CONCEPTUALIZING THE 'OLD-GROWTH' STAGE OF DEVELOPMENT ALONG CHRONOSEQUENCE AND PRODUCTIVITY GRADIENTS IN THE COASTAL MARITIME BOREAL FOREST

by
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ABSTRACT

I investigated stand development along chronosequence and site productivity gradients in Nova Scotia's coastal black spruce (*Picea mariana*) forests. I determined if gap-phase dynamics was contributing to uneven-aged structures, which is indicative of the 'old-growth' stage of stand development and increased structural complexity in lowland and upland ecosites. I found that small-scale disturbances were resulting in uneven-aged structures as the age of the oldest 30 % basal area increased. The upland sites had a higher growth rate, which was resulting in increased susceptibility and faster development of uneven-aged structures compared to the lowlands. Larger structural features and increased species diversity were not observed as stands aged. Older aged stands did exhibit decreased snag volume in the lowlands and increased snag density in the uplands. The onset of the 'old-growth' stage of development in the coastal boreal forest appeared to occur earlier than inland boreal forests located in Ontario and Quebec and other climax forest types in Nova Scotia. Because coastal black spruce forests are climax communities that exhibit unique structural features later in stand development, they should be included in regional old forest management practices.

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Old-growth forests are recognized as sanctuaries that reflect cultural and social values as well as being critical for preserving certain biodiversity and ecological values (Spies and Franklin 1996; Hunter 1998; Mosseler et al. 2003a, 2003b; Depsonts et al. 2004). In Canada, maintaining and managing old-growth forests is identified as an important policy and ecological issue (Mosseler et 2003b). With extensive forest management practices occurring across the country, the public has growing concern about the decline in the amount and distribution of old-growth forests at both regional-, and landscape levels (Mosseler et al. 2003b). Particularly in eastern Canada where Europeans first settled over five centuries ago, the amount of old-growth forests is estimated to comprise only 0.1 - 0.3% of the total forested landscape (Lynds 1992). Because old-growth forests are understood to contain rare features in an ecosystem, provincial governments have recognized the need to create policies and adapt management practices to identify, conserve and protect these diminishing communities.

Old-growth forests occur when autogenic or small-scale allogenic processes become the main agents influencing stand development (Oliver and Larson 1996; Chen and Popadiouk 2002). Stand development is defined as the change of stand structure over time. Although development is not a discrete and linear process, in the absence of stand-replacing events, most forests develop through four main developmental stages: stand initiation, stem exclusion, understory re-initiation and old-growth (Oliver and Larson 1996). Forests in the old-growth stage typically exhibit multi-cohorts and are dominated by long-lived species that have the ability to persist on a landscape through regenerating after small-scale disturbances (Oliver and Larson 1996).

Forest stand structures are broadly classified into two categories: even-aged (single cohort) or uneven-aged (multiple cohorts) (Kershaw et al. 2017). In general, even-aged stands are composed of trees that are relatively the same age and have originated from the same major disturbance (Oliver and Larson 1996; Spies 1996; Kershaw et al. 2017). Even-aged stands can result from successional dynamics with multi-aged cohorts, following the stem exclusion stage or understory re-initiation stage (Oliver and Larson 1996; Chen and Popadiouk 2002). A disturbance will either remove the overstory stems, enabling a new cohort to establish or a few stems will be removed, allowing remaining stems to occupy the newly created space in the canopy (Oliver and Larson 1996). Uneven-aged stands result from multiple smaller-scale disturbances that remove single or groups of trees from the stand (Kershaw et al. 2017). The stems suppressed in the understory are then able to grow into the canopy when a few stems are removed, resulting in cohorts from different disturbances occupying the canopy. This process is called gap-phase dynamics and allows the transition of a stand from an even-aged to uneven-aged condition composed of a mosaic of different ages, heights and diameters (Oliver and Larson 1996; Sturtevant et al. 1997). Therefore, large- and small-scale natural disturbance regimes dictate a forest's developmental pathway and its transition into the 'old-growth' stage of development.

A 'natural disturbance' can be defined as an event that disrupts the physical structure and/or resource availability of an ecosystem (White and Pickett 1985; Frelich 2002; Smith and Smith 2015). Natural forest disturbances regimes can be characterized by: 1) amount of forest removal above the forest floor; 2) frequency or return interval of the disturbance; 3) size and shape of the disturbed area and 4) amount of forest floor vegetation and soil removed (Frelich 2002; Neily et al. 2008). The impact of a disturbance also depends on the climate and weather, topography and landforms, soil type and properties, forest type and composition, age classes, and numerous other factors (Neily et al. 2008). Therefore, proper identification of the natural disturbances that affect an ecosystem is needed to gain an understanding of the forest dynamics that occur as a stand develops.

Along with stand age and natural disturbance regimes, site productivity also affects stand development by influencing development rates and altering the physical characteristics of the forest (White and Pickett 1985; Frelich 2002; Harper et al. 2002; Boucher et al. 2006; Brassard and Chen 2006; Kuttner et al. 2013; Smith and Smith 2015). Typically, stands with richer soil conditions (i.e. nutrients and moisture availability) develop quicker than sites with poorer soil conditions, resulting in uneven-aged structure (Boucher et al. 2006) and increased structural complexity occurring earlier (Harper et al. 2002; Brassard and Chen 2006; Kuttner et al. 2013; Moussaoui et al. 2019). Therefore, to define the ‘old-growth’ stage of development in forest communities where the late-successional features are unknown, the specific forest and site type as well as historical and current regimes of natural and human disturbances should be considered (Hunter 1998). The following section will discuss criteria typically used to identify and define a forest in the ‘old-growth’ stage.

Old-growth definitions

The term ‘old-growth’ encompasses numerous values, resulting in broad, conceptual definitions (Hunter 1998). Simplistic approaches to defining old-growth include Spies and Franklin's (1996) definition, which characterizes old-growth as late-successional trees, and free of human disturbance; Hunter's (1998) definition is relatively old and relatively undisturbed by humans. Davis (1996) also defines 'old-growth' as forests that have minor evidence of human disturbance, although he expands to include forests that have not experienced a catastrophic event and possess the characteristics of a 'virgin' forest condition. Furthermore, Cogbill (1996) suggests stands that have an average age of approximately half of the maximum longevity of the dominant tree species and contain maximum-aged trees are considered 'old-growth'. Although these definitions are broad, they fail to take into account the ecological process and perspectives of old-growth forests. Duchesne (1994) concluded that one, Canada-wide definition for 'old-growth' is contentious because of four main issues: 1) different values associated with old forests (i.e. ecological, social, economic); 2) different old forest conditions among forest regions and ecogeographic zones; 3) age criteria for the old-growth stage changing as forests age and; 4) definitions not flexible to accommodate all forest regions and old-growth ecosystems in Canada. Therefore, definitions need to incorporate the local ecology, forest type structure and development, and historical and current patterns of natural and human disturbance (Hunter 1998). Most definitions used in research have multiple criteria and can be fitted into one of the three definition categories: structural, successional, or biogeochemical (Wirth et al. 2009).

Structural definitions

Structural definitions of old-growth are typically based on quantitative measurements of structural conditions and usually identify a minimum age of a specific forest type (Kneeshaw and Gauthier 2003; Bergeron and Harper 2009). Franklin and Van Pelt (2004) identified two fundamental tendencies in structural old-growth characteristics: 1) accumulation of larger structures as both living and dead biomass and; 2) increase in structural complexity. Structural complexity is defined as the heterogeneous variability both vertically and horizontally across the landscape. These structural complexities have been understood to hold significant habitat and biodiversity values (Franklin and Van Pelt 2004; Bergeron and Harper 2009). Mosseler et al. (2003b) further identified three criteria that are important for old-growth age structure dynamics: 1) uneven-aged distribution; 2) mean age of dominant tree species is half the expected longevity of the species and; 3) some trees are close to their maximum longevity.

Structural characteristics such as height are typically correlated with age and can be used as proxies for determining the development stage of a stand (Wirth et al. 2009). Woody detritus, in the form of snags and downed woody debris (DWD), is another important structural component of forested ecosystems and can be an indicator of the mortality process based on the distribution and diversity of woody debris (Sturtevant et al. 1997; Brassard and Chen 2007). Typically, forests accumulate DWD in a ‘U-shaped’ temporal pattern following an initial stand-replacing disturbance with debris volume peaking during the transitional stage from even-aged to uneven-aged structure (Sturtevant et al, 1997; Spies et al., 1988; Brassard and Chen, 2007). Therefore, DWD decay class volume is used to define the stand’s development stage and the presence of gap disturbances.

These types of definitions focus on the physical attributes of a stand and are formulated to identify age thresholds that exhibit the appearance of gap-phase dynamics (Wirth et al. 2009). However, forest age thresholds are typically not abrupt or apparent

(Oliver and Larson 1996), and since there are numerous developmental pathways a forest can take to reach 'old-growth' state, discrete categories tend to contain arbitrariness (Hunter and White 1997; Hunter 1998; Pesklevits 2006). Therefore, the range of structural attributes that contribute to old forest conditions depends on the forest type, site productivity, and disturbance regimes (Duchesne 1994; Wirth et al. 2009). This contrast is evident when trying to define the Canadian coniferous forest. Duchesne (1994) used the example of Rowes' (1972) old-growth definition, which was based on the structural conditions of species situated in Pacific Northwest. Although the definition captures regional old-growth features, it does not accurately capture the structural conditions of old-growth forests dominated by white (*Pinus strobus*) and red pine (*P. reinosa*) forests in the Great-Lakes-St-Lawrence region (Day and Carter 1990).

Successional definition

Successional definitions of 'old-growth' can be used to address the ecological processes occurring as a forest develops. These processes include the transitions of early-successional cohorts following large-scale disturbances to late-successional species and the presence of gap-phase dynamics and single-tree replacement (Mosseler et al. 2003a; Fenton and Bergeron 2011). Based on such, Kneeshaw and Burton (1998) suggest a population-based definition that emphasizes cohort or age classes. Kneeshaw and Gauthier (2003) use this approach to define old-growth as 'the stage at which the original cohort begins to die and the understory stems are recruited to the canopy' (p.S102). By conceptualizing old-growth in this way, the mortality and recruitment processes of individual trees and cohorts associated with gap-phase dynamics are used to define ‘old-growth’, rather than structural attributes. Mosseler et al. (2003a), Wirth et al. (2009) and Fenton and Bergeron (2008, 2011) use generalized succession-based criteria, which includes the presence of late-successional tree species with ages close to their life expectancy or the mean age of trees is half the expected longevity of the dominating species and the presence of regeneration from gap-phase dynamics associated with the presence of shade-tolerant species, canopy gaps, large snags and logs in varying stages of decay.

Johnson et al. (1995) suggest that a proper concept of old-growth forests should be based on both landscape-level and stand-level properties. Spies and Franklin (1996) reiterate this concept by suggesting that the disturbance history of the cohorts of trees needs to be recognized rather than relying on age and structural characteristics. Therefore, alternative successional definitions determine a stand as ‘old-growth’ based on whether the age of the stand exceeds the expected return interval of the prevalent stand-replacing disturbances. From this definition, the identification of ‘old-growth’ is heavily dependent on the frequency and type of disturbance that influences a particular forest.

Biogeochemical definitions

Biogeochemistry refers to the natural cycle of biotic and abiotic elements being transferred and transformed within a natural environment or ecosystem (Butcher 1993). Examples of these biogeochemical cycles include the hydrological, carbon, nitrogen, and oxygen cycles. These cycles occur at all scales and can connect regional and global patterns and issues (Butcher 1993). Old-growth forests have been understood to function as regulators of the hydrological cycle and contribute to stable carbon and nutrient cycles. Therefore, old-growth forests' role in long-term carbon uptake and sequestration has been a topic of much discussion and debate (Wirth et al. 2009). Through studying carbon and nutrient cycles, Wirth et al. (2009) suggest that a decline in net primary production, biomass equilibrium, closed nutrient cycles and increased understory vegetation are all indicators of old-growth conditions and therefore use this criteria to define 'old-growth'. Although this type of definition can accurately account for functional processes across a multi-year ecosystem, quantification of these parameters is usually expensive and labour intensive (Wirth et al. 2009).

Application of old-growth definitions

Forests and natural disturbances regimes are diverse across Canada, resulting in definitions of 'old-growth' varying provincially. One strategy used by provincial governments to manage forests for multiple values, including old-growth forests, is through an ecosystem-based management approach. This approach accounts for the specific forest type and aims to emulate the inherent natural disturbance regimes (Oliver and Larson 1996; Bergeron et al. 1999; Frelich 2002). Therefore, to manage old-growth forests, many provincial forest managers have developed guidelines to identify the old-growth stage of development based on composition, structure and disturbance regimes (Bergeron et al. 1999; Rossi et al. 2009; Lecomte et al. 2016; Martin et al. 2018). Nova Scotia, Canada is a provincial example of applying an old forest definition that identifies an 'old-growth' age threshold based on structural and successional criteria.

Nova Scotia's 'old-growth' definition

The province of Nova Scotia is a peninsula located along Canada's east coast. The climate is influenced by its proximity to the Atlantic Ocean, resulting in harsh weather conditions, with milder winters and cooler summers compared to inland regions of Canada (ECCC 1990). Due to its climatic conditions and local geology, Nova Scotia's landscape is dominated by the Acadian Forest, with the exception of small areas of Maritime Boreal Forest located along the Atlantic Coast and Cape Breton Highlands (Neily et al. 2017; Figure 1.1.). The Acadian Forest is part of an ecological transition zone, which connects more northerly conifer forests and southerly temperate deciduous forests (Rowe 1972). The forest is characterized by the presence of red spruce (*Picea rubens*) and associated shade-tolerant species such as sugar maple (*Acer saccharum),* yellow birch (*Betula alleghaniensis)* and balsam fir (*Abies balsamea*). (Rowe 1972). In contrast, the Maritime Boreal Forest is characterized by the absence of red spruce and is dominated by black spruce (*P. mariana*), balsam fir, and white spruce (*P. glauca*) (Neily et al. 2017). Since European settlement, approximately 400 years ago, Nova Scotia's forests have been continuously exploited for their raw resources, resulting in the fragmentation of forests that exhibit pre-settlement conditions (Lynds, 1992). Therefore, the Nova Scotia government has recognized the need for identification and protection of these unique ecosystems through establishing and enacting the 'Old Forest Policy' (NSDNR 2012).

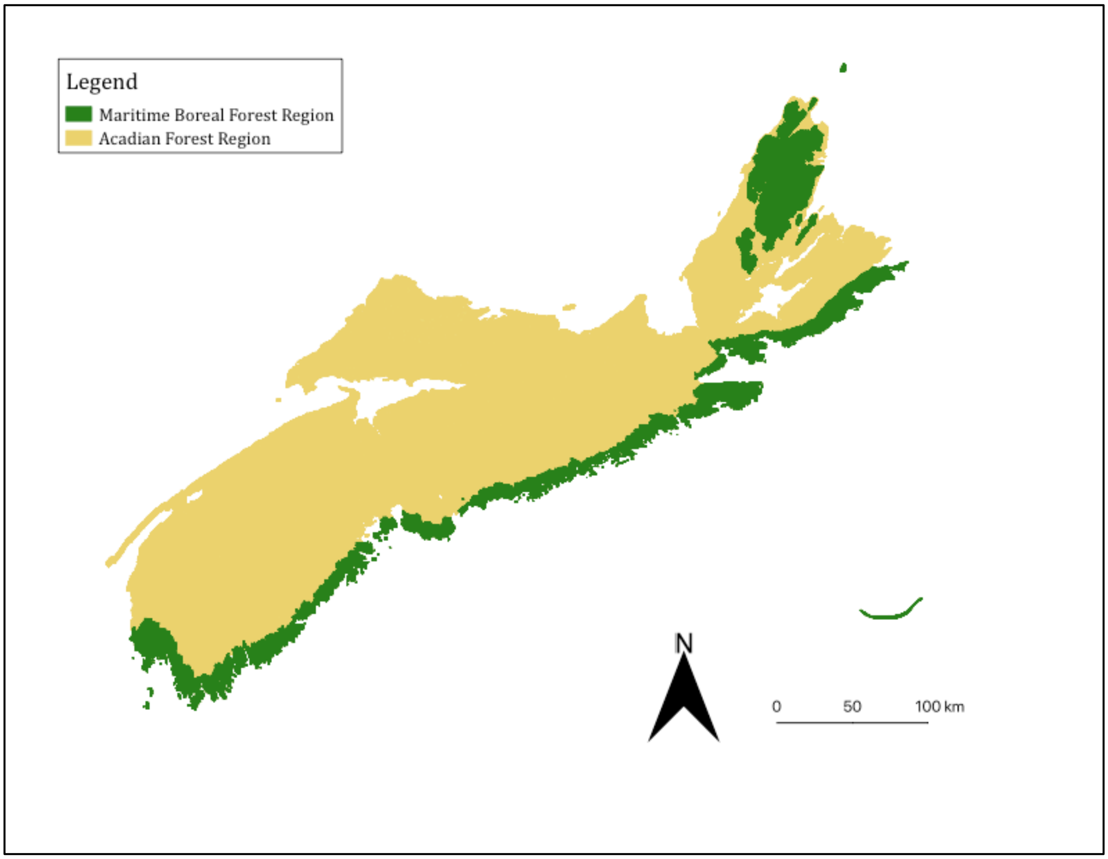

Figure 1.1. Nova Scotia's forest cover of Acadian and Maritime Boreal ecodististicts and ecoregions as identified by Neily et al. (2013).

Through this policy, Nova Scotia's Department of Lands and Forestry (NSDLF) has defined 'old-growth' as a forest that 1) contains 30% or more of the basal area in trees 125 years or older; 2) at least half of the basal area is composed of climax species and; 3) total crown closure is a minimum of 30%. This definition is based on the old-growth reference age (Stewart et al. 2003), majority of the stand (>50% basal area) occupied by climax species (Frelich, 2002) and canopy closure that distinguishes between the classification of a forested area and an open woodland (Neily et al. 2013). To quantify Nova Scotia's potential old-growth forests, an 'Old-growth Scoring' procedure is in place to allow NSDLF staff to identify and rank the 'old-growthness' of forest stands across the province (NSDNR 2012; Appendix A). 'Old-growthness' is defined as the degree of structural variability a forest stand expresses that which would be found in old-growth forests (Hunter and White 1997; Barbati et al. 2012). Hunter and White (1997) recommend using the degree of 'old-growthness' as an acceptable practice to gain an understanding of the overall stand characteristics and values.

However, the majority of old forest research in Nova Scotia has focused on the Acadian Forest types dominated by sugar maple*,* yellow birch, red spruce, American beech (*Fagus grandifolia),* eastern hemlock (*Tsuga canadensis)*, and eastern white pine (Lynds 1992; Mosseler et al. 2003a; Stewart et al. 2003; Pesklevits 2006), with minimal research (e.g. Neily et al. 2004) being conducted on zonal and edaphically limited Maritime Boreal climax species such as black spruce, balsam fir and red maple (*Acer rubrum*). Therefore, the 'Old-growth Scoring' and definition criteria are skewed towards species that dominate the Acadian Forest Region, which typically have greater longevity and exhibit larger structural features than the boreal (Stewart et al. 2003; Neily et al. 2004). To determine if the current definition applies to the coastal boreal forests, the characteristics of the old-growth stage need to be quantified. Currently, there are no forest data collected on the old-growth stage of Nova Scotia's coastal boreal forest. Therefore, the regional forest type and local disturbance regimes will be assessed to gain an understanding of the ecological processes that are contributing to late-successional coastal boreal forests.

Nova Scotia's coastal boreal forest

Forest type

From the list of Maritime Boreal climax species, black spruce typically dominates the coastal inland landscape (Rowe 1972; Davis and Browne 1996), is understood to have a longer life expectancy than the other listed climax boreal species (Lynds, 1992), and has the ability to self-replace after frequent or infrequent disturbance events (Spies and Franklin, 1996; Frelich, 2002). Spies and Franklin (1996) categorize black spruce as both a short-lived species, typically living less than 250 years, with the ability to mature through small- (i.e. < 0.1 ha) and large- (i.e. >0.1 ha) scale disturbances. Comparing this forest type to Nova Scotia's Acadian forest types, Lynds (1992) recognizes black spruce as a stable "non-climax" forest system and suggests this forest type, amongst others, deserves to be considered as regional successional old-growth.

To distinguish a forest's site productivity, Nova Scotia's Department of Lands and Forestry's (NSDLF) Forest Ecosystem Classification (FEC) guide (Neily et al. 2013) has determined that black spruce forests along the Atlantic coast have poor nutrient availability and a fresh to wet moisture regime. Depending on the moisture regime, coastal black spruce forest site productivity can be identified as either 1) Edaphic Wet-Poor Black Spruce (MB4) or 2) Edaphic/Zonal Fresh/Moist-Poor Black Spruce (MB2 and MB3).

Natural disturbance regimes

Natural disturbances influence forest and landscape dynamics and have shaped forests throughout Nova Scotia (Neily et al. 2008). Previous knowledge of Nova Scotia's Atlantic coast suggests that 72% of forests experience frequent disturbances, 7% experience infrequent and 0% experience gap dynamics (Neily et al. 2008). The following sections will detail the main types of natural disturbances occurring in Nova Scotia and discuss their current frequencies within the coastal Maritime Boreal Forest.

Wildfire

Fire is a major disturbance agent that has shaped Canada's boreal forest landscape. To determine the successional fire history of Nova Scotia's modern forests, Green (1981; 1982) and Livingston (1968) have analyzed pollen and charcoal deposits in lake sediments throughout Nova Scotia. Through these analyses, it is determined that the post-glacial vegetation consisted of spruce, pine and fir, matching surface strata found in the forested regions of Labrador (Livingston 1968). Spruce began to dominate the early forest landscape (10,500 – 9000 years B.P), resulting in a frequent fire regime (Green 1981). However, as the climate warmed, landscapes transitioned to pine-dominant and then pioneer hardwood-dominant forests (Green 1981). This transition created a mixing of conifer and hardwood species. Because hardwood species are less flammable, fewer intense fires and a lower fire frequency occurred between 6000 – 4000 and 3400 – 0 year B.P (Green 1981). With a less severe fire regime, shade-tolerant species such as American beech, sugar maple and yellow birch came to dominate. After 4000 B.P., the climate began to cool and become wetter, allowing for the resurgence of spruce mixed with fir and larch (*Larix*). The less severe fire regime also contributed to an 'equilibrium' period for vegetation community stability, which has resulted in the mixed forest structure present today (Green 1981). However, fire-adapted species such as jack (*Pinus banksiana*), eastern white and red pine and white and grey birch (*Betula populifolia*), and northern red oak (*Quercus rubra*) are evidence of the active presence fire still has on regional forest conditions (Louck 1962; Rowe 1972). This historic timeline of vegetation history, although simplified, outlines the role climate has had on the natural fire disturbance cycle and the complex composition structure of Nova Scotia's modern forests (Livingston 1968; Green, 1981; 1982).

During pre-European settlement times, the use of fire by the Mi’kmaq First Nations communities was evident (Drushka 2003; Joudry 2016), however Livingston (1968) concluded that there was no noticeable impact on forest composition during this time. Once Europeans began to explore and settle (1500-1914), human-caused wildfire became a prevalent disturbance occurring across Nova Scotia (Fernow 1912; Wein and Moore 1978). Vast amounts of unwanted forests were land-cleared by fire for agricultural use (Wein and Moore 1978; Drushka 2003) and localized encampment fires frequently became rampant. Particularly in the Atlantic coastal region, fires were used by settlers to expand their pasture land (Loucks 1962) and clear the forest undergrowth (Drushka 2003). Due to the pre- and post- settlement influences on Nova Scotia’s landscape, the true natural fire cycle is a contentious issue. Therefore, the following fire frequencies discussed may not only reflect the natural fire disturbance but a combination of human- and natural-caused occurrences.

Methods such as charcoal fragment analyses in lake sediment (Swain, 1973), pollen deposit analyses (Green 1981; 1982, Livingston 1963) and historical records (Fernow 1912; Wein and Moore 1977; 1978) have been used to determine the fire frequency and date the history of wildfires on the landscape. Black spruce research conducted in the interior boreal of Ontario and Quebec suggests fire frequency typically ranges between 47 to 172 years (Kneeshaw and Gauthier 2003); averaging around 100-year return intervals (Johnson 1992). However, frequency rates and rotation patterns are different within Maritime provinces (Fernow 1912; Wein and Moore 1977; 1978).

In recent history (1919 to 2018), the number of fires per year has not changed significantly, typically ranging between 200-500 fires, however the area of forests burned substantially decreased from 30,000 ha yr^{-1} to <500 ha yr^{-1} (Taylor et al. 2020).

Because of intense fire suppression activities, most of the fires in the last decade have been <10 ha (Wein and Moore 1978). Taylor et al. (2020) have mapped the locations of fires since the 1950s and identified fewer fires occurring in the Cape Breton Highlands and parts of the eastern and western ecoregions, particularly along the eastern coast and inland region (Figure 1.2.). The map compilation accounts for the temporal variation of fire frequency across the provincial landscape and shows that the fire frequency is not the same for the entire province.

Based on provincial fire records between 1915 and 1975, Wein and Moore (1978) calculated the return interval for Nova Scotia to be 1,000-2,500 years for the time after fire suppression was initiated. This interval is significantly higher than the pre-suppression return interval estimate of 200 years (Fernow 1912) and 400 years (Green 1981). Wein and Moore (1979) then examined return periods based on Louck's (1976) vegetation types and compared their findings with Fernow's calculations (1912). For the landscape along the coast, indicated as the spruce-fir coastal vegetation group, Fernow (1912) estimated the annual burn percentage to be 0.18%, a 555-year return period, while Wein and Moore (1978) determined the annual burn percentage to be much lower at 0.05%, a 2,000-year return period. The most recent estimate from Taylor et al. (2020) is based on the forest type and ecosite and suggests the annual burn percentage is 0.14%, which is a 600-year return interval for boreal forests located along the Atlantic coast.

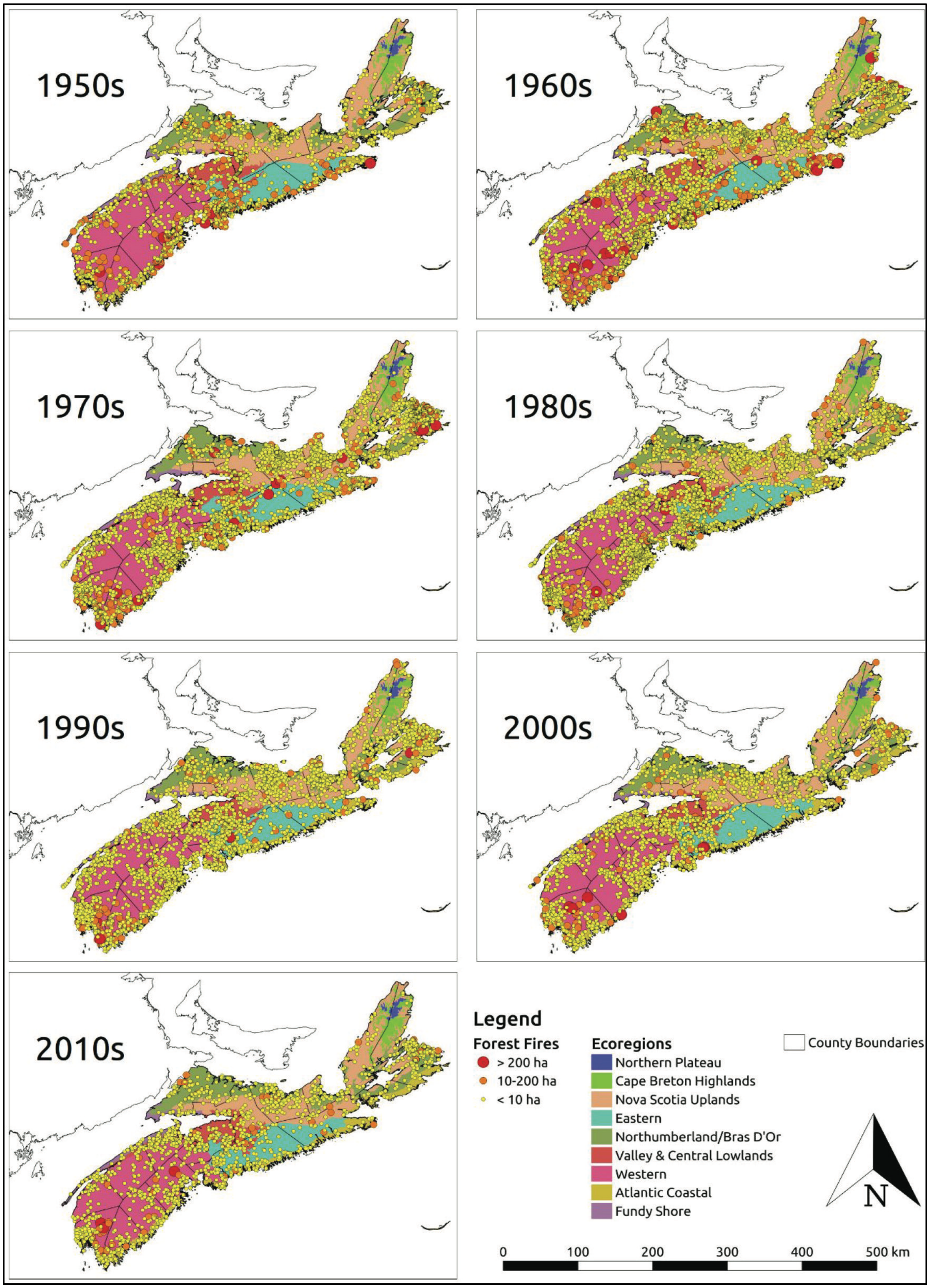

Figure 1.2. Maps of Nova Scotia compiled by Taylor et al. (2020) showing the locations and size of fires within Nova Scotia's ecoregions between 1950 to 2019. Minimal fire activity is noticeable in the Western and Eastern inland areas.

Spruce budworm

Similar to wildfires, spruce budworm (*Choristoneura fumiferana*) epizootics have been influential in the development of Nova Scotia's spruce-fir forests. Although balsam fir and white spruce are the most susceptible to spruce budworm defoliation, black and red spruce are also affected (Hennigar et al. 2007). There have been seven recorded widespread epizootics of the spruce budworm within the last 250-300 years in eastern Canada (NSDLF 1977; Blais 1983). In Nova Scotia, the spruce-fir forests in the Cape Breton Highlands are most affected, with evidence of epizootics occurring in 1846, 1819-1896, 1911-1915, 1922-1927, 1960-1963, and 1974-1981 (NSDLF 1977; Blais 1983; Ostaff and MacLean 1989). However, epizootics are not isolated to Cape Breton; major infestations have also occurred along with the eastern mainland counties between 1951-1955 (NSDLF 1977). Taylor et al. (2020) examined and compiled maps of defoliation between 1912 and 1986 and found that Cape Breton Island, the Northumberland, Bras D'Or, and Nova Scotia Uplands ecoregions were the most severely affected areas (Figure 1.3.). They also acknowledged a distinct line, where little to no spruce budworm defoliation occurs southward. Along with the western region, the eastern Atlantic coast has little to no evidence of spruce budworm activity. This observation is supported by Hardy et al.'s (1986) and Williams and Birdsey's (2003) spruce budworm map compilations of eastern North American (Figure 1.4.). These maps both identified three areas that were not affected by the spruce budworm: southern Maine, the northern Lake States and southern Nova Scotia. The main contributor to this is the localized climate and temperature, which can inhibit the overwintering survival of the larvae (Régnière et al. 2012). Taylor et al. (2020) estimate that the return interval for spruce budworm along the Atlantic coast is 0.05%, which is approximately every 2,000 years.

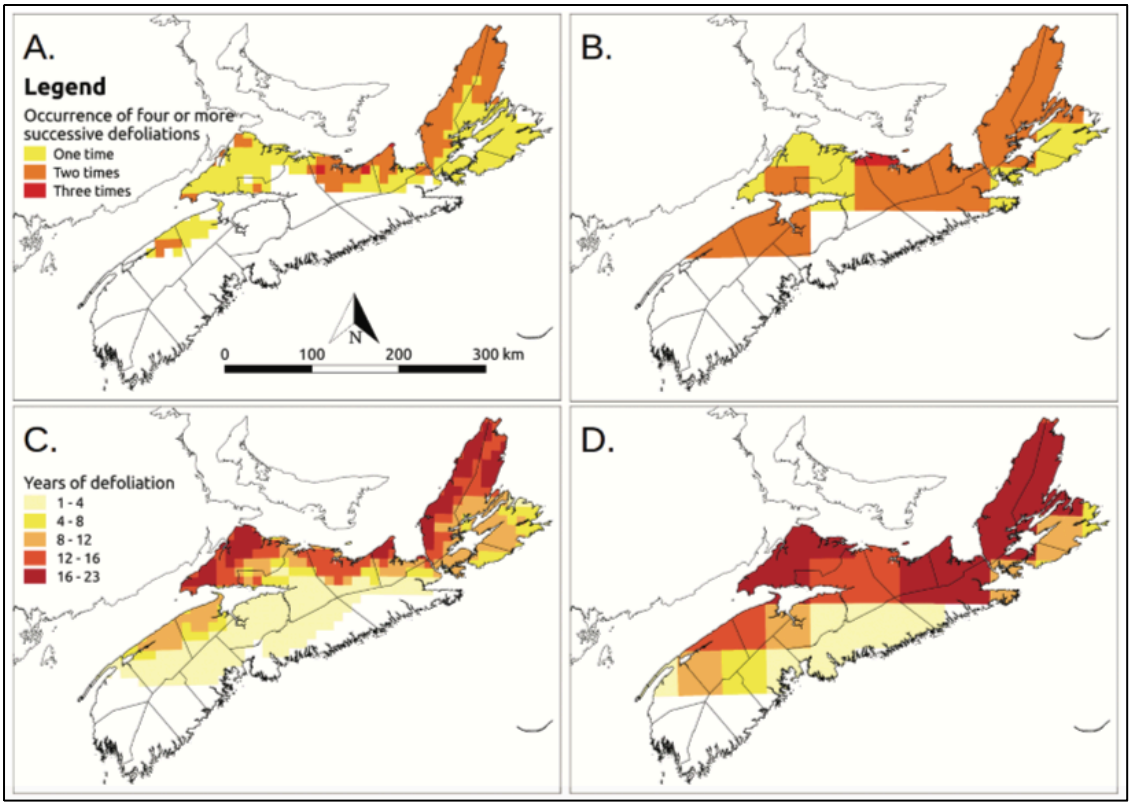

Figure 1.3. Maps compiled by Taylor et al. (2020) that summarize the location and severity of spruce budworm epizootics across Nova Scotia (1912-2018) in two scales: 10km x 10km (A, C) and 50km x 50km (B, D). Maps A and B show occurrences of defoliation every four or more successive years, while maps C and D show the total number of years of defoliation.

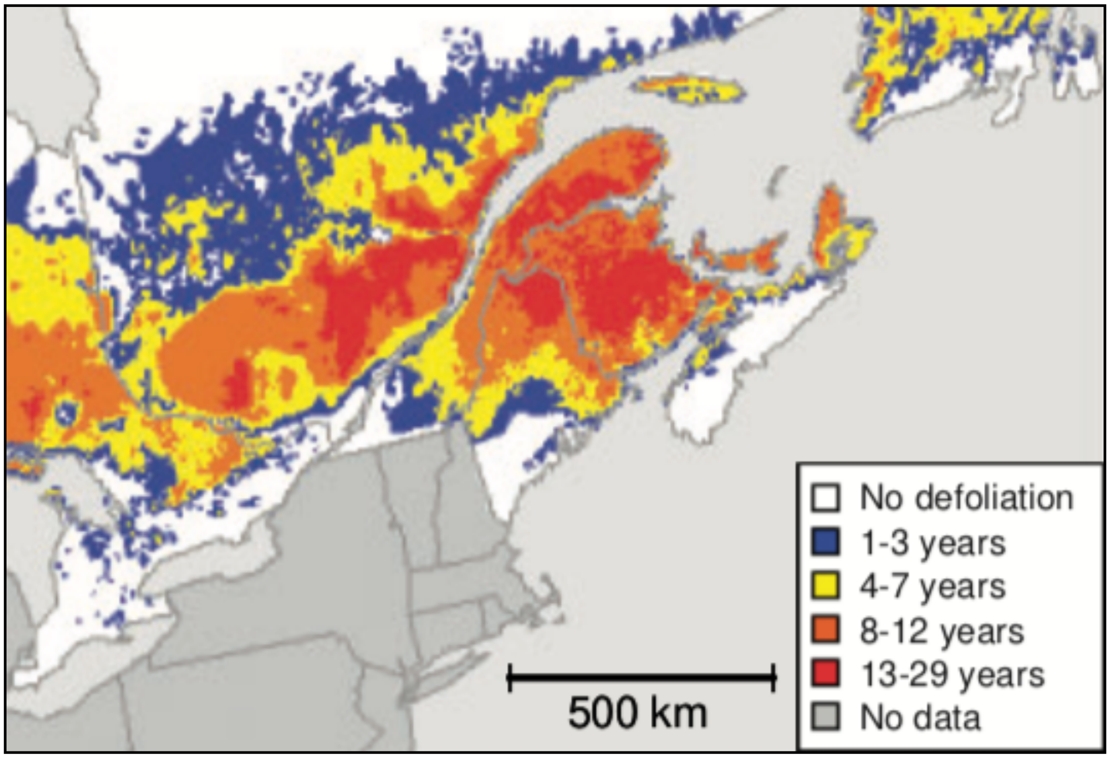

Figure 1.4. William and Birdsey's (2003) spruce budworm compilation. The areas are identified based on the frequency of defoliation between 1954 and 1988. A divide is evident in southern Maine, the northern Lake States and southern Nova Scotia between spruce budworm defoliation and no defoliation.

Wind events

Wind is a prevalent disturbance agent of forest dynamics in Nova Scotia due, in part, to the proximity to the ocean (Seymour et al. 2002; Neily et al. 2008; Taylor et al. 2019). The impact that wind has on a forest is influenced by a stand’s windthrow probability, which is determined by two components: the resistance threshold of a stand and the occurrence of strong winds (Bouchard et al. 2009; Taylor et al. 2019). The resistance threshold determines the stand’s ability to withstand severe wind and is dependent on soil characteristics and forest structure and composition (Bouchard et al. 2009). The occurrence of strong winds is dependent on topographic location and categorized by meteorological variables including the intensity and sustained wind speed, duration of the event, and precipitation before and during the event (Bouchard et al. 2009). Generally, Nova Scotia experiences two types of major wind events: windstorms and hurricanes.

Windstorms are considered to have wind intensities between 50-100 km/hr because events that have sustained winds of less than 50 km/hr are unlikely to cause significant wind damage (Stathers et al. 1994). In eastern North America, several researchers (Dunn et al. 1983; Canham and Loucks 1984; Boose et al. 1994; Foster et al. 1998; Frelich, 2002) found that 100-120 km/hr winds cause minor damage to trees, 140-180 km/hr winds cause partial destruction of the forest canopy, and > 200 km/hr winds cause severe canopy destruction, resulting in two thirds or more of the stand basal area to be removed in mature or old-growth stands.

The largest windstorms that affect Nova Scotia are extra-tropical cyclones (ETC), also referred to as mid-latitude cyclones, low-pressure systems or ‘nor’easters’ (Taylor et al. 2020). These windstorms can produce sustained northeast winds of 100 km/hr, bringing rain and/or snow. However, most of these windstorms have < 40 km/hr winds, with fewer than 2% of annual windstorms reaching > 90 km/hr winds (Plante et al. 2015). Another type of windstorm that is more compact and originates from the tropical ocean are tropical storms. With 56-104 km/hr winds, tropical storms can have the same widespread effect on forests.

The National Oceanic and Atmospheric Administration (NOAA) have tracked and recorded major wind events across the world since 1862. From this inventory, between 1900 and 2019 Nova Scotia experienced a minimum of 27 tropical storms, averaging to approximately one every four years (NOAA 2019). The most recent tropical storm was tropical storm Dorian in 2019, with sustained winds of 65 km/hr, producing extensive damage to trees and powerlines. Other windstorms include convection storms, tornados and severe thunderstorms, which are either uncommon or do not result in significant, widespread damage.

Taylor et al. (2020) used Nova Scotia's Department of Lands and Forestry's (NSDLF) inventory of permanent sample plot (PSP) network to estimate the windthrow damage rates caused by windstorms. They found that 93% of plots did not show evidence of any significant damage (i.e. > 5% downed tree biomass) between 2008-2017. The low severity windthrow is given a lower limit of 5% to account for the natural senescence of trees in the forest. Table 1.1 outlines the estimated annual disturbance rate and return intervals depending on wind severity. In the Atlantic coastal ecoregion, there is little evidence of any high to moderate severity events and the ecoregion experienced approximately the same annual disturbance rate as all of Nova Scotia (1.4%).

Table 1.1. Estimate of annual disturbance rate and return interval from wind severity based on NSDLF's PSP inventory (Taylor et al. 2020).

Severity	Downed tree biomass (%)	Mean Annual Disturbance Rate (%)	Return Interval
High	(>60)	0.02	5,000
Moderate	(30-60)	0.02	5,000
Low	(5-30)	1.4	71

Once a tropical cyclone has reached 104 km/hr winds or sustained winds of 119km/hr for one minute, it is then classified as a hurricane (NOAA 2019). Hurricanes are classified through Saffir-Simpson (SS) wind intensity index, which is a wind scale divided into five categories and based on the highest average one-minute interval. Taylor et al. (2020) found that from 1900 to 2018, approximately thirteen SS1 and four SS2 hurricanes passed through Nova Scotia, averaging one hurricane every seven years (NOAA 2019; Figure 1.5.). Similar to windstorms, hurricanes can cause widespread forest damage, however no reliable data has been recorded on the extent of damage in Nova Scotia (Taylor et al. 2019). The most recent SS2 hurricane, Hurricane Juan in 2003, has been the most documented (Bruce 2004; Taylor et al. 2019) and is used as a representation to estimate the wind damage rate. Through aerial photography and Landsat 5 imagery, NSDLF staff identified 91,484 ha of wind damage caused by Hurricane Juan. Taylor et al (2019) determined that the most influential variables affecting windthrow are wind speed and stand structural variables, particularly height and species composition. Taller stands dominated by spruce and balsam fir are more susceptible to windthrow than stands with higher proportions of pine and hardwood species (Taylor et al. 2019). Although Hurricane Juan was an unusually strong hurricane for Nova Scotia, global climate models predict that such events will become more common over the 21 century (Dale et al. 2001; Knutson et al. 2010; Taylor et al. 2017). Table 1.2 outlines Taylor et al.'s (2020) findings and concludes that, although the estimates may reflect the maximum disturbance levels, they are similar to disturbance rates found in the Lake States (Frelich and Lorimer 1991) and New England forests (Foster and Boose 1992; Lorimer and White 2003).

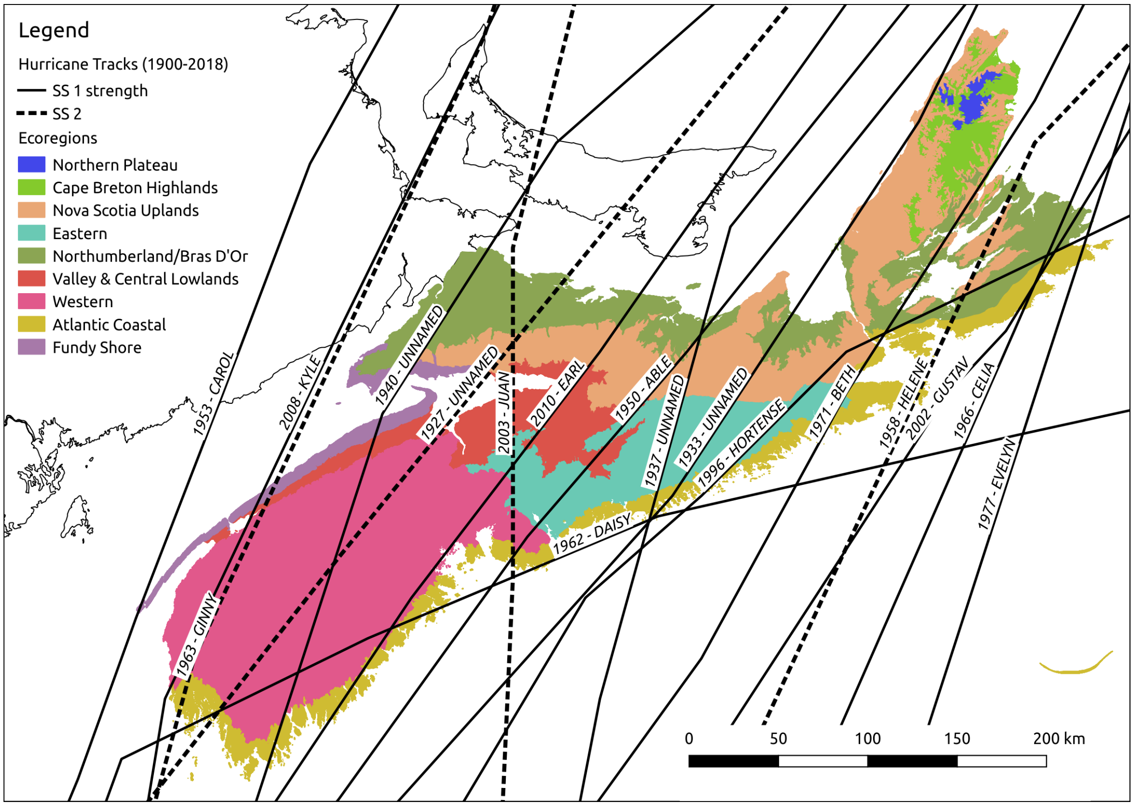

Figure 1.5. Hurricane tracks of the thirteen hurricanes passing through Nova Scotia between 1900- 2018 (Taylor et al. 2020).

Table 1.2. Estimates of forest damage, disturbance rate and return interval from wind severity after Hurricane Juan (2003) (Taylor et al. 2020).

Severity	Downed tree biomass (%)	Windthrow Damage (ha)	Forest Damage (%)	Mean annual disturbance rate (%)	Return Interval
High	(> 60)	22,871	25	0.08	1250
Moderate	(30-60)	41,083	49	0.14	714
Low	(<30)	26,530	29	0.09	1111

Nova Scotia's Maritime Boreal Forest development

Although extensive research has been conducted on Acadian Forest types (Mosseler et al. 2003a; Stewart et al. 2003; Pesklevits 2006), minimal research (e.g. Neily et al. 2004) has been conducted Nova Scotia's Maritime Boreal Forest. Recent research on old-growth boreal forests in eastern Canada suggest that, although stand-replacing disturbances remain an important agent for forest development, gap-phase dynamics are also an important process (Kneeshaw and Gauthier 2003; Pham et al. 2004; Harper et al. 2005; Boucher et al. 2006; Bergeron and Harper 2009; Lei et al. 2009; Rossi et al. 2009; Fenton and Bergeron 2011). However, the majority of this research has been conducted in interior boreal forests of Ontario and Quebec, where wildfire and spruce budworm epizootics are the two main natural disturbances contributing to stand development (Johnson 1992; Boucher et al. 2006). The research concludes that gap-phase dynamics are contributing to uneven-aged structures as forests develop. The uneven-aged forests typically have distinctly different structural attributes compared to even-aged, including increased diversity of heights and diameters (Kuttner 2013), larger deadwood features (Harper et al. 2005) and the presence of late-successional, shade-tolerant species (Rheault et al. 2009; Rossi et al. 2009; Wirth et al. 2009). Furthermore, it is understood that the transition from even-aged to uneven-aged stand structures can be significantly influenced by site productivity, resulting in less productive sites transitioning later in stand development (Harper et al. 2005; Boucher et al. 2006).

Currently, there is a knowledge gap in our understanding of stand development in forests located directly along Canada’s eastern coast. Due to higher precipitation levels and a moister climate, the boreal forests located along the coast of Nova Scotia are classified as ‘wet boreal’ (Rowe 1972) and experience a lower fire frequency (Wein and Moore 1978; McCarthy 2001; Thompson et al. 2003; Harper et al. 2005; Lecomte et al. 2006) and fewer spruce budworm epizootics (NSDLF 1977; Blais 1983) compared to other areas of eastern Canada. Instead, low severity windstorms are the prevalent natural disturbance occurring in this region (Fenton and Bergeron 2011; Taylor et al. 2019, 2020; Table 1.3). Therefore, the overarching goal of this research is to identify the successional processes (i.e. gap-phase dynamic or landscape-scale) and their influence on stand development in the boreal forest located directly along Nova Scotia's Atlantic coast.

Table 1.3. Main disturbance frequencies for Nova Scotia's coastal Maritime Boreal Forest (Taylor et al. 2020)

Disturbance	Severity	Mean annual disturbance rate (%)	Return Interval
Wildfire	High	0.16	600
Spruce budworm	High	005	2,000
Windstorm	High	0.02	5,000
	Moderate	0.02	5,000
	Low	1.4	71
Hurricane	High	0.08	1250
	Moderate	0.14	714
	Low	0.09	1111

Structure of thesis

This thesis is presented in a journal article format. Chapter 2 is formatted for the *Canadian Journal of Forest Research*. In Chapter 2, I investigate the characteristics associated with the 'old-growth' stage of development in Nova Scotia's coastal boreal black spruce forests. Based on the main disturbance of low severity windstorms and black spruce forest type, I hypothesize that gap-phase dynamics, opposed to landscape-scale processes, is the prevalent natural disturbance contributing to stand development. As a result, I predict that uneven-aged stand structures occur later in stand development and are more structurally diverse than even-aged structures. Site productivity can also influence stand development, therefore I further predict that richer, upland sites develop uneven-aged structures faster than poorer, lowland sites. I accomplish these tasks by examining three objectives that focus on successional and structural forest attributes across a chronosequence and between lowland (edaphic, wet-poor) and upland (edaphic/zonal, fresh/moist-poor) black spruce sites.

The first objective determines if stand age structure transitions from even-aged to uneven-aged. I classify each stand as even-aged or uneven-aged based on probability density functions and discuss when the temporal transition is occurring in each ecosite. The second objective assesses whether gap-phase dynamics are prevalent in the lowlands and uplands by examining the deadwood dynamics of downed woody debris (DWD) decay class volumes and snag decay class ages. For the final objective, I quantitatively compare structural parameters and determine if there is a difference in the structural conditions across the chronosequence and site productivity groups.

I have applied NSDLF's old-growth definition to the Maritime Boreal forests because it incorporates both structural and successional criteria and is practical for working within the jurisdiction. By using this definition, I can distinguish whether Nova Scotia's current 'Old Forest Policy ' (NSDNR 2012) is capturing late-successional black spruce forests located in the Maritime Boreal Forest Region or if altercations should be made. I summarize my findings in Chapter 3 and offer future research recommendations to continue improving our understanding of these unique forest communities. It is my objective that the results of this study be used as a tool for improved forest management practices and ensure that an ecosystem-based management approach is being applied to these regional forests.

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Chapter 2: An empirical study of the temporal and site dynamics occurring in Maritime Boreal black spruce (*Picea mariana*) forest communities

2.1 Abstract

Conditions of stand development and the ‘old-growth’ stage of development are dependent on the forest type, site productivity, and disturbance regimes. Currently, there is limited knowledge of the developmental processes occurring in boreal forests located directly along Canada’s Atlantic coast where low severity windstorms are the prevalent natural disturbance influencing stand development. To address this knowledge gap, coastal black spruce (*Picea mariana*) forests were examined along upland and lowland chronosequences in Nova Scotia, Canada. It was apparent that small-scale disturbances were occurring in both ecosites, which contributed to gap-phase dynamics and uneven-aged structures in stands with an older 30% basal area age (OLD3AGE). Uplands sites had a higher growth rate, which contributed to increased susceptibility to small-scale disturbances and faster stand development. Older aged stands did not exhibit larger structural features or increased species diversity. However, snag volume (ST) was lower in lowland sites and snag density (SD) was higher in uplands sites. The structural conditions and onset of the ‘old-growth’ stage of development occurred earlier than non-coastal boreal forests in Ontario and Quebec, as well as other climax forest types in Nova Scotia. The uniqueness of the coastal black spruce communities merits their inclusion in old forest management in the region.

2.2 **Introduction**

In the last twenty years, forest management strategies in Canada have incorporated more sustainable, ecosystem-based approaches by attempting to emulate regional natural disturbance regimes (NDR) (Bergeron et al. 1999; Harvey et al. 2002; Gauthier et al. 2009; Waldron et al. 2013). By imitating stand-scale processes, this management model results in a dynamic forest landscape comprising stands at different development stages with attributes closer to historical forest conditions (Gauthier et al. 2009). The NDR-based management approach is a partial response to the public's concern of extensive forest management practices occurring throughout Canada, which has contributed to the decline in the amount and distribution of forests in the 'old-growth' stage of development (Mosseler et al. 2003; Gauthier et al. 2009). Particularly in eastern Canada, where Europeans settled over five centuries ago, some estimates suggest that old-growth forests comprise only 0.1 - 0.3% of the total forested landscape (Lynds 1992). Because old-growth forests are understood to contain unique features in an ecosystem, provincial governments have recognized the need to create policies and adapt management practices to identify, and conserve these rare and diminishing communities (NSDNR 2012).

Studies on old-growth forests (Gauthier et al. 1996; Harper et al. 2005; Boucher et al. 2006; Lecomte et al. 2006; Fenton and Bergeron 2011) have defined older forests by their structural, successional, and/or biogeochemical attributes (Wirth et al. 2009). Definitions are typically created to associate stand age, or time since the last stand-replacing disturbance, with characteristics such as, but not limited to: the accumulation and diversity of woody detritus (Spies and Franklin 1988; Sturtevant 1997; Brassard and Chen 2007); transition of even-aged to uneven-aged structure (Frelich 2002; Mosseler et al. 2003; Martin et al. 2012; Kuttner 2013); increase in structural diversity (Franklin and Van Pelt 2004; Brassard and Chen 2006; Bouchard et al. 2009; Kane et al. 2010); presence of late-successional species (Rossi et al. 2009; Rheault et al. 2009; Wirth et al. 2009) and an increase in the sequestration of carbon (Wirth et al. 2009). These features typically occur when autogenic or small-scale allogenic processes become the dominant agents of tree regeneration within a stand (Oliver and Larson 1996). These gap-phase dynamics allow a forest to transition from even-aged to uneven-aged structure, creating a mosaic of different ages, heights and diameters as stands develop over time (Oliver and Larson 1996; Sturtevant et al. 1997). Although developmental pathways are not always discrete or linear processes, in the absence of stand-replacing events most forests develop through four main development stages: stand initiation, stem exclusion, understory initiation and old-growth (Oliver and Larson 1996).

Along with stand age, site productivity also affects stand development by influencing succession rates and altering the physical structure of the forest (White and Pickett 1985; Frelich 2002; Harper et al. 2002;Boucher et al. 2006; Brassard and Chen 2006; Kuttner et al. 2013; Smith and Smith 2015; Kershaw et al. 2017). Typically, sites that have richer soil conditions (i.e. nutrient and moisture content) develop quicker, resulting in uneven-aged structure (Boucher et al. 2006) and increased structural complexity (Harper et al. 2002; Brassard and Chen 2006; Kuttner et al. 2013; Moussaoui et al. 2019) occurring faster than sites with poorer soil conditions. Therefore, Hunter (1988) suggests that the site condition, forest type and disturbances regimes should be considered when identifying the natural processes contributing to stand development.

In Nova Scotia, old-growth definition criteria were established from the study of the Acadian Forest stands, characterized by the presence of red spruce (*Picea rubens*) and associated long-lived species such as sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia),* eastern hemlock (*Tsuga canadensis)*, and eastern white pine (*Pinus strobus)* (Lynds 1992; Mosseler et al. 2003a; Stewart et al. 2003; Pesklevits 2006). Nova Scotia's current 'Old Forest Policy', which aims to protect old-growth stands in the province, defines 'old-growth' as having 1) 30% or more of the basal area in trees 125 years or older; 2) at least half of the basal area is composed of climax species and; 3) total crown closure > 30% (NSDNR, 2012). However, these 'old-growth' criteria likely do not apply to the less common old-growth stands from the Maritime Boreal Forest Region in Nova Scotia, which are dominated by zonal and edaphically limited climax species such as black spruce (*Picea mariana*), balsam fir (*Abies balsamea*) and red maple (*Acer rubrum*). Of these climax species, black spruce typically dominates the coastal inland landscape (Rowe 1972; Davis and Browne 1996), is a late-successional species (Lynds 1992), and has the ability to self-replace after frequent or infrequent disturbance return intervals (Spies and Franklin 1996; Frelich 2002). However, black spruce does not live as long as typical Acadian climax species, with known maximum ages around 138 years for Maritime Boreal black spruce (Neily et al. 2004) that ranges between 250-300 years for the Acadian climax species (Stewart et al. 2003). Furthermore, black spruce forests exhibit smaller structural features, including smaller diameter at breast height (DBH) and height, compared to the Acadian climax species (Stewart et al. 2003; Neily et al. 2004). Given the lower longevity and contrasting structural features, Maritime Boreal black spruce forests are typically no considered in forest planning as mature or 'old-growth'.

Traditionally, species dominating the boreal forest have been understood to develop as even-aged stand structures (Johnson 1992). Research (Harper et al. 2005;

Boucher et al. 2006; Bergeron and Harper 2009; Rossi et al. 2009; Fenton and Bergeron 2011; Martin et al. 2018) has determined that, although stand-replacing disturbances are still an important catalyst in boreal forests, gap-phase dynamics also influence forest development. However, the majority of research has been conducted in the inland boreal forests of Ontario and Quebec, where wildfire and insect epizootics are the two main natural disturbances contributing to stand development (Johnson 1992; Boucher et al. 2006). The boreal forests located along the coast of Nova Scotia are characterized by high precipitation levels and a moist, cool climate resulting in lower fire frequency (Wein and Moore 1978; McCarthy 2001; Thompson et al. 2003; Harper et al. 2005; Lecomte et al. 2006; Taylor et al. 2020) and fewer insect epizootics (NSDLF 1977; Blais 1983) compared to other areas of eastern Canada. Instead, low severity windstorms, defined as 5-30% downed tree biomass accumulation, are the prevalent natural disturbance occurring approximately every 70 years in this region (Taylor et al. 2019, 2020).

The goal of this research is to characterize the conditions of the 'old-growth' stage of development, as defined by the presence of uneven-aged structures caused by gap-phase dynamic processes (Oliver and Larson 1996), in the coastal boreal forest. To understand the developmental processes occurring in these forest communities, the temporal and site productivity dynamics of lowland and upland stands will be examined through the following objectives: classify the stand age distribution structure as either even-aged or uneven-aged and identify the age of transition (Desponts et al. 2004; Martin et al. 2018), determine if the deadwood dynamics of downed woody debris volume and snag ages are the resulting from gap disturbances (Lorimer 1985; Frelich 2002; Wirth et al. 2009), and examine changes in 10 structural attributes associated with old-growth characters (Harper et al. 2005; Boucher and Gauthier 2006). Based on the main disturbance of low severity windstorms and late-successional black spruce forest type, I hypothesize that gap-phase dynamics, opposed to landscape-scale processes, is the prevalent natural disturbance contributing to stand development. As a result, I predict that uneven-aged stand structures occur later in stand development and are more structurally diverse than even-aged structures. Site productivity can also influence stand development. Therefore I further predict that upland sites with richer soil develop uneven-aged structures faster than poorer, lowland sites. The results of this study will be an important tool for improving forest management practices and ensuring that an ecosystem-based management approach is being applied to these regional forest groups.

2.3 **Methods**

Study area

The study area covered parts of the Atlantic coastline in the province of Nova Scotia, Canada, particularly in the Eastern shore (820) ecodistrict (Neily, et al. 2017; Figure 2.1). The Eastern shore ecodistrict was selected because of its conditions that support both edaphically limited lowland and upland black spruce forests and similar natural disturbance regimes (Neily et al. 2017). Extending from Chedabucto Bay (Guysborough County) to St. Margaret's Bay (Halifax County), this ecodistrict is the coldest on Nova Scotia's mainland due to a climate influenced by the ocean (Neily et al. 2017). Strong winds, extended periods of fog, salt sprays, cooler summer temperatures, a long frost-free period, high precipitation, and milder winters all contribute to Maritime Boreal forest conditions (Loucks 1961; Neily et al. 2017). Forested/woodlands area comprise 58% of the total ecodistrict land cover and are composed of zonal softwoods such as balsam fir, black spruce, and white spruce (*Picea glauca*), scattered red maple and white birch (*Betula papyrifera*) and the absence of red spruce (Loucks 1961; Neily et al. 2017). Based on settlement patterns, Neily et al. (2004) also concluded that the eastern shore appears to have the highest prospect of finding natural, undisturbed forests along Nova Scotia's shoreline.

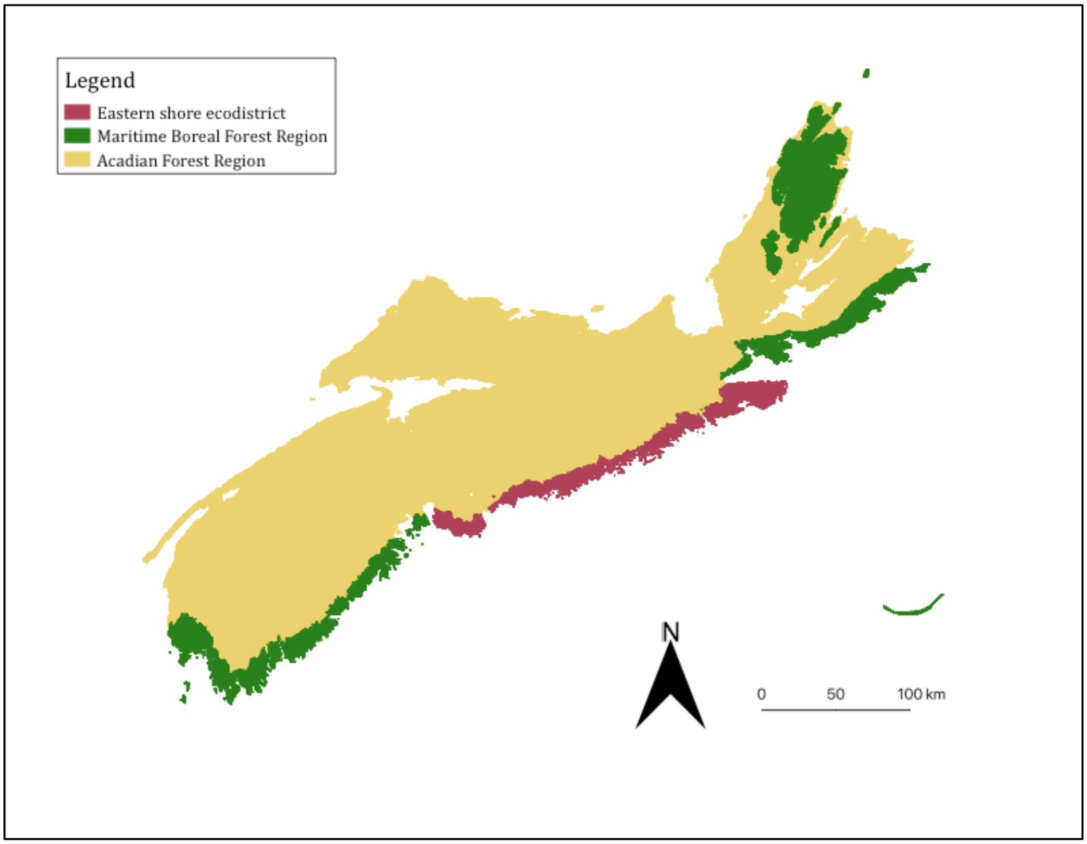

Figure 2.1. Nova Scotia's Eastern shore ecodistrict, Acadian Forest Region, and Maritime Boreal Forest Region (Neily et al. 2017).

Site selection

Ecosites, the smallest unit of the Ecological Land Classification (ELC) delineation, were used to distinguish a stand's site productivity (Neily et al. 2017). Neily et al. (2013) defines ecosites as units which represent ecosystems that develop under various conditions and influences, but share similar site productivity based on moisture and nutrient regimes. Therefore, the ecosite scale allows for delineation between forested sites of different productivity depending on the Forest Ecosystem Classification (FEC) soil type and vegetation type. Based on-site productivity, I selected stands for two forest ecosite groups: 1) Lowland: Edaphic Wet-Poor Black Spruce (MB4) and 2) Upland: Edaphic/Zonal Fresh/Moist-Poor Black Spruce (MB2 and MB3) (Neily et al. 2013).

Chronosequence methods were used to represent time-dependent development of a forest with homogenous disturbance regimes (Boucher et al. 2006; Fenton and Bergeron 2008; Johnson and Miyanishi 2008). Ten stands of different ages were surveyed in the two forest ecosite groups, allowing for the developmental stages to be examined along a chronosequence. Selected stands were black spruce dominated with homogenous site productivity, located less than 5 km away from the coastline, and greater than 2 ha in size. The sites had no visible or known evidence of human or recent stand-replacing disturbances in order to capture black spruce stands in later stages of development. Stand selection was based on aerial photographs, assessing Permanent Sample Plots (PSPs) and FEC plots, utilizing the Forest Inventory Database (FID), historical records and maps from previous harvest plans and disturbance events, and collaborating with local experts, government and industry.

The experiment is based on a nested design with 20 stands (samples) and 60 plots (subsamples) being assessed between the two ecosites. Frelich (2002) recommends not using random plot selections to capture stand disturbance history because disturbance regimes are spatial processes, causing tree chronologies to be dependent on the site. Systematic sampling is more appropriate approach to determine the disturbance history and assess the aerial extent of a disturbance; I selected three plots per stand using systematic with random starts via Avenza Maps (Avenza Systems Inc.).

Field methodology

Field data were collected between May 1, 2019 and October 1, 2019. A soil auger was used to determine the FEC soil type and forest floor vegetation was tallied by species to determine the FEC vegetation type, allowing for the categorization of a lowland (MB4) or upland (MB2 or MB3) site. At the plot center, basal area (m^2/ha), tree density (stems/ha) and live and dead tree composition were estimated using a BAF 2 prism at breast height (1.3 m). All live and dead trees captured in the prism sample were tallied and numbered, had one core extracted using an increment borer at breast height, and the species, status, diameter at breast height (DBH) and height recorded. All tree heights (nearest 0.1 m) were measured by using a sonic Vertex IV hypsometer (Haglof, Sweden). The same criteria were recorded for snags. Additionally, the top diameter was visually estimated (nearest 0.1 cm) to obtain the woody volume and the decay class was recorded (Stewart et al. 2003; Appendix D). Following NSDLF's research plot protocol, each core was mounted on boards, sanded by 220, 300, 400 and 600 sandpaper grit, and aged based on counting growth rings under a microscope (Appendix B). For snags, the outermost ring was used as the age of death (Aakala et al. 2008).

Any snag > 45° lean from vertical was considered downed and was tallied as downed woody debris (DWD). A fixed triangular linear intersect sampling (LIS) method was established from the plot centre with 30 m sides to capture DWD (Appendix C). All intersected DWD $\geq$ 7.5cm DBH (Neily et al. 2004; Kuttner 2013) was tallied and the species, diameter at the point of intersection and decay class were recorded (Stewart et al. 2003; Appendix D).

A LIS method was also used to determine gap fraction. Gap fraction was defined as the ratio of gap length to transect length and was used as a general measure of extent of canopy disturbance (Runkle 1982; Martin et al. 2018). Following Martin et al.'s (2018) methodology, gaps were defined as sections of transects where the canopy was below two-thirds the height of the dominant tree (Pham et al. 2004) and greater than 2 m in length. Based on these criteria, the natural separation of tree crowns could be accounted for and true gaps identified (Martin et al. 2018). From the plot centre, five fixed 25 m transects were assessed to establish the overall percentage of canopy openings (Appendix C).

In total, 923 live tally trees were cored at breast height, sanded and aged by counting growth rings to estimate the stand age dynamics. Trees were cored at breast height to comply with typical forest management practices. However, there are errors of age underestimation and the assumption of similar growth rates for the first 1.3 m growth increment when coring trees at breast height (Wong and Lertzman 2001). Therefore, the derived stand ages discussed throughout this study should be recognized as the minimal age of the oldest 30% basal area obtained at breast height. Following Stewart et al.'s (2003) 'old reference age' approach, the age of the oldest cohort of trees was estimated by averaging the age of the oldest 30% of trees in each plot (OLD3AGE).

Statistical methods

Even-aged structures are typically defined as those having a symmetrical unimodal, bell-shaped or bimodal diameter distribution, while uneven-aged structures exhibit a skewed distribution (Oliver and Larson 1996; Kershaw et al. 2017; Martin et al. 2018). I fitted Weibull probability density functions to quantitatively represent the age distribution of each stand (Bailey and Dell 1973). The Weibull shape parameter (WSP) (Bailey and Dell 1973) and symmetry index (SI) (Lorimer and Krug 1983) models were used to classify age distributions as even- or uneven-aged structures (Frelich 2002; Desponts et al. 2004). The WSP was estimated through EasyFit 5.6 Professional distribution fitting software (Mathwave Technologies) using the following equation:

$$f(x) = \left(\frac{a}{b}\right) \times \left(\frac{x}{b}\right) \times \left\{-\left(\frac{x}{b}\right)^{a}\right\} ;x \ \geq 0; a > 0; b \ > 0$$

where *f(x)* represents Weibull density function, *b* is the scale parameter, *c* is the shape parameter (WSP) and *x* is the stems/ha (Bailey and Dell 1973). Thresholds have been established for the WSP, which indicates the distribution type based on the calculated value. I used the suggested WSP threshold of 1.5, with WSP values > 1.5 indicating a symmetric distribution, and values ≤ 1.5 representing a right skewed distribution (Bailey and Dell 1973; Martin et al. 2018).

SI was calculated by applying the following equation:

$$SI \ = \frac{(M - XL)}{(X.95 - XL)}$$

where *M* is the mode of the distribution, *XL* is the lowest age in the distribution, and *X.95* is the 95th percentile age in the distribution (Lorimer and King 1983). The SI threshold interprets values close to 0.5 as reflecting a true symmetric distribution and 0 representing a right skewed distribution (Lorimer and King 1983). Therefore, a SI value of > 0.25 was interpreted as symmetrical and a SI value of ≤ 0.25 as a right skewed distribution.

Linear mixed effects models were used to determine the deadwood dynamics and disturbance patterns. Decay class and ecosites were fixed factors while stand was applied to the intercept as a random effect and p-values < .05 were considered significant. By assessing the fixed and random effects for downed woody debris volume and snag ages, tree mortality can be evaluated across the chronosequence and between ecosites. Model comparisons were conducted through a log-likelihood ratio to determine the model of best fit and chosen based on the lowest chi-squared p-value.

One-sided and two-sided Kolmogorov-Smirnov (KS) distribution tests and a two-side one-tailed t-test (TOST) of equivalence were used to explore the conditions of 10 structural attributes across the chronosequence and between the ecosites (Table 2.1). The combination of these methods enabled examination of how an observed cumulative frequency distribution (CFD) conformed to an expected frequency distribution (Sokal and Rohlf 1969; Zar 2014) and if differences exceeding a minimum negligible difference of 10% could be detected (Robinson and Froese 2004). The sample size in this study limits the ability to conduct traditional mean differences tests; therefore, by applying distribution tests and equivalence tests, structural attributes (Table 2.1) CFDs could be compared across the chronosequence and between ecosites to validate if there were any meaningful differences. If structural attributes values were exactly the same across the chronosequence, a uniform distribution would be expected. Therefore, the one-sided KS tests were tested against a uniform distribution for any significant differences from the mean values (Table 2.7).

Table 2.1. Description of the structural and successional variables measured at each plot in the study.

Type	Variable	Acronym	Unit	Description
Structural				
	Basal area	BA	m^2/ha	Amount of area occupied by tree stems using a BAF 2 prism.
	Live tree density	TD	#/ha	The number of living trees per hectare. Calculated based on sum of trees in DBH class, multiplied by the Tree Density Factor (TDF) and divided by number of plots/stand[1] (Kershaw et al. 2017).
	Snag density	SNAG_N	#/ha	The number of dead snags per hectare. Calculated based on sum of snags in DBH class, multiplied by the TDF and divided by number of plots/stand[1] (Kershaw et al. 2017).
	Downed woody debris	DWD_v	m^3/ha	Volume of dead woody <45 degrees vertical calculated using McRae et al.'s (1979) volume equation[2].
	Snag volume	ST	m^3	Volume of standing timber >45 degrees vertical. Volume (m^3) calculated using Smalian's formula[3] and multiplied my the individual snag density to obtain volume per hectare (m^3/ha)
	Gap fraction	GF	%	Percent of gaps across a five 25m linear transects from plot centre using Runkle's (1982) gap ratio[4] (Martin et al. 2012).
	Diameter at breast height	DBH	cm	Diameter at breast height determined by the quadratic mean of the stand.
	Height	HT	m	Heights based on the unweighted mean of the stand.
	Coarse woody debris DBH	CWD_dbh	cm	Diameter at breast height for snags and diameter at point of intersection for DWD.
	Species composition	SC	-	Shannon and Weaver's (1949) formula[5] to indicate diversity of tree species based on the basal area (X) and density (D) importance value[6] (Kershaw et al. 2017).
Successional				
	Stand age	OLD3AGE	years	The minimum age of the oldest 30% of the basal area obtained at each plot.
	Snag decay class age	SA	years	Age of snags based on decay class.
	DWD decay volume	DWD_decay	m^3/ha	Volume of downed woody debris based on decay class.

[1] $TD = TDF \times \frac{(\#\ tallied)}{\#\ plots/stand}$

$$TDF = \frac{BAF}{(0.0000785)\times(DBH)^2}$$

[2] $DWD(\mathrm{V}) = \left(\frac{1.23}{L}\right) * \sum\left(d^2 * \frac{S}{T}\right)$

$$S = \sqrt{[1 + (ps/100)^2]}$$
$$T = \cos(h)$$

[3] $ST(V) = \left[\frac{B\times T}{2}\right] \times h$

B = area at diameter at breast height (m^2)
T = area at top diameter of snag (m^2)
h = height of snag (m)

[4] $GF(\%) = \frac{sum\ of\ canopy\ gap}{total\ length\ of\ transects}$

[5] $SI = \sum p_i \times ln(p_i)$

p_i = importance value (I_i) of the ith species

[6] $I_i = 100(\frac{n_j}{N} + \frac{d_j}{D})$

I_i = importance value of the ith species
n_i = the number of sampling units where the ith species is present
N = total number of sample units
d_i = the number of individuals of the ith species present in the sample population
D = total number of individuals in the sample population ($D = \sum di$)

2.4 **Results**

Age structure classification

Stand ages (OLD3AGE) ranged between 75 to 108 years in the lowlands, and between 66 and 104 years in the uplands. Heartwood decay was present in 11 upland trees and 11 lowland trees, resulting in 3% of trees not being aged. Across all stands, black spruce was the oldest individual found on both the lowlands and uplands, with the oldest being 155 years in the lowlands, and 132 years in the uplands. The overall black spruce mean age for the two groups differed, with lowland sites averaging 84 years (21.1 sd) and upland sites 72 years (16.2 sd). In general, lowland live tree ages were significantly older than the uplands ($p = <.001$).

The age distribution from lowland to upland chronosequences is based on the stems per hectare and associated age (Figure 2.2). From the sampled stands, two of the ten lowland sites and four of the ten upland sites were identified as having uneven-aged stand structure (Figure 2.3). Lowland stands with an OLD3AGE value of 100 and 103 years and upland stands with an OLD3AGE values of 70, 82, 92 and 104 years were classified as having uneven-aged structure, while the remaining stands were classified as having even-aged structure based on the thresholds of WSP values > 1.5 and SI values > 0.25 indicating a symmetric distribution and WSP values ≤ 1.5 and SI values ≤ 0.25 representing a right skewed distribution.

The lowest (1) to highest (10) stand age values did not exhibit a gradual reduction from even-aged structure values (top right) to uneven-aged structure values (bottom left) and there was no distinct divide between the ecosites (Figure 2.3). Based on the structural definitions and methods of calculating stand age, uneven-aged structures were primarily identified in stands with an older OLD3AGE value. From the sampled stands, six out of nine upland stands with an OLD3AGE of 70 years or greater were classified as having uneven-aged structure. At the 80-year threshold, three out of four stands with an older OLD3AGE age were considered to have uneven-aged structures (Figure 2.4). In the lowlands, uneven-aged structures did not appear until later in the chronosequence. After the OLD3AGE was greater than 100 years old, two out of three lowland stands were identified as having uneven-aged structures, with all of stands younger than the 100-year OLD3AGE threshold classified as even-aged structures (Figure 2.4).

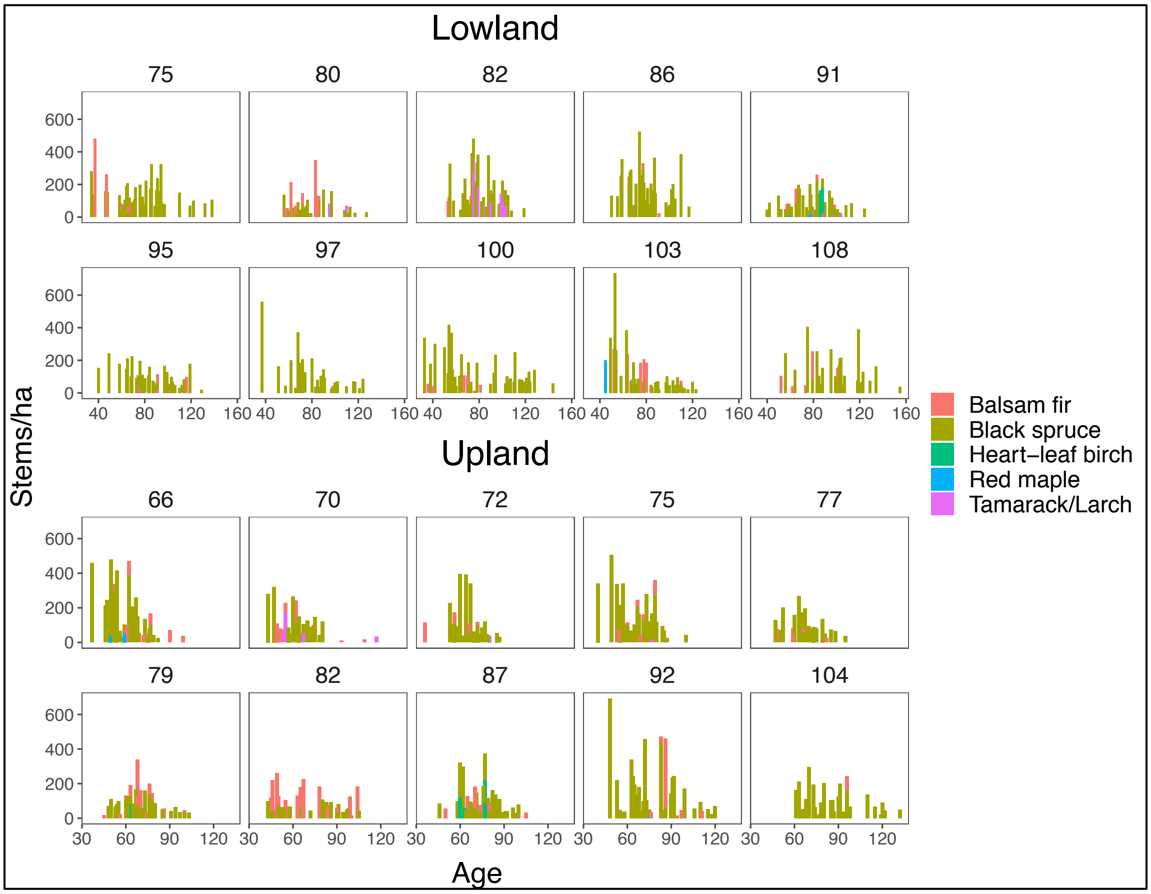

Figure 2.2 Age distribution of live density (stems/ha) in the lowland and upland ecosites ordered by stand age (OLD3AGE).

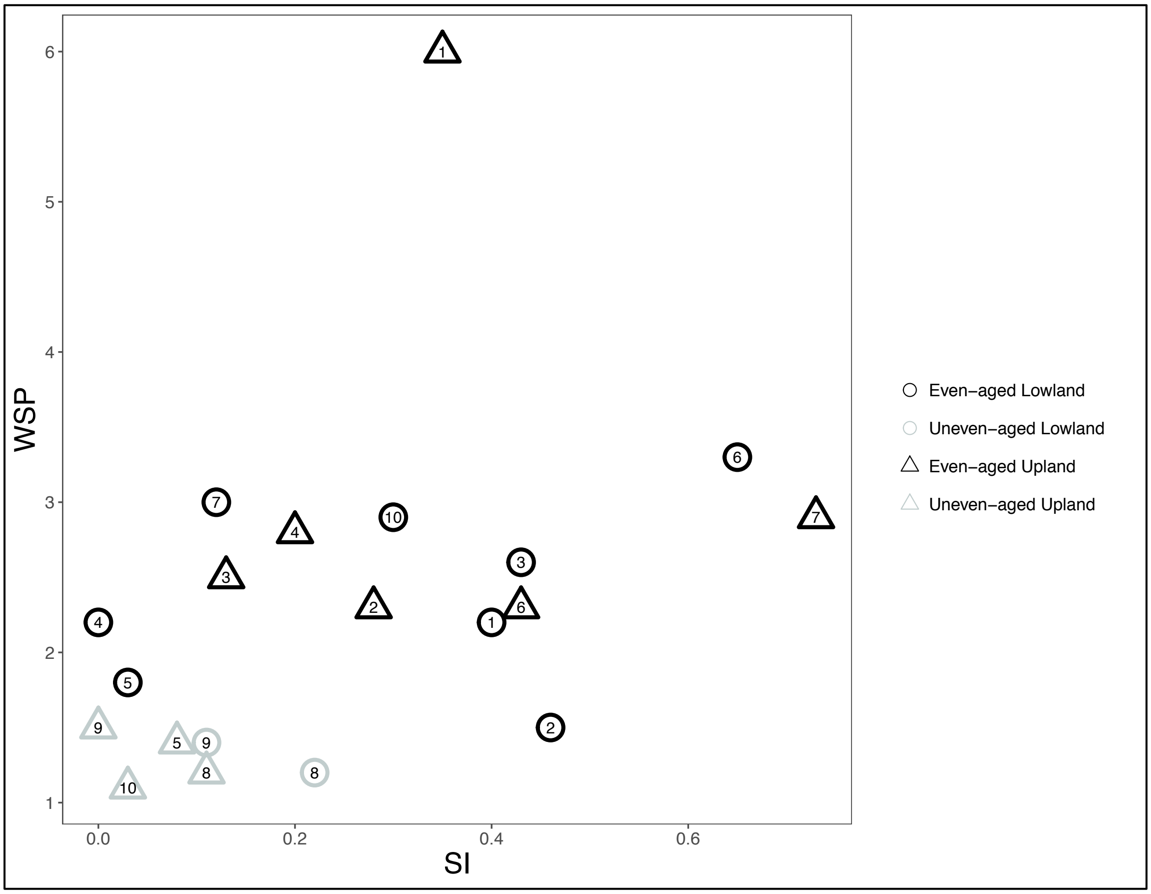

Figure 2.3. Weibull shape parameter (WSP) and symmetry index (SI) values based on the age distribution in the lowland and upland stands from the lowest (1) to highest (10) OLD3AGE value.

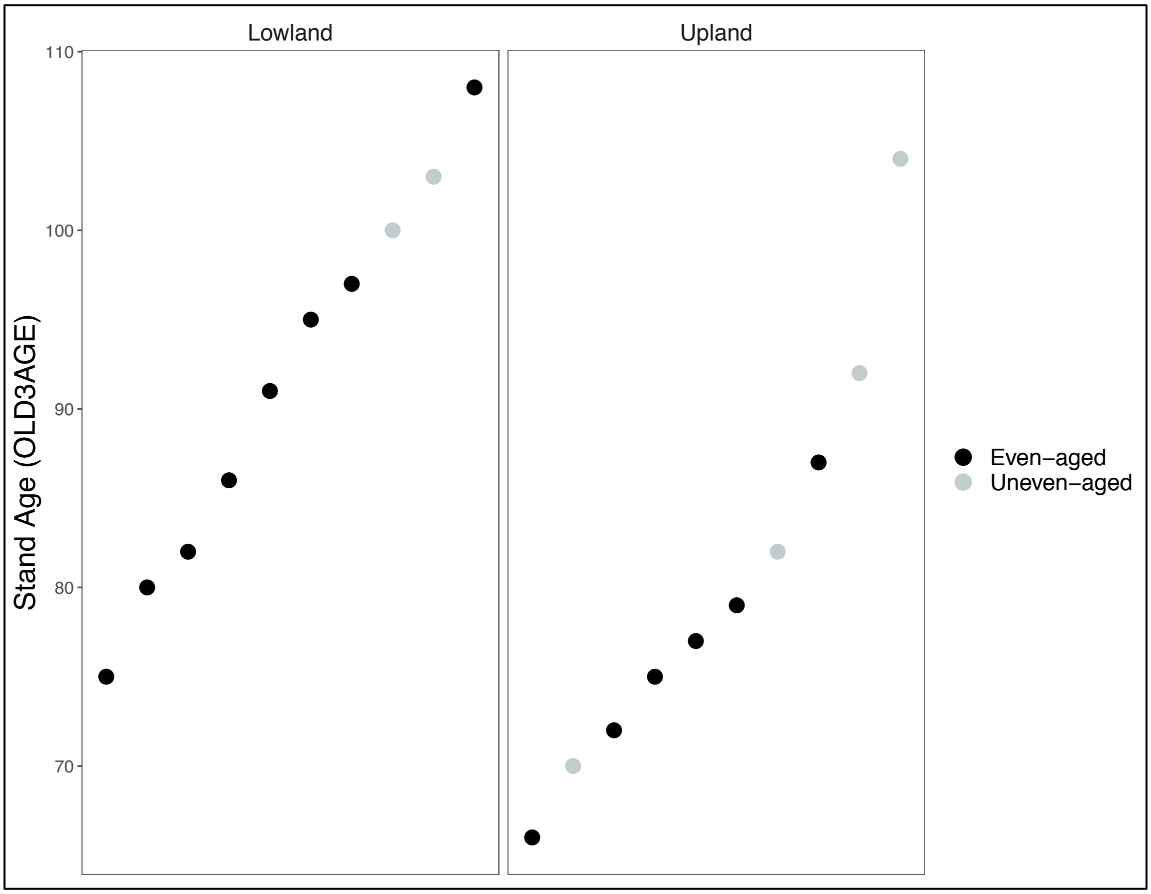

Figure 2.4. Stand age (OLD3AGE) and structure by position along ecosite chronosequences.

Deadwood dynamics

Downed woody debris

Black spruce accounted for the majority of the DWD volume in both ecosites, comprising 59% of the lowland and 55% of the upland volume. Balsam fir (38% and 43% respectively) and tamarack (*Larix laricina*; 3% and 2% respectively) comprised the remaining volume. From examining the DWD decay data, there were no noticeable patterns of species dominating total DWD volume across the chronosequence or occupying a particular decay class.

Based on the model comparison, there was a significant interaction between ecosite and decay class and significant variation explained when adding the random effects associated with stand (Table 2.2). The distribution of DWD_decay was different between the ecosites, resulting in 20% of the variation being explained by the fixed effects (Table 2.3). In the lowlands, DWD_decay was more equally distributed across the more advanced decay classes, with similar volume observed in decay class IV and significantly more volume in decay class II (Table 2.4). However, in the uplands the majority of DWD volume was observed in the lesser decay classes (I, II and III), with significantly less volume in the more advanced decay classes (IV and V; Table 2.4). A continuous distribution of decay was evident in the lowlands with the gradual reduction of volume, however volume abruptly decreased between the decay class III and IV for the uplands (Table 2.4).

The model explained approximately 30% of the total variation (the fixed plus random effects; Table 2.3). The addition of the random effects associated with the stand accounted for significant ($p < .0001$) additional amounts of DWD_decay variation, suggesting that the volume distribution varied by stand. In the lowlands, the highest distribution (20.41 m^3/ha) occurred when OLD3AGE was greater than 80 years (Figure 2.5). However, the lowest amount of DWD_decay (1.58 m^3/ha) is observed around the same age (84 years). In the lowlands, the lowest OLD3AGE sites accounted for the lowest DWD_decay values, increased and then slightly decreased in the stands with the greatest OLD3AGE value. In the uplands, there was less volume distributed in the younger stands, peaked at 31.55 m^3/ha, and then decreased and leveled off in the largest OLD3AGE stands (Figure 2.5).

There was also a noticeable increase in decay class I across the lowland chronosequence. Stands with an OLD3AGE value < 97 years contained 34% of the total decay I volume while stands with values ≥ 97 years contained 67% (Figure 2.5). In the uplands, the volume of lesser decayed logs was distributed in the stands with a lower OLD3AGE value and did not appear to exhibit a difference in decay class distribution across the chronosequence. A small distribution of later decay classes was evident within each stand, however less decayed (I, II and III) was still dominant.

Table 2.2. Log-likelihood model comparison to determine the model of best fit for downed woody debris decay class volume (DWD_decay) based on the fixed effects of Ecosite and Decay and the random effects associated with Stand.

Variable	Equation	X^2	df	pvalue
DWD_decay	Ecosite + Decay_Class			
	Ecosite + Decay_Class + Stand	14.613	1	0.0001
	Ecosite * Decay_Class	0.000	3	1.000
	Ecosite * Decay_Class + Stand	15.435	1	< 0.0001

Table 2.3. Linear mixed effects model for DWD_decay based on the significant interaction of the fixed effects (Ecosite and Decay) and random effects associated with Stand ($s(b_0)$).

Factor	Parameter	Estimate	Standard Error
Fixed Effects	Intercept	1.6866	0.6924
	Decay2	2.0638	0.8139
	Decay3	0.6500	0.8139
	Decay4	-1.1752	0.8139
	Decay5	-1.589	0.8139
	Upland	2.8517	0.9792
	Decay2:Upland	-2.1763	1.1510
	Decay3:Upland	-0.9207	1.1510
	Decay4:Upland	-1.8441	1.1510
	Decay5:Upland	-2.7211	1.1510
Random Effects	Stand ($s(b_0)$)	1.482	
Regression Summary	rMSE	3.152	
	pseudo R^2 (fixed)	0.2011	
	pseudo R^2 (fixed + random)	0.3048	

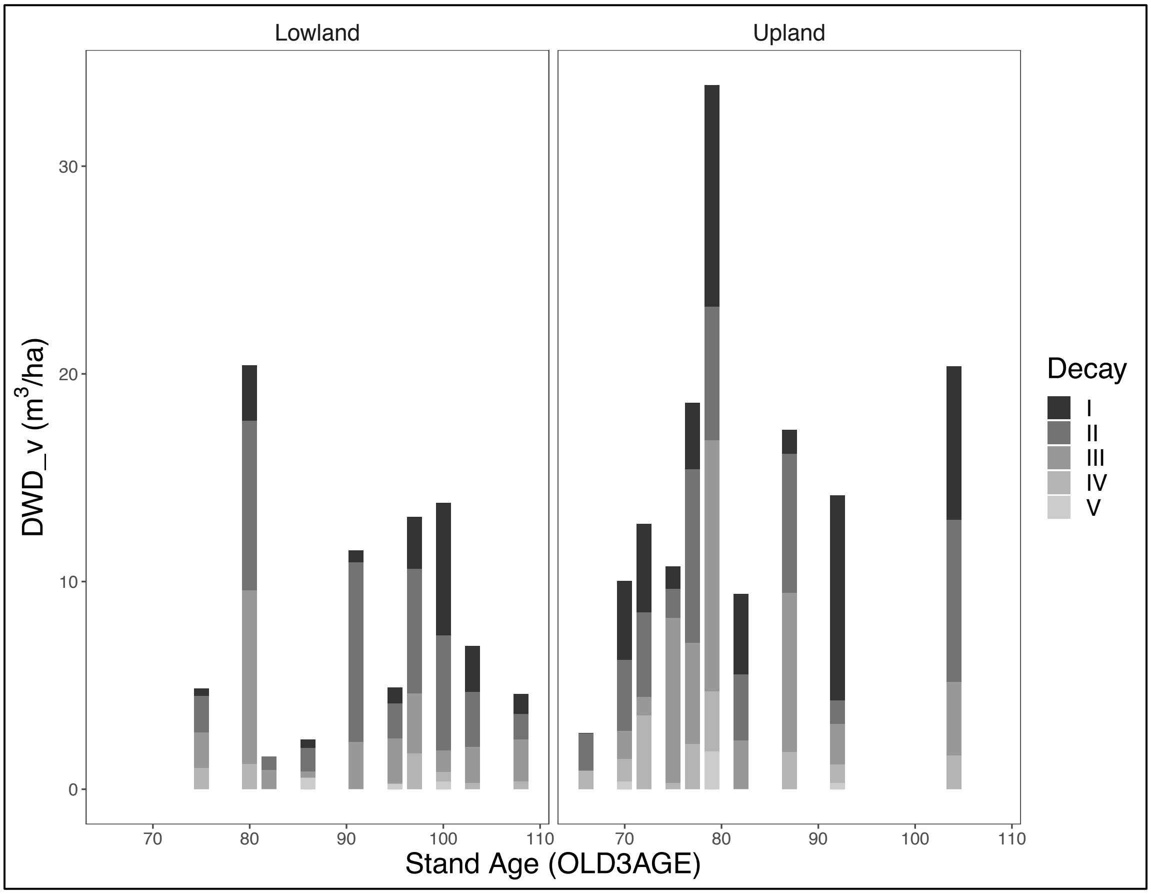

Figure 2.5. The distribution of downed woody debris volume (DWD_v) based on decay class along the lowland and upland chronosequences.

Table 2.4. Mean, standard deviation (sd) and range of the DWD decay class volume (DWD_decay) and snag decay class ages (SA) in the lowlands and uplands.

Variable	Lowlands			Uplands		
	Mean	sd	Range	Mean	sd	Range
DWD_decay						
I	1.69	1.91	0.00 – 6.39	4.53	3.67	0.00 – 10.67
II	3.75	3.05	0.66 – 8.65	4.42	2.70	1.12 – 8.37
III	2.33	2.24	0.29 – 8.35	4.26	3.87	0.00 – 12.11
IV	0.511	0.61	0.00 – 1.73	1.52	1.12	0.00 – 3.56
V	0.18	0.20	0.00 – 0.55	0.25	0.57	0.00 – 1.82
SA						
I	71.69	19.83	29.5 – 103	71.10	10.29	55 – 91
II	70.64	20.19	36 – 119.3	51.38	13.43	24.5 – 83
III	58.40	24.11	44 – 108	50.86	20.66	28 - 84
IV	41.5	8.85	33 – 51	NA	NA	NA

Snag decay age

In total, 255 snags were cored and aged. Thirty-seven upland and twenty lowland snags were rotten and excluded from analyses. The model comparison showed that there were significant interactions between the decay class and ecosite when determining the snag age (SA), however there was no additional variation accounted for with the inclusion of the random effects of stand ($p < 0.011$; Table 2.4). Therefore, the random effects associated with stand, including the OLD3AGE value, did not have a significant effect on the SA value. The SA was significantly different based on the decay class and ecosite (Figure 2.6). Fixed effects accounted for approximately 20% of the total snag age variation (Table 2.5). The average lowlands' SA across all decay classes was larger than the uplands, with total ages averaging 66 years and 58 years respectively.

In the lowlands sites, the SA of decay classes I and II were similar (Table 2.6) and had comparable range of ages (Table 2.7). The snags in a more advanced state of decay (decay class III and IV) were younger, resulting in the SA increasing as decay class decreased (Figure 2.6). A similar distribution was observed in the uplands, however only trees identified as decay class I were senescing at a similar age. The SA standard deviation (sd) slightly decreased in the earlier decay classes, resulting in less decayed trees having a similar distribution of ages than trees earlier in stand development. No decay class IV snags (aged or unaged) were observed in the upland sites and upland decay class II SA was significantly lower than the lowlands (Table 2.5).

Table 2.5. Log-likelihood model comparison for snag decay class age (SA) based on the fixed effects of Group and Decay and the random effects associated with Stand.

Variable	Equation	X^2	df	pvalue
SA	Ecosite + Decay_Class			
	Ecosite + Decay_Class + Stand	0.0000	1	1.000
	Ecosite * Decay_Class	6.5095	1	0.011
	Ecosite * Decay_Class + Stand	0.0000	1	1.000

Table 2.6. Linear model for snag decay age (SA) based on the significant interaction between Ecosite and Decay_Class[1]

Factor	Parameter	Estimate	Standard Error
	Intercept	71.6905	3.8504
	Decay2	-1.0547	5.3830
	Decay3	-13.2857	6.0879
	Decay4	-30.1905	9.6259
	Upland	-0.5869	5.5129
	Decay2:Upland	-18.6739	7.5129
	Decay3:Upland	-0.6907	9.8542
	Decay4:Upland	NA	NA
Regression Summary	pseudo R^2 (fixed)	0.2037	

[1] Random effects associated with stand were not significant ($p > .05$).

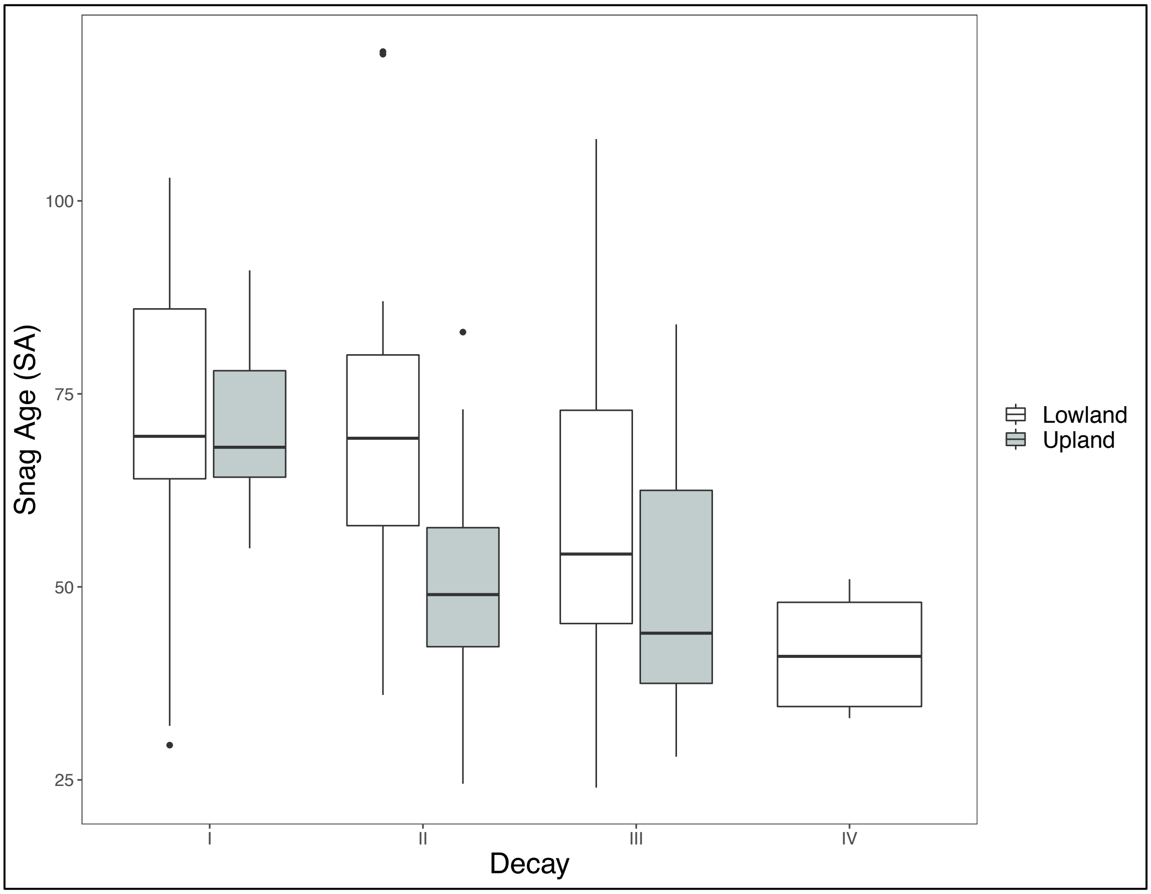

Figure 2.6. Boxplots indicating the mean and upper and lower quartiles of the snag decay class age (SA) within the lowlands and uplands.

Structural complexity

The majority of structural parameters in the two ecosites were not significantly different across the chronosequence. Live black spruce DBH and HT in the coastal forests did not significantly increase as the OLD3AGE value increased, with stand averages remaining relatively constant (Figure 2.10). Larger structural features, both live and dead, also remained constant along the chronosequence. There was also no difference in the composition of live trees (SC) as stands developed.

In the lowland stands, snag volume (ST) was the only structural attribute that was significantly different from the uniform distribution (p = .004). Eight of the ten stands' values were less than the mean (34.26 m^3/ha) causing a right skewed distribution (Figure 2.7). Because snag density (SNAG_N) was not significantly different from the uniform distribution, the snag frequency did not explain the change in volume.

In the uplands, snag density (SNAG_N) significantly differed (p = 0.033) from a uniform distribution, with six of the ten stands exhibiting values less than the uniform value of 1882 stems/ha, causing a right skewed distribution (Table 2.5; Figure 2.9). From the total stems/ha, 84% of snags were black spruce, 15% were balsam fir and 1% was tamarack. SNAG_N was consistent across the younger stands, with stands that have an OLD3AGE value less than 97 years exhibiting SNAG_N less than the mean. When OLD3AGE was older than 82 years, there was a significant increase in stems/ha, with the four stands with the highest OLD3AGE value all being higher than the average (Figure 2.10).

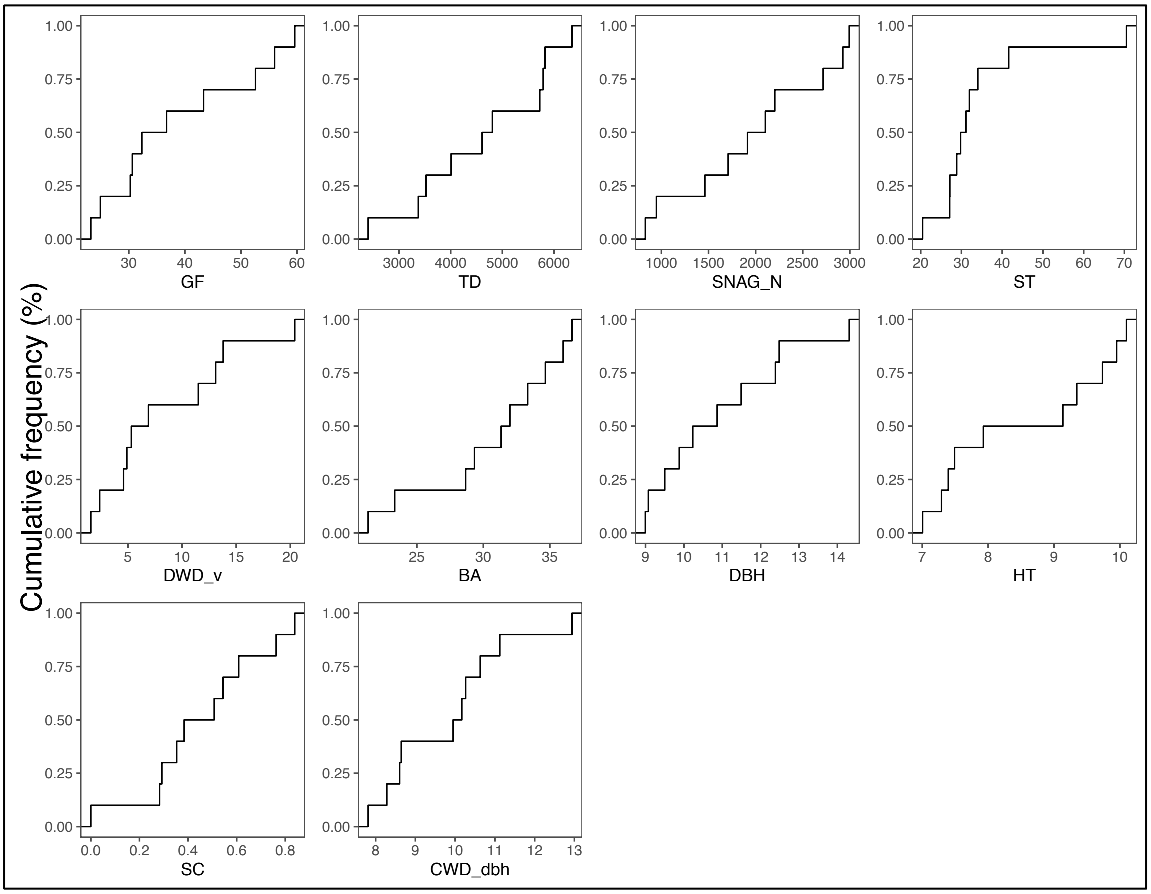

Figure 2.7. Cumulative frequency distributions (CFDs) of the 10 structural attribute in the lowland coastal black spruce stands. Gap fraction (GF), live tree density (TD), snag density (SNAG_N), snag volume (ST), downed woody debris volume (DWD_v), live basal area (BA), black spruce diameter at breast height (DBH), black spruce height (HT), species diversity (SC) and coarse woody debris diameter (CWD_dbh).

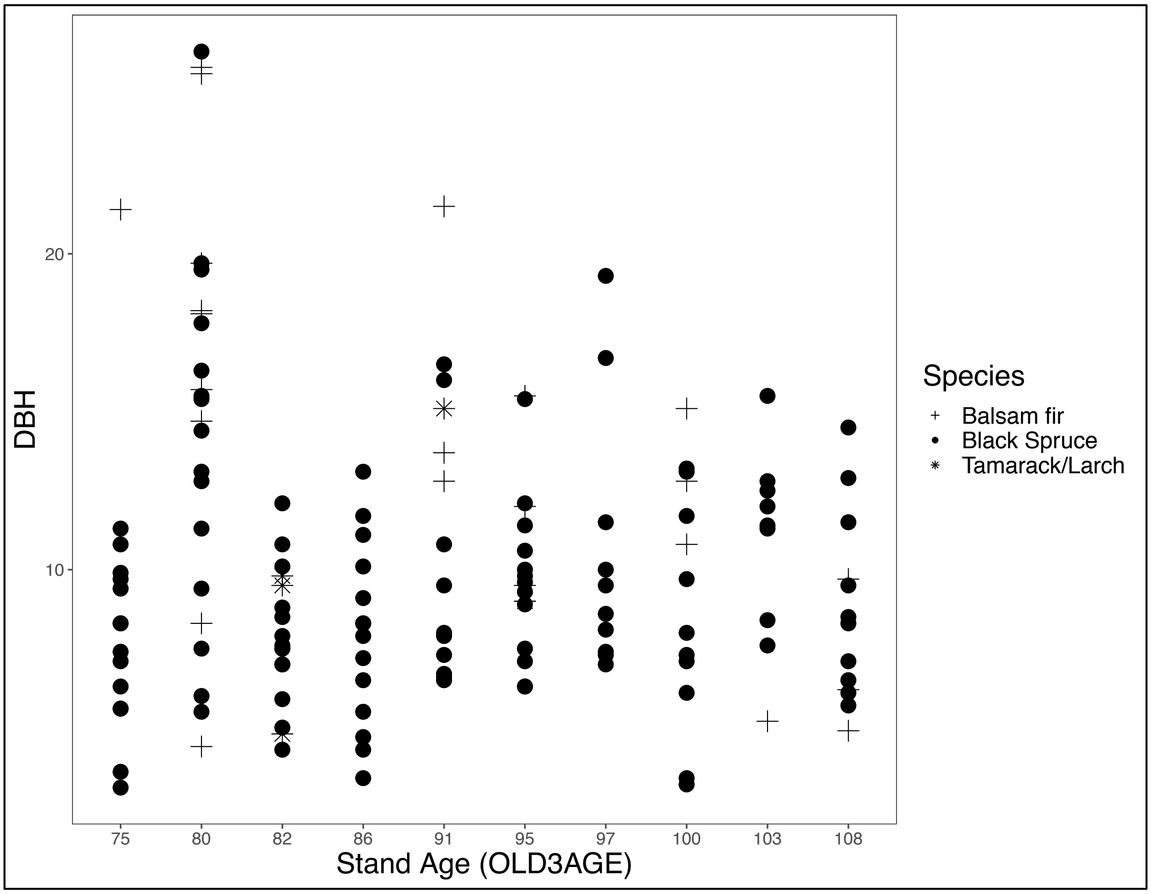

Figure 2.8. Lowland snag DBH sizes across the lowland chronosequence.

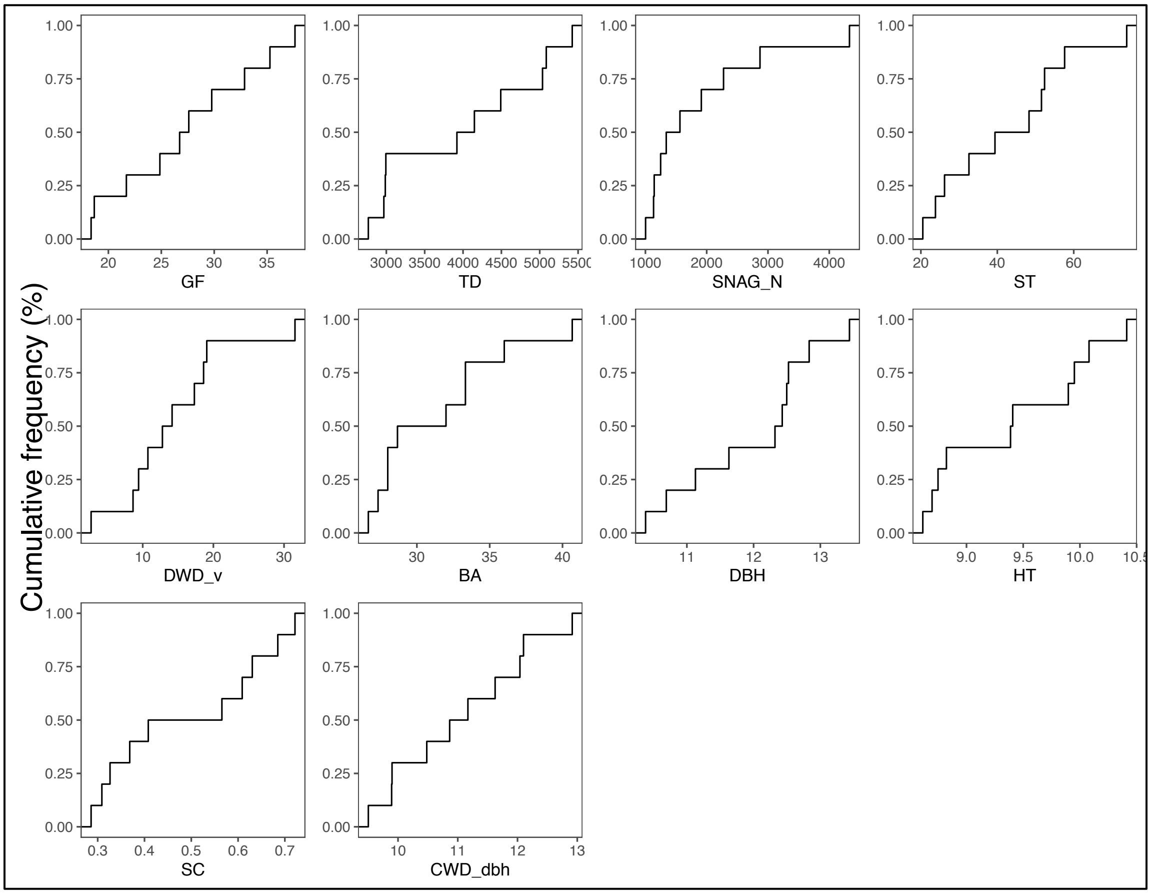

Figure 2.9. Cumulative frequency distributions (CDFs) of the structural attributes in the upland coastal black spruce stands. Gap fraction (GF), live tree density (TD), snag density (SNAG_N), snag volume (ST), downed woody debris volume (DWD_v), live basal area (BA), black spruce diameter at breast height (DBH), black spruce height (HT), species diversity (SC) and coarse woody debris diameter (CWD_dbh).

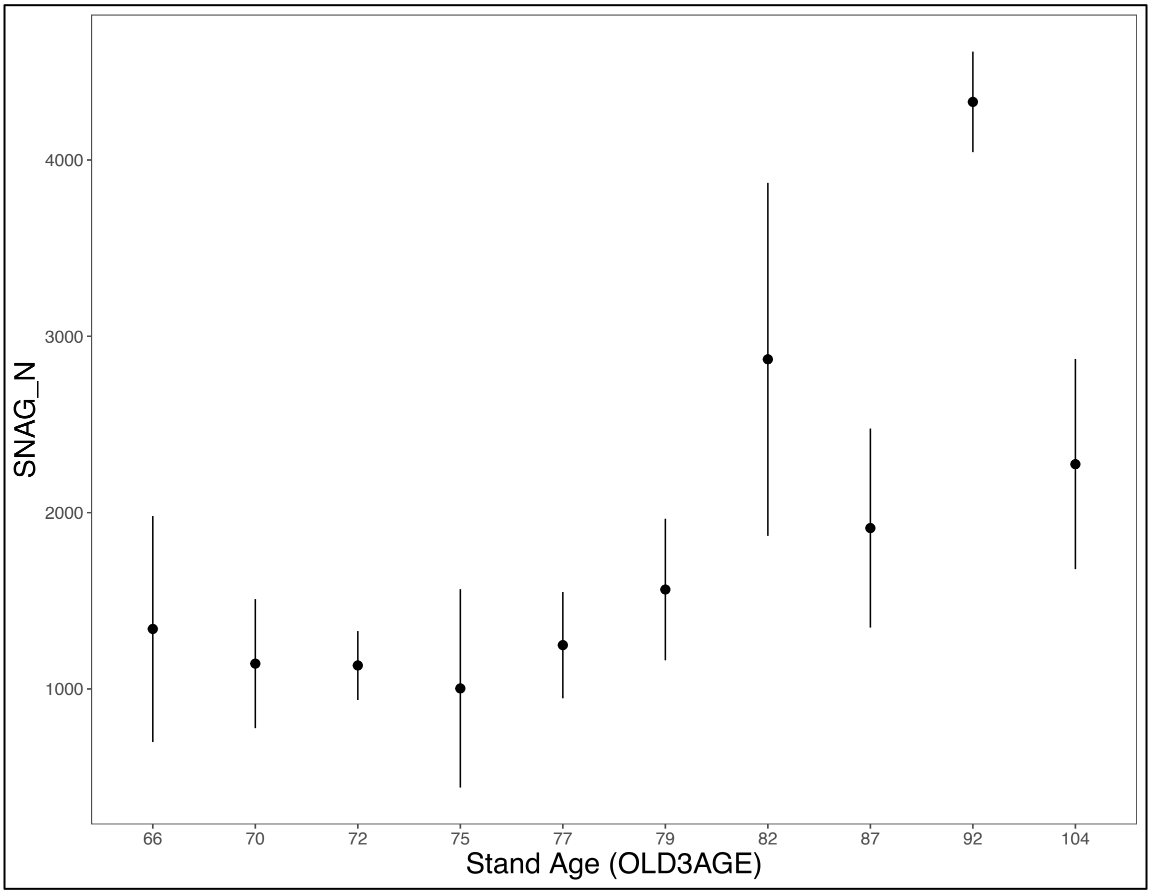

Figure 2.10. Mean and standard error values for the upland snag density (SNAG_N) across the upland chronosequence.

Table 2.7. Mean, standard deviation (sd) and range of live basal area (BA), live tree density (TD), snag density (SNAG_N), downed woody debris volume (DWD_v), snag volume (ST), gap fraction (GF), diameter at breast height (DBH), height (HT), coarse woody debris diameter (CWD_dbh), and species diversity (SC).

Variable	Lowland			Upland		
	Mean	sd	Range	Mean	sd	Range
BA	30.67	5.13	21.33 – 36.67	31.4	4.53	26.67 – 40.67
TD	4641	1295	2402-6347	3982	1010	2765 - 5423
SNAG_N	1980	765	829-2993	1882	1043	1002 - 4329
DWD_v	8.45	6.02	1.58 – 20.41	14.50	7.84	2.69 – 31.55
ST	34.26	13.84	20.46 – 70.51	42.62	17.10	20.51 – 73.86
GF	38.97	13.16	23.23 – 59.6	27.35	6.66	18.37 – 37.63
DBH	10.92	1.73	9.00 – 14.31	11.99	0.99	10.38 – 13.44
HT	8.54	1.23	7.00 – 10.10	9.35	0.66	8.62 – 10.41
CWD_dbh	9.84	1.55	7.81 – 12.94	11.05	1.12	9.5 – 12.92
SC	0.46	0.25	0.00 – 0.84	0.49	0.17	0.29 – 0.72

Table 2.8. P-values for one-sample Kolmogorov-Smirnov (KS) test versus a uniform distribution by ecosite and stand variables; two-sample KS test and Welch's two sample TOST equivalence test (epsilon = 0.1) for lowland vs. uplands by stand variable. Live basal area (BA), live tree density (TD), snag density (SNAG_N), downed woody volume (DWD_v), snag volume (ST), gap fraction (GF), diameter at breast height of black spruce (DBH), height of black spruce (HT), coarse woody debris diameter (CWD_dbh) and species diversity (SC).

Variable	One-sample KS test		Lowlands vs. Uplands	
	Lowland	Upland	Two-sample KS test	Equivalence test
BA	0.353	0.156 ..	0.988	0.140 ..
TD	0.525	0.225	0.418	0.689
SNAG_N	0.883	0.033 **	0.787	0.415
DWD_v	0.2145	0.174	0.168 ..	0.920
ST	0.004 ***	0.725	0.418	0.718
GF	0.485	0.827	0.168 ..	0.960
DBH	0.401	0.568	0.168 ..	0.458
HT	0.518	0.329	0.168 ..	0.432
CWD_dbh	0.465	0.829	0.418	0.566
SC	0.552	0.645	0.995	0.436

In general, the uplands appeared to have larger structural features compared to the lowlands (Table 2.7). From the two-sample KS tests, there were no significant differences ($p > .05$) between any structural attributes from the lowland versus upland ecosites. The equivalence tests also concluded that none of the attributes were statistically equivalent at epsilon = 0.1 (Table 2.8). There were noticeable differences between the ecosites at $p < 0.2$ (Table 2.8). The structural attributes of gap fraction (GF), black spruce diameter at breast height (DBH), black spruce height (HT) and downed woody debris volume (DWD_v) tended to be different ($p < 0.2$) between the two ecosites (Figure 2.11). Live tree density (TD), live tree basal area (BA), snag density (SNAG_N), snag volume (ST), coarse woody debris diameter (CWD_dbh) and species diversity (SC) were not significantly different or statistically equivalent (Figure 2.11).

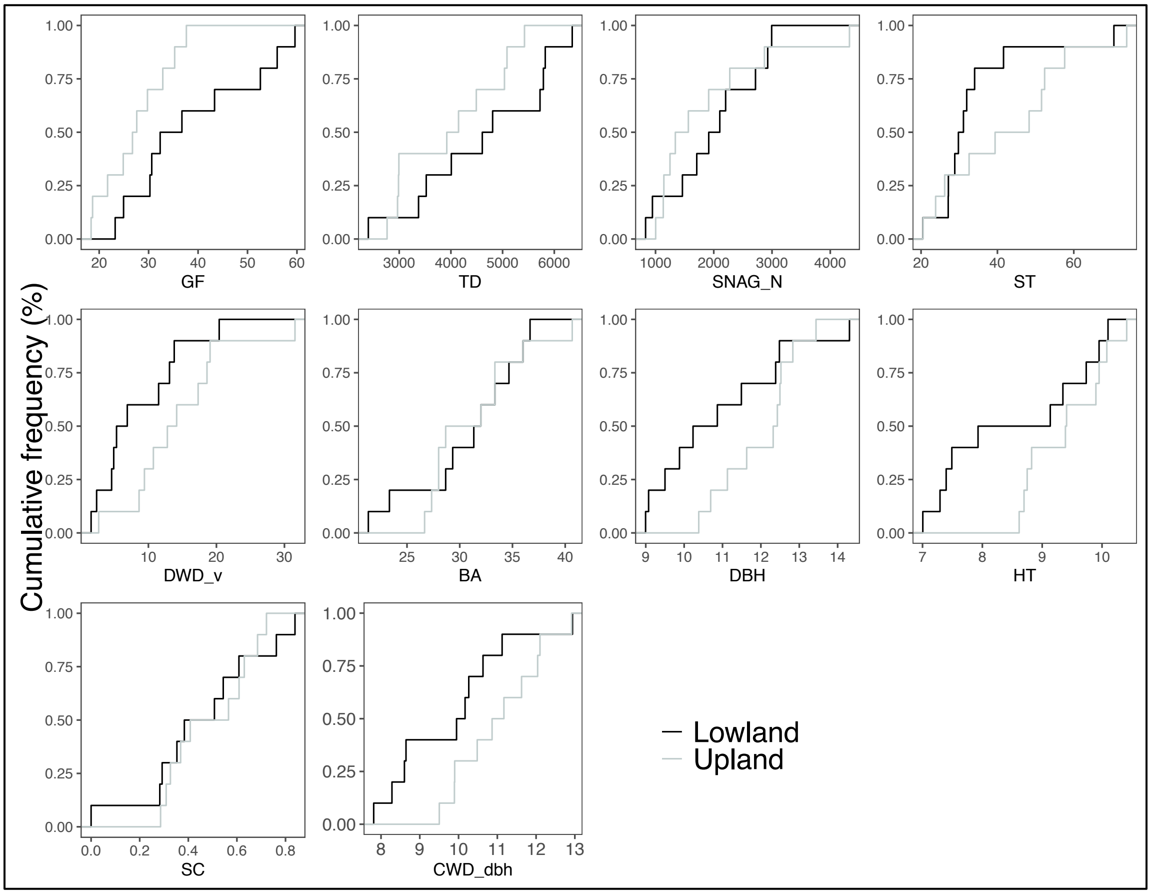

Figure 2.11. Cumulative frequency distributions (CFDs) of the structural parameters between the in the lowland and upland coastal black spruce stands. Gap fraction (GF), live tree density (TD), snag density (SNAG_N), snag volume (ST) downed woody debris volume (DWD_v), live basal area (BA), black spruce diameter at best height (DBH) and black spruce height (HT), species diversity (SC) and coarse woody diameter (CWD_dbh).

2.5 Discussion

Gap dynamics and scale of disturbance

Previous studies on forest development have identified the agent and scale of disturbance through observing the temporal pattern of deadwood and the distributions of decay classes (Spies et al. 1988; Sturtevant et al. 1997; Brassard and Chen 2006; Campbell and Laroque 2007; Edman et al. 2007). Particularly in balsam fir and black spruce forests located in Cape Breton, Nova Scotia, the rate of decay is understood to take on average 12 years to move from one decay class to the next, resulting in a decay period of approximately 60 years (Campbell and Laroque 2007). Therefore, the progression of decay classes can be assessed to understand the dynamics of woody debris over a relatively long period of time.

For the stands observed in this study, the distribution of downed woody debris volume (DWD_v) was examined along each ecosite chronosequence, resulting in the site productivity (as defined by ecosite) not accounting for the differences of DWD_v as the OLD3AGE values increased. Past research (Spies et al. 1988; Sturtevant et al. 1997; Brassard and Chen 2006), suggested that DWD volume typically followed a U-shaped temporal pattern, with a large amount of volume occurring after a stand-replacing event, reducing in the intermediate stages of development and accumulating exponentially as the forest ages and live trees begin to senesce. Contrary to the typical U-shaped pattern, the initial high accumulation earlier in development was not apparent in the coastal boreal stands observed in this study (Figure 2.5). Although an attempt was made to obtain a broad range of stand ages, the lack of DWD volume earlier in development could be due to inadequate sampling in stands that experienced a recent stand replacing disturbance, resulting in an under-representation of the dynamics occurring at the beginning of stand development (Harper et al. 2005). A similar distribution was evident in the intermediate coastal boreal stands, with the lowest DWD_decay values being accounted for in stands with a lower OLD3AGE value (Figure 2.5). However, the distribution of volume appeared to level off or slightly decline in the sites with the greatest OLD3AGE value instead of accumulating exponentially as observed in other forest communities (Spies et al. 1988; Sturtevant et al. 1997; Brassard and Chen 2006).

The volume distributed later in stand development has also been associated with trees becoming larger with age and a transition of species composition (Brassard and Chen 2009). However, coarse woody debris diameter (CWD_dbh) did not significantly differ for either of the ecosites (Table 2.8) and there was no apparent transition of species comprising deadwood volume as stands aged. Therefore, the increase of volume across the lowlands and uplands appeared to be due to abiotic or biotic disturbances as oppose to site-specific conditions.

The distribution of decay class volume can also be used to understand the scale and timing of disturbances. Volume distributed evenly across all decay classes is indicative of a constant disturbance pattern, while an unequal distribution is evidence of disturbances occurring at relatively different times throughout development (Spies et al. 1988; Delong and Kessler 2000; Jonsson 2000; Karjalainen and Kuuluvainen 2002). Although the coastal stands did not exhibit an even distribution of volume across all decay classes, the majority of decay classes within a stand had similar volume. The oldest decay class (V) accounted for significantly less volume, with the lesser decay classes contributing the majority of the volume across most of stands (Table 2.3). Therefore, it was apparent that constant disturbances as oppose to infrequent disturbances were contributing to the distribution of DWD volume in lowland and upland stand development (Table 2.3; Figure 2.5).

The increase of decay class dominance could also be assessed to understand when disturbances were occurring throughout stand development. Residual wood from a previous large-scale disturbance typically contributes to an increase in later deadwood decay earlier in stand development (Sturtevant et al. 1997). More advanced decay classes could also be the result of stem exclusion. However, because stem mortality typically occurs in smaller individuals, the DWD accumulated during this stage is small and debris could have decayed quickly (Lang 1985; Sturtevant et al. 1997). Therefore, younger stands typically have greater deadwood debris volumes in a more advanced decay class, while older stands begin to accumulate lesser decay classes (Spies et al. 1988). In the coastal boreal, more advanced DWD decay classes had the least distribution of volume (Table 2.3). The significantly less distribution of volume could be the result of previous large-scale disturbance activity and/or stem exclusion processes. The increase of decay class I volume was noticeable in the lowlands, with less total decay class I volume in the stands aged younger than 97 years and increased after the OLD3AGE is older than 97 years (Figure 2.5). However, the uplands did not exhibit an increase of the lesser decay classes (I, II, III) as stands developed and instead have equal distribution of across all stands (Figure 2.5).

The history of disturbance could also be assessed based on the dynamics of snag ages. Snags typically have a slower decomposition rate compared to DWD because they remain standing and are therefore a better indicator of the stand age and history (Hély et al. 2000). Although the agent of mortality was not recorded for each snag and cross-dating was not conducted, it was evident that as decay class decreased, SA increased in both ecosites. Because the random effects associated with stand were not significant, it is apparent that SA did not differ depending on the OLDAGE value ($p < 0.01$). Instead, an even distribution of SA was evident across the chronosequence. Stands were producing mortality earlier in stand development, resulting in longer standing snags senescing at a younger age. It should be noted that although an effort was made it accurately count the age of each snag, the reduced age of more advanced decay class snags could be influenced by the issue of an increase in missing rings with more decomposed wood

(Aakala et al. 2008). Although all snags were attempted to be aged, true ages of later decay classes might not be accurate because of the inability to obtain the age of trees that were too decayed. From examining the unaged snags in both ecosites, ages were missing across all decay classes and black spruce accounted for the majority of missing ages. Therefore, the snag decay classes ages did not exhibit missing species or decay classes, allowing for the samples obtained to be used as estimates of the decay class age (Aakala 2008). For the purpose of this research, the age trends were of more importance instead exact tree ages, allowing for the estimates to be used to understand the dynamic of snags throughout stand development.

The gradual reduction in SA indicated even-aged development processes were occurring throughout the stand development in both ecosites (Figure 2.6; Oliver and Larson 1996). However, with similar means and a larger distribution of recently decayed snag ages (Table 2.4), there did appear to be a transition to uneven-aged mortality structures later in lowland stand development (Figure 2.6). Because of the low range of ages in decay II and III (Table 2.4), this transition to uneven-aged mortality structures was not observed in upland stand development. Instead, the upland decay II (51 years) was significantly younger than the lowland decay class II (71 years), which implied that the upland sites were inducing snag mortality faster than the lowlands. Decay IV was present in lowlands and not in uplands, suggesting the mortality of snags could be occurring earlier in development in the lowlands and/or upland snags were not remaining standing long enough to reach decay class IV. Therefore, the lowlands were exhibiting the typical distribution of SA associated with uneven-aged structure from small-scale disturbances later in stand development (Figure 2.6). Although constant small-scale disturbances were also contributing to upland stand development, the implications on stand development from the minor disturbances was resulting in faster senescence of trees (Figure 2.6) and consistent distribution of lesser decay volume (Figure 2.5) as stands aged (OLD3AGE).

Age and structural development

Uneven-aged structures were primarily identified in the older aged (OLD3AGE) stands. Although uneven-aged structures were present by the 70-year threshold, the likelihood of a stand having uneven-aged structure was higher after the 80-year threshold and therefore was a better indicator of the transition from even-aged to uneven-aged structures. Transition ages of 80 years (OLD3AGE) in the uplands and 100 years (OLD3AGE) in the lowlands are the best estimates for uneven-aged structures for the stands observed in this study (Figure 2.4). However, the majority of structural attributes were not significantly different as OLD3AGE values increased and there was low variation from the mean (Table 2.7; Table 2.8). Therefore, larger live structures were not apparent and instead remained small, resulting in low diameter and height diversity as stands aged. Along with physical live tree structure, no significant differences ($p > .05$) were observed in the area occupied by trees, with live tree density (TD) and live tree basal area (BA) values not different from the uniform distribution (Table 2.8). Increased species diversity or transition of live species composition also were not present as the coastal boreal forest developed. Larger deadwood features were not evident, with the distribution of snags and downed woody debris diameter (CWD_dbh) for the lowlands and the uplands not being significantly different from the uniform distribution (Table 2.8). However, older stands were not more compositionally diverse and did not exhibit larger structural features or a transition of species composition. Black spruce accounted for the majority of snags and DWD, overstory trees, and understory recruitment. Because black spruce remained dominant throughout stand development, the coastal black spruce forest types are climax communities within the Maritime Boreal Forest Region.

Although larger structural features were not observed in the older aged stands, there were differences in the structural conditions of snags based on the OLD3AGE value. In the uplands, snag density (SNAG_N) was significantly larger later in stand development, with the stands that exhibited a larger OLD3AGE having a greater value than the mean of 1882 stems/ha ($p = 0.033$). Past research (Lee et al. 1997; Sturtevant et al. 1997; Harper et al. 2005; Brassard and Chen 2006) observed that the accumulation of SNAG_N typically followed a bimodal temporal distribution with density highest in the younger, post stand-replacing stage of succession, reducing to lower density in the intermediate-aged stands, reaching the maximum in the mature stands before decreasing slightly again in the oldest stands. In the coastal uplands, the significantly higher values in SNAG_N was evident later in stand development (Figure 2.10) and could be the result of stem competition (Oliver and Larson 1996; Chen and Popadiouk 2002), trees reaching their maximum longevity (Chen and Popadiouk 2002; Brassard and Chen 2006) or other small-scale disturbances (Clark 1988; Oliver and Larson 1996; Hély et al. 2000). There was no evidence of SNAG_N peaking in earlier development. However, this could be due to the lack of sampling in stands at the very beginning of succession (i.e. 0 – 50 years old). The increase in SNAG_N also did not appear to be due to a transition in species composition, with black spruce accounting for the majority of snag density across all stands. SNAG_N was significantly larger when OLD3AGE was greater than 82 years, which was also the onset of when three out of four upland stands begun to exhibit uneven-aged structures. Because of the presence of uneven-aged structures and a significant increase in SNAG_N, it appeared that the newly created space in canopy allowed the regenerating cohort to establish as opposed to being filled by the dominating cohort. Therefore, small-scale processes such as trees reaching life longevity or death due to external minor disturbances as opposed to stem exclusion processes appeared to be contributing to tree mortality, resulting in the initiation of the suppressed understory layer.

The lowlands exhibited a decrease in snag volume (ST) ($p = 0.004$). From referencing the snag data, it was apparent that large balsam fir snags greater than 20 cm were common in stands with a lower OLD3AGE value, and gradually reduced as OLD3AGE values increased (Figure 2.8). Particularly when OLD3AGE was older than 80 years, the larger balsam fir snags contributed to the highest volume (70.5 m^3/ha). Similar ST dynamics were observed in Canada's Aspen-dominated (Lee et al. 1997) and mixed boreal forests (Chen and Popadiouk 2002). Large gaps promote balsam fir establishment, resulting in balsam fir growing quicker after a large-gap or stand-replacing disturbance (Chen and Popadiouk 2002). Snags produced in the later stages of development were smaller due to competition and self-thinning (Lee et al. 1997; Chen and Popadiouk 2002). Therefore, the large balsam fir snags were evidence of previous large gap formation in the lowlands. Contrary to the lowlands, live DBH typically increased with stand age, causing trees to become larger again during canopy transition. As trees get larger, they inherently occupy more of the forest canopy, which inhibits other trees to grow. Typically, forests that exhibit larger trees in the later stages of development also experience a reduction in live tree density (Spies and Franklin 1996). Therefore, snags that died of age-related mortality later in development tended to be larger, causing another increase in ST in the oldest stands (Lee et al. 1997). Because the coastal lowlands lacked larger live trees in the later stages of development, the stands did not experience the typical increase in ST volume as seen in other forest types (Spies and Franklin 1996; Mosseler et al. 2003a).

Influence of site productivity on stand development

The presence of right skewed age distributions in the older aged stands indicated that uneven-aged stand structures were occurring in the upland and lowland black spruce stands (Figure 2.2). The uplands appeared to be developing uneven-aged structures at an earlier OLD3AGE than the lowlands, with uneven-aged transitions of 80 years in the uplands and of 100 years in the lowlands (Figure 2.4). In the uplands, black spruce trees have considerably larger diameters at breast height (DBH) and heights (HT) compared to the lowlands (Table 2.8). Half of the lowlands' mean DBH values were less than 10 cm, while none of the upland stands had values less than the lowland mean (Figure 2.11). Similarly, half of the lowland sites had HT values less than 8 m, while all the upland sites had values greater than 8 m (Figure 2.11). The larger values in the uplands indicated that trees were experiencing a higher growth rate. Growth rates are typically lower in harsh environmental or unfavourable sites and result in increased tree longevity (Wagener and Schulman 1954; Laberge et al. 2000). Richer sites with greater growth rates induce earlier tree senescence and typically have faster development rates (Romme and Knight 1981; Prach et al. 1993). In general, black spruce tree mortality has been related to height, with taller trees being more susceptible to wind events because of their shallow root system (Farrar 1995).

The growth rate and susceptibly of trees in the coastal ecosites were assessed through examining the decay dynamics of deadwood features throughout stand development. In the uplands, recent tree mortality appeared to be contributing to a significant increase in early DWD volume and even-aged development pattern of snags. The cumulative DWD volumes were considerably different between the lowland and upland groups, with averages of 8.14 m^3/ha in the lowlands and 14.50 m^3/ha in the uplands (Table 2.7). From comparing the ecosites, the lowlands exhibited a right skewed distribution, with half of the stands having less than 8.14m^3/ha (Figure 2.11). In the uplands, the distribution was relatively symmetric, however only one of the ten stands had less than the lowland mean (Figure 2.11). The volume of DWD was influenced by both the input of volume from dead trees and the decay rate. Decay rates are predominantly determined by biotic and abiotic factors such as disturbance regimes, temperature, soil moisture content, species chemical properties and physical properties of the substrate (Harmon and Hua 1991; Sturtevant et al. 1997). Although the lowlands and upland have the similar disturbance regimes, the higher distribution of DWD volume and significantly earlier decay class II snag mortality in the uplands suggests that the uplands were more severely impacted from minor disturbances compared to the lowlands. In terms of decay rate, coarse woody debris diameter (CWD_dbh) was not significantly different or statistically similar (Table 2.8) and there was no apparent distribution of deadwood species composition between the ecosites. The higher soil moisture content is also known to speed up the decay rate of spruce logs because of increased exposure to decomposers (Næsset 1999; Hély et al. 2000). Therefore, it appeared the difference in the soil condition, particularly moisture regime, was contributing to higher susceptibility and slower decay rate in the uplands. The site quality also influenced the timing of DWD volume distribution, with upland sites exhibiting more volume at an earlier age, causing a shift of the temporal distribution to the left. Based on these observations, the trees located in the uplands appeared to grow quicker and reach the point of susceptibility faster than the lowlands. Additional environmental variables other than the moisture regime, such as elevation, soil depth (Boucher et al. 2006) and slope (Martin et al. 2018) could also be influencing the susceptibility and longevity of trees, however these attributes were not assessed.

Another noteworthy difference between the ecosites was the distribution of the gap fraction (GF) values. The lowlands had considerably higher values of canopy openings than the uplands. All the upland stands exhibited values lower than 40%, while almost half of the values in the lowland sites had GF greater than 40% (Figure 2.11). The lowland sites had a greater range in values, while the uplands did not significantly deviate from its respective mean (Table 2.7). McCarthy (2001) determined that site productivity has been understood to influence individual tree crown sizes and distribution of gap sizes in the boreal forests. Although these gap characteristics were not assessed, it can be hypothesized that the differences of tree crowns and/or gaps sizes could be resulting in considerably different gap fractions between the ecosites.

Old forest management implications

The coastal black spruce forest communities are a climax forest type in the Maritime Boreal because black spruce was self-perpetuating throughout stand development. However, these forests lacked the typical structural features and compositional diversity that are found in other 'old-growth' forests. Instead, the stand dynamics occurring throughout coastal stand development were unique and could potentially be important for regional biodiversity (Bergeron and Harper 2009). Because the forestry industry is gradually moving towards more ecosystem-based approaches, the natural processes occurring in the coastal boreal should be considered in old forest management practices. It was apparent that site productivity (as defined by ecosite) was influencing when the transition from even-aged to uneven-aged structures occurred, with the uplands exhibiting uneven-aged structures at an earlier OLD3AGE than the lowlands. Both ecosites did transition to uneven-aged structures, which is indicative of the 'old-growth' stage of development, faster than other climax forest types in Nova Scotia (Stewart et al. 2003). However, based on Nova Scotia's current 'old-growth' definition, the coastal black spruce stands exhibiting features associated with the old-growth stage of development would not be identified. Although all the stands had more than 50% climax species and over 30% canopy closer, none were older than the OLD3AGE threshold of 125 years.

Black spruce forest communities are also identified as a climax forest type in Ontario and Quebec. In these forests, uneven-aged structures occurred in the later stages of development and shared similar structural attributes as the coastal boreal, including a lack of large structural features (Harper 2005; Rossi et al. 2009), no differences in species composition or diversity (Boucher et al. 2006; Bergeron and Harper 2009), and the presence of diverse deadwood decay (Hély et al. 2000; Ter-Mikaelian et al. 2008; Bergeron and Harper 2009). However, it was apparent that the dynamics of snags and timing of uneven-aged structures were unique to the coastal boreal. Stand ages of 150 years (Bergeron and Fenton 2012) and 160 - 170 years (Martin et al. 2018) since the most recent fire disturbance and maximum tree age of 200 years (Rossi et al. 2009) are identified as being accurate age estimates of stands transitioning to the old-growth stage of development for the inland boreal. Furthermore, maximum black spruces ages of 340+ years in Quebec (Boucher et al. 2006; Rossi et al. 2009) and 200+ years in Ontario (Uhilig et al. 2003) were higher than the oldest black spruce found in the coastal boreal (155 years in the lowland and 132 years in the upland). Therefore, uneven-aged structures and the onset of the old-growth stage of development is occurring earlier in the coastal boreal compared to the inland boreal and other climax forest types in Nova Scotia. Because of the different structural attributes and timing of uneven-aged structures throughout stand development, this study supports the knowledge that forest communities should be understood in a regional context; findings from Ontario and Quebec should not be readily applied to forest management practices in Nova Scotia or other geological areas. To address the different features associated with the 'old-growth' stage of development across Canada's forested landscape, forest managers should establish old forest definitions and management practices based on a scale that incorporates both the regional forest type and site productivity factors to ensure these unique communities are being identified.

It was evident that gap-dynamics is a prevalent natural disturbance occurring later in Nova Scotia's coastal black spruce forest development. The diversity of decay classes was indicative of constant small-scale processes. A gradual increase in snag decay age in both ecosites suggested that even-aged processes occurred during the more advanced stages of snag decay, with a transition to uneven-aged dynamics for the lesser decayed snags in the lowlands. For both ecosites, uneven-aged stand structures and a change in structural attributes were apparent as stands temporally progressed. However, site productivity did influence when this transition occurred, with the upland sites exhibiting uneven-aged structures at an earlier OLD3AGE than the lowlands. When stand age (OLD3AGE) was older than 80 years for the coastal uplands and 100 years for the coastal lowlands, uneven-aged structures were likely. Although larger live and deadwood features and species composition did not change as stands aged (OLD3AGE), attributes associated with snags differed. The lowlands exhibited a decrease in large balsam fir (>20 DBH) snag volume and the upland had an increase in snag density later in development. Because of the significant increase in snag density, earlier DWD decay classes, and even-aged snag decay age dynamics, it was apparent that minor disturbances had more severe impacts on stand development in the uplands compared to the lowlands. The increased impact could be attributed to the noticeably greater DBH and HT in the uplands, which was resulting in higher growth rate compared to the lowlands. The uplands' increased growth rate appeared to be causing trees to reach the point of susceptibility faster, resulting in uneven-aged structures occurring earlier than the lowlands.

Based on the Nova Scotia's current definition of 'old-growth', coastal black spruce forests in the 'old-growth' stage of stand development would not be identified. The climax black spruce forest types in Ontario and Quebec transition to uneven-aged structure later than the coastal boreal. The difference in stand development characteristics between these regional boreal forests supports the knowledge of understanding regional forest communities as opposed to applying practices from a different geological area or forest type. For an ecosystem-based management approach to be applied to these forests, provincial old forest management practices should be implemented at a scale that incorporates both the regional forest type and site productivity factors.

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Chapter 3: Conclusion

3.1 Overview of Thesis

In Chapter 2, stand development was assessed along a chronosequence of lowland and upland sites. I examined three objectives to quantitatively assess the successional and structural processes occurring as stands developed. My first objective determined that uneven-aged structures were occurring in the black spruce forest communities along Nova Scotia's eastern shore. The Weibull shape parameter (WSP) and symmetry index (SI) determined that there was no distinct gradient of stands transitioning from even-aged to uneven-aged based on stand age (OLD3AGE) or ecosite. However, all uneven-aged structures, except for upland stand aged 72 years, were identified in the older aged sites. The onset OLD3AGE of uneven-aged structures was approximately 80 years in the uplands and 100 years in the lowlands. Upland sites appeared to have a higher development rate than the lowlands because uneven-aged structures were occurring earlier in stand development. Black spruce maintained dominance of deadwood and overstory and regenerating cohorts. Therefore, it was apparent that the lowland and upland black spruce forest communities are climax forest types in the Maritime Boreal Forest Region.

My second objective examined DWD volume and snag ages based on decay classes within and between the ecosites. Based on the linear mixed effects model, the fixed effects of ecosite and decay had a significant interaction and the random effects associated with stand accounted for significant variation of DWD decay volume. The temporal distribution did not follow the typical U-shaped pattern. Although an increase in volume was observed, in both the lowland and uplands sites, total volume declined or leveled off in the oldest stands. The majority of decay class volume within the ecosites was not significantly different. For snag ages, the fixed effects of ecosite and decay class had significant interaction while the random effects associated with stand did not account for any additional variation. Therefore, snag decay ages did not differ depending on the OLD3AGE of the stand. The upland sites had lower decay II value, which implied that the upland sites were inducing snag mortality faster than the lowlands. Snag mortality did exhibit even-aged development at the beginning of stand development. However, in the lowlands it appeared that mortality structures transitioned towards more uneven-aged conditions. These findings confirmed the presence of gap-phase dynamics caused by small-scale disturbances in both ecosites. However, trees in the uplands appeared to be senescing earlier and contributed to a significant increase in earlier DWD volume.

My third objective determined that snag volume (ST) was significantly lower in the lowlands and snag density (SD) significantly increased in the uplands as the OLD3AGE value increased. Balsam fir snags >20 DBH were present in the younger lowlands sites and were contributing to an increase in ST. In the oldest stands, the larger size of balsam fir snags was not present and overall snag DBH was less than younger OLD3AGE stands. The significant increase in upland SD was the same age-threshold when three out of four of the stands exhibited uneven-aged structures. The natural senescence of trees and/or external small-scale disturbance appeared to be inducing significant upland snag mortality, resulting in the regeneration layer occupying the newly created space in the canopy. The other parameters were not significantly different as stands aged (OLD3AGE). Therefore, older boreal forests did not exhibit larger live tree structural features or compositional change. No parameters were significantly different between the ecosites, however uplands had noticeably ($p < 0.2$) greater DBH and HT values, which suggested a higher growth rate. The higher growth rate appeared to cause increased susceptibility and more severe impacts on stand development than the lowlands. Along with DBH and HT, the uplands exhibited noticeably higher downed woody debris volume (DWD_v) and lower gap faction (GF) values compared to the lowlands. Chronosequence or site productivity gradients did not account for live tree density (TD), basal area (BA), species diversity (SC), and coarse woody debris diameter (CWD_dbh), which suggests these attributes were either inherently similar or another factor was contributing to their value.

My objectives determined that gap-phase dynamics is a prevalent natural disturbance occurring later in coastal boreal black spruce stand development. Uneven-aged structures are identified in the older (OLD3AGE) stands, with the uplands exhibiting uneven-aged structures earlier than the lowlands. Although the majority of structural attributes are not significantly different from a uniform distribution, variables associated with snags differed. It was apparent that black spruce is a coastal climax community, however the onset of attributes associated with the ‘old-growth’ stage of development was different compared to the boreal forests of Quebec, Ontario and the climax forest communities currently identified in Nova Scotia. Therefore, both the regional forest type and site productivity factors should be incorporated into old forest management policies and practices.

3.2 Application of Old-growth Definition

Nova Scotia's current 'old-growth' definition did not apply to the coastal black spruce forests. However, the lowland and upland coastal black spruce forest types are climax forest communities occurring within the Maritime Boreal Forest and they exhibit unique conditions indicative of the 'old-growth' stage of development. Therefore, the definition criteria currently used should be altered to address the stand dynamics occurring in coastal black spruce forests. Through this research, I used a combination of structural and successional definition parameters to understand when the transition to the 'old-growth' stage of development was occurring. Successional definition criteria included the presence of late-successional, climax forest types and gap-phase dynamics. Structural definitions criteria included the presence of uneven-aged structures and changes in structural attributes. By utilizing both successional and structural parameters, the processes occurring later in stand development were identified. From incorporating a combination of these criteria, an appropriate approach for determining an 'old-growth' definition based on the regional forest type and site productivity factors can be established.

3.3 Other Boreal Forest Management

Black spruce forest types have been identified as late-successional forest communities in the inland boreal forests of Ontario and Quebec. Similar to the coastal, species composition and increased species diversity were not significantly different throughout Ontario and Quebec stand development (Harper et al. 2002, 2005; Boucher et al. 2006; Bergeron and Harper 2009; Kuttner et al. 2013). Boucher et al. (2006) attribute this to both a lack of species composition change and the fact that black spruce forests have inherently low species diversity. It was also identified that black spruce forests lacked the key structural attributes that were typically associated with old-growth forests, including the abundance of large live structural features (Harper et al. 2005; Bergeron and Harper 2009; Rossi et al. 2009). Other similarities included diversity of snag and DWD decay class throughout stand development (Bergeron and Harper 2009). However, volume was higher than values observed in the coastal boreal, with averages of 34 m^3/ha in northwestern Quebec (Hély et al. 2000) and 46.7 m^3/ha in Ontario (Ter-Mikaelian et al. 2008). The structural features observed in the inland boreal were slightly larger than values in the coastal boreal, with DBH mean values ranging from approximately 11.5 cm – 16.5 cm and height ranging from approximately 8.5 m – 14 m (Ter-Mikaelian et al. 2008; Rossi et al. 2009). Although slightly larger, live structural features were still similar, which suggests that the higher DWD volume could be attributed to an increase in DWD log frequency instead of larger deadwood pieces. Higher accumulation of DWD logs has been understood to indicate the timing and severity of disturbances (Brassard and Chen 2006; Bergeron and Harper 2009). Although small-scale disturbances are both identified as processes influencing boreal stand development, it is apparent that the scale and severity of disturbances have different impacts on stand development in these regional forests.

Although the Ontario and Quebec boreal forests exhibited some differences in the temporal progression of structural attributes, there are still similarities associated with the ‘old-growth’ stage of development. Because of these similarities, management recommendations from the inland boreal could be adjusted to represent the coastal boreal stand development. Management recommendations include stand structures being diversified by age rather than size (Rossi et al. 2008), maintenance of structural attributes, particularly deadwood features, associated with later stand development (Bergeron and Harper 2009) and addressing the importance of stand development based on site productivity (Boucher et al. 2006). These recommendations could be incorporated into other management practices other than old forest management, allowing for features associated with each stage of development to be maintained throughout the coastal boreal landscape.

3.4 **Recommendations**

Future climate predictions suggest the coastal boreal will experience an increase in the frequency and severity of storms (Taylor et al. 2019). Therefore, this study can be used as a reference point for current wind disturbances' influence on forest development. From this research, deadwood features appear to be the best indicator for understanding the temporal dynamics of stands in the upland and lowland ecosites. However, the agent of mortality was not assessed. Therefore, I suggest future research focus on the mortality agent of deadwood structural features within each ecosite to understand if trees are senescing due to wind, from reaching the peak of longevity or other external disturbances. Therefore, future changes in disturbance regimes and their influence on the structural condition of the coastal forests can be determined.

My research focused on structural and successional tree features within a forest and did not take into consideration the richness of herbaceous plants, bryophytes, and animals. Because forests in the later stages of development are known to have an increase in biodiversity features (Spies and Franklin 1996; Hunter 1998; Mosseler et al. 2003a, 2003b; Desponts et al. 2004), I recommend future research focus on plant and animal habitat richness in relation to forest structure. My research identified differences based on the site and temporal conditions of the stand, therefore I recommend including these as factors in future habitat research. This would allow for a holistic approach to forest and habitat management within this region.

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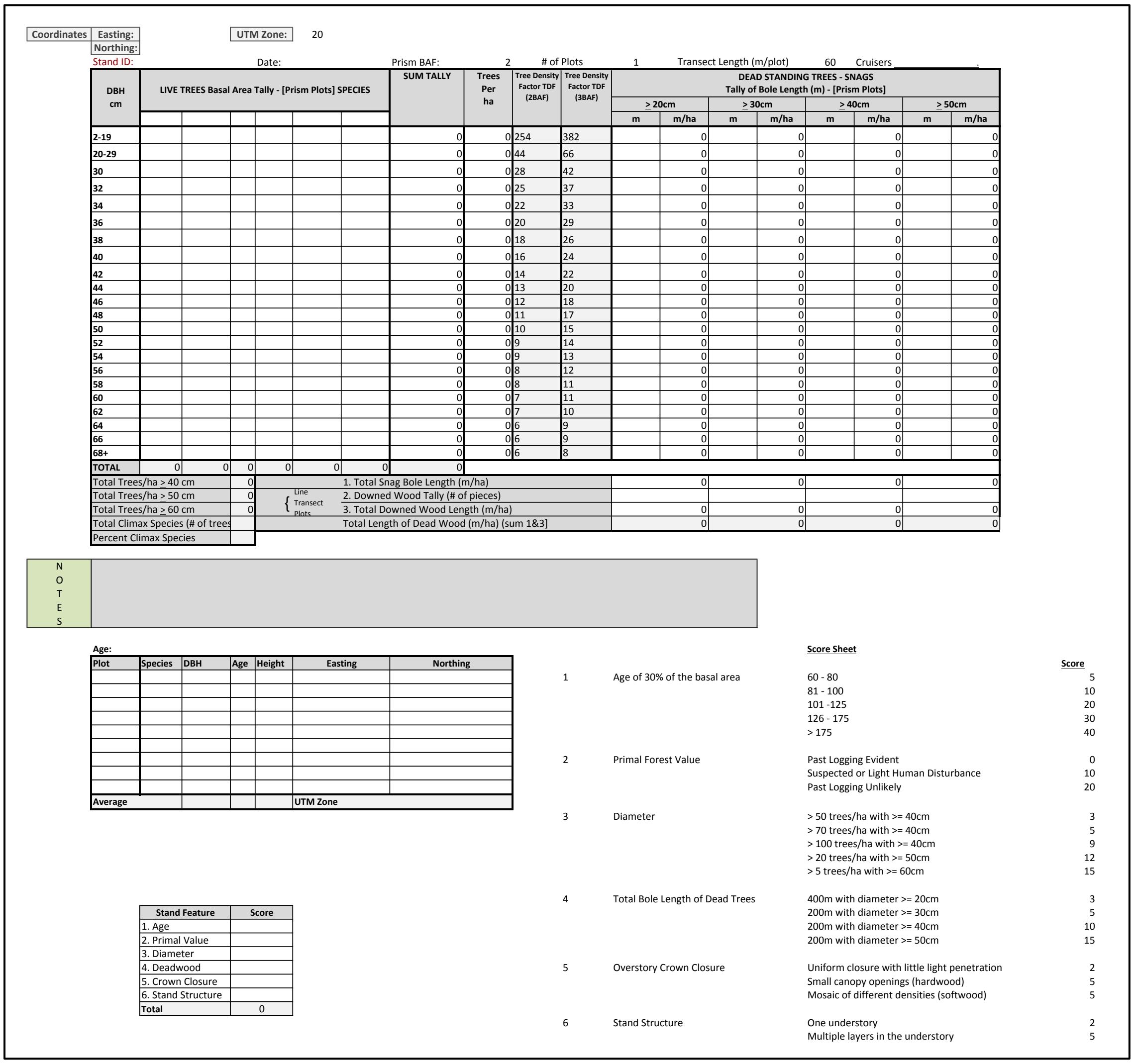
Appendix A: Nova Scotia Department of Lands and Forestry ‘old forest scoring’ sheet



Coordinates Easting:
Northing:
UTM Zone: 20

Stand ID: Date: Prism BAF: 2 # of Plots 1 Transect Length (m/plot) 60 Cruisers _______________.

DBH cm	LIVE TREES Basal Area Tally - [Prism Plots] SPECIES						SUM TALLY	Trees Per ha	Tree Density Factor TDF (2BAF)	Tree Density Factor TDF (3BAF)	DEAD STANDING TREES - SNAGS Tally of Bole Length (m) - [Prism Plots]							
											≥ 20cm		≥ 30cm		≥ 40cm		≥ 50cm	
											m	m/ha	m	m/ha	m	m/ha	m	m/ha
2-19							0	0	254	382		0		0		0		0
20-29							0	0	44	66		0		0		0		0
30							0	0	28	42		0		0		0		0
32							0	0	25	37		0		0		0		0
34							0	0	22	33		0		0		0		0
36							0	0	20	29		0		0		0		0
38							0	0	18	26		0		0		0		0
40							0	0	16	24		0		0		0		0
42							0	0	14	22		0		0		0		0
44							0	0	13	20		0		0		0		0
46							0	0	12	18		0		0		0		0
48							0	0	11	17		0		0		0		0
50							0	0	10	15		0		0		0		0
52							0	0	9	14		0		0		0		0
54							0	0	9	13		0		0		0		0
56							0	0	8	12		0		0		0		0
58							0	0	8	11		0		0		0		0
60							0	0	7	11		0		0		0		0
62							0	0	7	10		0		0		0		0
64							0	0	6	9		0		0		0		0
66							0	0	6	9		0		0		0		0
68+							0	0	6	8		0		0		0		0
TOTAL	0	0	0	0	0	0	0											

Total Trees/ha ≥ 40 cm	0	1. Total Snag Bole Length (m/ha)	0	0	0	0
Total Trees/ha ≥ 50 cm	0	{ Line Transect Plots 2. Downed Wood Tally (# of pieces)				
Total Trees/ha ≥ 60 cm	0	3. Total Downed Wood Length (m/ha)	0	0	0	0
Total Climax Species (# of trees		Total Length of Dead Wood (m/ha) (sum 1&3)	0	0	0	0
Percent Climax Species						

N
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S

Age:

Plot	Species	DBH	Age	Height	Easting	Northing
Average					UTM Zone	

Stand Feature	Score
1. Age	
2. Primal Value	
3. Diameter	
4. Deadwood	
5. Crown Closure	
6. Stand Structure	
Total	0

Score Sheet

			Score
1	Age of 30% of the basal area	60 - 80	5
		81 - 100	10
		101 -125	20
		126 - 175	30
		> 175	40
2	Primal Forest Value	Past Logging Evident	0
		Suspected or Light Human Disturbance	10
		Past Logging Unlikely	20
3	Diameter	> 50 trees/ha with >= 40cm	3
		> 70 trees/ha with >= 40cm	5
		> 100 trees/ha with >= 40cm	9
		> 20 trees/ha with >= 50cm	12
		> 5 trees/ha with >= 60cm	15
4	Total Bole Length of Dead Trees	400m with diameter >= 20cm	3
		200m with diameter >= 30cm	5
		200m with diameter >= 40cm	10
		200m with diameter >= 50cm	15
5	Overstory Crown Closure	Uniform closure with little light penetration	2
		Small canopy openings (hardwood)	5
		Mosaic of different densities (softwood)	5
6	Stand Structure	One understory	2
		Multiple layers in the understory	5

Appendix B: Nova Scotia Department of Lands and Forestry research plot protocol

Age and Structural Characteristics of Remnant Red Spruce Old Growth Forests at Cape Chignecto

"Field Sampling Procedures"

General Description

The project will involve non-destructive sampling of remnant old growth red spruce forests at Cape Chignecto. The primary objective is to develop a scientific understanding of age structure and long term stand dynamics in old growth forests through extensive increment coring. Macro features of coarse woody debris, snags, tree size (diameter), basal area, vertical structure and canopy condition will be measured to assist in the evaluation and development of the N.S. Old Growth Scoring system.

Purpose

Develop a scientific understanding of the age structure and stand dynamics of Old Growth Forests. Evaluate the Nova Scotia Old Growth Scoring System.

Objective

Obtain detailed measurements of stand age and stand structural elements.

Methods

Up to 5 sample points will be established systematically through selected old growth stands. At each point, live and dead tree composition will be measured by point sample using a 1, 2, and 3 BAF prisms. All sampled trees will be increment cored, and cores will be taken to the lab for preparation and aging. Other noteworthy trees will also be selectively sampled.
Coarse wood debris will be sampled along a 105 m triangular shaped line transect (35 m sides). Stand vertical structure and canopy condition will be visually assessed.

Results

Data will be summarized to provide a quantitative description of stand conditions. Age data will be analyzed and stand age class structure will be determined and used to describe stand disturbance dynamics. The overall results will be used to evaluate the old growth scoring system.

In each stand, all sample trees will be aged by extracting increment cores, that will be prepared and aged in the lab using stand tree chronology techniques. Cores will be permanently mounted and be available for future study if occasion arises.

Study Sites

Remnant old growth stands of red spruce were identified from the Cape Chignecto area using photogrametry. These remnant forest stands occur within a larger landscape of younger red spruce that arose following clearcut harvesting in the mid 1990's.

Sampling Instructions

- Establish 3 -5 sample plots per stand
- Collect a minimum of 50 increment cores per stand, representing the full range of age/diameter classes in the stand. This will include a full sampling of all trees tallied by prism sample, as well as other selected individuals with noteworthy characteristics suggesting very old age (the intention being to capture the maximum stand age, as well as the age distribution of the stand).

At each sample plot:

1. Collect or record gps location (utm nad83)
2. Use 2 or 3 BAF prism (15 - 20 live trees/plot) to record live and dead trees by species by 2 cm dbh class. For snags record the length of bole by 10cm diameter class. For trees less than 10 cm dbh sample using a 1 BAF prism.
3. Establish a 105 m line transect triangle (35 m sides) beginning at each sample point. For all transected downed wood > 9.0 cm, Record diameter at intersection (mm), species, and decay class.
4. Visually inspect and record the overstory canopy condition (uniformly closed, canopy openings, mosaic of densities)
5. Visually inspect and record the number of understory layers not including seedling (0, 1, 2, >2)
6. Record evidence of past human or natural disturbance (type, amount, when)
7. Measure and record depth of duff layer near plot center
8. Sample all trees tallied by prism sample, as well as other selected individuals with noteworthy characteristics suggesting very old age

For each sample tree record:

- a. Tree number
- b. Species
- c. Dbh
- d. Height
- e. Status (Live or Dead)
- f. Amount of crown dieback (stag tree?)

Store and Label cores:

- a. Store core in straw in order of extraction and affix label at the bark end of the straw.
- b. On label record: date, species, dbh, stand name, plot#, tree#

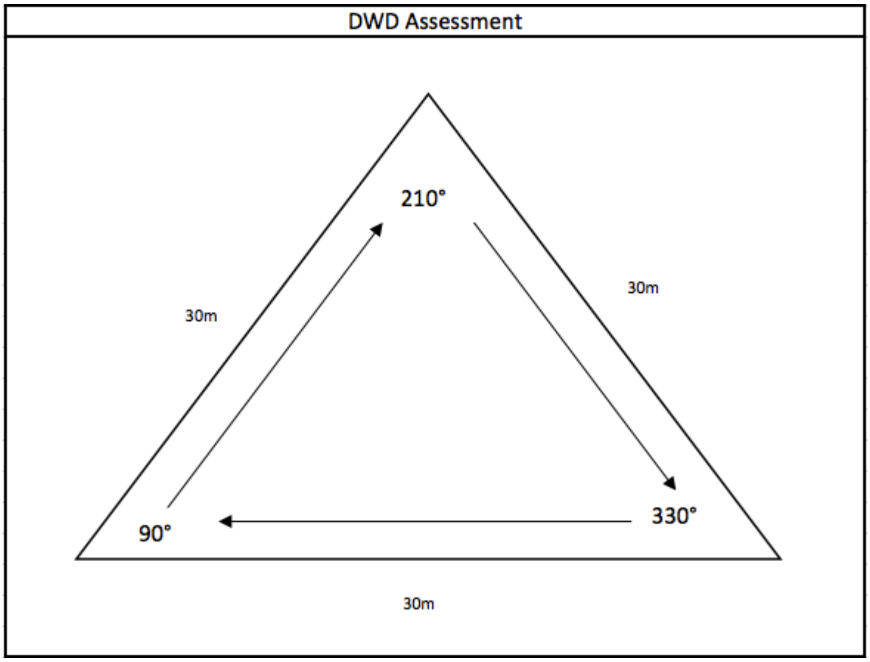
Increment Core Preparation (from David W. Stahle, tree chronologist):
recommended websight: http://web.utk.edu/~grissino/

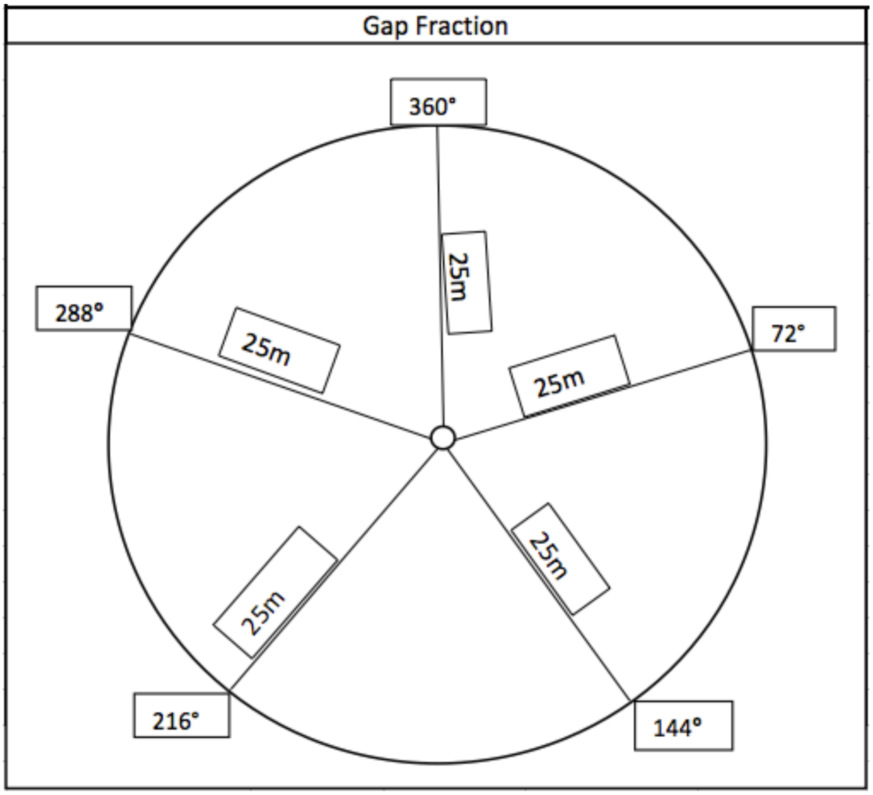
1. Upon collection, store cores in straws in the order of extraction from the tree. Attach label to the straw at the “bark” end of the core.
2. In the lab, slice open straws, and leave cores to dry inside straw for a few days.
3. Permanently mount cores using wood glue into a shallow 2mm wide groove cut into a narrow board. Cores should have the tracheids extended vertically (ie. see radial/cross sectional surface)
4. Polish cores with sandpaper through the following grit sequence: 220, 300, 400, 600
5. Count rings using strong magnifying glass, or dissecting microscope.

Materials

1. Prisms (2 & 3 BAF)
2. Diameter Tape
3. Increment Borer
4. Compass
5. 30 m tapes (2)
6. Laser Hypsometer
7. GPS
8. Straws
9. Labels (for straws)
10. Marker
11. Masking tape
12. Clipboard
13. Cruise Sheets
14. Aerial Photos
15. Grooved 1" Pine boards for mounting cores
16. Wood Glue
17. Sandpaper 220, 320, 400, 600 (Lee Valley Tools)
18. Windendro system

Appendix C: Downed woody debris (DWD) and gap fraction (GF) fixed linear transects





Appendix D: Stewart et al. (2003) modified decay classes based on Sollin (1982)

Decay Classes	
I	Freshly dead, bark intact, branches intact (including small), needle/leaf retention, bole sound, bole raised off group on branches.
II	Beginnings of decay but rot not well established in wood that was sound at time of death. Bark mostly intact, branch stubs, bole not raised on branches, bole mostly sound.
III	Rot becoming established but sound at core. Bark loose and mostly flaked off, bole beginning to rot but maintaining structural strength – round, straight, not sinking into ground
IV	Advanced decay. Bark mostly absent, bole mostly decayed with little or no sound wood present. Colonized with vegetation. Lacking structural strength – bole oval and bending to shape of ground. Last stage for snag, which will be rotted, wobbly, and could be easily pushed over.
V	Rotted through, becoming humus. Sunken into mound on the ground, but retaining a woody character, not yet part of the soil.

Curriculum Vitae

Candidate's full name: Emily Katelyn Woudstra

Universities attended:

University of Guelph, BA, International Development, 2015

Awards:

Dorothy and Kenneth Langmaid Forest Soils and Tree Growth Scholarship, 2020/2021

Publications: None

Conference Presentations: None