and change (III)

Spatial variation (**II**) and temporal change (**III**) in canopy cover were analyzed at multiple spatial scales. For this, the scale derivative analysis (Pasanen et al. 2013; **II**–**III**), Bayesian scale space multiresolution analysis (MRBSiZer; Holmström et al. 2011, **II**), and Bayesian scale space analysis for images (iBSiZer; Holmström and Pasanen 2012; Pasanen and Holmström 2015; **III**) were used. Detailed descriptions of the analysis pathways are given in the chapters (**II**–**III**). Briefly, when used to analyze images, both MRBSiZer and iBSiZer rely on the idea that the image consists of a sum of components at various spatial scales. Hence, smoothing the image can reveal features that occur at different spatial scales. In MRBSiZer, the smoothed components are separated from each other, whereas only smoothing is performed in iBSiZer. The spatial scales used for the smoothing should represent the scales at which the most salient variation or change occurs (i.e. characteristic scales; Wu 1999). Hence, the first step in the analysis was to identify the characteristic scales to be used in smoothing. We identified the characteristic scales with an objective approach which is based on a concept of ‘scale-derivative’ (Pasanen et al. 2013).

A scale-derivative is the derivative of the smooth with respect to the logarithm of the smoothing level, and in scale-derivative analysis the characteristic scales are detected based on the smoothing levels that minimize the scale-derivative vector norm. For example, in a signal that is a sum of two components with different scales, the location of such a local minimum represents a level at which the smaller scale is smoothed out and the large-scale component, not yet affected by smoothing, is revealed (see Pasanen et al. 2013 for details). In **II**–**III**, sequences of smoothing levels were defined by identifying the local minima of the scale-derivative vector norms for the newest canopy cover map (**II**) and all the maps of canopy cover change (**III**).

Using MRBSiZer, the canopy cover maps depicting canopy cover at the time of the newest photographs were decomposed into scale-dependent components based on the smoothing level sequences identified in scale-derivative analysis (**II**). The maps were smoothed using a Nadaraya-Watson smoother with a Gaussian kernel. When smoothing was used to reveal features with small spatial scale, the data points were averaged over a small neighborhood. To reveal large-scale features, data points were averaged over larger spatial scales. After smoothing the canopy cover maps, the smooths were subtracted. This resulted in maps that depict canopy cover at a location relative to its surroundings (i.e. relative canopy cover map; Fig. 2 in **II**), the sizes of the locations and surroundings depending on the smoothing level (with increased smoothing, larger areas are compared to their surroundings). In relative canopy cover maps, high canopy cover means high canopy cover in relation to the surrounding areas, and vice versa. Maps depicting relative basal area of dead wood were produced in the same manner (Fig. S6 in **II**).

Chapter **III** focused on analyzing spatial patterns of canopy cover change at multiple spatial scales. For this, absolute changes in canopy cover were analyzed (not relative as in **II**). Hence, iBSiZer instead of MRBSiZer was used to smooth the maps of canopy cover change that depict canopy cover change between two time points. Similar to **II**, also the maps of canopy cover change were smoothed based on the smoothing level sequences identified in the scale-derivative analysis (Pasanen et al. 2013).

Theoretically, the combination of scale-derivative analysis and iBSiZer/MRBSiZer is close to the wavelet analysis, which can be used to detect spatial patterns in two dimensional ecological data (as in James et al. 2011). However, our approach has some advantages over the wavelet analysis. Firstly, in our approach, the characteristic scales are objectively identified using the scale-derivative analysis. The scale-detection in wavelet analysis is sensitive to wavelet template selection, introducing an element of subjectivity in the scale-detection of wavelet analysis (James et al. 2010). Secondly, compared to the wavelet analysis where nonstationary subregions or hotspots are identified, our approach provides a more intuitive interpretation of the results (areas that differ credibly from their surroundings or areas that have changed credibly are identified in MRBSiZer or iBSiZer, respectively; see Holmström et al. 2011 for a more detailed comparison).

To produce comparable and intuitive numerical information on the spatial scales at which canopy cover varies or changes (**II**–**III**), the characteristic size of a feature within an identified scale was quantified using a combination of scale-derivative analysis (Pasanen et al. 2013), and the diameter of the representative circle approach (cf. Pasanen et al. 2018). Due to the size estimation, the scale sizes could be reported in hectares instead of uninformative smoothing parameter values.

Credibility of canopy cover variation and change

Error distributions in the calibration models, quantified in chapter **I**, were used to develop posterior predictive distributions of canopy cover for each canopy cover map and for each map of canopy cover change. These posterior predictive distributions were analyzed in a Bayesian framework to assess the credibility of the general patterns of canopy cover change (**I**), spatial variation in canopy cover (**II**), and canopy cover change at multiple spatial scales (**III**), and to distinguish credible phenomena from the visual interpretation error. The approach used to examine the credibility of the results depended on the aims of the particular study. In chapter **I** the aim was to quantify the magnitude of forest structural change that could be detected with the proposed methodology. In this spatially implicit analysis, the credibility of the general patterns of canopy cover change were distinguished from the interpretation error by estimating the point-wise posterior mean of the canopy cover change as the cell-wise mean of 10000 draws from the canopy cover change posterior distribution (Erästö and Holmström 2005). The cells where 99% of the samples where positive or negative were considered as cells with credible canopy cover increase or decrease, respectively.

In the multiscale analyses (**II**–**III**), the credibility of the results was assessed in a spatially explicit manner using the method of highest point-wise probabilities (HPW; Erästö and Holmström 2005). The cells where the joint posterior probability exceeded a threshold of 95% were flagged as cells with credibly higher or lower relative canopy cover (**II**) or as cells with credible canopy cover increase or decrease (**III**). The main difference between the point-wise and the highest point-wise approach is that in HPW canopy cover variation or change in a cell is compared to that of the whole landscape, while considering the 5% error marginal. This means that in HPW, the error margin is given for the whole canopy cover map, whereas in the spatially implicit point-wise approach the margin is given separately for each cell. The purpose of the comparison over the whole landscape is to account for the multiple testing problem and the consequent false positive observations. As the consideration of the multiple testing problem is embedded in HPW, a lower credibility threshold than in the point-wise approach could be used.

RESULTS AND DISCUSSION

Changes in forest structure were credibly detectable using time series of aerial photographs (I)

To develop and apply a methodology to study changes in forest structure using time series of aerial photographs, altogether 61440 individual canopy cover interpretations were made from the five study landscapes, using stereopairs of aerial photographs taken at three time points between the years 1959–2011. The visual interpretation of canopy cover was compared to canopy cover values reconstructed based on field- and tree ring measurements. The difference between the canopy cover values reconstructed using field- and tree-ring measurements and the visually interpreted canopy cover varied between the oldest, middlemost and the newest aerial photographs. For oldest and middlemost photographs, the mean differences were 5 and 3 percentage points (pp), respectively, considering all landscapes (Fig. 3; **I**). For the newest photographs, the mean difference was -3 pp. (Fig. 3; **I**). This suggested bias in the visual canopy cover interpretation and indicated that canopy cover was typically systematically underestimated using the oldest and middlemost, and overestimated using the newest aerial photographs. The interpretation bias also varied among the studied landscapes, and depended on the reconstructed canopy cover in the interpreted cell (Fig. 3; **I**). The canopy cover overestimation increased with increasing canopy cover when interpreting the newest photographs. For the oldest and middlemost photographs, canopy cover underestimation increased with increasing canopy cover, independent of the studied landscape.

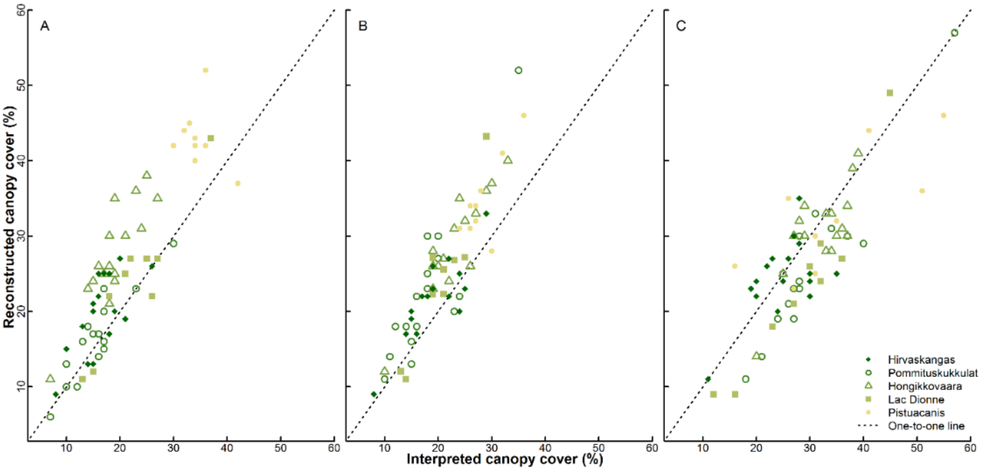

Figure 3. Difference between the canopy cover reconstructed using the field and tree-ring measurements, and the visually interpreted canopy cover at the time of the oldest (A), middlemost (B), and newest aerial photographs (C).

The results supported the earlier findings on how differences in aerial photo scale and quality can cause bias in visual aerial photo interpretation (Danby and Hik 2007; Fensham and Fairfax 2007). A potential explanation for why canopy cover was underestimated using the oldest and middlemost photographs and overestimated using the newest photographs is that the individual tree crowns appear larger and are easier to delineate from the recent high-quality aerial photographs compared to the older low-quality photographs. This applies especially to trees close to the applied diameter limit of 10 cm at 1.3-m height. Trees close but above this limit were not clearly visible in the oldest and middlemost photographs. While visible, they were hard to separate from trees just below the diameter limit using the newest photographs that also had the highest quality. The dependency between the visual interpretation bias and the quality of the aerial photographs, as well as between the studied landscape and the tree species composition and cover signifies that the interpretation bias cannot be assumed constant between different forest landscapes (Massada et al. 2006), but should be quantified separately when these landscape characteristics or aerial photo quality change.

In Quebec, the regeneration after the spruce budworm outbreak (from 1970s to mid-1980s; Bouchard and Pothier 2010) was ongoing at the time of the newest photographs (2011). Consequently, many trees were close to the 10 cm at 1.3-m height limit at the time of the newest photographs. It is plausible that the relatively high random interpretation error of the newest aerial photographs in Quebec was caused by the difficulty to separate the field-measured trees from those below the limit using the aerial photographs. This difficulty could also partly explain the lack of connection between the photo quality and interpretation success.

Because the bias and error in the visual interpretation of canopy cover varied between different landscapes and between the aerial photographs with different quality (different photo years), the magnitude of the credibly detectable change in canopy cover differed during among the studied landscapes and between different time intervals (Fig. 4). This influenced the changes that were credibly detected in chapters **I** and **III**. Similarly, the relatively high error in the interpretation of the newest aerial photographs decreased the amount of spatial variability in forest structure that could be credibly detected using different scenes (**II**). The results in chapter **I** indicated that in most cases, multiple tree crowns were needed to cover an area that would exceed the limit of credibly detectable change, the specific area depending on the absolute canopy cover in a particular cell. This means that changes that occur at a level of an individual tree (e.g., individual tree mortality) could not always be credibly discerned. However, changes that influenced a few trees could already be credibly separated. While boreal forest structure typically changes at individual tree scale, changes that influence forest structure at the level of a few trees up to stand scale are also common (Pham et al. 2004; St-Denis et al. 2010), as are changes that occur at even broader spatial scales (De Grandpre et al. 2000; Bergeron and Fenton 2012; Kuuluvainen et al. 2014). Consequently, credible canopy cover increases and decreases were identified during all time intervals (Fig. 4). This suggests that time series of aerial photographs together with canopy cover reconstructions based on field- and tree-ring measurements can be used to detect the slow and continuous changes in forest structure that occur over several years, in addition to the abrupt change detection to which time series of aerial photographs are typically applied to (Beaty and Taylor 2001; D’Aoust et al. 2004; Morgan and Gergel 2013).

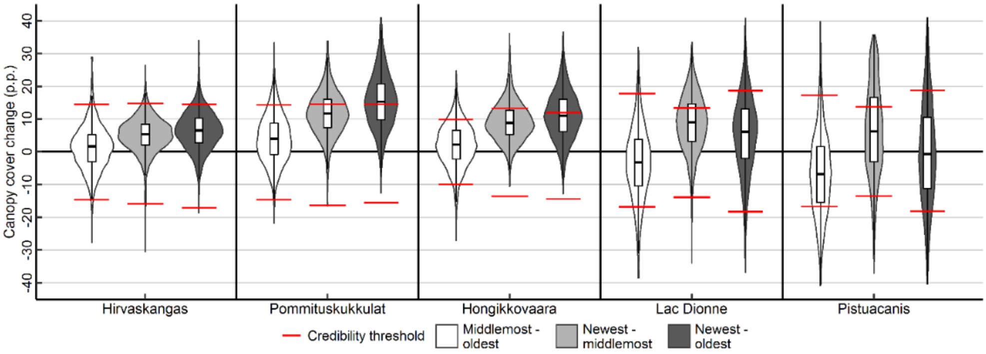

Figure 4. Distributions of canopy cover change for the 0.1-ha cells for the first time interval (white), the second time interval (light grey), and the whole time interval (dark grey) in each landscape as percentage points. The violins indicate the distribution of the change values in the given landscape and the study interval, and the red lines are the credibility thresholds. The cells above the topmost threshold have credible canopy cover increase, and the cells below the bottom threshold have credible canopy cover decrease.

Natural boreal forests displayed characteristic spatial scales at which forest structure varied (II)

To identify the spatial scales at which the structure of natural boreal forests varies, and to analyze the variation at these scales, canopy cover in the five study landscapes at the time of the newest aerial photographs was studied in detail. With scale-derivative analysis (Pasanen et al. 2013), three spatial scales at which forest structure varied were identified in each landscape studied. The typical features within these scales had an area of 0.1 ha, 1.3–2.8 ha, and 20.1–321.4 ha, the exact feature size depending on the studied landscape. These three scales are henceforth denoted small, mid, and large scale, respectively. The successful identification and decomposition of the distinct scales of variation concurred with the premises of hierarchy theory (O'Neill et al. 1986) that expect multi-scale variation and scale decomposability from ecological systems. Furthermore, the multiple scales at which forest structure varied were in agreement with the hierarchical patch dynamics concept, which assumes that forest ecosystems are mosaics that consist of hierarchical patches (Wu and Loucks 1995). The results indicated that the analysis of forest structural variation can be performed without relying on the delineation of distinct patches or on *a priori*-selected study scales. The scale selection that is based on the examined data increases the likelihood that the ecological systems are studied at the scales most where the most relevant processes occur (Hay et al. 2002; Scholes 2017; Estes et al. 2018).

The superimposed scales at which forest structure varied demonstrated hierarchical structure in the studied landscapes. This means that the small-scale variation occurred within the larger variation levels in a nested manner (Kotliar and Wiens 1990; Hay et al. 2002). Such hierarchical structure is a characteristic feature of ecological systems (O'Neill et al. 1986). It is well-known that forest structure varies at multiple spatial scales (Elkie and Rempel 2001). In the boreal region, the three commonly reported levels at which forest dynamics occur are gap, patch, and landscape scales (e.g., Zackrisson 1977; Pham et al. 2004; Kuuluvainen et al. 2014). However, the spatial scales at which forest dynamics occur are typically described only qualitatively (Angelstam and Kuuluvainen 2004, Bouchard et al. 2008). In chapter **II**, an objective identification and quantification of these scales was provided.

The largest scale at which variation in forest structure was identified differed the most between the landscapes. In contrast, the scales at which the mid- and small-scale variation occurred were remarkably similar in all five landscapes. The different spatial scales at which forest structure varies reflect the influence of drivers that shape forest structure at different scales, and their cumulative effects (Elkie and Rempel 2001, Wong and Daniels 2017). Because landscapes with different dominant tree species and disturbance regimes were analyzed, also the scales at which forest structure varies were expected to differ. The observed similarity of the mid-, and small-scale variation suggests that at these scales natural boreal forests may display characteristic levels of variation that are somewhat independent of the dominant tree species or disturbance regime of a landscape. At large-scales, the characteristic scales of variation differed between the studied landscapes.

Scale-dependent processes caused variation in forest structure at multiple spatial scales (II)

In an effort to determine the processes that cause scale-dependent variability in the structure of natural boreal forests, patterns of spatial variability at the three spatial scales identified in chapter **II** were analyzed in relation to factors that could be underlying these variation patterns. Key assumptions in the analysis of the factors that cause variation in forest structure is that the variation patterns at a particular scale are indicative of driving processes (Wu and Loucks 1995; Elkie and Rempel 2001), and that the examination of these patterns and their linkages to driving processes can be used to analyze how forest ecosystems function (Craver and Bechtel 2007). The results indicated that the processes that cause spatial variability in forest structure were scale-dependent. This means that the studied processes influenced forest structural variability at a specific spatial scale. However, certain processes partly crossed spatial scales, meaning that these processes created structural variation at multiple spatial scales.

The examined topographical variables included elevation, slope steepness, slope aspect, and topographic position. Of these variables and at large scale, canopy cover variation had the strongest correlation with elevation in all landscapes. At large scale, Spearman’s rho (r) between the relative canopy cover and elevation ranged from -0.34 to -0.89 in Hirvaskangas, Hongikkovaara and Pistuacanis. In Pommituskukkulat and Lac Dionne the relationship between relative canopy cover and elevation was positive (r = 0.21, 0.18, respectively). The negative correlation between relative canopy cover and elevation was suggestive of limited nutrient and moisture availability with increasing elevation (Seibert et al. 2007), a mechanism previously noted to influence forest structure in both studied regions (Roiko-Jokela 1980; Boucher et al. 2006). The modest elevation differences in the three landscapes (100–150 m) further suggest that soil characteristics instead of weaker growth conditions due to decreasing temperatures with increasing elevation could explain the dependency between the relative canopy cover and elevation. In Lac Dionne, the positive relationship could be due to elevational change in hydric conditions, as the low-lying areas are prone to paludification, and consequently have low productivity and relative canopy cover (De Grandpré et al. 2000; Simard et al. 2007). In Pommituskukkulat the positive relationship could be due to disturbance history more than an elevational effect *per se*. The high elevation areas experienced a fire in 1831 (Aakala 2018) and were dominated by deciduous trees at the time of the newest photographs. Also the canopy cover was relatively high in these areas.

At mid-scale, topographic position correlated negatively with relative canopy cover in Lac Dionne. This indicates that the areas with lower elevation than the surrounding areas also had lower canopy cover than the surrounding areas. Similar to the large-scale dependency between elevation and relative canopy cover in Lac Dionne, this relationship was probably explained by the low productivity of the low topographic positions associated with paludification (Simard et al. 2007).

The influence of recent disturbances on forest structural variability was examined by testing for the dependency between relative canopy cover and relative dead wood basal area at all scales. Recent disturbances influenced forest structure at mid- and small-scales, indicating that the influence of disturbances to forest structural variability crossed spatial scales. At mid-scale (1.3–2.8 ha), this dependency showed wide spatial variability (Fig. 4 in **II**), the credible correlations being both positive and negative. The counter-intuitive positive relationship between relative canopy cover and relative dead wood basal area could have be due to soil properties. The more productive sites sustain more trees compared to the less productive sites. Consequently, the more productive sites can also have more dead trees than the less productive sites (De Grandpré et al. 2000; Kuuluvainen et al. 2014). The negative relationship indicated that tree mortality due to recent disturbances caused patch-scale structural variation in the studied natural boreal forests (D’Aoust et al. 2004; Kuuluvainen et al. 2014), as well as at small, stand-scale (0.1 ha). Especially the stand-scale variability due do disturbances is common in boreal forests (e.g., Pham et al. 2004; St-Denis et al. 2010).

Many of the credible variation patches at mid-scale were located in areas where tree species composition changed, suggesting a dependency between tree species composition and forest structural variability at this scale. This dependency was attributed to edaphic conditions and/or time since the last stand-replacing, both of which are reflected on the tree species composition and tree density (De Grandpré et al. 2000; Kuuluvainen et al 2017).

Recent and historical disturbances and tree species composition were identified as the primary drivers of forest structural variability at mid scale. However, soil characteristics influence tree species composition (Rowe 1972; Sutinen et al. 2002) and fire occurrence (Wallenius et al. 2004; Mansuy et al. 2010) in both studied regions. Tree species composition further influences the susceptibility of a forested stand to a specific disturbance. For example, *A. balsamea*-stands in Quebec are especially vulnerable to spruce budworm defoliation (D’Aoust et al. 2004; Hennigar et al. 2008), while windthrow is a common disturbance type especially in *P. abies*-stands of Fennoscandia (Shorohova et al. 2011). Similarly, topography may change the predisposition of forest stands to high winds (Ruel et al. 1998). These examples indicate that the scale-dependent variability in forest structure is ultimately caused by interactions between multiple driving factors. Hence, similar to an analysis of forest ecosystem change, the linkages between the driving processes and forest structural variability should be interpreted carefully (Emmett et al. 2019).

Further, the studied landscapes were only 4 km² in size. This is well below the area of stand-replacing fires that occur in Quebec (De Grandpré et al. 2000). For example, fire that occurred in 1810 covered the Lac Dionne landscape completely (Bouchard et al. 2008). Due to the small landscape size, the influence of stand-replacing fires to forest structural variability could not be analyzed, and the occurrence of some relevant forest structural variability at scales beyond the extent of the study is evident.

Large scale processes drove canopy cover increase in most landscapes (I, III)

Visual canopy cover interpretations from three time points were used to examine how natural boreal forest structure changes in time. First, general changes in canopy cover were analyzed by quantifying mean canopy cover changes during three different time intervals in the five study landscapes (**I**). The time intervals are denoted whole time interval (newest photograph – oldest photographs, 38 – 52 years), first time interval (middlemost photograph – oldest photograph, 16 – 32 years), and second time interval (newest photograph – middlemost photograph, 20 – 24 years). Second, how boreal forest structure changed at different spatial scales over the same time intervals was examined (**III**). The calibrated raster maps and error distributions presented in chapter **I** were utilized for these purposes.

The mean canopy cover (quantified over the whole landscape) increased in the Finnish landscapes, independent of the studied time interval (Table 2, **I**). Mean canopy cover increased most during the whole time interval, and more during the second than during the first time interval. In Quebec, mean canopy cover decreased during the first and increased during the second time interval. The decrease was larger in Pistuacanis than in Lac Dionne landscape. Consequently, mean canopy cover increased in Lac Dionne during the whole time period, while in Pistuacanis the mean canopy cover change was zero (**I**).

Consistent with the hierarchy theory (O'Neill et al. 1986) and the hierarchical patch dynamics concept (Wu and Loucks 1995), three to four distinct, hierarchical spatial scales at which canopy cover changes occurred were identified with scale-derivative analysis (Pasanen et al. 2013), the exact number of scales depending on the studied landscape and time interval (**III)**. Examining the whole time interval, canopy cover changes occurred at three spatial scales. During this time interval, the credible changes at the largest identified scale (15.4–125.6 ha) indicated canopy cover increase in the Finnish landscapes and in Lac Dionne, Quebec, while Pistuacanis landscape showed both credible increase and decrease in canopy cover. These large-scale patterns were reflective of the cover changes in mean canopy cover (**I)**.

While the drivers of canopy cover change were not explicitly analyzed, the identification of the scales at which forest structure changes allows for speculation of the factors driving these changes (Elkie and Rempel 2001). The mean canopy cover increase (**I**) together with the large scale canopy cover increase (**III**) suggest that the Finnish landscapes and Lac Dionne landscape in Quebec were responding to large scale drivers that cause an increase in tree canopy cover. Pistuacanis landscape did not show similar canopy cover development. Instead, the temporal pattern of canopy cover development is probably reflective of the well-documented spruce budworm *Choristoneura fumiferana* (Clem.) outbreak that occurred in the region from the 1970s to the mid-1980s (Bouchard and Pothier 2010), and the consequent recovery of the forest after the end of the outbreak.

Table 2. The mean canopy cover change (as percentage points), its standard deviation and range in the studied landscapes during the three time intervals.

	Hirvaskangas			**Pommitus-kukkulat**			**Hongikkovaara**			**Lac Dionne**			**Pistuacanis**		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Whole time interval	7	6	-18–34	16	9	-13–41	11	7	-13–37	6	12	-37–41	0	15	-40–41
First time interval	1	7	-28–39	4	8	-22–34	2	7	-27–25	- 3	11	-39–32	-7	13	-42–40
Second time interval	5	5	-31–27	12	7	-17–34	9	6	-11–36	9	8	-34–33	7	13	-37–36

The potential factors driving the canopy cover increase in the four landscapes are less evident compared to canopy cover change dynamics in Pistuacanis that could be attributed to disturbance and the following succession. Recent research conducted in the studied regions suggests that changes in forest structure that have occurred after the late 19th century could be related to changes in climate (Aakala et al. 2018; Hofgaard et al. 2018, Sulla-Menashe et al. 2018), as annual temperature and precipitation have significantly increased in both regions during this period of time (Yagouti et al. 2007; Kivinen and Rasmus 2015). This supports the notion that the observed canopy cover increase could indeed be due to improved growth conditions. However, other factors such as changes in disturbance regime (particularly prolonged fire return interval; Wallenius 2011; Drobyshev et al. 2017; Aakala 2018) and atmospheric nitrogen deposition (Henttonen et al. 2017) have also influenced forest growth and dynamics during the same period of time. Because multiple factors drive changes in forest ecosystems, the influence of a particular driver is difficult to differentiate (Emmett et al. 2019), and the drivers of the canopy cover increase cannot be explicitly determined based on the results.

Superimposed on the changes at large spatial scales, changes in canopy cover were identified at two smaller hierarchical scales (1.3–2.8 ha, mid-scale; 0.1 ha, small-scale) in all landscapes and during all time intervals (**III**). These scales correspond to the scales of patch and gap dynamics, respectively, that have been identified from boreal forests in both regions (Pham et al. 2004, Kuuluvainen and Aakala 2011; Shorohova et al. 2011), and attributed to disturbances (D’Aoust et al. 2004; Bergeron and Fenton 2012; Kuuluvainen et al. 2014). However, the results indicate changes at these scales even in landscapes where patch-scale disturbances were mostly absent (**II**). Together with the changes that occurred at large spatial scales, these multiscale changes demonstrate that forest dynamics occurs simultaneously at various spatial scales (Elkie and Rempel 2001). While the occurrence of gap- and landscape-scale dynamics in natural boreal forests is well-known (e.g., Zackrisson 1977; Kuuluvainen 1994), the occurrence of changes also at other scales further illustrates that natural boreal forest structure changes also at spatial scales other than these two commonly proposed scales (Bergeron and Fenton 2012; Kuuluvainen et al. 2014).

Canopy cover increased and decreased variably at small scales, but either predominantly increased or decreased at the large scale, depending on the landscape (**III**). This indicates scale-dependency in how forest structure changes. Due to this scale-dependency, studies which examine forest ecosystem change at different spatial scales may reveal changes with different magnitude or even with different direction (Marchand et al. 2018). This emphasizes that comprehensive understanding of forest dynamics necessitates that the scale of observation is explicitly considered in forest ecosystem change analyses.

CONCLUSIONS

Due to their long time span, broad spatial coverage, and wide availability, aerial photographs are a valuable resource in examining how forest ecosystems change over time. Similarly, the high quality of modern aerial photographs enables detailed spatial analysis of forest structural variability. A major issue in using aerial photographs to address how forest ecosystems change has been the lack of spatially explicit ground-truth values especially for the historic photographs. The results showed how the quantification of forest structural attributes from aerial photographs is prone to bias and random error, caused for example by differences in aerial photo quality and variation in tree species composition. Lacking the calibration data has meant that the influence of bias and random error has generally been neglected, limiting the usage of the extensive aerial photo records. This thesis presents a methodology with which the calibration data can be produced retrospectively using field- and tree-ring measurements, and showcases how the methodology can be used to study both abrupt changes (due to, e.g., disturbances) and the slow continuous changes (due to, e.g., tree growth) in forest structure. The presented methodology enables taking advantage of the extensive aerial photo records in forest ecosystem change analyses in biomes where tree-rings form.

Natural boreal forest landscapes showed characteristic scales at which forest structure varied and changed, and some (but not all) of these scales could be objectively discerned. The identifiable characteristic scales were consistent with the hierarchy theory which predicts that due to the loose coupling between the different scales, they can be identified and discerned. Moreover, the results supported the premises of both hierarchy theory and hierarchical patch dynamics concept by showing that forest ecosystems are hierarchically structured, and consist of nested levels that are separable. The successful identification of scales at which forest structure varied and changed indicated that forest ecosystem analysis does not need to rely on *a priori* identified study scales. Instead, the salient scales at which forest ecosystem varies can be identified from the analyzed data. Because of *a priori*-selected study scales, relevant information may remain outside the scale of observation. Hence, the selection of analysis scales based on the data is a valuable tool for forest ecosystem analysis.

As expected from the current ecological theory, natural boreal forest landscapes were dynamic environments, and their structure showed variability at spatial scales corresponding to gap, patch and landscape-level dynamics. This variability was further connected to driving processes such as disturbances that shaped forest structure at various spatial scales, and caused differences in how forest structural variability occurred among the landscapes and at different time intervals. The findings of this dissertation highlight the importance of gap and patch dynamics as drivers of natural boreal forest development. However, the change analyses that were based on an exceptionally long time series of calibrated aerial photographs also indicate that the majority of the studied landscapes are currently responding to large scale drivers that cause a trend-like increase in their canopy cover. This contradicts the conventional view that changes in the boreal old-growth forest structure are mostly due to gap dynamics, and further suggests that the ongoing changes may profoundly alter the structure and functionality of natural boreal forests in the studied regions.

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