# Quantifying Tree Community Assemblages on Habitation sites in the Great Bear Rainforest

by

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## Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners

I understand that my thesis may be made electronically available to the public

# Abstract

Identifying how past human actions have influenced their environment is important for understanding how current ecosystems function. Heavy intertidal resource use by Indigenous Peoples for the past several millennia has led to habitation sites containing vast shell midden deposits within their soils, with long-term impacts on soil chemistry and drainage. Here we examine how these shell middens have impacted various forest metrics, such as species diversity, dissimilarity, structure, and seedling recruitment to determine if forest composition on habitation sites differs from the surrounding matrix. Field data was collected within Hakai Lúxvbálís Conservancy on Calvert and Hecate Islands within the Great Bear Rainforest along British Columbia's Central Coast. Known habitation sites, places with archeological evidence indicating past year-round human occupation, along the coast of Calvert and Hecate Island were used as study sites. Two to three 11.28 m radius plot were randomly placed on habitation sites where adult species were tallied, height (m), and diameter and breast height (DBH) (cm) data was collected. Within the 11.28 m radius plot were five 1 m x 4 m sub-plots, where all seedlings were tallied, and their growing substrate recorded. For adult trees there was no significant between control sites and habitation sites. (p = 0.07). Adult tree communities on habitation sites were significantly dissimilar from the surrounding matrix (p = 0.008). There was no significant difference between seedling diversity on habitation sites and control sites (p > 0.05), and there was no significant difference in dissimilarity between communities (p = 0.1). We found that there were no significant differences between height or DBH for all tree species analyzed. Both western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) adult trees were the main drivers of community dissimilarity by having reduced abundance on habitation sites compared to our control sites. Finally, we found that nurse logs, fallen trees that act as a seedbed,

were the primary substrate for seedling recruitment with little regeneration on the forest floor (p < 0.001). Our results demonstrate that forest communities on habitation differ only in their measure of stem density, quantified through community dissimilarity, and that no differences in diversity or physiology are seen between control and habitation sites.

# Acknowledgement

I would like to start out by acknowledging my supervisor Dr. Andrew Trant for all his diligent work in assisting me in this project. His knowledge in forest ecology, cultural history, experimental design and data analysis were invaluable in the completion of my master's thesis. Through countless meetings, headaches and bungled R sessions he was always present when things felt dire. It is through this that I wish to thank him. I would also like to thank my committee member Dr. Brad Fedy on his expertise in experimental design and data analysis. Through various meetings and Skype calls his knowledge in data analysis was pertinent in developing the statistical know-how required to address my seeming insurmountable data quarrels. Also, of great assistance to this project was Kieran Cox for his assistance in furthering my knowledge of the quantification of diversity and its various parameters.

I would also like to thank fellow lab mates Alana Closs, Sara Wickham, Emma Davis, Alexandra Johnson for all their suggestions with project building, analysis, interpretation, and editing. These acknowledges also extend to those who braved the field season with me including Sharon Wilson, who was a key figure in helping me during my field season with data collection and Jennifer Walkus, who also assisted me with field surveys.

Furthermore, I would like to thank Hakai for both funding this project and making this thesis a possibility. Finally, I would like to acknowledge the Indigenous communities for giving me the unique opportunity to work on their lands and by their sides.

# Dedications

This project is dedicated to all those who love trees! Or science in general!

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# Chapter 1: Introduction and Background Information
## Background & Research Questions:

Within the Pacific Northwest (PNW) lies the largest remaining temperate rainforest in the world, the Great Bear Rainforest, a 6.4-million-hectare area within British Columbia of ecological, economic and cultural significance (Clapp, 2004; Gottesfeld, 1992; Price, Roburn, & MacKinnon, 2009; Riddell, 2005). The Indigenous communities' occupation of these lands for the last 14,000 years have led to various landscape level modifications through land use practices and management. Given the heavy reliance of Indigenous communities on surrounding intertidal resources, the majority of known habitation sites, places with archeological evidence of past human settlement, are found along the coastal margins of these areas (McLaren et al. 2015). Some of these modifications include: manipulation of intertidal areas through stone relocation to support clam gardens (Deur et al. 2015), the burning of trees leading to accumulations of anthropogenic soil charcoal (Hoffman et al. 2016), stripping of bark from the western redcedar (*Thuja plicata* Donn ex D. Don) to use as material for clothing or household objects, or the depositing of shell middens from the use of intertidal resources (McLaren et al. 2015).

The focus of this thesis project lies in the deposition of shell middens (mixtures of shellfish, artifacts, roots, charcoal and bone) starting around 6,000 years ago (McLaren et al. 2015) and their effects on the forest community structure. These shell midden deposits are highly variable in shape and extent, with larger deposits reaching over 5 m in depth (McLaren et al, 2014). These shell midden deposits can be used as proxies to help determine segments of the coastal land that were used as village sites by Indigenous communities. While much work has gone into the archeological and anthropological significance of these habitation sites, little has been done to quantify the ecological impacts of these human-mediated modifications.

Previous work within the Great Bear Rainforest has generally focused around Calvert and

Hecate Islands (51.5559° N, 128.0365° W) which contains the Calvert Island Ecological

Observatory, an interdisciplinary research station which facilitates coastal science through

collaborative measures with various universities, organizations and Indigenous communities.

The research station's close proximity to a host of well-documented habitation sites along the

coast of Calvert and Hecate Islands offers a unique opportunity to study these shell middens and

their influence on forest community structure.

Previous studies on Calvert and Hecate island have shown an increase of productivity

from forest stands found on habitation sites relative to those in the surrounding matrix (Trant et

al. 2016). Western redcedar trees growing on habitation sites were taller and wider then trees in

the surrounding area with increased levels of wood calcium (Trant et al. 2016). Another

interesting finding was how the shell middens modified various soil characteristics such as pH

and nutrient availability where a significant increase in pH, calcium and phosphorus were

detected (Trant et al. 2016). Finally, a previous study showed increased levels of herbaceous

plant diversity, more culturally important plants associated with habitations sites and elevated

soil nutrient levels (Fisher et al. 2019).

The composition of shell middens varies depending on location, but their primary

constitutes complement the activities of those sites by containing clam shells, fish bones,

terrestrial and aquatic mammal bones, and other organic elements such as human remains. Given

the composition of these shell middens, their impacts may be viewed analogously to other

marine-derived inputs in a terrestrial system. This is prominently seen when foraging bears, or

other vertebrates, leave salmon carcasses in riparian areas, altering soil chemical regimes leading

to an influx salmon derived nitrogen ($\delta^{15}N$) and phosphorus (P) (Bilby et al. 2003, Hocking and

Reynolds 2012). These marine-derived nutrients can then be detected within the foliage of above ground vegetation where previous studies have found that sites closest to high density salmon spawns contain the highest levels of ($\delta^{15}$N) (Bilby et al. 2003) and ultimately plant diversity (Hocking and Reynolds 2012). The impacts that marine-derived nutrients can have on terrestrial systems is especially important within the context of this study where acidic soils and poor drainage has limited nutrient availability for above ground vegetation (Gessel et al. 1973, Prescott et al. 2000, Richardson et al. 2004). The soils in this region are dominantly organic soils, more specifically nutrient-poor Ferro-Humic Podzols and therefore have a relatively low pH (Ministry of Environment, 2017). As a result of this, calcium, a key element found in the calcium carbonate shells fragments found in the shell middens, is often leached from the soils. The calcium input from this marine source can act to buffer pH, similar to how biochar can increase the pH of acidic soil (Chintala et al. 2014). These nutrient poor soils often limit the growth of various conifer species found in the region such as western redcedar, yellow cedar (*Cupressus nootkatensis* D. Don), Sitka spruce (*Picea sitchensis* B. C.), mountain hemlock (*Tsuga mertensiana* B. C.), Pacific yew (*Taxus brevifolia* N.) and shore pine (*Pinus contorta* D.*)* (Spies and Franklin 1989, Klinka et al. 1996). Of the common conifers found along coastal British Columbia, western redcedar and western hemlock generally have the lowest nutrient requirements for growth, and the potential ability to alter soil chemistry and microbial content (Brockett, Prescott, & Grayston, 2012; Canham, LePage, & Coates, 2004; Messier, 1993; Prescott & Blevins, 2005; Wang, Qian, & Klinka, 1994). Low nutrients and poor soil drainage have contributed to the abundance of western redcedar and western hemlock in low altitudinal forest stands, while limiting the growth of Pacific yew and shore pine (Minore 1990, Banner et al. 2005).

Nutrient requirements are not the only factor limiting growth, as light availability often dictates the success of conifer seedling recruitment. There is variation in the light requirements of conifer seedlings where interspecific competition shows western redcedar achieves maximum growth rates with the least amount of light (Minore 1990, Drever and Lertzman 2001). However, there have been some inconstancies in the literature in regard to the shade tolerance of western redcedar. One study found that western redcedar saplings had higher shade tolerance than western hemlock, which is thought to be the most shade tolerant tree species along coastal British Columbia (Harrington 2006). Shade tolerance levels can also vary depending on soil drainage, an important factor to consider given that shell middens increase soil drainage (Carter and Klinka 1992, Trant et al. 2016). The forest floor of these low altitudinal forest stands are often complex and well-developed, being dominated by salal (*Gaultheria shallon* P.), blueberry (*Vaccinium spp.*) and false azalea (*Menziesia ferruginea*) (Banner et al. 2005). The resulting interspecific competition for light gives advantages to seedlings which establish on coarse woody debris, henceforth referred to as nurse logs (Harmon and Hua 1991). These nurse logs offer a physical advantage in height, increasing seedling survivorship (Harmon & Hua, 1991). However, it is not known what role nurse logs play within the Great Bear Rainforest, and whether these nurse logs offer the same advantages as seen in previous studies.

My research builds off previous work done in this system by examining if shell middens have altered the forest community structure and composition. As previously mentioned, this study was conducted on Calvert Island and Hecate Islands, located along the central coast of British Columbia. These study sites fall in the Very Wet Hypermaritime, a subzone of the Coastal Western Hemlock zone (CWH); one of the 14 biogeoclimatic zones within British Columbia denoted by high levels of precipitation and a cool mesothermal climate (Meidinger

and Pojar 1991). Of particular interest of this location pertains to the local tectonic attributes, where both Calvert and Hecate Islands are situated on a sea level hinge in which local sea level dynamics have remained relatively stable post glaciation (McLaren et al. 2014). These stable sea levels enabled Indigenous communities to occupy these lands for over 14,000 years, where various habitation sites in these areas still see use. This lack of disturbance via glaciation has allowed researchers the unique opportunity to study these persistent effects left behind by past Indigenous stewardship, leading to my overarching thesis question:

> *How has the presence of shell middens on habitation sites altered forest community composition and structure?*

More specifically, has the presence of these shell midden deposits lead to changes in species compositions or physical structure of both adult trees and seedlings on habitation sites. Community composition in this system is fairly well understood, with western hemlock and western redcedar being the most common species at lower altitudes, and mountain hemlock (and yellow cedar being the most common species at higher altitudes within this region (Banner et al. 2005). However, when looking at the site level (i.e., a habitation site) the relative proportions of these dominant and rarer species is not well-understood. As western redcedars growing on habitation sites have been found to have enhanced growth (Trant et al., 2016), here we seek to understand if this relationship is seen in other tree species on habitation sites.

## Approach:

In order to answer my research question, community structure and composition will be quantified using of a combination of field techniques. The most traditional of these diversity indices delve into the inherent relationship between species richness and evenness such as the Shannon-Weiner index or Simpson's index (Jost 2010, Moreno and Rodríguez 2011, Zhang et al.

2012). While there is value in the use of these indices, it has been argued that their use alone may fail to capture the complexities of the system of interest. (Anderson et al. 2011, Leinster and Cobbold 2012)

In order to properly assess differences, I will be using multiple analytical tools to assess community structure and diversity. Taxonomic diversity will be explored using Shannon-Weiners H' and Simpson's Reciprocal (1/D). Given the low species richness of this system, the use of multiple indices that reflect different values will elucidate differences in diversity between communities. Shannon H' places more weight on rare species while Simpson's reciprocal (1/D) favors the presence of common species (Smith & Wilson, 1996, Jost 2010, Tuomisto 2012).

While these indices provide insight into overall diversity, they fail to identify compositional differences that may exist between communities. As such, ecologist often require other analytical tools to determine community differences. In addition to diversity indices, measures of community dissimilarity will be determined using a Permutational Analysis of Variance (PERMANOVA). These PERMANOVA's will be performed using Bray-Curtis Dissimilarities, one of the most common and widely used dissimilarity measures by ecologist (Clarke 1993). Finally, the last tool to detect community differences will be Similarity Percentages (SIMPER) analysis. While the two previous techniques can elude to community differences the specific species responsible for this aren't known. SIMPER analysis helps by identifying which species are responsible and also the degree of influence they have on overall community dissimilarity.

## Broader Context:

Ultimately, this thesis is but one part of a larger, ever-evolving process to better understand how these eco-cultural legacies, i.e persistent effects left behind by past human activity, have shaped both current and future ecological processes. There are two main goals with this thesis regarding a larger sustainability concept, with the first being:

1) *To generate site level species data within the Great Bear Rainforest to determine community composition and structure.*

Generating site level species data is the first step towards generating modelling accurate future projections of this system. Having an inventory of both adult and seedling species compositions provides baseline data that future studies can build on to asses other ecological principles such as successional trajectories and how climate change will affect this system. Additionally, some of the tree data gathered for this project, specifically that of the western redcedar, overlaps with previously collected data from similar locations in a 2016 study by Trant et al.. The results of this study will assist the validation of these previous study while providing further evidence of the effects of these shell middens. Finally, this thesis is complementary, yet entirely independent, to a recent thesis completed by a Master's student at the University of Victoria, Julia Fisher, in which shell midden effects on the herbaceous plant diversity were quantified (Fisher et al., 2019). This leads to the second goal of this thesis:

2) *To contribute empirical evidence to a growing body of literature describing how Indigenous cultures have facilitated landscape level modifications through land use and management.*

While aspects such as western redcedar tree height and shrub/ephemeral diversity have been quantified on these habitation sites (Trant et al. 2016, Fisher et al. 2019), community composition and structure data for a wider breadth of tree species remains unknown. With this study, we hope to add to the growing body of knowledge that humans have directly contributed to landscape level modifications for thousands of years.

# Chapter 2: Data collection and analysis

## 1.0 Introduction

Human influence on global biodiversity and ecosystem process have been well-documented, with post-industrial ecosystem loss increasing as human populations continue to climb (Steffen et al. 2015, Watson et al. 2016). Modern human land-use patterns are often associated with negative ecological impacts such as habitat destruction (McIntyre and Hobbs 1999, Hoekstra et al. 2005), soil degradation (Lamb et al. 2005, Lal 2015), and global biodiversity loss (Butchart et al. 2010). However, there is a growing body of evidence that suggest alternative spatial-temporal models for how humans have influenced their environment. These include phenomena such as constructed clam gardens, which increase shellfish productivity (Deur et al., 2015; Groesbeck, Rowell, Lepofsky, & Salomon, 2014; Smith et al., 2019), anthropogenic fires during the Holocene, which increase floral and faunal biodiversity (Hoffman et al. 2016), terrestrial deposition of shell middens which enhance forest productivity, expressed through forest height, width and greenness (Trant et al. 2016), increases of the presence of cultural important plants (Fisher et al. 2019), and an increased abundance of culturally important trees near archeological sites in the Amazon as a result of ancient plant domestication (Levis et al. 2017). A better understanding of these ecological legacies, or effects of past human mediation, is imperative in the understanding of current and future ecosystem functioning through providing a more accurate baseline to assess patterns and process (Swetnam, Allen and Betancourt, 1999).

Marine-derived nutrient loading to near-shore vegetation is a well documented phenomenon, often seen through nitrogen loading via salmon carcases (Ben-David et al. 1998,

Hilderbrand et al. 1999). These marine-derived subsidies can act as fertilizers on riparian zones and enhance their productivity and alter vegetative community structure (Bartz and Naiman 2005, Hocking and Reynolds 2012). Similarity, anthropogenically-mediated nutrient inputs, such as the accumulation of charcoal and shell middens, have altered soil chemistry in habitation sites across North America (Vanderplank et al. 2014, Cook-Patton et al. 2014, Hoffman et al. 2016, Fisher et al. 2019). For example, the accumulation of shell middens, which are composed of bivalve shells, bones, plant remains, and rich organic soils, result in the deposition of large amounts of calcium (Ca) and phosphorous (P) in systems where they might not be readily abundant (Cook-Patton et al. 2014), leading to higher nutrient levels and less acidic soils on habitation sites compared to the surrounding forest (Trant et al. 2016). Increased levels of nutrients have varying ecological impacts depending on the ecosystem affected; locations such as wetlands or tundra communities have shown decreases in plant diversity (Theodose and Bowman 1997, Bedford et al. 1999), whereas semi-arid environments can experience increases in plant diversity (Perroni-Ventura et al. 2006). Forest community composition in ecosystems containing shell middens have shown that community assemblages on these sites tend to be more diverse and structurally complex then the surrounding matrix (Cook-Patton et al. 2014, Fisher et al. 2019).

The west coast of British Columbia is a place of cultural and ecological importance to the Indigenous peoples who have been occupying the landscape for over 14,000 years (McLaren et al. 2015). Long-term intergenerational occupation of these lands has led to a variety of landscape level modifications, including the development of shell middens that have resulted from sustained resource-use of the intertidal environment (McLaren et al. 2015) and is tied to the intertidal resource dependency of the Indigenous peoples (Sawbridge and Bell 1972, Deur et al.

2015). Shell midden deposits, often found along the shorelines of costal regions, can be used alongside other unique landscape features, such as clam gardens or estuarine root gardens, to locate previously occupied habitation sites - places of repeated, long-term, or high occupancy human settlement (McLaren et al. 2015). While occasional resource-use at these habitation sites still occurs, the overall intensity of resource-use has significantly decreased since the mid-1800s (McLaren et al. 2015) thus habitation sites, which were once mostly cleared of vegetation, have since been colonized by western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) . Previous dendrochronology work with western redcedars on habitation sites have dated adult species to be over 150 years old, representing a climax community typical of this region (Banner et al. 2005)

Western hemlock and western red cedar form the dynamic climax community present at lower altitudes in the Great Bear Rainforest (Banner et al. 2005). This region is dominated by old-growth forests where gap dynamics and fine-scale canopy gap disturbances dictate forest turnover (Daniels 2003). Post-disturbance interspecies competition for these fine-scale canopy gaps are often dominated by western redcedar and western hemlock seedlings due to their efficiency in both low light and nutrient environments (Messier 1993, Brown et al. 1996, Canham, LePage, & Coates, 2004, Lacourse 2005). Local climatology and microclimates often act as limiting factors for seedling recruitment as the local topography of these coastal sites is often highly complex, leading to high levels of variation between soil and air temperature of the understory (Banner et al., 2005). Coarse woody debris, henceforth referred to as nurse logs, often offers a plant habitat in this system, allowing seedlings an opportunity to germinate without the cover of dominant understory vegetation such as *Gaultheria shallon* (Salal) (Harmon and Hua 1991).

In this paper, we seek to quantify the effect of shell middens on the composition of old-growth forests in the Central Coast of British Columbia by addressing the following four questions: 1) How has the presence of shell middens impacted the diversity of adult old-growth forest stands on habitation sites? We hypothesized that adult tree species assemblages will be more diverse on habitation sites, as previous work with shell-middens have found the herbaceous layers to be more diverse than surrounding areas through increased availability of nutrients (Fisher et al. 2019). Furthermore, positive correlation between tree species diversity and shrub diversity resulting from increased soil pH have been seen in temperate systems (Vockenhuber et al. 2011). 2) How has presence of shell middens altered the diversity of seedlings that have recruited on habitation sites? We again hypothesized an increase in recruitment diversity as shell middens tend to increase vegetative diversity more generally. 3) How has the presence of shell middens affected adult tree species height or Diameter at Breast Height (DBH)? Previous work has shown that western redcedar on habitation sites are both taller and wider than those found in surrounding areas (Trant et al. 2016). Our study builds on these findings by quantifying these phenomena for all adult species present within plots in both habitation sites and the surrounding area and we hypothesized that our results would be similar to those found in previous studies. 4) Finally, what role does coarse woody debris – fallen trees that act as seed beds, henceforth known as nurse logs – play in forest regeneration? Given the high density of shrubs and ephemerals in the forests understory, it is predicted that nurse logs will act as the primary substrate for seedling germination due to less access to light on the forest floor (Harmon and Hua 1991). Past studies have focused primarily on either herbaceous diversity, the presence of culturally important species, or a mix of herbaceous and woody diversity. To our knowledge, this study is the first to exclusively study the woody plant diversity and community composition of

these habitation sites. In doing so, we are able to quantify ecological legacies within the Great

Bear Rainforest to gain a better understanding how ancient human settlements have shaped these

lands.

## 2.0 Methods
## 2.1 Study Area

All data collection was performed in the Hakai Lúxvbálís Conservancy on Calvert and Hecate Islands within the Great Bear Rainforest. The Great Bear Rainforest is a 6.4 million-hectare temperate rainforest along the coast of British Columbia within the Pacific temperate rainforest ecoregion (N 51° 38′–W 128° 05′). The study sites are located within the Coastal Western Hemlock zone (CWH) which is characterized by a high annual rainfall (1000 to 4400 mm), a cool mesothermal climate and poorly drained organic soils (Gessel et al. 1973, Meidinger and Pojar 1991, Prescott et al. 2000, Richardson et al. 2004). Within this regions lies the Very Wet Hypermaritime zone (CWHvh), a sub-variant of the Coastal Western Hemlock zone (CWH) classified by its continentality and precipitation (Meidinger and Pojar 1991, Banner et al. 2005). This zone is dominated by western redcedar and western hemlock stands that are situated on high-water tables with low nutrients and poor drainage. (Banner et al., 2005; Messier, 1993). However, other species such as yellow cedar (*Cupressus nootkatensis*), Sitka spruce (*Picea sitchensis*), Pacific yew (*Taxus brevifolia*), and shore pine (*Pinus contorta*) can also be found in these areas (Spies and Franklin 1989, Klinka et al. 1996).

High levels of precipitation and poor soil drainage often limit the occurrence of natural understory fires, such that this system experiences few large-scale disturbances of this type (Hoffman et al. 2016). However, the Pacific Northwest (PNW) often experiences high intensity windstorms via the Pacific Decadal Oscillation that can influence coastal tree growth (Knapp and Hadley 2012). While lightening seldomly causes fires within the PNW, there is evidence of controlled burning on habitation sites from Indigenous communities that have led to an elevated level of charcoal within the naturally nutrient-poor soil (Hoffman et al. 2016).

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Calvert and Hecate islands contain four different types of vegetative areas that vary altitudinally and are classified based on dominant species (Banner et al. 2005). All habitation and control site samples were taken from the zonal forest, the highly productive riparian interface between the coast and the bog forest further upland. Given their close proximately to the intertidal region it allowed for altitudinal parameters to remain relatively constant.
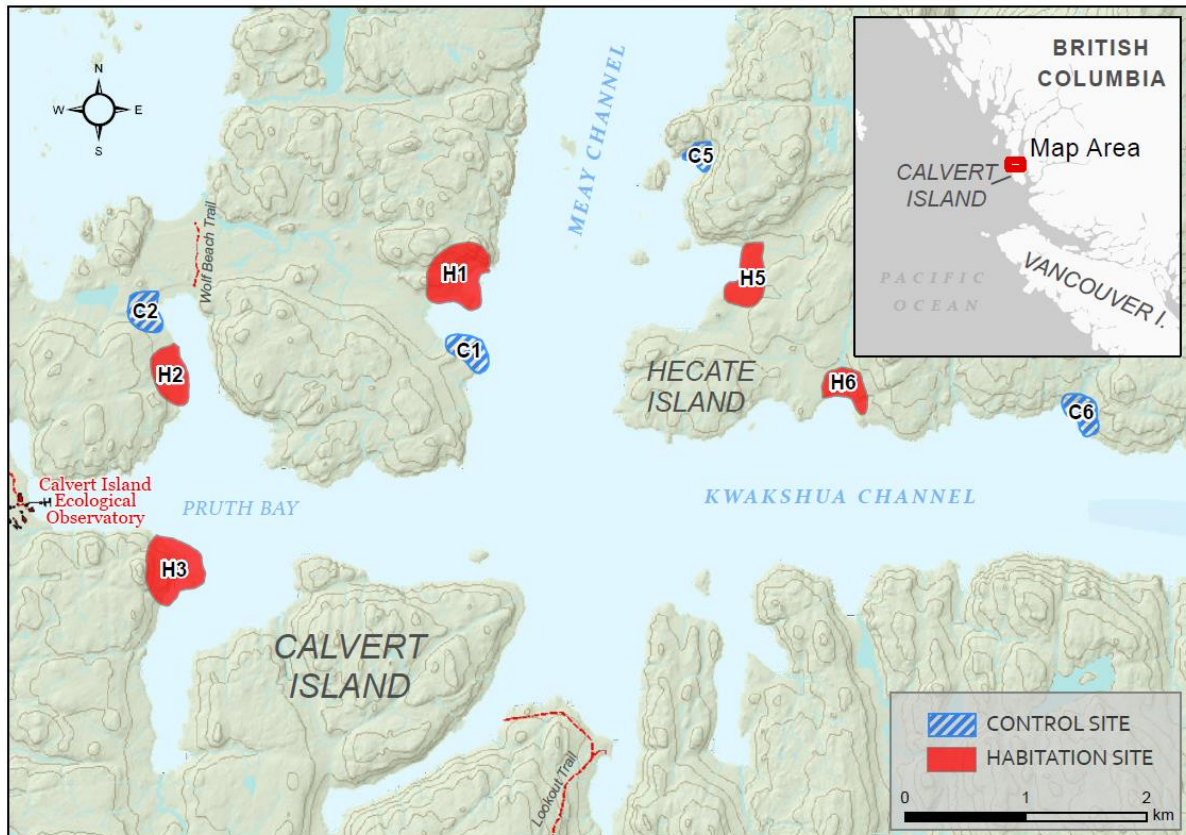


Figure 1: Map of Calvert and Hecate Islands showing habitation (red polygons) and control sites blue hashed polygons).

## 2.2 Field Samples

Five habitation and four control sites (Fig. 1) were chosen based on several criteria. Habitation sites were identified using a combination of archeological and ecological data that contain strong evidence of past human settlement. Archeological data includes soil augers containing shell middens, artifacts, and human remains, while ecological evidence includes

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culturally modified trees (western redcedars with scars from bark stripping) and the presence of elevated charcoal levels in the soil (McLaren et al. 2015, Hoffman et al. 2016). Control sites were chosen based on proximity and ecologically relevant parameters, such as aspect and slope, to reflect the conditions of the habitation sites while having no evidence of the previously mentioned anthropogenic affects. Within each site, three 11.28 m radius plots, roughly 400 $m^2$, (Fig. 2) were established, with the exception of two treatment sites that contained only two plots due to the smaller extent of shell midden at this site. 11.28 m plots were chosen as the larger area compared to 200 $m^2$ and 30 $m^2$ allows for more accurate estimations from remote sensing estimations (Næsset et al. 2015). The edge of one plot was positioned at least 10 meters apart from the edge of the next, and at least 10 meters from the forest edge to avoid any confounds from edge effects such as top die back and increased light penetration. Altogether, we had 13 plots nested within five habitation sites and 12 plots nested within four control sites. The initial plot locations at each site chosen using stratified random subsampling with the use of GE path (v1.4.6) to superimpose a square grid onto imagery in Google Earth Pro (v.7.3.1.). Grid lines were set at 2.5 m and were positioned over locations of known shell middens for habitation sites. Any 2.5 m by 2.5 m quadrat that landed outside of the suspected shell midden boundaries, or only partially covered the suspected shell midden boundaries were excluded from sampling eligibility. All remaining quadrats were then assigned a number and using a random number generated in R (v3.6.2), where three numbers were chosen to represent locations that were sampled. The Universal Transverse Mercator (UTM) at the center of each quadrat was determined using Google Earth Pro so that the locations could be found in the field. Within each quadrat, all living adult species (>7.5 DBH) were tallied and had their height and DBH measured (Fig. 2).

Five 4m x 1m regeneration sub-plots were established within the plots to capture all seedling and saplings (<7.5 DBH) within them (Fig. 2). At the center of each regeneration plot, digital cover photography, which captures a straight vertical field of view, was used to determine canopy cover. Each photo was taken with a Sony Cyber-shot DSC-RX100 Digital Camera with a 35 mm equivalent lens mounted on a tripod. All photos were taken 1-meter off the ground and balanced using a hand-held level with the top of the frame facing uphill from the coastal line. Both the exposure and shutter speed settings were automated by the camera. All photos were recorded in the JPEG format with a resolution of 5472 x 3648 pixels. Analysis of photos was done in GIMP v 2.10 using the Select by Colour tool to identify all between canopy gaps. Limited access to these remote sites resulted in some photos being taken without an overcast sky, thus causing some photos to be taken during broad daylight which may result in an underestimate of canopy cover.

Aspect and slope were obtained using LiDAR data captured by Terra Remote Sensing Inc. of both Calvert and Hecate island in 2012. Climatic variables were not included as the high-resolution climate data required to accommodate the close proximately of our sampling sites is unavailable for our study location. Due to the cultural sensitivity of these lands no soil data was available for collection on habitation sites.
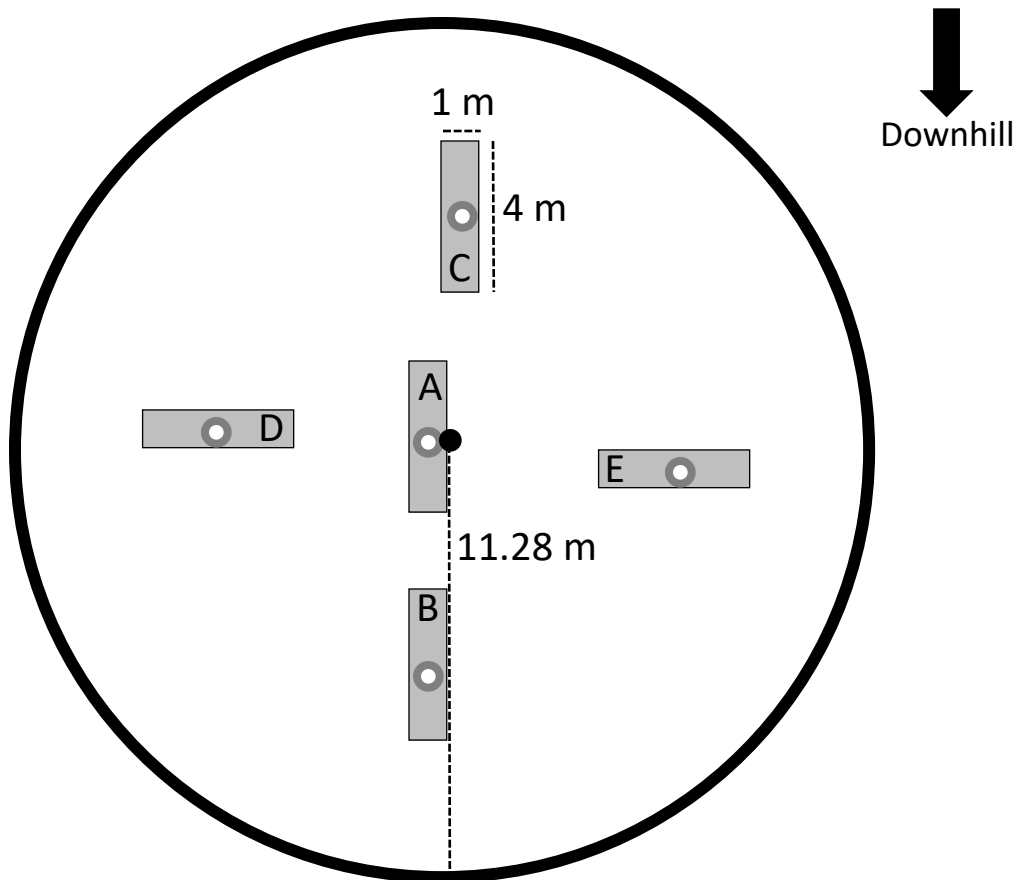
Figure 2: Sample plot design used to generate species inventories. The outer ring represents the 11.28 m radius outer boundaries of the plot. 11.28 m radius were chosen as the total area covered is 400 m². Gray rectangles represent regeneration sub-plots labelled in order of assessment. Grey circles with white centers represent canopy photographs take taken 1-meter off the ground with the top of the frame facing uphill.

2.3 Statistical Analysis

Species composition was characterized using two diversity indices to capture any variation between habitation and non-habitation sites. The first used was Shannon-Weiner index (Shannon's H), the most commonly used metric that explores the relationship between species

richness and evenness that places less weight on dominant species (Jost 2006, Tuomisto 2012, Zhang et al. 2012). The next index used was Simpson's reciprocal D, which considers both species richness and evenness while weighing dominant species. A value for both indices was generated for each plot (n=25). Having sampled in a system with low diversity, the use of multiple indices may elucidate patterns that may not be captured using a single metric. All analysis were done using R statistical software v.3.6.5 (R core team 2019). Shapiro-Wilk tests were conducted to test for normality of our response variables. All models had their residuals plotted against fitted and visualized using the Q-Q plot function in R.

For adult tree communities, indices of Shannon's H' and Simpson's reciprocal (1/D) in the form of a continuous variable modeled against treatment type (habitation or control site), a two-level categorical variable, using a one-way nested Analysis of Variance (ANOVA) a type of Generalized Linear Model (GLM) where individual plots were nested within treatment type. Both Shannon-Weiner's H' and Simpson's reciprocal (1/D) values were obtained using the 'vegan' package (Oksanen et al. 2007). Only one model was generated for both indices, so no model comparison was performed.

For seedling data, the same response variables (diversity indices of Shannon's H' and Simpson's reciprocal [1/D]) were used modeled against treatment type and canopy cover using one-way nested ANOVA's where our plots were nested within treatment type. Canopy cover was treated as a categorical variable where percent cover was assigned one of four bins (0-24%, 25-49%, 50-74%, 75-100%).

Dissimilarities between both adult and regenerative communities were determined using a nested Permutational Multivariate Analysis of Variance (PERMANOVA) with the 'BiodiversityR' package in R (Kindt 2005). Bray-Curtis coefficients were used to calculate

community density matrices of all sites (s = 6). To account for the hierarchical nature of our data, a nested PERMANOVA can factor in the non-independence of our data collection. 999 permutations were performed where two fixed factors, treatment type and site, were included in the nested PERMANOVA. A single model was generated for both adult and seedlings and no model comparisons were performed. Community compositions were then visualised using non-metric multidimensional scaling (nMDS). Finally, SIMPER analysis was performed using the 'vegan' package in which the contribution of species contribution to the community dissimilarity was determined. The average dissimilarity between each species to the standard deviation of the dissimilarities were measured as (Diss/SD) to elucidate which species are consistently contributing to community dissimilarity (Clarke 1993).

Forest stand structure data contained the two continuous variables height (m) and diameter at breast height (DBH) (cm) for each adult tree sampled (n=835). Both were modelled against treatment type and site (five treatment and four control) using Generalized Linear Mixed Model's (GLMM), where plot was fitted as a random intercept using the 'lme4' package in R (Bates, D, Sarkar, D, Bates, M. D, & Matrix, L, 2007). Given a single value was collected at each site for slope and aspect they're represented through the inclusion of site as a fixed effect. Thus, the inclusion of site will delineate any variation between sites that will be overlooked if excluded from the model. Western redcedar and western hemlock analysis was fit with a Gamma distribution, as model residuals demonstrated a positive right skew; Sitka spruce was fit with a Gaussian distribution as plotted residuals fit the assumptions of normality. Aspect was transformed using a cosine transformation where $x = -1\cos[\theta\left(\frac{\pi}{180}\right)]$, where $\theta$ is the aspect angle in degrees to account for the issues associated with comparing aspect in degrees (Whittington et al. 2005). After transformation, values closer to 1 represent aspects better aligned

to receive maximum solar radiation while those closer to -1 represent areas of lower solar radiation (Whittington et al. 2005). A tukey multiple comparisons post hoc test was performed using the glht function from the 'multcomp' package in R on any significant interactions of our fixed treatment effect (Hothorn, Bretz and Westfall, 2008). A single model was developed for each species tested for both height and DBH. Thus, no model selection was performed.

Finally, to test for the establishment preference of seedlings, species were tallied and counted as either establishing on a nurse log or the forest floor as count data. The amount of space occupied by the nurse logs within the four by one-meter plots was also determined as the percent of plot occupied by nurse logs. However, due to time constraints this data was only collected by six of nine sites. Generalized Linear Models (GLM) fitted to a Poisson distribution were performed, where seedling counts were modeled against location (nurse log or forest floor) and treatment type.

## 3.0 Results

Overall, the results of this study showed there was no significant difference of diversity indices between habitation and control sites. There was no statistical differences between the average height or DBH of all species examined on habitation and control sites. While significant differences in community composition were detected for adult species between treatment type, this response was not seen in seedlings. Finally, there was significantly more seedling recruitment on nurse logs than on the forest floor.

### 3.1 Community analysis

Six different species of adult trees (western redcedar, western hemlock, Sitka spruce, yellow cedar, Pacific yew and shore pine) were found across all sites while only five different species of seedling were encountered (western redcedar, western hemlock, Sitka spruce, Pacific yew and shore pine). When looking at adult species composition, there was no significant difference between habitation and control sites for both Shannon-Weiner's H' (F = 4.23, P = 0.07, Fig 3a) and the reciprocal of Simpson's D (1/D) (F = 2.56, P = 0.15, Fig 3b).

Significant differences at the community level were detected following a nested PERMANOVA analysis, where there was significant dissimilarity between habitation sites and control sites (F = 9.13, p = 0.008) following 999 permutations. nMDS plots (Fig. 4) had a stress of 0.07, indicating a good model fit between habitation and control sites (Clark 1993). The SIMPER analysis (Table 1) elucidated that habitation sites were 34.64% dissimilar to control sites. The largest contributors of this dissimilarity between treatment types were western hemlock (Diss/SD = 1.55) and western redcedar (Diss/SD = 1.35). The average density of western hemlocks and western redcedars on control sites were 193% and 165% higher than on

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habitation sites and contributed over 75% of the total cumulative dissimilarity seen between communities (Table 2). Sitka spruce also contributed regularity to community dissimilarity despite a low density on both habitation and control sites.
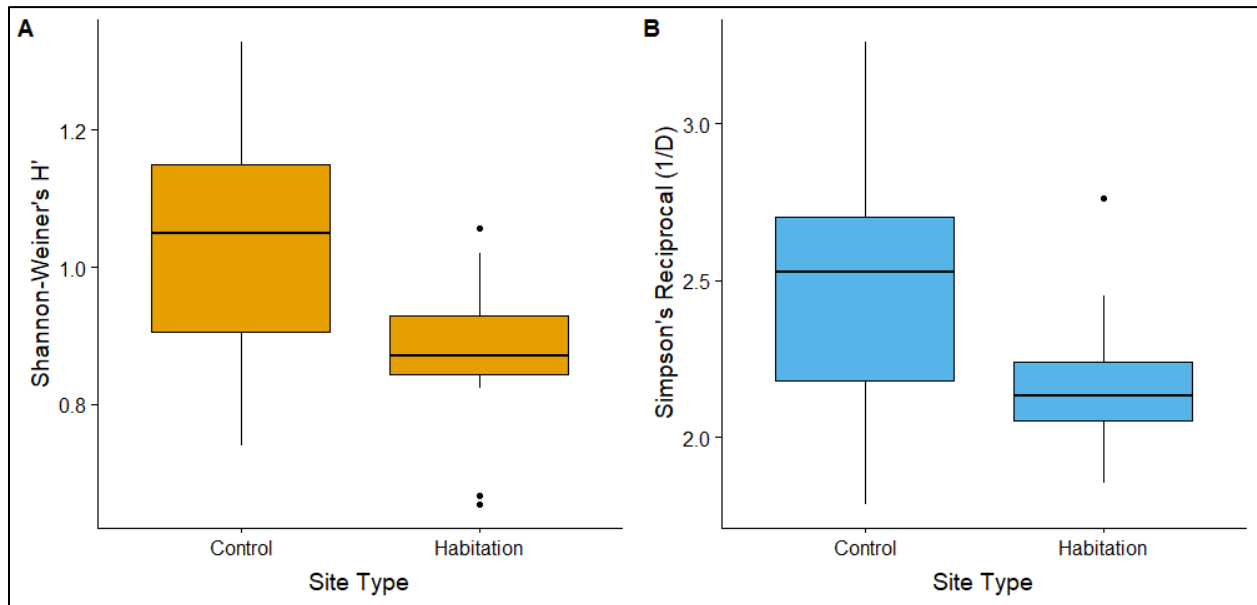


Figure 3: Box and whisker plot comparing, A) Shannon-Weiner's H' and B) Simpson's reciprocal (1/D) between control sites and habitation sites (n = 9). Outliers are represented as black dots and represent samples that are >1.5 times the interquartile range. There was no statistical significance for either Shannon-Weiner's H' (F = 4.23, P = 0.07), or Simpson's Reciprocal (1/D) (F = 2.56, P = 0.15).

Figure 4: nMDS plot (stress 0.07) of adult community composition between control (Red polygons) and habitation (Green polygons) sites. Each point represents a plot, with plots of similar shapes being from the same site.

Table 1: Similarity Percentage (SIMPER) table showing the dissimilarity contributions of each species found on habitation and control sites for adults. A Diss/SD value > 1 represent species that regularity contribute to community dissimilarity while a Diss/SD value < 1 represent those which contribute little. The average dissimilarity between habitation to control sites was 34.64%.

| Species | Average Density | Average Density | Average Dissim. (%) | Diss/ SD | Cont. (%) | Cum. Dissim. (%) |
|---|---|---|---|---|---|---|
| | Control | Habitation | | Total Average Dissimilarity = 34.64% | | |
| Western hemlock | 21.83 | 11.15 | 13.65 | 1.55 | 39.41 | 39.41 |
| Western redcedar | 25.25 | 15.30 | 12.65 | 1.35 | 36.52 | 75.93 |
| Yellow cedar | 3.58 | 0.00 | 3.85 | 0.87 | 11.12 | 87.05 |
| Sitka spruce | 2.92 | 2.23 | 2.97 | 1.13 | 2.97 | 95.63 |
| Pacific yew | 0.75 | 0.46 | 1.02 | 0.98 | 1.40 | 98.60 |
| Shore pine | 0.5 | 0.00 | 0.4 | 0.42 | 0.00 | 100 |

Seedling species diversity showed the opposite visual trend of our adult species composition, with diversity being higher on habitation sites. However, these patterns were not significant (Fig. 5). There was no significant difference in Shannon-Weiner's H' (F = 2.85, P = 0.17, Fig 5a) or Simpson's Reciprocal (1/D) (F = 2.69, P = 0.15, Fig 5b) between habitation and control sites. Canopy cover was also an insignificant factor for Shannon-Weiner's H' (F = 0.081, P = 0.78) or Simpson's Reciprocal (1/D) (F = 0.16, P = 0.70).

There was no significant differences found at the community level between control and habitation sites (F = 1.55, p = 0.24) following 999 permutations. nMDS plots (Fig. 6) had a stress of 0.04, indicating a good model fit. SIMPER analysis (Table 2) demonstrated that habitation sites were 36.66% dissimilar at the community level. The largest contributors to dissimilarity in seedling composition between treatment types were western hemlock (Diss/SD = 1.37) and western redcedar (Diss/SD = 1.48). The average density of western hemlocks was slightly lower on habitation sites while average western redcedar density was 169% higher on habitation sites (Table 2). Both western hemlock and western redcedar contributed over 75% of the total dissimilarity seen between communities. While the average density of Sitka spruce was 388% higher on habitation sites these results should be interpreted with caution as their average densities were low on both control and habitation sites.
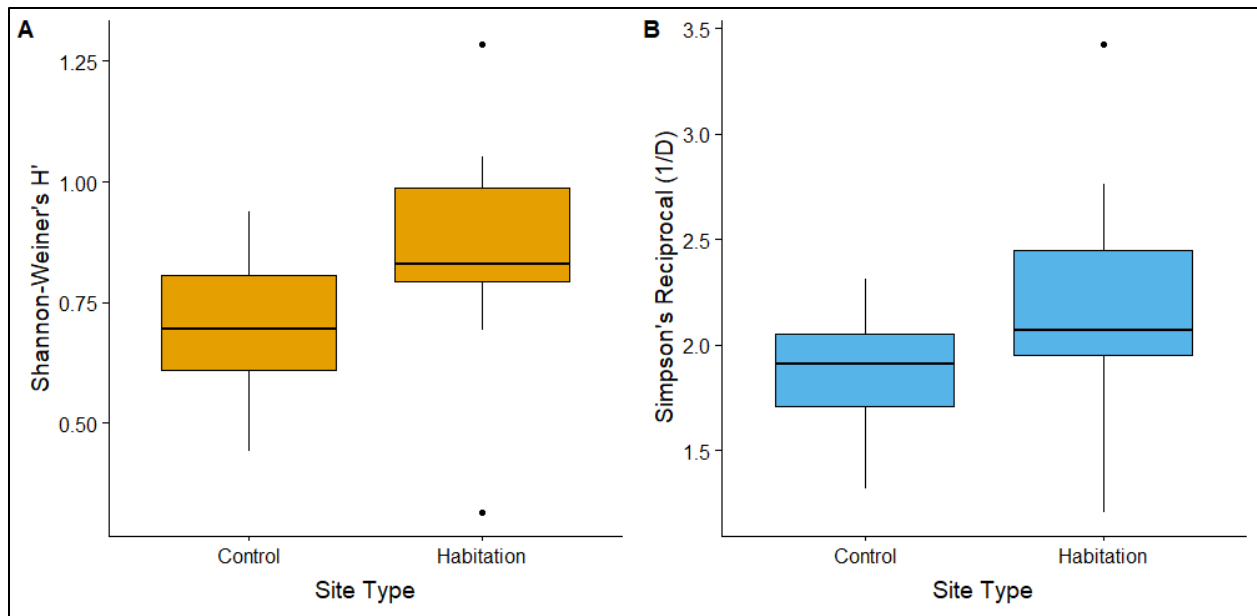
Figure 5: Box and whisker plot comparing seedling diversity using, A) Shannon-Weiner's H' and B) Simpson's reciprocal (1/D) indices between control sites and habitation sites (n = 9). Outliers are represented as black dots and represent samples that are >1.5 times the interquartile range. There was no statistical significance for either Shannon-Weiner's H' (F = 2.85, P = 0.17) or Simpson's Reciprocal (1/D) (F = 2.69, P = 0.15).
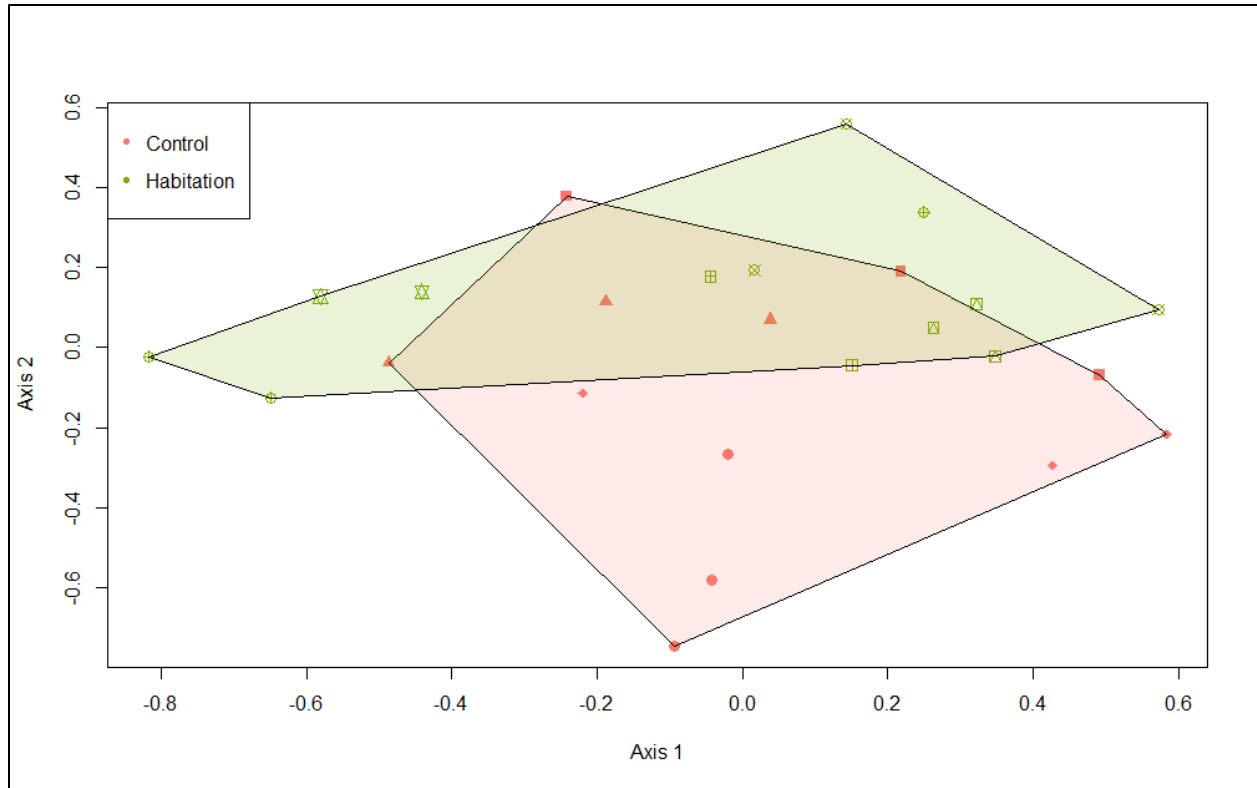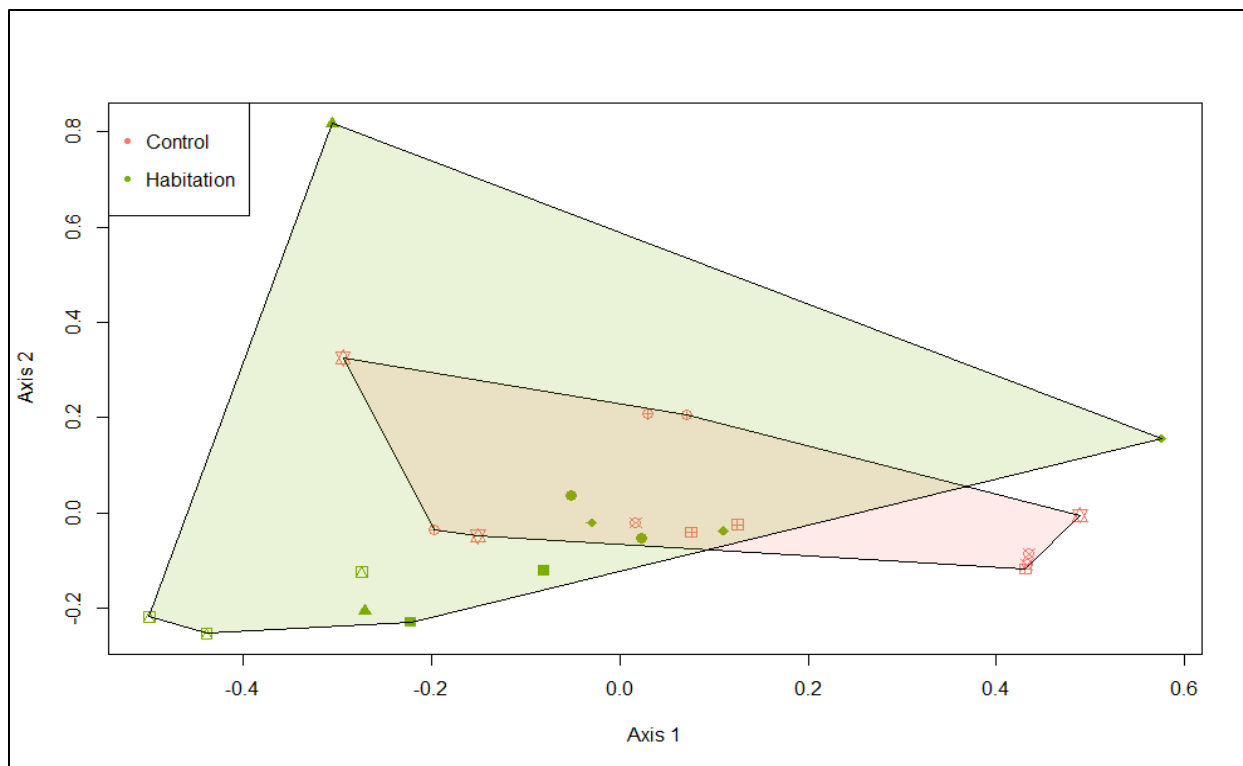
Figure 6: nMDS plot (stress 0.04) of seedling community compositions between Control (Red polygons) and habitation (Green polygons) sites. Each point represents a plot, with plots of similar shapes being from the same site.

Table 2: Similarity Percentage (SIMPER) table showing the dissimilarity contributions of each species found on habitation and control sites for seedlings. A Diss/SD value > 1 represent species that regularity contribute to community dissimilarity while a Diss/SD value < 1 represent those which contribute little. The average dissimilarity between habitation to control sites was 36.66%.

| Species | Average Density | Average Density | Average Dissim. (%) | Diss/ SD | Cont. (%) | Cum. Dissim. (%) |
|---|---|---|---|---|---|---|
| | Control | Habitation | | Total Average Dissim. = 36.66% | | |
| Western hemlock | 29.92 | 25.33 | 16.78 | 1.38 | 45.78 | 45.78 |
| Western redcedar | 13.83 | 23.42 | 15.00 | 1.49 | 40.90 | 86.68 |
| Sitka spruce | 1.33 | 5.08 | 4.69 | 0.94 | 12.79 | 99.47 |
| Pacific yew | 0.00 | 0.08 | 0.11 | 0.29 | 0.29 | 99.76 |
| Yellow cedar | 0.08 | 0.00 | 0.00 | 0.29 | 0.24 | 100 |

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## 3.2 Forest Structure

Due to yellow cedar and lodgepole pine only being present on control sites they were omitted

from structural analysis. Despite Pacific yew being present on both habitation and control sites,

we were unable to obtain model convergence due to low sample size (n=10). (Table 3) shows

summary statistics for each model produced for western redcedar, Sitka spruce and western

hemlock. (Figure 7 & Figure 8) are boxplots that provide a visual representation of the spread of

data for height and DBH respectively.

Table 3: Generalized Mixed Model (GLMM) results for height and DBH for all tested species.
Treatment and site were treated as fixed effects while plot was treated as a random effect. p-
values represent the statistical power of the treatment fixed effect. A Tukey multiple
comparisons post hoc test was performed on the western redcedar DBH model, yet the results
were non-significant (Est = 5.11, z = 1.59, p = 0.11). Only one model was created for each
species per category, thus no model comparison was performed.

| Species | Model | Estimate | Std. Error | p-value |
|---|---|---|---|---|
| **A) Height** | | | | |
| Western redcedar | Height ~ Treatment + Site + (1\|plot) | -2.55 | 0.51 | 0.11 |
| Sitka spruce | Height ~ Treatment + Site + (1\|plot) | 5.21 | 0.94 | 0.32 |
| Western hemlock | Height ~ Treatment + Site + (1\|plot) | -0.42 | 0.94 | 0.66 |
| **B) DBH** | | | | |
| Western redcedar | Height ~ Treatment + Site + (1\|plot) | 19.32 | 7.00 | 0.11 |
| Sitka spruce | Height ~ Treatment + Site + (1\|plot) | 16.93 | 6.96 | 0.22 |
| Western hemlock | Height ~ Treatment + Site + (1\|plot) | -2.09 | 0.70 | 0.30 |
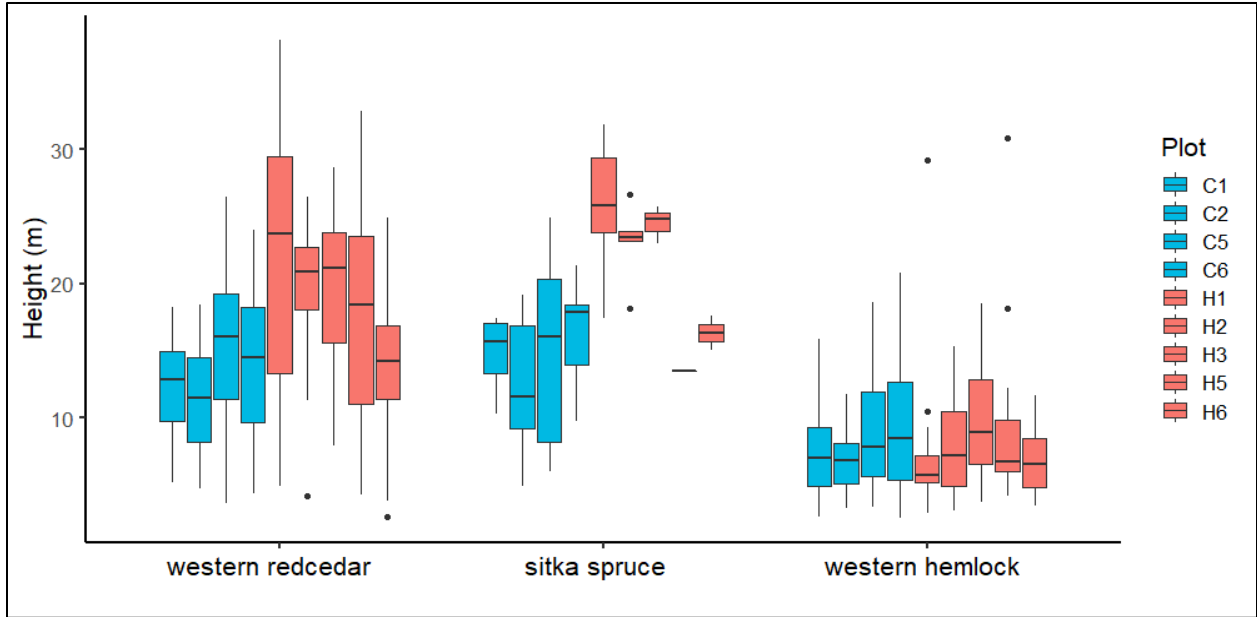
Figure 7: Box and whisker plot showing tree height in meters of western redcedar, Sitka spruce and western hemlock on habitation sites (H1-H6) and control sites (C1-C6). Outliers are represented as black dots and represent samples that are >1.5 times the interquartile range.
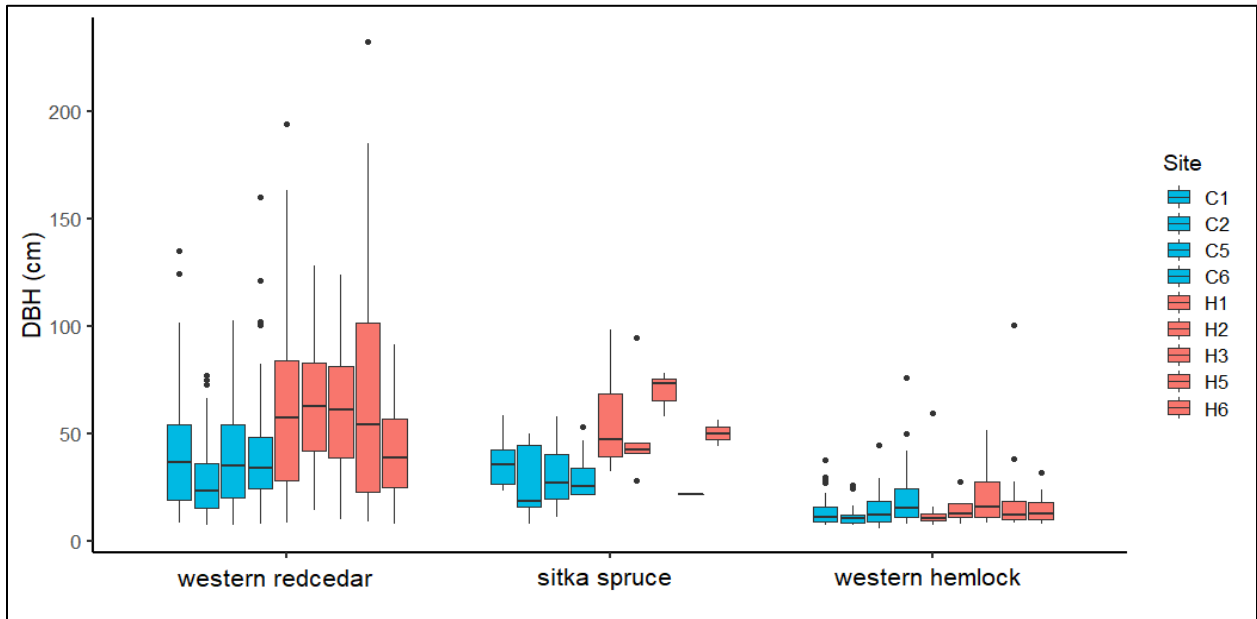


Figure 8: Box and whisker plot showing DBH in centimeters of western redcedar, Sitka spruce and western hemlock on habitation sites (H1-H6) and control sites (C1-C6). Outliers are represented as black dots and represent samples that are >1.5 times the interquartile range.

## 3.3 Nurse Log

Nurse log coverage differed only slightly between treatment type, with control sites having 19.55% ± 2.14% coverage while habitation sites had 23.43% ± 3.33% coverage within regeneration plots. There was significantly more seedling recruitment on nurse logs than on forest floors (Est = 2.13, Z = 22.86, P < 0.01), and there was a significantly higher recruitment of seedlings on nurse logs within habitation sites compared to control sites (Est = 0.12, Z = 2.00, P = 0.04).
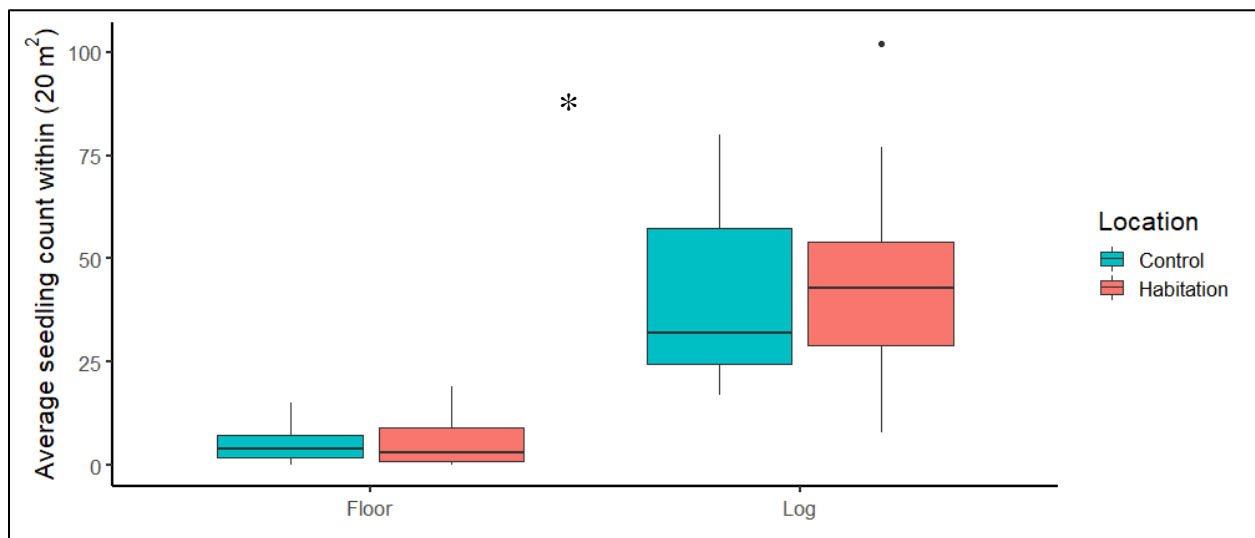


Figure 9: Boxplot showing the total number of seedlings found on nurse logs versus the forest floor. Pink boxes represent treatment sites while blue bars represent control sites. Outliers are represented as black dots and represent samples that are >1.5 times the interquartile range. * denotes a significant difference between locations (Floor and Log). There was significantly more seedling recruitment on nurse logs then on the forest floor (Est = 2.13, Z = 22.86, p < 0.01). Nurse logs made up on average 23.43% ± 3.33 of the forest floors on habitation sites vs 19.55% ± 2.14 on control.

## 4.0 Discussion

The presence of shell midden deposits provide a unique opportunity to understand how these persistent effects may impact above ground vegetative community composition and structure. Our results show that while long term year-round occupation of habitation sites by Indigenous communities have had some influence on community dynamics, there were more similarities between habitation sites and control sites then differences.

The results of our diversity analysis fail to support our first two hypothesis' in which there was no significant difference in diversity between habitation and control sites. The lack of difference in diversity between habitation and control sites is in contrast to previous work, where species richness was often higher on sites with shell middens compared to surrounding areas (Vanderplank et al. 2014, Fisher et al. 2019). However, these previous studies have only focused on the herbaceous layer of these systems. In studies of both woody and herbaceous composition, a decrease in woody species abundance was detected as a result from a shift towards a more diverse herbaceous composition due to anthropogenic nutrient inputs (Cook-Patton et al. 2014). Increased forest productivity on shell middens resulting in reduced, or a unimodal pattern of diversity is documented among both the herbaceous layer (Gough et al. 2000, Rajaniemi 2002), and the woody layer (Trant et al. 2016). The two species found only on control sites, yellow cedar and shore pine, had little affect on the overall diversity of this system as their representation was relatively minor compared to the dominance of western redcedar and western hemlock. Despite our results being nonsignificant, the idea of varied diversity may of interest to future studies seeking to use variables, such as soil characteristics or high-resolution climate data unavailable to this study. However, it should be noted that given the low species richness values

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(n=6) detected across all sites that ecolgcal relevance of such inferences may be difficult to interpret should a statistically significant signal be detected.

The results of our comparisons of community dissimilarity via nested PERMANOVA showed that habitation sites were significantly dissimilar to control sites despite sharing nearly all species present between sites. A SIMPER analysis eluded to difference this by showing that over 75% of the cumulative community dissimilarity was being represented by both western hemlock and western redcedar as a result of the changes in their densities. These differences where seen via the overall reduction in stem density on habitation sites as opposed to variations in species composition, most prominently detected in western hemlock and western redcedar given their contributions. However, overall community dissimilarity was low (around 36%) as western hemlock and western redcedar, the dominant species, were seen on all habitation and control sites. This in combination with the low species richness of the zonal coastal forest could likely result the lower dissimilarity value seen in this study. Differences in community structure presented here between habitation and control sites could also be as a result of differences in stand age or successional stage; however, tree core samples taken from habitation sites in our study area have documented western redcedars to be over 150 years old (A Trant, personal communication, October 8,2019), representing a mature forest stand. Therefore, we would argue that the successional stage is similar to the surrounding forest matrix and that our results are due to nutrient inputs facilitated by the presence of middens. However, the models used to derive these inferences were of the simplest form, and lacked features, such as climatic variables, that may influence composition beyond the effects of shell middens.

Similar to adults, both western hemlock and western redcedars seedlings made up over 85% of the community dissimilarity from changes in density. This inverse relationship between a

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reduced western redcedar adult density on habitation site and increased seedling density is of particular note given their limited dispersal range compared to western hemlocks and Sitka spruce (Minore 1990). While regeneration in this system is primarily driven by gap-forest dynamics, we found little difference in canopy cover between control and habitation sites. However, given the differences in stem density between habitation and control sites, complex canopy differences, such as angular light penetration, that were undetectable within our study design could be present. The ability of western redcedar seedlings to establish in higher density on habitation sites may be a result of these differences and should be the focus of future studies within this system.

The results of our structural data failed to support our third hypothesis that adult species growing on habitation sites would be both significantly larger and wider than those growing on control sites. The variation among sites was a more prominent signal than the variation between treatments. A potential cause for the high level of variation between sites is the depth of the shell midden. While shell midden depth was not explored in this study, previous research found forest productivity, measured by height and greenness, to be correlated to shell midden depth in which the deepest middens contained the most productive forest stands (Trant et al. 2016). Differences in sampling and methodology may explain these differences, as this previous study only looked at the tallest trees on habitation and control sites. There is also evidence to the contrary, where in another study along the Rhode River in Maryland found that trees found on shell middens had significantly smaller DBH compared to those on surrounding sites (Cook-Patton et al. 2014). These inconsistences between studies may be the result of differences in methodology, systems examined, or breadth of variables explored. For example, the variability in species-level responses between specific sites may be due to interspecific competition for N and P. Soils on

habitation sites are less acidic then those in surrounding areas which have been shown to decrease soil C:N ratios and elevate rates of N mineralization, leading to an increase in the availability of useable N for above ground vegetation (Fisher et al. 2019). An exploration into the relationships between elevated rates of N mineralization and shell midden depth may be of interested to future studies

It is unsurprising that nurse logs in temperate rainforests are the primary substrate for seedling recruitment and forest regeneration. Our findings supported our fourth hypothesis, and are consistent with past work in the Pacific Northwest where nurse logs contained over 94% percent of Sitka spruce and western hemlock seedlings (Graham and Cromack. Jr. 1982). Of note, while nurse logs are the primary substrate for recruitment, they occupy less than 30% of the forest floor within our study plots, similar to other studies within the Pacific Northwest (Graham and Cromack. Jr. 1982, Christy and Mack 1984). Despite nurse logs containing fewer nutrients than surrounding soils (Takahashi et al. 2000), they allow for a competitive advantage for light by avoiding shading from the herbaceous layer. However, the advantages provided by a greater access to light come at a cost, as previous work has documented an increase in mortality rates associated with seedling established on nurse logs (Harmon et al., 1986).

The results of this study are in contradiction of several previous studies, in which no differences in stand diversity or structure was seen between habitation and control sites. A closer look at adult forest stands on habitation sites within the Great Bear Rainforest have shown that there are community dissimilarities, however, they are only expressed by a decreased stem density on habitation sites as opposed to compositional differences. However, this is not to dissuade the notion that Indigenous practices have influenced their environment, but that these signals may not be ubiquitous in their strength and influence of ecosystem dynamics. Accounting

for the role that Indigenous practices played in governing landscapes is a practice we, as

researchers, should adapt as to account for any effects, as large or small they may be, that

influence their system.

# Chapter 3: Discussion and Future Directions

## Context:

The main goal of this thesis was to better understand in what capacity have shell middens influenced forest community structure on habitation sites in the Great Bear Rainforest. Overall, it was found that forest communities on habitation sites only differed slightly from the surrounding matrix when looking at diversity, dissimilarity and structure. We also found that seedlings primarily established on nurse logs as opposed to the forest floor. The data provided from this thesis provides the groundwork for my first overarching goal: To provide high-resolution tree community composition and structure within the Great Bear Rainforest In total, more than 1300 adult trees and over 2400 tree seedlings were measured to generate high-resolution data of species compositions and structure on Calvert and Hecate Islands.

The methodology employed differs from previous work in these systems, where a greater focus was put on the historic reconstruction of species populations and their successional turnover using pollen records and radiocarbon dating (Banner et al. 1983, Turunen and Turunen 2003, Galloway et al. 2009). Site level species composition data along coastal British Columbia has been gathered in the past near Prince Rupert Island. However, their study used Two-Way INdicator SPecies Analysis (TWINSPAN) to assess community compositions and placed a greater focus on vegetative dynamics and successional turnover (Banner et al. 2005). To my knowledge, the data presented here is the only other source of high-resolution species compositional data within this vast geographic area.

The second goal of this thesis was to contribute empirical evidence to a growing body of literature describing how Indigenous peoples have facilitated landscape level modifications through land-use and management. Within the context of British Columbia, this can be seen by

the work of David Sawbridge in the early 1970's, where it was found that shell middens altered soil qualities and vegetation (Sawbridge & Bell, 1972). Since then, work looking at how Indigenous communities have influenced their environment has increased tremendously, with researchers looking at clam gardens (Groesbeck et al. 2014, Deur et al. 2015, Toniello et al. 2019), anthropogenic fire history (Hoffman et al. 2016a, Hoffman et al. 2016b), and finally the impacts of shell middens on plant and tree communities (Trant et al. 2016, Fisher et al. 2019). While these previous studies found that Indigenous practices had large consequences on their environment, the results of this study only eluded to a weak signal expressed by communities on habitation sites in the form of reduced stand density on habitation sites.

## Implications

While it was initially hypothesised that habitation sites would have reduced diversity to the surrounding matrix, it was rejected as our analysis failed to achieve statistical significance. With the visual trend of (Figure 3; Chapter 2) of adult trees having reduced diversity on habitation sites, a larger sample size may have detected this. Forest communities having decreased diversity while being on more productive soils is consistent with Michael's Rosenzweig's 'Paradox of Enrichment', where increasing essential nutrients can destabilize system stability (Rosenzweig 1971). The way vegetative communities react to increases in nutrients is neither consistent in experimental manipulations nor in naturalised studies (Huston & McBride 2002). More recent theoretical and experimental literature has shown this paradox of enrichment isn't always the case, as increasing species richness can increase system stability and ecosystem function (Schwartz et al. 2000, Perroni-Ventura et al. 2006). A recent study within the Great Bear Rainforest demonstrated that an increase of nutrients resulting from shell middens led to species specific responses and an increase in culturally important plants (Fisher et al. 2019).

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These contradictory interpretations of the link between species diversity and ecosystem function may demonstrate the role that both geographic location and organisms of interest plays in the interpretation of this phenomenon.

The species-specific response of adult trees to the presence of shell middens in chapter two also raises some interesting questions and provides the opportunity for future studies. Western redcedar and Sitka spruce both had increases in height and DBH on habitation sites while western hemlock displayed no obvious physical differences. Competitive exclusion of western hemlock is one potential possibility as western redcedars, and western hemlocks may be better suited in nutrient rich environments. Previous work looking at silvicultural growth of western hemlock seedlings showed equally competitive responses to consistent and exponential increases in N fertilization (Hawkins et al. 2005). While in isolation western hemlocks are capable of increasing in biomass when exposed to elevated nutrient levels, that appears to not hold true in a competitive environment. To what degree, if any, that competitive exclusion is the driving force behind trends found in this study provides a strong foundation for future work.

Nurse logs being the primary substrate for seedling recruitment doesn't come as a surprise despite there being little literature regarding this phenomenon in the Pacific Northwest. Nurse logs can provide refuge from the wildly fluctuating elements of the forest floor such as soil depth, water table levels, fungal pathogens and understory vegetation (Harmon and Franklin 1989, O'Hanlon-Manners and Kotanen 2004). These role of microsite complexities on seedling survival within the Great Bear Rainforest is currently unknown, but previous work has shown that nurse logs may allow seedlings to escape excess shading from understory vegetation (Harmon and Franklin 1989). Given the structural complexity of the understory within this

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system I would argue that escaping understory shading is the largest driver of the trends reported here.

Interestingly, despite adult stem density being almost twice as high on control sites there was only a small difference (less then 4% difference in cover) in the percent cover of nurse logs in a plot. Despite such large differences in stand density canopy cover remained relatively similar between control and habitation sites and had little explanatory power in determining patterns of recruitment. However, while Digital Cover Photography (DCP) provides high-resolution of vertical canopy gaps between, and within, tree crowns they fail to capture the multiple zenith angles of Digital Hemispherical Photography (DHP) (Chianucci et al. 2014). While DCP can be used to determine Leaf Area Index (LAI) and other relevant parameters they require additional assumptions about leaf angle and shape (Chianucci et al. 2014). With large structural differences and variations in density between habitation and control sites more rigorous analysis, of which will be discussed possible future directions, of the canopy may shed some light on variations within the crown not detected in this study.

While the concept of the Anthropocene has been ambitiously debated in the last decade, its 'start point' or the transition point away from the Holocene remains even more uncertain and problematic (Chernilo 2017). While the industrial revolution of the 1700's is often touted as the boundary between epochs, alternative temporal boundaries are becoming increasing present in today literatures as an increasing body of literature demonstrates how humans have altered normal cycles of nature (Crutzen 2006, Smith and Zeder 2013). The persistent impacts of shell middens on above ground forest stands in this study support other proposed boundaries, such as those proposed by Giacomo Certini & Riccardo Scalenghe or William Ruddiman that argue humans impacts can be seen long before the industrial revolution (Ruddiman 2003, Certini and

Scalenghe 2011). Others view the start somewhere near 14,000 – 15,000 years ago with prehistoric megafaunal extinctions (Corlett 2013). While the intention of this study wasn't to argue the potential the lower boundary of the Anthropocene, contextualising this study, and other that focus on long term Indigenous impacts, amongst those who incorporate Indigenous values into their Interpretations of the Anthropocene is of interest (Todd 2015).

## Limitations

Acknowledgment of self-reported limitations is a critical step in the research process to ascribing credibility, and something that is often neglected within scientific inquiry (Ioannidis 2007). First, the inability to collect soil data as a result of working on culturally sensitive lands prevented me from drawing any direct correlations between the presence of shell middens and differences in community structure. However, previous work on similar locations around Calvert and Hecate Islands have eluded to the increase of available nutrients on habitation sites (Trant et al. 2016, Fisher et al. 2019). It is through the results of these studies that I maintain high confidence in the inference made that forest communities on habitation sites differ due to the presence of shell middens.

The geographical remoteness of Hakai's Tula Centre and the general difficulty in transportation between nearby islands this limited my study area to only Calvert and Hecate Islands. This in combination with a limited field season limited the total number of available sites we were able to include in this study (n = 9). While multiple plots at each site provided a substantial data, which enabled the analysis done in this thesis, a more intricate investigation of the effects of shell middens was not possible. For example, looking at trends between midden size and the response seen in above ground vegetation. In this study, the site with the largest

western redcedars (Figure 7; Chapter 2) has the deepest shell midden at 5 m (McLaren et al. 2015). While our data suggests a relationship between midden depth and an above ground vegetative response exists, greater sampling effort must be done to draw statistically meaningful conclusions and provides grounds for future studies.

## Future directions

As described previously, we detected no differences in canopy structure using DCP. Reduced density of adult trees on habitation sites can decrease the amount of between crown gaps seen compared to control sites, thus potentially increasing light penetration from non-vertical zenith angles. With fine-scale gaps being the dominant disturbance regime in western redcedar and western hemlock old growth forests, this increase in light penetration may alter seedling establishment and survival, giving less shade tolerant species an opportunity to thrive (Carter and Klinka 1992, Daniels 2003). A more rigorous analysis of canopy structure could utilize DHP to test for changes in non-vertical light penetration or photosynthetically active radiation (PAR) meters for canopy light transmittance (Leblanc et al. 2005, Leiterer et al. 2015). With the possibility of differences in light transmittance between habitation and control sites, seedling recruitment may reflect these variations with an increase in the shade intolerant Sitka spruce (Mason et al. 2004).

The results found in this study can provide a foundation for future studies to build upon. While there was no differences between the height and DBH of trees between habitation and control sites, their specific interactions with the shell midden were not explored. To determine how each tree interacts with the shell midden, stable isotope δ15N fractionation of woody and vegetative parts can provide insight on specific species interactions. This type of analysis can be

seen when assessing how marine derived subsidies fertilize land vegetation or riparian zone

productivity (Ben-David et al. 1998, Bartz and Naiman 2005). As $\delta15N$ occurs more naturally in

aquatic environments, fractionation can provide $\delta15N/ \delta14N$ ratios that elude to how much of the

nitrogen in foliar or woody tissue is derived from the shell midden vs from a terrestrial source

(Owens 1988). Isotope fractionation may explain the species-specific responses we see in height

and width by showing how much of the available nutrients each species is using and their

allocation of them. Sample collection over a gradient from the boundaries of a known shell

midden to the surrounding matrix can determine how far off the known shell midden range a

signal can be seen. This information provided can be useful in mapping out the true extent of

which the shell midden has influence.

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