QUANTIFYING KEY METRICS OF ECOSYSTEM BIODIVERSITY IN NATURAL AND MANAGED SUB-BOREAL FORESTS OF BRITISH COLUMBIA

by

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Abstract

Forest management in the central interior of British Columbia has been active for over a century. Industrial forest practices in the region are based on the premise that harvest and subsequent stands regeneration is sustainable, but recent investigations raise questions about long-term ecological sustainability and impacts on biodiversity. I evaluate here, using a chronosequence of forest stands, the impacts of stand harvest on biodiversity status and recovery. Aerial laser scanning is used to enhance analysis and model impacts spatially. I provide a novel assessment of key biodiversity metrics of diversity, richness, abundance, and modeling using linear discriminant analysis and random forest frameworks. Results show that vegetation community composition and coarse woody debris (CWD), a key habitat for numerous taxa, are both impacted by harvest history. Predictive mapping of CWD provides insights and a further tool for decision makers to manage and ensure natural levels of CWD are maintained on the landscape.

Acknowledgements

This project would not have been possible without the support and encouragement of the Aleza Lake Research Forest Society. Much thanks to Michael Jull who has been a mentor to me as a forester and as a forest scientist. Thanks to Samantha Gonzalez, Kailee MacKinnon, John Mainville, Alicja Muir, Rachelle Winsor, Keaton Freel, Saskia Hart, Marie Garnier, Autin Bartel, and Yuxiao Zhao for their assistance with data collection. Dr. Nicholas Coops and members of the UBC Integrated Remote Sensing Studio provided me time and space as I learned how to use lidar remote sensing data. Dr. Brian Menounos provided in-kind support for the acquisition and initial data processing of the lidar dataset. I am very thankful for the efforts of Dr. Che Elkin, who supervised, taught, challenged, and encouraged me throughout the entire project. I am grateful to the additional members of my examining committee: Dr. Roger Wheate, Dr. Hugues Massicotte, and John Pousette for their questions and review of this document. Financial support for the project was provided by the Sustainable Forestry Initiative and a UNBC research seed grant.

Finally, I am grateful to my family, my partner in life Tina, our son Samuel, our parents Earle and Dorothy Chisholm, and Gordon and Mary Townsend for their support throughout this time of study and learning.

Dedication

I dedicate this work to my son Sam to encourage him to “do hard things” and to “never stop learning”.

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Chapter 1

Research background

My motivation and central question

As an introduction for the motivation to undertake this research, I provide this personal reflection from my experience of working in the forests. I am a practicing forester and am accredited as a Registered Professional Forester with the Association of British Columbia Forest Professionals. Much of my career has focused on the regeneration of forests following clear-cut harvest, including management of operations to prepare sites for planting, overseeing the planting of millions of trees, and stand tending including competing vegetation management after planting. These activities took me across much of the Central Interior of British Columbia, from 100 Mile House north to Fort Ware, and Fraser Lake and east into Alberta. In Alberta, these activities extended from Kananaskis north to Peace River and west to the provincial border. The story of forestry practices across all these regions is generally the same: harvest of old natural forest and regenerate planted trees. Through my career one question has continually returned to my mind: are we growing forests or are we simply growing trees? The following research has provided an opportunity to explore this question and present quantitative answers to the impact and patterns of recovery of forests on the landscape through the examination of key metrics of biodiversity, following harvest and planting.

Consideration of the issues

The conservation of biodiversity in forested lands is critically important for the long-term sustainable management of forest ecosystems (Gao et al., 2014; Harrison et al., 2014). Old-growth forests, those that are old in age and free from human disturbance, are frequently identified as areas with high biodiversity value (Kane et al., 2010a; Mladenoff et al., 1993). This richness in biodiversity is assumed to derive from the fact that these areas are highly complex systems (Filotas et al., 2014; Messier et al., 2013) though attempts to quantify forest complexity to support the ecological theory that forests are complex adaptive systems is highly challenging (Parrott, 2010).

The oldest forest stands, generally those with the largest trees, are assumed to have emergent properties that support a greater variety of species in addition to species that require an old forest state (Burton, 2013; Levin, 1998). Key physical attributes that make up the old-growth forests, characterizing the physical structures that make them unique, include higher levels of large dead wood in the form of coarse woody debris (CWD) (Harmon et al., 1986b; Stokland et al., 2012), standing snags (Spies et al., 1988), and live stand characteristics including canopy gaps (DeLong et al., 2003), high variability in canopy shape, and old large trees (Kane et al., 2010a). With the increasing availability of 3-dimensional remote sensing data from lidar, opportunities to assess a plethora of forest metrics across whole landscapes are now accessible (Ahmed et al., 2015; Coops et al., 2016; Filotas et al., 2014; Gao et al., 2014); it is expected that this novel remote sensing data, paired with empirical data, will provide new insights into characterizing and quantifying forest structures that are indicative of biodiversity and forest ecosystem complexity.

For decades there has been the recognition that forests provide a richness in biodiversity and that they should be managed for numerous values or ecosystem services (Franklin, 1989; Harrison et al., 2014). Cardinale et al. (2012) provides a succinct definition:

“Biodiversity is the variety of life, including variation among genes, species and functional traits.” Examining biodiversity is critically important when considering ecosystem services to humanity as well as ecosystem function. Organisms are known to influence their own local environment and generally, with increases in biodiversity, greater biomass production and nutrient cycling are afforded. Additionally, biologically diverse systems are considered to be more stable while remaining dynamic providing for higher ecosystem resilience (Cardinale et al., 2012; Parrott and Lange, 2013).

While recognizing the importance of biodiversity, governments, non-governmental organizations, as well as industrial resource-based companies make commitments to the conservation of biodiversity. For example, Canadian federal law provides for the conservation of Biodiversity through The Species at Risk Act, the Canadian Environmental Protection Act, the Migratory Birds Convention Act, and the Canada Wildlife Act. In addition, numerous voluntary forest certification systems or organizations market the conservation of biodiversity as a priority and companies that manufacture products from forest harvest include these certification standards into their business model. Gulbrandsen (2004) reviews the potential of forest certification regimes to ‘fill the gaps’ in legislation, though the effectiveness of these systems is debated (Castka, 2016; Gullison, 2003; Kalonga et al., 2016).

In British Columbia, Canada forest lands are dominantly publicly owned (95%) and managed by the government (Canadian Council of Forest Ministers, 2017). The conservation of biodiversity is given high priority and is one of the resource values protected under the Forest and Range Practices Act. Of particular importance for landscape level planning is the establishment of Biodiversity Orders which are set at provincial and regional scales, that is Forest Districts or Timber Supply Areas; these ‘orders’ issued under the Government Action Regulation set minimum old forest target levels (MSRM, 2004). A specific example of the Aleza Lake Research Forest has government targets set to conserve 30 percent of the forest lands in an old forest state (ILMB, 2009).

Forest ecosystems are theorized to be complex adaptive systems (CAS, Levin, 1998; Parrott, 2010). This concept comes from "Complexity Systems Science", originally from the fields of non-linear physics and information theory, and is being used to understand and describe ecosystems – even suggesting that it could unify the study of global forests providing a common understanding for all forest types from tropical to boreal (Filotas et al., 2014). Forest ecosystems are excellent examples of complex systems as they are heterogeneous, self-organizing, dynamically optimizing their internal components and processes and thereby attaining maximum complexity. This 'maximum-complexity' is considered to be an emergent and distinct attribute of an ecosystem (Messier et al., 2013).

Forest disturbance occurs both naturally and from anthropogenic sources and varies in scale and severity. Large scale disturbances occur in the 1000 to 100,000s of hectare range and can include impacts by fire or insect outbreaks (Burton, 2013). These large scale disturbances provide a "legacy of structure" in the forms of standing dead trees burnt or otherwise, an influx of CWD, and small patches of undisturbed or moderately disturbed refugia; long return disturbance intervals occur in the 300-1000 year range (Franklin et al., 2002; Spies et al., 1988). In periods between major disturbances, smaller scale events occur creating canopy gap dynamics. For example, wind events may uproot or snap small clusters of trees often weakened by fungal pathogens or rots. These small scale natural disturbances also leave high levels of physical structures as a legacy. In contrast, conventional timber harvesting methods generally remove most of the biomass from a site, reducing structures that may be essential for ecosystem development.

In landscapes with a mosaic of old natural, "naturally disturbed" and "management disturbed" stands, it is important to consider the complex dynamics occurring. CAS theory suggests that naturally disturbed stands experience shift from a state of theoretical maximum complexity to one of increased disorder. While managed stands, in particular those that are artificially regenerated and managed for a particular tree species, move towards a highly ordered or homogenized system (Messier et al., 2013). Following these disturbances, forest systems will begin returning to a state of maximum complexity. However, it is unclear if there are different ecological processes at work between the natural and managed stands and if they are moving towards similar or unique maximum diversity states. While concepts of the CAS theory may be indicative of ecosystem health and resilience, studies examining this theory are limited (Parrott, 2010).

These central and related conceptual pillars –forest as complex adaptive systems and biodiversity– are useful but represent thousands of species, their interactions and their habitats. It is neither feasible nor practical to quantify in its entirety the biodiversity at work and to monitor the development of forest complexity. However, it is possible to examine key metrics of biodiversity and to examine if these are indicative of CAS.

At large scales, climate and natural disturbance patterns compose the major drivers of biodiversity and the processes driving forest complexity. Areas with high energy input are (e.g. equatorial / tropical sites) more diverse than those at higher latitudes (Kimmins, 1996). The availability or access to resources needed for growth, reproduction, and the ultimate survival of an organism within a given ecology depend on numerous factors. In a very broad sense, this can be placed into two categories: a) sustenance - sources of energy and nutrients essential for survival and b) a safe space to live and reproduce. These two categories are highly dependent on the structures that form habitats and the climate that surround the habitat. What then are the essential structures driving ecological processes? Soils form a substrate: a safe place for numerous organisms to further colonize and develop. The local topography of a site will influence the availability of nutrients at any given site. Water flows from ridge tops to depressions or valley bottoms and consequently, this local topological structure has a strong influence on the water availability for organisms. Trees that form the forest stands grow to maturity and provide incredible opportunities for vertical structure that may enhance habitat for some organisms while reducing available resource availability for others (e.g. creating elevated structures for birds while reducing light availability in the lower canopy). It is this variety of physical structures within forests that provide an array of diverse habitats, microhabitats and niche spaces for organisms to interact and live (complexity and biodiversity).

The examination of vegetation provides a direct measure of diversity for one kingdom of organisms. Plant species diversity has also been found to correlate well with overall diversity, as demonstrated by Gao et al. (2014). Understanding that plant communities are both a measure of one group of organism diversity and an indicator of overall biodiversity, one must consider how plant communities function in forested ecosystems. These systems are complex not simply in the sense of many processes happening simultaneously but in the sense of complexity theory described above. Plant communities develop and in many ways the 'whole exceeds the sum of their parts'.

McElhinny et al. (2005) provide a review of physical structural complexity and suggest a definition and recommendations for measuring it. Their work focuses on the ability to use structure as an indicator of biodiversity at the forest stand scale with the ultimate goal of generating a metric that could be used to classify various forest types. Forest structural characteristics they suggest as important include: canopy cover, understory vegetation, deadwood, and forest tree sizes, abundance and distributes. However, it should be noted that, for many of the attributes listed (a list generated from their literature review), links to biodiversity were assumed with few studies giving definitive linkages. As such, there seems to be a general sense in the scientific community that forest structure is strongly linked to biodiversity, yet the authors themselves suggest that this assumption may need significant substantiation.

Harmon et al. (1986b) provided a thorough examination of CWD in the Pacific Northwest: it highlighted the use of CWD by numerous organisms as well as examined sources of CWD and rates of decomposition. More recently, Stokland et al. (2012) provided a comprehensive exploration of the ecological role played by dead wood structures in ecosystems with a focus on biodiversity. The authors demonstrate the importance of dead wood to the conservation of biodiversity, estimating that between 400,000 and a million different species use these structures for habitat or food sources.

The contribution of dead wood to biodiversity is striking. The sources of dead wood, that is the recruitment of these materials, are dependent on the ecological processes that cause individual trees to die. Sources of CWD come from two pools: the pre-disturbance stand (i.e. pre-fire / stand replacement disturbance) and from within an existing stand (Spies et al., 1988). Generally, following a major disturbance (e.g. fire, clear-cut harvest), some remnant pieces may provide large individual pieces that begin a slow decay. This is more distinctly the case following a fire where, although much of the material may have burnt, remaining dead trees will provide CWD. These large pieces will decay relatively slowly, given their low surface to volume ratios. In contrast, in maturing forest, the recruitment of CWD significantly depends on forest stand dynamics: patterns of growth and mortality of trees. Following a stand-replacing disturbance, forest re-establishes (naturally or through management intervention) and as the young trees mature, they compete with one another (e.g. at crown closure), entering a stem-exclusion phase where intra-tree competition will cause some individuals to die as they are outcompeted for resources. The dead stems are relatively small as these stands have not yet matured, they have a higher surface to volume ratio and will decay relatively quickly – thereby contributing CWD for a shorter period. For example, second growth plantations in the central interior of British Columbia will enter a stem exclusion phase at approximately 30 years of age and individuals may only be 15 – 20cm diameter at breast height (author's professional experience). At later ages, through ongoing stem exclusion processes or additional impacts by wind, pathogens, and localized insect attacks, large trees will be recruited to CWD. These large structures provide high quality habitat especially for larger organisms that require larger sites for roosting and cavity nesting. Additionally, large dead wood takes longer to decay given low surface to volume ratios and thereby provide relatively long lasting structure.

Parrott (2010) suggests the following approaches to measure or examine complexity in forest ecosystems: (a) Temporal Measures – change of state over time; (b) Spatial Measures – describe the configuration of the system at a point in time (raster based data from remote sensing or modelling is often used here); (c) Spatiotemporal measures – involving 3-dimensional modeling of information layers and time; and (d) Structural Measures (Ecological topology) – describing the organization and relationships in the system.

Aerial Laser Scanning (ALS) / Light detection and ranging (lidar) is a remote sensing technique that provides 3-dimensional point cloud data of the area surveyed. This system is an active sensor, usually mounted to either a helicopter or airplane, emitting lasers towards the ground and capturing a return signal that provides a datapoint with a real-world coordinate (easting, northing, and elevation) with sub-metre accuracy. Additional data includes signal intensity, and meta-data (e.g. time, signal return sequence, flight path identifier). Numerous models are generated from this type of data – two of the most common are digital terrain models and crown height models (White et al., 2016).

The enhancement of traditional forest inventories through the use of ALS/lidar has been well documented (Wulder et al., 2008a, 2013). Forest inventory modelling is traditionally done through airphoto interpretation where human operators evaluate stereo images to identify similar forest stands and provide general forest attributes based. In contrast, lidar provides opportunities to directly measure forest stand in an automated system. Metrics from lidar point cloud data are highly correlated with numerous forest timber metrics including: tree height, stand height, basal area, and volume (White et al., 2016).

More recently, studies have begun to examine the use of lidar for mapping areas for biodiversity monitoring. Guo et al. (2017) examined the capacity of lidar to regionally map vegetation structure for biodiversity monitoring. This research team was able to automatically classify nine distinct forest types based across the forested ecologies of Alberta. In a companion study, a forest structure habitat index and model of avian species richness was developed (Coops et al., 2016).

Additional studies have examined structural complexity (Kane et al., 2010b,a), correlated lidar metrics for avian (Melin et al., 2016b; Vauhkonen and Imponen, 2016) and moose (Melin et al., 2016a) habitat. Another study has examined similarities and differences between old natural stands and mature second growth stands (Sverdrup-Thygeson et al., 2016). A discussion paper has been put forward to examine the use of lidar data for the classification of ecosystems (Campbell et al., 2017). Regarding CWD there has been some analysis using lidar to indicate fire fuels loading (Kramer et al., 2014) and gap analysis (Tanhuanpää et al., 2015).

Following a review of literature to date, the following gaps or areas for future research are noted:

- Attempts to quantify forest complexity supporting ecosystem as complex adaptive systems are limited. With the increasing availability of lidar datasets, opportunities to assess a plethora of forest metrics now exist which may provide insights into quantifying forest complexity and biodiversity.
- Regional landscapes (sub-boreal plateau): sub-boreal plateau landscapes are subtle. Subtle in the sense that very minor changes in topography can create very significant differences in ecology both in how an ecology presents as well as the underlying processes in a forest stand.
- In the central interior of British Columbia, there are no known examinations of forest ecology using lidar.
- Remote sensing of coarse woody debris is very limited.

Project objectives

Using indicators of biodiversity and forest ecosystem complexity, including empirical and remotely sensed metrics (e.g. forest stand, live tree, snags, coarse woody debris and understory vegetation), this thesis will examine and provide indices to quantify biodiversity and forest ecological complexity.

The following chapters address gaps in the literature and are written as stand-alone-papers that are intended for publication. Chapter 2 examines the response of vegetation communities across a chronosequence of forest stands that encompass examples from the entire history of industrial forest harvesting in the Central Interior of British Columbia. Key metrics from this study include using measures of biodiversity and quantitative ecology (note that lidar data is not used).

Chapter 3 examines coarse woody debris (CWD) as a key indicator of biodiversity and ecosystem processes. Comparing empirical and remotely sensed lidar data, it is possible to quantify and characterize CWD. Questions around the ability to detect and characterize CWD, and any limitations for doing so are answered. Additionally, the examination of different stand histories provides distinct insights into the impacts of disturbance history on CWD quantity and quality indicative of biodiversity.

Chapter 2

Long term impacts of forest harvesting on stand structure and vegetation in sub-boreal forests of British Columbia

Introduction

Forest management in British Columbia is thought to be sustainable. However, recent publications and reports highlight concerns that forest management may be having long-term impacts on forest biodiversity and threaten the ecological sustainability of this industry (Price et al., 2020; Gorley and Merkel, 2020). Literature highlights that long term impacts of forest harvesting in the Canadian context are not fully known given the relatively short age of the forest industry (Venier et al., 2014; Hart and Chen, 2006). Our study provides insight in the long term impacts of forest harvesting in the sub-boreal forests of British Columbia comparing key biodiversity metrics of vegetation across a sequence of managed stand development stages to natural old-growth.

DeLong (2007) highlights how the Province of British Columbia has developed harvest patterns similar to wildfire disturbance in an effort to mimic patch size and seral stage distributions of historical wildfires across a range of ecologies (e.g. short-fire return interval to long fire return interval forest types).

> “In effect, wildfire is the disturbance process we are generally attempting to

> replace with harvesting." – *DeLong (2007)*

However, recent studies emphasize that clear-cut harvesting does not fully mimic natural ecological processes. DeLong (2007) had recognized that harvesting would not mimic wildfire in many aspects but creating the patterns of disturbance would address other forest management issues (e.g. excessive road building and forest fragmentation). Of particular concern is that disturbance by wildfire is primarily chemical disturbance where in contrast, forest harvesting is dominantly a physical disturbance; these key differences result in different site conditions and successional pathways of vegetation and concern that biodiversity is impacted. (Hart and Chen, 2006, Venier et al. (2014)). Similarly, in their study in Alberta, Macdonald and Fenniak (2007) also found that vegetation community composition were likewise altered across a variety of partial harvest systems suggesting that impacts may not be limited to clear-cut harvesting.

Metrics of plant species diversity provides a direct measure of biodiversity for that kingdom and are considered indicative of total biodiversity (Gao et al., 2014). Boutin et al. (2009) suggests specific means for measuring biodiversity in plants which include trends in the abundance and distribution of species.

In this study we examine the response of past harvesting disturbance on forest plant communities to examine how they respond across a sequence of stand development stages from juvenile, immature, and mature sites, and how these plant communities compare with natural old-growth forests. Key questions examined include:

1. Are there measurable losses or changes in biodiversity.
2. How does stand development stage impact the abundance, richness, and diversity of vegetation.
3. Do managed stands become natural with time.

Methods

Study location

Investigation took place at the Aleza Lake Research Forest (ALRF, $N.54^o03.8'$, $W.122^o04.3'$). Forest stands within the ALRF are coniferous-leading dominated by hybrid spruce (*Picea glauca* (Moench) Voss x *engelmannii* Parry ex Engelm.), and sub-alpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and small dispersed numbers of douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Deciduous tree species include paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and cottonwood (*Populus trichocarpa* Torr. & A. Gray). The birch is a common but minor portion of the conifer-leading stands while the poplar species may form pure stands or have dispersed individuals in the common conifer-leading stands. The area is within the sub-boreal spruce wet-cool ecological unit (DeLong, 2003). Soils are fine textured lacustrine (DeLong et al., 2003).

The ALRF was established as a research site in 1924 with a key objective of demonstrating sustained yield forestry. Since then it has been actively managed for timber harvesting amongst other research endeavours. Pedersen (2003) describes how various harvest systems were used historically throughout British Columbia highlighting that thin-from-above harvest systems (i.e. intermediate utilization) were used in the first half of the century and focused on targeting larger diameter trees, with a transition in the 1960s to clear-cut harvesting which remains the dominant harvest system to today. The ALRF generally followed this pattern with with the earlier harvest systems focused on the removal of large spruce (Aleza Lake Research Forest Society, 2019).

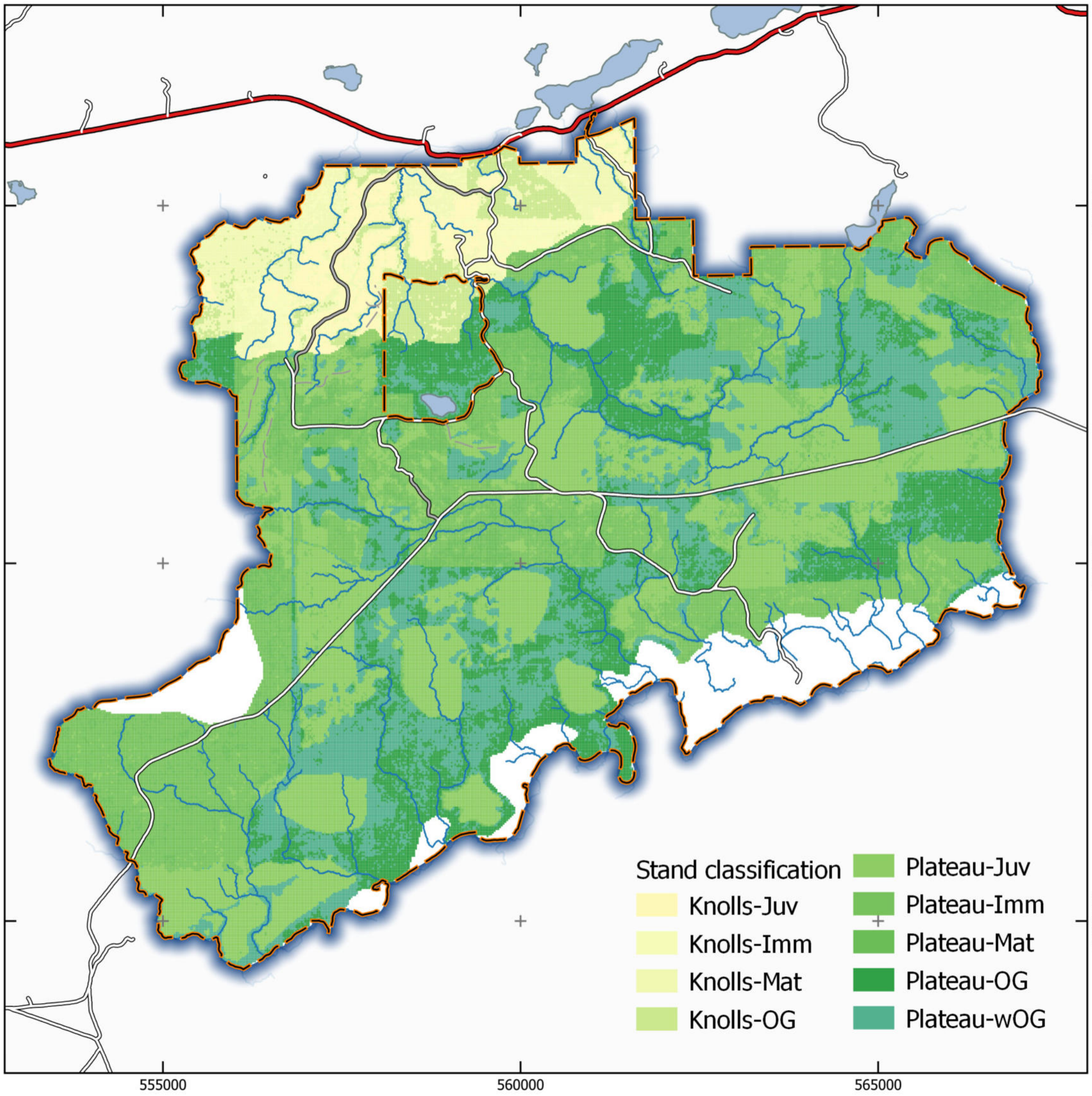

Figure 2.1: The Aleza Lake Research Forest highlighting the landscape units and stand development stages.

Table 2.1: Stand development stages examined in this study.

Class	Name	Height Range(m)	Managed Forest
juv	Juvenile	5 - 19.9	Yes
imm	Immature	20 - 29	Yes
mat	Mature	>29	Yes
OG	Old-growth	>29	No
wOG	Forested Wetlands	20 - 29	No

Sampling design and data collection

The research forest was divided into two main landscape units (see Figure 2.1). The *Knolls*, in the northern portion of the forest, is gently rolling with slopes ranging between 8 and 24% (1st and 3rd quartile). The *Plateau* unit is distinctly flatter with slopes ranging from 0 to 9%. Both landscape units are drained by deeply incised gullies. Sets of sample plots of 1ha were established across each landscape unit using stratified random sampling. Stratification was based on wall-to-wall lidar metrics to place the forest into height classes of relative stand maturity (table 2.1). Height classes were based on minimum height thresholds. Heights were extracted from a $1m^2$ resolution lidar derived crown height model; a minimum of 1% the pixels had to exceed the height threshold to be considered within a given class. Known harvest history polygons were used to further stratify the forests between managed and natural stands. Within each plot, 4 nested plot centres were established to collect the following: tree species identity and diameter at breast height (dbh): for trees larger than 10cm dbh, a circular $200m^2$ was used, and a $50m^2$ plot was used for smaller trees: 2.0 - 9.9cm dbh. Vegetation identity and abundance was measured by pooling the data from two $1m^2$ quadrats located at four metres north and four metres south of nested plot centre. All plant species within the quadrat were identified including an ocular estimate of percent cover.

Statistical processing

Data processing and statistical analyses were completed in `R` version 4.02 (R Core Team, 2020). Statistical processing for species richness, abundance, and diversity used the `vegan` package (Oksanen et al., 2019). Linear discriminant analyses were completed following methods in Borcard et al. (2018) using the R libraries `vegan` (Oksanen et al., 2019), `MASS` (Venables and Ripley, 2002), and additional scripting provided by Borcard et al. (2018).

Stand structure

Forest stand structure was evaluated for each treatment comparing basal area by: total, leading species, and diameter class. Tree density was standardized to total stems per hectare. ANOVA was used to compare results across the stand development stages (SDS) and landscape units (i.e. the treatments).

Species richness, diversity, and abundance

The biodiversity of understory vegetation was examined to compare the differences between the SDS and landform influences (i.e. the treatments). Key metrics of richness, abundance (i.e. percent cover), and diversity were generated for all species which were compared using ANOVA. Abundance of vegetation communities was compared by functional groups (bryophytes, forbs, shrubs, grasses, and lichen) and further by abundance of individual species. Abundance metrics used the Hellinger transformation (Legendre and Gallagher, 2001). To compare functional group abundance, a MANOVA framework was used as per Warton and Hudson (2004) and more recently Hart et al. (2019). To highlight specific differences and the potential drivers of differences, linear discriminant analyses (LDA) were completed. LDA analysis examined if SDS could be determined using vegetation functional group abundance and further by individual species abundances. A series of LDAs using individual species were completed using Hellinger-transformed abundance of observed species. Four LDA runs were made with a minimum of 5, 10, 20, and 40 species observations; this was done so that unique observations would not dominate the discrimination process. Further, results were leave-one-out validated as recommended by Borcard et al. (2018). Summary tabular results are provided for each of the LDAs, while detailed results for the LDA using 40-observation are presented here.

The Hellinger transformation is the square root of the proportional abundance within a given site where i is the index of the site and j is the index of the species (i.e. where the data is organized by sites in rows and species in columns). As such y_{ij} is the abundance of the individual species within a site, and y_i is the total abundance within the one site or row[a].

$$y'_{ij} = \sqrt{\frac{y_{ij}}{y_i}}$$

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[a] As described by Legendre and Gallagher (2001)

Results

Stand structure

Initially, following harvest (i.e. juvenile stage), total stems per hectare was elevated while total basal area was reduced. Stems per hectare decreases with SDS with both landscape units following similar patterns ($F(4, 181)= 19.378, p = 0.000$). Total basal area recovers to natural ranges (i.e. compared to old-growth) by the immature or mature SDS; in addition, the pattern of basal area recovery differed between the landscape units (Figure 2.2).

In the Knolls landscape units the immature, mature, and old-growth stands all had similar basal areas. In the Plateau the pattern of basal area recovery differed with a pattern of basal area increasing from juvenile through to mature and reduced basal area in the old-growth sites. Figure 2.2 highlights the significant differences in basal area. ANOVA demonstrated that these differences were a result of SDS, landscape, and the SDS-landscape interactions ($F(3, 183) = 3.667, p = 0.013$). Coefficient of basal area variance indicated significant difference based on SDS with the immature having higher variability than all others ($F(4, 39) = 4.445, p = 0.005$)

Tree species richness and diversity did not show significant differences across the treatments. However, differences in species composition by basal area indicated that the dominant leading species changed over this chronosequence. On average juvenile stands were spruce leading, immature sites were sub-alpine fir leading, while mature and old-growth sites were spruce leading (Figure 2.3). Figure 2.4 highlights the increase in frequency of larger diameter class trees. Old-growth sites have the largest individuals with trees in the 90 and >100cm dbh classes.

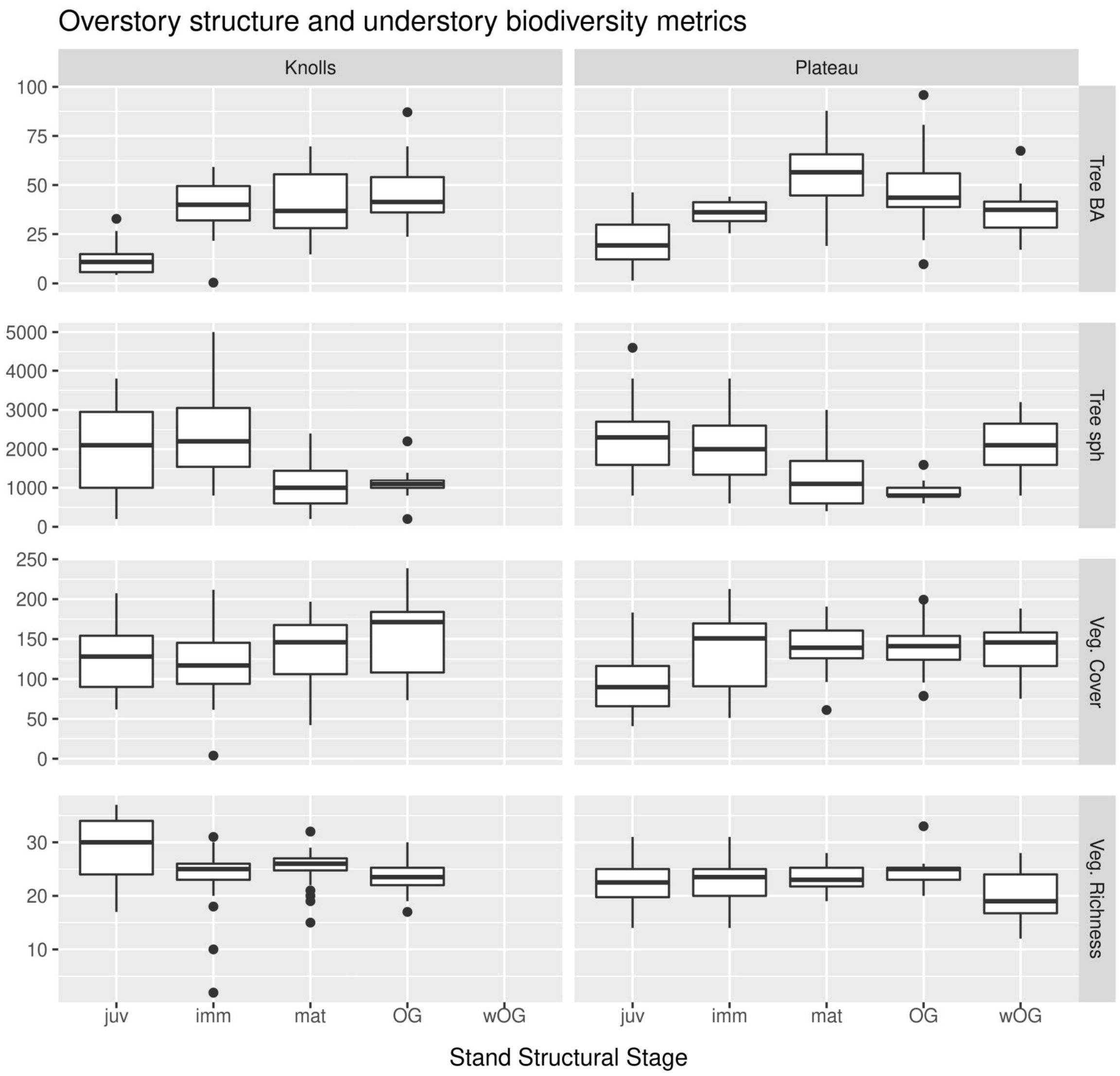


Figure 2.2: Key metrics of stand structure with corresponding biodiversity metrics of understory vegetation comparing stand development stage and landscape units. Total basal area (m^2 per hectare) recovers to natural levels. Likewise stems per hectare decrease over time towards natural levels. Vegetation response, using total abundance (percent cover) and total species richness (number of unique species), shows little response.

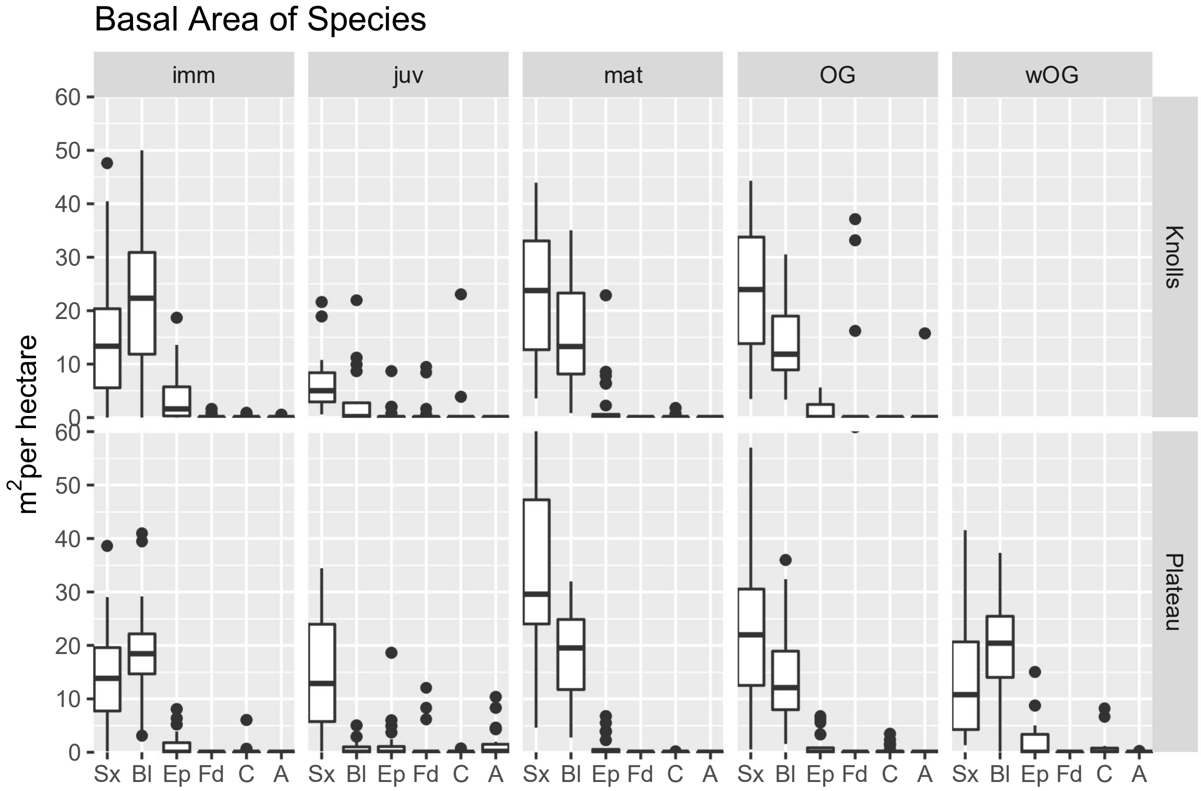


Figure 2.3: Basal area (m^2 per hectare) of species by stands development stage and landscape unit. Species include spruce (Sx), sub-alpine fir (Bl), birch (Ep), other conifers (C), and poplars (A).

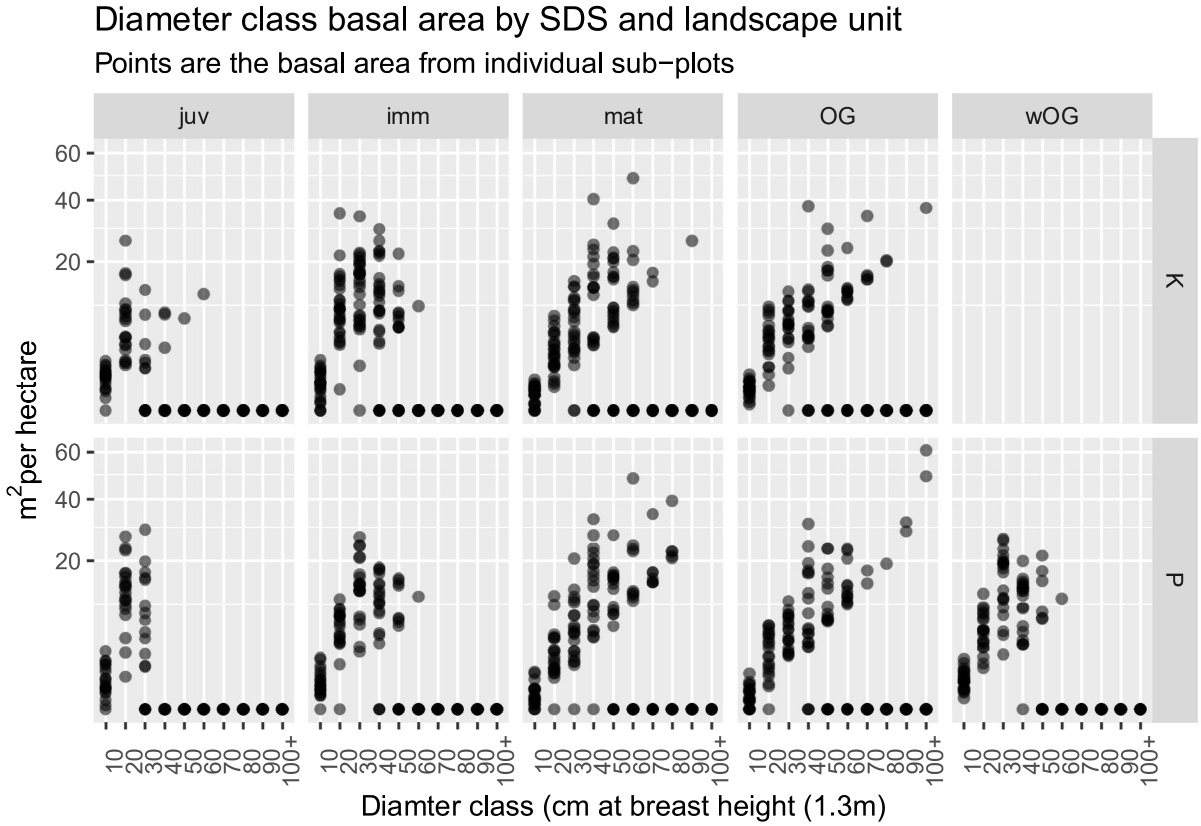


Figure 2.4: Basal area by diameter class. Each point represents the basal area contribution within each sub-plot. OG sites are the only sites with trees in the 90 and 100cm dbh classes.

Vegetation

No significant differences were seen in total species diversity while a few differences are noted in the total abundance and richness – specific differences were determined through Tukey post hoc analysis (Figure 2.2). Juvenile stands in the Plateau had lower total abundance than the old-growth and mature sites of both landscape units, and the immature and forested wetland sites in the Plateau ($F(4, 176)= 4.910, p = 0.001$). Two significant differences in species richness were noted with juvenile sites in the Knolls unit had higher richness while the forested wetlands sites had lower richness ($F(3, 176) = 3.631, p = 0.014$).

Abundance by functional group

MANOVA analysis of Hellinger-transformed functional group abundance demonstrated that there are significant differences in the understory vegetation cover by SDS ($F(4, 179) = 5.454$, $p = 0.000$), though no differences were attributed to the landscape units. Figure 2.5 highlights that in the juvenile stages, bryophyte cover was reduced. Linear discriminant analysis was used to determine if stand development stages could be separated; results of the LDA are provided in Figure 2.6 with A1 providing the biplot and A2 providing the confusion matrix. The biplot suggests high levels of confusion when using functional groups to determine stand development stage. The confusion matrix highlights that the juvenile sites are classified with an accuracy of 73%; however, accuracy for other stand development stages is low.

Species abundance

A series of LDA were completed to determine if the abundance of individual species could be used to classify the sites into SDS. Table 2.2 provides a summary of the LDA results. The more species used in the LDA, the higher the accuracy of classifying the sites correctly. However, this was at a cost of higher mean-misclassification error (mmce) in

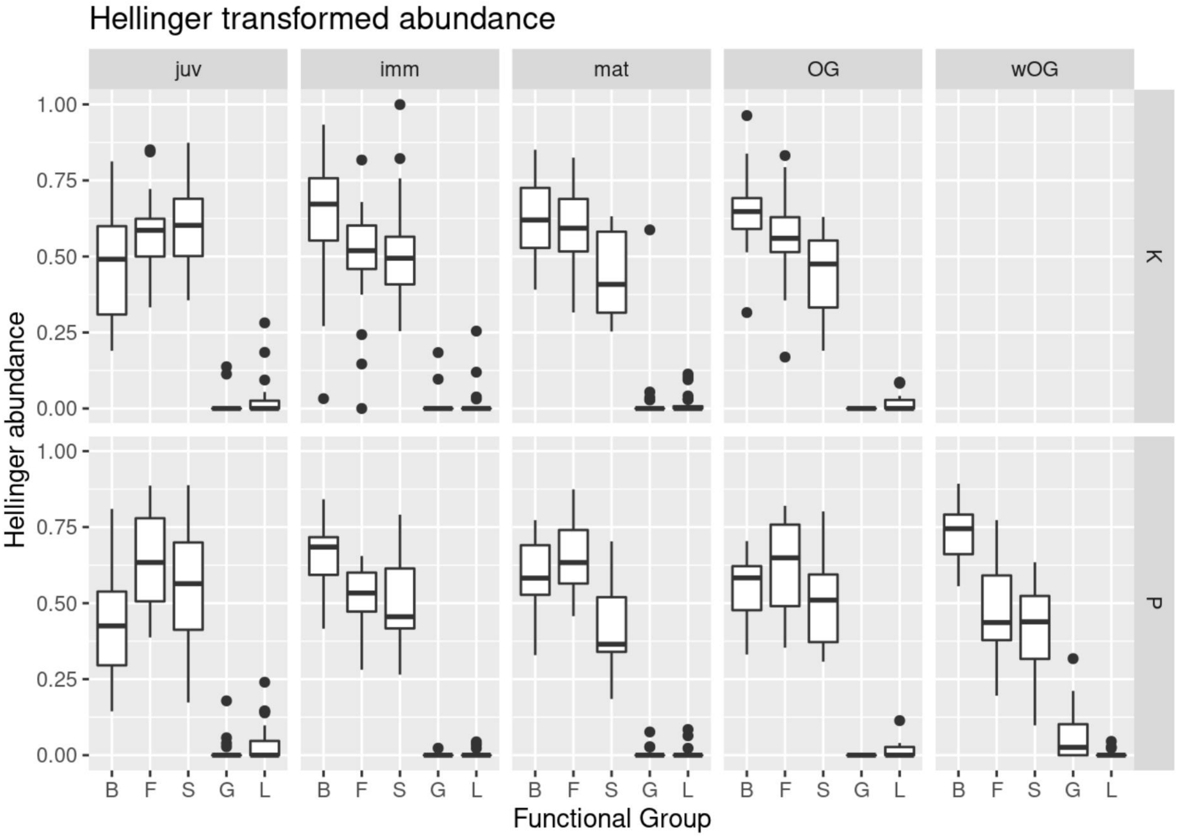
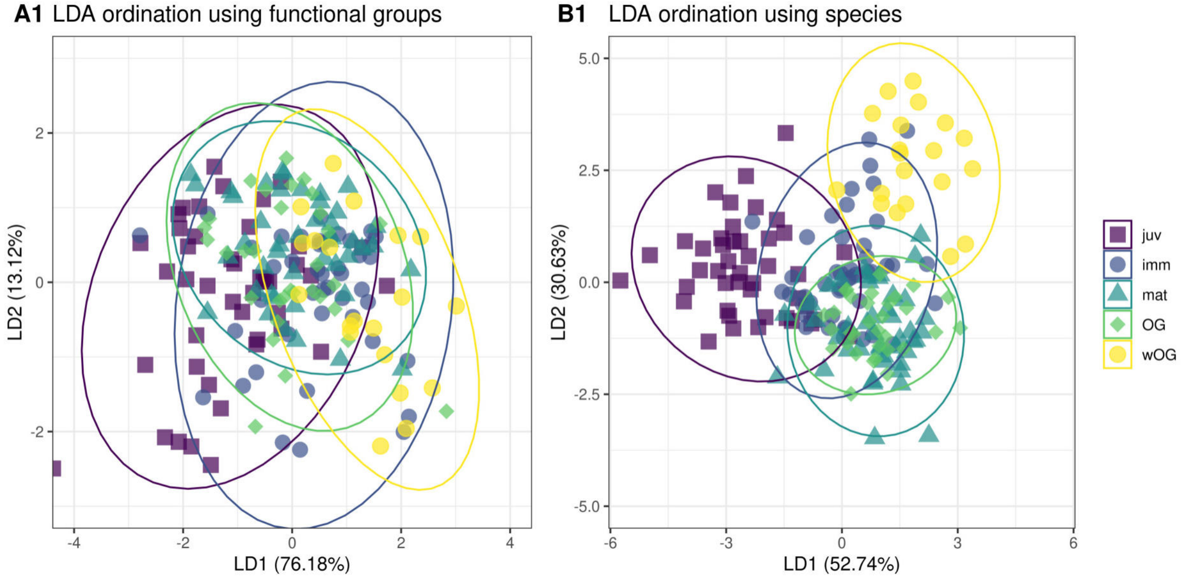


Figure 2.5: Hellinger-transformed abundance of functional groups arranged by stand development stage and landscape unit. Functional groups include Bryophytes (B), Forbes (F), Shrubs (S), Grasses (G), and Lichens (L).

Table 2.2: Summary of all linear discriminant analyses. When more species are used accuracy increases; however there is little change to the mean misclassification error (mmce).

			Accuracy						
Min. Observations	Species Observed	Percent of total Species	juv	imm	mat	OG	wOG	mmce	cv-mmce
FnG	all grouped	all	0.73	0.47	0.52	0.00	0.45	0.57	0.60
5	98	59%	0.98	0.96	0.93	0.94	1.00	0.04	0.43
10	74	45%	0.95	0.93	0.80	0.84	1.00	0.09	0.44
20	58	35%	0.86	0.78	0.82	0.72	0.95	0.17	0.45
40	39	23%	0.86	0.76	0.70	0.72	0.95	0.20	0.47



A1 LDA ordination using functional groups

B1 LDA ordination using species

A2

	juv	imm	mat	OG	wOG
juv	32	6	6	0	0
imm	9	21	12	0	3
mat	8	11	23	0	2
OG	8	13	10	0	1
wOG	0	6	5	0	9

B2

	juv	imm	mat	OG	wOG
juv	38	5	1	0	0
imm	2	34	2	3	4
mat	2	4	31	6	1
OG	0	2	7	23	0
wOG	0	0	1	0	19

B3

	juv	imm	mat	OG	wOG
juv	28	8	7	0	1
imm	6	24	5	4	6
mat	4	7	19	12	2
OG	0	5	12	15	0
wOG	1	4	3	0	12

Figure 2.6: Linear discriminant analyses to determine if understory vegetation can be used to differentiate logging history. Site classification using vegetation functional groups including biplot (A1) and confusion matrix (A2). Classification of the sites using species with a minimum of 40 observations including biplot (B1), confusion matrix (B2), and leave-on-out validated confusion matrix (B3)

the leave-one-out validated models. All LDA runs demonstrate that sites can be classified correctly the majority of the time.

In Figure 2.6, B1-B3 provide LDA results for the run using species that were observed within a minimum of 40 individual quadrats. The biplot shows graphically good separation of the juvenile and forested wetlands sites. This plot graphically displays the discrimination of the SDS with a total of 83.7% of the variance explained (LD1: 55.3% and LD2: 28.4%). Despite not being graphically separated, the confusion matrix (B2) highlights that immature, mature, old-growth, and forested wetlands are also accurately classified. B3 provides the leave-one-out validated confusion matrix highlighting that strong separation remains for all SDS. Old-growth shows the lowest accuracy (65%) and is most often confused with mature and then immature sites. Species mean Hellinger transformed abundance are listed in descending order of influence in Appendix A.1.

Discussion

No differences in biodiversity metrics were associated with the trees (i.e. Shannon's H', and richness); however, there are distinct changes in stand structure. Stand structure changes from initial harvest disturbance through to maturity follows well established stand dynamics. Initial stratification of the stands types was based on differences in height; total basal area increased with stand development with full site occupancy developing in the immature stage; and total tree density fell from the youngest to the oldest sites. These changes in the physical characteristics of the stand can affect light and moisture, and influence understory plant communities (Venier et al., 2014). Importantly is the fact that mature and old-growth are indistinguishable from each other using the stand structure metrics selected here. One component of stand structure that was not examined here were the dynamics of dead wood, namely: standing snags and coarse woody debris (CWD) may separate managed from unmanaged stands (see Chapter 3 for an examination of CWD). In their review of stand structure dynamics Brassard and Chen (2006) found that CWD was reduced in managed stands and that this could potentially be detrimental to biodiversity.

Vegetation response, based on total abundance, richness, and diversity showed few differences. Total species richness was highest in the juvenile sites in the Knolls, while seemingly contradictory, vegetation cover was lowest in the juvenile Plateau. Reduced cover may have been a result of closed canopy often associated with earlier stand development stages, and this would be consistent with other studies (Kumar et al., 2018b). However, this appears to be in conflict with higher cover and significantly higher species richness found in the Knolls juvenile sites, a point consistent with Venier et al. (2014) who found vascular plant diversity increased following harvesting. Significantly lower species richness was also found in the wOG sites. This is believed to be a response to the different site conditions and productivity of these forested wetlands.

Further examination of vegetation response, using abundance by functional group, does clarify that juvenile sites are distinct from the other stand types. The juvenile is classified correctly 70% of the time (based on Table A2 in Figure 2.6). In the juvenile sites bryophyte cover was lowest and shrub cover was highest. This is consistent with Kumar et al. (2018b) and Venier et al. (2014) who found that increased shrub cover resulted in the suppression of non-vascular plants (e.g. bryophytes). Kumar et al. (2018b) further suggests that this may be a function deciduous leaf little causing physical inhibition or an allelopathic effect on the non-vascular species. A challenge to using the functional group analysis is that there is no separation of the other stand types.

Examination of abundance using species, as opposed to functional groups, highlights that there are differences between all of the stand development stages (Figure 2.6 B1-B3). The juvenile and forested wetland sites are the most distinct with accuracy in excess of 85% and 95% respectively. The immature, mature, and old-growth sites are also accurately classified at a minimum of 70% and as high as 93% (see table 2.2). These results highlight that differences in disturbance history and differences in local, site levels, environmental conditions are measurable and likely long lasting. When classification errors does occur it is most often associated with sites in neighbouring stand development stages. This suggests that there is a progression of vegetation community composition from early to late development stage.

Using species to differentiate the sites is more effective than using functional groups as species have differing ecological niches. Specifically, species abundance in response to disturbance history is influenced by light and moisture availability (Barbier et al., 2008; Kumar et al., 2018b). For example, two shrubs *Lonicera involucrata* (black twinberry) and *Oplopanax horridus* (Devil's club), are respectively shade intolerant and shade tolerant with *L. involucrata* most abundant in the juvenile sites and *O. horridus* abundant in the mature and old-growth sites. Similarly for the forbs group, the ferns *Dryopteris expansa* and *Gymnocarpium disjunctum* are shade tolerant and most abundant in mature and old-growth sites; in comparison, the *Galium spp* (Bedstraw) are more abundant in the juvenile sites. Differences in the bryophytes highlight ecological differences *Sphagnum* moss, a hydrophylic species, is most abundant in the forested wetlands with little to no representation in other sites. Beaudry et al. (1999) or Klinkenberg (2021) provide descriptions of specific species.

Cross validation highlights that the LDA results are robust demonstrating similar trends to the raw results; sites are classified into their stand development stages, though with reduced accuracy. Where classification into SDS errors do occur, these are most often placed in a neighbouring SDS. This suggests a continuum or progression between the stand development stages and that the managed forests are developing towards old-growth condition.

This work focused on the impacts from management disturbance. In comparison, natural

disturbances, particularly those from fire are known to have more distinct differences from managed stands. A primary cause of differences is that fire-based disturbances are primarily chemical in nature versus physical. The chemical nature of disturbance by fire causes increased soil disturbance, releases nutrients that were immobile in organic compounds and raised pH (Hart and Chen, 2006).
Fire origin stands and those harvested have different plant communities, with burned areas supporting pyrophilic species and young harvested areas showed greater similarity to old forest plant communities. On a longer time scale natural spruce-sub-alpine fir stands similar to those in this study have a long fire return interval. DeLong (2011) states an average return interval of 220 years. With active harvest management there is concern that shortened disturbance return intervals could negatively impact biodiversity (Venier et al., 2014)

Works discussing the theory of forest recovery from disturbance suggest that this development towards the old-growth condition is not direct or determinant and that the complexity of ecological factors could cause forests to not return to original forest condition (Messier et al., 2015; Parrott, 2010). The fact that mature and old-growth can be separated, despite having similar stand structure, suggests that the return to natural condition is either incomplete or that a new condition is being established. Similarly, Venier et al. (2014) suggests that harvest with truncated harvest rotation cause concern for long term biodiversity.

Management of forest should take into consideration that harvest disturbance changes understory plant vegetation communities and that full recovery of these communities takes significant time and may not return to previous conditions. This study suggests that mature sites remain somewhat distinct from old-growth forest condition. In order to mitigate long-term impacts to the biodiversity of plant communities and ensure that natural distributions of plant communities remain representative, unharvested forest reserves, that represent the ecology of the harvested areas, should be maintained adjacent to the site. In addition, consideration should be given to harvest rotation length. The oldest managed stands in this study were most similar to old-growth.

Future work should: a) Continue to monitor the development of second growth plantations. In this study the immature and mature managed stands originated from thin-from-above partial harvest and relied on natural regeneration. In contrast, the juvenile sites were planted, with regular spacing, as such the stand structure development may differ and likewise may cause alternate vegetation community responses than those observed here. b) Consider additional stand structure metrics including the abundance of dead wood and canopy closure. Direct crown closure measurements may provide greater insights into the distributions of plant communities.

Conclusion

This study examined a series of stand development stages with and without historic forest harvest and demonstrated that there are long term impacts to understory vegetation communities. Vegetation communities remain distinct, despite forest stand structure returning to nearly natural old-growth conditions. Juvenile stands and forested wetlands are most distinct, highlighting that stand structure and localized environmental conditions are important factors influencing community composition. Vegetation communities in the later stand development stages converge towards natural old-growth but still provide unique signatures. Forest managers should be mindful that changes in vegetation communities due to harvesting are long lasting and options to mitigate potential loss in biodiversity include extending harvest rotation length and provide unharvested reserves that represent the local ecology of the areas.

Acknowledgements

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Chapter 3

Quantifying the recovery of coarse woody debris in British Columbia's managed sub-boreal spruce forests

Introduction

Coarse woody debris (CWD) is an integral component of forest ecosystems, providing key habitat features for a wide range of species (Stokland et al., 2012; Harmon et al., 1986b). It is recognized that forest management impacts on CWD need to be considered when developing stand and landscape level plans given that managed forests have a deficit of coarse woody debris compared to natural stands (Brassard and Chen, 2008; Spies et al., 1988). To address this issue various CWD targets in the form of minimum acceptable volumes of CWD immediately following harvest, while at the landscape scale targets are set for minimum percent areas in old forest condition (SFI, 2015; Forest Practices Board, 2012; Müller and Bütler, 2010; Berry et al., 2018). Here I examine the differences in the quantity and character of CWD in a sequence of stands comparing managed and old-growth natural forests, evaluating how CWD recovers over time, both within stands and how it is distributed across the landscape.

CWD has been shown to be critical for maintaining biodiversity, as well as supporting a broad range of ecological functions (Arsenault, 2003; Stokland et al., 2012). Saproxylic species depend on dead wood as a structure for reproduction or as a direct source for nutrient uptake (Langor et al., 2008; Maňák and Jonsell, 2017). Fauteux et al. (2012) highlighted the importance of CWD for use by small mammals in eastern Canada. In western Canada Keisker (2000) provides a review of functional use of CWD by numerous animals.

The character of the CWD changes through time due to the biological degradation/decay processes, with concomitant impacts on the ecological functions that the CWD play (Langor et al., 2008). Harmon et al. (1986b) and more recently Stokland et al. (2012) provided thorough overviews of the functions provided by CWD. In addition to the biological use of CWD, these woody materials provide a valuable carbon sink (Fredeen et al., 2005; Bois et al., 2009). Ehnström (2001) stresses the usefulness of CWD by claiming that: "Dead wood is perhaps the most important substrate for the maintenance of the diversity of insects, cryptogams and fungi in the boreal forests."

The importance of high volume and large piece size CWD, as described by diameter and piece length, is often stressed when evaluating the importance of CWD inputs. This is partially due to the fact that large pieces remain in the environment for the longest periods of time, contribute large carbon and nutrient pools, and provide large structural habitat features (Stone et al., 1998; Harmon et al., 1986b) In addition to size, the state of decay is important, and ranges from material that is very firm with little decay to pieces that have high levels of decay (i.e from biological degradation) where wood cellular structures have been broken down creating soft material. These differences in the type of material are critical for the ecological function that the material provides (Kumar et al., 2018a; Siitonen, 2001).

In natural forest stands CWD is generally input into the ecosystem through disturbance events such as wind, fire, and the influences of pests and pathogens on the live stand. CWD sources include materials: from before disturbance, generated as a result of, and trees that remain following a disturbance (Spies et al., 1988). In contrast, managed stands, and in particular those that are clear-cut harvested, lose the vast majority of their biomass. Siitonen (2001) highlights that though there may be an initial flush of CWD in a newly harvested juvenile stand this is relatively short and then the harvest areas lacks opportunities for CWD input.

While potentially not as intensely disturbing as clear-cut harvesting, partial cutting may also have a large impact on CWD volume and attributes. Lee et al. (2017) demonstrates that partial retention harvest systems can support natural saproxylic beetle assemblages. However, they raise concern that even with partial retention there may not be enough CWD recruitment to support native diversity.

Historically, in British Columbia, diameter limit cutting, a thin-from-above silvicultural system, was common practice from the early 1900s through to the 1960s (Stevenson et al., 2011; Pedersen, 2003). Diameter limit harvesting removed the largest and most desirable trees; while smaller diameter trees commonly in the sub-canopy and understory were left to regenerate the site. With the removal of the main canopy the potential input of large diameter CWD is removed; large diameter CWD recruitment is thereby delayed until the stand matures further.

In our region, many of the stands that were diameter limit logged are now mature and viable for a second harvest. Understanding the current CWD loading and distribution of these previously harvest sites (i.e. understanding the impact of harvesting legacy) is therefore important as it will assist in determining future impact on CWD inputs.

The importance of CWD volume and character for biodiversity and ecosystem functioning emphasize the need to manage CWD at the landscape scale, and be able to assess and project CWD inputs following management interventions (Brassard and Chen, 2008). Remote sensing via Aerial laser scanning (lidar) techniques have been used to describe stand structure for timber (White et al., 2017; Næsset, 2002) and characterize stand structure as indicators of biodiversity (Guo et al., 2017; Zellweger et al., 2014). In their review Davies and Asner (2014) encourages the research community to use ALS to characterize critical habitats. Detection of CWD has been attempted using direct and indirect lidar metrics (Joyce et al., 2019; Tanhuanpää et al., 2015). In addition to providing metrics to characterize stands, modelling empirical data with lidar allows for the generation of predictive maps across landscapes (Hengl et al., 2018; White et al., 2013).

In this study, the influence of recent and historic harvest patterns on CWD quantity and characteristics are examined. This work compares natural forest stands with forest stands of varied harvest legacies, from 20 - 90 years since disturbance. My aim is to quantify the impacts of forest harvesting on the CWD structures within each stand type and across the forested landscape. Known harvest histories provide a chronosequence of stands that were clear-cut, diameter limit harvested, or are natural old-growth. CWD is evaluated using a combination of field plots and lidar providing opportunities to characterize CWD within stands and across the landscape. Key structural components of the CWD are examined including size, volume, and decay class. Lidar provides detail on the detection of CWD and allows for predictive mapping of CWD across the landscape. My work aims to address these main questions:

1. What are the differences in CWD volume and characteristics across different forest management histories?
2. Does CWD recover over time and specifically within timber rotation period?
3. Can lidar be used as an effective tool for detecting CWD and provide predictive mapping useful for meeting landscape level objectives?

Methods

Study site

This study was completed at the University of Northern British Columbia's Aleza Lake Research Forest ($N.54^o03.8', W.122^o04.3'$). This 9,000 hectare forest is dominated by hybrid white spruce (*Picea glauca* (Moench) Voss x *engelmannii* Parry ex Engelm.) and sub-alpine fir (*Abies lasiocarpa* (Hook.) Nutt.) with minor components of Douglas-fir *Pseudotsuga menziesii* (Mirb.) Franco), trembling aspen (*Populus tremuloides* Mich), and paper birch (*Betula papyrifera* Marsh.). Topographically the area is part of a larger plateau landscape with elevations ranging from 660 – 720 metres resulting from flooding following the end of previous glaciation (i.e. Glacial Lake Prince George) as described by Tipper (1971). Topography is generally flat with gently rolling terrain in the north with lacustrine soils that are incised by various streams. The area was established as a experimental station in 1924 with the key objective "*to demonstrate sustained yield forestry at a practical level*" (Schmidt, 1992). Since then, the forest has been actively managed for timber and other values (Aleza Lake Research Forest Society, 2019).

Sampling design

Eight forest stand types were sampled in a $2\,x\,2\,x\,3$ design: defined by two landscape units, two harvest histories (i.e. harvested or old-growth), and three stand height classes. The landscape units included first the *Knolls* in the northern portion of the forest distinguished by gently rolling terrain with moderately well drained soils (silt-clay loams to clay-loams), and slopes ranging from 2-25%. Second, the *Plateau*, a generally flat landscape with slopes outside of stream gully areas ranging from 0-10% with moderately to poorly drained soils (clay loams to clays). See Chapter 2, Figure 2.1 for a map of the landscape units. In each landscape unit plots were randomly located in each harvest history and height strata.

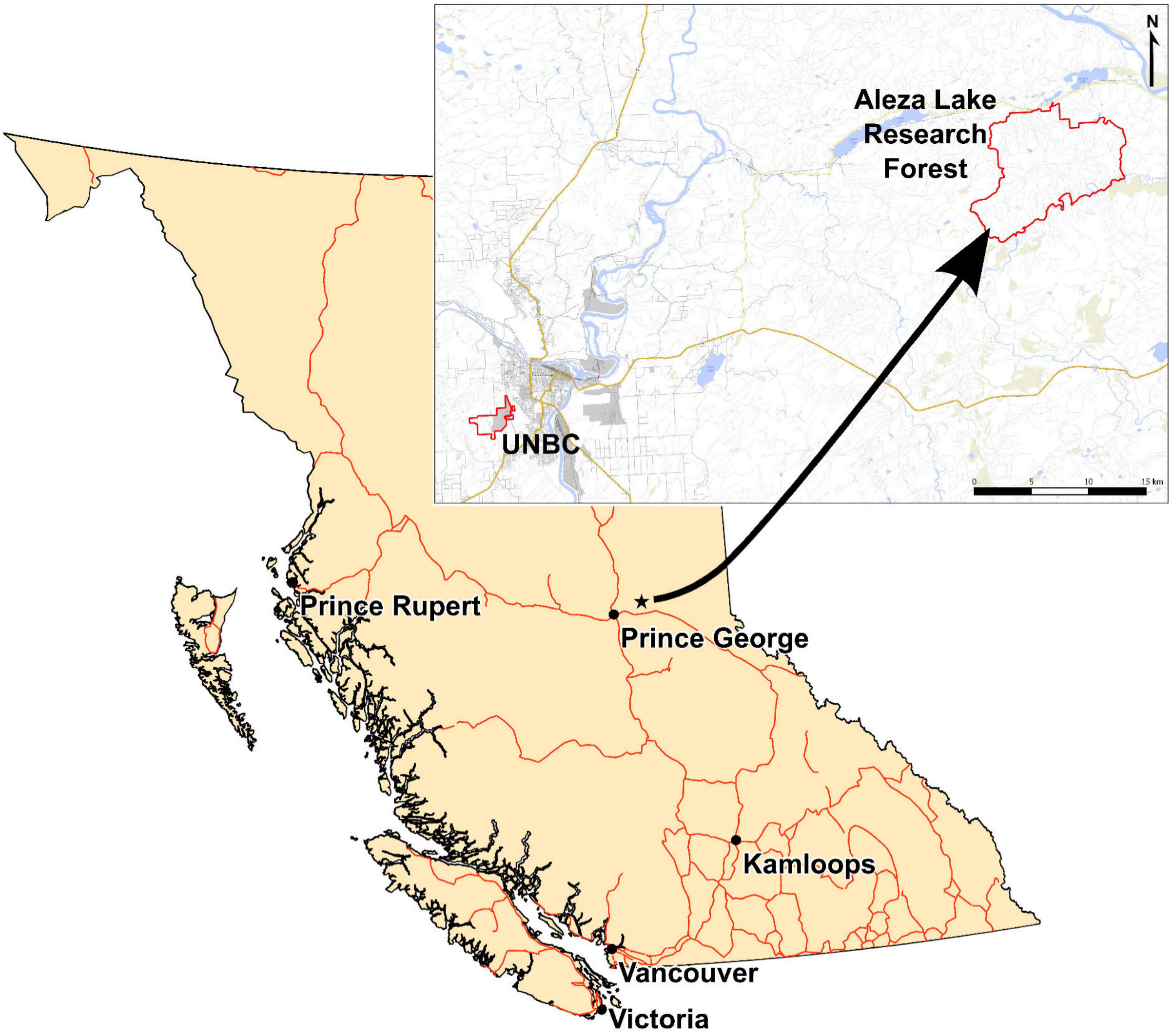

Figure 3.1: The 9,000 hectare Aleza Lake Research Forest is the focus of this study. This forest was established in 1924 to demonstrate sustained yield harvesting.

This was done based on known harvest history records with stand heights determined from a 1m resolution crown height model derived from lidar. The natural forests were divided into old-growth (OG; heights $\geq 29m$), and natural immature sites (NI; heights $20-29m$). Areas with harvest history (HH) were divided into three height classes: juvenile (juv ; $5-19.9m$), immature (imm; $20-28.9m$), and mature stands (mat; $\geq 29m$). Younger stands with heights less than 10m were not examined in this study.

Harvest history records are available for the research forest dating back to the 1920s. Prior to 1966 the most common harvest system were methods of intermediate utilization or diameter limit cut (DLC, Pedersen, 2003). These DLC sites are distinct from the current dominant regional practice of clear-cut management followed by tree planting, used from the late 1960's to present, though planting programs were not common until the 1980s. In contrast, the DLC sites were thin-from-above silviculture retaining small diameter stems (less than either 12 or 9 inches at dbh), and sites were left to regenerate naturally. These differences in silvicuture systems are considered when examining the results of this study. Immature and mature managed stands were harvested in the era of intermediate utilization.

CWD field data collection

A series of four 30m long linear transects were established to measure CWD from within four sub-plots (Figure. 3.2). Transect locations were established in the forest using the iSXBlue II (sub-metre accuracy GPS). This was done to ensure that empirical data could be matched with the lidar data. All CWD larger than 7.5cm in diameter at the point they intersect with the transect were measured. For each piece of CWD the length, diameter, decay class, and location along the transect were recorded.

The decay class of the CWD was placed into a discrete scale from 1 to 5 as described in British Columbia (2010). A decay class of 1 has no significant decay to 5 where the wood

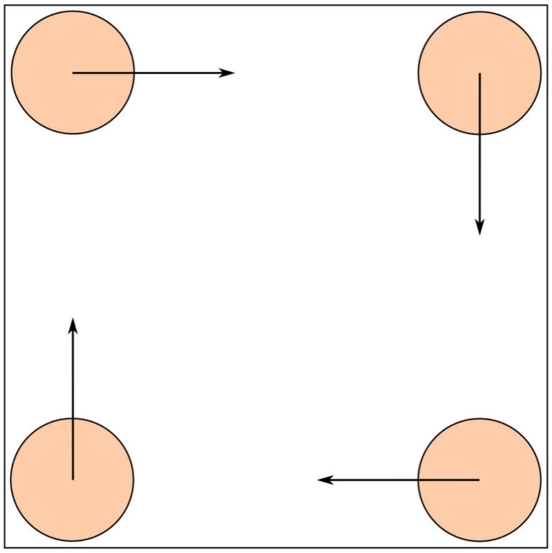

Figure 3.2: One hectare plot layout including four $400m^2$ sub-plots and associated 30 metre CWD transects.

is highly decomposed. This transect survey did not consider CWD that had decomposed to the point that it was considered part of the soil profile as defined by $\geq 50\%$ of the CWD piece being embedded in the soil. The volume of CWD was calculated using the Van Wagner formula Equation: (3.1) as described in Van Wagner (1968) and Fraver et al. (2018) where d is the piece diameter in metres and L is the length of the transect in metres.

$$V = \left(pi^2 \sum \frac{d^2}{8L}\right) \times 10,000 \tag{3.1}$$

Statistical analysis was done using R 3.6.2 (R Core Team, 2019). CWD attributes were evaluated using ANOVA testing and post-hoc comparisons were made using Tukey Honest Significant Differences. A significance level of 0.05 was used throughout. Eta-squared (η^2) was used to quantify effect size or strength of relationships. Shannon's diversity index was used to compare the diversity of decay classes as suggested by Brassard and Chen (2008).

Lidar analysis

On May 11, 2015 the study area was Aerial Laser Scanned (lidar) using UNBC's Riegl VQ-580 lidar scanner mounted on a fixed wing plane. The timing of this data collection provided for snow free and leaf off conditions. The plane flew at an elevation of approximately 500m above the ground. Scan frequency was 380 kHz with a scan angle of 30^o from vertical (60^o field of view). Laser divergence was 0.2 mrad equaling a 10cm on-ground footprint (vertical pulses). The resulting data provided 10 first pulse returns per square metre. Lidar data was processed using LASTools software (Isenburg, 2016) and the the R package `lidR` (Roussel and Auty, 2020).

In order to determine to what extent individual CWD pieces were identifiable from ALS, a 0.25m^2 resolution near-ground-surface-model (NGSM) was generated using a height cutoff of 1.3m (i.e. ALS data higher than 1.3m above the ground was removed). This was visualized in QGIS (QGIS Development Team, 2019) with a digital representation of the transect location. Empirical transect data including piece size and location along the transect was cross referenced with a digital version of the transect overlaying the NGSM and where possible CWD pieces were identified (Figure 3.3).

Wall-to-wall lidar coverage of the study area provided the opportunity to model CWD across the landscape. To do this standard ALS area based approach metrics (ABA) were generated corresponding to the transect data collection (White et al., 2013; White et al., 2017; Næsset, 2014; and Rousse, 2018). In addition, a metric of near-ground-point-density (NGPD) was used to characterize the amount of material in the CWD layer, that is non-ground classified lidar points with elevations of 0.1m to 1.3m above ground were used (equation (3.2)). Figure 3.3 illustrates the area around the empirical transect for which the ABA metrics were generated (30m long transect x 13.33m wide, a 400m^2 area). A *random forest* regression model was fit to the empirical data and then used to predict the volume of CWD across the landscape. Key processing packages include: `mlr` (Bischl

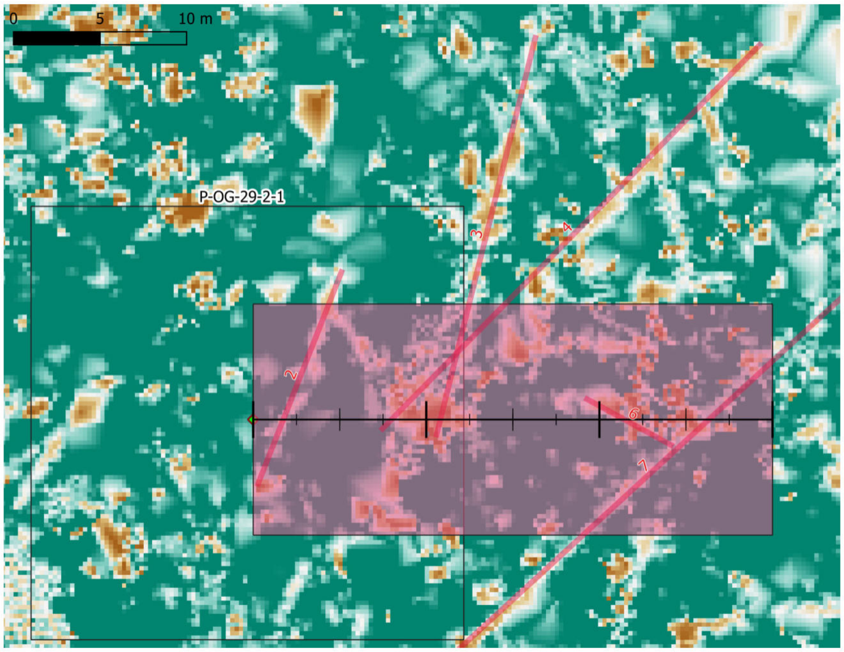

Figure 3.3: Surface model highlighting CWD generated from lidar data using a 1.3m height cut-off. Identifiable individual pieces of CWD that crossed the transect were digitized and labelled corresponding to the piece in the empirical data. The digital transect includes tick-marks every 2.5m to compare with piece locations in the empirical data. The boxed area represent the area from which the ABA lidar metrics were generated.

et al., 2016), `ranger` (Wright and Ziegler, 2017), `stars` (Pebesma, 2020), and `sf`(Pebesma, 2018). Prediction accuracy was assessed using the r^2 coefficient. The predictive model was validated using the *leave-one-out* method described by Tompalski et al. (2019)

$$NGPD = \frac{CWD_{130}}{CWD_{130} + G} \tag{3.2}$$

> Equation (3.2): To generate the near-ground-point-density ($NGPD$) the lidar data is height limited between 0.1 and 1.3m above ground (CWD_{130}) and normalized against the sum of this CWD_{130} and the ground classified points (G).

To evaluate the utility of the predictive map zonal statistics were conducted using existing forest inventory polygons greater than 5 hectares in size. A spatial union of the ALRF's harvest history database and provincial forest inventory polygons[1] was completed. A negative 20m buffer was applied to all polygons to reduce potential edge effects. Mean raster values from the predicted CWD layer were generated for each polygon using zonal statistics process in QGIS. Managed stands younger than 30 years were considered juvenile, age 30 - 59 as immature, and over 60 years as mature. Old-growth stands were all those that did not have a harvest history. In addition, old-growth polygons were reviewed against aerial photography to remove sites that were distinctly forested wetlands.

Results

Empirical assessment of CWD

I tested if there were differences in CWD volume between the Knolls and Plateau areas. No significant differences attributed to landscape unit were found (*F(1, 182) = 1.749, p = 0.1877*). As such the results presented are in relation to stand history and development

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[1] BC Data's Vegetation Resource Inventory

stage ($F(4,\ 182) = 20.0121,\ p = 0.000$).

During field data collection it was noted that the natural immature sites in the Knolls landscape unit were previously unmapped harvest areas as evidenced by old cut stumps. These plots were subsequently classified with the managed immature. In the Plateau landscape unit the natural immature sites were unique in that they were not upland productive forest but were forested wetlands as evidenced by their herb and shrub plant communities (unpublished data). These were reclassified as old-growth forested wetlands (*wOG*).

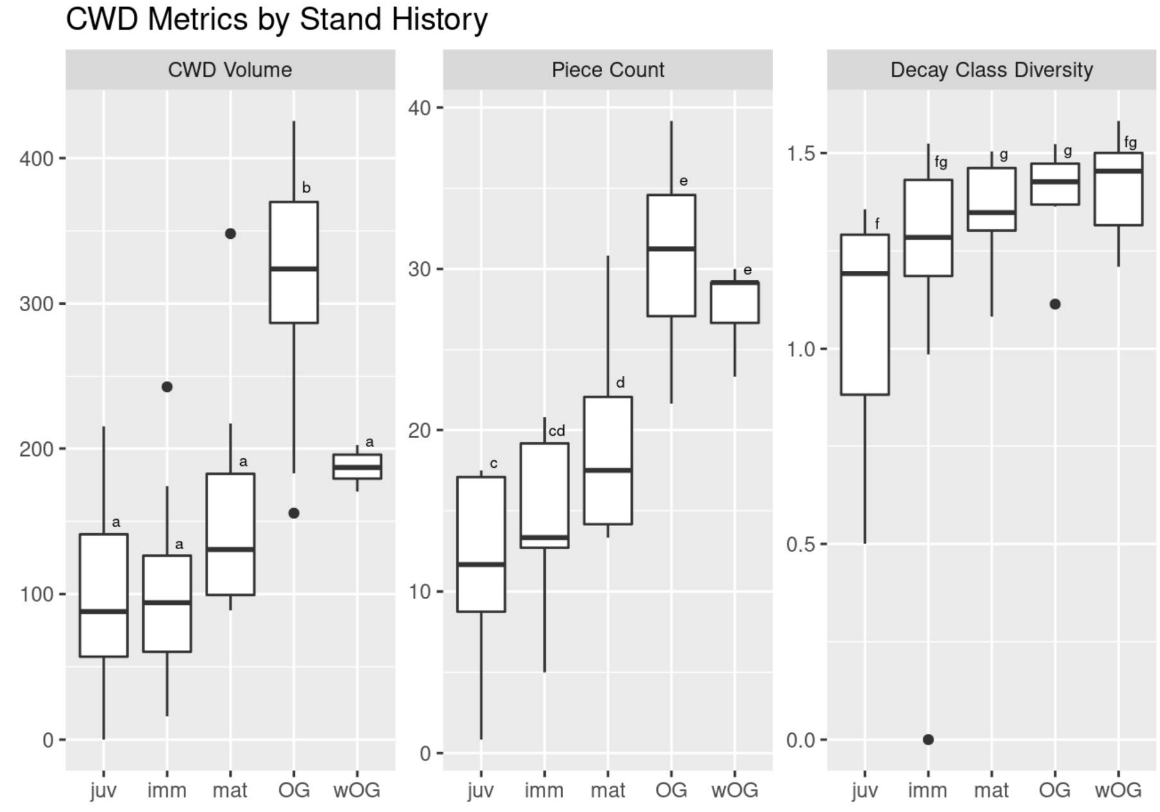

Figure 3.4: Empirical metrics of CWD highlight that younger stands have lower total volume ($m^3/ha.$), lower piece counts in transects (pieces / 100m), and diversity across decay classes (Shannon's H'). Letters above boxplots indicate treatments that are statistically similar.

There was a distinct pattern in the volume of CWD across harvest histories with the lowest volume in the younger stands increasing in the mature forest sites. The old-growth

Table 3.1: Summary of empirical CWD volume, piece count, and Shannon's diversity index (H).

Treatment	Plot N	CWD Volume	v se	Piece Count	pc se	Decay Class	Shannon's H	H se
juv	11	101.23^{a}	20.12	11.74^{c}	1.74	3.34	0.976^{f}	0.128
imm	12	102.87^{a}	18.07	14.72^{cd}	1.41	2.77	1.192^{g}	0.119
mat	11	155.95^{a}	23.36	18.79^{d}	1.75	2.52	1.36^{g}	0.038
OG	10	310.01^{b}	27.52	30.58^{e}	1.86	2.77	1.405^{g}	0.037
wOG	5	186.99^{a}	5.69	27.67^{e}	1.22	2.89	1.412^{fg}	0.067

sites had distinctly more volume than the previously harvested stands ($F(4, 44) = 15.483$, $p = 0.000$, $\eta^2 = 0.585$). Tukey Honest Statistical Difference post-hoc analysis indicated there were significant differences between the old-growth and all of the other stand types. This is highlighted in Figure 3.4 where stands that are statistically similar have the same letter ($p \geq 0.05$). Mean CWD volume in the old-growth sites was 310m^3, twice that of the mature HH sites, and three times higher than the juvenile and immature HH sites. Although HH sites were statistically indistinguishable a trend of increasing volume corresponding to stand development appears to exist. Table 3.1 provides a summary of the CWD volume, piece counts, average decay class, and average piece size.

Piece count shows a similar pattern with significant differences between the old-growth and the managed forest sites (Figure 3.4; $F(4, 44) = 21.654$, $p = 0.000$, $\eta^2 = 0.663$). Based on post-hoc analysis the mature stands were shown to have significantly more pieces of CWD than the juvenile though they were not significantly different than the immature stands. Analysis of piece size across treatment showed some significant differences. However, there was no distinct pattern and the strength of these differences was weak ($\eta^2 = 0.023$).

Shannon's diversity index (H) was used to determine what differences exist in the character/ types of CWD. A similar pattern to volume and piece count is seen as diversity increases with stand development. Significant differences between the diversity indices were observed (Figure 3.4; $F(4, 44) = 3.721$, $p = 0.011$, $\eta^2 = 0.253$). Post-hoc analysis showed that juvenile and immature stands were statistically similar, and lower than the mature and

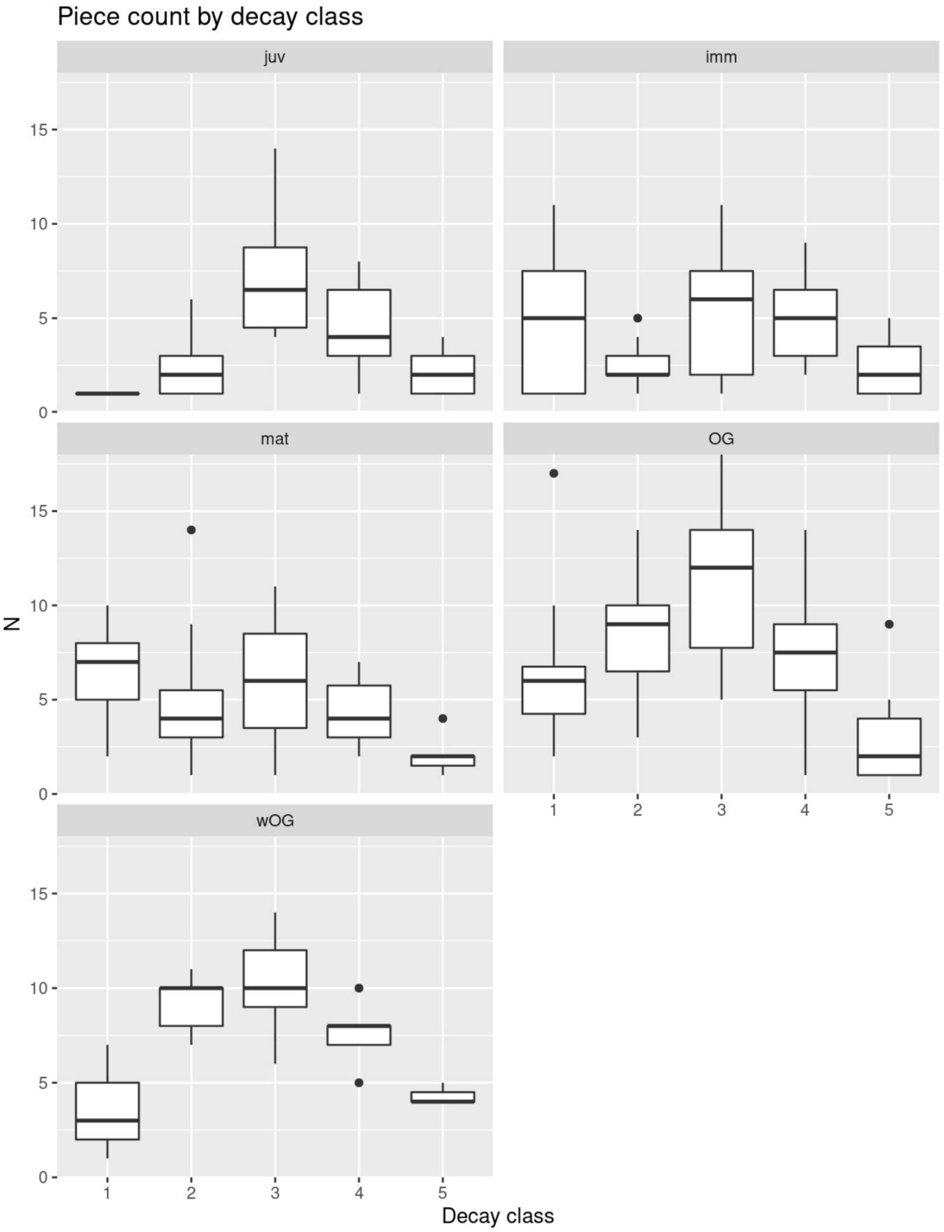

Figure 3.5: Decay class abundance arranged in panels of stands development stages. Old-growth sites have CWD in all decay class with the greatest amount in decay class 3. In comparison, juvenile stands have small counts in decay class 1 and 2; while immature and mature sites have elevated levels of decay class 1.

old-growth sites.

Patterns in the different CWD decay classes are visible in Figure 3.5. The old-growth stands have the greatest about of CWD in decay class three with a smaller number of pieces in the other decay classes. In comparison, the harvest history sites have different patterns especially in the classes 1 and 2 (newly recruited CWD). The juvenile stands are effectively void of decay class 1 materials and have lower proportions of class 2 than that of the old-growth sites; in comparison, data from the immature and mature stands suggest that these classes are accumulating.

Lidar detection of CWD

On average the detection rate of individual CWD pieces from lidar was 23.7%. However, detection rates are dependent on the size of individual pieces (Figure 3.3), decay class (Figure 3.6), and stand canopy characteristics (Table 3.2). To examine the influence of decay on detection rates, only logs of 30cm in diameter or larger were considered; Table 3.3 highlights that CWD with higher levels of decay were less likely to be detected. To examine the influence of stand development stage, large logs with little decay were used (i.e. logs 30cm - 45cm in diameter in decay classes 1-3); Table 3.4 shows that stand structural differences associated with stage development stage affect the ability to detect individual pieces. Mature and old-growth sites had individual piece detection rates that were more than double that of juvenile stands.

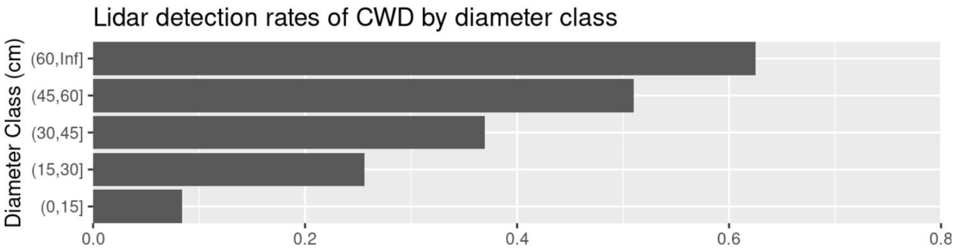

Figure 3.6: The comparison of detection rates of CWD from lidar demonstrates that larger pieces of CWD are more likely to be detected.

Table 3.2: Detection rates of CWD by diameter class across all sites treatments.

Diameter	Field Measured	Lidar detected	Detection Rate
0-15	370	31	0.08
15-30	469	120	0.26
30-45	246	91	0.37
45-60	49	25	0.51
60+	8	5	0.62

Table 3.3: Detection rates of CWD by decay class across all treatments. For this table only CWD between > 30cm in diameter was used.

Decay Class	Field Measured	Lidar detected	Detection Rate
1	20.0	17.0	0.85
2	50.0	27.0	0.54
3	95.0	50.0	0.53
4	96.0	20.0	0.21
5	42.0	7.0	0.17

Table 3.4: Detection rates of CWD by treatment. For this examination only CWD of 30-45cm diameter and in decay classes 1-3 were used.

Stand Type	Field Measured	Lidar detected	Detection Rate
juv	21	6	0.29
imm	16	6	0.38
mat	38	25	0.66
OG	76	53	0.70
wOG	14	4	0.29

Predictive mapping

In order to provide a prediction of CWD across the landscape, area-based-approach lidar metrics were used. Results from the leave-one-out validated *random forest* regression model provides an $r^2 = 0.2221$ (Figure 3.7). Variables that were determined to be the most important for providing the prediction included key stand structural characteristics of height (i.e. zq90, zq95, zq85, zq25, zmax) and stand height variability (zsd, zkurt, Rumple indices). In addition, the NGPD metric was listed as the fourth most important variable (Figure 3.8). Using the model a wall-to-wall predicted CWD map was generated (Figure 3.9).

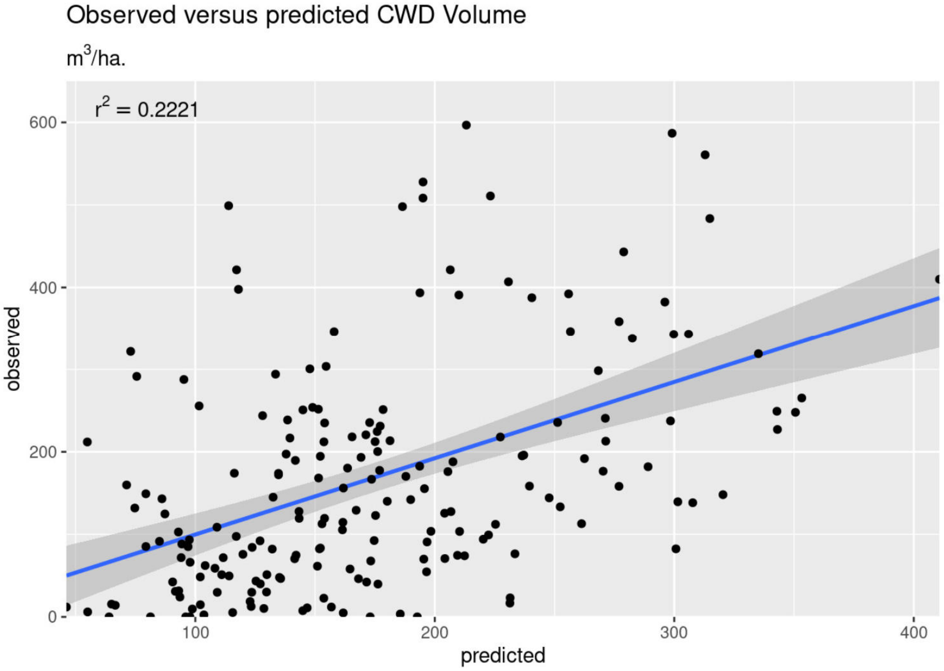

Figure 3.7: Observed vs. predicted coarse woody debris volume from leave-one-out validation from the random forest regression model.

Predictive map efficacy

Mean predicted CWD volume was determined for the forest inventory polygons and showed a clear separation between all stand types ($F(4, 184)$, $p = 0.000$, $\eta^2 = 0.607$).

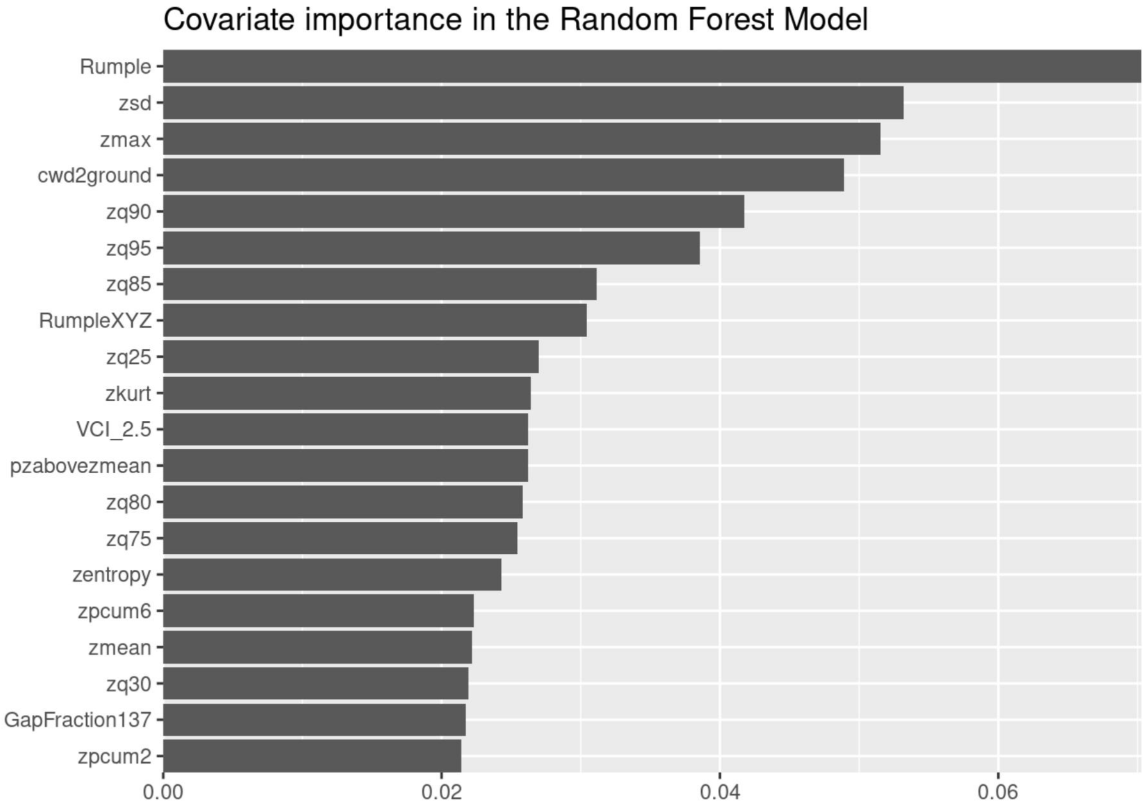

Figure 3.8: Random forest models allow for the determination of which of the covariates were most important in generating the model. Key metrics for predicting CWD include stand structural metrics of canopy variability (e.g. Rumple, RumpleXYZ, zsd), height (e.g. zmax, zq90, zq95), and the custom near-ground-point-density (i.e. cwd2ground).

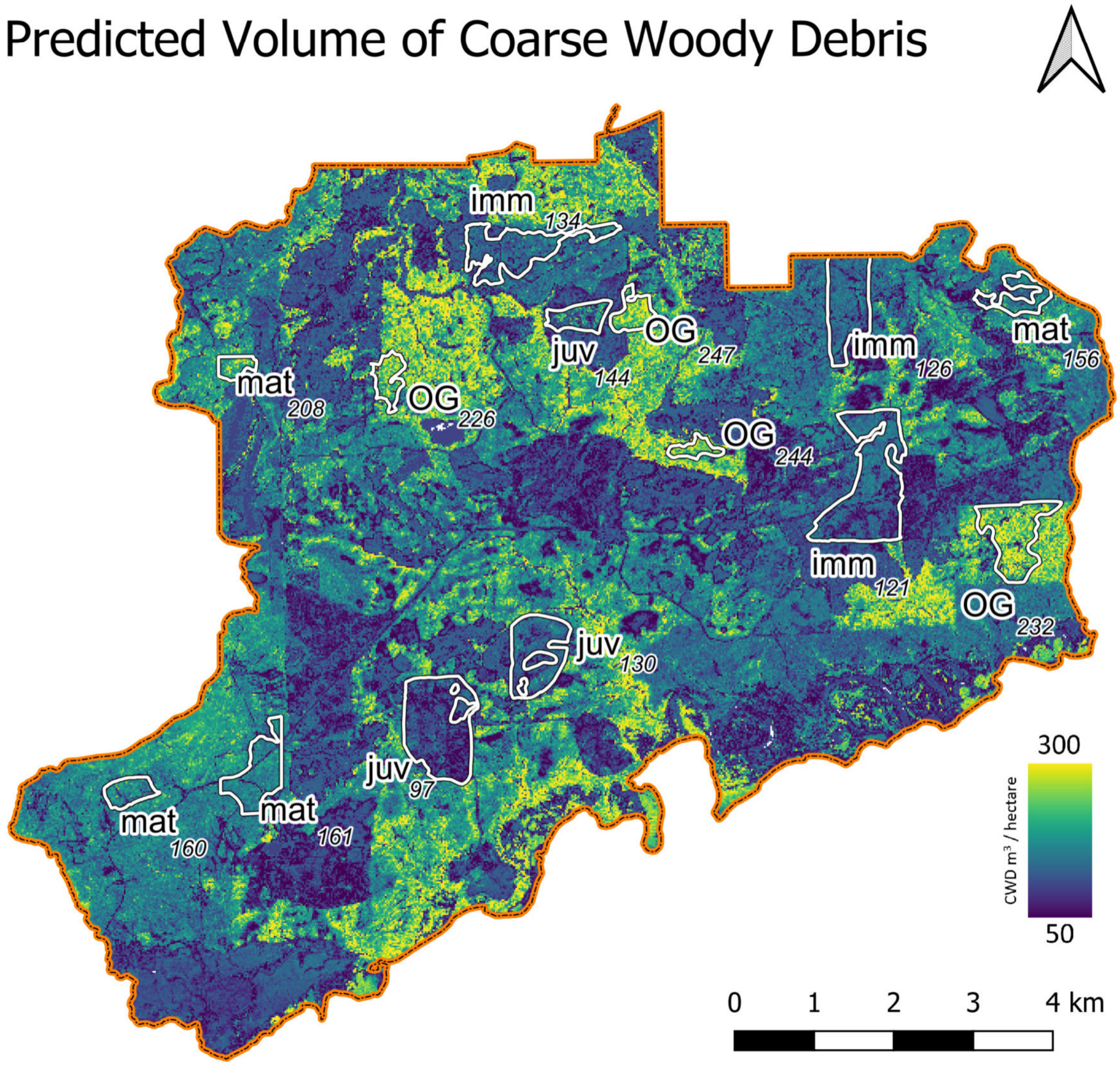

Figure 3.9: A predictive map of CWD across the Aleza Lake Research Forest. Polygons with known disturbance histories highlight the CWD volumes differences between the treatments consistent with empirical analysis. Polygon labels include the stand type with the mean predicted CWD volume per hectare for the polygon.

Tukey Honest Statistical Difference post-hoc analysis demonstrated that all treatments were significantly different from one another (Figure 3.10). At the stand level, predicted mean CWD volumes ranged from 103m^3 in the juvenile stands to 209m^3 in the old-growth stands.

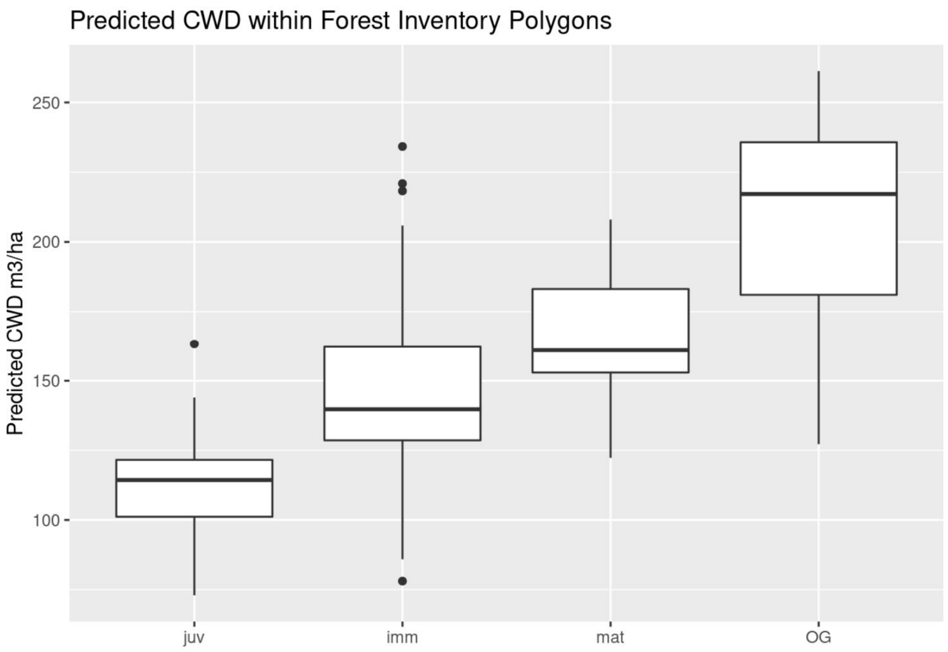

Figure 3.10: Average predicted CWD volume within forest inventory polygons.

Discussion

Empirical differences

Volume of CWD

My empirical results clearly demonstrate that CWD volumes in managed stands, regardless of time since disturbance and method of logging, have distinctly lower levels of CWD than natural stands, by a factor of 2-3. This difference is not only in the volume of CWD but is also reflected in a lower number of pieces, and shifts in the character and diversity of the CWD material (i.e. decay class; Figure 3.4). The trend that managed stands have less CWD than natural stands findings is consistent with numerous studies (Spies et al., 1988; Siitonen, 2001; Brassard and Chen, 2008).

CWD material can be classified as inputs that were present pre-disturbance, and CWD that originated from the remaining trees following a disturbance (Spies et al., 1988;

Sturtevant et al., 1997). Stands in earlier stages of stand development lack sources of CWD. As the stands mature small stems may die as a result of self-thinning. However, these smaller stems are relatively low in volume and due to their small size are expected to decay faster (Freschet et al., 2012; Harmon et al., 1986a).

Mature stands, those that were partially harvested, indicate a trend of increasing CWD as shown by stands having 50 percent more CWD than immature sites. However, this increase still remains half of what is in natural stands. As these stands are mature, and thereby available for harvest, it raises the question if a return to natural levels is actually possible. If harvest scheduling is primarily based on the maturity of the forest then the natural disturbance pattern will be shortened and as a result CWD loading will not return to natural levels. The additional levels of CWD in these sites may be a function of natural self-thinning processes. Our data is inconclusive as far as partial cutting, causing an increase in CWD volume.

Character of CWD

The character of CWD in the managed stands differs from that of the old-growth. Results from Shannon's diversity index shows a trend of low decay class diversity increasing with each stand developmental stage; Figure 3.5 provides insight on the abundance of each decay class. Old-growth sites have CWD represented in all decay classes with decay class 3 having the most. In contrast, juvenile sites are generally devoid of decay classes 1 and 2 (materials with low levels of decay). Juvenile sites, having been clear-cut harvested, have effectively no new potential inputs of CWD except perhaps along the mature edges surrounding these sites. Immature, and mature sites have elevated levels of decay class 1 which may be indicative of stem exclusion stand dynamics as suggested by Brassard and Chen (2006). Though the Shannon H' diversity index values between mature and old-growth are effectively the same the actual abundance within each class differs (as noted above).

All sites have decay class 3 as the most abundant class. This is likely due to the fact, that as stems decay they remain in decay class 3 the longest period of time, consistent with finding of Newberry et al. (2004) who examined time since death based on CWD decay metrics. All sites show lower abundance of decay class 4 and 5 (highly decomposed materials). This is likely due to a lower amount of time that material would remain in decay class 4 relative to decay class 3. Our sampling method likely discounted the amount materials in decay class 5, as logs that were 50% of greater embedded in the forest soil profile were not measured. The managed mature and immature forest stands do have similar decay class distributions, however, the abundance of material remains far less and there are numerous decades in which the managed stands have lower volume and an altered distribution of CWD decay classes.

The old-growth forested wetlands share some similar CWD characteristics with the upland forest old-growth stands in terms of piece counts and diversity of decay classes; they differ however in that the total CWD volume is lower. The lower volume compared with the old-growth sites is attributed to lower site productivity (the site was not capable of producing larger trees and thereby high total volume on the site).

Evidence suggests that the ecological functions provided by CWD debris may be compromised in managed forests given that total amount of material is significantly reduced and the character of that material takes significant time to recover. Brassard and Chen (2006) note that a varied decay class may be just as important as the volume of CWD. Our study does suggest that decay classes differ and that there may be several decades in which not all decay classes are represented (i.e. juvenile sites). Kumar et al. (2018a) found that decay class had a strong influence on epixylic plant communities. Langor et al. (2008) found that saproxylic insects communities were likewise influenced by decay class.

Given that there are strong differences between old-growth and stands with harvest histories, to ensure that ecosystem integrity is met, it is important to identify where areas of high CWD are on the on the landscape.

Detection of CWD using lidar, and landscape management

Review of CWD transects in the near-ground surface models highlight that CWD can be detected using lidar. However, successful detection of individual pieces is reliant on a number of factors. Individual CWD pieces influences detection rate where large pieces with lower levels decay (i.e. decay classes 1-3) have higher detection success rates (tables 3.2 and 3.3). The structure of the live forest canopy also influences detection rate. Detection rates are highest in old-growth stands and lowest in the juvenile sites, as the latter had closed canopies and lacked canopy lift such that tree branches remained visible in surface model and obscured visualization of the near-ground surface model. Likewise, immature stands had slightly higher detection rates though it is suspected that the degree of canopy closure reduced detection rates. Highest detection rates are in mature and old-growth stands where crown lift is highest, and the canopy is more transparent due to stand dynamics (e.g. gap generation). Direct CWD detection in this study was done through manual comparison of CWD surface model with empirical data. Image segmentation algorithms should be investigated to automate this process and provide opportunities to map individual CWD across a landscape.

Area based metrics were used to generate models of CWD and demonstrate that it is possible to generate predictive maps of CWD across a landscape. Figure 3.8 highlights that metrics of stand structural diversity are predictive of CWD. These include standard deviation (zsd), and rumple indices[2], which are measures of crown surface roughness, and metrics of stand height (zmax and zq90). Kane et al. (2010b) highlights that these metrics are consistent with stand structural development where increasing values of these metrics corresponds with increasing stand structural diversity. Finally, the custom NSPD

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[2] $Rumple_{pts}$ used Delaunay triangulation of lidar points, and $Rumple_{chm}$ used a raster based method following Jenness (2004)

metric was highlighted as a variable useful for determining CWD.

The *Random Forest* model provides an $r^2 - value = 0.2221$ which is strong enough to demonstrate distinct trends but not adequate enough to provide pixel-for-pixel certainty. The forest stand polygon analysis demonstrates that, despite a lower r^2 value, there is a clear separation of the stand development stages. This confirms that there is strong utility to highlight where areas of CWD are on the landscape. Some caution is needed in that modelled CWD volumes tallied at the polygon stand level differ from values expected from the empirical data. Juvenile and immature stands had predicted volumes that fell within the empirical ranges expected (e.g. juvenile: 113; immature: 145; mature: 166; and old-growth: 209; see Figure 3.10). Our predictive map (Figure 3.9) shows a clear distinction between areas with harvest history and old-growth. More careful examination of Figure 3.9 shows that the recovery of CWD volume is visible on the landscape; highlighted areas show increasing amounts of CWD corresponding with their stand development stages.

Management Opportunities

Ecological Differences

Results from this study are consistent with others suggesting that high volumes of CWD can be considered a good indicator of old forest condition (Kunttu et al., 2015; Ulyshen et al., 2018). However, ecological drivers including natural disturbance patterns need to be considered. For example, areas with higher frequency forest fire may still see low levels of CWD in old forest stands. Ulyshen et al. (2018) examined longleaf pine forests with frequent fire return intervals and determined that following fire, there was a large input of CWD in the stand development stage immediately following fire disturbance and over time CWD levels fell and were lowest in the oldest stands. However, one could argue that such landscapes never have the opportunity to become old (Arsenault, 2003).

Bauhus et al. (2009) suggests that silvicultural manipulation of maturing and mature second growth stands could allow for the recruitment of old forest structures. This is supported by Sandström et al. (2019) who reviewed numerous studies covering temperate and boreal forests of North American and Europe, and concluded that artificially increasing volumes of CWD significantly increased abundance and richness of saproxylic insects and wood-inhabiting fungi, although they caution that manipulating CWD while providing volume does not address potential issues relating to mimicking natural distribution of decay classes.

Designated areas

Providing areas reserved for natural processes, including natural disturbance, may be critically important to ensure that islands of natural CWD volume and distribution of varied CWD decay classes remain on the landscape as these may be essential for the survival of some saproxylic species. Predictive mapping of CWD, as used in this study, provides an opportunity to highlight areas to either implement silvicultural treatments to enhance CWD and to consider for reserve designation. In considering future research, predictive mapping methods could be to highlight other forest attributes or create indices for ecological function.

Conclusion

My research compared natural old-growth fforests to managed stands, and found that managed stands have much lower CWD volume and differ in the character of CWD (i.e. decay class). Old-growth stands have twice as much volume than the mature managed stands and while mature managed stands did show an increase in CWD compared with the immature stands, indicating that recruitment of CWD has started, more time will be needed to return to the natural levels. The character of CWD, in its various decay classes, also differs in managed stands; of particular concern are the juvenile sites which were nearly devoid of decay class 1 and 2. Recovery of CWD volume and character to natural levels does not occur within timber rotation period, raising concerns that the lack of CWD could impact the biodiversity of numerous taxa requiring CWD in its various forms. Without management intervention to create CWD it will therefore not be possible to see natural levels of CWD within the managed forests. Managing CWD at the landscape, including identifying where stands rich in CWD are located, provide options for management to maintain stands rich in CWD on the landscape. The use of lidar in this study demonstrated that CWD can be detected. Modelling of empirical data with the lidar allows for the production of predictive maps of CWD, which could be used by decision makers to manage CWD at the landscape scale.

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Chapter 4

Synopsis

Introduction

The forest landscapes of Canada are being progressively changed by forest management (Venier et al., 2014). Although regarded as sustainable, concerns have been raised over the last number of decades about the impacts of forestry practices on biodiversity and ecological integrity (Harmon et al., 1986a; Hart and Chen, 2006; Brassard and Chen, 2006). In their consideration of forest disturbance and recovery, Messier et al. (2015) promote the concept of forests as complex adaptive systems and that forest stands develop from a stand initiating event (e.g. harvest or fire) and converge towards old-growth condition though this may not be linear or determinative. For the purpose of measuring forests as complex adaptive systems, Parrott (2010) encourages the research community to develop tools to measure how ecosystems are developing, to use remote sensing to supplement research, and to be spatially and temporally explicit in measurements. Remote sensing from aerial laser scanning (lidar) provides excellent detail of the 3-dimensional structure of forests (Wulder et al., 2008b). Davies and Asner (2014) encourages the use of lidar to describe habitat condition and ecosystem function. My previous chapters have demonstrated the use of research tools to quantitatively measure the impacts of forest management disturbance and patterns of recovery. Here, based on findings of Chapters 2 and 3 I consider:

1. Are the forest stands converging towards old forest condition?
2. Provide recommendations for forest land management.
3. Highlight areas for further research.
4. Are we growing forests or are we growing trees?

Forest disturbance and patterns of recovery

Methods

In the previous chapters impacts on forest biodiversity were quantitatively investigated. Chapter 2 provided direct measurements to biodiversity by examining plant response to changes in forest structure. Metrics of biodiversity included impacts to stand structure and diversity: tree species composition, sizes, and density. Understory vegetation community composition was measured using total species diversity, richness, and abundance. Analysis of vegetation abundance was considered as total abundance, abundance by functional group, and individual species abundance.

Chapter 3 provided indirect measurements of biodiversity by examining coarse woody debris (CWD) as key structual features in forests essential for the support of numerous taxa especially those that are considered epixylic or saprophylic (Stokland et al., 2012). This chapter measured both the character and quality of CWD. In addition, the use of lidar provided opportunity to evaluate differences in CWD volume across the landscape.

In both chapters, the same series of forest stands was used covering two landscape units and a range of stand development stages, stratified by height class, and presence or absence of harvest history. Managed stands included plantation forest stands: juvenile, and stands that were thinned from above: immature, and mature. Natural stands included old-growth and forested wetlands. With the exception of the forested wetlands this series of stands formed a chronosequence allowing for insight into the impacts and recovery of key biodiversity metrics both spatially and temporally.

Indicators of forest recovery

The results from Chapter 2 suggest that there is very little impact from forest management on metrics of biodiversity. Managed forest stand structure was distinct from natural through the juvenile and immature stages while the mature stands, based on the metrics used, were indistinguishable from the old-growth. Results showed that total species diversity and richness for the main canopy and the understory vegetation showed only slight differences linked to management and these returned to natural levels by the immature stage. Vegetation community abundance by functional groups indicated impacts from forest harvesting on the juvenile stage of stand development with recovery by the immature stage. The examination of abundance by individual species is where a signature of long term impacts forest harvesting were discernible. All harvested stands could uniquely be identified. Patterns from the linear discriminant analysis do suggest that vegetation communities are converging towards old forest condition as the mature harvested sites and old-growth sites showed overlap and some classification confusion (Figure 2.6).

Chapter 3 found distinct differences in the total volume of CWD. Volume of CWD in the juvenile and immature sites were one third that of old-growth. Mature sites did see some recruitment of CWD but remained half that of the old-growth. The number of CWD pieces showed a pattern of recovery but all managed stand types were lower than old-growth stands. The types of CWD, indicated by decay class, was also altered, being less diverse in the managed stands (Figure 3.4). This chapter also demonstrated that it was possible to use lidar to detect and model the spatial distribution of CWD on the landscape providing a visual tool to identify where CWD pools are most impacted and where opportunities for conserving areas high in CWD are located.

These chapters demonstrate that there are patterns of recovery. Vegetation community composition converges to old-growth with stand maturity. The greatest area of concern in the management of CWD, as patterns indicate a trajectory towards old-growth; however, managed stands remain distinct and well below natural conditions even at stand maturity.

Recommendations

The forest manager needs to be mindful that the impacts forest management has on vegetation and CWD are long lasting. Although there are indications of some return to natural conditions managed forests are distinct from natural old-growth. Given that mature stands, as their name implies, are ready for a subsequent harvest, this raises further concern that full recovery of these stands will never be achieved as they will be harvested prior to full convergence with natural conditions (Venier et al., 2014; Hart and Chen, 2006). Options for the full recovery to natural condition requires more time or, as Bauhus et al. (2009) suggests, treatment of maturing stands could be conducted to encourage the development of old-growth attributes. Alternatively, action can be taken in the spatial management of old-growth or development of mature stands towards old-growth. Areas of reserve, with the objective of conserving or restoring old-growth condition should be established. This can be done at both the stand level and landscape level.

Additional research to refine my findings is also needed. The series of stands used in this study included plantation forests and those that were thinned from above. Future work needs to continue to monitor the development of plantation forests which may develop different vegetation communities and patterns of CWD recruitment. Further, lidar metrics could be used with the community vegetation data to examine in greater detailed the impacts of stand structural conditions. For example, lidar can provide a direct measure of canopy closure impacting light conditions in the understory.

Are we growing forests or growing trees?

We are growing forests but perhaps not in their entirety. Through my research it is evident that managed forests and in particular mature managed forests continue to differ from natural old-growth. The vegetation communities though somewhat distinct are converging towards natural stand condition. The greater concern appears to be the long-term management of CWD on the landscape. In the management of forest lands, indications are that it will be possible to see the return of natural levels of CWD. However, as a land manager I need to be mindful that this will not occur without action. Rotation forestry, harvesting stands as soon as they are mature, will never allow the return of old-growth attributes and the services they provide. To manage for CWD, it must be done spatially to either conserve existing areas or define areas for recruitment of natural CWD condition.

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Appendix A

Mean Species Abundance

Table A.1: Mean Hellinger-transformed species abundance from linear discriminant analysis using the species that were observed a minimum of forty times.

Fn	Genus	Species	SCode	juv	imm	mat	OG	wOG
Bryophytes	Brachythecium	spp	BRACHSPP	0.168	0.169	0.188	0.189	0.167
Bryophytes	Hylocomium	splendens	HYLOCSPLEN	0.024	0.098	0.078	0.133	0.091
Bryophytes	Plagiomnium	medium	PLAGIMEDIU	0.122	0.078	0.123	0.102	0.161
Bryophytes	Pleurozium	schreberi	PLEURSCHRE	0.183	0.191	0.158	0.123	0.168
Bryophytes	Ptilium	crista-castrensis	PTILICRIST	0.121	0.243	0.185	0.214	0.376
Bryophytes	Rhizomnium	glabrescens	RHIZOGLABR	0.047	0.040	0.135	0.077	0.085
Bryophytes	Rhytidiadelphus	triquetrus	RHYTITRIQU	0.139	0.322	0.302	0.331	0.185
Bryophytes	Sphagnum	squarrosum	SPHAGSQUAR	0.013	0.082	0.014	0.009	0.289
Bryophytes	Timmia	austriaca	TIMMIAUSTR	0.023	0.024	0.014	0.002	0.016
Forbes	Aralia	nudicaulis	ARALINUDIC	0.128	0.133	0.120	0.149	0.006
Forbes	Athyrium	filix-femina	ATHYRFILIX	0.106	0.053	0.178	0.083	0.121
Forbes	Clintonia	uniflora	CLINTUNIFL	0.074	0.105	0.086	0.115	0.000
Forbes	Cornus	canadensis	CORNUCANAD	0.246	0.147	0.157	0.197	0.143
Forbes	Dryopteris	expansa	DRYOPEXPAN	0.024	0.038	0.104	0.085	0.111
Forbes	Equisetum	arvense	EQUISARVEN	0.018	0.012	0.011	0.003	0.047
Forbes	Equisetum	sylvaticum	EQUISSYLVA	0.023	0.032	0.016	0.006	0.080
Forbes	Galium	trifidum	GALIUTRIFI	0.012	0.005	0.011	0.004	0.000
Forbes	Galium	triflorum	GALIUTRIFL	0.042	0.005	0.025	0.017	0.015
Forbes	Gymnocarpium	disjunctum	GYMNODISJU	0.135	0.151	0.226	0.197	0.101
Forbes	Linnaea	borealis	LINNABOREA	0.086	0.058	0.037	0.039	0.016
Forbes	Lycopodium	clavatum	LYCOPCLAVA	0.014	0.036	0.047	0.032	0.038
Forbes	Mitella	nuda	MITELNUDA	0.025	0.021	0.048	0.036	0.017
Forbes	Petasites	palmatus	PETASPALMA	0.063	0.048	0.018	0.009	0.000
Forbes	Prosartes	hookeri	PROSAHOOKE	0.056	0.031	0.027	0.085	0.000
Forbes	Rubus	pedatus	RUBUSPEDAT	0.022	0.089	0.120	0.105	0.146
Forbes	Rubus	pubescens	RUBUSPUBES	0.038	0.039	0.010	0.026	0.056
Forbes	Streptopus	lanceolatus	STREPLANCE	0.087	0.135	0.152	0.151	0.028
Forbes	Tiarella	trifoliata	TIARETRIFO	0.125	0.151	0.228	0.183	0.178
Shrubs	Alnus	viridis	ALNUSVIRID	0.080	0.068	0.014	0.062	0.083
Shrubs	Lonicera	involucrata	LONICINVOL	0.192	0.071	0.033	0.058	0.084
Shrubs	Oplopanax	horridus	OPLOPHORRI	0.029	0.079	0.177	0.192	0.101
Shrubs	Ribes	lacustre	RIBESLACUS	0.038	0.040	0.057	0.049	0.004
Shrubs	Rosa	acicularis	ROSAACICU	0.110	0.055	0.039	0.073	0.041
Shrubs	Rubus	parviflorus	RUBUSPARVI	0.209	0.138	0.186	0.193	0.005
Shrubs	Spiraea	betulifolia	SPIRABETUL	0.107	0.067	0.053	0.045	0.016
Shrubs	Spiraea	douglasii	SPIRADOUGL	0.127	0.104	0.017	0.018	0.179
Shrubs	Vaccinium	membranaceum	VACCIMEMBR	0.025	0.074	0.061	0.109	0.038
Shrubs	Vaccinium	ovalifolium	VACCIOVALI	0.030	0.091	0.055	0.067	0.139
Shrubs	Viburnum	edule	VIBUREDULE	0.093	0.074	0.066	0.061	0.013