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The Impacts of Clearcutting on Understory Plants and Culturally Significant Species In Coastal Western Hemlock Forests of Vancouver Island

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The Impacts of Clearcutting on Understory Plants and Culturally Significant Species
In Coastal Western Hemlock Forests of Vancouver Island

by

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A THESIS

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Abstract

The goal of the study is to understand successional changes in an understory plant community after clear-cut timber harvesting. The forest ecosystem is within the Southern Very Wet Hypermaritime biogeoclimatic subzone in the broader Coastal Western Hemlock zone along the west coast of Vancouver Island. The ecosystem is located in Huu-ay-aht First Nations traditional territory, and the subzone falls within various Nuu-chah-nulth First Nations traditional territories. A chronosequence was used to categorize various stages of forest growth in five successional stages: Regeneration, Immature, Thinning, Mature, and Old-growth. Forests censused ranged in age from 1 to 354 years old with old-growth stages described as stands over 250 years. The leaf cover and stem density of understory plant species were recorded within 83 subplots. These metrics were evaluated with regard to environmental variables (slope aspect, elevation, canopy openness, soil pH, A horizon depth, soil profile depth, tree basal area, tree stem density, ground moss cover, and bare ground cover) to determine which, if any, factors influenced understory species composition and structure. Out of 45 species identified, 19 are culturally significant plant species to the Nuu-chah-nulth First Nations. The species restricted to one successional stage were identified, with emphasis on opportunistic species in early stages and rare species in the Old-growth stage. There was a large decrease in many culturally significant species immediately after clearcutting. There was a large decrease in species (stem density, leaf cover, species richness, species diversity) from the Regeneration stage to the Thinning stage (1 to 80 years); however, these values steadily increased thereafter. Plant leaf cover and stem density were influenced by the amount of light reaching the understory. The natural disturbance regime that shade-tolerant plants are adapted to in these old-growth forests is small-scale gap formations, which clearcutting does not mimic. Timber harvesting options are

recommended to better mimic the natural disturbance regime in this region, which is optimal for the understory species in this region. Many rare and culturally significant plant species were negatively impacted by clearcutting. Protecting rare plant species in old-growth forests is important for maintaining forest biodiversity and indigenous cultural practices in the future.

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I would like to acknowledge that my study area is within the Huu-ay-aht First Nations traditional territory. My gratitude to the Huu-ay-aht First Nation for sharing their cultural knowledge and for the ability to do research within their traditional territory. As a Mi'kmaq First Nation, it is very important to me to include traditional knowledge within my research, and I hope that future ecological research holds this same value.

Thank-you to BC Parks for the opportunity to conduct research within the Pacific Rim National Park Reserve; a truly beautiful area that will forever hold my heart. Also, I would like to thank the staff at the Bamfield Marine Sciences Centre for their support and use of facilities.

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Chapter 1: Introduction

1.1 Background

The aim of this study is to understand the succession of forest understory plant communities following timber harvesting in the Southern Very Wet Hypermaritime biogeoclimatic subzone, and to determine patterns of understory biodiversity and species composition as forests recover from logging. Most previous studies (Wulder et al., 2009; Weber et al., 2014; Weetman and Prescott, 2001; Daniels, 1994) have been largely focused on how logging affects tree species regeneration and composition, with few investigations into the effects of logging disturbance on understory vascular plants and their recovery after a disturbance. I would also like to focus on the regeneration of indigenous culturally significant species after timber harvesting. This is a perspective is understudied in forest science, yet I believe to be vital to understanding forest health.

The large-scale logging occurring on Vancouver Island allows the opportunity to conduct research into the changes in forest structure and diversity through time (Ryan et al. 2009). The conifer-dominated forests of coastal British Columbia have large accumulations of biomass, and most literature has focused on tree biomass rather than focusing on understory biomass (Waring and Franklin, 1979). Understory vegetation is considered to be an indicator of site quality because of its restricted ecological tolerance (Spurr and Barnes, 1980). Halpern and Spies (1995) state that few scientific studies related to forest succession in the Pacific Northwest examine the diversity of understory vegetation in every stand development stage. In the nearly 25 years since their assessment, there are still few published studies on the diversity of understory vegetation in various stand development stages for this region. Many of the biodiversity studies of forests in the Pacific Northwest focus on wildlife, rather than community-level plant species diversity,

although vegetation supports faunistic diversity (Halpern and Spies, 1995). Organisms that dwell in a forest ecosystem depend upon overall health of the forest, including both the understory and the overstory species. Traditional forest studies predominantly focus on trees in the overstory, thus, the nature of understory plant succession in southwestern Vancouver Island is largely unexplored. Acquiring a more comprehensive view of the vegetation composition of these forests will provide a baseline of information useful to foresters, land managers, and indigenous communities. Information about the understory community can contribute to a better understanding of forest health, how anthropogenic use impacts the forest, and can be applied towards logging practices, restoration, and conservation initiatives.

Indigenous knowledge of these forest ecosystems may provide valuable information in the preservation and regeneration of harvested stands, as well as provide cultural importance of understory vegetation. There has been a multitude of ethnobotany studies done on culturally significant species to the Nuu-chah-nulth First Nations; However, there has not been specific focus on the regeneration of culturally significant species after forest stand harvesting. Timber harvesting, as well as the regeneration of species post-harvest, may have impacts on understory species that are integral to indigenous culture, such as loss of species used for food and medicinal purposes. The study region falls within Huu-ay-aht First Nations traditional territory, and I would like to further explore the regeneration of their culturally significant species.

1.2 Literature Review

1.2.1 Disturbances

White and Pickett (1985) define a disturbance as a discrete event in time that ends up disrupting the structure of an ecosystem, community, or population, which alters the physical environment, resources, or the availability of substrate. Disturbances play a unique role in

controlling the regeneration and health of the forest ecosystem and occur at varying spatial and temporal scales. Different types of disturbances can lead to varying understory vegetation regeneration.

There are four common disturbances that occur in the forests of the Pacific Northwest region of North America: gap formation, forest fires, windstorms, and logging. The first three disturbances occur naturally in these forests; however, the fourth disturbance is an anthropogenic cause. Commercial logging in British Columbia began in the 1820s, with sawmills established on Vancouver Island by the 1860s (Green et al. 2014). During the last century, the dominant disturbances in the Pacific Northwest have shifted from natural disturbances like individual tree-fall, windstorms, and fire, which are variable in size and frequency, to more frequent and intense anthropogenic disturbances such as timber harvest and prescribed burns (Halpern and Spies, 1995).

Through windthrow and individual tree mortality, trees fall over and decompose, thus returning nutrients to the soil (Kimmins, 1997). After a forest fire, minerals that were once held in the trees are now in an available form on the forest floor (Kimmins, 1997). By contrast, a logging disturbance removes the trees from the stand, also removing nutrients that might have returned to the soil (Kimmins, 1997). In this manner, logging has a larger impact on the soil and vegetation.

Spurr and Barnes (1980) divide forest disturbances into three separate categories; the disturbances that alter forest structure; disturbances that alter the composition of species; and finally, the disturbances that alter the long-term climate of the forest. Some of the types of disturbances in the first category includes windthrow, fire, logging, and other activities that clear land (Spurr and Barnes, 1980). The second category can be characterized by the introduction or

elimination of new animals and plants into the environment (Spurr and Barnes, 1980). The third category regarding long-term climate involves climate extremes and climate changes over time (Spurr and Barnes, 1980). For the purpose of this paper, I focus on the large-scale destructive disturbances from the first category that are pertinent to the forest management of the Pacific Northwest coast; windthrow, fire, and logging. Windthrow and fire are the natural large-scale disturbances, whereas logging is an anthropogenic large-scale disturbance. Disturbances play a large role in influencing the ecology of a forest because adaptations of certain understory plants arise in response to disturbances, which aids in maintaining biodiversity (Agee, 1993; Spies et al. 2006).

1.2.1.1 Gap formation

Small-scale gap formations from individual fallen trees within a forest ecosystem are important for maintaining species richness and structural diversity (Alaback and Tappeiner, 1991). Alaback and Tappeiner (1991) note that herb, shrub, and tree species in this region are adapted to small gaps created in the canopy from natural disturbances, most notably wind. Older stands are distinguished from younger stands by the presence of structural characteristics caused by individual tree mortality events leading to gaps in the forests (Lertzman et al. 1995). Small-scale disturbances lead to gaps in the canopy, along with remaining logs and snags, which all influence understory vegetation dynamics and tree recruitment (Lertzman et al. 1995). Lertzman et al. (1995) found that 56% of the forests within their study area in southwest Vancouver Island were influenced by canopy openings. These small-scale, low-intensity disturbances are vital to forest regeneration in coastal environments of British Columbia (Lertzman et al. 1995).

1.2.1.2 Windthrow

In the Pacific Northwest coastal temperate rainforests dominated by western hemlock (*Tsuga heterophylla*), windthrow is the dominant natural disturbance (Alaback, 1991). Windthrow is defined as multiple treefalls of larger tree size classes within a forest due to wind (Peterson, 2000), leading to changes the forest structure. According to Lang et al. (2009), the changes resulting from windthrow can alter light patterns, temperature, and soil water and nutrients within a forest. The damage and the recovery from windstorms may be affected by soil characteristics, tree species composition, tree age and size, topography, and previous disturbances (Everham and Brokaw, 1996). The damage from windthrow can be separated into multiple categories; damage to stems, damage to branches, damage to the canopy, mortality, changes to tree volume or biomass, or a combination of multiple categories as they are not mutually exclusive (Everham and Brokaw, 1996). Tree species in the Pacific Northwest have differing tolerance to wind; some are adapted to intense wind, whereas others are more susceptible to windfall. For example, western red cedar and Sitka spruce are considered to be windfirm, western hemlock is more likely to experience windthrow, and Douglas-fir has intermediate wind tolerance (Boe, 1965; Moore and MacDonald, 1974; Ruth and Yoder, 1953).

1.2.1.3 Fire

Fire is a recurring disturbance that typically returns at regular intervals, with the interval length depending upon the geographic location of the forest (Spurr and Barnes, 1980). There are many processes in a forest that are dependent on fire, such as regeneration, reproduction, competition reduction, seedbed preparation, dry-matter accumulation, nutrition, thinning, fuel removal, succession, and wildlife ecology (Spurr and Barnes, 1980). The vegetation composition, quality of habitat, carbon balance, and probability of fire recurrence are determined by the attrition of dead matter, herb and shrub growth, and tree recruitment after a forest fire

(Acker et al. 2017). I could not find literature regarding the regeneration of understory plants after a forest fire in southwestern Vancouver Island. The available literature focuses on tree regeneration.

The fire return interval of the cedar, spruce, and hemlock forest type on the west coast in Washington State averages 937 years (Fahnestock and Agee, 1983). This relatively long forest fire return interval is most likely due to this region having a higher moisture level (Franklin and Dyrness, 1973). The forests in this region have a high severity fire regime, where the amount of the basal area that is removed in a fire is 70% or more (Agee, 1990). The increased fire severity is caused by significant organic matter build up during long time intervals between forest fires (Spurr and Barnes, 1980). The fires in the Pacific Northwest are mostly caused by lightning strikes during the dry season (Agee, 1993).

Fire increases the availability of several soil nutrients, particularly calcium and magnesium (Agee, 1993). A forest fire also increases the amount of available nitrogen in the soil, while simultaneously decreasing the total amount of nitrogen in the soil, an important nutrient in vascular plant growth (Agee, 1993; Brady and Weil, 2008). Therefore, fire is important because of its ability to return nutrients into the soil for further plant growth and forest regeneration.

1.2.1.4 Logging

Logging is defined as the removal of timber from a forest environment for utilization by humans, which includes cutting, further processing, and extraction (Canadian Forest Services, 1999). Logging practices cause a disturbance to the vegetation and soil, which initiates the process of secondary succession (Cromack et al. 1978). The regeneration of vegetation after a logging disturbance is dependent upon the logging method used, environmental conditions, plant succession patterns that are unique to a location, and post-logging regeneration practices

(Cromack et al. 1978). The response of vegetation post-harvest will be impacted by slash biomass, physical damage, and the patterns of disturbance to the soil (Halpern et al. 2005).

Other forest types that have undergone logging have varying impacts on the regeneration of understory species. Studies show that the understory species in northern hardwood forests are tolerant to logging, whereas Appalachian hardwood forests experience a reduction of understory (Scheller and Mladenoff, 2002). This reduction was due to slow recovery of various herbs, climate, change, and loss of microsites (Scheller and Mladenoff, 2002). There are few studies done on the regeneration of understory after logging in the Pacific Northwest. Herbs and shrubs are more abundant in a logged area 10 to 20 years after timber harvest than they are in mature forests with little disturbance (Alaback, 1984; Hanley et al. 1989). Common shade-tolerant understory species that are prominent in old-growth forests are slow to regenerate in second-growth post-logging forests (Alaback and Tappeiner, 1991).

The definition of forestry provided by Nyland (2016) is the art, science, practice, and business of the organization and management of forests and their resources, with the purpose of benefiting people. Silviculture – a critical part of forestry – is defined as the methods used for the establishment and maintenance of healthy tree communities, along with other plant and animal species that are deemed important by people (Nyland, 2016). Silviculture ensures the health and the productivity of managed forest ecosystems (Nyland, 2016). Environmental Reporting BC (2018) describes three silvicultural system categories in British Columbia: clearcutting, partial cutting, and clearcutting with reserves. Clearcutting with reserves leaves residual patches of trees for various ecological purposes (Environmental Reporting BC, 2018; Nyland 2016).

Environmental Reporting BC (2018) states that the main silviculture system that has been in place over the last 15 years has been clearcutting with reserves. Clear cutting with reserves is the

dominant silviculture system found within the study area. This important to note because different types of forest harvesting can lead to varying patterns of understory regeneration.

1.2.2 Succession

Ecological succession is “any process of change with time in communities which is regular and directed by properties of a component species” (Gibson and Brown, 1985). Spurr and Barnes (1980) defined succession as the replacement of biota in a certain area by biota that is of a different nature, which influences dynamic changes in the composition and structure of the forest. Secondary succession occurs after a disturbance to plant community that does not remove all biota, as opposed to primary succession, which begins at a point with no presence of biological materials (Gibson and Brown, 1985). Secondary succession can follow multiple developmental stages (Oliver & Larson, 1996). The first developmental stage is stand initiation, the second stage is stem exclusion, the third stage is understory initiation, and the final stage is known as old-growth (Oliver & Larson, 1996). Every developmental stage has its own unique set of characteristics and level of plant diversity that varies depending on site (Qian et al. 1997). Alaska’s Forests and Wildlife (2018) denotes three stages in secondary succession coastal rainforests: Regrowth stage, Second-growth forest, and Old-growth forest. In the first successional stage, understory plants will sprout from seeds of roots that were buried in the soils, whereas others will sprout from seeds carried by the wind or animals (Alaska’s Forests and Wildlife, 2018). The second-growth forest of crowded conifer sites with few understory plants able to grow in deep shade and is comprised of few shrubs with moss and liverworts as the primary ground cover (Alaska’s Forest and Wildlife, 2018). The old-growth forest contains all aged stands, with increased sunlight reaching the understory, leading to increases presence of shrubs and herbs in the understory (Alaska’s Forest and Wildlife, 2018). In a slightly different

naming convention, Ryan et al. (2016) categorized successional stages as regeneration, immature, mature, and old growth. A characteristic of productive conifer forests is the lack of understory plants found in second growth stands with closed canopies, meaning a healthy, mid-succession stand will have lower quantities of understory plants (Alaback 1982; Alaback and Herman 1988; Oliver 1981). Schoonmaker and McKee (1988) note that plant diversity in the Pacific Northwest peaks during intermediate stages of succession.

1.2.2.1 Natural Succession

Natural disturbances are vital for species richness and structural diversity in many different temperate forest ecosystems (Alaback and Tappeiner, 1991). Natural canopy gaps in a forest provide safe areas for seedlings to regenerate over time (Harper, 1977). There have not been many studies conducted on the natural succession of forests in this region and none completed on one single biogeoclimatic subzone. Alaback and Tappeiner (1991) note that many types of species such as herb, shrub, and tree species are adapted to growing and reproducing within small canopy gaps created from natural disturbances. Natural succession in coastal forests, measured by leaf cover, typically requires several decades and is much slower than in deciduous forests (West et al. 1981).

Many species in this region are adapted to growing and reproducing within small canopy gaps (Alaback and Tappeiner, 1991). The small-scale tree mortality of this region leads to canopy gaps that have a profound impact on understory vegetation dynamics (Alaback and Tappeiner, 1991). The composition of species in temperate forests of the Pacific Northwest is affected by gaps of varying types and sizes (Spies and Franklin, 1989). The canopies of forests in coastal British Columbia are structurally heterogenous and have many canopy gaps, which

promotes shrub and herb growth (Banner and LePage, 2008). Canopy gaps influence understory plant diversity by affecting understory light regimes (Canham et al. 1990).

In studies conducted on a variety of forest types within the Pacific northwest region there was an initial increase in understory vegetation within the first one to two decades after clearcutting occurred, followed by a decrease once the canopy closed, and then another slow increase as the forest matured into old-growth (Alaback, 1982; Klinka et al., 1985; Banner and LePage, 2008).

1.2.2.2 Timber Harvesting

The majority of the forest stands in the wet temperate forests of the Pacific Northwest region were originally managed on a harvest rotation, where they were kept within the first three stages of stand development: stand initiation, stem exclusion, and understory re-initiation (Qian et al. 1997). But recently, with the introduction of new silvicultural practices, harvest rotations are evolving to allow a mosaic of young and old-growth stands.

On Vancouver Island, recently logged stands in the first successional stages tend to have more understory plant species than later successional stages (Ryan et al. 2009). In a variety of second-growth forest stands, there is a lack of understory vegetation due to high levels of competition with western hemlock seedlings (Alaback, 1982; Alaback and Tappeiner, 1991). Common shade-tolerant understory species that are prominent in old-growth forests are slower to regenerate within second-growth forests (Alaback and Tappeiner, 1991). Mueller-Dombois (1965) conducted a study on Douglas-fir and western hemlock forests on Vancouver Island and found that after logging there was an increase in species richness, and the regenerating species were predominantly shade-intolerant. These shade-intolerant species were not found in later successional stages (Mueller-Dombois, 1965). Late-seral species regenerate promptly, and the

original vascular plants regenerate quickly after disturbance in sites within the Drier and Wetter Coastal Western Hemlock subzones on southern Vancouver Island (Klinka et al. 1985).

Hanley (2005) stated that in old-growth forests, once a canopy gap occurs the majority of plants are able to establish early on; however, they grow at different rates. Ferns and forbs are the quickest to respond to a gap in the canopy, shrubs grow after two to three years, and conifer trees require several years more than shrubs (Tappeiner and Alaback, 1989). Other chronosequence studies conducted in the northern temperate rainforest show that shrubs and herbs dominate a site in biomass one to two years after a disturbance, such as logging; however, they are not as successful in mature forests that undergo less frequent, small-scale disturbances (Alaback, 1984; Hanley et al. 1989). The varying growth responses of vegetation in response to light coming through a canopy gap provides an environment where no individual species is able to dominate in the understory (Hanley, 2005). This is due to the constant shifting of the light environment and the high spatial heterogeneity on a small scale (Hanley, 2005). Small-scale canopy gaps lead to different regeneration than that of a logging disturbance. Alaback (1982) noted that clear-cutting creates a large-scale and spatially uniform environment, because it is a disturbance that has a high-magnitude and low frequency.

In southeast Alaska, shrubs in the understory increased in numbers primarily in the first 10 to 20 years after a harvesting event, but by 25 to 30 years there was a decrease in understory vegetation due to regenerating conifers overtopping and shading out the understory (Alaback 1982). Sparse understory vegetation persisted until the stands reached 150 years old, after which the understory plants slowly started to increase again in volume (Alaback, 1982). This study found that the average timber harvesting rotation age was 100 years, therefore between 30 and 100 years, there is sparse vegetation present in the understory, which is very low-quality habitat

for wildlife. Hanley et al. (1989) reported that after thinning treatments, the understory that regenerates is dominated by a few woody shrub species rather than exhibiting a balanced composition of shrubs, tree seedlings, forbs, and ferns. The forbs and ferns together composed less than 1-4% of the understory biomass, whereas in an old-growth stand the ferns typically account for 3-7%, and the forbs 3-9% of the understory biomass (Hanley et al. 1989, Hanley, 2005). Site productivity in the inland Pacific Northwest was substantially lower 15 to 25 years after clearcutting, due to soil compaction, forest floor displacement, and soil displacement (Clayton et al. 1987; Bosworth and Studer, 1991).

A study conducted on southwestern Vancouver Island showed that early successional stands had the largest number of species, which decreased when moving into older, forested plots, largely attributable to an overall decrease in herb diversity (Ryan et al. 2009). Ryan et al. (2009) state that the decrease in herb diversity after the regeneration stage may be due to the initial colonization of invasive species being slowed by canopy closure in immature forests. There was a general increase of cryptogams with an increase in stand age on southwestern Vancouver Island (Ryan et al. 2016). Cryptogam cover in regenerating sites was limited by high light levels and prescribed burning, which is not an ideal environment for cryptogam growth (Ryan et al. 2016). Shrubs were more common in regenerating and old-growth plots, as opposed to immature and mature growth plots (Ryan et al. 2016). Ryan et al. (2016) also noted the highest herb cover in regenerating plots, followed by a decrease of herb cover in immature plots, then an increase in mature plots, and another decrease in old-growth plots.

1.2.3 Light Dynamics

Photosynthetically active radiation (PAR) is important to plant growth and plant regeneration (Frazer et al. 1997). Canopy gaps influence understory plant diversity by affecting

understory light regimes, meaning they regulate PAR levels infiltrating the canopy and reaching the forest floor (Canham et al. 1990). Forest gaps range from fine-scale single tree deaths to broad-scale gap processes whereby thousands of hectares are damaged from wildfire (Spies and Franklin, 1989). Plant species have varying light requirements and are generalized as either shade-tolerant or shade-intolerant (Spurr and Barnes, 1980). Thus, after canopy closure shade-intolerant plant species will become less abundant, due to the lower levels of solar radiation, and other shade-tolerant species will be better suited to the darker conditions. The composition of species in temperate forests of the Pacific Northwest is affected by gaps of varying types and sizes (Spies and Franklin, 1989).

For fine-scale disturbances in the Pacific Northwest, the canopy-return interval for a gap is long, ranging from 50 to 200 years (Spies and Franklin, 1989; Gray et al. 2012). Western hemlock, western red cedar, and Pacific silver fir tend to regenerate and dominate in small gaps because of their shade tolerance (Spies and Franklin, 1989). Yet even shade-tolerant tree species require canopy gaps to reach canopy height. For example, western hemlock does not require an opening in the canopy to grow, but to become part of the overstory it needs the additional light from a gap (Stewart, 1986; Spies and Franklin, 1989). Interior cedar-hemlock forests have lower canopy openness than other coniferous forests, yet they have a high light transmission at the stand level because of the more frequent canopy gaps (Canham et al. 1999).

The nature of canopy gaps caused by the death of mature trees effects stand structure and vegetation (Gray et al. 2012). Canopy gaps affect succession because they allow for new growth in the understory, continued growth of already established vegetation, and space for mature trees to expand their canopy (Gray et al. 2012). Gaps can negatively affect the trees found in the surrounding intact forest by increasing their exposure to solar radiation, decreasing soil moisture,

and increased exposure to wind, which can all lead to higher rates of tree mortality (Gray et al. 2012). Changes to the canopy can influence the duration and the timing of sunflecks, as well as change the ratio of diffuse and direct solar radiation (Canham, 1988; Chazdon, 1988). Sunflecks are the intensity and duration of sunlight on the tree canopy and understory forest plants, that create a continually changing patterns of sun and shade patches (Smith and Berry, 2013). Sunflecks can contribute half of the PAR during the growing season in the understory of closed-canopy coniferous forests (Drever and Lertzman, 2002).

1.2.4 Culturally Significant Species

The western coast of Vancouver Island is home to the Nuu-chah-nulth First Nations (Castleden et al. 2009). The Huu-ay-aht First Nation is one of the 14 Nuu-chah-nulth First Nations that reside in this region (Castleden et al. 2009). The Nuu-chah-nulth First Nations territory covers a long stretch along the west coast of Vancouver Island (Figure 1.2), and part of this territory along the coastline is within the Very Wet Hypermaritime biogeoclimatic subzone (CWHvh1). The Huu-ay-aht traditional territory (Hahoothlee) spans 78,000 kilometers and is located around the town of Bamfield region (Figure 1.1), approximately 250 kilometers northwest of Victoria (Castleden et al. 2009). The territory has been described as having inland mountains, coastline beaches, channels, rocky peninsulas, estuaries, river valleys, and lakes, but the landscape is mostly dominated by temperate rainforest (Castleden et al. 2009). The Huu-ay-aht First Nation use the extensive forest resources within their territory (Castleden et al. 2009). To manage these resources, they use principles of World view (Hishuk Tsawak), which means “everything is one, everything is connected” (Castleden et al. 2009). Many species in the forest are depended upon for culturally uses such as food, clothing, shelter, food, medicines, and other life necessities (Garibaldi and Turner, 2004).



Figure 1.1 - Haa-ay-aht First Nation Traditional Territory (Haa-hoothlee) (Morgan and Castleden, 2014).



Figure 1.2 – Traditional territory of Nuu-chah-nulth First Nations (Morgan and Castleden, 2014).

While conducting ecological research in forests within First Nations traditional territory it is important to recognize the relationship of culturally significant plant species to indigenous peoples. Culturally significant species are depended upon for food, clothing, shelter, food, medicines, and other life necessities (Garibaldi and Turner, 2004). These species are also important components of people’s traditions, narratives, ceremonies, spiritual practices, dances, songs, language, and discourse (Garibaldi and Turner, 2004). Within these culturally significant species there are also Cultural Keystone species, which are represented by a few culturally salient species that shape cultural identity of people, specifically in their relation to diet,

materials, medicine, and spiritual practices (Garibaldi and Turner, 2004). In a spatial context, there are multiple factors defining whether species are culturally significant, such as proximity to other culturally significant species, availability of the plants, and plant community structure (Garibaldi and Turner, 2004). There is a lot of traditional knowledge about the spatial distribution of plants throughout the land, but I wanted to add the perspective of plant distribution over time and after clear-cut timber harvesting. The goal is to understand the impact of timber harvesting on these culturally significant species' spatial distributions and composition, how their stem density and leaf cover change over time as the forest regenerates, and how this may potentially impact indigenous communities. Indigenous communities in this region rely a lot on the land, "Everything we have, came from the land" (Huu-ay-aht First Nations, 2016).

The field sites in my study area fall within the traditional territory of the Huu-ay-aht First Nations and within the broader language group, the Nuu-chah-nulth First Nations. Information shared by the Huu-ay-aht First Nation was gathered from elders in their community who talked about the importance of the connection to their ancestors and traditional territory (Huu-ay-aht First Nations, 2016). Their land has always been abundant with life-sustaining resources, such as their ancestors' first foods (Huu-ay-aht First Nations, 2016). I combined the traditional knowledge, referenced from Huu-ay-aht First Nation text (Huu-ay-aht First Nations, 2016), with ethnobotanical information referenced from numerous papers authored by Dr. Nancy Turner (Turner, 1995), which details culturally significant species to the Nuu-chah-nulth First Nations (Table 1.1). This information is a combination of both historical uses and modern day uses. It is also important to note that what species may be culturally significant to one First Nation may not be culturally significant to another (Garibaldi and Turner, 2004).

Various parts of plants were consumed as food, medicine, and gathered for other cultural uses, such as the roots, flowers, berries, and leaves. Certain plants were also only consumed at a particular stage of their life cycle. The Huu-ay-aht First Nations Elders note berries (qawii) as a very important traditional food (Huu-ay-aht First Nations, 2016). Berries have been prepared and eaten either fresh, jarred, pressed, or dried between planks and stored in baskets, or cooked into a jam (Huu-ay-aht First Nations, 2016). The berries that are listed are cultural significant species that were found throughout the study sites (Table 1.1).

There are many traditional medicines and recipes of Huu-ay-aht First Nations that are still used today (Huu-ay-aht First Nations, 2016). However, this information is not readily shared because many Elders believe that if the recipe is revealed, the medicine may lose strength (Huu-ay-aht First Nations, 2016). Knowledge of medicinal practices, recipes, and plants are shared within families and are generally kept by a keeper (Huu-ay-aht First Nations, 2016). I am very grateful to have the opportunity to learn and help share some of this knowledge from the Huu-ay-aht First Nation and Nuu-chah-nulth First Nations.

Table 1.1 – List of culturally significant vascular plant species to the Huu-ay-First Nation and the Nuu-chah-nulth First Nations.

Oval-leaf blueberry - Wild blueberries	Oval-leaf blueberry is commonly found in moist, coniferous forests, and stream banks with increased shade (Turner, 1995). The berries are eaten raw or cooked by all west coast indigenous peoples (Turner and Kuhnlein, 1991).
Red huckleberry – Red (his?inwa) huckleberry	This berry species, consumed as food by the Huu-ay-aht First Nations and Nuu-chah-nulth, are commonly found in shaded forests and rotting woody matter (Turner, 1995). They can be eaten raw, used in cakes for winter, eaten with sugar, jarred, frozen, or baked into pies, as the berries are known to make superior jellies (Turner and Kuhnlein, 1991).
Evergreen huckleberry - Cynamoka Berries	Evergreen huckleberries are important source of food to the Nuu-chah-nulth, as the berries can be harvested throughout late autumn and into December, whereas the berries of other species will have rotten and fallen by that time (Turner, 1995). This important berry species can be found in dense forest stands and in moist conditions,

	and on eastern slopes (Turner, 1995). Today they are often used in cooking and to make jams (Turner and Kuhnlein, 1991).
Canada bunchberry	These berries were gathered by the Nuu-chah-nulth, along with other coastal peoples, and eaten raw or stored for later consumption (Turner and Kuhnlein, 1991). The Huu-ay-aht First Nations note these berries as edible (Huu-ay-aht First Nations, 2016).
Thimble berry (Hup?aal)	The Huu-ay-aht First Nations use many parts of the Thimble berry plant as food, such as the berries, the shoots, and young sprouts as a vegetable (Huu-ay-aht First Nations, 2016). Nuu-chah-nulth peoples were also known to boil the leaves with fish as flavouring (Turner and Kuhnlein, 1991).
Salal (Yama)	Salal berries were eaten fresh or preserved for winter by using a maul to pound them and drying them in the sun (Huu-ay-aht First Nations, 2016; Turner, 1995). Historically, the Nuu-chah-nulth people ate them with whale or seal oil (Turner and Kuhnlein, 1991). The chewing of small, young Salal leaves can be used to aid with indigestion (Huu-ay-aht First Nations, 2016).
Black raspberry	Black raspberry, also known as Blackcap, is found in open woods, clearings, and burned areas (Turner, 1995). The berries are consumed as food.
Salmonberry	Salmon berry shoots are collected in the early spring to be peeled and eaten raw (Huu-ay-aht First Nations, 2016). The salmon berries are some of the earliest to ripen and be eaten (Huu-ay-aht First Nations, 2016). They are often eaten raw, frozen, canned, or made into jams and jellies (Turner and Kuhnlein, 1991). Some Nuu-chah-nulth peoples boiled the leaves with fish as flavouring (Turner and Kuhnlein, 1991).
Common horsetail	The Nuu-chah-nulth peeled off the outer parts of young plants including the sheathing, leaves and branches, and ate the vegetative shoots (Turner, 1995).
Skunk cabbage	The central and northern Nuu-chah-nulth gathered Skunk Cabbage roots in the fall and ate the fleshy rhizomes of skunk cabbage by first steaming them (Turner and Kuhnlein, 1991; Turner, 1995). They were also previously widely used in food preparation in the form of using the big leaves as wax paper for wrapping food, lining cook pits, separating foods that were being cooked together, and as a surface for drying berries (Turner and Kuhnlein, 1991).
Bracken fern	The Nuu-chah-nulth ate the fiddle heads of the Bracken fern after they have been boiled
Sword fern	The rhizomes of the Sword fern were either cooked or steamed and then peeled to be eaten (Turner, 1995).
Deer fern	Nuu-chah-nulth peoples ate the shoots to suppress hunger and used fronds for lining steaming pits (Turner and Kuhnlein, 1991).
Licorice fern (hihit'aqtlmapt)	Licorice fern has been used as a medicine to treat respiratory infections (Huu-ay-aht First Nations, 2016). Nuu-chah-nulth peoples used licorice fern rhizomes as mouth sweetener and appetite

	stimulant (Turner and Kuhnlein, 1991). The plant was also used widely in cough syrups, for sore throats and colds, and as added sweeteners to other medicines (Turner and Hebda, 1990).
Wild crabapples	Iron-rich Wild crabapples were used as medicine, to increase strength, and for many other purposes (Huu-ay-aht First Nations, 2016). Apples were picked to be eaten and stored, and the bark was carefully stripped, boiled, and at times stored in jars to be used later as medicine (Huu-ay-aht First Nations, 2016).
Cascara	The bark of Cascara can be used as a medicine to aid in relieving constipation due to its laxative properties (Huu-ay-aht First Nations, 2016; Turner, 1995). The bark can either be used fresh or dried and boiled to create a tonic (Huu-ay-aht First Nations, 2016).
Pacific yew	Boiling and drinking the inner bark is said to be beneficial for the health of all the internal organs and boost immunity (Huu-ay-aht First Nations, 2016).
Western red cedar (Huumiis)	Though the western red cedar has many cultural uses for the Huu-ay-aht First Nations, the medicinal properties are believed to help support the body's immunity and to fight fungal, bronchial, and urinary infections (Huu-ay-aht First Nations, 2016). The inside of the bark was used to repel mosquitos (Huu-ay-aht First Nations, 2016).
Western hemlock	The boughs of western hemlock are used to collect herring spawn by being submerged in the water of inlet and estuaries or by being tied to floating logs anchored close to the shore (Turner and Kuhnlein, 1991). Western hemlock boughs are flexible and easily handled, and the mild needles provide a resinous flavour to the herring spawn.
Red alder (qaqmapt)	The alder tree is believed by elders to have numerous healing properties (Huu-ay-aht First Nations, 2016). The bark is prepared by peeling it and then soaking it in boiling water, and this tonic can be drunk to heal illnesses (Huu-ay-aht First Nations, 2016). It was also used by many indigenous peoples along the west coast as fuel for smoking salmon and other foods (Turner and Kuhnlein, 1991).

1.3 Research Objectives

The main focus of this study is to identify successional changes in forest understory vascular plants and culturally significant species after clear cut logging within the Very Wet Hypermaritime Coastal Western Hemlock subzone of Vancouver Island. This can be broken down into five objectives.

The first objective is to evaluate how time since logging affects species stem density and leaf cover of the forest understory. Understory plant species stem density and leaf cover are two metrics that provide insight into understory species composition, measuring how much of each species is present and how many individuals. By measuring these metrics in various successional stages, the values contribute to our understanding of how time influences understory plant growth after timber harvesting.

The second objective is to measure understory plant species diversity, richness, and evenness at various stages of succession. These ecological metrics describe how plant communities and forest health are changing over time after clear cut logging. Forest ecosystem health can be defined by the level of biodiversity (Simberloff, 1999). Species diversity is a community level characteristic defined by the relative abundance of species and species richness (Russel et al., 2010). Species richness is defined as the number of species and species evenness is a measure of relative abundance, which is the number of individuals in a species relative to the total number of individuals (Russel et al. 2010).

The third objective is to evaluate how various environmental and topographic variables influence plant composition throughout time. Environmental factors and topography influence what type of species can grow in a given area. The third objective will be achieved through

obtaining information on topography, such as slope aspect, slope angle, and elevation, as well as environmental factors including soil characteristics, light dynamics, and stand information.

The fourth objective is to identify common, indicator, opportunistic, rare, restricted, and invasive species at various successional stages. In this study, common species are described as species that are found throughout all successional stages. Indicator species are understory plant species indicate the conditions for the Southern Very Wet Hypermaritime subzone. These understory plant communities will only grow, reproduce, and survive under specific ecological conditions (Ceska and Scagel, 2011). Opportunistic plant species are adapted to take advantage of newly available habitats and resources, such as in clear cut forests (Freedman, 2023). Invasive alien species are plant species that are introduced to a new habitat and spread outside their past distributions, threatening local biological diversity (Weber, 2017). In this study, restricted species are found in only one successional stage and rare plants are the restricted plants that are only found within old-growth stands.

The fifth objective is to evaluate how indigenous culturally significant species to the Huu-ay-aht First Nation and Nuu-chah-nulth First Nations respond to clearcutting over time.

- 1) Evaluate how time since clear cut logging affects species density and cover of the forest understory.
- 2) Measure understory plant species diversity, richness, and evenness at various stages of succession.
- 3) Evaluate how various environmental and topographic variables influence plant composition throughout time

- 4) Identify common, indicator, opportunistic, rare, restricted, and invasive species at different successional stages.
- 5) Evaluate how indigenous culturally significant species to the Huu-ay-aht First Nation and Nuu-chah-nulth First Nations respond to clearcutting over time.

Chapter 2: Methods

2.1 Study Area

The study area (Figure 2.1) is located around Bamfield, British Columbia, Canada, on the western coast of Vancouver Island (48° 47' 59" N, -125° 5' 31" W). It falls within the Pacific Rim National Park Reserve, crown land, and Huu-ay-aht First Nations land. The site is comprised of Coastal Temperate Rainforest ecozone and is within the Western Vancouver Island ecoregion (Pojar et al. 1991; Demarchi, 2011). The study area is within the Very Wet Hypermaritime (CWHvh) and the Very Wet Maritime (CWHvm) Biogeoclimatic subzones, which are a part of the Coastal Western Hemlock Biogeoclimatic zone (Pojar et al. 1991). The driest and warmest months in Bamfield (the nearest climate station) are July and August with total precipitations of 144 mm and 138 mm, and mean temperatures of 15.9 °C and 17.5 °C respectively (Climate Change Canada, 2019). The wettest and coolest months are January and December with mean total precipitations of 563 mm and 573.3 mm, and mean temperatures of 8.2 °C and 9.9 °C (Climate Change Canada, 2019). The average annual mean temperature for Bamfield in 2018 was 11.6 °C and the sum of total annual precipitation in 2019 was 2030.1 mm (Wiebe, 2018).

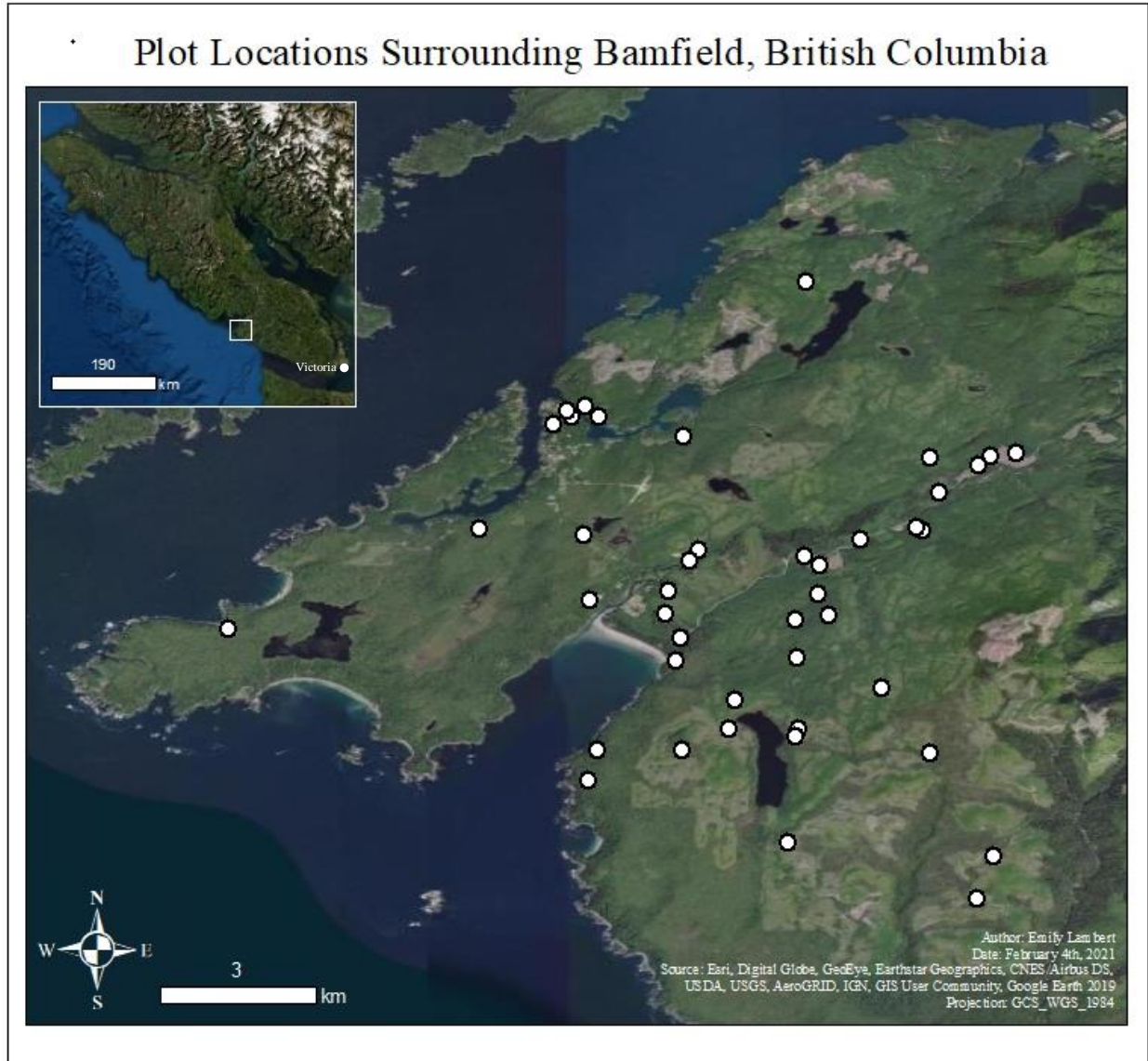


Figure 2.1 - Map showing the 44 site locations within the study area. The study area is located in the southwestern portion of Vancouver Island, BC, surrounding the town of Bamfield.

The southwestern portion of Vancouver Island was covered by the Cordilleran ice sheet during the late Pleistocene (Alley and Chatwin, 1979). Following the retreat of this ice sheet, what remained was bed rock rich glacial deposits, also known as colluvial material (Alley and Chatwin, 1979; Preston and Trofymow, 2000); providing the parent material for the soils that are found there today. The soils within the Coastal Temperate Rainforest ecozone are young podzols, which began to develop when the region was deglaciated around 12,000 years ago

(Spurr and Barnes, 1980; Alley and Chatwin, 1979). The two predominant soil associations in the area are Sarita soils and Sprise soils (Jungen, 1985). These soil associations occur within elevation that ranges from sea-level to 600 meters (Jungen, 1985). The soil classifications of the Sarita soils are Duric Ferro-Humic Podzols and Duric Humo-Ferric Podzols and are moderately-well to well-drained soils (Jungen, 1985). The classifications of the Sprise soils are Orthic Ferro-Humic Podzols and Orthic Humo-Ferric Podzols, and are well drained soils (Jungen, 1985). The soils in this moist temperate region have undergone podsolization, where through acid leaching minerals are carried downward through soil profile, commonly occurring in hemlock-dominated temperate rainforests (Spurr and Barnes, 1980).

Pojar et al (1991) note that the dominant tree species in this biogeoclimatic subzone include western hemlock (*Tsuga heterophylla*), amabilis fir (*Abies amabilis*), western red cedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), red alder (*Alnus rubra*), and Alaska-cedar (*Cupressus nootkatensis*). Some common shrubs are oval-leaf blueberry (*Vaccinium ovalifolium*), salal (*Gaultheria shallon*), and red huckleberry (*Vaccinium parvifolium*) (Pojar et al. 1991). Common herbaceous species are deer fern (*Blechnum spicant*), fern-leaved goldthread (*Coptis asplenifolia*), false lily-of-the-valley (*Maianthemum dilatatum*), and false azalea (*Menziesia ferruginea*) (Pojar et al. 1991). The forest floor is also covered with various species of mosses; flat moss (*Buckiella undulata*), lanky moss (*Rhytidiadelphus loreus*), and step moss (*Hylocomium splendens*) (Pojar et al. 1991). The Western hemlock dominated forests of the Pacific Northwest characteristically have extremely low light levels and wet or damp sites (Spurr and Barnes, 1980). The most prevalent trees noted within the plots were the Western red cedar, a tree species tolerant to shade, and the western hemlock, which is very tolerant to shade (Spurr and Barnes, 1980). This region has undergone clear-cut timber harvesting, as well as clear-

cutting with reserves. They use a slash burning treatment on the cut stands, to remove access woody debris (M. Hallaway, personal communication, June 12, 2019).

2.2 Data Collection

2.2.1 Vegetation

Vegetation was sampled using a chronosequence approach (Barbour et al. 1987). A chronosequence is defined as a set of sites that were formed from the same parent material and differ in the time since formation (Walker, 2010). Chronosequences can be used to measure differences in characteristics overtime and throughout ecological succession (Walker, 2010). Stands of varying ages were found using the VRI – Forest Vegetation Composite Polygons and Rank 1 Layer data set from the Ministry of Forests, Lands, Natural Resource Operations and Rural Development – Forest Analysis and Inventory of British Columbia (Rousseau & Fong, 2019). This data set provided information on tree age, derived from time since logged, and tree density. Plots were sampled across a wide range of stand ages, from 1 to 354 years old. Sites in stands from the Regeneration to the Mature stage all had evidence of logging from “cut stumps”, however the prior disturbances to old-growth forests are unknown. All harvested stands had a harvest pattern of clear-cutting, or in more recent years clear-cutting with remnant patches.

There were 42 plots sampled in total in both logged and unlogged (old growth) stands. The nested quadrat method was used for the plots, a common sampling method to census various types and sizes of vegetation (Barbour et al. 1987). Forest plots of 10 x 10 meters, 10 x 20 meters, or 20 x 20 meters were used for stand sampling and varied in size due to differences in tree density (Figure 2.2). The standard plot size was 20 x 20 meters. Within forest stands that had numerous small trees or were difficult to navigate on foot, a smaller 10 x 10 meters or 10 x 20

meters plot sizes were chosen. Within each forest plot, trees (> 5 cm dbh) were identified and counted. Two 5 x 1-meter subplots were located at opposite corners of each forest plots but were relocated to adjacent corners if inaccessible (tree remnants made the field too difficult to traverse). There were a total of 83 subplots. The subplots were then divided into five 1 x 1-meter sections to record tree seedlings (< 30 cm tall), tree saplings (> 30 cm tall, < 5cm dbh), shrub, forb, and herbaceous leaf cover, and stem counts. Additionally, in each quadrat I recorded percent moss cover and percent bare ground of the forest floor. Within the quadrats, herb and shrub leaf cover, moss cover, and bare ground cover were estimated visually using a 10 x 10 cm square, equally 1% of cover.

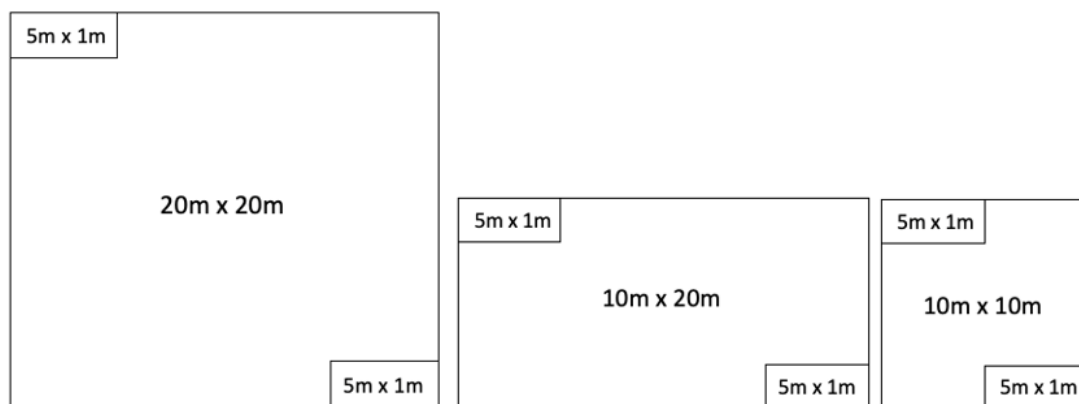


Figure 2.2 - Plot sizes; 20 by 20 meters, 10 by 20 meters, and 10 by 10 meters, each containing two 5 by 1-meter subplots.

2.2.2 Landscape Position

A Suunto Tandem inclinometer/compass (Suunto Tandem /360PC/360R G Clino/Compass) was used to measure slope angle and aspect. The slope angle remained under 13 degrees across all sites (with the exception of one site that was 18 degrees) to reduce topographic

variability. A hand-held Garmin inReach Explorer+ GPS was used to collect coordinates and elevation data.

Plots were located away from edges or roads to ensure that light levels were consistent with the canopy cover, and to avoid edge effects (Spurr and Barnes, 1980). The selection of plot locations was constrained by logging road access, trail access, and varying topography. For the majority of site sampling, I only sampled forest stands that were accessible by logging roads. Some stands that were selected to be sampled had logging road closures that were not indicated on forestry maps, therefore could not be accessed. Some old-growth sites selected to be sampled within the Pacific Rim National Park Reserve could not be sampled due to limited accessibility by hiking trails and physical limitations from carrying equipment over long distances and through dense understory. Some younger sites that were selected to be sampled could not be accessed on foot due to difficult topography such as large fallen woody debris. Low-lying areas with water accumulation and steep slopes were also avoided, to remove any unnecessary variables and keep plant species consistent. Two subplots were removed from analysis because of their high moisture levels and pooling water.

2.2.3 Soil

Soil was environmental variable measured to test the relation between understory plant species and various soil characteristics. A soil single soil sample was taken from the middle of each plot. This sample location was chosen through random sampling, by walking into the middle of the plot and throwing a stick. Wherever the stick landed was the location of where the soil sample would be collected. The soil characteristics evaluated included depth of A and O horizons, depth to bedrock and pH. A small soil pit was dug to differentiate the depths of the A and O horizons. The depth to bedrock was measured using a metal rod and measuring tape,

measuring from the top of the organic layer, down to bedrock. One soil sample of the A horizon was collected for the centre of each plot. The pH was measured the same day as the sample was collected using an Accumet Portable 115 pH meter. Approximately 100 grams of soil was collected from the A horizon from immediately beneath the O horizon. A slurry was created of water and soil at a 2:1 ratio, 50 g soil to 100 ml water. This slurry was left to sit for 30 minutes and mixed every 5 minutes. It was then measured with the Accumet Portable AP115 pH/ORP meter while being continuously stirred (Hendershot et al. 2008).

2.2.4 Understory Light

Canopy openness was an environmental variable measured to understand the relation between understory plant species and light levels. Understory light levels were assessed using hemispherical (fisheye) photographs taken of the tree canopy (Anderson, 1964; Frazer et al. 1997). Hemispherical photographs were taken in the middle of each subplot by pointing a Nikon Fisheye Converter (FC-E9) 183° hemispherical lens directly upwards. The camera was stabilized with a tripod to avoid angular distortion (Frazer et al. 1997). The photo was taken at 150 cm to estimate light reaching the understory layer. The images were processed using the WinSCANOPY hemispherical canopy analysis software, where light variables were calculated including Canopy Openness and Gap Fraction. The software paired the images with temporal data and sun track data to produce outputs that correlated with the time of year and the angle of incidence. The pixel threshold was adjusted based on visual presentation of each image, to ensure that software accurately analyzed the difference between vegetation and sky (Figure 2.3). At times, cloud cover was similar in brightness to vegetation, or the reflectance on leaves was similar in brightness to the sky, therefore the pixel threshold was adjusted to account for these similarities in each image.

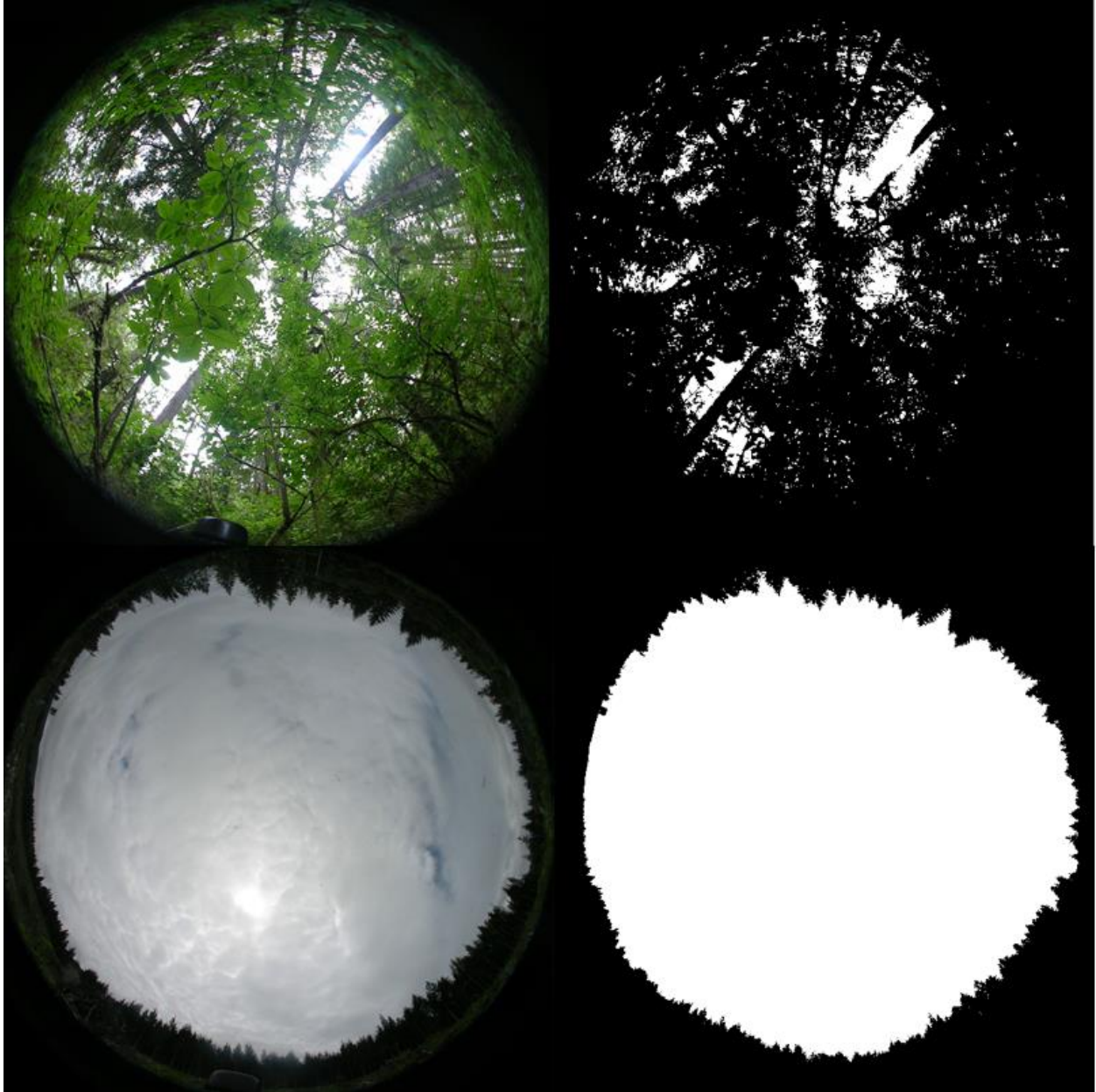


Figure 2.3 – Images from WinSCANOPY software, providing canopy openness values. The pixel threshold of the top image is 200 and the pixel threshold of the bottom row is 9.

2.3 Data analysis

2.3.1 Vegetation Summary Statistics

The field sites were divided into 5 separate successional groups, based on stand age. Regeneration (1 – 9 years), Immature (10 – 39 years), Thinning (40 – 79 years), Mature (80 – 250 years), and Old-growth (250+ years). These successional stage age ranges were based on a combination of previous literature on forest succession, patterns found within the data, and differences found while visually analyzing the sites. Plots from each successional stage are summed and then average to correctly account for the different number of plots between each stage.

2.3.1.1 Species Richness, Diversity, and Evenness

Species richness was calculated by summing the total number of species within each successional stage. Species diversity was calculated from species density data using the Shannon Diversity Index, which is defined as

$$H = -\sum_{i=1}^k p_i \ln p_i$$

where k is the total number of species in the community, and p is the proportion of k that is made up of a specific species (i) (Marcon et al. 2014). A higher level of species diversity is present when the H-value is higher (Marcon et al. 2014). Species evenness was calculated using Shannon's Equitability (E_H):

$$E = H / \ln S$$

where H is the Shannon Diversity value and S is the total number of species (Marcon et al. 2014). The equitability value ranges from 0 to 1, where 1 is high community evenness and 0 is low community evenness (Marcon et al. 2014).

2.3.1.2 Species Density and Cover

The mean cover and density of all vegetation within each successional stage was calculated, along with the mean cover and density various vegetation types, within each successional stage. These general vegetation types included shrubs, herbaceous plants, ferns, and tree seedlings and saplings.

2.3.2 Descriptive Statistics

The field sites were divided into 5 separate successional groups, based on stand age. Regeneration (1 – 9 years), Immature (10 – 39 years), Thinning (40 – 79 years), Mature (80 – 249 years), and Old-growth (250+ years).

The regeneration group consisted of tree seedlings, some tree saplings, and understory vegetation. The immature group consisted of predominantly trees, tree saplings, some tree seedlings, and understory vegetation. The Thinning group consisted of plots that had predominantly even-aged tree stands, with little understory growth. The Thinning stage was used to define the beginning part of the stem exclusion development stage, where existing trees in an even-aged stand begin to die and go through the thinning process (Oliver and Larson, 1996). There is reduced understory vegetation during this stage. The mature stands had larger trees, some tree seedlings and saplings, and an increased amount of understory growth. The old-growth stands consisted of all-aged tree stands, with large, old trees, and a dense understory. In the coastal region of BC, old-growth forests are classified as stands aged 250 years and older (BC Ministry of Forests, 2022). There were 12 regeneration subplots, 18 immature subplots, 22 Thinning subplots, 18 mature subplots, and 13 old-growth subplots.

I calculated mean and standard deviation for both the vegetation cover and vegetation density in each successional stage. Kruskal-Wallis non-parametric H tests were performed using

the SPSS Statistics (Ver 24) software from IBM, to test for significance. I used five groups, representing each stage of succession ($k=5$). When a significant difference was identified by the Kruskal-Wallis test, a post-hoc pairwise Tukey test with a Bonferroni correction was run to identify significant differences between groups (Rice, 1989).

Descriptive statistics were also calculated for environmental variables; bare ground cover, moss cover, A soil horizon depth, soil profile depth, soil pH, canopy openness, stand basal area, and stand stem density.

Restricted species were identified, meaning they were only observed in one specific successional stage. Culturally significant species to the Huu-ay-aht First Nation and Nuuchahnulth First Nations were also identified.

2.3.3 Multivariate Ordination

Canonical correspondence analysis is an ordination technique used to classify species distributions along environmental gradients (Palmer, 1993). The length of an axis describes the importance of an environmental variable, the axis direction describes the correlation with species composition axes, the angle between two environmental axes indicates correlation between environmental variables, environmental characteristics of a site are indicated by the location of site scores relative to the axes, and the species positions relative to the axes describes which environmental variables influences each species (Palmer, 1993).

The environmental data was first analyzed using the Pearson's Correlation Matrix to narrow down which environmental variables to use, by excluding highly correlated environmental variables. Data was then analyzed using canonical correspondence analysis (CCA) to discover how the environmental data related to the understory species cover and diversity. Four separate canonical correspondence analyses were done comparing plant cover,

plant density, plots, and plant species to various environmental variables. The axes consisted of Canopy openness, Bare ground cover (%), Moss cover (%), A horizon depth, Soil pH, Stand basal area (m²), Stand stem density (stems/ha), Slope angle, and Slope aspect (calculated in Eastness and Northness).

Chapter 3: Results

3.1 Vegetation metrics across developmental stages

Forty-five species were identified, including 13 shrubs, 20 herbs, six ferns, and six trees (Appendix A). Five of the six tree species were found as mature trees in the overstory, as well as seedlings and saplings in the understory, whereas one tree species, Pacific yew (*Taxus brevifolia*) was only found in the overstory as a mature tree. There were 44 native species and one invasive species, rush skeleton weed (*Chondrilla juncea*) (Invasive Species Council of BC, 2021).

3.1.1 Understory Leaf Cover and Stem Density

The overall mean (\pm standard error [SE]) understory stem density (stems/m²) and understory leaf cover (%) per subplot varied by successional stage (Figure 3.1). The overall mean density in the Thinning stage was significantly lower than both the Immature stage (Kruskal Wallis, $p < 0.05$) and the Old-growth stage (Kruskal Wallis, $p < 0.05$). The overall mean cover in the Thinning stage was significantly lower than both the Immature stage (Kruskal Wallis, $p < 0.05$) and the Old-growth stage (Kruskal Wallis, $p < 0.05$). There was a decrease in mean understory leaf cover (%) and mean stem density (stems/m²) from the Immature stage to the Thinning stage, and an increase in mean understory leaf cover (%) and mean stem density (stems/m²) from the Thinning stage to the Old-growth stage.

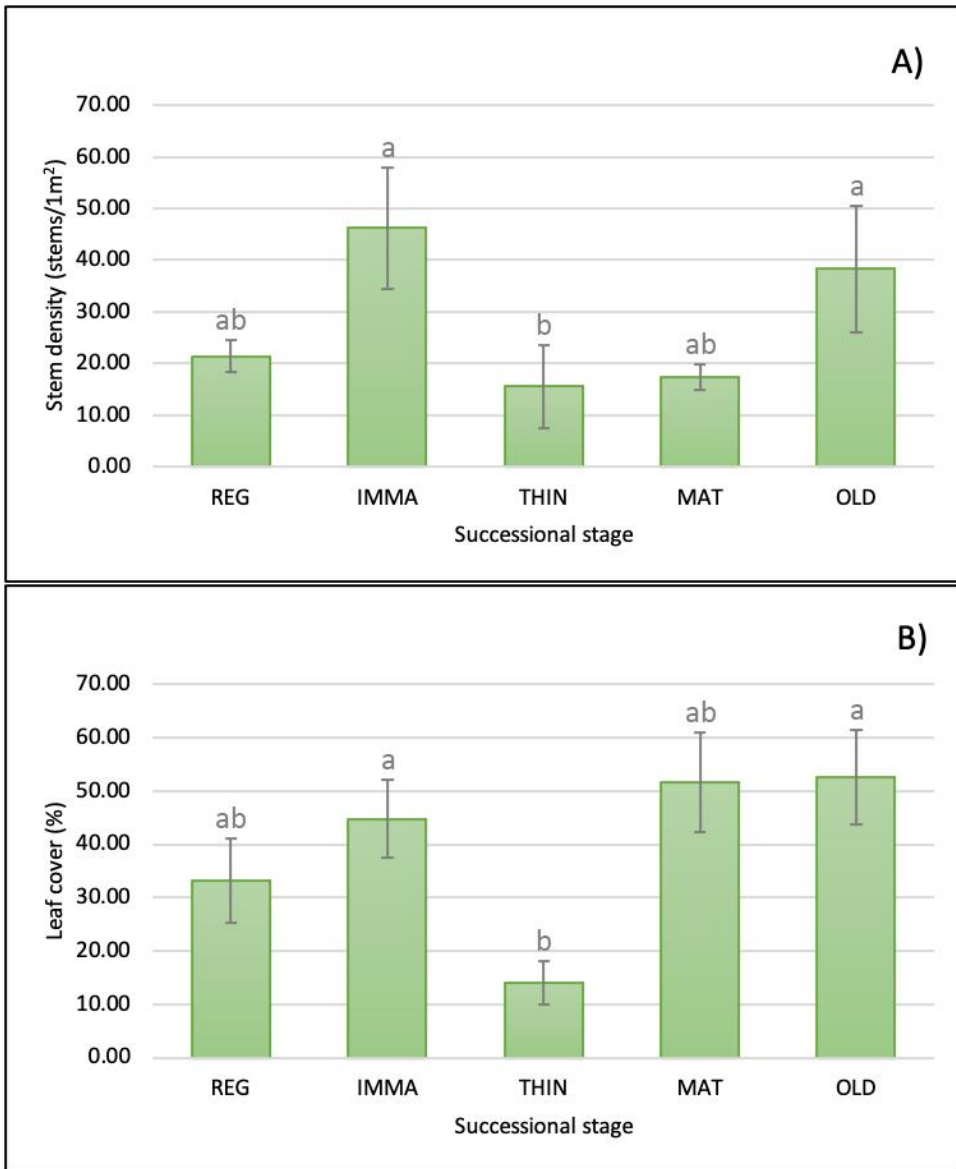


Figure 3.1 – A) Mean (\pm SE) understory stem density (# of individuals) and B) mean (\pm SE) understory leaf cover (%) per 1 m² plot. Error bars represent standard error. X-axis labels: REG=regeneration, IMMA = Immature, THIN = Thinning, MAT = Mature, OLD = Old-growth. Lowercase letters indicate groupings as determined by a Kruskal-Wallis statistical test. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different ($p < 0.05$).

The mean (\pm SE) shrub and herb stem density differed significantly in one successional stage (Figure 3.2, Table 3.1). The Thinning stage shrub and herbaceous plant stem density values were significantly lower than the Regeneration, Immature, and Old-growth values (Table 3.0). The tree seedling and sapling stem density values were not significantly different between stages.

Regeneration stage stem density was dominated by shrubs at 48.95% (Figure 3.3). Immature, Mature and Old-growth stages stem densities were dominated by herbaceous plants: Immature at 68.98% (12.2% ferns, 56.78% other herbs), Mature 52.43% (13.55% ferns, 38.88% other herbs), and Old-growth at 61.65% (14.12% ferns, 47.53% other herbs). Finally, the Thinning stage stem density was dominated by tree saplings and seedlings at 65.14% (0.06% sapling, 65.08% seedling). Other herbs dominated over ferns for herbaceous plant stem density in all successional stages (Figure 3.3).

The shrub and herb stem density of the Regeneration stage was significantly (Kruskal-Wallis, $p < 0.05$) higher than the Thinning stage. Thinning stage stem density was also significantly lower than Immature and Old-growth stages. Seedling and sapling stem densities were not significant between successional stages (Table 3.0).

Table 3.1 – Average stem density (stems/m²) \pm standard error per plant type category: shrubs, herbaceous plants, and tree seedlings/saplings. Statistical comparisons are based on Kruskal-Wallis tests for each plant type. Lowercase letters indicate statistically ($p < 0.05$) similar groupings.

Plant type	Regeneration	Immature	Thinning	Mature	Old-growth
Shrub	10.50 \pm 1.35a	13.52 \pm 1.66ac	2.46 \pm 0.60b	6.53 \pm 1.13abc	12.48 \pm 2.72ac
Herb	9.68 \pm 1.78a	31.92 \pm 11.26ac	2.94 \pm 1.80b	9.11 \pm 2.27abc	23.65 \pm 8.82ac
Seed/Sap (n.s.)	3.15 \pm 0.32	0.83 \pm 0.27	10.09 \pm 7.60	1.73 \pm 0.64	2.23 \pm 1.24

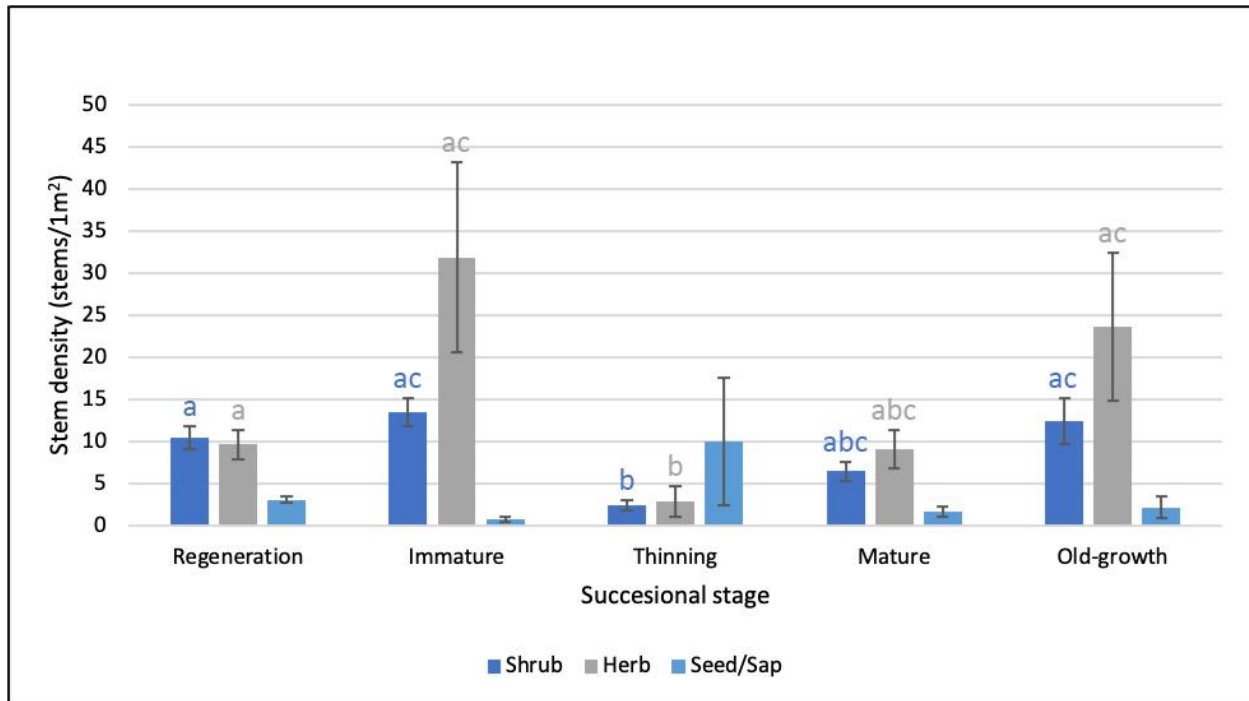


Figure 3.2 - Mean (\pm SE) understory stem density per m² subplot, for every successional stage. Stem density of shrubs, herbaceous plants, and tree saplings and seedlings. Error bars represent the variation of understory stem density between plots within each successional stage.

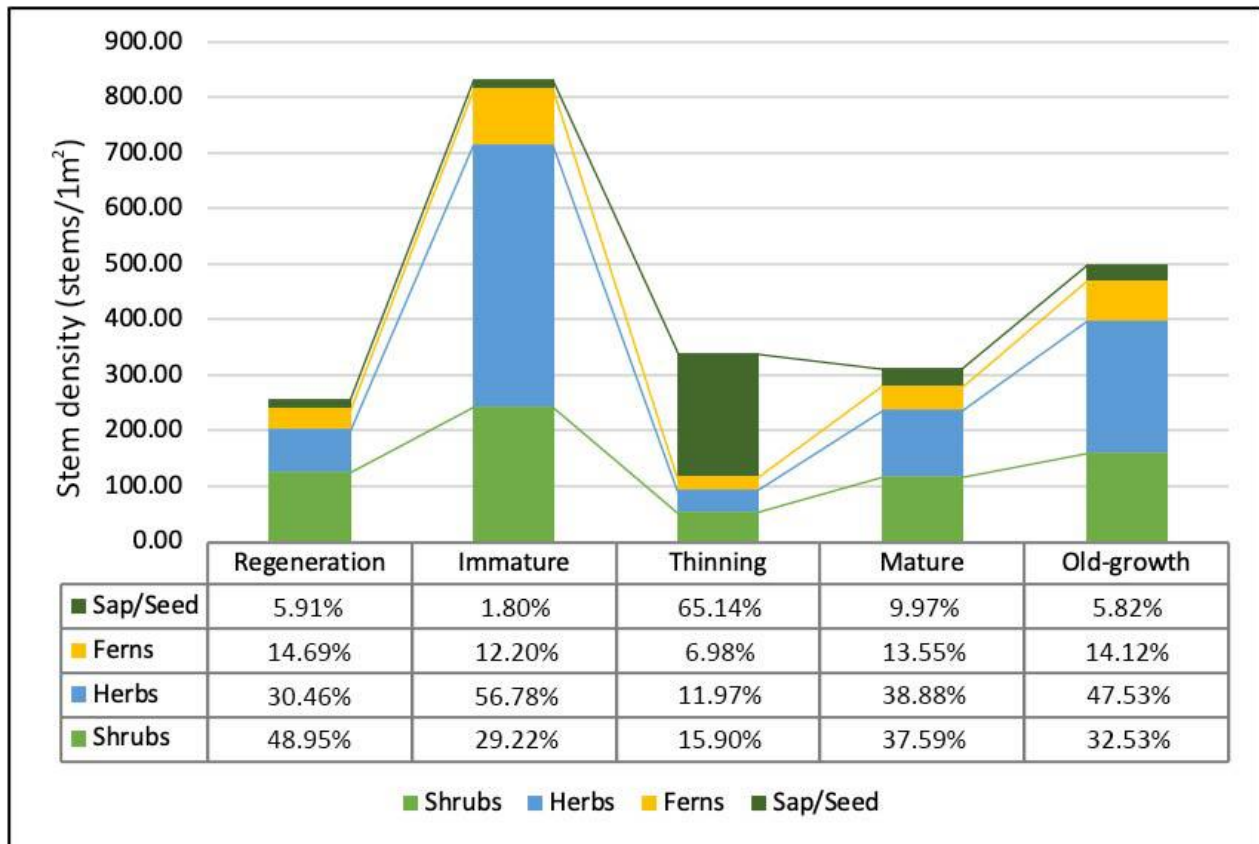


Figure 3.3 - Proportion of stem density by plant type averaged from all plots within each successional stage. Total mean stem density/m² of understory vegetation in subplots along the y-axis and successional stage along the x-axis.

The average shrub leaf cover (%) per plot differed significantly in one successional stage (Figure 3.4, Table 3.1). Shrubs had a significantly higher average leaf cover (Kruskal-Wallis, $p < 0.05$) in Immature, Mature, and Old-growth stages, compared to the Thinning stage. The average herb leaf cover (%) was significantly higher (Kruskal-Wallis, $p < 0.05$) in the Immature stage compared to the Thinning stage. Seedling and sapling average leaf cover (%) was significantly higher (Kruskal-Wallis, $p < 0.05$) in both Regeneration and Immature stages than in Thinning.

The Regeneration, Immature, Mature, and Old-growth successional stages leaf cover (%) were dominated by shrubs, at 59.41%, 54.62%, 76.50% and 76.11%, respectively (Figure 3.5).

The Thinning stage leaf cover was dominated by herbaceous plants at 50.3%. Ferns dominated over other herbaceous leaf cover in the Immature, Thinning, Mature, and the Old-growth stages, however other herbs dominated herbaceous leaf cover in the Regeneration stage (Figure 3.5).

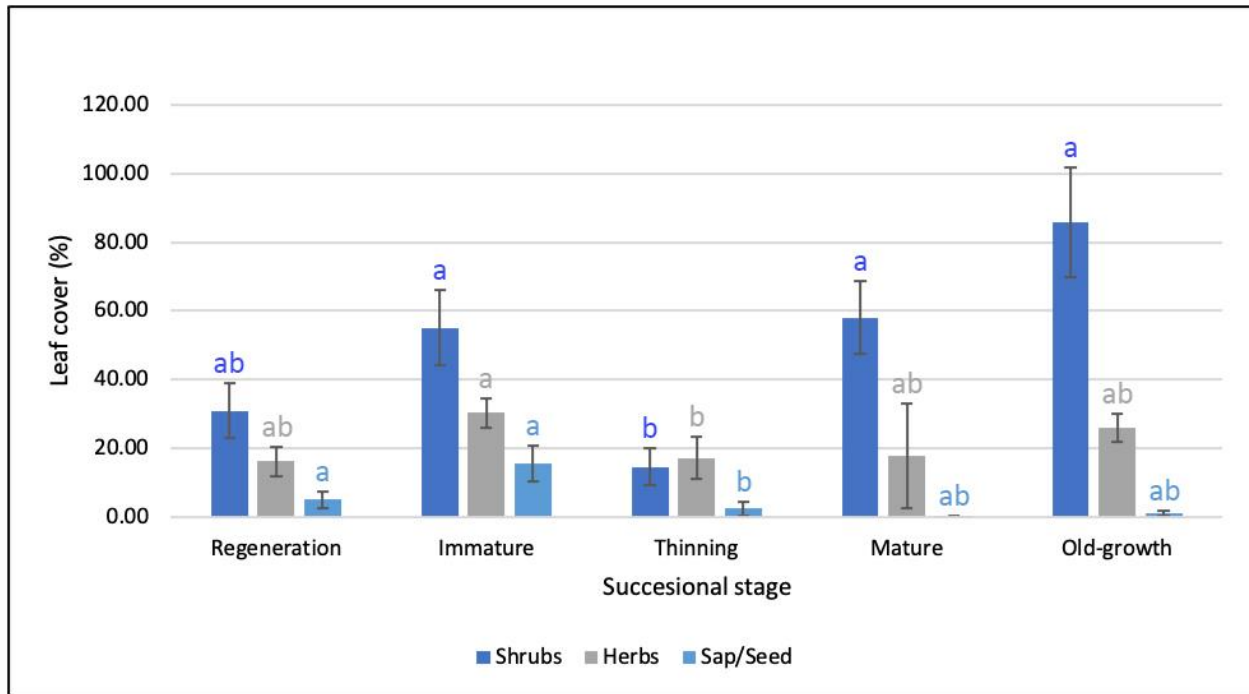


Figure 3.4 - Mean (\pm SE) understory leaf cover/m², for every successional stage. Leaf cover of shrubs, herbaceous plants, and tree sapling and seedlings. Error bars represent the variation of understory leaf cover between plots within each successional stage.

Table 3.2 - Average leaf cover (%) per plant type in 1 m² subplots, with standard error (SE).

Plant type	Regeneration	Immature	Thinning	Mature	Old-growth
Shrub	30.85 \pm 8.05ab	55.06 \pm 10.88a	14.47 \pm 5.47b	58.08 \pm 10.65a	86.03 \pm 16.00a
Herb	16.15 \pm 4.20ab	30.25 \pm 4.32a	17.02 \pm 6.16b	17.62 \pm 3.05ab	25.97 \pm 3.99ab
Seed/Sap	4.92 \pm 2.35a	15.49 \pm 5.19a	2.36 \pm 2.07b	0.23 \pm 0.09ab	1.03 \pm 0.65ab

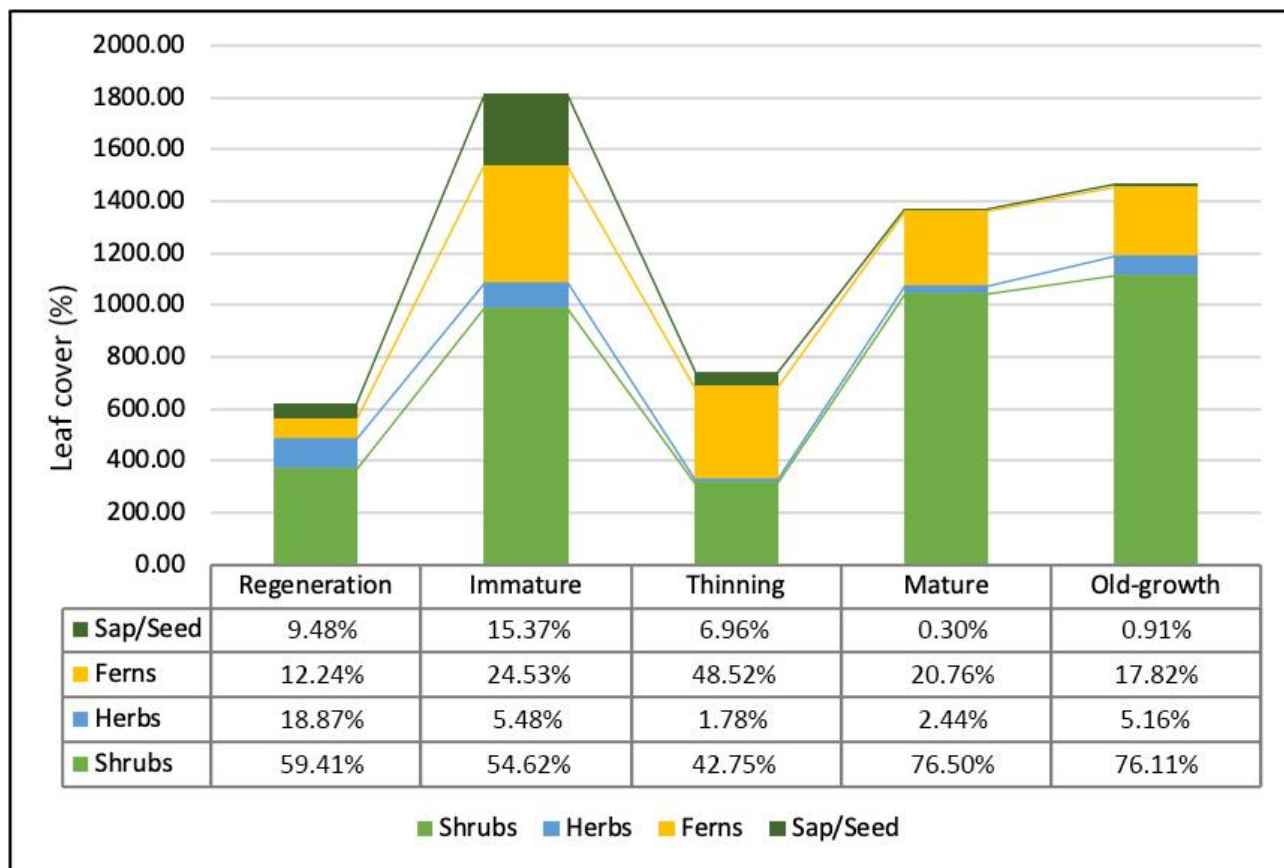


Figure 3.5 - Proportion of leaf cover by plant type averaged from all plots within each successional stage. Total mean leaf cover of understory vegetation in subplots along the y-axis and successional stage along the x-axis.

Table 3.3 – Mean (\pm SE) understory stem density (stems per m^2) and mean (\pm SE) understory leaf cover (%) for each successional stage per $1 m^2$ plot. Lowercase letters indicate groupings as determined by a Kruskal-Wallis statistical test. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different ($p < 0.05$).

	Regeneration	Immature	Thinning	Mature	Old-growth
Stem Density	21.45 \pm 3.13ab	46.28 \pm 11.82a	15.50 \pm 8.09b	17.38 \pm 2.55ab	38.35 \pm 12.25a
Leaf Cover	33.15 \pm 7.86ab	44.79 \pm 7.28a	14.02 \pm 4.16b	51.63 \pm 9.33ab	52.59 \pm 8.76a

3.1.2 Species Richness, Evenness, and Diversity

In total, 31 species were found across the Regeneration stage plots, 22 species in the Immature stage, 13 species in the Thinning stage, 20 species in the Mature stage, and 20 species in the Old-growth stage.

The Regeneration stage had a significantly higher Shannon-Weiner diversity than the Immature, Thinning, and Mature stages (Table 3.4 Figure 3.6A). The Immature stage had a significantly (Post hoc Tukey, $p < 0.05$) higher Shannon-Weiner diversity than the Thinning stage. The Thinning stage had the lowest Shannon-Weiner diversity out of all the stages; however, there was no statistical evidence of a difference between Thinning and Mature (Kruskal Wallis, n.s.). The Regeneration stage had significantly higher evenness than the Immature stage (Post hoc Tukey, $p < 0.05$) (Table 3.3, Figure 3.6B). Mean (+SE) species richness varied by successional stage (Table 3.3, Figure 3.6C). The Regeneration stage had a significantly (Post hoc Tukey, $p < 0.05$) higher species richness than the Thinning and Mature stages. The Thinning stage had a significantly (Post hoc Tukey, $p < 0.05$) lower species richness than all stages except the Mature stage.

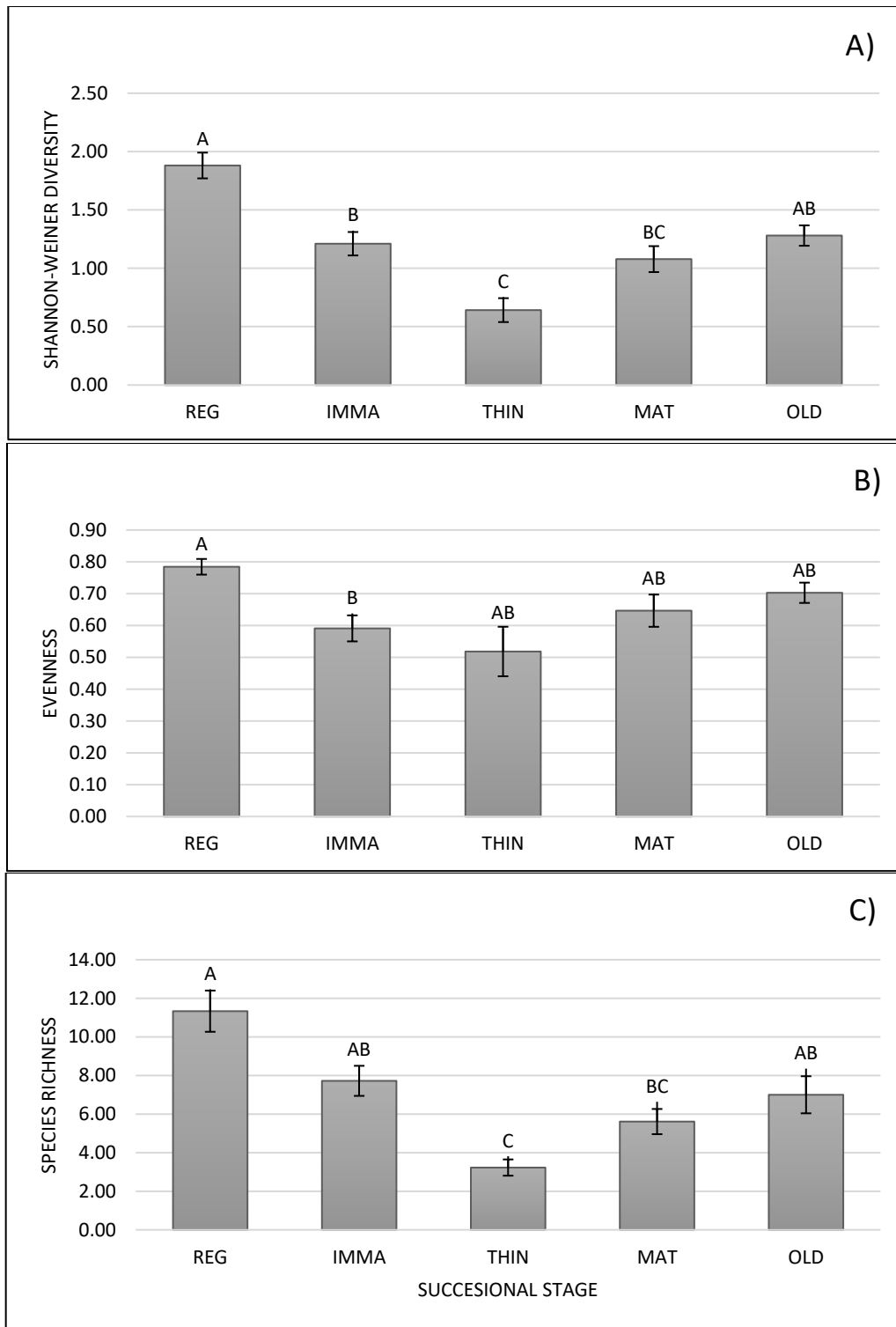


Figure 3.6 – A) Mean Shannon-Weiner diversity (\pm SE), B) mean species evenness (\pm SE), and C) mean species richness (\pm SE) of each successional stage. Refer to Figure 3.2 for X-axis label descriptions. Letters above the bars represents significance groupings (Refer to Table 3.2 for detailed description).

Table 3.4 - Mean and standard error of Shannon-Weiner diversity (\pm SE), evenness (\pm SE), and species richness (\pm SE) in each successional stage. Lowercase letters indicate groupings as determined by a Kruskal-Wallis statistical test. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different (Post hoc Tukey, $p < 0.05$).

	Regeneration	Immature	Thinning	Mature	Old-growth
Shannon-Weiner	1.88 \pm 0.11a	1.21 \pm 0.10b	0.64 \pm 0.10c	1.08 \pm 0.11bc	1.28 \pm 0.09ab
Evenness	0.78 \pm 0.02a	0.59 \pm 0.04b	0.52 \pm 0.08ab	0.65 \pm 0.05ab	0.70 \pm 0.03ab
Richness	11.33 \pm 1.07a	7.72 \pm 0.78ab	3.23 \pm 0.42c	5.61 \pm 0.65bc	7.00 \pm 0.96ab

3.1.3 Overstory metrics

The proportion of stand stem density (stems/ha) and basal area (m^2/ha) of each tree species present in the canopy varied by successional stages (Figure 3.7). There were no mature trees present in the Regeneration stage. Two species dominated by stem density but varied by stage: western red cedar in the Immature and Old-growth stage, and western hemlock in the Thinning and Mature stages. Pacific yew was only present in the Mature and Old-growth stages. There were two dominant tree species through all of the successional stages for basal area: western red cedar and western hemlock. The dominant tree species by basal area varied by stage: western red cedar in the Immature and Old-growth stages, and western hemlock in the Thinning and Mature stages.

The mean stand basal area (m^2/ha) was significantly different (Post hoc Tukey, $p < 0.001$) between Regeneration and every other successional stage, and between Immature and Thinning (Table 3.4). The stand basal area peaked in the Thinning stage and was the lowest in Regeneration, however there is no statistical evidence of this difference. The stand stem density (stems/ha) significantly differed (Post hoc Tukey, $p < 0.001$) between successional stages, with the highest stem density in Immature and lowest in the Regeneration.

Table 3.5 – Means and standard errors of stand basal area (m²/ha) and stem density (stems/ha) in each successional stage. Lowercase letters indicate groupings as determined by a Kruskal-Wallis statistical test. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different.

	Regeneration (n=6)	Immature (n = 15)	Thinning (n = 11)	Mature (n = 6)	Old-growth (n = 7)	p- value
Stand basal area (m ² /ha)	0.00a	9.11 ± 2.24ac	72.71 ± 4.70b	159.21 ± 37.55b	91.23 ± 33.04bc	0.001
Stand stem density (stems/ha)	0.00a	1530.00 ± 352.02b	1588.64 ± 351.90b	958.33 ± 236.49ab	596.42 ± 173.68ab	0.001

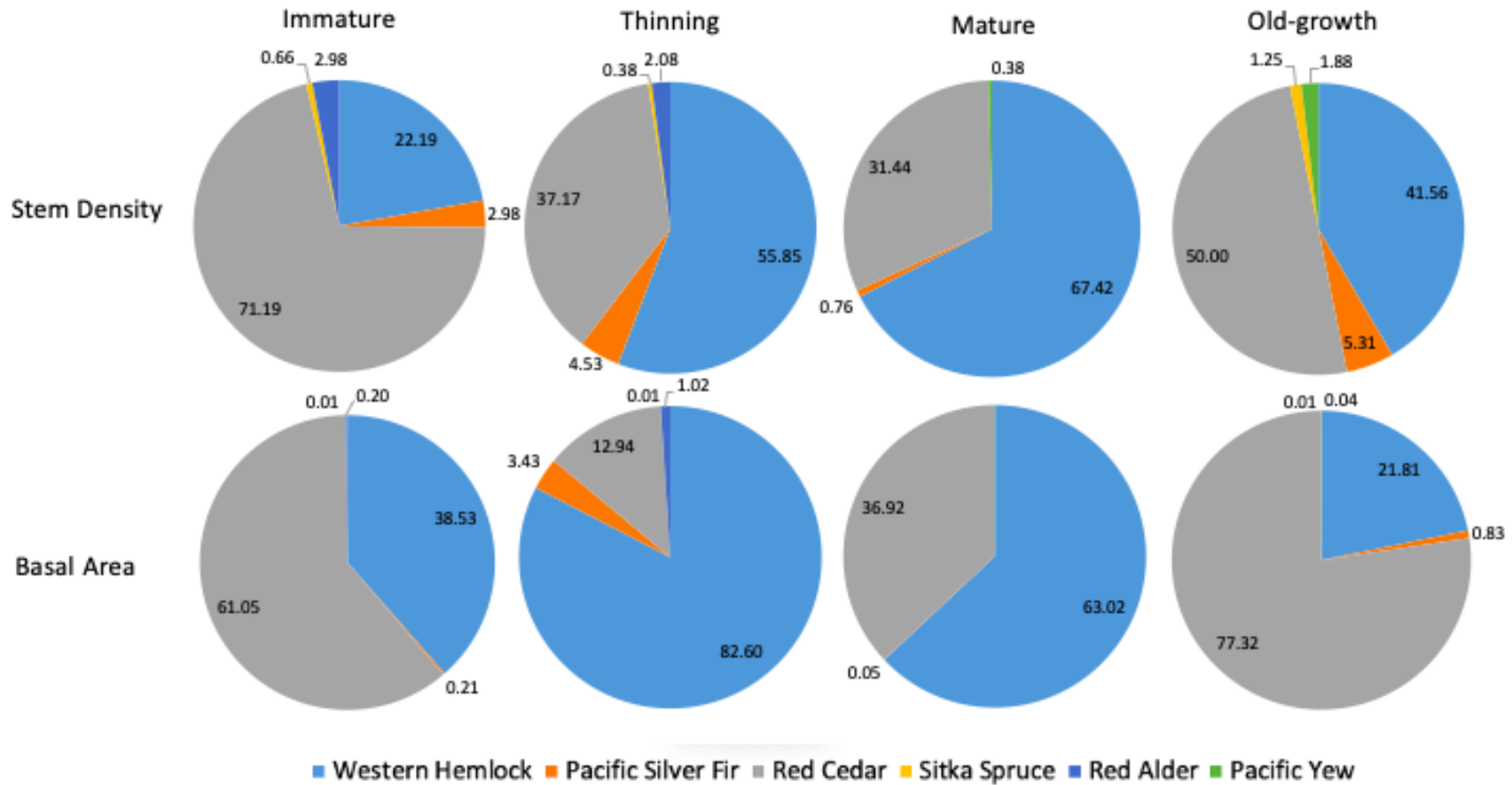


Figure 3.7 - Percent of tree species present in the overstory in each successional stage, based on tree stem density (stems/ha) and tree basal area (m²/ha). Regeneration stage is excluded since no mature trees (> 5 cm dbh) were present.

3.2 Ecological and Environmental Variables

All the environmental variables, bare ground cover (%), moss cover (%), A horizon depth (cm), soil profile depth (cm), soil pH, canopy openness (%), and elevation (m) differed significantly (Post hoc Tukey, $p < 0.05$) between successional stages (Table 3.5). The pairwise comparisons show that bare ground cover (%) was significantly different (Post hoc Tukey, $p < 0.001$) between the Regeneration stage and every other successional stage (Table 3.5). Moss cover was significantly lower (Post hoc Tukey, $p < 0.001$) in Regeneration stands compared to Thinning and Mature stands, while Immature and Old-Growth stands had intermediate moss cover values (Table 3.6). There was a significant difference (Post hoc Tukey, $p < 0.001$) in A horizon depth (cm), with thinner depths in the Regeneration stage compared to all other successional stages (Table 3.6). Soil profile depth (cm) showed a significant difference (Post hoc Tukey, $p < 0.001$) between Regeneration and Mature stages. There was a significant difference (Post hoc Tukey, $p < 0.05$) in mean soil pH found between Old-growth and every other successional stage. The mean canopy openness (%) was significantly different (Post hoc Tukey, $p < 0.001$) between the Regeneration and Thinning stage.

Table 3.6 – Means and standard errors of environmental variables in each successional stage. Lowercase letters indicate groupings as determined by a Kruskal-Wallis statistical test. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different. The Post hoc Tukey test is represented by the p-value.

	Regeneration (n=12)	Immature (n = 18)	Thinning (n = 22)	Mature (n = 18)	Old-growth (n = 13)	p- value
Bare ground cover (0 – 500%)	69.33 ± 17.34a	3.33 ± 1.19b	4.14 ± 0.94b	5.44 ± 0.92b	7.85 ± 3.88b	0.001
Moss cover (0 – 500%)	11.43 ± 4.52a	26.44 ± 8.33ab	57.77 ± 9.64b	53.67 ± 10.18b	30.92 ± 10.74ab	0.001
A horizon depth (cm)	7.83 ± 1.41a	19.18 ± 2.58b	16.27 ± 1.36b	28.33 ± 2.84b	20.08 ± 2.51b	0.001
Profile depth (cm)	20.33 ± 1.88a	30.78 ± 2.18ab	28.14 ± 2.40ab	38.06 ± 2.93b	26.54 ± 2.95ab	0.001

pH	4.73 ± 0.10a	4.62 ± 0.05a	4.59 ± 0.12a	4.46 ± 0.07a	4.32 ± 0.06b	0.009
Canopy openness (%)	77.58 ± 1.64a (n=12)	34.34 ± 5.14ac (n=18)	10.88 ± 0.60bc (n=22)	9.92 ± 0.70b (n=18)	10.25 ± 0.99b (n=13)	0.001
Canopy openness* (%)	77.58 ± 1.64a (n=12)	34.34 ± 5.14ac (n=18)	10.88 ± 0.60b (n=22)	11.22 ± 1.87bc (n=5)*	13.29 ± 1.00bc (n=5)*	0.001
Elevation (m)	139.83 ± 43.47ab	137 ± 14.69a	62.45 ± 8.71b	26.56 ± 2.96b	102.08 ± 34.69ab	0.001

The asterisk (*) represents a separate Canopy Openness calculation, with a smaller sample size, to account for the understory vegetation presence in hemispherical images of mature and old-growth stands.

3.3 Species-Specific Statistics

3.3.1 Shrubs

From the 13 shrub species identified in the study, there were a few dominant patterns in both leaf cover (%) and stem density (stems/m²). False azalea, oval leaf blueberry, red huckleberry, salal, and salmonberry were found in all successional stages, and are considered common species. Black raspberry, thimbleberry, and red elderberry were found only in the Regeneration stands (Table 3.6, Table 3.7). The stem density and leaf cover of Salmonberry was found to be significantly higher (Post hoc Tukey, p<0.001) in Regeneration and Immature stands. False Azalea was significantly (Post hoc Tukey, p<0.05) lower in stem density and leaf cover in the Thinning stage, compared to Immature and Mature stages (Table. 3.6, Table 3.7). The stem density of Salal was significant lower (Post hoc Tukey, p<0.001) in the Thinning stages and higher in the Immature. The stem densities of red huckleberry and oval-leaf blueberry were significantly higher (Post hoc Tukey, p<0.001) in the Old-growth stage compared to the Thinning stage (Table 3.7). The two species exhibited significant differences (Post hoc Tukey, p<0.05) in stem density between stages, but not in leaf cover.

Table 3.7 – Mean density (stems/m²) and standard error of shrubs in each successional stage. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different.

	Regeneration (n = 12)	Immature (n = 22)	Thinning (n = 18)	Mature (n = 16)	Old-growth (n = 15)	p- value
Black Raspberry	0.10 ± 0.068a	0.00b	0.00b	0.00b	0.00b	0.001
Cascara Sagrada	0.034 ± 0.034	0.034 ± 0.034	0.00	0.012 ± 0.012	0.016 ± 0.016	n.s.
Evergreen Huckleberry	0.00	0.212 ± 0.126	0.018 ± 0.018	0.4 ± 0.332	0.37 ± 0.254	n.s.
False Azalea	0.084 ± 0.068ab	1.14 ± 0.51a	0.018 ± 0.018b	0.67 ± 0.39a	0.31 ± 0.13ab	0.001
Oval-Leaf Blueberry	0.28 ± 0.12ab	0.27 ± 0.12ab	0.01 ± 0.01a	2.7 ± 0.17ab	0.57 ± 0.26b	0.036
Pacific Crab Apple	0.00	0.012 ± 0.012	0.00	0.00	0.00	n.s.
Red Elderberry	0.92 ± 0.45a	0.00b	0.00b	0.00b	0.00b	0.001
Red Huckleberry	0.27 ± 0.14a	0.64 ± 0.15ab	1.07 ± 0.38ab	1.77 ± 0.64ab	3.37 ± 1.08b	0.022
Salal	2.7 ± 1.004ac	10.54 ± 1.39b	1.21 ± 0.31a	3.36 ± 0.76ac	7.8 ± 2.08bc	0.001
Salmon berry	5.15 ± 1.26a	0.67 ± 0.20ab	0.14 ± 0.09b	0.06 ± 0.04b	0.046 ± 0.034b	0.001
Thimble berry	0.97 ± 0.33a	0.00b	0.00b	0.00b	0.00b	0.001
Black Twinberry	0.00	0.04 ± 0.04	0.00	0.00	0.00	n.s.
Twinflower	0.00	0.58 ± 0.38	0.00	0.00	1.48 ± 0.94	n.s.

Table 3.8 – Mean leaf cover % and standard error of shrubs in each successional stage. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different.

	Regeneration (n = 12)	Immature (n = 22)	Thinning (n = 18)	Mature (n = 16)	Old-growth (n = 15)	p- value
Black Raspberry	0.64 ± 0.58a	0.00b	0.00b	0.00b	0.00b	0.001
Cascara Sagrada	0.42 ± 0.42	0.18 ± 0.18	0.00	0.006 ± 0.006	0.25 ± 0.25	n.s.
Evergreen Huckleberry	0.00	1.03 ± 0.59	1.91 ± 1.91	6.45 ± 3.80	7.02 ± 6.19	n.s.
False Azalea	0.19 ± 0.18ac	1.40 ± 0.69a	0.50 ± 0.50bc	1.86 ± 1.39a	2.34 ± 2.30ac	0.002
Oval-Leaf Blueberry	0.85 ± 0.48	1.96 ± 1.01	0.054 ± 0.054	5.00 ± 3.89	5.19 ± 3.75	n.s.
Pacific Crab Apple	0.00	0.11 ± 0.11	0.00	0.00	0.00	n.s.
Red Elderberry	4.00 ± 2.82a	0.00b	0.00b	0.00b	0.00b	0.001
Red Huckleberry	0.79 ± 0.53	1.11 ± 0.29	0.78 ± 0.42	5.30 ± 2.00	2.82 ± 1.34	n.s.
Salal	3.61 ± 1.72a	45.54 ± 10.32b	5.83 ± 3.00a	39.42 ± 10.47b	68.41 ± 14.76b	0.001

Salmon berry	15.17 ± 4.66a	3.74 ± 1.16ab	5.40 ± 4.46bc	0.02 ± 0.02c	0.004 ± 0.002bc	0.001
Thimble berry	5.19 ± 2.78a	0.00b	0.00b	0.00b	0.00b	0.001
Black Twinberry	0.00	0.11 ± 0.11	0.00	0.00	0.00	n.s.
Twinflower	0.00	0.20 ± 0.14	0.00	0.00	0.29 ± 0.17	n.s.

3.3.2 Herbaceous Plants

There were 20 herbaceous plant species identified in the study sites. False lily of the valley was the only common herbaceous plant that was present in every successional stage, with a significantly higher ((Post hoc Tukey, $p < 0.001$) stem density and leaf cover in Immature and Old-growth stages compared to the Thinning stage (Tables 3.8 & 3.9). Grass cover was significantly higher (Post hoc Tukey, $p < 0.001$) in the Regeneration stage than any other stage, in both stem density and leaf cover. Douglas spirea was significantly higher (Post hoc Tukey, $p < 0.03$, $p < 0.01$) in both values in the Regeneration stage, compared to Thinning, Mature, and Old-growth, however, did not significantly differ from the Immature stage. Fireweed was significantly higher (Post hoc Tukey, $p < 0.01$) in the Regeneration stage than any other stage for stem density and leaf cover. Foam flower is significantly higher (Post hoc Tukey, $p < 0.02$) in the Regeneration stage compared to the Thinning stage.

Table 3.9 – Mean density (stems/m²) and standard error of herbaceous plants in each successional stage. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different.

	Regeneration (n = 12)	Immature (n = 22)	Thinning (n = 18)	Mature (n = 16)	Old-growth (n = 15)	p- value
Bunchberry	0.18 ± 0.18	6.82 ± 3.72	0.00	0.00	8.63 ± 6.12	n.s.
Canada Thistle	0.12 ± 0.08ac	0.00b	0.00b	0.00b	0.00bc	0.018
Clasping Twisted Stalk	0.08 ± 0.07	0.00	0.00	0.02 ± 0.02	0.00	n.s.
Common Horsetail	0.00	0.08 ± 0.07	0.00	0.00	0.00	n.s.
Douglas Spirea	0.08 ± 0.05ac	0.11 ± 0.11bc	0.00b	0.00b	0.00b	0.012
Fern-leaved Goldthread	0.00ab	0.00ab	0.00a	0.00ab	1.12 ± 1.09b	0.028

Green False Hellebore	0.00	0.00	0.00	0.00	0.016 ± 0.016	n.s.
False Lily of The Valley	0.52 ± 0.41ab	9.52 ± 2.88a	1.85 ± 1.68b	6.16 ± 1.84ab	5.94 ± 2.00a	0.001
Fireweed	1.25 ± 0.40a	0.08 ± 0.05b	0.00b	0.00b	0.00b	0.001
Foam Flower	0.35 ± 0.19a	0.00ab	0.00b	0.44 ± 0.43ab	0.00ab	0.020
Fringed Willowherb	0.03 ± 0.02ac	0.00b	0.00b	0.00b	0.00bc	0.018
Grass	1.12 ± 0.38a	0.13 ± 0.07b	0.00b	0.00b	0.80 ± 0.80b	0.001
Northwestern Twayblade	0.00ab	0.00ab	0.00a	0.00ab	0.23 ± 0.21b	0.028
One-flowered Wintergreen	0.00	0.00	0.00	0.13 ± 0.13	0.00	n.s.
Pearly Everlasting	1.02 ± 0.72a	0.00b	0.00b	0.00b	0.00b	0.001
Rush Skeleton Weed	0.33 ± 0.23ac	0.00b	0.00b	0.00b	0.00bc	0.018
Smooth Cats Ear	0.38 ± 0.32ac	0.00b	0.00b	0.00b	0.00bc	0.018
Wall Lettuce	1.00 ± 0.60a	0.00b	0.00b	0.00b	0.00b	0.001
Western Boykinia	0.00	8.79 ± 6.89	0.00	0.00	0.00	n.s.
Western Skunk Cabbage	0.07 ± 0.04a	0.03 ± 0.03ab	0.00b	0.00ab	0.016 ± 0.016ab	0.041

Table 3.10 – Mean cover % and standard error of herbaceous plants in each successional stage. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different.

	Regeneration (n = 12)	Immature (n = 22)	Thinning (n = 18)	Mature (n = 16)	Old-growth (n = 15)	p-value
Bunchberry	0.06 ± 0.06	1.15 ± 0.72	0.00	0.00	2.69 ± 1.77	n.s.
Canada Thistle	0.13 ± 0.10ac	0.00b	0.00b	0.00b	0.00bc	0.018
Clasping Twisted Stalk	0.08 ± 0.07	0.00	0.00	0.04 ± 0.04	0.00	n.s.
Common Horsetail	0.00	0.06 ± 0.05	0.00	0.00	0.00	n.s.
Douglas Spirea	0.78 ± 0.51ac	0.27 ± 0.27bc	0.00b	0.00b	0.00b	0.011
Fern-leaved Goldthread	0.00ac	0.00bc	0.00ac	0.00ac	0.08 ± 0.07a	0.028
Green False Hellebore	0.00	0.00	0.00	0.00	1.08 ± 1.08	n.s.
False Lily of The Valley	0.07 ± 0.06ab	1.77 ± 0.48a	0.60 ± 0.50b	1.72 ± 0.53ab	2.32 ± 0.82a	0.001
Fireweed	5.75 ± 3.42a	0.20 ± 0.12b	0.00b	0.00b	0.00b	0.001
Foam Flower	0.18 ± 0.11a	0.00b	0.00b	0.07 ± 0.07ab	0.00ab	0.019
Fringed Willowherb	0.03 ± 0.03a	0.00bc	0.00bc	0.00bc	0.00ac	0.018
Grass	0.17 ± 0.07a	0.03 ± 0.02b	0.00b	0.00b	0.08 ± 0.08b	0.001
Northwestern Twayblade	0.00ab	0.00ab	0.00a	0.00ab	0.006 ± 0.004b	0.028

One-flowered Wintergreen	0.00	0.00	0.00	0.02 ± 0.02	0.00	n.s.
Pearly Everlasting	0.58 ± 0.35a	0.00b	0.00b	0.00bb	0.00b	0.001
Rush Skeleton Weed	1.29 ± 1.17ac	0.00b	0.00b	0.00b	0.00bc	0.018
Smooth Cats Ear	0.16 ± 0.11ac	0.00b	0.00b	0.00b	0.00bc	0.018
Wall Lettuce	0.26 ± 0.12a	0.00b	0.00b	0.00b	0.00b	0.001
Western Boykinia	0.00	1.06 ± 0.83	0.00	0.00	0.00	n.s.
Western Skunk Cabbage	0.24 ± 0.24a	0.67 ± 0.67ab	0.00b	0.00ab	0.14 ± 0.14ab	0.044

3.3.3 Ferns

There were five fern species identified in the study sites, with an additional category for unidentified ferns. Deer fern was found present in every successional stage, making it a common species (Table 3.10 & 3.11). Deer fern had a significantly higher (Post hoc Tukey, $p < 0.001$) stem density in the Immature and Old-growth stages than the Thinning stage. Bracken fern was only found in the Old-growth stage and licorice fern was found only in the Mature stage. Lady fern was only found within the Regeneration and Thinning stages, with similar stem densities, but had a much higher leaf cover in the Thinning stage (Post hoc Tukey, n.s). Sword fern was not found within the Old-growth stage, however, was present in all other stages. Though there was a higher stem density of sword fern in the Regeneration stage, the Thinning stage had a higher leaf cover (Post hoc Tukey, n.s).

Table 3.11 – Mean density and standard error of ferns in each successional stage. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different.

	Regeneration (n = 12)	Immature (n = 22)	Thinning (n = 18)	Mature (n = 16)	Old-growth (n = 15)	p-value
Bracken Fern	0.00	0.00	0.00	0.00	0.016 ± 0.016	n.s.
Deer Fern	2.63 ± 0.67ac	5.58 ± 0.94a	0.71 ± 0.25bc	2.22 ± 0.48ac	5.4 ± 1.55a	0.001
Lady Fern	0.07 ± 0.07	0.00	0.08 ± 0.08	0.00	0.00	n.s.
Licorice Fern	0.00	0.00	0.00	0.02 ± 0.02	0.00	n.s.
Sword Fern	0.32 ± 0.18	0.07 ± 0.04	0.21 ± 0.09	0.09 ± 0.06	0.00	n.s.
Other Ferns	0.13 ± 0.10	0.00	0.08 ± 0.06	0.03 ± 0.02	0.00	n.s.

Table 3.12 – Mean cover % and standard error of ferns in each successional stage. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different.

	Regeneration (n = 12)	Immature (n = 22)	Thinning (n = 18)	Mature (n = 16)	Old-growth (n = 15)	p- value
Bracken Fern	0.00	0.00	0.00	0.00	0.46 ± 0.46	n.s.
Deer Fern	3.68 ± 0.96ac	24.69 ± 4.00c	2.67 ± 1.39a	13.65 ± 2.60bc	19.68 ± 3.95bc	0.001
Lady Fern	0.006 ± 0.006	0.00	0.17 ± 0.17	0.00	0.00	n.s.
Licorice Fern	0.00	0.00	0.00	0.006 ± 0.006	0.00	n.s.
Sword Fern	2.55 ± 1.51	0.04 ± 0.02	12.95 ± 5.33	1.85 ± 1.27	0.00	n.s.
Other Ferns	0.13 ± 0.12	0.00	0.62 ± 0.48	0.26 ± 0.26	0.00	n.s.

3.3.4 Tree Seedlings and Saplings

There were five tree species present as seedlings and saplings. There is a significantly higher (Post hoc Tukey, $p < 0.05$) leaf cover for Western hemlock seedlings in Thinning stands than in Regeneration. Western hemlock seedlings were found in every successional stage (Tables 3.12 & 3.13). Western red cedar saplings were found to have a significantly higher (Post hoc Tukey, $p < 0.001$) stem density and leaf cover in the Immature stage than in all other stages, whereas the only significant difference (Post hoc Tukey, $p < 0.05$) between western red cedar seedlings was higher values in the Regeneration stage than Thinning (Tables 3.12, 3.13). Pacific fir saplings were only found in regeneration stands. Sitka spruce seedlings and saplings have significantly higher (Post hoc Tukey, $p < 0.05$) stem density and leaf cover in Regeneration stands than other stands.

Table 3.13 – Mean density (stems/m²) and standard error of tree seedlings and saplings in each successional stage. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different.

	Regeneration (n = 12)	Immature (n = 22)	Thinning (n = 18)	Mature (n = 16)	Old-growth (n = 15)	p- value
Red alder sapling	0.00	0.02 ± 0.02	0.00	0.00	0.00	n.s.
Red alder seedling	0.00	0.07 ± 0.07	0.00	0.012 ± 0.012	0.00	n.s.
Pacific silver fir sapling	0.05 ± 0.04ac	0.00b	0.00b	0.00b	0.00bc	0.018

Pacific silver fir seedling	0.00ab	0.00a	0.63 ± 0.55b	0.04 ± 0.04ab	0.00ab	n.s.
Western red cedar sapling	0.00a	0.21 ± 0.08b	0.00a	0.00a	0.06 ± 0.06a	0.001
Western red cedar seedling	0.13 ± 0.05a	0.28 ± 0.17ab	0.00b	0.012 ± 0.012ab	0.62 ± 0.55ab	0.008
Western hemlock sapling	0.00	0.13 ± 0.10	0.01 ± 0.01	0.012 ± 0.012	0.06 ± 0.05	n.s.
Western hemlock seedling	0.88 ± 0.27a	0.11 ± 0.05b	9.45 ± 7.24ab	1.66 ± 0.64ab	1.43 ± 0.77ab	0.001
Sitka spruce sapling	0.05 ± 0.04a	0.00b	0.00b	0.00b	0.00ab	0.018
Sitka spruce seedling	0.15 ± 0.09a	0.00b	0.00b	0.00b	0.06 ± 0.05ab	0.001

Table 3.14 – Mean leaf cover % and standard error of tree seedlings and saplings in each successional stage. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different.

	Regeneration (n = 12)	Immature (n = 22)	Thinning (n = 18)	Mature (n = 16)	Old-growth (n = 15)	p-value
Red alder sapling	0.00	0.17 ± 0.17	0.00	0.00	0.00	n.s.
Red alder seedling	0.00	0.09 ± 0.09	0.00	0.002 ± 0.002	0.00	n.s.
Pacific silver fir sapling	0.60 ± 0.46ac	0.00b	0.00b	0.00b	0.00bc	0.018
Pacific silver fir seedling	0.00	0.00	0.52 ± 0.51	0.016 ± 0.016	0.00	n.s.
Western red cedar sapling	0.00a	12.33 ± 4.95b	0.00a	0.00a	0.17 ± 0.17a	0.001
Western red cedar seedling	0.43 ± 0.25a	0.38 ± 0.34ab	0.00b	0.002 ± 0.002ab	0.16 ± 0.13ab	0.005
Western hemlock sapling	0.00	2.44 ± 1.33	0.06 ± 0.06	0.03 ± 0.03	0.37 ± 0.31	n.s.
Western hemlock seedling	0.42 ± 0.20a	0.07 ± 0.04ab	1.77 ± 1.57b	0.17 ± 0.06ab	0.31 ± 0.51ab	0.025
Sitka spruce sapling	3.33 ± 2.26a	0.00b	0.00b	0.00b	0.00ab	0.018
Sitka spruce seedling	0.13 ± 0.11a	0.00b	0.00b	0.00b	0.03 ± 0.02ab	0.001

3.3.6 – Tree species

The Thinning and Mature stages were significantly higher (Post hoc Tukey, $p < 0.01$) in western hemlock mean basal area (m^2/ha) and mean stem density (stems/ha) than the Regeneration and Immature stages (Table 3.14 & 3.15). Pacific silver fir mean basal area was significantly higher (Post hoc Tukey, $p < 0.01$) in the Mature stage compared to Regeneration and

Thinning stages. There was a significant difference (Kruskal-Wallis, $p < 0.03$) in western red cedar stem density between stages, with the post-hoc Tukey test ($p < 0.05$) identifying differences between the Regeneration and Mature stages, as well as a significant increase in basal area between the Regeneration Old-growth stage. Pacific yew had a significantly higher (Post hoc Tukey, $p < 0.01$) mean basal area in the Old-growth stage compared to Regeneration and Thinning stages. Red alder and Sitka spruce showed no statistical difference between any successional stage.

Table 3.15 – Mean stem density (stems/ha) and standard error of trees species per hectare. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different.

	Regeneration (n = 6)	Immature (n = 5)	Thinning (n = 11)	Mature (n = 6)	Old-growth (n = 7)	p- value
Western hemlock	0.00a	110.00 ± 69.86ac	829.55 ± 143.59b	612.5 ± 152.04bc	260.71 ± 68.67ab	0.001
Pacific silver fir	0.00	90.00 ± 69.86	52.27 ± 20.69	4.17 ± 3.80	32.14 ± 6.6	n.s.
Western red cedar	0.00a	1260 ± 313.50b	659.09 ± 231.27ab	337.5 ± 168.51b	282.14 ± 104.70ab	0.003
Sitka spruce	0.00	20.00 ± 7.62	4.55 ± 4.33	0.00	10.71 ± 9.92	n.s.
Red alder	0.00	50.00 ± 34.64	43.18 ± 20.85	0.00	0.00	n.s.
Pacific yew	0.00	0.00	0.00	4.17 ± 3.80	10.71 ± 4.68	n.s.

Table 3.16 – Mean basal area (m²/ha) and standard error of trees species per hectare. Categories with the same lowercase letter are statistically similar, while those with different letters are significantly different.

	Regeneration (n = 6)	Immature (n = 5)	Thinning (n = 11)	Mature (n = 6)	Old-growth (n = 7)	p- value
Western hemlock	0.00a	0.59 ± 0.40a	41.37 ± 6.18b	90.96 ± 30.56b	14.30 ± 5.03ab	0.001
Pacific silver fir	0.00a	0.46 ± 0.32ab	6.55 ± 2.98bc	0.39 ± 0.35c	3.10 ± 1.15bc	0.001
Western red cedar	0.00a	7.83 ± 2.17ab	22.25 ± 6.30b	67.81 ± 37.77ab	73.68 ± 29.23b	0.009
Sitka spruce	0.00	0.08 ± 0.07	0.15 ± 0.15	0.00	0.03 ± 0.02	n.s.
Red alder	0.00	0.15 ± 0.08	2.38 ± 1.65	0.00	0.00	n.s.
Pacific yew	0.00a	0.00ab	0.00a	0.05 ± 0.04ab	0.13 ± 0.07b	0.01

3.3.5 Restricted Species

There were a number of ‘restricted’ or ‘indicator’ species found in only one successional stage (Table 3.16). There was a mix of both herbaceous and shrub species restricted within the understory of the Regeneration successional stage including, three shrubs and six herbaceous plants. The Immature stage had one shrub species and three herbaceous plant species. There were no understory species restricted in the Thinning stage. The Mature successional stage had two restricted understory herbaceous plant species. Finally, the old-growth stage had four restricted species that were herbaceous plants and one tree species in the overstory.

In contrast, there were eight species that were found throughout every successional stage including: false lily of the valley, false azalea, oval-leaf blueberry, red huckleberry, salal, salmon berry, deer fern, and western hemlock seedlings.

Table 3.17 - Species restricted to each successional stage.

Regeneration			
<i>Rubus leucodermis</i> (Black raspberry)	<i>Sambucus racemosa</i> (Red elderberry)	<i>Cirsium arvense</i> (Canada thistle)	<i>Epilobium ciliatum</i> (Fringed willowherb)
<i>Anaphalis margaritacea</i> (Pearly everlasting)	<i>Chondrilla juncea</i> (Rush skeleton weed)	<i>Hypochaeris glabra</i> (Smooth cat’s ear)	<i>Mycelis muralis</i> (Wall lettuce)
<i>Rubus parviflorus</i> (Thimbleberry)			
Immature			
<i>Malus fusca</i> (Pacific crab apple)	<i>Lonicera involucrate</i> (Black twinberry)	<i>Boykinia occidentalis</i> (Western boykinia)	<i>Equisetum arvense</i> (Common horsetail)
Thinning			
Mature			
<i>Polypodium glycyrrhiza</i> (Licorice fern)	<i>Moneses uniflora</i> (One-flowered wintergreen)		
Old-growth			
<i>Coptis asplenifolia</i> (Fern-leaved goldthread)	<i>Neottia banksiana</i> (Northwestern twayblade)	<i>Pteridium aquilinum</i> (Bracken fern)	<i>Veratrum viride</i> (Green false hellebore)
<i>Taxus brevifolia</i> (Pacific yew)			

3.4 Multivariate Ordination

3.4.1 Site ordination

Canonical correspondence analysis (CCA) illustrates vegetation community patterns based on the presence and abundance of species in each site. Sites are distributed in the ordination space CCA based on similarities in species composition such that points that are near reflect a similar species composition, while points that are widely separated in ordination space share few, if any, species. Based on understory plant stem density, the sites in the Regeneration stage are mostly congregated together in the lower left quadrant (Figure 3.8). This grouping indicates similar species compositions, associated with higher values of bare ground cover (%), soil pH, northness (north-facing slopes), and canopy openness (%), and lower values of soil profile depth (cm), moss cover (%), stand age, tree stem density (stems/ha), and tree basal area (m^2/ha). The Thinning and Mature stage sites are generally overlapping, indicating similar species compositions between these two stages, and are found mainly in the mid-range of most environmental variables, however, are associated with lower elevations, and most associated with eastness (east-facing slopes). With three exceptions, nearly all immature sites are grouped tightly in the middle of the ordination space suggesting highly similar species composition and an association with mid-range values for all environmental and ecological variables. Much like Immature understories, Old-growth sites were found mainly grouped in the middle of the graph, associated with intermediate values of the environmental and ecological variables. This largely overlapping of Immature and Old-growth sites suggests similarities in species composition based on understory plant stem density.

Environmental variables are closely related to each other shown through the grouping of vectors in the ordinations. For example, bare ground cover has high values related with canopy

openness, soil pH, and north facing slopes, demonstrated through the grouping of their vectors in the ordination (Figure 3.8). Stand basal area, moss cover, soil profile depth, and stand age are also grouped together, meaning they have high values related to one another (Figure 3.8).

Like the CCA ordination based on stem density (Figure 3.8), the ordination based on understory plant leaf cover has some grouping (Figure 3.9). The Regeneration sites are mostly grouped together on the left side of the graph, associated with higher values of bare ground cover (%), soil pH, northness, and canopy openness (%), and associated with lower values of soil profile depth (cm), moss cover (%), stand age, tree stem density (stems/ha), and tree basal area (m^2/ha). Three Immature sites, along with two old-growth sites have higher values associated with elevation, whereas the four Thinning sites had lower values. The remaining sites in other stages (Regeneration, Mature, and Old-growth) were grouped together on along the right side of the graph, with similar species compositions, and associated with slightly higher values of eastness, moss cover, tree basal area (m^2/ha), soil profile depth, stand age, and tree stem density (stems/ha).

3.4.2 Species ordinations

In the Canonical Correspondence Analysis used to analyze the three different species types – herbs, shrubs, tree seedlings and saplings – in relation to various environmental and ecological variables, multiple patterns were found for both stem density (Figure 3.10) and leaf cover (Figure 3.11). Shrubs, herbaceous plants, and tree seedlings and saplings all have even distribution throughout the graphs (Figure 3.10; Figure 3.11). The overall trend seems to be a grouping of species, in both stem density and leaf cover graphs, that have high values associated with bare ground cover, openness, and to a lesser degree pH and northness. There is a small group of species that have high values associated with elevation, and another group with values

negatively associated with elevation values. In Figure 3.10, there is a group of species concentrated around the center, alluding to similar values across all environmental variables. There is a group species in the leaf cover graph (Figure 3.11) that have higher values relating to basal area, eastness, basal area, profile depth, age, moss cover, and stem density. Herbaceous plants appear to have a slightly broader spread. Tree sapling and seedling species are clumped in a linear stretch from the upper left to the lower right, showing intermediate stem density values for most of the environmental variables (Figure 3.10). The herbs appear to be associated with both higher and lower values for the environmental variables; however, have a larger spread when it comes to leaf cover. Aside from the light loving species, shrubs appear to be associated with intermediate stem density values for all environmental variables (Figure 3.10).

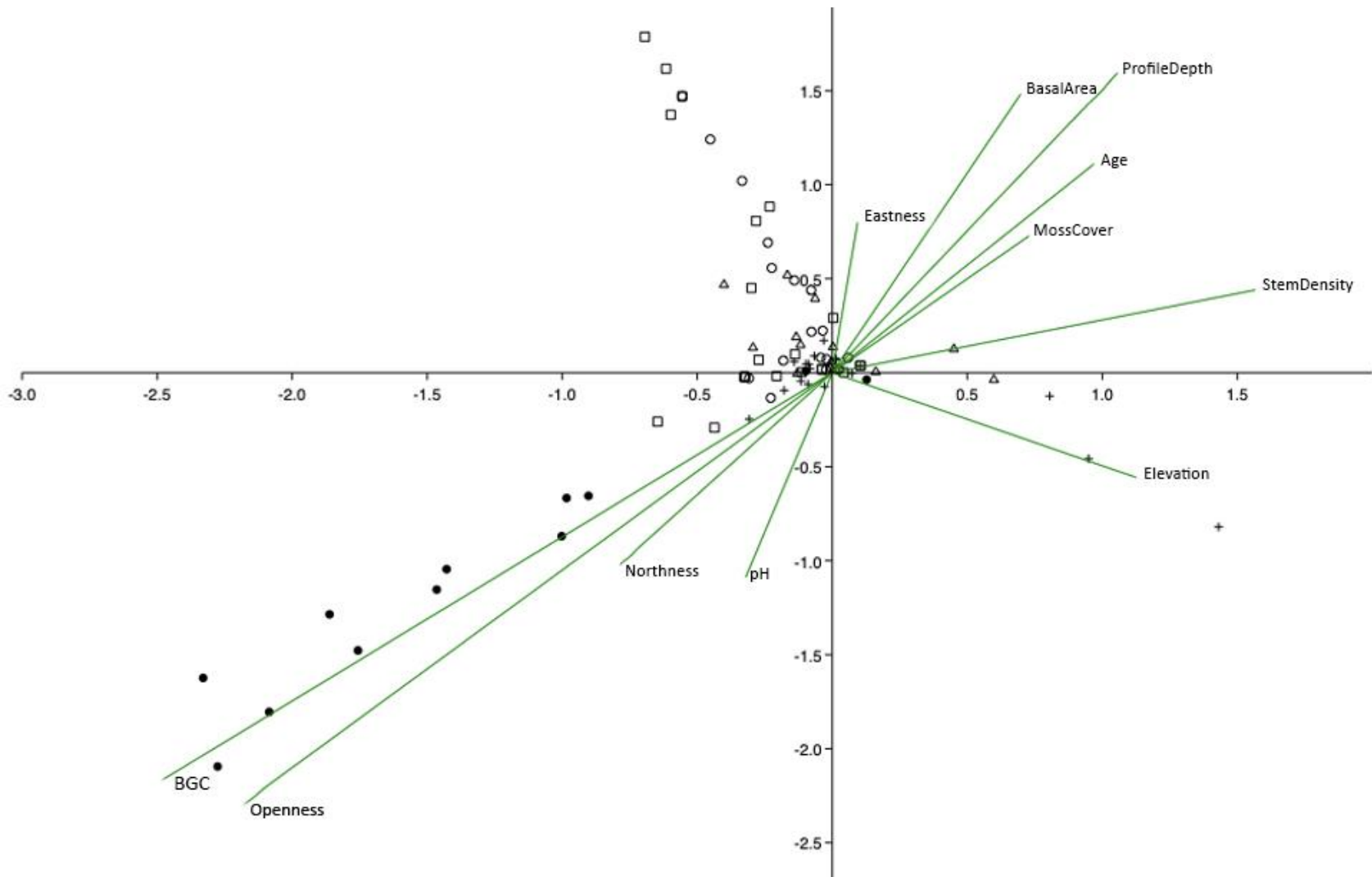


Figure 3.8 - Canonical Correspondence Analysis of the forest plots by successional stages, related to the stem density of understory species. Environmental variables include Stand Age (Age), Elevation, Tree (StemDensity), Tree (BasalArea), Soil (ProfileDepth), Northness, Eastness, Moss Cover), Bare Ground Cover (BGC), Canopy Openness (Openness), and Soil Acidity (pH).

[●] Regeneration [+] Immature [□] Thinning [○] Mature [△] Old-growth.

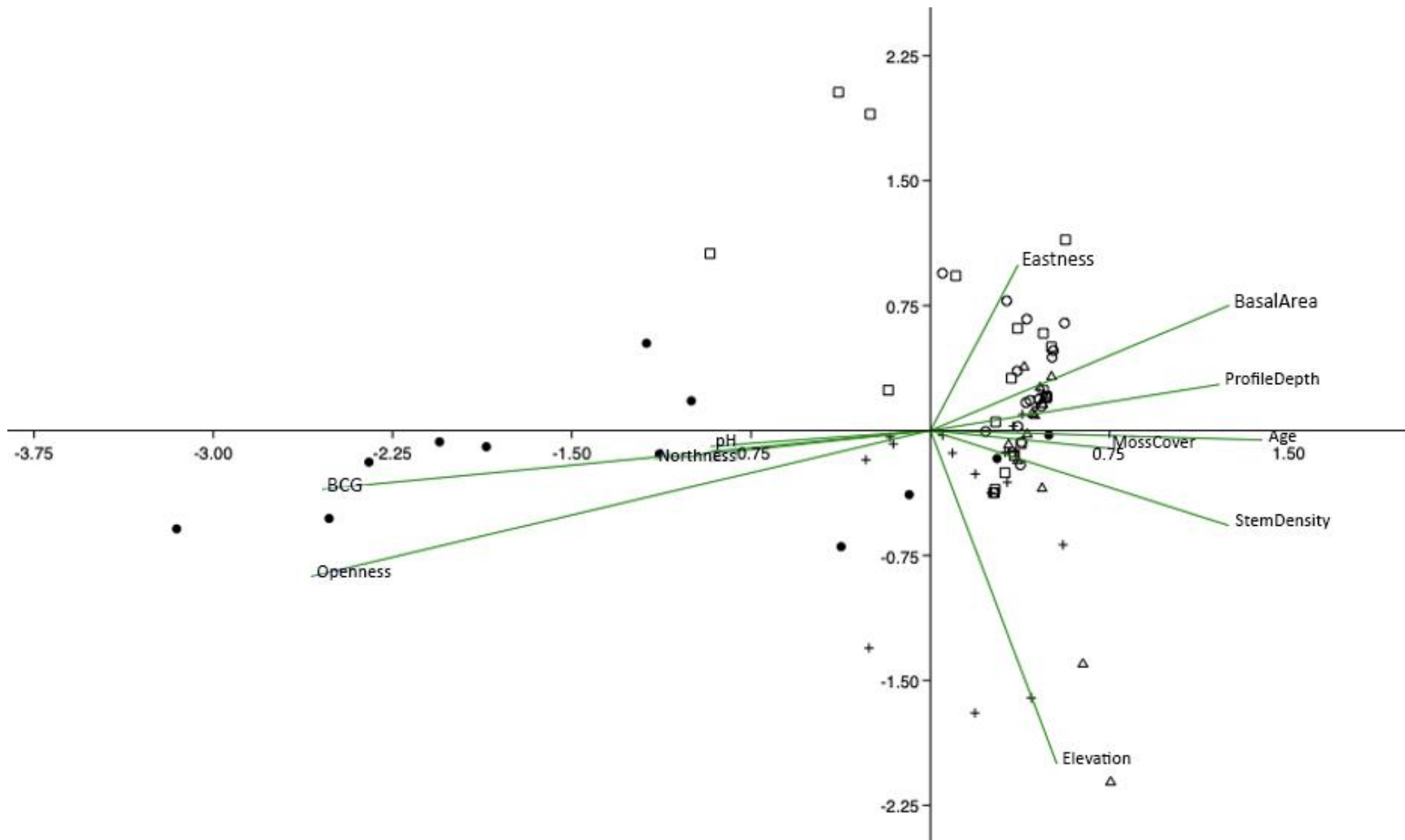


Figure 3.9 - Canonical Correspondence Analysis of the forest plots by successional stages, related to the leaf cover of understory species. Environmental variables include Stand Age (Age), Elevation, Tree (StemDensity), Tree (BasalArea), Soil (ProfileDepth), Northness, Eastness, Moss Cover), Bare Ground Cover (BGC), Canopy Openness (Openness), and Soil Acidity (pH).
 [●] Regeneration [+] Immature [□] Thinning [○] Mature [△] Old-growth.

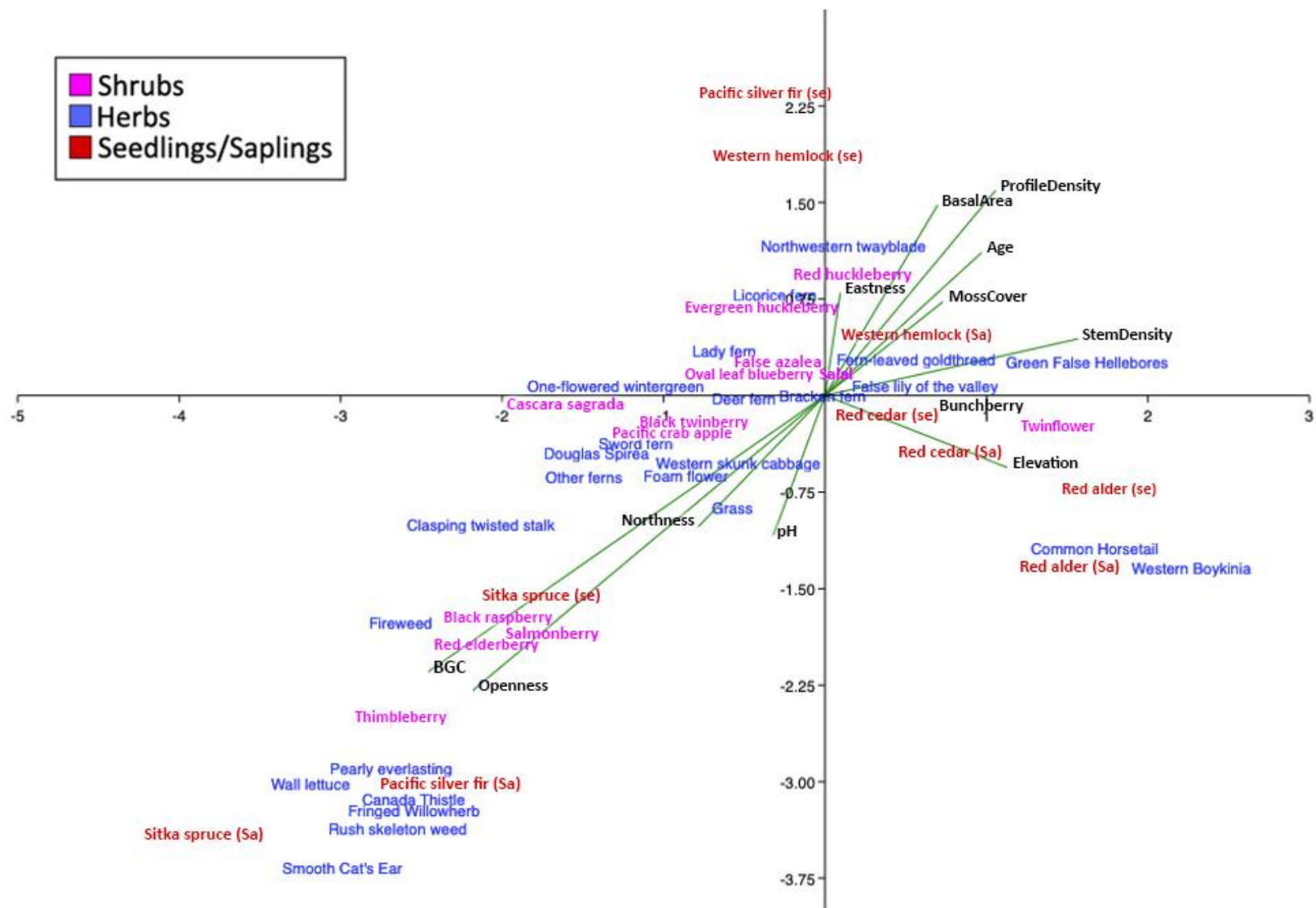


Figure 3.10 - Canonical Correspondence Analysis of the forest plots by species type, related to the stem density of all understory species. Environmental variables include Stand Age (Age), Elevation, Tree (StemDensity), Tree (BasalArea), Soil (ProfileDepth), Northness, Eastness, Moss Cover), Bare Ground Cover (BGC), Canopy Openness (Openness), and Soil Acidity (pH).

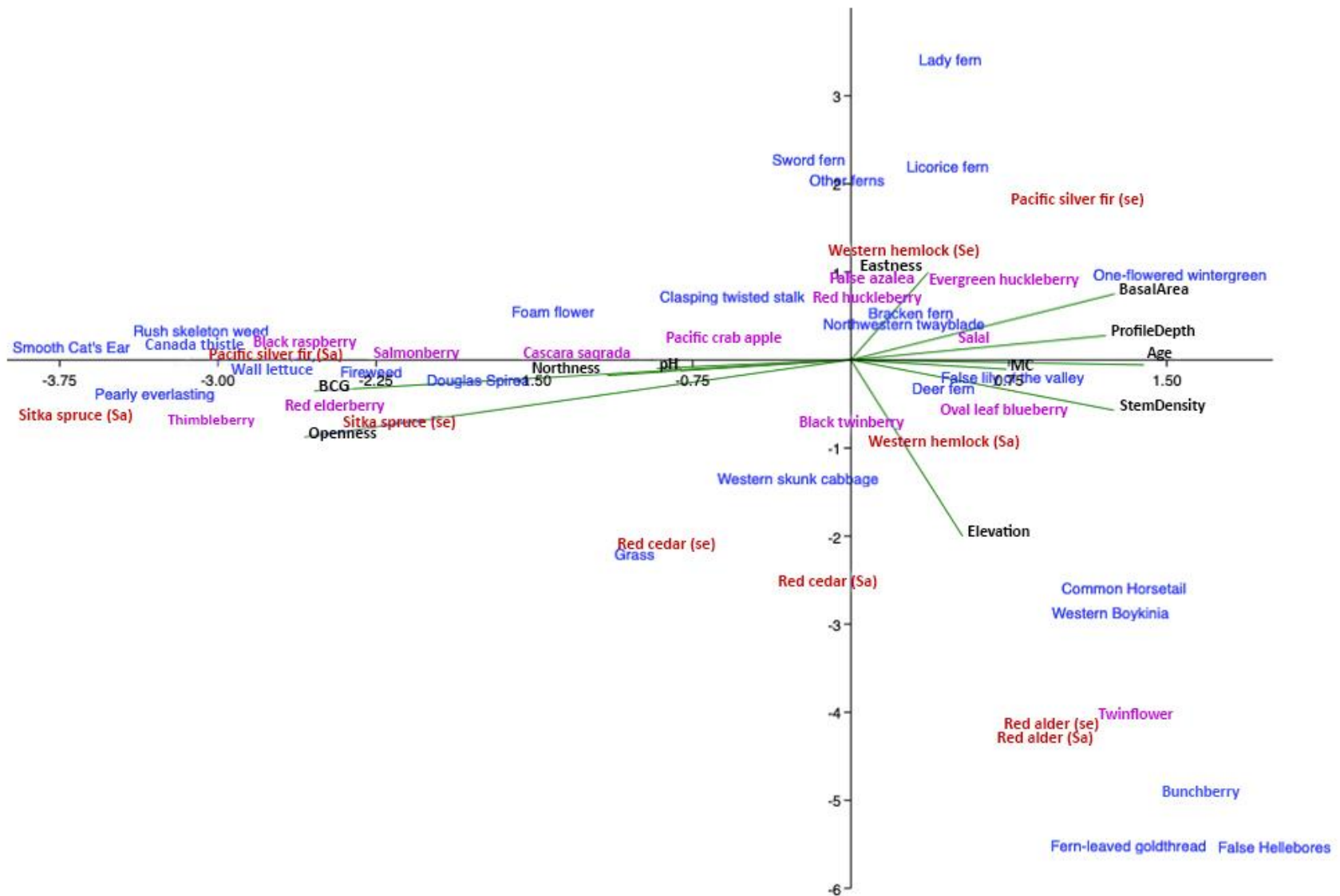


Figure 3.11 - Canonical Correspondence Analysis of the forest plots by species type, related to the leaf cover of all understory species. Environmental variables include Stand Age (Age), Elevation, Tree (StemDensity), Tree (BasalArea), Soil (ProfileDepth), Northness, Eastness, Moss Cover), Bare Ground Cover (BGC), Canopy Openness (Openness), and Soil Acidity (pH).

3.4.3 Vegetation Groups Ordinations

Ordinations completed for each vegetation type focuses on the differences found between species in each category. The broad patterns for all vegetation types together are addressed in Figure 3.10 and Figure 3.11, however, in this section, more specific patterns found within vegetation types can be addressed. The following canonical correspondence analysis (CCA) graphs depict the species composition of herbaceous plants, shrubs, and tree seedlings and saplings through plant stem density and leaf cover, in relation to 11 environmental variables (Figures 3.12 - 3.17). These graphs each focus on one vegetation type, along with either leaf cover or stem density. Some plots were not included as they did not contain the plant type pertaining to the analysis: herbaceous plants, shrubs, or trees. In Figures 3.12 and 3.13, 10 plots had to be removed from the analysis as they contained no herbs. In Figures 3.14 and 3.15, five plots had to be removed from the analysis as they contained no shrubs. And in Figure 3.16 and 3.17, 36 plots had to be removed as they contained no tree seedlings or saplings.

The CCA shown in Figure 3.12 demonstrates patterns of the stem density of herbaceous plants in relation to 11 ecological and environmental variables. Grouped in the top left quadrant is smooth cats ear, rush skeleton weed, fringed willowherb, Canada thistle, wall lettuce, and pearly everlasting, which are associated with higher values of bare ground cover and canopy openness, and to a lesser degree, northness (north-facing slopes), and soil pH. These species have low stem density values associated with soil profile depth, stand age, tree stem density, and tree basal area. Sword fern, Douglas spirea, and western skunk cabbage have high stem density values associated with Bare ground cover, canopy openness, northness, and pH, while having lower values associated with elevation (Figure 3.12). Fern-leaved goldthread, False hellebores, and Bunchberry have high values stem density values related to moss cover, stem density, profile

depth, elevation, age, and basal area (Figure 3.12). Common horsetail and Western boykinia have intermediate environmental values; however, these two species have values associated with higher elevation (Figure 3.12).

Leaf cover values in herbaceous plants follow similar patterns in relation to the environmental and ecological variables, but with a few notable differences (Figure 3.13). Douglas spirea and fireweed can now also be found in the group of herbaceous plants that has high values associated with bare ground cover and canopy openness. Bunchberry, fern-leaved goldthread, and green false hellebores are associated with values of high elevation. Grass and western skunk cabbage are found associated with high elevation, open canopy, and bare ground cover, and associated with low values of pH and east-facing slopes. One-flowered wintergreen has values associated with a large tree basal area. Western boykinia and common horsetail are largely related to elevation and age. Deer fern, false lily of the valley, and northwestern twayblade are herbs that have values that are associated with slightly higher elevation, stand age, moss cover, tree stem density, and soil profile depth (Figure 3.13).

Stem density and leaf cover for shrubs shows thimbleberry, red elderberry, black raspberry, and salmonberry have high values associated with bare ground cover, canopy openness, northness, and slightly with soil pH (Figures 3.14 & 3.15). Evergreen huckleberry and black twinberry are both strong outliers in relation to leaf cover. Pacific crab-apple is strongly related to a high pH, indicative of Regeneration stands (Figure 3.14, 3.15). Red huckleberry and oval-leaf blueberry have high values associated with elevation for leaf cover, however the stem density values for red huckleberry are associated with eastness and oval-leaf stem density values are equal across all variables (Figure 3.14, 3.15). Cascara sagrada has low values associated with stand stem density and high values associated with northness (Figure 3.14, 3.15). Twinflower has

leaf cover values associated with high basal area, stem density, stand age, and to a lesser degree moss cover (Figure 3.15). Twinflower stem density values are associated with higher elevation and stand stem density (Figure 3.14). False azalea has stem density values associated with higher tree stem density and leaf cover values slightly associated with higher eastness (Figure 3.14 & 3.15). The stem density and leaf cover values for salal are slightly related to higher elevation and deeper profile depth, respectively, however, due the central placement of salal on the graphs, it is evenly associated with multiple environmental variables.

Red alder seedlings and saplings have a higher stem density in plots with higher values associated with high tree stem density, however, looking at the size of the plants through the measure of leaf cover, they were associated with high values of bare ground cover, openness, northness, and pH (Figure 3.16, 3.17). Western red cedar saplings were grouped with red alder in the leaf cover graph (Figure, 3.17). The stem density of western red cedar saplings had high values related to stand stem density, elevation, and to a lesser degree, northness and pH, whereas the seedlings were had high values associated with elevation. Pacific silver fir had values associated with openness, basal area, age, moss cover, and soil profile depth, with saplings having an association with high bare ground cover and low stem density. Sitka spruce seedlings stem density had high values associated with elevation, however leaf cover had low values associated with elevation (Figures 3.16, 3.17). Western hemlock had higher values associated with eastness and stand stem density, for both leaf cover and stem density graph, whereas seedlings had intermediate stem density values for all environmental variables and leaf cover values associated with moss cover, pH, and age (Figure 3.16, 3.17).

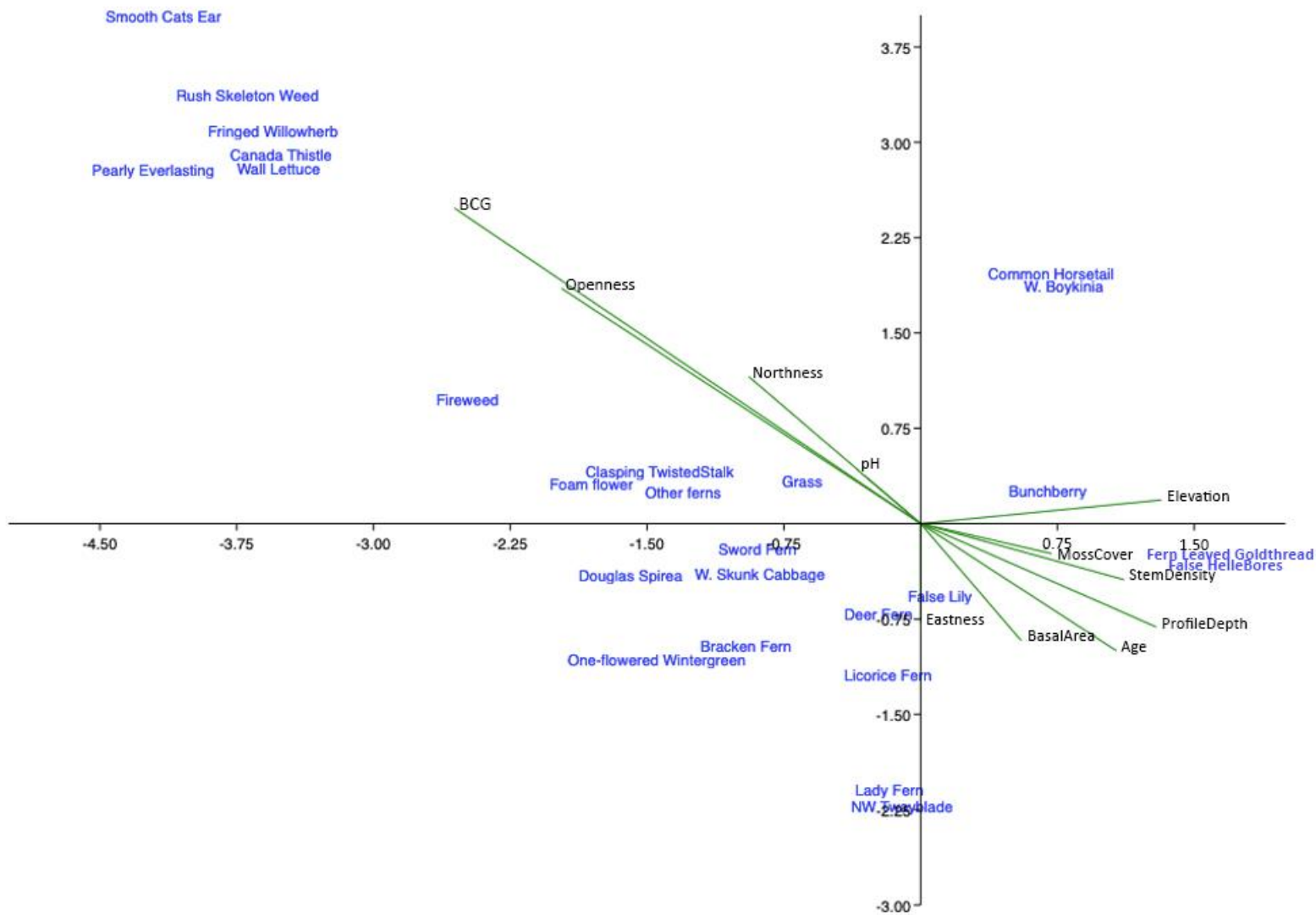


Figure 3.12 - Canonical Correspondence Analysis of the forest plots for herbaceous understory species, related to the stem density. Environmental variables include Stand Age (Age), Elevation, Tree (StemDensity), Tree (BasalArea), Soil (ProfileDepth), Northness, Eastness, Moss Cover), Bare Ground Cover (BGC), Canopy Openness (Openness), and Soil Acidity (pH).

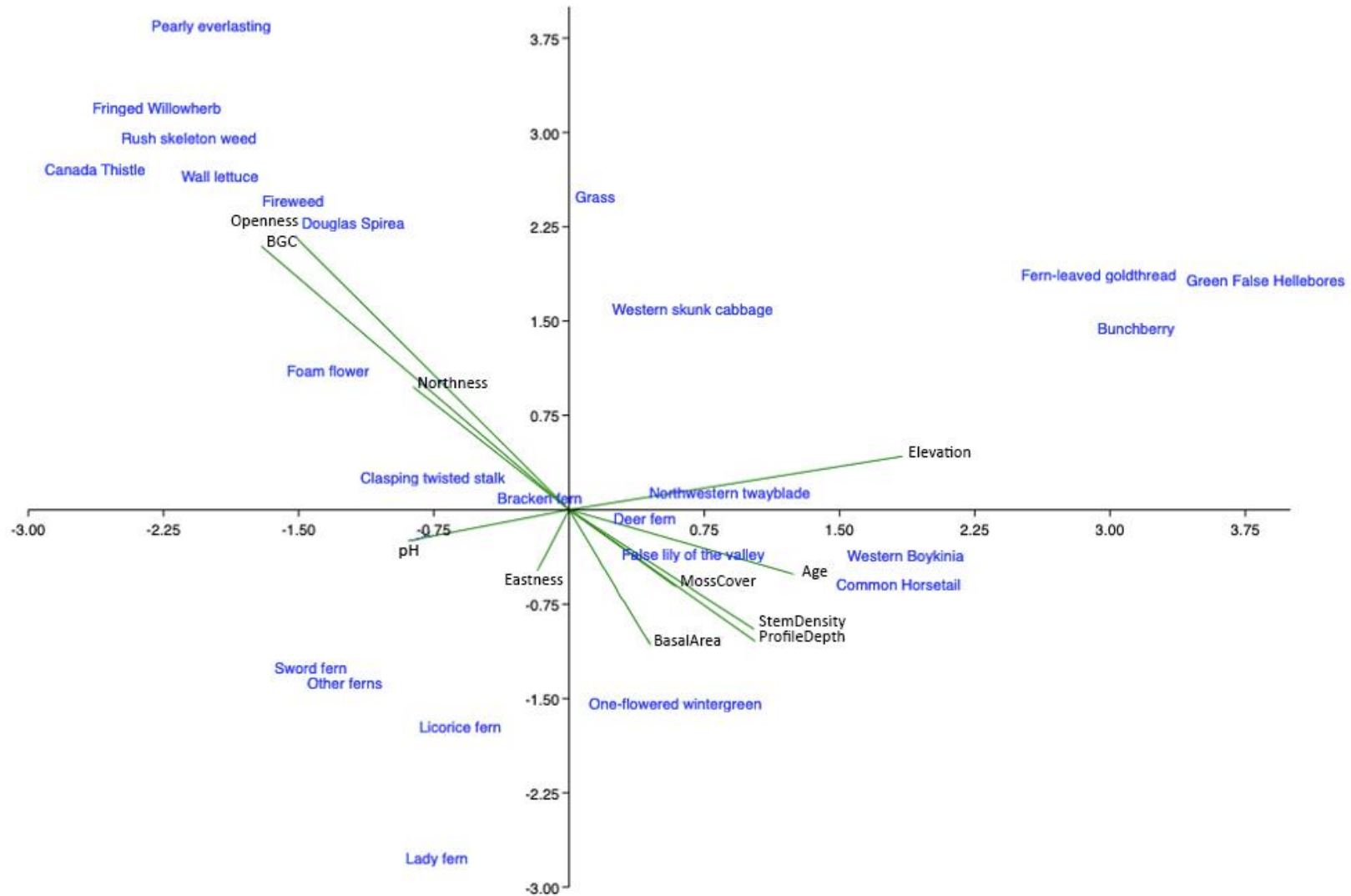


Figure 3.13 - Canonical Correspondence Analysis of the forest plots for understory herbaceous species, related to the leaf cover. Environmental variables include Stand Age (Age), Elevation, Tree (StemDensity), Tree (BasalArea), Soil (ProfileDepth), Northness, Eastness, Moss Cover), Bare Ground Cover (BGC), Canopy Openness (Openness), and Soil Acidity (pH).

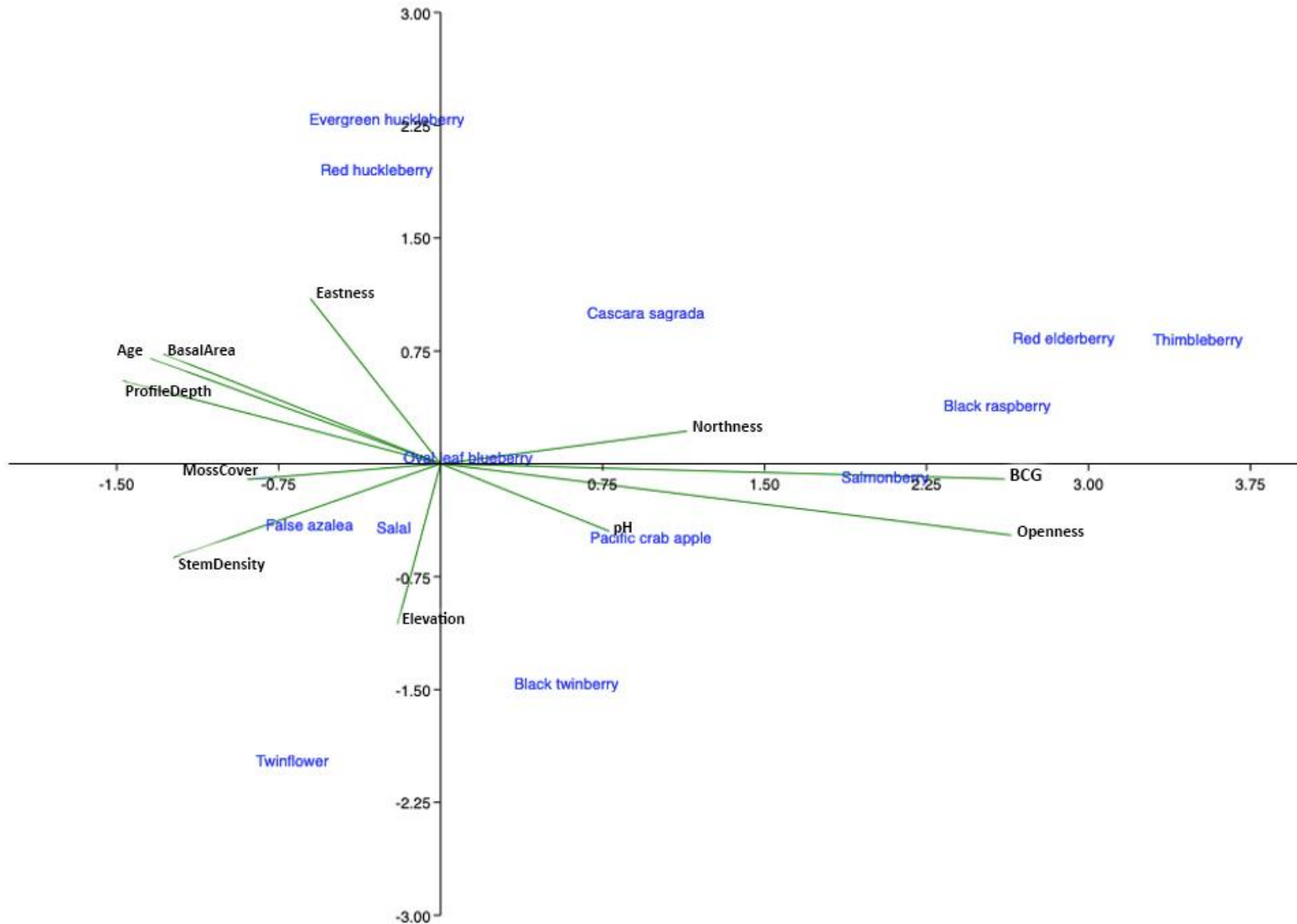


Figure 3.14 - Canonical Correspondence Analysis of the forest plots for understory shrub species, related to the stem density. Environmental variables include Stand Age (Age), Elevation, Tree (StemDensity), Tree (BasalArea), Soil (ProfileDepth), Northness, Eastness, Moss Cover), Bare Ground Cover (BGC), Canopy Openness (Openness), and Soil Acidity (pH).

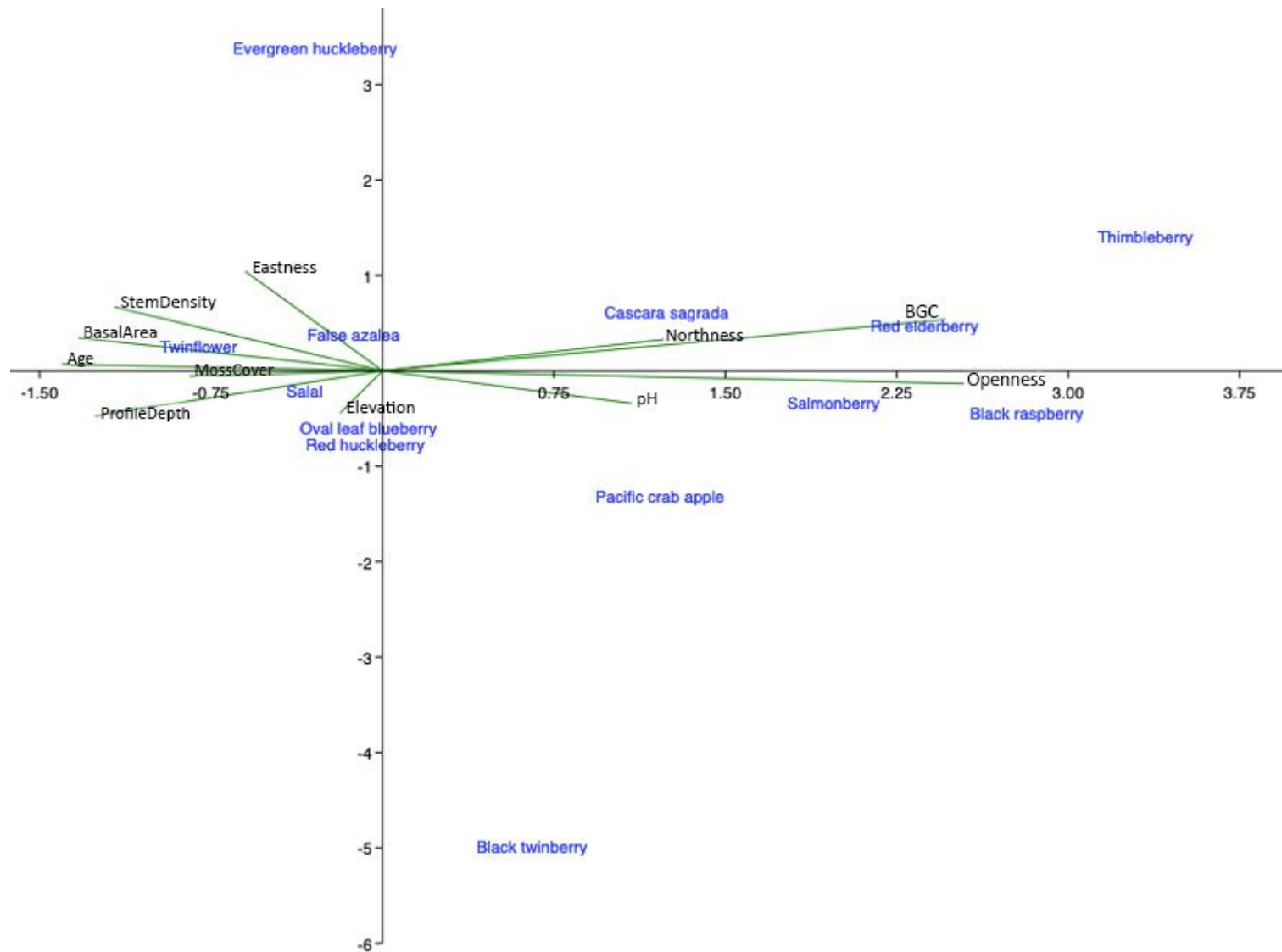


Figure 3.15 - Canonical Correspondence Analysis of the forest plots for understory shrub species, related to the leaf cover. Environmental variables include Stand Age (Age), Elevation, Tree (StemDensity), Tree (BasalArea), Soil (ProfileDepth), Northness, Eastness, Moss Cover), Bare Ground Cover (BGC), Canopy Openness (Openness), and Soil Acidity (pH).

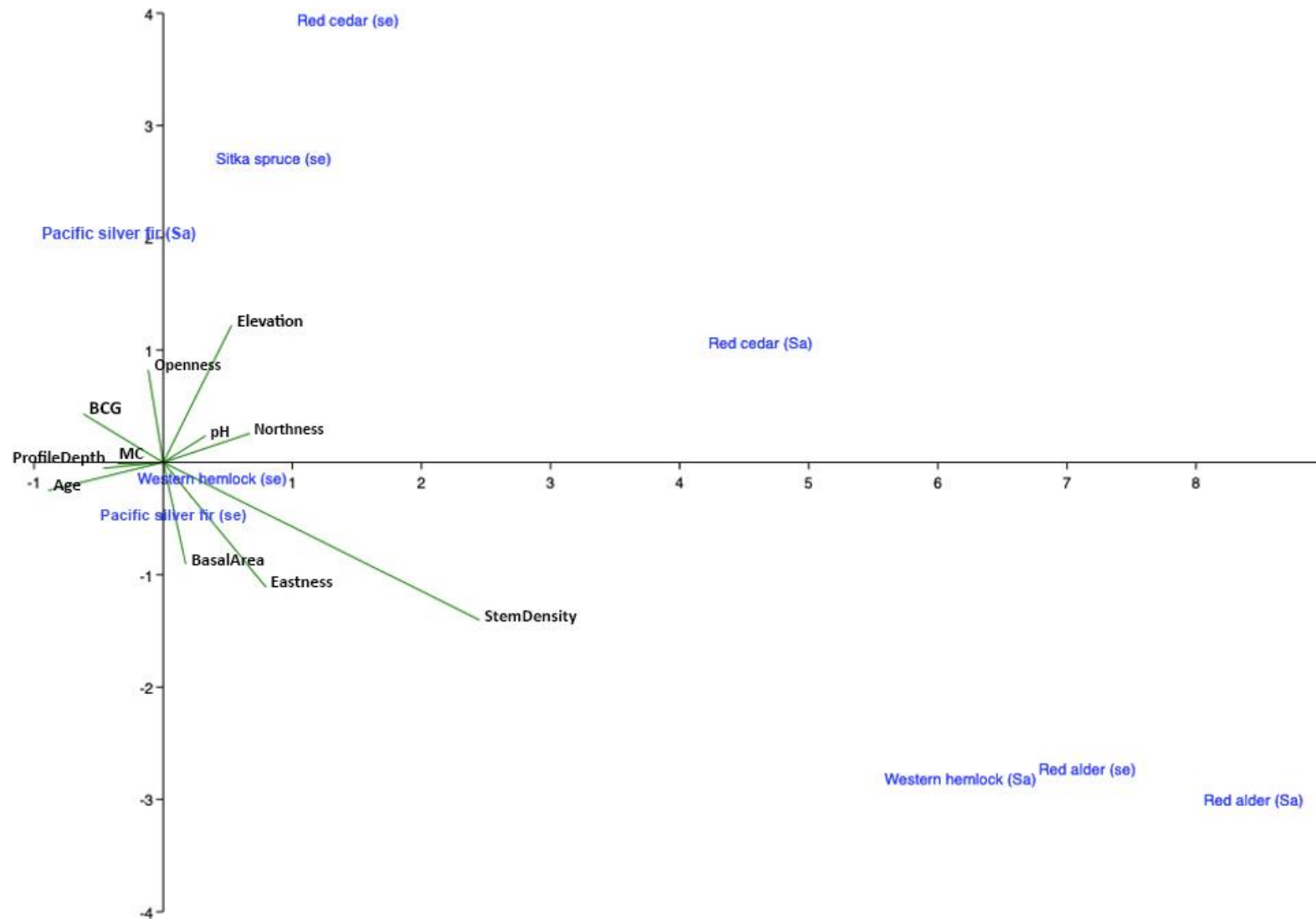


Figure 3.16 - Canonical Correspondence Analysis of the forest plots for understory tree seedling and sapling species, related to the stem density. Environmental variables include Stand Age (Age), Elevation, Tree (StemDensity), Tree (BasalArea), Soil (ProfileDepth), Northness, Eastness, Moss Cover), Bare Ground Cover (BGC), Canopy Openness (Openness), and Soil Acidity (pH).

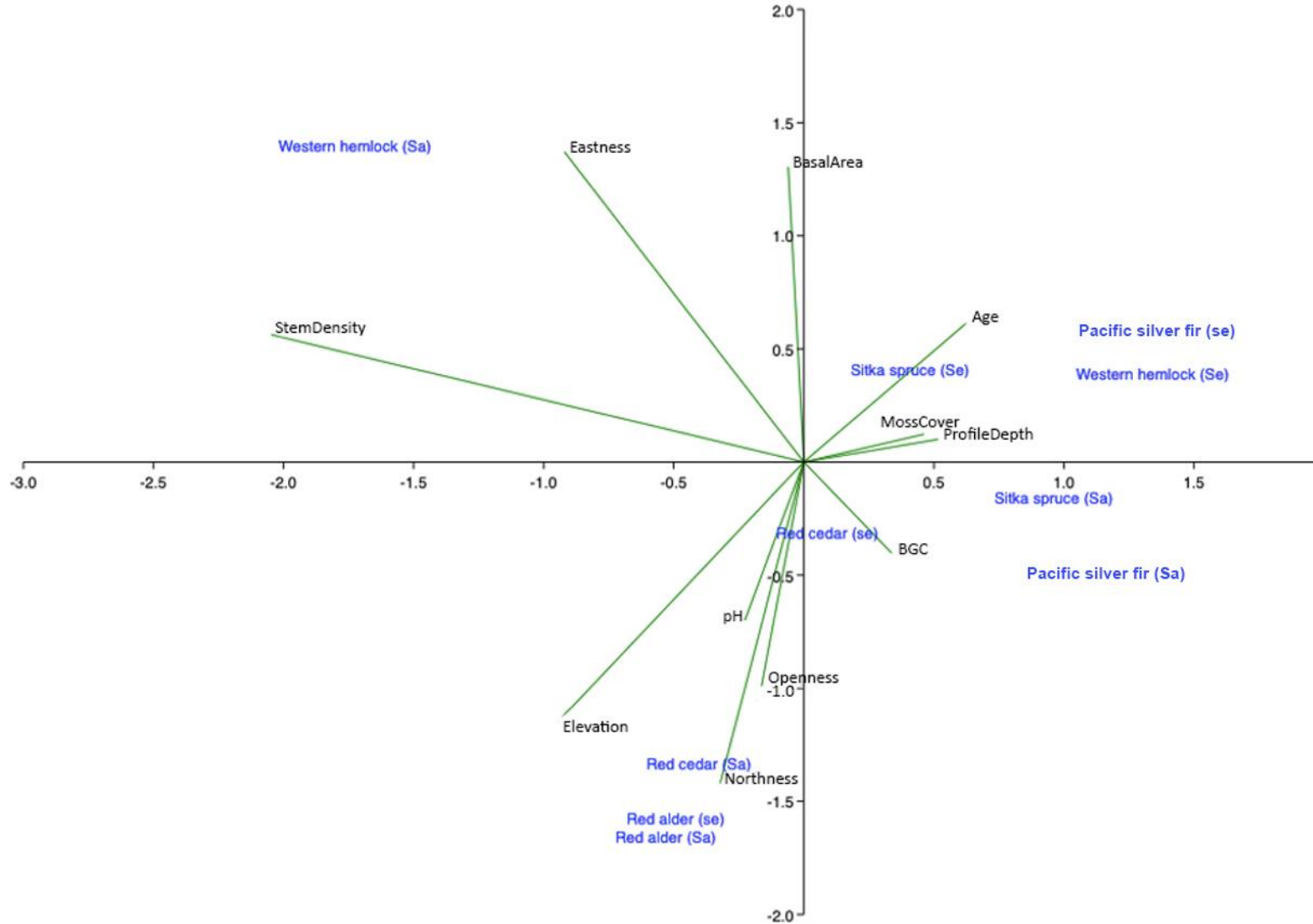


Figure 3.17 - Canonical Correspondence Analysis of the forest plots for understory tree seedling and sapling species, related to the leaf cover. Environmental variables include Stand Age (Age), Elevation, Tree (StemDensity), Tree (BasalArea), Soil (ProfileDepth), Northness, Eastness, Moss Cover), Bare Ground Cover (BGC), Canopy Openness (Openness), and Soil Acidity (pH).

Chapter 4: Discussion

4.1 Environmental Variables

There are a variety of factors that influence understory growth, creating complex relationships between environmental variables and understory productivity. Few forest succession models have considered the relationship between understory growth and canopy structure (Alaback, 1982). Some authors have tried to create links between understory plant communities with percent canopy cover, tree basal area, and tree density (Alaback, 1982); however, it is a variety of factors together that will have varying impacts on understory growth. The environmental variables that were measured in this study all play a unique role in influencing understory plant growth, such as tree stem density, tree basal area, canopy openness, slope aspect, ground cover, elevation, slope angle, and various soil characteristics.

4.1.1 Soils

There was significantly more bare ground in the Regeneration stage due to the recent timber harvesting. In this study, clear cut harvesting disrupted the forest floor and removed vegetation cover, leaving open patches of bare ground. Variables such as disturbance from machinery and changes in light levels can reduce the vegetation cover and leave bare ground (Dynesius and Hylander, 2007). Understory vegetation is an integral part of nutrient circulation in the forest (Spurr and Barnes, 1980). In the early and the late stages of succession, with high light levels reaching the forest floor, understory vegetation can contribute up to 28% of total litter (Bray and Gorham, 1964). Clear cutting leads to thinner and underdeveloped soil profiles, due to the mixing of mineral soil that occurs during the harvesting process (Johnson et al. 1991). An old-growth forest has had centuries for a soil profile to slowly develop, and the process of clear cutting disrupts the soil, and the forest flora loses this important resource, which can impact

species composition. Alaback (1982) states that clearcuts that had the most topsoil disturbance or mass-movement erosion are colonized by shade-intolerant species, whereas clearcuts with minimal topsoil disturbance favor the reestablishment of species that were established prior to logging. Site productivity in the inland Pacific Northwest has been found to be substantially lower 15 to 25 years after clearcutting, due to soil compaction, forest floor displacement, and soil displacement (Clayton et al. 1987; Bosworth and Studer, 1991). In this study Old-growth stages were found to have the most acidic soils, indicating that as a forest ages, the soil pH decreases. Similarly, in a study conducted in Scots pine forests, there was a gradual decrease in soil pH during the regeneration of a forest stand after clear cutting, however in Coastal Western Hemlock forests, the soil pH was found to be lower in younger stands than in the old-growth stage (Gustiene et al. 2022). Soil profile depth also showed a significant increase between the Regeneration and Mature stage, and the A horizon was deeper in all stages compared to Regeneration, both indicating that the soil profile is developing and growing over time as the forest matures. Covington (1981) notes that forest floor depth increased 50-60 years after cutting and then remained consistent into Old-growth stands, whereas Covington (1976) showed an increase in forest floor depth up until 90 years after cutting in the northern hardwood forests of New York. In both studies, there is an increase in soil profile depth from the Regeneration stage.

Moss cover was associated with tree basal area, soil profile depth, stand age, eastern slope aspect and tree stem density, which are all environmental variables closely related to both Immature and Mature stands. There was a lack of moss cover in the Regeneration stage likely due to an increase in light levels, varying moisture and temperature, changes in leaf litter, and mechanical disturbance to the forest floor from machinery (Dynesius and Hylander, 2007). In the results of this study, bare ground cover was negatively related to moss cover. Dynesius and

Hylander (2007) noted that total bryophyte species richness in boreal forests decreased after clear cutting and did not recover 30-50 years after harvesting. The most moss cover occurred during the Thinning and Mature stages, which have the lowest levels of light. This is similar to the Southeast forests of Alaska, where once canopy closure has occurred, from 50-70 years, moss cover increases and extensively carpets the ground and exceeds the biomass of the vascular plants in the understory (Alaback, 1982). This increase in moss biomass peaks at 140-160 years after disturbance and decreases going into the final stage of succession (Alaback, 1982). Immature stands had intermediate levels of moss cover, which was lower than the Thinning stage. These two stages have a higher number of herbaceous plants covering the forest floor, leaving less room, soil moisture, and light for moss growth.

4.1.2. Light

Light availability under the main forest canopy influences the development of understory vegetation (Spies and Franklin, 1989), and thus is an important factor in understory plant succession. Alaback (1982) noted that the most drastic change in the environmental variables throughout the chronosequence in their study was the change in light reaching the forest floor, making light a key environmental factor in relation to understory plant growth. The composition of species in temperate forests of the Pacific Northwest is affected by gaps of varying types and sizes (Spies and Franklin, 1989). The canopies of forests in coastal British Columbia are structurally heterogenous and have many canopy gaps, which promotes shrub and herb growth (Banner and LePage, 2008). Canopy gaps influence understory plant diversity by affecting understory light regimes (Canham et al. 1990). The increased light levels reaching the understory due to large scale canopy gaps from clear cutting, has an impact on understory vegetation. Canopy openness was associated with bare ground cover, northern slope aspects, and soil pH.

When the forest is harvested there is a massive disturbance to the forest floor, leaving areas of disturbed soil, which explains the relation between canopy openness and bare ground cover. Canopy openness was found to be higher in Regeneration stands and lower in Thinning stands, which follows the expected pattern. Timber harvesting leads to large opening in the canopy, allowing an increased amount of light to reach the understory, followed by a canopy closure once the trees regrow and reach a point of maximum stem density in the Thinning stage. Similarly, Alaback (1982) found that in the first 100 years after disturbance, percentage of canopy cover had a negative relationship with understory plant development. Other chronosequence studies in British Columbia showed an increase in understory vegetation cover with stand age, after the stem exclusion phase, or in this case, the Thinning stage (Banner and LePage, 2008; Well, 1996). Closed canopies in second-growth stands have limited light penetrating to the forest floor, therefore reducing understory development (Banner and LePage, 2008).

4.1.3 Elevation

Elevation is an environmental variable in this study that had a strong influence over the leaf cover and stem density of certain understory species. There were some sites that were sampled within another biogeoclimatic subzone due to limited site access. After the field sites were selected and inventoried, the study was then narrowed down to the Southern Very Wet Hypermaritime Subzone (CWHvh1). However, seven plots were sampled outside of this region and within the adjacent subzone: Submontane Very Wet Hypermaritime (CWHvm1). The CWHvm1 occurs up to 600 meters above sea-level, whereas the CHWvh1 occurs up to 200 meters above sea-level, and the seven sites were sampled above 200 meters (Green, 1994). Four of these sites were within the Old-growth stage. The elevation of a forest stand plays an important role in the growth of vegetation due to the changes in sun exposure and moisture levels

(Spurr and Barnes, 1980). Higher elevations will typically have lower soil moisture due to downhill runoff of rain (Spurr and Barnes, 1980). For this reason, the leaf cover and stem density of some species were strongly associated with a higher elevation, which can be seen in the canonical correspondence analyses. The main differences in vegetation between these two subzones is a decrease in deer fern, salal, false lily-of-the-valley and evergreen huckleberry in the CWHvm1, which could impact the leaf cover and stem density results. There was also a notable visual difference between the Old-growth forests of these subzones: salal thickets were taller and more encompassing of the understory at lower elevation sites, in closer proximity to the ocean. These results show that elevation has a strong influence over vegetation, further providing evidence that each biogeoclimatic subzone is unique and should be managed with this information in mind.

4.2 Fifth Successional Stage

Alaback (1982) noted that a characteristic of a productive second growth stand with a closed canopy is the lack of understory vegetation. In the present study, the overall mean stem density and leaf cover was lowest in the Thinning stage. The results are both indicative of a fifth successional stage, in this middle of the four successional stages, that is not discussed in previous literature. At this age of forest regeneration (46 – 79 years), tree mortality or natural thinning occurs, which is the result of competition for soil and light resources amongst trees in the stand (Oliver and Larson, 1996). The competition leads to the death of the smallest and weakest trees below the closing canopy, while the largest individuals use the liberated resources (Oliver and Larson, 1996). As found in our study, before the stands start to thin, the density of trees is at its highest in the Thinning stage, preventing large amounts solar radiation from reaching the forest floor. The low levels of light due to canopy closure impede the growth of understory plants, as seen in a study in Sitka spruce-western hemlock forests in southeast Alaska (Alaback, 1982). In

the stages of stand development, this would be known as the stem exclusion stage, where there is crown closure, competition is intense, and self-thinning occurs (Oliver, 1980). In the forest development model (Daniels and Gray, 2006) stand initiation is represented by the Regeneration and Immature stage, stem exclusion is represented by the Thinning stage, understory re-initiation is represented by the Mature stage, and old-growth is represented by the Old-growth stage.

Previous forest ecological studies (Ryan et al. 2009) describe only four stages of development; however, this often spreads the Thinning stage across the Immature and Mature stages, which could skew data representing successional stages. The higher mean stem density and mean leaf cover in the Immature and Mature stages coincided with an open canopy and higher light levels. Successional stages were originally derived from the regeneration of trees, not specifically considering the forest understory plants. Though forest succession is best represented as a continuum, to study plant dynamics over time, age groups must be created for comparison. Studying plant succession based on four successional stages is not sufficient at representing the major structural changes that occur in a stand over time and how those impact vegetation. There is very little understory growth during the Thinning stage, making this stage in succession very different from the previous Immature and the following Mature stages. In this study, the age range for the Thinning stage was based on visual observations made in the field. However, there is evidence in the results that suggest a fifth successional stage, such as the significant difference found in shrub leaf cover (%) between the Thinning and Mature stages (Table 3.4). Once trees begin to outcompete one another and the canopy begins to open and let light reach the forest floor, understory plant leaf cover will increase due to the increased ability to photosynthesize. Alaback (1982) noted that after canopy closure, there was a decline in understory standing crop biomass and annual production of the understory. There is also

substantial evidence showing a difference in understory plant stem density and leaf cover between the Immature stage and Thinning stage. Considering that most timber harvest rotations are 80 years (Western Forest Products, 2006; British Columbia Ministry of Forest, 1999), which falls at the end of Thinning stage, it is important to further understand the understory vegetation at this time in forest succession.

Further ecological studies conducted regarding forest secondary succession should consider this additional successional stage, especially because this stage is representing a major event that occurs to the stand during secondary succession. Understory plant studies will increase in accuracy once including this division in successional stage. This can be further applied to forest studies in various Biogeoclimatic zones and subzones, and successional stage age ranges can be adjusted for various forest types. Different tree species will grow at various rates and become old-growth forests at different ages, therefore the age ranges in this study should only be applied to western hemlock-western red cedar forests in the Southern Very Wet Hypermaritime Biogeoclimatic subzone. It is important to note that forest succession is homogenous between different regions, therefore this model should be carefully applied to forests with a similar secondary succession.

4.3 Overall Trends for Plant Types

In this study conducted within the Southern Very Wet Hypermaritime biogeoclimatic subzone, understory vegetation increased initially in the Regeneration (1 – 9 years) and Immature (10 – 39 years) stages, then decreased in the Thinning (40 – 79 years) stage, followed by another gradual increase throughout the Mature (80 – 250 years) and Old-growth stages (250+ years). In a similar study in southeast Alaska, shrubs in the understory increased in numbers primarily in the first 10 to 20 years after a harvesting event, however by 25 to 30 years there was a decrease in understory vegetation due to regenerating conifers overtopping and shading out the

understory (Alaback 1982). Sparse understory vegetation persisted until the stands reached 150 years old, after which the understory plants slowly started to increase again in volume (Alaback, 1982). The increase in understory plant volume in this study is like the increase shown in Alaback (1982), where the volume increases again after the Mature stage and into the Old-growth stage due to the opening of the forest canopy. In the Very Dry Maritime and the Very Wet Maritime Coastal Western Hemlock subzones on Vancouver Island understory vegetation increased in cover and density in Mature and Old-growth stands, in comparison to earlier successional stages (Klinka et al. 1985). Banner and LePage (2008) noted a general increase in shrub and herb cover as the forest ages from very young forests (<40 years) to old-growth (>250 years).

In this study, after logging, shrub stem density was higher in Old-growth and Regeneration stages than Thinning. The understory was dominated by shrubs in the Regeneration stage, by herbs in the Old-growth stage, and by tree seedlings and saplings in the Thinning stage. Other chronosequences studies conducted in the northern temperate rainforest show that one to two years after logging, shrubs and herbs dominated the understory of a site, however, in mature forests that undergo less frequent, small-scale disturbances, trees will dominate (Alaback 1984; Hanley et al. 1989). Within stands in the Very Wet Hypermaritime biogeoclimatic zone of coastal British Columbia, a study found that herb and shrub cover were highly related to stands age (Banner and LePage, 2008).

4.3.1 Herbaceous plants

In old-growth stands, ferns typically account for 3-7%, and the forbs 3-9% of the understory biomass (Hanley et al. 1989, Hanley, 2005). This study did not measure understory biomass, however, found that understory leaf cover in the old-growth stage for ferns is at 17.82%

of the total understory leaf cover and herbs (forbs) at 5.16%, whereas the stem density of ferns was 14.12% of total understory stem density and herbs at 47.53%. Banner and LePage (2008) studied forests within the same biogeoclimatic subzone and found a statistically significant increase in herbaceous plant cover in the understory over time (1 to 250 years). In this study, though there was only a significant difference between the higher cover in the Immature stage compared to the Thinning stage, there was still another increase in herb leaf cover from the Thinning stage to the Mature stage, and then from the Mature stage to the Old-growth stage (Kruskal Wallis, n.s.).

An interesting finding within the Thinning stage is the low cover of herbaceous plants as compared to ferns. Within the Thinning stage ferns were dominant with regards to leaf cover, meaning they are tolerant to stands with low light. A study done by Alaback (1982) in forests of southeast Alaska show a similar dominance of ferns over herbs in the understory production starting at 50-60 years after disturbance. The Immature, Mature, and Old-growth stages also showed the dominance in fern leaf cover over herbaceous leaf cover, however, this could also just be explained by the increased size of ferns as compared to other herbaceous species. Sword ferns for example can growth up to 1.5 m tall, whereas small herbaceous plants like bunchberry will only grow 5 to 25 cm tall (Pojar et al. 1994). Ryan et al. (2009) also noted the highest herb cover in regenerating plots, followed by a decrease of herb cover in immature plots, then an increase in mature plots, and another decrease in old-growth plots. A fully developed soil profile and increased light levels would allow for more herbs to grow on the forest floor, then on a freshly logged area where there is massive soil profile disturbance.

4.3.2 *Shrubs*

There is a higher percentage of shrubs in the Regeneration stage than the Old-growth stage, indicating that shade-intolerant shrub species (i.e., Thimbleberry) have a slight advantage over herbs in recently logged stands, whereas the shrub to herb ratio decreased in an older, established forest. Ryan et al. (2016) found that shrubs were more common in regenerating and old-growth plots, as opposed to immature and mature growth plots. Regarding leaf cover percentage, shrubs had the highest percent coverage out of the plant types, with exception in the Thinning stage. Shrubs leaf cover was highest in the Old-growth successional stage, but only significantly different between the Thinning stage and three other stages. Banner and LePage (2008) also found an increase in shrub cover in the understory over time, peaking in old-growth forests (>250 years). There was shrub cover increase from 7% to 46% in maturing forests (41-100 years) and 4% to 50% in old-growth forests (Banner and LePage, 2008). Immature, Mature, and Old-growth stages all had higher shrubs leaf cover than the thinning stage. This was also likely due to low light levels in the Thinning stage. Much like the high levels of shrub leaf cover found in this study, Alaback (1982) noted an increased amount of woody shrub regrowth in young stands, due to low tree density and higher soil disturbance. Old-growth forests also had high light levels, along with more developed soil profiles and lower pH levels, which is more optimal habitat for native understory growth.

4.3.3 *Tree seedlings and saplings*

The low light levels of the Thinning stage would account for the understory being dominated by tree seedlings and saplings, because they are shade tolerant species that can grow within these light conditions. The majority (65.14%) of the understory stem density in the Thinning stage were tree seedlings and saplings, whereas this number was under 10% in all other

stages. Another interesting percentage to note is the increased tree seedling and sapling leaf cover within the Immature stage. Similar to the high tree seedlings and sapling leaf cover found in this study, Alaback (1982) noted an increased amount of tree seedlings regrowth in young stands, due to low tree density and higher soil disturbance. During this time, trees are beginning to regrow and many tree saplings are on the edge of becoming trees. There is a lot of competition to outgrow other surrounding saplings and acquire the most space in the canopy.

4.4 Ecological Metrics

The highest Shannon-Weiner diversity was found in Regeneration and Old-growth stages. The stages have similarities with high light availability, however there are vast differences in soil, the type of species that were present, the stem density and leaf cover of understory plants, and the density and diameter of trees. Qian et al (1997) noted an increase in Shannon-Weiner diversity from 40-year-old Immature stands to Old-growth stands on southwestern Vancouver Island. The increased diversity in the Regeneration stage can be explained by the increase in opportunistic (ruderal) species from an open canopy, however the increased species diversity in the old-growth stage is possibly influenced by a number of factors, including the difference in soil conditions. Qian et al (1997) wrote that species diversity was influenced by soil conditions such as nutrients, acidity, and cation availability. When the forest transitions from Mature to Old-growth, the canopy becomes increasingly heterogenous, leading to re-initiation of understory species, increases in understory diversity, and increases in understory productivity (Lertzman et al. 1996). Old-growth forests can be attributed to high native species diversity. The significant difference in evenness between the Regeneration stage and Immature stage can be attributed to the influx of opportunistic species immediately post-harvest. Shafi and Yarranton (1973) noted a gradual decrease in evenness in the early years of stand regeneration in the boreal forest of northern Ontario. The Thinning stage had the lowest

species richness and diversity, likely due to the higher stem density of trees leading to canopy closure and therefore less light reaching the forest floor to allow plant growth. Similarly, Schoonmaker and McKee (1988) found in their study of western hemlock-Douglas fir forests in the Western Cascade Mountains of Oregon, that after the tree canopy closes, understory species diversity declines until reaching the lowest diversity values at 40 years.

The highest species richness was 31 species in the Regeneration stage, which also had a higher average species richness likely due to increased light levels leading to an increase in opportunistic species and the remnant understory species that were present in the stand prior to the clear cut, but this is speculation. In the Regeneration stage, two years post-disturbance in forests of the Washington Cascade Range, richness values exceeded pre-harvest values (Halpern and Spies, 1995). Halpern and Spies (1995) also indicated an early increase in species richness that exceeded levels prior to forest fire. Therefore, site burning like slash burning, could lead to an increase in species richness in the Regeneration stage. Logging showed more of an increase in invading species than residual species in the early years of succession as compared to the richness post-fire (Halpern and Spies, 1995), which is similar the increase in opportunistic species in the Regeneration stage of this study. A study conducted on southwestern Vancouver Island showed that early successional stands that had recently been logged showed the highest number of understory plant species, which decreased when moving into older, forested plots, largely attributable to an overall decrease in herb diversity (Ryan et al. 2009). Ryan et al. (2009) suggests the decrease in herb diversity after the regeneration stage may be due to the initial colonization of invasive species being slowed by canopy closure in immature forests. Schoonmaker and McKee (1988) noted that late seral species that accounted for 99% of the vegetative cover in old-growth forests were almost completely eliminated after harvesting,

however they increased five years, peaking at 40 years. Mueller-Dombois (1965) found that after a disturbance, species richness initially increased. Similarly in this study, the species richness did show an initial increase after timber harvesting occurred and was significantly higher than the Thinning and Mature stages. Alaback (1982) noted the highest understory production was within the 15 to 25 years age class. Similar to this study, the Immature stage showed the highest mean understory stem density, however, the Old-growth stage had the highest mean understory leaf cover. An understory study of Sitka spruce-western hemlock forests of Southeast Alaska showed that production of herbs and shrubs increased with time, likely due to the decreased competition with trees, increased light availability due to an open canopy, favorable temperatures, and nutrient availability (Alaback, 1982; Liken et al., 1978). Similar to this study, these articles (Ryan et al. 2009; McKee, 1988; Mueller-Dombois, 1965; Alaback, 1982) describe an initial decrease in seral understory vegetation and an increase in opportunistic species due to an open canopy and increased light availability. This is followed by an increase in seral species into the Immature stage and eventually leading to a decrease in understory species in the Thinning stage due to canopy closure.

The Regeneration stage likely had a higher species richness than the Thinning and Mature successional stages due to the greater presence of shade-intolerant species able to colonize and grow in open canopy areas. Halpern and Spies (1995) showed a similar recovery in diversity post-harvest explained by the colonization of ruderal or non-forest 'invader' species. Similarly, why the species diversity was higher in Regeneration than it was in Thinning and Mature stands. Shade-intolerant plant species have a growth advantage in freshly harvested stands, where there are high levels of sunlight reaching the forest floor. The crown closure from

tree growth causes understory species richness to decrease, as the shade-intolerant species die off.

Banner and LePage (2008) noted an increase in species richness between very young forests (<40 years) and old-growth forests (>250 years), as well as increase in Simpson's diversity. Their regression model predicted that only 75% of the species richness found in old-growth forest would be found in 80-year-old-forests (Banner and LePage, 2008), which is average stand age for clear cut harvesting to occur in this region (British Columbia Ministry of Forest, 1999). In this study, species richness may not be as high in old-growth forests as Banner and LePage (2008) because bryophytes and lichens were not included in understory vegetation samplings, which is what Clark et al. (2003) mentioned in their study.

4.5 Stand Metrics

Stand information directly correlates with understory species composition. Tree species composition can change stand attributes such as light dynamics, soil properties, and the presence of various animal species. Both the size and number of trees in a stand will change the understory plant dynamics.

Forest stand information was gathered using two different metrics: stem density (stem/ha) and basal area (m^2/ha). These two metrics provide varying information about a forest stand. For example, a stand that has a high stem density is likely to be an intermediate stage of succession. In this stage, trees are in high competition with one another, competing to reach the top of the canopy for light resources (Oliver, 1980). Alaback (1982) mentions that shade-intolerant tree species form denser canopies than that of seral intolerant trees. Western hemlock and western red cedar, the two main tree species found in this study, are both shade tolerant species which produce denser forest canopies. The cooler growing seasons in Southeast Alaska provide a

conducive environment for the quick re-establishment of dense canopies post-harvest (Alaback, 1982). This can be seen in the dense canopies comprised of shade-tolerant tree species in the Thinning stages of this study, however the canopy opens as the forest moves into climax or equilibrium.

An Old-growth stand typically has a low density and high basal area because the older trees are large in diameter leading to less trees taking up an area, and large canopy gaps in old growth forests leads to less mature trees in an area –. A high stem density and low basal area is indicative of a young forest, a stand with low stem density and high basal area is indicative of an old forest, and both an average stem density and basal area could indicate an intermediate or a ‘mature’ forest.

There were no trees present in the Regeneration stage, because at this stand age the trees are still saplings. Western hemlock and western red cedar were the two dominant tree species throughout the later successional stages for both basal area and stem density, which is the typical tree composition of this biogeoclimatic subzone, along with Pacific silver fir (Green and Klinka, 1994). In the Immature and Old-growth stages there was a higher percentage of western red cedar compared to western hemlock, however, in the Thinning and Mature stages western hemlock had a higher percentage over western red cedar. A study in the northern coast of British Columbia shows a co-dominance of western red cedar in old-growth forests, however a lower presence in second growth stands (Banner and LePage). Banner and LePage (2008) also found that western hemlock had a strong relationship with younger forests. Due to the large time variation and the undocumented land tenure ownership in the past, it is unknown which species were planted during what time periods. Reforestation requirements and practices varied over time within the chronosequence in this study. Based on Carter and Klinka (1992), western red

cedar has a higher shade tolerance than western hemlock, however shade tolerance can also be influenced by soil moisture. Minore (1979) classified western hemlock as a more shade tolerant species than western red cedar, therefore there is no consensus on the difference in shade tolerance between these species. Amabilis fir, western hemlock, and western red cedar are all tree species with high shade tolerance (Carter and Klinka, 1992). The higher presence of western red cedar in Immature stands may be due to western red cedar acting as a pioneer species (McKenzie and Tinker, 2013). There are also differences in shade tolerance between seedlings and adult trees, along with differences in shade-tolerance between species that may impact stand composition (Weber et al. 2017).

4.6 Understory Plant Species

This section reviews the common species found throughout all stages of succession, indicator species for the Southern Very Wet Hypermaritime Subzone, restricted species that are only found in one stage of succession, rare species (restricted species in old-growth forests), and culturally significant species. Out of all species that were sampled in the understory, 60% of species showed significant differences ($P < 0.05$) in constancy among successional stages, whereas in the Cascade Range and Oregon Coast Range it was only 11-16% of species (Halpern and Spies, 1995). Therefore, the understory plants in this region show more variability between successional stages comparatively.

Some species are labelled with their common name, as well as their traditional name used by the Huu-ay-aht First Nations and broader Nuu-chah-nulth language group. Many of the Nuu-chah-nulth names are referenced from Hesquiaht First Nations (University of Victoria, 2013). Indigenous communities may have varying perspectives and interpretations of plant species that are based in traditional uses, cultural connections, and language, which reflect local systems of

categorizing biodiversity (O'Flaherty et al. 2008; Turner et al. 2009; Wilder et al. 2016). This traditional ecological knowledge that differs from scientific taxonomy can provide a biocultural lens that enhances ideas grounded in ecological thinking, by including the role that people play in ecological processes (Wilder et al. 2016; Lepofsky, 2009). Some traditional uses for plants with the Huu-ay-aht First Nation are still being utilized, therefore present-tense is used, however, it is unknown if some traditional plant uses that were historically recorded within the Nuu-chah-nulth First Nations are still practiced, therefore past-tense is used for those scenarios.

4.6.1 Indicator and Common Species

For the purpose of this study, indicator species are understory plant species that are typically found within the Southern Very Wet Hypermaritime Subzone (CWHvh1), noted in Green (1994). These understory plant communities will only grow, reproduce, and survive under specific ecological conditions (Ceska and Scagel, 2011). In this study, common species are described as species that are found throughout all successional stages. There are multiple indicator species for the Southern Very Wet Hypermaritime Subzone (CWHvh1). The indicator shrubs include false azalea, Alaska blueberry, oval-leaved blueberry, red huckleberry, salal, and evergreen huckleberry (Green, 1994). The indicator herbaceous plants include deer fern, false lily-of-the-valley, bunchberry, fine-leaved bramble, twinflower, and sword fern. The common species that were found in all successional stages in the study was false azalea, oval-leaf blueberry, red huckleberry, salal, and salmonberry. Klinka et al (1985) noted some species that were present in all stages, such as salal (*Gaultheria shallon*) and trailing blackberry (*Rubus ursinus*) but had a higher presence among the young stands.

The huckleberry species (genus *Vaccinium*) are an important part of the forest communities in the Pacific Northwest (Kerns et al. 2004). Economically, they are extensively

used by humans in the floral market, as wild food, as medicinal plants, and landscaping (Kerns et al. 2004). They are also valued by Indigenous peoples for cultural use and as a food source (Kerns et al. 2004; Turner, 1995).

Evergreen huckleberry (p'ap'aʔismapt) is a shade-tolerant understory plant that typically grows slowly, however, can grow at an increased rate if found within shady and moist conditions (Kerns et al, 2004). Evergreen huckleberry is noted to be a good indicator of the Southern Very Wet Hypermaritime Subzone and is also considered a rare species in this subzone (Green, 1994). Evergreen huckleberry leaf cover and stem density did not significantly differ between successional stages, however, did show a preference for eastern slopes and forest stands with higher tree stem density in the CCA. Evergreen huckleberry was not present in the Regeneration stage, however, had a higher presence in later stages. A higher tree stem density leads to higher shade and moister forest conditions due to denser canopy cover, meaning these results coincide with Kerns et al. (2004), stating this evergreen huckleberry grows at an increased rate in shady and moist conditions. Clear cutting can reduce the presence of forest stands with these conditions, therefore reducing the abundance of evergreen huckleberry. The culturally significant evergreen huckleberry produces Cynamoka berries (p'ap'aʔis), which are an important source of food to the Nuu-chah-nulth (Turner, 1995). They can be harvested later than other berries, throughout late autumn, and December (Turner, 1995).

The berries (hisʔinwa) of the red huckleberry (hisʔitqmapt) are a culturally significant plant food to the Huu-ay-aht First Nations and to the Nuu-chah-nulth (Huu-ay-aht First Nations, 2016; Turner, 1995). Red huckleberry is commonly found in conifer forests, under canopy openings, in soils rich in decaying wood, and on stumps and logs (Pojar et al. 1994). There is a higher mean density of red huckleberry found in Old-growth forests compared to younger

Regeneration forests (Table 3.7). Clear-cutting therefore reduces old-growth forests and therefore reduces the density of red huckleberry. Alaback (1982) found that *Vaccinium* species (along with *Rubus spectabilis* and *Ribes laxiflorum*) made over 90% of the understory production in the young stands of southeast Alaska, and small decumbent red huckleberry plants will persist after canopy closure beside root mounds, logs, or tree stumps. Red huckleberry plants may grow in every successional stage; however, in closed canopy forest stages they may not receive enough sunlight to produce berries (Green, 1994). Therefore, though red huckleberry is present in the young Thinning stands, this does not mean they are productive in this stage of forest succession.

Oval-leaf blueberry (tł'itsx^waanushmapt) had higher leaf cover at associated with elevation and higher as well, however stem density was even across environmental variables, meaning the amount of plants did not change based on a certain variable, only the size. There was a higher mean stem density of oval-leaf blueberry found in Old-growth forests compared to younger Thinning forests. This species is commonly found in moist conifer forests and openings (Pojar et al. 1994). Oval-leaf blueberry is a dominant understory shrub in western hemlock forests and has high shade tolerance (Tappeiner and Alaback, 1989). After clear-cut logging, this species only becomes dominant over herbs after three to seven years by resprouting from intact rhizomes, however if it establishes from seed, then it may take even longer to become dominant (Alaback and Tappeiner, 1991). The berries from oval-leaf blueberry are consumed as food by indigenous peoples on the west coast (Turner and Kuhnlein, 1991). Clear cutting and reducing forest stand age decreases the density of oval-leaf blueberry. Oval leaf blueberry is similar in appearance to dwarf blueberry, bog blueberry and Alaskan blueberry. Oval-leaf blueberry often grows aside Alaskan blueberry (Pojar, 1994). In the field, these species were accidentally

combined when conducting plant surveys. The results for oval-leaf blueberry are not completely accurate due to the combining of similar species and therefore are not reliable. Alaska blueberry (*Vaccinium alaskaense*) is Bog blueberry (*Vaccinium uliginosum*) is a culturally significant plant species to the Nuu-chah-nulth and the berries are consumed fresh or in dried cakes (Pojar, 1994).

Salal (Yama, y'am'apt) is a culturally significant food and medicinal plant to the Huu-ay-aht First Nations (Huu-ay-aht First Nations, 2016). The salal berries (y'am'a) are consumed fresh or preserved for winter, and the young salal leaves are chewed to aid with indigestion (Huu-ay-aht First Nations, 2016). Salal was found in all stages in varying quantities, making it a common species in this forest type. The stem density of salal was highest in Immature and Old-growth stands, and salal leaf cover was highest in Immature, Mature, and Old-growth stages and lowest in Regeneration and Thinning stages. In the Drier Maritime Coastal Western Hemlock biogeoclimatic subzone, salal was most abundant in young stands (Klinka et al. 1985), whereas in this study the abundance is higher in a variety of successional stages, particular older stages. Low stem density and leaf cover values in the thinning stages is similar to the findings of Messier (1992) in coastal forests of northern Vancouver Island, suggesting that light intensity is an important factor influencing salal growth, leaf size, biomass, and structure. Light intensity in northern Vancouver Island forests varied from 5% to full sunlight to 25% full sunlight, differing in Forest stands in the Thinning stage have high stem density and low light levels, creating unideal growing environment for Salal. While there are many opportunistic species growing within the Regeneration stage, salal persists and grow alongside them. Salal's occupation of these sites in this regeneration period is due to the ability to rapidly reoccupy sites through pre-disturbance rhizomes, and also through its ability to acquire nutrients in advance of the invasion of other species (Messier and Kimmins, 1991). Salal's ability to acquire nutrients post clear cut

may be due to their associated mycorrhizal fungi presence in the soil, providing access to nitrogen (Xiao and Berch, 1999). The quality of light may be important too, as Messier et al. (1989) noted that the photosynthetic photon flux density (PPFD) red:far-red ratio decreased with canopy closure, leading to the decrease in salal cover. Similarly, in the current study salal showed a significant decrease in leaf cover between the Immature and Thinning stages, followed by a significant increase in the Mature stage. Salal stem density showed a significant decrease between the Immature and Mature stage, and a significant increase between the Thinning and Old-growth stages. The interesting finding for salal in old-growth forests is that though salal increased in both leaf cover and stem density again in old-growth forest, stem density did not show as much of an increase. Similar to this study, Klinka et al. (1985) found salal in all successional stages, but it had a higher presence among the young stands, however, the values were also higher in Mature and Old-growth stands. As the forest advanced into the Old-growth stage, salal leaf cover increased but the stem density did not show as much of an increase. Salal plant growth was shown in increased leaf cover rather than number of stems. This suggests that over time salal plants outcompete each other and expand in size (leaf cover). This increase in leaf cover is important because it contributes to leaf litter, and we know that 28% of total leaf litter is contributed by understory plants (Bray and Gorham, 1964).

Twinflower is considered an indicator species for the Southern Very Wet Hypermaritime Biogeoclimatic subzone (Green, 1994). In this study Twinflower was found only within the Immature and Old-growth successional stages, consistent with where it is commonly found; open to dense forests and in shrub thickets (Pojar et al. 1994). The stem density for twinflower was related to higher values of elevation, whereas the leaf cover correlated with tree basal area, stem density, age, moss cover, and profile depth. This indicates that a higher number of twinflowers

grew within sites sampled outside the Southern Very Wet Hypermaritime Subzone, within the Submontane Very Wet Hypermaritime, whereas a larger volume of twinflower grew in forests old forests with large trees. Only one site out of the stages where twinflower was found was within the Southern Very Wet Hypermaritime Biogeoclimatic Zone, therefore, within the subzone twinflower was restricted to the Old-growth stage.

False lily of the valley (kuuw'iikmapt) is found in every stage of forest succession and is considered a common species, as well as an indicator species of the Southern Very Wet Hypermaritime Biogeoclimatic subzone (Green, 1994). The leaf cover and stem density of the Immature and Old-growth stages are significantly higher than the Thinning stage, indicating that false lily-of-the-valley does not prefer a highly closed canopy. False lily-of-the-valley is commonly found in moist to wet, shady woods (Pojar et al. 1994). Understory species like False lily-of-the-valley that typically grow in moist environments, also seem to be found in Immature and Old-growth stages. This is likely due to the increased understory volume, which leads to more shade and less evaporative water loss.

Canada bunchberry (hast'aachiqmapt) is a culturally significant plant species to the Nuu-chah-nulth and other coastal peoples that produces berries that can be eaten raw or stored for later consumption (Turner and Kuhnlein, 1991). Canada bunchberry has high stem density values related to moss cover, tree stem density, profile depth, elevation, age, and basal area, indicative of Immature and Old-growth stands. They are commonly found in moist conifer forests and forest openings, from valley bottoms to the subalpine (Pojar et al. 1994). Canada bunchberry had highest values in Immature and Old-growth stands, though these results were not significant.

As a culturally significant species to the Nuu-chah-nulth, the rhizomes of the sword fern (ʔitsmakt, ʔitsmapt) could be cooked, peeled, and eaten (Turner, 1995). Historically, the fronds

of the sword fern were used in a pilaa-pilaa contest, which was a game for boys to see who could hold their breath the longest, which was important in diving to harvest bull kelp for fishing lines and harpoon lines, as well as dive underneath the body of whale during the hunt (Turner, 2014). In this study, sword fern was found in every stage of succession, except for Old-growth, and had values related to canopy openness, North facing slopes, stand basal area, profile depth, stand stem density, and low elevation. Sword fern had higher leaf cover values in the Thinning stage, indicating a shade-tolerant species that grows better in forests with high stand stem density. Sword fern is an indicator species of the Southern Very Wet Hypermaritime Biogeoclimatic subzone (Green, 1994).

Deer fern (kaatskuuxsmapt) is a culturally significant species to the Nuu-chah-nulth people, with young shoots eaten to suppress hunger and the fronds used to line steaming pits (Turner and Kuhnlein, 1991). Deer fern stem density is positively related to an east-facing slopes, whereas the leaf cover is not related to any specific environmental variables. Like the sword fern, deer fern is also an indicator species for the Southern Very Wet Hypermaritime subzone. This species was also found within all stages of succession, meaning it is a common species of these forest types, adapted to growing throughout all stages of succession to varying amounts. Alaback (1982) noted that *Blechnum* ferns, such as deer fern, grow in dense clumps when there is sparse tree regeneration in younger stands.

4.6.2 Restricted Species

4.6.2.1 Rare Species

Biodiversity loss is a global scale concern, especially with increasing biodiversity loss within forest ecosystems (Gilliam, 2007). Forest land use can destroy or alter habitats, decreasing the number of native species and introducing invasive species (Gilliam, 2007). Typically, when

talking about biodiversity loss within the forest environment, the herb layer is omitted from discussions, however, species that exist within this layer have a higher rate of natural extinction than species that live within other forest strata (Gilliam, 2007). Herbaceous layer species richness is therefore an indicator of forest biodiversity, and the threats seen by both are interdependent (Jolls, 2003). Over 80% of total plant species richness in temperate forests is represented within the herbaceous layer (Gilliam, 2007). Species-rich understories are often correlated with species-rich overstories, and total richness, all of which vary with forest type (Gilliam, 2007). The occurrence of rare species in the understory layer are important indicators for biodiversity, due to the habitat specificity of rare plants (Gilliam, 2007; Spyreas and Matthews, 2006). Habitat loss, habitat fragmentation, introduction of invasive species, and overexploitation are all anthropogenic factors that can negatively impact the presence of rare species (Jolls, 2003), some of which are a factor when logging operations are undertaken.

Rare species are defined as species that “occurs in widely separated, small sub-populations so that interbreeding between sub-populations is seriously reduced or is restricted to a single population” (Dury, 1974). Old-growth forests are a widely separated and endangered habitat. The restricted species that are found only in old-growth forests may remain rare because their optimal habitat is within fragmented and small stands (Ryan et al. 2009). These climax forests are home to multiple rare species, that can only be found in more developed forest stands. For example, in this study five rare species, were only found within the Old-growth successional stage, one tree species and four understory species: Pacific yew, fern-leaved goldthread, northwestern twayblade, bracken fern, green false hellebore (Table 3.12). Pacific yew, bracken fern, and green false hellebore are all culturally significant species to the Huu-ay-aht First Nations, for both traditional medicine and food.

Northwestern twayblade, bracken fern (shitlmapt), fern-leaved goldthread, and green false hellebore were only found in the old-growth forest stands. Bracken fern is a culturally significant species to the Nuu-chah-nulth. Fiddle heads from this fern were eaten once boiled and the rhizomes were roasted in underground pits and consumed (Turner, 1995; Turner and Kuhnlein, 1991). Bracken fern is correlated with intermediate values of all environmental variables, indicating old-growth forests. Fern-leaved goldthread is an important species for deer forage and is commonly found in moist forests (Pojar et al. 1994). Green false hellebore is a medicinal plant used by the Nuu-chah-nulth and is a culturally significant species (Turner, 1995). The mashed roots can be used topically to stop pain (Pojar et al. 1994). This understory species can be found in moist to wet, open forests (Pojar et al. 1994). Fern-leaved goldthread and green false hellebore were both associated with higher values of elevation, moss cover, tree stem density and soil profile depth, indicating old-growth forests. One-flowered wintergreen was only found in the Mature stage and had values associated with high tree basal area. This species can be commonly found in open to dense, moist coniferous forests with high moss ground cover, which correlates with the higher moss cover in Mature forests (Table 3.6) (Pojar et al. 1994). Pacific yew (tlatmapt) was only found in old-growth forests overstory and is a culturally significant plant species the Huu-ay-aht First Nations, used as medicine (Huu-ay-aht First Nations, 2016). In a similar study in coastal old-growth forests on Vancouver Island, the only restricted species found were bryophytes, which was most likely due the shaded and moist environment provided by old-growth tree stands (Ryan et al. 2009).

The restricted species that are found only in old-growth forests may remain rare because their optimal habitat is within fragmented and small stands (Ryan et al. 2009). The conversion of old-growth forest to second-growth forest from timber harvesting, leads to more regenerating

stands and therefore an increase in the species that are restricted to younger stands (Ryan et al. 2009). Therefore, the old-growth rare species such as, Pacific yew, fern-leaved goldthread, Northwestern twayblade, bracken fern, and green false hellebore will continue to remain rare, the more that we clear cut harvest forests. Halpern and Spies (1995) also noted a local extinction of four species from sites that were harvested in cascade and coastal forests of Washington and Oregon, USA, including *Tiarella trifoliata* (foam flower).

4.6.2.2 *Opportunistic Species*

In Vancouver Island forests Ryan et al. (2016) found that the highest number of restricted species were found soon after disturbance, similar to our results finding the highest number of restricted species found in the Regeneration stage. This is due to light-loving, opportunistic species colonizing the newly disturbed site (Ryan et al. 2016). Pearly everlasting, rush skeleton weed, fringed willowherb, smooth cats ear, wall lettuce, and Canada thistle (sachkmapt) are restricted species that were only found in the Regeneration stage which are often found in open forests, clearings, meadows, and fields (Pojar et al. 1994). Wall lettuce is commonly located in both moist forests and clearings (Pojar et al. 1994). They have values associated with high bare ground cover and canopy openness, indicative of a recently harvested stand. These species all had stem density and leaf cover values associated with high bare ground cover and canopy openness. Fireweed is an opportunistic species that found was to have a significantly higher leaf cover and stem density in the Regeneration stage than other stages, however it was present in both Regeneration and Immature stages.

Thimbleberry (tl'ach?almapt, ch'ashxiqmapt) is a culturally significant plant to the Huu-ay-aht First Nations. Many parts of the plant were used as food, such as the berries (tl'aach?aal), shoots (ch'aashxiw'a), and young sprouts (Huu-ay-aht-First Nations, 2016). The leaves could

also be boiled with fish as flavouring (Turner and Kuhlein, 1991). Thimbleberry shoots were often brought to halibut fishing ground to share and trade (Turner, 2014). Thimbleberry is a restricted species that was only present in the Regeneration stage consistent with the typical habitat of thimbleberry, in open wooded areas, clearings, along roadsides and shorelines (Turner, 1995). Based on the results of this study, clear cutting can increase the presence of thimbleberry. Black raspberry (hisshitlmapt) is a culturally significant species and produces berries (hisshitl) that are consumed as food (Turner, 1995). In this study, black raspberry was only present in Regeneration stands, with high levels of light and open canopy, meaning it can be classified as both a restricted and opportunistic species. Dyrness (1973) found that blackcap raspberry preferred disturbed-unburned, moist sites. Black raspberry was associated with higher levels of canopy openness and bare ground cover. They are typically found in thickets, open forests, and disturbed sites such as burned clearcuts (Pojar et al. 1994). Red elderberry (ts'iwiipt), which was only found within the Regeneration stage, are typically found within open forests, moist clearings, stream banks, and swampy thickets (Pojar et al. 1994).

It is interesting to note that some of the species found in the Regeneration stage may not be representative of this successional stage if the stand had been logged within the year. Some species may be temporarily persisting from a more developed forest that was logged. They may require an additional year to die off, as the habitat is no longer suitable. These are called 'residual' species, which is defined as species that are characteristic of the undisturbed forest (Halpern and Spies, 1995). This characterization is based on knowledge of the vegetation of undisturbed forests and pre-harvesting samples (Halpern and Spies, 1995). For example, foam flower was found in both Regeneration and Mature stands, however, this plant typically grows in moist forests with partial shade (Pojar et al. 1994). The foam flowers were observed in a recently

harvested forest stand. Therefore, it is correct to say that foam flower only grows in more developed forest stands. Another example of this would be western skunk cabbage, living within Regeneration, Immature, and Old-growth forests, however, the western skunk cabbage observed in recently logged stands were dwindling. The leaves were turning yellow from sun bleaching, drying up, and shrinking. To reduce this sampling issue in future studies, I would recommend avoiding stands logged within 1 to 2 years, to allow time for species found in previous mature stands to decrease. Lady fern was present in both Thinning and Regeneration stages and the stem densities were similar, however, the leaf cover was disproportionately larger in the Thinning stage, indicating a species that has the most growth in shaded forests and is a residual species in recently logged forests.

4.6.3 Other Culturally Significant Species

Pacific crab apple (*tsitsih?aqtlmapt*) is a culturally significant species to the Huu-ay-aht First Nations that was used as both food and medicine (Huu-ay-aht First Nations, 2016). The apples were used as food and do increase strength, and the bark was stripped to use as medicine (Huu-ay-aht First Nations, 2016). Pacific crab apple was restricted to the Immature stage. In the canonical correspondence analyses, it had values associated with higher soil pH and higher elevation. Pojar et al (1994) note that it can commonly be found in places with higher levels of moisture.

Cascara (*q'ay'aax^wasmapt*) is a culturally significant species to the Huu-ay-aht First Nations. The bark has laxative properties which can be used as a medicine (Huu-ay-aht- First Nations, 2016). Cascara sagrada was found throughout every successional stage, except for the Thinning stage. The stem density was associated with higher values of Northness (north facing slopes) and Eastness (east facing slopes), whereas the leaf cover associated with northness and

bare ground cover. Cascara sagrada is commonly found in dry to wet, shady sites, in mixed woods, and on southern aspects (Pojar et al. 1994), which is the opposite aspect of what was found in this study. This understory plant species is unlikely to grow in forests that are in the Thinning stage of succession (aged 46 to 79 years), though 80-120 years is the average harvesting age range for a stand in this region (Western Forest Products, 2006; British Columbia Ministry of Forest, 1999).

Licorice fern (hihit'aqtlmapt) is a culturally significant fern species to the Huu-ay-aht First Nations and Nuuchahnulth peoples that has been used both as food and for medicinal purposes. It can be used to treat respiratory infections, as mouth sweetener, and as an appetite stimulant (Huu-ay-aht First Nations, 2016; Turner and Kuhnlein, 1991). Licorice fern is a restricted species that was only found within the Mature stage in this study and was associated with Eastness. Licorice fern can be found on wet, mossy ground, logs and rocks, tree trunks, and at low elevations (Pojar et al. 1994). The plots sampled did not include areas with rocks, and plant growth on large tree trunks was not counted when sampling understory species, therefore this could reduce the amount of licorice fern found in old-growth sites.

Salmonberry (qawashmapt, m'ashmapt) is a culturally significant plant species to the Huu-ay-aht First Nations and Nuuchahnulth people. The peeled young shoots can be eaten, and the leaves were boiled with fish as flavouring (Huu-ay-aht First Nations, 2016; Turner and Kuhnlein, 1991). Some Nuuchahnulth First Nations correspond the ripening of salmonberries to the return of sockeye salmon to the spawning ground (Turner, 2014), and the ripening of these berries can be related to the song of the Swainson's thrush bird (Turner, 2014). These are phenological indicators of ripening and events that would help with scheduling harvest and travelling times (Turner, 2014). In this study, salmonberry was found predominantly in younger

forest stands, with higher light levels. Alaback (1982) found that in forests of Southeast Alaska, *Rubus spectabilis* (salmonberry) was eliminated during the closing of the forest canopy, similar to this study where salmonberry was not found in the Thinning stage. It was associated with higher levels of canopy openness and bare ground cover. There was a significantly higher presence in Regeneration and Immature stands, meaning this species grew better in increased light conditions. In young stands of in Sitka spruce-western hemlock forests of Southeast Alaska, Salmonberry (along with various species of *Vaccinium* and *Ribes laxiflorum*) make up over 90% of the understory production (Alaback, 1982). However, this study excluded areas with high moisture levels to reduce the number of variables, so this data may not accurately depict presence of salmonberry throughout successional stages. Salmonberry is typically an indicator of very moist to very wet soil moisture conditions (Qian et al.1997).

4.6.4 Tree Seedlings and Saplings

Seedlings and saplings in early successional stages are predominantly dependent upon what trees have been replanted, what species were present in the stand prior to harvest that naturally regenerated, and which trees species thrive with high light levels. It is unknown which trees were selected for replanting or if free growing occurred, especially in older successional stages, however; reforestation did become legally required in British Columbia in 1987 (British Columbia, 2017), so we can assume stands past this date were planted with tree seedlings. There is a higher presence of western red cedar and western hemlock seedlings in this study compared to other tree species.

Red alder (qaqmapt) is a culturally significant plant species to the Huu-ay-aht First Nations and Nuu-chah-nulth peoples that is believed by the elders to have numerous healing properties (Huu-ay-aht First Nations, 2016). The bark is used in a tonic that can be drunk to heal

illnesses, and the tree can also be used by many indigenous peoples along the West coast as fuel for smoking salmon and other food (Huu-ay-aht First Nations, 2016; (Turner and Kuhnlein, 1991). Red alder saplings were restricted to the Immature stage and the seedlings were only present in Immature and Mature forests. Red alder is the only commercial tree species located west of the Rocky Mountains with the ability to fix atmospheric nitrogen (Harrington, 1949), therefore making this species important in forest management. These seedlings prefer to grow in moist organic surfaces such as litter, and are shade-intolerant, therefore they grow well in full sunlight (Harrington, 1949). The Immature stage has a moister soil than the Regeneration stage and still plenty of light from an open canopy, explaining the increased presence of red alder seedlings and saplings in this stage.

Pacific silver fir (w'ihmapt) saplings were restricted to the Regeneration stage, whereas the seedlings were found in the Thinning and Mature stage (Table 3.13), indicating a shade tolerant species that can regenerate in low light conditions. Green and Klinka (1994) confirm that Pacific silver fir is a shade tolerant species. Sitka spruce (tuuhmapt) saplings and seedlings were highest in the Regeneration stage, initially having a larger density and cover, but outcompeted by western hemlock and western red cedar in more mature stands. Sitka spruce will not survive in environments with too little of light (Page and Cameron, 2006), which is similar to the Thinning stage of succession. Since western hemlock and western red cedar are more shade tolerant, they will dominate in this stage of succession, where the canopy is closed.

Western red cedar (huumiis) is a culturally significant tree to West coast peoples and has many different cultural uses for the Huu-ay-aht First Nations (Huu-ay-aht First Nations, 2016). This tree has medicinal properties that used to help support the body's immunity and fight infections such as urinary, fungal, and bronchial infections (Huu-ay-aht First Nations, 2016). The

inside of the bark was also used to repel mosquitoes. This tree species has a variety of cultural uses such as basket and hat making by weaving the bark, and using the entire tree to make boats (Huu-ay-aht First Nations, 2016). There was a significant decrease in western red cedar seedlings between the Regeneration and Thinning stage, when the canopy is closing, leading to lower light conditions. Western red cedar seedlings were present in every successional stage except the Thinning stage. The highest density of western red cedar saplings was in the Immature stage, indicating tree saplings that are growing into trees. Saplings were also found in Old-growth stands, which is an indicator of an all-aged stand. The largest trees by basal area within Old-growth forests were western red cedars, indicating that western red cedars dominated within old-growth forests of the Southern Very Wet Hypermaritime Biogeoclimatic subzone. In earlier successional stages western hemlock trees dominated in density and basal area; however, western red cedars dominate in climax forests.

Western hemlock (*q^witł'aqmapt*) is a culturally significant plant species to the Nuuchahnulth peoples on the east coast of Vancouver Island. The boughs were used to collect herring spawn in inlets and estuaries, and (Turner and Kuhnlein, 1991). There is a story within the Nuuchahnulth First Nations that explains the origin of sunlight, where Raven transforms into a tiny needle of a hemlock (Turner, 2014), which is one example of how plants are intertwined within the culture and traditional stories of First Nations. There was a significantly higher leaf cover of western hemlock seedlings in the Thinning stage as compared to Regeneration, indicating this species grows better in shaded forest stands. Western hemlock is a shade tolerant tree species (Green and Klinka, 1994), therefore this difference found in the study agrees with current literature. Due to its competitive edge in shaded forests, the western hemlock is most likely to become dominant in a site after a natural disturbance or thinning (Alaback and Tappeiner, 1991).

4.7 Culturally Significant Species

Culturally significant species that are used for food, clothing, shelter, food, medicines, and other traditional uses (Garibaldi and Turner, 2004) are important to preserve. Some of these species can only be found in old-growth forests and some of these species have higher stem density and leaf cover in old-growth forests. Multiple culturally significant species in the understory have a reduced presence in coastal forests after clear cut timber harvesting, which could have potential impacts on indigenous traditional practices.

The importance of these plant species is shared through traditional ecological knowledge and wisdom (TEKW) of indigenous peoples, which reflects their long-standing close relationship with the environment (Turner et al. 2000). Traditional ecological knowledge is passed down in families through generations, through traditions, narratives, recipes, spiritual practices, dances, songs, language, and discourse (Garibaldi and Turner, 2004). There are stories that use plant species and have important life lessons, like the example of story about eating too many berries is how the idea of greediness was taught within the Nuu-chah-nulth culture (Turner, 2014). Knowledge of these understory plant species are intertwined into the cultural practices and hold incredible value amongst indigenous peoples. Industrial logging has caused a reduction in the abundance of large western redcedar trees, which are used in cultural practices such as carving dugout canoes, totem poles, and traditional buildings (Benner et al. 2023). The type of western red cedar needed for these practices are rare, and now extirpated from the landscape due to logging (Benner et al. 2023). This is an example of how timber harvesting can impact culturally significant species. There has not been much research on how logging impacts understory culturally significant plant species.

The forest understory is important in indigenous communities, and understory plants have long been managed and harvested. The Nuu-chah-nulth people on the west coast of Vancouver

Island are an indigenous community that have harvested a large range of plant species for food, medicines, materials, ceremonies, and other traditional uses (Armstrong et al. 2022; Turner, 2020). They have all managed the land and plants for many millennia, with the use of forest gardens and other ethnobotanical methods (Armstrong et al. 2022), including berry patches, orchards, root gardens, and wetland crops. Indigenous groups have been caretakers and promoters of food and other resources (Turner, 2020). Plants also played an important role in diet and trade economies, which is why some plant species were actively managed (Armstrong et al. 2022).

The plant species sampled in this study, within Huu-ay-aht First Nation traditional territory, are also found throughout the traditional territories of the Nuu-chah-nulth First Nations along the western coast of Vancouver Island. Nineteen culturally significant understory plant species were impacted in stem density and leaf cover by timber harvesting: nine of those species decreased after clear-cutting, seven increased after clear cut harvesting, two decreased in the Thinning successional stage, and one increased in the Thinning stage. Various parts of these species were consumed or used for other traditional purposes, including the roots, flowers, berries, and leaves (Huu-ay-aht First Nations, 2016). Twelve of these plant species are used as food, nine species are used for medicines, three were used as materials for various purposes from cooking to building, and five were used for other traditional and spiritual practices. There is a complex bond between the plants and First Nations in this region and is tightly woven into a variety of aspects of life. The cycle of life is integral to the Traditional Ecological Knowledge of the Nuu-chah-nulth because seasonal changes influence food and harvesting (Turner, 2014).

Providing ethnobotanical traditional knowledge about these understory plant species provides another important perspective in forest management. These plants species and their

traditional values in indigenous communities should be taken into consideration when designing and implementing management regimes. The Nuu-chah-nulth have a phrase ‘hishukish tsawaak’ meaning ‘everything is one’, talking about how all things are related., which is a kincentric approach explaining how all things (abiotic and biotic) are interconnected with each other and with the land (Turner, 2014). This type of ideology is one that should be considered in forest management. Consultation with indigenous communities should be an important part of forestry silviculture prescriptions in British Columbia. Acknowledging and learning from the importance of plant species to various First Nations is an important part of reconciliation.

4.8 Old-growth Forests

Old-growth forests are described as natural ecosystems with a complex structure that is generated through the landscape’s natural disturbance regime (Karen et al. 2021). Not only are old-growth forests home to rare and culturally significant understory plant species, as described in this study, but they also hold unique populations of fungi and wildlife. Trees, understory plants, fungi, and wildlife are all dependent on one another to form an ecosystem that supports life. The understory layer in forests of the Pacific Northwest directly and indirectly supports floristic and faunistic diversity (Halpern and Spies, 1995). Old-growth forests are home to species that are totally and partially dependent on this climax forests for their life cycles (Green, 1994). Some old-growth forest features that create a suitable habitat include the structural diversity from multiple canopy layers, wide variation in trees sizing and spacing, canopy gaps, coarse woody debris, snags and wildlife trees, cool and moist environment, abundant understory vegetation, abundant epiphytic lichens, and abundant mycorrhizal fungi. The Coastal Western Hemlock forests experience infrequent large-scale disturbances and are driven by small scale tree fall gaps, meaning these old-growth forests have much older trees than forests with other natural disturbance regimes (Karen et al. 2021; Daniels and Gray 2006; Lertzman 1992).

Old-growth forests in British Columbia have been subject to extensive logging over the last centuries, which has reduced these old-growth forests by over 99% (Karen et al. 2021). Economic gain has previously – and still does – take precedent over forest health. Current forest policy and timber harvesting priorities does not aim to preserve forest ecosystems (Bunnell 1995; Spies and Franklin 1996; Franklin et al. 2002). What remaining old-growth forest that is left outside of provincial parks is threatened by logging. The rare and culturally significant understory plants found within the Coastal Western Hemlock old-growth forests are at risk of disappearing if management regimes are not changed and old-growth logging is not drastically reduced. These forests are diminishing quickly due to a high rate of clear-cut harvesting, which is prohibiting the return to a natural old-growth state due to short harvest rotations. The recommendations for harvesting and forest management practices in coastal British Columbia are not based on adequate data regarding how forests respond and recover from past disturbances (Banner and LePage, 2008). Studies of forest ecosystem recovery following disturbance in temperate rainforests of coastal British Columbia are virtually nonexistent (Banner and LePage, 2008), which is why studies that record ecosystem and understory plant recovery after disturbance in each biogeoclimatic subzone is highly important. We need records of growth in every successional stage in order to ensure forests are being managed in a way that prioritizes forest health and old-growth recovery.

Forests on southwestern Vancouver Island are currently being harvested on average at around 80 to 120 years old (Western Forest Products, 2006; British Columbia Ministry of Forest, 1999). It would be beneficial to manage forests on longer harvest rotations (150 to 300 years) to maintain understory plant species and to allow for certain species to recover after disturbance (Halpern and Spies, 1995). Since the old-growth stage begins at 250 years and the natural

turnover rate of old trees is 350-950 years (Daniels and Gray, 2006), I would suggest the harvest age be moved to a longer time period, well over 250 years, to allow for old-growth forests to persist and provide ecosystem resilience.

4.9 Harvesting Impacts on Old-growth Forests

Common shade-tolerant species that are prominent in old-growth forests are slower to regenerate within second-growth forests, and many regenerating species are shade-intolerant (Alaback and Tappeiner, 1991). The slow regrowth of species such as Northwestern twayblade, bracken fern, fern-leaved goldthread, green false hellebores, and one-flowered wintergreen can be seen through this study. Within the CWHvh1 shade tolerant species are commonly found, therefore an increase in shade-intolerant species is outside of what is typical for this ecosystem. Many species in this region are adapted to growing and reproducing within small canopy gaps (Alaback and Tappeiner, 1991), which can be seen by the difference in plant composition post clear cut as compared to the plant composition within an old-growth forest. The small-scale tree mortality of this region leads to canopy gaps that have a profound impact on understory vegetation dynamics (Alaback and Tappeiner, 1991).

Forest management based on mimicking natural disturbances is called emulating natural disturbance regimes (ENDR) and is defined as management strategies with the goal of producing forest ecosystems that are similar to ecosystems resulting from natural disturbances (Long, 2009). The Coastal Hemlock Zone is an example of a forest type that is characterized by a wind-gap disturbance regime (Daniels and Gray, 2006). The pit and mound microtopography and associated gaps produced from wind fall are important structural legacies for species richness and diversity (Schaetzl et al., 1989a; Oliver, 1980). Since forests on the Southeastern coast of Vancouver Island have a tree fall gap dynamic for the natural regime, it would be best to have a harvesting type that mimics this regime. Fires occur at a much lower interval, from 750 to 1000

years, meaning it is not the dominant disturbance regime in these forests (Daniels and Gray, 2006). Daniels and Gray (2006) suggest that forest fires are an infrequent, low- and mix-severity events in the Hypermaritime Coastal Hemlock subzone, and that fine-scale gap dynamics is the dominant process explaining the dynamics and structure of these forests. When considering various disturbance types, small gap-scale mortality events leave an intact forest and the forest matrix dominates, however stand-level mortality events destroy dominant cover and the matrix is altered to a post-disturbance environment (Franklin et al. 2007).

The current forest management regime is clear cutting with reserves; however, this harvesting type more closely mimics large spatial scale and small temporal scale natural disturbance regimes such as fire. West et al. (1981) notes that large-scale disturbance regimes can be described by the size of the disturbance, the frequency, the recurrence interval, predictability, rotation period, and magnitude. You can then classify a disturbance by intensity and severity, which is usually inversely related to frequency (West et al., 1981). Based on the severity of the impact to the understory vegetation, the large scale, and the high frequency; I would classify clearcutting as an intense and severe unnatural disturbance to the forests within the CWHvh1. An example of harvesting that may more closely mimic the gap dynamics and windfall seen in forests with shade-tolerant species would be shelterwood cutting or selective logging. The shelterwood retention system would only remove select individuals from a stand, whereas clear cutting with reserves removes the entire stand of trees while only leaving small remnant patches (British Columbia, 2003). Clear cutting is designed to manage areas as even-aged stands, which is not like stands on the uneven-ages forests of the Coastal Hemlock zone. Using a shelterwood system would allow trees to persist, with the objective to shelter the next generation and understory (British Columbia, 2003). Since these forests contain many shade-

tolerant tree and understory species, this is the best silvicultural system to use as it allows for a shaded environment. And irregular shelterwood system would allow longer periods of time between initial establishment and removal, allowing the understory regeneration to occur for a longer time (British Columbia, 2003).

4.9 Limitations

The sampling method used in this study holds limitations. Using a quadrat method for sampling could possibly miss the true number of species found within the forest, whereas an inventory approach, where one walks around and simply recording the species found may encounter an increased number of species (Gilliam, 2007). Compared to inventory sampling, plot-based sampling underestimates species richness (Gilliam, 2007). However, for the context of this study, it was important to quantify the stem density and leaf cover of each species, which is possible with a quantitative method like quadrats, however, not feasible in an inventory approach. The age ranges in the chronosequence could have been made smaller, to avoid the changes that are seen in transition years between stages, this would have provided better results within the descriptive statistics. For example, the Immature stage was from 10 to 45 years, and Thinning stage was 46 to 79 years, however this could have been changed to 15 to 35 years and 50 to 70 years. Halpern and Spies (1995) left five and twenty years between their three successional stages. The successional stages that were used in Ryan et al (2009) included Regeneration (3-8 years), Immature (25-45 years), Mature (65-85 years), and Old-growth (> 200 years), meaning there was 17, 40, and 15 years between the four successional stages. Klinka et al (1985) based their successional stages upon on forest structure rather than age.

The reforestation practices and policies changed drastically over the past decades, therefore the plots sampled in this study had a variety of backgrounds with regards to the stand regeneration. It is unknown what species and composition were replanted in each stand, or if any

replanting occurred at all post-harvest. The main assumption of a chronosequence approach is that the only difference between sampled plots is the age, however within this study it is not possible to know the planting history, which is therefore another limitation to take into consideration.

The limitations of this study included technological malfunctions. In the field, the camera malfunctioned, corrupting the images at multiple field sites (3, 28, 29, 31, 34, 36, 41, 44, 45, 48, 79, and 81). Near the end of the study, the camera broke, and the remainder of the photographs had to be taken with an iPhone 10 with the camera fish-eye lens. This created minor differences in images collected from earlier and later plots, introducing slight bias into the results. Another limitation of collecting the light data included the height restriction of the camera tripod.

According to Drever and Lertzman (2002), any plant that is greater than 2 m in height will have an impact on the light conditions in the understory, therefore photographs should be taken at a height of 2 meters. Observation shows that the canopy was very open in old-growth forests, however the results show a decrease in canopy openness in old-growth forests (Table 1). This is most likely due to the height at which the images were taken. All images were taken at 150 cm (due to limitations of the equipment); however, the height of the understory shrub layer was higher than this in several plots. Therefore, the camera was taking images of canopy cover that included the cover of the dense understory shrubs. The data would have been more representative if the camera was positioned higher, above the understory shrub layer. This limitation introduced bias into the light data results. For future understory research in this region, I would recommend setting the camera at a height of above 2 m or higher, to accurately measure canopy openness. The old-growth stage has a mean canopy openness percent of 9.97 ± 3.38

(n=16), however if you exclude all the plots that had understory vegetation over 150 cm, then the mean percent openness would be 13.88 ± 2.08 (n=4).

Other limitations of the study included the collection of soil data ground cover data. There was not enough time or resources to measure various soil characteristics in both field and laboratory settings, such as concentrations of various minerals, and bulk density. I collected data regarding percent moss cover and percent bare ground cover; however, this information would have had increased accuracy with more ground cover categories. For example, in Ryan et al. (2009) understory vegetation study, had four ground cover categories: Humus, Wood, Rock, and Mineral soil. In several of our plots there was low bare ground and low moss cover recorded, but no description of what material was covering the remaining ground. During these occasions, there was increased amounts of remnant woody debris, which accounted for most of the ground cover in Regeneration plots. This wood cover could be important in understanding the plant species present, due to the potential effects on the soil profile. O'Connell (1997) noted that woody debris from slash may add important nutrients to the soil for plant regrowth, whereas Ramovs and Roberts (2003) explained the importance of coarse woody debris in mature stands as critical habitat for vascular understory plant species. However, there aren't many studies conducted in the Pacific Northwest on the impacts of woody debris on understory plant growth. Based on these limitations regarding soil and ground cover, I would recommend a further study on the soils of successional stages in this region, to relate to the changes in vegetation seen over time after timber harvesting. It would also be important to record detailed ground cover information.

Distinguishing between certain species proved to be a difficulty in the field setting. Species such as oval-leaf blueberry and Alaska blueberry, described as very similar to one

another by Turner (1995), were difficult to distinguish in the field. Therefore, in the results, these two species were identified as one: oval-leaf blueberry. This grouping may have skewed the results for Oval-leaf blueberry stem density and leaf cover, though these two species are often found in similar environments (Turner, 1995). There was also difficulty distinguishing between various species of ferns in this region, so the unknown or similar species were grouped together under the category of 'other ferns'. The last identification issue surrounded grasses, which were also grouped together under the category of 'grasses'. Improvements for future research would involve more in depth understanding of botany and plant characteristics of various families found in this region, prior to conducting field work. This may involve having a local First Nations person as a guide, to learn local species identification.

The final limitation of this study involved the access to site locations. Sites were chosen based on a combination of remote sensing data and logging maps, to ensure access to forest sites that varied in space and age. A few selected sites turned out to be inaccessible due to logging road closure. The maps provided of logging roads in that region were not kept up to date. The areas logged are constantly changing and not all roads are frequently maintained, and these changes were not always updated on the provided maps. Therefore, a lot of sites that had initially been chosen were inaccessible due to road closure, or the roads had been unmaintained and had grown over with encroaching vegetation. Inaccessibility restricted the number of sites in the various age groups that could be surveyed, explaining the unevenness in the number of plots between successional stages. As previously mentioned, there were also some sites that were selected within another biogeoclimatic subzone due to limited site access. Though the majority of sites were found within the Southern Very Wet Hypermaritime Subzone (CWHvh1), seven plots were sampled outside of this region and within the adjacent subzone: Submontane Very

Wet Hypermaritime (CWHvm1). The CWHvm1 occurs up to 600 meters above elevation, whereas the CHWvh1 occurs up to 200 meters above elevation, and the seven sites were sampled above 200 meters (Green, 1994). The inclusion of sites outside of the CWHvh1 could influence the understory vegetation findings in this study. In future studies, it will be important to sample within elevation limits for each individual subzone to avoid the influence elevation may have on species distribution, species composition, leaf cover, and stem density.

4.10 Future Research

I would recommend conducting future temporal forest research using five successional stages, because results show varying stem densities and leaf covers of understory vegetation between these stand ages. More research is needed to confirm the upper and lower limits of stand age for these 5 successional stages within the Southern Very Wet Hypermaritime Biogeoclimatic subzone and within various other Biogeoclimatic subzones. Ryan et al. (2016) talks of the importance of different species in older stands and the variations between subzones, meaning that ecological results collected from a study of one ecosystem should not be applied to other ecosystems, as each region has its own unique characteristics and biodiversity. The presence of one species in an older successional stage may be rare to one subzone, but common to another. Klinka et al (1985) notes that climax plant associations represent different environmentally different ecosystems and that site associations should be classified according to climate, soil moisture, and soil nutrients, hence the importance of studying within the proper biogeoclimatic subzone.

For future studies surrounding understory vegetation on southwestern Vancouver Island, I would recommend pairing this type of ecological study with soil research. To take this research one step further, one could examine the changes in soil characteristics through various successional stages after timber harvesting. The understory vegetation is integral to nutrient

cycling through the entire forest stratum, from overstory to soil, and holds the highest level of nutrients (Gilliam, 2007). Soil and vegetation are highly connected and influence the development of one another. Testing for soil characteristics as well as soil nutrient levels would give a broader picture to what is occurring in these second-growth forests over time. Good indicators of nutrient presence throughout soil development include C:N, C:P, and N:P ratios, that are found within the topsoil (Tian et al. 2010). These ratios in soils are affected by vegetation cover, plant composition, geomorphology, and seawall (Zhang et al. 2014).

Another part of the understory that can be studied through successional stages would be fungi, mosses, and animals. More can be researched about how species within these categories can be impacted by logging, as well as their importance on the old-growth forest ecosystem in the Southern Very Wet Hypermaritime biogeoclimatic subzone.

A beneficial contribution to the literature would be successional understory vegetation studies conducted in each subzone on Vancouver Island. Every subzone has unique compositions of understory vegetation due to biogeoclimatic differences in each region, and these varying understories have not yet been thoroughly documented. There are chronosequences studies, like Ryan et al. (2009), that include a few subzones, however, there has not been one study conducted of every subzone, that includes soil attributes, overstory vegetation composition, and understory vegetation compositions. A downfall in ecological field-based studies is that there is so much variation in the methods that are used, leaving it more difficult to note similarities between studies. Using one method across many subzones would be beneficial in seeing the true variation in understory vegetation between regions.

There are few studies done on the relationship between plant species richness and productivity, and how this relationship changes from forest management (Leuschner et al. 2009;

Reich et al. 2002). There are large differences in the relationship plant diversity and productivity, between herbaceous and woody species in the understory, and between the different canopy layers (Laanisto et al. 2008; Burton et al. 2013). The herbaceous and woody plants that make up the understory layer consist of two to ten times the number of species that can be found in the overstory of a northern temperate forest (Gilliam, 2007). I recommend studies within each subzone on Vancouver Island to research further into the connection between understory species richness, diversity, and productivity.

Through this study, I looked at the impact of clear-cut logging over time on the forest understory, however there is still research needed on how different logging methods will impact the understory vegetation. We need more information to compare the regeneration over time from various harvesting techniques. It is known that using different harvesting techniques such as shelterwood cutting or selective cutting, can maintain understory light levels, and therefore influence understory composition (British Columbia Ministry of Forests, 2003).

In modern day, climate change is growing issue to the planet, with a lot of focus on how to manage carbon in the atmosphere. As we know, forests act as carbon sinks through carbon sequestration, specifically old-growth forests (Karen et al. 2021). It could be beneficial to further research how forest clear-cutting and loss of understory could contribute to reduced carbon storage in forest ecosystems. As we are trying to move towards a greener planet and conserve forest ecosystems for climate mitigation, we should investigate how deforestation impacts the forest ecosystem's ability to store carbon, rather than solely focusing on the overstory. The overstory can store over 200 times more carbon than the understory of a northern temperate forest (Smithwick et al. 2002). Though understory vegetation typically only accounts for 1% of carbon stored in old-growth Pacific Northwest forests, understory vegetation has a big influence

on soil development, which stores 50 to 59% of forest carbon (Birdsey et al. 1993; Smithwick et al. 2002). Lyu et al. (2019) determined that fern litter and roots accounted for 54 to 61% of total soil carbon in pine forests. Though living ferns within the understory do not store a large percentage of carbon, their litter and DOM contribute to a large percentage of the carbon stored in forest soil. Temperate old-growth forests have a higher level of carbon storage in plant matter and soil than disturbed early succession forests, which is dramatically reduced through human disturbance (Smithwick et al. 2002). Understory plants also contribute around 20% of leaf litter to the forest floor, that contains the higher levels of nutrients than the litter produced from tree (Gilliam, 2007). I would recommend a baseline study of how old-growth forests in the Southern Very Wet Hypermaritime subzone store carbon throughout the stratum and finding the upper bounds (Smithwick et al. 2002). From there, you can study how this carbon storage changes overtime after clear-cut logging, this would be through the “difference” approach, which measures the changes in forest inventory data over a time (Smithwick et al. 2002; Turner et al. 2000). Bender et al. (2006) states that you need a baseline study of an unimpacted region to compare carbon nutrient and carbon dynamics from pre-industrial environments to the impact on the environment from modern humans. Carbon sequestration in old-growth forests is only estimated using models due to the lack of field studies, as well as the lack of accounting for all manageable pools of carbon within the forest ecosystem in the field studies (Smithwick et al. 2002). A step forward in measuring forest ecosystem level carbon storage could be done by applying Smithwick et al. (2002) study, including field sampling, to the varying subzones on Vancouver Island, for varying stages of succession. Few studies have investigated the links between forest carbon storage and understory plants, though most of the plant diversity is found within the understory vegetation (Burton et al. 2013). Along with decreases in carbon storage

from deforestation, increases in atmospheric carbon can potentially change the forest understory species composition (Gilliam, 2007). Harmon et al. (1990) found that the carbon storage of a harvested forest does not return to original old-growth capacity until a minimum of 200 years, resulting in an influx of CO₂ to the atmosphere from timber harvesting.

Remote sensing technology like LiDAR, once perfected, can be used to model forest understory. Analysts have not yet created a method to use LiDAR data for understory inventory and classification. This type of research method could possibly replace field sampling in the future. LiDAR can be used to create a three-dimensional representation of the understory, with the use of laser light pulses reflecting off vegetation (Venier et al. 2019). This technology can estimate canopy height and cover, basal area, tree density, and has the potential to measure understory characteristics as well (Venier et al. 2019).

Future forest understory vegetation research should include indigenous knowledge from those First Nations that have traditional territory within the region of study. Many First Nations are closely connected to the landscape and have cultural practices that are tied to many forest plants. This study has shown there are culturally significant plant species that are significantly impacted by timber harvesting. Indigenous ways of knowing and the interconnectedness between people and the land provides another important perspective to consider in forest management and scientific research.

Chapter 5: Conclusion

This study identified gaps in the literature regarding ecological studies on understory vegetation within Biogeoclimatic subzone-specific forests of British Columbia. There has been a lack of focus on understory vegetation when studying the impacts of timber harvesting on forest health. This study has detailed the succession of understory vascular plants after clear-cut timber harvesting and identified the major shift in plant composition in these ecosystems as a result. This study has also addressed the need of a fifth successional stage when studying secondary forest succession in this region. During the Thinning stage, leaf cover and stem density of most of the important understory plants decreases, along with species diversity and species richness. The standard harvest rotation in British Columbia occurs at 80 years, long before the forest has matured to a climax state at 250 years. This highlights the need to extend harvest rotations to allow the regeneration and persistence of important understory vascular species, as well as preserving more old-growth forest stands. Through the study I have also identified rare species that are only present in old-growth forests, which are endangered ecosystems in British Columbia. Clearcutting was found to significantly reduce the presence of many rare species, while increasing the presence of opportunistic species in young stands. Culturally significant species experienced both increases and decreases from clear cutting, which highlights the need to explore traditional knowledge and forest management practices from First Nations in this region. Future scientific studies should aim to include traditional ecological knowledge of culturally significant species for food, medicine, materials, spiritual practices, and more. This provides us with a perspective of the human relationship to the forests we study and the interconnectedness of all things.

Chapter 6: References

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Chapter 7: Appendices

Appendix A

Common Name	Scientific Name	Veg Type
Black raspberry	<i>Rubus leucodermis</i>	Shrub
Black twinberry	<i>Lonicera involucrata</i>	Herb
Bracken fern	<i>Pteridium aquilinum</i>	Fern
Canada bunchberry	<i>Cornus canadensis</i>	Herb
Canada thistle	<i>Cirsium arvense</i>	Herb
Cascara sagrada	<i>Rhamnus purshiana</i>	Shrub
Clasping twisted stalk	<i>Streptopus amplexifolius</i>	Herb
Common horsetail	<i>Equisetum arvense</i>	Herb
Deer fern	<i>Blechnum spicant</i>	Fern
Douglas spirea	<i>Spirea douglasii</i>	Herb
Evergreen huckleberry	<i>Vaccinium ovatum</i>	Shrub
False azalea	<i>Menziesia ferruginea</i>	Shrub
Fern-leaved goldthread	<i>Coptis asplenifolia</i>	Herb
Green false hellebores	<i>Veratrum viride</i>	Herb
False lily of the valley	<i>Maianthemum dilatatum</i>	Herb
Fireweed	<i>Chamaenerion angustifolium</i>	Herb
Foam flower	<i>Tiarella trifoliata</i>	Herb
Fringed willowherb	<i>Epilobium ciliatum</i>	Herb
Grass	Poaceae (family)	Herb
Lady fern	<i>Athyrium filix-femina</i>	Fern
Licorice fern	<i>Polypodium glycyrrhiza</i>	Fern
Northwestern twayblade	<i>Neottia banksiana</i>	Herb
One-flowered wintergreen	<i>Moneses uniflora</i>	Herb
Oval leaf blueberry	<i>Vaccinium ovalifolium</i>	Shrub
Pacific crab apple	<i>Malus fusca</i>	Shrub
Pearly everlasting	<i>Anaphalis margaritacea</i>	Herb
Red elderberry	<i>Sambucus racemosa</i>	Shrub
Red huckleberry	<i>Vaccinium parvifolium</i>	Shrub
Salal	<i>Gaultheria shallon</i>	Shrub
Salmonberry	<i>Rubus spectabilis</i>	Shrub
Western skunk cabbage	<i>Lysichiton americanus</i>	Herb
Rush skeleton weed	<i>Chondrilla juncea</i>	Herb
Smooth cat's ear	<i>Hypochaeris glabra</i>	Herb
Sword fern	<i>Polystichum munitum</i>	Fern
Thimbleberry	<i>Rubus parviflorus</i>	Shrub
Twinflower	<i>Linnaea borealis</i>	Shrub
Wall lettuce	<i>Mycelis muralis</i>	Herb

Western boykinia	<i>Boykinia occidentalis</i>	Herb
Other ferns	Polypodiaceae (family)	Fern
Red alder	<i>Alnus rubra</i>	Tree
Amabilis fir	<i>Abies amabilis</i>	Tree
Western red cedar	<i>Thuja plicata</i>	Tree
Western hemlock	<i>Tsuga heterophylla</i>	Tree
Sitka spruce	<i>Picea sitchensis</i>	Tree
Pacific yew	<i>Taxus brevifolia</i>	Tree