

Ecological understandings of Indigenous landscape management shape the study of Pacific yew  
(*Taxus brevifolia*)

by

Geneviève E.M. Reynolds  
B.A., University of Ottawa, 2018

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of the Requirements for the Degree of

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*We acknowledge and respect the lək̓ʷəŋən peoples on whose traditional territory the university  
stands and the Songhees, Esquimalt and W̱SÁNEĆ peoples whose historical relationships with  
the land continue to this day.*

## **Supervisory Committee**

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## Abstract

Indigenous landscape management has transformed ecosystems for millennia, with long-lasting impacts on the productivity and abundance of plant species. While western science based ecological research is beginning to investigate these impacts, less abundant species of cultural importance remain understudied. Pacific yew (*Taxus brevifolia* Nutt.), an uncommon understory conifer found in old-growth forests of the Northwest Coast of North America, has not received sustained ecological interest despite its importance to Indigenous Peoples throughout its range. In the first chapter, I synthesize the current ethnobotanical and ecological literature discussing Pacific yew to identify knowledge gaps and dominant paradigms that have shaped the study of the species. I find that many mechanisms behind Pacific yew's habitat selection and ecosystem functions are unknown to western science and that the impacts of Indigenous landscape management are largely unacknowledged within the western scientific literature. In the following chapter, in partnership with the Heiltsuk First Nation, I examine the growth and abundance of Pacific yew on sites that were inhabited intensively by First Nations on the Central Coast of British Columbia for over 10,000 years. I find that habitation histories are not a strong driver of patterns of tree size and that Pacific yew abundance is largely driven by site aspect. These findings shed light on the habitat preferences of Pacific yew, which have rarely been studied in this region. They also illustrate variation in the response of culturally important species to landscape modification and highlight the need for nuanced understanding of the diversity of plant management strategies employed by Indigenous Peoples. This work is part of a broader attempt to incorporate cultural histories and questions into ecological study

and to recognize the continuing ecological influences of Indigenous Peoples, who have stewarded their homelands for millennia.

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## Dedication

“Of vast circumference and gloom profound

This solitary Tree! -a living thing

Produced too slowly ever to decay;

Of form and aspect too magnificent

To be destroyed.”

- Yew-Trees, William Wordsworth

## Chapter 1: General Introduction

### 1.1 Humans and Landscapes

The histories of humans and plants are inextricably linked. Throughout time, human activities have altered the distribution, abundance, and productivity of plant species, both directly and indirectly (Boivin et al., 2016; Ellis et al., 2021; Thuiller et al., 2008; Tilman & Lehman, 2001). Direct changes include movements of species, horticultural, and agricultural activities (Boivin et al., 2016; Ellis et al., 2021; Hofman & Rick, 2018) and indirect changes are caused by landscape development, habitat changes and destruction, and alterations to climate and fire cycles (Ellis et al., 2021; Hoekstra et al., 2005; Tilman & Lehman, 2001). These activities affect vegetation community composition and ecosystem functions, with associated changes to animal communities and entire landscapes (Boivin et al., 2016; Ellis et al., 2021; Hofman & Rick, 2018). Anthropogenic influences have therefore fundamentally altered natural ecosystem processes and created ecosystems that are maintained by human activities (Boivin et al., 2016; Ellis et al., 2021; Stephens et al., 2019). These human impacts on landscapes can linger long after management activities have ceased, meaning that human landscape histories can explain or drive present vegetation communities and ecosystem processes (Boivin et al., 2016; Hofman & Rick, 2018; Trant et al., 2016).

While many of the human legacies on landscapes that may come to mind leave large footprints and are associated with landscape degradation (Williams et al., 2020), the legacies of Indigenous landscape management are often non-harmful or beneficial to ecosystems and leave “light footprints” (Ellis et al., 2021; Turner, Lepofsky, et al., 2013) that may not be

immediately apparent to outsiders. On the Northwest Coast of North America, widespread forms of landscape management include altering plant abundance, selecting for morphological characteristics of food, medicine, and resource species, transplanting species to different areas, creating ideal habitat for plant species, maintaining certain successional stages, and improving soil quality to increase plant productivity (Armstrong et al., 2021; Turner et al., 2000; Turner, Lepofsky, et al., 2013; Turner et al., 2021; Turner & Peacock, 2005). The effects of Indigenous landscape management also continue to influence plant community composition and productivity in areas where traditional active management no longer takes place (Cook-Patton et al., 2014; Fisher et al., 2019; Trant et al., 2016). Forms of landscape management vary across space and time and are often linked to culture, community, and spirituality (Ogar et al., 2020; Turner et al., 2000). Indigenous Peoples continue to steward their lands today, with benefits to environments and humans alike due to ecosystem services provided by Indigenous landscape management (Garnett et al., 2018; Schuster et al., 2019).

## **1.2 Indigenous Landscape Management on the Central Coast of British Columbia**

On the Central Coast of British Columbia, First Nations management has profoundly impacted local landscapes and ecology. The lush coastal temperate rainforests of the region have been home to the Heiltsuk, Wuikinuxv, Nuxalk, and Kitasoo-Xai'xais Nations since time immemorial and all four Nations continue to engage in stewardship of their territories (CCIRA, 2022). The mild, rainy climate, lack of major industrial disturbance in the region, and relatively stable sea levels over the past 14,000 years mean that the imprints of human dwelling are still present in many areas (Klinka et al., 1996; Mackie et al., 2018; McLaren et al., 2014, 2015; Trant et al., 2016).

One of the most common and important forms of archaeological evidence in the region is the presence of shell middens – intentional accumulations of shells, bone, and food waste built up in soil over generations (Grier et al., 2017; Mackie et al., 2018). In addition to their utility as a waste management method, middens can improve soil drainage and act as nutrient subsidies for vegetation grown in midden soils (Cook-Patton et al., 2014; Hunter, 2021; Vanderplank et al., 2014). Other evidence of habitation includes hearth features, stone tools, and human footprints found preserved in an intertidal zone that date to around 13,200 cal BP (Mackie et al., 2018; McLaren et al., 2015). Sites on the Central Coast that show evidence of intensive habitation and use over millennia that leave a physical record are known as habitation sites (McLaren et al., 2015; Trant et al., 2016).

Interdisciplinary research on the Central Coast in the last decade has demonstrated the lasting impacts of habitation and stewardship practices on the ecology of Central Coast habitation sites. Habitation histories affect the height and productivity of forests (Trant et al., 2016), assemblages and nutrient densities of culturally important plants (Fisher et al., 2019; Hunter, 2021), the landscape distributions of culturally important plants (Hunter, 2021), and fire intervals (Hoffman et al., 2017). Most research to date has focused on culturally important species with high abundance and cover values, but much less is known about how habitation histories and landscape management influence less abundant culturally important species.

### **1.3 Pacific yew**

Pacific yew (łémq̓ in Heiltsuk, also known as *Taxus brevifolia* Nutt. or Western yew) has long been a prized material for Indigenous Peoples throughout its range (Gunther, 1973; Turner & Bell, 1971), but it has not always received in-depth ecological or ethnobotanical attention in

western science. It is a shade-tolerant understory tree or shrub that displays a distinct preference for old-growth environments (Busing, Halpern, et al., 1995a; Halpern & Spies, 1995). The species has been integral to the daily lives of numerous Indigenous Peoples of the Northwest Coast, who have used Pacific yew to make tools such as bows, canoe paddles, digging sticks, and other important implements requiring high tensile strength (Turner, 1998). It is of little timber value to settler societies and thus was not a focus of ecological research until an anticancer compound, taxol, was identified in its bark (Campbell & Nicholson, 1995). While this discovery spurred a burst of ecological research into Pacific yew's ecology and silvicultural potential (e.g. Kelsey & Vance, 1992; Minore et al., 1996; Minore & Weatherly, 1994), interest faded after semisynthetic taxol became widely available in the late 1990s (Nicolaou et al., 1996). As a result of this history, investigations into Pacific yew's ecology and ecosystem functions have been limited by past conceptions of the species' value and many questions remain about its growth and distribution.

The relationships between Indigenous Peoples and Pacific yew have been well-documented in ethnobotanical studies (e.g. Compton, 1993; Gunther, 1973; Turner, 1998), but knowledge is missing around management activities undertaken to steward Pacific yew and how these activities may have influenced its abundance and distribution on landscapes. The question of management and stewardship of Pacific yew is therefore central to deepening both ethnobotanical and ecological understandings of the species. At a broader scale, this research contributes to the growing body of work integrating human histories and Indigenous landscape management into understandings of ecological patterns and processes (e.g., Boivin et al., 2016; Ellis et al., 2021; Hoffman et al., 2021; Schuster et al., 2019).

## 1.4 Thesis Objectives

In this thesis, I explore how Indigenous landscape management has influenced the ecology of Pacific yew and how interactions between western science and Indigenous knowledge and management systems have shaped the study of the species. I also examine the scientific paradigms and attitudes that have created gaps in our understanding of yew. I use interdisciplinary analytical methods to examine both the management techniques themselves and the ways in which western science has engaged with – or overlooked – Indigenous impacts on landscapes.

In Chapter Two, I conduct a literature review and synthesis of the prior ethnobotanical and ecological literature on Pacific yew that has taken place throughout the Northwest Coast of North America. Given that most research on Pacific yew took place over 20 years ago and that the species does not currently receive much attention in either discipline, I establish the aspects of its ecology and relationships with Indigenous Peoples that are well-understood and identify knowledge gaps where further research is needed. I also identify the dominant priorities and frameworks of understanding that have contributed to those knowledge gaps and suggest ways in which current understandings of Indigenous landscape management may alter how we interpret ecological patterns and processes.

In Chapter Three, I investigate the impacts of First Nations habitation and management on Pacific yew on the Central Coast of British Columbia. I ask two questions: *Do habitation histories influence the growth of Pacific yew on habitation sites?* and *Do habitation histories influence the abundance of Pacific yew on habitation sites?* Using a paired habitation site-control site study design, I compare the height, diameter, abundance, and foliar nutrient

content of Pacific yew on sites with long-term First Nations habitation histories and on control sites with no known habitation histories or middens. I hypothesize that the height and diameter of yews on habitation sites will be greater than yews on control sites and that habitation sites will have higher abundances of yew than control sites. I also hypothesize that yew foliage on habitation sites will have higher levels of calcium, potassium, nitrogen, phosphorus, and sodium than control site trees. This chapter explores how Pacific yew responds differently to habitation histories than other culturally important species and demonstrates that the design of such studies must be informed by the stewardship histories of the species.

This thesis brings renewed attention to a culturally important species that has not received sustained ecological or ethnobotanical study in over 20 years. My findings also add nuance to our understandings of the long-term impacts of Indigenous landscape management, which will help to inform future research. Including Indigenous communities in ecological studies and acknowledging the depth and breadth of their relationships with their territories not only improves understandings of landscape patterns and processes, but also supports their sovereignty and resource management (Ellis et al., 2021; Ogar et al., 2020).

## **Chapter 2: Revisiting Pacific yew (*Taxus brevifolia* Nutt.): An ethno-ecological review**

### **2.1 Abstract**

The old-growth forests of the Northwest Coast of North America are complex ecosystems that provide many important ecosystem functions, but not all old-growth species have been fully investigated. The declines and range shifts of understudied species, and the loss of ecosystem services they provide, may have unknown consequences for old-growth forests. Despite its long relationship with Indigenous Peoples and its brief time in the spotlight as the source of the effective anti-cancer drug taxol, Pacific yew (*Taxus brevifolia* Nutt.) remains one such understudied species. Given the abundance of new techniques and perspectives that have emerged in the 20 years since Pacific yew was last studied intensively, this review synthesizes prior ethnobotanical and ecological research about Pacific yew to identify important gaps in knowledge and the dominant paradigms and priorities that have shaped the study of the species.

While its ethnobotany has generally been well-documented throughout the Northwest Coast, documentation of tending practices applied to Pacific yew has been limited by past conceptions of the scope and breadth of Indigenous landscape management. The habitat, responses to disturbance, and responses to overstory removal of the species are generally well-understood due to the focus of prior research on harvesting and tree cultivation, but geographic biases affect the applicability of research to different regions. Pacific yew's ecosystem functions remain virtually unknown in many areas. The study of Pacific yew, and most other plant species, has been limited thus far in its acknowledgement of the depth of Indigenous landscape management and the extent to which those practices have influenced the

ecology and distribution of species. This review demonstrates that applying new techniques and paradigms to older bodies of literature has the potential to identify important ecological relationships and create holistic understandings of ecosystems.

## **2.2 Introduction**

Old-growth forests are important hubs of biodiversity, cultural knowledge, and can provide important ecosystem functions, but are increasingly under threat from climate change and natural resource extraction (Bergeron & Fenton, 2012; Lindenmayer et al., 2012; Turner, 2001; Wirth et al., 2009). In the coastal temperate rainforests of the Northwest Coast of North America, old-growth forests, defined as late-successional, multi-age forests with old trees and small-scale, frequent disturbances (Hoffman, Starzomski, et al., 2021; Spies, 2004), can provide important habitat and are hubs of carbon sequestration (Strittholt et al., 2006). The structural complexity of old-growth forests means that they can even create cooler microclimates than in surrounding regions and act as climate refugia, maintaining biodiversity in the face of warming temperatures (Frey et al., 2016). Old-growth forests, particularly those that have not been logged or intensively modified through the processes of colonization, are also the sites of long-standing relationships between plant species and Indigenous Peoples, who have tended and managed these landscapes for millennia (Lepofsky & Geralda Armstrong, 2018; Turner, Lepofsky, et al., 2013). Effective and ecosystem-specific management regimes are needed to conserve and argue for old-growth environments, requiring detailed knowledge of their ecology and the factors that maintain local biodiversity and ecosystem functioning (Spies, 2004).

Some non-dominant old-growth species, defined as species with low constancy and cover values (Crawford & Johnson, 1985) remain understudied, leaving gaps in ecological

knowledge that can negatively affect the efficacy of population modeling and management (Case & Lawler, 2017). Where ecosystem functions and services provided by understudied species have not been thoroughly investigated, their declines and range shifts could have unknown consequences for old-growth ecosystems. Addressing knowledge gaps related to understudied tree species is therefore a key component of effective old-growth conservation and management and supports Indigenous sovereignty.

Pacific yew is of particular interest in this regard due to the lack of ecological attention it has received in the last two decades. A slow-growing species found predominantly in old-growth forests from northern California to Alaska (Busing, Halpern, et al., 1995a; Scher & Jimerson, 1989), Pacific yew received the bulk of its ecological interest from the 1970s to the early 2000s in response to the identification of potent anti-cancer compound taxol in its bark (Campbell & Nicholson, 1995). Following the creation and distribution of semisynthetic taxol in the late 1990s (Nicolaou et al., 1996), public interest declined and ecological research on Pacific yew largely ceased. Given that this research was largely focused on the impacts of harvesting, and the abundance of relevant new techniques that have emerged in the last 20 years, many aspects of Pacific yew's ecology and ecosystem functions remain unstudied. At present, it is listed as near threatened on the IUCN Red List and populations are decreasing (Thomas, 2013). It is not considered a timber species (Ministry of Forests, n.d.). As a tree with such a strong preference for old-growth environments, gaining a fuller understanding of Pacific yew's habitat and potential ecosystem functions is important for its conservation in the face of ongoing climactic and human-driven changes to old-growth ecosystems (Rogers et al., 2011).

Revisiting the study of Pacific yew is also important due to its sensitivity to disturbance and its significance to Indigenous Peoples along the Northwest Coast of North America. Although the species can survive low-severity ground fires and millennia of cultural burning surrounding Indigenous village sites (Hoffman, 2018), it is not resistant to stand-replacing fires and struggles to re-establish in disturbed sites (like clear cuts) or to colonize new sites (Busing, Halpern, et al., 1995a; Halpern, 1989; Stickney, 1980). Threats and major disturbance to old-growth forests therefore directly threaten the viability and stability of Pacific yew populations (Arsenault & Bradfield, 1995). The species is also important to many Indigenous Peoples throughout its range, who use Pacific yew for a variety of technological and medicinal applications (Turner, 1998). While parts of Indigenous Peoples' relationships with Pacific yew have been well-documented in ethnobotanical research, the reciprocity of these relationships and potential Indigenous management strategies have not been fully considered in ecological studies. As with other tree species in this region (Schang, 2020; Trant et al., 2016), Indigenous Peoples may have influenced the distribution, physiology, and abundance of Pacific yew as part of stewardship practices, with influences on local ecology. Understanding these influences can contribute to the conservation and stewardship of Pacific yew in the present.

This paper aims to revisit and synthesize the current body of ethnobotanical and ecological literature on Pacific yew to establish the aspects of its ethnobotany and ecology that are well-understood and to identify knowledge gaps where further research is needed. Doing so will assist in the development of more comprehensive old-growth management plans and highlight the need for further study of a species that has received little ecological focus in the past 20 years.

## **2.3 Ethnobotany and Human-Plant Relationships**

### **2.3.1 Ethnobotany in Context**

Pacific yew is mentioned frequently in ethnobotanical studies of the Northwest Coast and is an important technological resource for coastal and interior Indigenous Peoples (Table 1). Sources included in this review are largely ethnographic, linguistic, and ethnobotanical accounts focused on the relationships between Indigenous Peoples and plant species in their homelands. Many focus on folk taxonomies and plant classifications as well as the various uses of plants and their cultural significance, as recorded by settlers through interviews with Indigenous people. While these references cover most of Pacific yew's range, sources are concentrated in southern and central British Columbia due to the abundance of ethnobotanical work that has taken place in these regions. The lack of inclusion of certain peoples or regions in this review does not mean that those peoples did not use Pacific yew, and instead likely reflects gaps in the available ethnobotanical literature.

### **2.3.2 Significance of Pacific yew**

Pacific yew is an important species for Indigenous Peoples across the Northwest Coast of North America, with many technological and medicinal uses. Recorded ethnobotanical uses of the species closely match its ecological distribution, with coastal peoples from present-day California to northern British Columbia and interior peoples in British Columbia all using Pacific yew (Bocek, 1984; Campbell & Nicholson, 1995; Rundel, 1968; Turner, 1973, 1979, 1988).

Most recorded uses of Pacific yew are technological, with the species being used by many peoples to make implements and equipment. Bowmaking is the most commonly recorded use of Pacific yew (Table 1), with at least 19 peoples ranging along the Northwest

Coast utilizing the tree in this way. In many languages, the names for Pacific yew or parts of the tree are linked to bows or bowmaking, indicating the significance of this use to conceptions of the species and perhaps that Pacific yew is the best material for bowmaking (Turner, Burton, et al., 2013). Many applications are also linked to boatmaking and fishing, such as using Pacific yew to make paddles, fishing and whaling tools, canoes, fishing hooks, and boat ribs (Table 1). Recorded ocean-related uses of the species appear to be concentrated in present-day Oregon and on the Central and North Coasts of present-day British Columbia. Pacific yew's fine-grained, hard wood has made it a prized material in the creation of tools requiring durability by many peoples (Gunther, 1973; Turner & Bell, 1971), including digging sticks, wedges for removing bark strips from trees (Hebda & Mathewes, 1984; Turner, 1973), adze handles, and other implements not specified in the literature (Table 1). The widespread and varied uses of Pacific yew point to its importance in the daily lives of Indigenous Peoples along the Northwest Coast as a vital technological resource.

Some medicinal uses of Pacific yew are also recorded in the ethnobotanical literature, but not always in detail. Parts of Pacific yew have been used by the Swinomish, Sts'ailes, and Cowlitz peoples in present-day Oregon and by the Nlaka'pamux of the present-day interior of British Columbia for unspecified medicinal purposes (Gunther, 1973; Turner, 1988). Other uses tend to be specific to certain peoples and concern different ailments and parts of the body (Table 1), and in some cases are not shared between neighbouring groups. This indicates that medicinal knowledge and use of Pacific yew was widespread and fairly common along the Northwest Coast as a whole, though gaps in the ethnobotanical literature exist and further research may be needed. Limited information has been recorded on the social and spiritual

aspects of Indigenous relationships with Pacific yew, but the species has been used for games and plays a role in the bereavement process for the Nlaka’pamux (Table 1).

Pacific yew was so valuable as a material that some Indigenous Peoples living in areas outside of yew’s range would trade with other peoples to obtain it, as has been documented in some ethnobotanical accounts (Turner, 1979, 1997). The In-SHUCK-ch of the lower Lillooet River in British Columbia would trade Pacific yew for silverberry (*Elaeagnus commutata* Bernh. Ex Rydb.) bark and basketmaking fibres with the St’at’imc of the southern Coast Mountains (Turner, 1979). The St’at’imc and Halkomelem peoples of the Fraser River valley had a similar trading agreement (Turner, 1997). These relationships demonstrate the significance of Pacific yew not only as a resource, but as part of the connections that exist between Indigenous Peoples in different areas. Pacific yew is still used by Indigenous carvers today, but its availability as a carving material has been limited by past harvesting and habitat destruction (Turner, 1979).

**Table 1:** Summary of ethnobotanical uses of Pacific yew throughout the Northwest Coast of North America.

<i>Use category</i>	<i>Use</i>	<i>Cultural Group (and References)</i>	<i># of peoples with recorded uses</i>
Technological	Bows	Coast Salish (Turner & Bell, 1971); Klamath (Coville, 1897); Kwakwaka’wakw (Turner, 1973); Ohlone (Bocek, 1984); Wuikinuxv, Hanaksiala, Haisla (Compton, 1993); Haida, Upper St’at’imc (Turner, 1973); Snohomish, Swinomish, Samish, Sts’ailes, Klallam, Makah, Quinault (Gunther, 1973; Sprague & Walker, 1980); Nlaka’pamux,	19

	St'at'imc (Turner, 1988); Secwépemc (Turner, 1979)	
Digging sticks	Wuikinuxv, Hanaksiala, Haisla (Compton, 1993); Quinault, Swinomish, Cowlitz (Gunther, 1973); Nlaka'pamux, St'at'imc (Turner, 1988); Kwakwaka'wakw (Turner & Bell, 1973; Turner & Peacock, 2005); Klallam (Sprague & Walker, 1980)	10
Paddles	Kwakwaka'wakw (Turner, 1973); Wuikinuxv, Hanaksiala, Haisla (Compton, 1993); Coast Salish (Turner & Bell, 1971); Klallam, Makah, Quinault (Gunther, 1973; Sprague & Walker, 1980)	8
Fishing & whaling implements	Coast Salish (Turner & Bell, 1971); Klickitat, Samish, Swinomish (Underhill & Division, 1945); Makah, Quinault, Samish, Swinomish (Gunther, 1973)	8
Wedges	Kwakwaka'wakw (Turner, 1973); unspecified nation (Hebda & Mathewes, 1984); Coast Salish (Turner & Bell, 1971); Cowlitz, Samish, Swinomish (Gunther, 1973); St'at'imc (Turner, 1988)	7
Unspecified tools	Wuikinuxv, Tsimshian (Compton, 1993); Nlaka'pamux, Klamath (Turner et al., 2011); Haida (Turner, 1973); St'at'imc (Turner, 1988)	6
Clubs	Hanaksiala, Haisla (Compton, 1993); Quinault, Samish, Swinomish (Gunther, 1973)	5
Boat ribs	Hanaksiala, Haisla (Compton, 1993); Klickitat, Samish, Swinomish (Underhill & Division, 1945)	5
Fishing hooks	Hanaksiala, Haisla (Compton, 1993); Coast Salish (Turner & Bell, 1971)	3
Combs	Coast Salish (Turner & Bell, 1971); Cowlitz, Quinault (Gunther, 1973)	3
Containers	Wuikinuxv (Compton, 1993); Makah (Gunther, 1973)	2

	Spears	Kwakwaka'wakw (Turner, 1973); St'at'imc (Turner, 1988)	2
	Serving bowls	Wuikinuxv (Compton, 1993); Makah (Gunther, 1973)	2
	Utensils	Makah, Quinault (Gunther, 1973)	2
	Snowshoes	Nlaka'pamux, St'at'imc (Turner, 1988)	2
	Adze handles	Kwakwaka'wakw (Turner, 1973)	1
	Spades	Kwakwaka'wakw (Turner, 1973)	1
	Unspecified weapons	Coast Salish peoples (Turner & Bell, 1971)	1
	Catapult	Coast Salish (Turner & Bell, 1971)	1
	Drum frame	Cowlitz (Gunther, 1973)	1
	Pipes	Karuk (Anderson, 2013)	1
	Rod in deer trap	Quinault (Turner, 1979)	1
	Sea urchin gathering tool	Kwakwaka'wakw (Turner, 1979)	1
	Paint	Syilx Okanagan (Turner, 1979)	1
Medicinal	Smoking	Klickitat, Samish, Swinomish (Underhill & Division, 1945); Klallam (Gunther, 1973)	4
	Unspecified medicine	Swinomish, Sts'ailes, Cowlitz (Gunther, 1973); Nlaka'pamux (Turner, 1988)	4
	Treatment for urinary disorder	Hanaksiala, Haisla (Compton, 1993)	2
	Pulp applied to wounds	Cowlitz, Quinault (Gunther, 1973)	2
	Unspecified, for stomach and digestive tract	Tsimshian (Compton, 1993)	1
	For rheumatism, arthritis, muscular disorders, paralysis, contraceptive, abortive	Haida (Turner, 1973)	1
	Bath for babies and elders	Sts'ailes (Gunther, 1973)	1
	Unspecified internal injury and pain	Klallam (Gunther, 1973; Sprague & Walker, 1980)	1
	Lung medicine	Quinault (Gunther, 1973)	1
	Incense or cleansing agent	Nlaka'pamux (Turner, 1988)	1

Social	Unspecified games	Klickitat, Samish, Swinomish (Underhill & Division, 1945); Karuk (Anderson, 2013)	4
	Gaming disks	Coast Salish (Turner & Bell, 1971)	1
	Strength test by twisting tree trunk	Kwakwaka'wakw (Turner, 1979)	1
	Unspecified games	Karuk (Anderson, 2013)	1
Spiritual	Chief of plant spirits	Kwakwaka'wakw (Turner, 1973)	1
	Death or bereavement	Nlaka'pamux (Turner, 1988)	1
Food	Arils eaten in small quantities	Haida (Turner, 1973); St'at'imc (Turner, 1988)	2

**2.3.3 Knowledge Gaps and Limitations**

While the current body of ethnobotanical literature on Pacific yew effectively illustrates the diversity of roles the species plays in Indigenous cultures of the Northwest Coast, gaps exist in the literature geographically and temporally. Most studies documenting uses of Pacific yew focus on coastal peoples, and less attention has been paid to the roles of Pacific yew in the lives of interior peoples. Their interactions with the species may differ due to differences in resource availability, climate, environment, and lifestyles, all as results of living in different ecosystems than coastal peoples (Turner, 1979). These potential differences have not been thoroughly explored in ethnobotanical literature and represent components of the species' cultural history that may be relevant to conservation and co-management initiatives. In addition, while the sources presented here range in age from the late 19<sup>th</sup> to the early 21<sup>st</sup> century, few, if any, repeat studies or surveys have been conducted to explore changes in plant use over time, so contemporary uses for Pacific yew may differ from those recorded in the literature.

While some ethnobotanical and historical-ecological studies of other species document tending and management practices in detail (e.g., Armstrong et al., 2018; Turner, Lepofsky, et

al., 2013), that knowledge is currently lacking for Pacific yew. Tending practices including pruning, transplanting, and soil enhancement were (and are) common among numerous Northwest Coast Indigenous Peoples, with the goals of sustainable resource harvest and increasing species productivity (Armstrong et al., 2018; Lepofsky et al., 2017; Lepofsky & Geralda Armstrong, 2018; Turner et al., 2000). These practices were likely applied to Pacific yew but have not been well-documented in the existing literature, which, in accordance with paradigms of the time (Turner, 2020), is largely focused on the benefits that humans have derived from plant species. This approach does not describe the reciprocity inherent in many relationships between Indigenous Peoples and organisms in their environments and can lead to overlooking the key roles that Indigenous Peoples have played in altering ecosystems (Armstrong et al., 2021; Boivin et al., 2016; Ellis et al., 2021; Hoffman, Davis, et al., 2021; Trant et al., 2016; Turner, 2020b).

Newer ethnobotanical and historical-ecological research that began after interest in Pacific yew began to wane is far more aware of active landscape management by Indigenous Peoples as part of a broader paradigm shift (Turner et al., 2021). Indigenous peoples of the Northwest Coast were once considered “hunter-gatherers” who obtained food and materials opportunistically from a resource-rich landscape, but did not exert much influence over the productivity, distribution, and availability of plant and animal resources (Turner, 2020; Turner et al., 2000). While this perspective describes some aspects of Indigenous Peoples’ activities, it does not encapsulate the full depth of Traditional Ecological Knowledge possessed by Indigenous Peoples and the active roles that they play in landscape management (Turner et al., 2000). Newer research considering Northwest Coast Indigenous Peoples as “hunter-gather-

agriculturalists” and incorporating Indigenous histories into ecological studies is therefore in closer alignment with Indigenous knowledge holders in describing landscape management activities used to alter and shape environments, and in acknowledging the spirituality and reciprocity inherent in these stewardship practices (Ellis et al., 2021; Grier et al., 2017; Turner, 2020; Turner et al., 2000; Turner, Lepofsky, et al., 2013). Pacific yew has received little discussion in research conducted from this newer perspective. Some sources note that certain stands of Pacific yew may have been harvested by Indigenous Peoples intensively for specific uses (Anderson, 2013; Turner & Peacock, 2005), and recent research indicates that Pacific yew has been managed and translocated in the Northwest Coast (Turner et al., 2021), but in general the management practices applied to Pacific yew have not been well documented. This makes teasing out biological and anthropogenic influences on species ecology and identifying mechanisms behind observed patterns more challenging. Expanding ethnobotanical focuses to include discussions and documentation of reciprocity with Pacific yew would fill a critical knowledge gap and benefit ecological study, conservation, and management, but must be done with appropriate community engagement and communication (Schang et al., 2020).

## **2.4 Ecological Research**

### **2.4.1 Ecology in Context**

In contrast with the attention paid to Pacific yew by Indigenous Peoples and ethnobotanists, the species received little Western scientific inquiry until 1967, when taxol, an anti-cancer compound derived from Pacific yew bark, was identified (Heiken, 1992; Rowinsky et al., 1990; Turner, 2001). Taxol prevents the chromosomes of cancerous cells from aligning during mitosis, thereby stopping cancer from spreading (Heiken, 1992). In the early 1990s, taxol

caused ovarian cancer remission in 30 to 50% of cases, considered a high success rate (Heiken, 1992). Prior to this discovery, Pacific yew was mentioned in ecosystem descriptions (Anderson, 1967; Whittaker, 1960) but was rarely the focus of ecological or biological research. The identification of taxol led to widespread harvesting of wild Pacific yew stands, including poaching from federal lands (Willits, 1995), often with little consideration for the cultural and technological value of the species for Indigenous peoples (Turner, 2001). Harvesting throughout the Northwest Coast was intensive, with approximately 7270kg of bark required to produce 1kg of taxol (Minore & Weatherly, 1994a). This process usually involved stripping the bark from trees, killing them in the process (Minore & Weatherly, 1994a). Harvesting from wild populations was recognized as unsustainable in the long-term due to Pacific yew's slow growth and relative rarity (Campbell & Nicholson, 1995; Minore & Weatherly, 1994a), so scientific research in this period largely focused on the reproduction and regrowth viability of the species to alleviate harvesting pressures.

In this body of work on yew, key mechanisms behind habitat selection, light availability adaptation, and disturbance responses have not been thoroughly investigated. The ecosystem functions of Pacific yew and its role in forest structure are also understudied, leaving gaps in ecological knowledge of Pacific yew that may hinder conservation initiatives and future habitat modeling for old-growth environments. In addition, most past research does not consider the impacts of long-term Indigenous management on old-growth ecosystems or on Pacific yew, which may represent an important paradigm shift in understandings of ecosystem processes.

## **2.4.2 Habitat**

### **2.4.2.1 Biogeoclimatic Zones**

Pacific yew grows in many biogeoclimatic zones of the northwest of North America and shows a distinct preference for old-growth environments. In British Columbia, it is most common in Coastal Western Hemlock zones (Chourmouzis et al., 2009) and can also be found in Coastal Douglas-Fir, Interior Douglas-Fir, and Interior Cedar-Hemlock zones (Campbell & Nicholson, 1995). It is most commonly an understory tree or shrub (Campbell & Nicholson, 1995; Crawford, 1983). At higher elevations, Pacific yew is found in Montane Spruce, Mountain Hemlock, and Engelmann Spruce-Subalpine Fir zones (Campbell & Nicholson, 1995). Its habitat in northern Montana is similar, where the species has been noted as an understory shrub in Western redcedar-Western hemlock communities (Habeck, 1968). In northwestern California, Pacific yew is likewise found consistently in Douglas-fir ecosystems (Willits, 1995). It is widespread but non-dominant in many of these ecosystems (Busing, Halpern, et al., 1995a; Crawford, 1983; Habeck, 1968; Lamb & Megill, 2003; Scher & Schwarzschild, 1989), except in north-central Idaho where it can form the dominant forest cover (Crawford, 1983).

### **2.4.2.2. Old-growth Habitat**

Throughout its range, multiple studies have identified Pacific yew's strong preference for old-growth ecosystems. Halpern & Spies (1995), investigating species diversity of old-growth Douglas fir forests in western Washington and Oregon, found that the basal area of Pacific yew was up to 75 times greater in old-growth plots than in plots of younger age classes. Busing et al. (1995) found similar results in the same region, where the abundance of Pacific yew was positively correlated with stand age and peaked in stands around 400 years old. In western

Montana, Pacific yew is more abundant in old-growth stands over 150 years old than in immature stands less than 90 years old (Antos & Habeck, 1981). This pattern continues in southern British Columbia, where Arsenault and Bradfield (1995) found the mean cover of Pacific yew in old-growth forests was 7.7% but near 0% in mature and young forests. While scattered individuals are present in the region in forests of all ages, the authors suggest that the species may require old-growth ecosystems to maintain population viability. Bailey and Liegel (1998), in an investigation of Pacific yew's growth and site factors in Oregon, confirmed that Pacific yew primarily occurs in the understory of old-growth forests that have not experienced recent major disturbance. Some research has suggested that the species be considered an old-growth forest indicator on the Northwest Coast of North America as a result of its strong preferences for old-growth environments (Scher & Jimerson, 1989).

Although Pacific yew's preference for old-growth is well-established, the mechanisms behind this habitat choice have not been fully investigated. Some research has suggested that the species regenerates most successfully in old-growth forests due to its shade tolerance (Busing, Halpern, et al., 1995a; Scher & Schwarzschild, 1989), but the main factor theorized to explain Pacific yew's habitat preferences is its responses to disturbance. The species is slow to re-grow following stand-replacing disturbances such as clear-cut logging (Anderson, 2001; Halpern, 1989; Rowinsky et al., 1990; Stickney, 1980). It is also very sensitive to high-intensity fire, which has been demonstrated to hinder re-growth and re-establishment of Pacific yew, though it can tolerate low-intensity burns (Busing, Halpern, et al., 1995a; Halpern & Spies, 1995; Hoffman, 2018; Scher & Jimerson, 1989). Old-growth forests of the Northwest Coast do not typically encounter stand-replacing disturbances or widespread fire naturally, so Pacific yew

populations may be more successful at establishing and regenerating in these environments than in young or mature forests that experience more frequent, higher-intensity disturbance (Anderson, 2001; Busing, Halpern, et al., 1995; Halpern & Spies, 1995; Scher & Jimerson, 1989). Although these hypotheses have been discussed in some research on the ecology of Pacific yew, they could benefit from further research to clarify the mechanism(s) behind yew density and stand age. This will allow for more informed conservation planning in regions where old-growth ecosystems are limited in extent or are at risk of higher-intensity disturbance and will allow for more accurate predictions of the impacts of clear-cut logging and wildfires on Pacific yew populations.

#### **2.4.2.3 Microhabitat**

Within old-growth areas, data available on Pacific yew's microhabitat preferences are limited and anecdotal, representing an important avenue for further study. Sometimes considered a riparian species, multiple habitat descriptions state that Pacific yew may grow best near or along stream banks (Bolsinger & Jaramillo, 1990; Crawford, 1983; Hicock et al., 1982; Scher & Schwarzschild, 1989; Service, 1908), although one of the only quantitative studies of Pacific yew microhabitats found that the basal area of yew increases with distance from streams and that seedlings are more numerous further from streams (Minore & Weatherly, 1994b). Descriptions also suggest a preference for lower parts of slopes or ravines (Bolsinger & Jaramillo, 1990; Campbell & Nicholson, 1995; Crawford, 1983; Hicock et al., 1982; Scher & Jimerson, 1989; Scher & Schwarzschild, 1989; Service, 1908). Sources differ in their assessment of Pacific yew's microclimate preferences, with some (e.g. Bolsinger & Jaramillo, 1990; Hicock et al., 1982; Scher & Jimerson, 1989; Scher & Schwarzschild, 1989) stating that the

species prefers microenvironments of high humidity and moisture, while others suggest that it may prefer warmer, drier microclimates (Crawford, 1983; Klinka et al., 2000). Contradictions therefore exist in described trends in microhabitat throughout the ecological literature, though very few studies appear to have thoroughly and quantitatively investigated the fine-scale habitat preferences of Pacific yew. This knowledge gap impacts our understanding of Pacific yew's role in forest structure and the ecosystem functions and services it may provide, as well as our ability to predict habitat suitability for Pacific yew.

Such analysis would also be very useful in testing the contrasting hypothesis that Pacific yew is a habitat generalist, which is likewise stated throughout the available literature but has not always been investigated in depth. Busing, Halpern, et al. (1995) in a study of Pacific yew ecology in western Washington and Oregon, found that "*Taxus [brevifolia]* tolerates a wide range of site conditions but, because of its small stature, is never dominant in . . . tall coniferous forests." Further research in the same region has found little evidence of narrow habitat selection in Pacific yew (Busing, Halpern, et al., 1995a). This finding is congruent with other reviews and technical summaries that demonstrate the diverse ecosystems and climates where Pacific yew is found, and therefore its broad environmental tolerances (Bolsinger & Jaramillo, 1990; Campbell & Nicholson, 1995). Future investigations could potentially clarify habitat selection in the species and whether it is an environmental generalist or shows distinct preferences for slopes and stream banks, as has been suggested.

#### **2.4.2.4 Knowledge Gaps and Limitations**

Although the habitat of Pacific yew has been investigated in multiple studies throughout its range, questions remain about the mechanisms behind its habitat selection. The processes

leading to Pacific yew's abundance in old-growth environments, theorized to be linked to slow tree growth and disturbance intensity (Busing, Halpern, et al., 1995a; Halpern, 1989), could benefit from further investigation. For example, understanding Pacific yew's regeneration potential after different disturbance intensities would allow for better prediction of the impacts of natural and anthropogenic disturbance on Pacific yew population viability and may shed light on its habitat preferences.

Information available about Pacific yew's microhabitat preferences is incomplete. The differences between tolerable and ideal habitat for the species in different parts of its range have not been investigated, and we lack thorough understanding of its microhabitat preferences as a result. Findings from Montana suggest that Pacific yew may be more abundant on sites with higher soil nitrogen (McCune & Allen, 1985), but very little else is known about Pacific yew's soil preferences. Methods and data sources that were less available when prior research took place, such as habitat suitability modeling and analyses of community science data, may prove useful in identifying Pacific yew's fine-scale habitat preferences due to the breadth and quantity of information they are able to analyze. This information may be necessary for understanding Pacific yew's landscape distribution and population dynamics in different regions.

Information is also lacking on Pacific yew's habitat in the northern parts of its range. Most research available has focused on Pacific yew in the United States and southern British Columbia, and much less is known about Pacific yew in vegetation communities on the central and north coasts of British Columbia and into Alaska. Given that these environments have very different climates and less intensive human disturbance than the southern parts of Pacific yew's

range (Banner et al., 2005; Busing, Halpern, et al., 1995a), Pacific yew's habitat and microclimate preferences may differ in these regions in ways that are relevant to land managers. Deepening ecological understandings of Pacific yew's habitat enables more effective decisions about land management and the creation of more accurate habitat suitability and range shift modeling.

### **2.4.3 Disturbance Responses**

#### **2.4.3.1 Responses to Fire and Logging**

Pacific yew is largely fire intolerant throughout its range. Fire frequency affects the landscape distribution of Pacific yew in northern California, where areas with high fire frequencies have low frequencies of Pacific yew (Scher & Jimerson, 1989). Similarly, fire frequency in western Washington and Oregon may limit the abundance of Pacific yew in the Coast Range (Busing, Halpern, et al., 1995a). Post-fire succession data from Montana also shows that Pacific yew struggles to re-establish on burned sites in the years immediately following disturbance (Stickney, 1980). In north central Idaho, one of the only areas where Pacific yew can form dominant dense stands, areas dominated by Pacific yew show little evidence of fire and stand ages tend to exceed the typical fire interval of the region (Crawford & Johnson, 1985). These results suggest that fire regimes may play an important role in determining the abundance and distribution of Pacific yew, though further research may be needed to validate this hypothesis.

The species also has difficulty surviving and re-establishing on sites that experience both logging and burning, as has been demonstrated in Washington and Oregon. In studies of old-

growth responses to disturbance over decades, Pacific yew showed “minimal post disturbance recovery” (Halpern, 1989). On sites that had been clear-cut and broadcast burned 30 years prior to the study, Pacific yew was able to survive in lightly burned areas but experienced local extinctions on watersheds that had been heavily burned (Halpern & Spies, 1995). The authors theorize that its sensitivity to intense fire, coupled with its slow growth rate, mean that Pacific yew could take centuries to recover and return to pre-fire densities. The individual effects of clear-cutting and burning cannot be isolated; however, due to the disturbance histories of the study sites. In population modeling of the impacts of tree harvesting in the same region, Pacific yew exhibits slow recovery from major harvests and may take centuries to return to pre-harvest abundance (Busing, Spies, et al., 1995). The responses of Pacific yew to disturbance illustrate its sensitivity to environmental change and its relatively slow population dynamics (Busing, Spies, et al., 1995).

#### **2.4.3.2 Knowledge Gaps and Limitations**

As discussed briefly in the previous section, Pacific yew shows strong responses to natural and anthropogenic disturbance. Ecological literature repeatedly demonstrates that the species is slow to re-establish on sites that have encountered major stand-replacing disturbance (Anderson, 2001; Halpern, 1989; Scher & Jimerson, 1989; Stickney, 1980), which has implications for population stability and genetic diversity (Arsenault & Bradfield, 1995; Busing, Spies, et al., 1995). Results are consistent across studies, though those related to regeneration of Pacific yew in Washington and Oregon (Halpern, 1989; Halpern & Spies, 1995) took place on the same plots and may not be fully generalizable to other regions and

ecosystems. As with other knowledge areas discussed in this review, region- and ecosystem-specific studies may be necessary for fine-grained management and predictions.

In addition, currently available research focuses largely on high-intensity disturbance, but Pacific yew's responses to moderate- and low-intensity disturbance are less understood. Findings suggest that the species can survive low-intensity burns (Halpern & Spies, 1995), though more research may be needed to quantify these results. The interactions between logging and burning disturbances and site conditions in the regeneration of Pacific yew are also poorly understood and may be necessary for environmental impact assessments and management. These findings are relevant to current management concerns due to the increased susceptibility of old-growth forests to fire as a result of climate change (Rogers et al., 2011) and due to logging and forestry taking place in old-growth areas.

#### **2.4.4 Ecosystem Functions and Services**

##### **2.4.4.1 Predation and Herbivory**

Despite concern from land managers and researchers over the loss of Pacific yew's ecosystem functions and services as a result of overharvesting (Bailey & Liegel, 1997; Campbell & Nicholson, 1995; Minore & Weatherly, 1994a), these aspects of its ecology are relatively unexplored. The red aril of Pacific yew has been documented as a food source for birds and rodents, which contribute to seed dispersal and population regeneration (Anderson, 2001; Bailey & Liegel, 1997; Bolsinger & Jaramillo, 1990; El-Kassaby & Yanchuk, 1994; Scher & Schwarzschild, 1989). At the same time, frugivory of this kind can limit seed production, as demonstrated in a western Oregon study where Pacific yew branches bagged to exclude vertebrate predation had significantly higher seed production than unbagged, predated

branches (Difazio et al., 1998). A study on southern Vancouver Island found similar results, where predation of Pacific yew was linked to high seed abortion rates (Anderson, 2001). The effects of seed predation therefore appear to be complex, with benefits to seed dispersal and detriments to seed development and production.

Pacific yew can also be an important food source for larger vertebrate species such as elk, moose, and deer. It is the second most common winter food source for elk (*Cervus elaphus*) in the Cascade Mountain forests of Washington, and elk feces analyzed in the study also contained higher proportions of Pacific yew after snowfall (Jenkins & Starkey, 1993). This demonstrates Pacific yew's importance as an available food source in harsh climatic conditions when other herbaceous forage is scarce. In northeastern Oregon, Pacific yew is a significant component of mid- and late-summer elk diets and was "the most consistently eaten browse species" through the summers of the study period (Korfhage et al., 1980). This browse activity can lead to the near-extirpation of seedlings and saplings and therefore negatively affect Pacific yew's population regeneration (Parks et al., 1998). Similarly, the species provides winter habitat for moose (*Alces alces*) in north-central Idaho (Pierce & Peek, 1984) and they use it extensively as a winter food source (Pierce, 1984). Pierce & Peek (1984) demonstrated that moose showed strong selection preferences for areas with high cover values of Pacific yew, despite the scarcity of this cover type in the study area. It is also one of the most important forage species they use in autumn and winter (Pierce & Peek, 1984; Pierce, 1984). Work conducted in California suggests that forage by black-tailed deer (*Odocoileus hemionus columbianus*) may inhibit the recruitment of Pacific yew into taller size classes (Willits, 1995). Given the significance of Pacific yew as habitat and forage to large vertebrate populations, the interactions between predation,

herbivory, and yew abundance and regeneration may be important ecological relationships that would benefit from further study.

#### **2.4.4.2 Other Ecosystem Functions**

Other ecosystem functions of Pacific yew have been noted in scientific literature but not in detail. The species may provide protective cover for wildlife and shade streams to maintain cool water temperatures for salmonids and other fish (Service, 1908; Scher & Jimerson, 1989). Its root system may also contribute to stream bank stabilization (Scher & Jimerson, 1989). These ecosystem functions do not appear to have been thoroughly investigated, however, and the sources do not describe if these functions are undertaken solely by Pacific yew or if they are generalizable to other understory trees and shrubs.

#### **2.4.4.3 Knowledge Gaps and Limitations**

Many gaps exist in ecological understandings of Pacific yew's roles in ecosystem structures and functioning. While its relationships with large mammal species have been explored to some extent (Anderson, 2001; Difazio et al., 1998; Jenkins & Starkey, 1993; Willits, 1995), Pacific yew's relationships with other species and roles in food webs throughout its range remain largely unknown. Its potential to provide habitat for bryophyte and epiphyte communities, as other old-growth tree species do (Kenkel & Bradfield, 1981), has also not been explored. The roles of mycorrhizal networks in assisting the establishment of Pacific yew seedlings, as has been demonstrated in other old-growth species (Beiler et al., 2010), is also not known. As a result, we currently have little understanding of the ecosystem functions and services provided by Pacific yew and its importance to old-growth community ecology.

Additionally, Pacific yew's role in forest structure has not been investigated. If the species does have a habitat preference for slopes, as has been suggested in prior literature (Bolsinger & Jaramillo, 1990; Campbell & Nicholson, 1995), it may contribute to bank stabilization in a way that has not been thoroughly investigated. Given the very limited body of research to date studying the roles of Pacific yew in ecosystems, many avenues of study may improve our understanding of the importance of Pacific yew to ecological communities.

As with studies of Pacific yew's habitat, most of the research investigating its ecosystem functions and services seems to have been conducted in the southern part of its range. Expanding research to focus on Pacific yew at higher latitudes, which in some cases can have different ecosystems, climates, and species interactions (Banner et al., 2005; Busing, Halpern, et al., 1995a), would provide a more complete picture of the roles that Pacific yew can play in ecosystem functioning. Investigating this spatial variation in Pacific yew's ecosystem functions would increase our understanding of the complex interspecies relationships present in old-growth forests. It would also allow us to better understand and predict the broader ecological impacts of future changes in Pacific yew populations as a result of habitat loss and climate change.

## **2.4.5 Responses to Light Availability**

### **2.4.5.1 Physiological and Morphological Adaptations**

As primarily an understory tree or shrub, Pacific yew is tolerant of shaded conditions (Bolsinger & Jaramillo, 1990; Busing, Halpern, et al., 1995a) but can adapt to some extent to changes in light availability. A study on southern Vancouver Island measuring Pacific yew's growth in shade and in full sun found that shade-grown trees had "larger and more efficient

light harvesting and utilization capacities than trees grown in sun” (Mitchell, 1998b), indicating physiological adaptation to changes in light conditions. That study also found that shade-grown trees had longer needles and higher specific leaf area than sun-grown trees – as did similar research in Oregon (DiFazio, 1995; Kelsey & Vance, 1992) and Idaho (Crawford, 1983). Further morphological adaptations identified by DiFazio (1995) include the production of denser foliar tissue, increased branching, and self-shading in full-sun conditions. Crawford (1983, cited in DiFazio, 1995) also found that overstory openness was positively correlated with tree branching. Together, these findings demonstrate Pacific yew’s ability to adapt physiologically and morphologically to changes in light availability.

#### **2.4.5.2 Growth Releases and Productivity**

In areas where the overstory has been removed, Pacific yew may experience growth releases and increases in productivity. This effect was demonstrated in a limited capacity by Bailey and Liegel (1997), who found a strong increase in 10-year incremental growth of Pacific yew following overstory harvest compared to yew in unharvested stands in the Cascade Mountains of Oregon. In similar ecosystems, DiFazio (1995) found that 5-year growth increments of Pacific yew were positively associated with overstory openness. This study noted that sun-grown trees seemed to be more vigorous than shade-grown trees, in contrast to Crawford (1983), who noted that overstory removal seemed to result in decreased tree vigour in Idaho. DiFazio (1995) also notes that while overstory removal may increase tree growth, it does not necessarily increase tree fitness and survival rates of offspring.

#### **2.4.5.3 Reproductive Potential**

Overstory removal and increased light availability have mixed effects on the reproductive potential of Pacific yew that could benefit from further investigation. Multiple studies have found that the production of reproductive structures, or strobili, is positively correlated with light availability and overstory openness (Anderson, 2001; DiFazio et al., 1997). Reproductive potential does not seem to translate to reproductive output, however, as Difazio et al. (1997) in western Oregon found that the proportion of ovules that develop into mature seeds, or seed efficiency, is negatively correlated with overstory openness and that there is no overall association between seed production and overstory openness. When branches were bagged to exclude predators, Difazio et al. (1998) found an interaction between canopy openness and predation, where seed production on predator-excluded branches was positively associated with canopy openness. This indicates that there are higher levels of predation under open canopies than closed canopies, though there was a lot of variation in this pattern among sites and years (Difazio et al., 1998). Crawford (1983) likewise found that following clearcut overstory harvests in Idaho, Pacific yew left growing under open canopies showed decreased seed production compared to yew growing under intact canopies. Together, these results indicate that canopy openness increases the reproductive potential of Pacific yew but that factors such as predation may interact to decrease the production of mature seeds under open canopies.

#### **2.4.5.4 Knowledge Gaps and Limitations**

The impacts of light availability on the growth and reproduction of Pacific yew are better understood than other aspects of its ecology, largely due to the forestry context in which the

research took place. Many studies investigate the responses of Pacific yew to overstory removal and changes in light availability as a result of silvicultural activity and to assess the viability of growing Pacific yew in open clearings for harvesting purposes (Mitchell, 1998b). The available data on Pacific yew's responses to changes in light availability suggest that while the species can adapt to tolerate overstory removal and full-sun conditions, these adaptations do not increase Pacific yew's reproductive success and may decrease seed efficiency. Findings related to physiological and morphological adaptations are consistent throughout the available literature and have been demonstrated in different ecosystems and climates throughout Pacific yew's range, though the body of work available for review is relatively small (Crawford, 1983; DiFazio, 1995; Kelsey & Vance, 1992; Mitchell, 1998b). Growth release responses have likewise been identified in multiple studies (Bailey & Liegel, 1997; DiFazio, 1995), but within the same geographic area. The impacts of overstory removal on the growth and reproduction of Pacific yew in different regions and forest types are unknown, which represents a major gap in our understanding of the species' responses to disturbance. This affects our ability to predict the impacts of forestry operations and wide-scale disturbance on Pacific yew populations.

Findings related to the reproductive capacity of Pacific yew under different overstory conditions could also benefit from further study and clarification. Anderson (2001) and DiFazio (1997) both found increases in strobilus production following increases in light availability, but viable seed production seems to decrease with canopy openness (Crawford, 1983; DiFazio et al., 1997). The mechanism behind this effect is not widely investigated but may be dependent on predation or other environmental factors that can vary widely between sites and study systems (Bailey & Liegel, 1998; DiFazio et al., 1998). Further investigations of this relationship

conducted in varied ecosystems would likely be useful for assessing light availability impacts on Pacific yew population dynamics and regeneration. This topic remains relevant to the conservation and management of Pacific yew, given that logging of old-growth stands drastically alters light availability in the subcanopy (DiFazio, 1995).

## 2.5 Broad Findings and Knowledge Gaps

While useful information about Pacific yew is available to land managers and conservationists, questions remain that need to be addressed. The scientific literature available is likely sufficient to make broad-scale, general predictions about the responses of Pacific yew to environmental change and disturbance, but changes in data availability and paradigm shifts regarding Indigenous landscape management in the 20 years since Pacific yew was studied intensively mean that many aspects of its ecology could be better understood in the present (Table 2). This would facilitate more effective conservation strategies for old-growth areas and understanding of Pacific yew’s role in old-growth ecosystems.

**Table 2:** Summary of major knowledge gaps in ethnobotanical and ecological literature on Pacific yew.

<i>Topic</i>	<i>Major knowledge gaps</i>
Ethnobotany and human-plant relationships	<ul style="list-style-type: none"> <li>• Uses by interior Indigenous peoples</li> <li>• Stewardship and management practices</li> <li>• Influences of Indigenous landscape management on growth and landscape distribution</li> </ul>
Habitat	<ul style="list-style-type: none"> <li>• Habitat selection mechanisms</li> <li>• Microhabitat preferences</li> <li>• High latitude habitat information</li> </ul>
Disturbance responses	<ul style="list-style-type: none"> <li>• Responses to low-intensity disturbance</li> </ul>
Ecosystem functions and services	<ul style="list-style-type: none"> <li>• Roles in food webs</li> <li>• Potential to provide habitat</li> </ul>

	<ul style="list-style-type: none"> <li>• Role in forest structure</li> <li>• Functions and services at high latitudes</li> </ul>
Responses to light availability	<ul style="list-style-type: none"> <li>• Responses to overstory removal in different regions and forest types</li> <li>• Seed production and light availability mechanisms and interactions</li> </ul>

Reviewing the available literature shows that Pacific yew has strong habitat preferences for old-growth and that most of its abundance seems to be found in old-growth forests (Antos & Habeck, 1981; Arsenault & Bradfield, 1995; Halpern & Spies, 1995). The mechanisms behind this preference have not been fully investigated but may be linked to the species' slow recovery from stand-replacing disturbances (Busing, Halpern, et al., 1995a). Quantitative research is needed to investigate the habitat selection of Pacific yew (Busing, Halpern, et al., 1995a). Due to its sensitivity to intense fire, fire intervals likely play an important role in determining the abundance and distribution of Pacific yew on landscapes (Crawford & Johnson, 1985; Scher & Jimerson, 1989) and populations are slow to recover from clear-cutting and broadcast burning (Halpern, 1989). Beyond its role as a food source for birds, rodents, and large mammals (Anderson, 2001; Jenkins & Starkey, 1993; Pierce & Peek, 1984; Willits, 1995), the ecosystem functions and services of Pacific yew are poorly understood and require further study. Pacific yew's responses to changes in canopy openness vary between sites and study systems.

These key findings have not been demonstrated throughout Pacific yew's range, however, and geographic biases may limit the applicability of this information to areas outside of the study regions. Most studies of Pacific yew ecology and biology have been conducted in the United States, with much less of a focus on its ecology and ecosystem roles in the northern

parts of its range. Almost no information exists on Pacific yew north of Vancouver Island, except for brief mentions in ecosystem descriptions (Lamb & Megill, 2003) and in a small body of recent work on the Central Coast of British Columbia (Hoffman, 2018; Hunter, 2021; Schang, 2020). Old-growth forests on the central and north coasts of British Columbia differ from their southern counterparts in biogeoclimatic zones, anthropogenic disturbance histories, and vegetation communities (Banner et al., 2005), so Pacific yew's ecology and population dynamics may require region-specific study. Understanding its ecology at higher latitudes is also important because the species' range is predicted to shift northwards in the coming decades due to climate change (Case & Lawler, 2017). Methods that were not widely available when most studies of yew took place, such as remote sensing and habitat suitability modeling, may be especially useful in examining geographic variation in Pacific yew ecology.

Information on Pacific yew's ecosystem functions is extremely limited, presenting one of the most important avenues for future study. Its roles in forest structure and function are unknown, as are its relationships with most other organisms. Limited work in Washington, Idaho, and California suggests that Pacific yew is an important forage species for large mammals (Jenkins & Starkey, 1993; Pierce, 1984; Willits, 1995), but these patterns have not been investigated elsewhere and thus Pacific yew's roles in food webs are largely unknown. As a result, scientists and land managers are not able to fully predict the impacts of changes in Pacific yew's range and landscape distribution on old-growth ecosystem dynamics and food webs.

Additionally, paradigms regarding Indigenous landscape management have shifted since the bulk of ecological and ethnobotanical research on Pacific yew took place (Turner et al.,

2021). While skepticism regarding the extent of Indigenous Peoples' roles in ecosystem process remains (Turner et al., 2021), recent research highlights the extent and diversity of landscape changes that have been brought about and maintained by Indigenous Peoples worldwide (Armstrong et al., 2021; Boivin et al., 2016; Cook-Patton et al., 2014; Ellis et al., 2021; Engdawork & Bork, 2014; Fisher et al., 2019; Hoffman, Davis, et al., 2021; Hoffman et al., 2018; Trant et al., 2016; Vanderplank et al., 2014). The impacts of these changes can persist even after active management has ceased due to colonialism and the removal of Indigenous peoples from their lands (Fisher et al., 2019; Trant et al., 2016). Given that this paradigm shift started happening relatively recently, most older studies included in this review do not consider the impacts of Indigenous landscape management. While some sources mention or describe the ethnobotanical significance of Pacific yew to Indigenous Peoples (e.g. Anderson, 2001; Campbell & Nicholson, 1995), most do not consider the social or cultural significance of the species beyond its applications in western medicine, nor do they recognize their study environments as landscapes with potential human management histories that could impact study results. These omissions potentially miss the human elements of landscape ecology and reflect beliefs and attitudes that can still be prevalent in ecological research today (Boivin et al., 2016; Schang et al., 2020).

Given that much of the globe has been modified by human activities for at least the past 12,000 years (Boivin et al., 2016; Ellis et al., 2021), including human influences in ecological studies is therefore a core component of ecological understanding, from the scale of individual tree species to entire biomes (Boivin et al., 2016; Ellis et al., 2021; Ogar et al., 2020; Schang et al., 2020). Future ecological research on Pacific yew, and most other species and ecosystems,

would benefit greatly from the recognition and integration of Indigenous landscape management and human histories into ecological study, done with the consent and consultation of Indigenous communities (Boivin et al., 2016; Ogar et al., 2020; Schang et al., 2020).

## **2.6 Conclusion**

Pacific yew populations in British Columbia appear to be stable and protected at present (Chourmouzis et al., 2009), but gaps in our knowledge of the species' ecology could lead to unpredictable impacts as Pacific yew's range and distribution change in the coming century. Prior ethnobotanical research shows that Pacific yew is a very important technological and medicinal resource for Indigenous peoples throughout the Northwest Coast, but few management practices for the species have been documented. Pacific yew's microhabitat preferences, ecosystem functions, and responses to overstory removal would all benefit from further study, as would variation in Pacific yew's ecology geographically. Prior research largely omits discussions of Indigenous landscape management as a factor in explaining ecosystem patterns and species distribution, which represents a major area of future study that could alter our understanding of species and landscape ecology. Continuing to study Pacific yew will facilitate more effective conservation of the species in future and will contribute to our knowledge of the structure and function of old-growth ecosystems. Applying new techniques and paradigms of Indigenous landscape management to older bodies of literature has the potential to identify important ecological relationships and create holistic understandings of ecosystems.

# Chapter 3: Coastal habitat characteristics influence growth of Pacific yew (łémq, *Taxus brevifolia* Nutt.) on traditional landscapes of the Central Coast, British Columbia

## 3.1 Abstract

First Nations on the Central Coast of British Columbia have modified landscapes in ways that have altered local ecology since time immemorial, but these contributions and processes have not always been considered in ecological studies. Although a growing body of work integrates Indigenous ecosystem management into ecological studies at the community level, much less is known about the effects of traditional management on the growth, abundance, and landscape distribution of individual and rarer species of cultural importance like Pacific yew (łémq in Heiltsuk , also known as *Taxus brevifolia* Nutt. or Western yew). A non-dominant understory tree and shrub that grows almost exclusively in old-growth forests of the Northwest Coast of North America, Pacific yew has long been of value to Indigenous Peoples throughout the range of the tree, beloved for its for technological and medicinal purposes. However, most aspects of Pacific yew's ecology have not received detailed study.

In partnership with the Heiltsuk First Nation, I investigated the impacts of long-term First Nations habitation on Pacific yew by comparing the size and abundance of yew trees on sites that were inhabited intensively by the Heiltsuk Nation until 120 years ago to sites that received little to no use. Although this method has detected the impacts of First Nations modification on other tree and shrub species in prior studies, I found that landscape histories were not a strong driver of patterns of tree size, nor were habitat conditions. In this study area,

patterns of Pacific yew abundance are largely driven by site aspect and not by First Nations management histories. These findings shed light on the habitat preferences of Pacific yew, which have rarely been studied in this region. They also illustrate variation in the response of culturally important species to landscape modification and highlight the need for nuanced understanding of the diversity of management strategies employed by First Nations.

### **3.2 Introduction**

First Nations have dwelt in the forests of British Columbia, Canada, since time immemorial, but the depth of their relationships to the land and the ecological impacts of their traditional land use practices have not always been considered in ecological studies (Cook-Patton et al., 2014; Lepofsky & Lertzman, 2008; Schang et al., 2020). A growing body of ecological and archaeological work over the past few decades is in line with Indigenous knowledge that has always described these forests as carefully tended landscapes, though they have long been considered “untouched” or “undisturbed” in most Western descriptions (Armstrong et al., 2018, 2021; Fisher et al., 2019; Trant et al., 2016). The long-term, diffuse environmental impacts of continuous human inhabitation over long timescales, termed *eco-cultural legacies*, have been found worldwide, from Alaska (Hrdlička, 1937), to Mexico (Vanderplank et al., 2014), to Ethiopia (Engdawork & Bork, 2014).

In coastal British Columbia, eco-cultural legacies have been found to impact many aspects of old-growth forest ecology. These effects are concentrated on sites of repeated and long-term landscape inhabitation by First Nations, known as habitation sites. Dominant tree species growing on habitation sites are taller and more productive than in surrounding areas, likely due to increased levels of limiting nutrients in the soil as a byproduct of daily life

(Lepofsky & Lertzman, 2008; Trant et al., 2016). Plant community composition on habitation sites is also typically different than that of the surrounding forest, with higher concentrations of culturally important species present due to historic cultivation practices (Fisher et al., 2019; Hunter, 2021; Turner et al., 2021). In ‘forest gardens’ cultivated near habitation sites, plant functional trait diversity and species richness are also higher than in surrounding forests that did not receive intensive modification (Armstrong et al., 2021). Indigenous habitation histories thus strongly shape the ecology of old-growth forests, with impacts on the distribution and abundance of culturally important species that continue to be detectable into the present.

The Heiltsuk and Wuikinuxv Nations have dwelt in the forests and along the coastlines of the Central Coast of British Columbia for over 14,000 years (Heiltsuk Nation, n.d.; Lepofsky & Lertzman, 2008). These Nations continue to engage in active stewardship and management of their territories. In this region, the ecological impacts of eco-cultural legacies on dominant tree and understory species are documented at the community level (Fisher et al., 2019; Trant et al., 2016), but much less is known about these effects on individual, and rarer, species of cultural importance like Pacific yew (łémq̓ in Heiltsuk , also known as *Taxus brevifolia* Nutt or Western yew).

Pacific yew is a shade-tolerant understory tree or shrub found throughout the temperate coastal rainforests of BC (Busing, Halpern, et al., 1995b; Halpern, 1989; Mitchell, 1998a). This near-threatened evergreen conifer is slow-growing and able to tolerate a variety of environmental conditions, but is sensitive to disturbance (Busing, Halpern, et al., 1995a; Campbell & Nicholson, 1995; Halpern, 1989), and is found almost exclusively in old-growth stands (Arsenault & Bradfield, 1995; Busing, Halpern, et al., 1995a). Pacific yew is of value for

many Indigenous Peoples throughout the tree's range from present-day California to northern BC due to its strong, hard wood (Sprague & Jr, 1980; Turner & Bell, 1971; Turner, 1988) and is used by the Heiltsuk and Wuikinuxv Nations for technological and medicinal purposes (Compton, 1993; W. Housty, personal communication, July 28, 2020). The wood of Pacific yew has very high tensile strength, making it ideal for tools such as bows, digging sticks (which were instrumental in root garden stewardship), splitting wedges used to split Western redcedar (*Thuja plicata* (Donn ex D. Don in Lamb)), paddles, fishing hooks, and spears (Compton, 1993; N. J. Turner, 1973, 1998). The tree has also been a vital medicine for many Indigenous Peoples, used to treat various ailments including urinary and muscular disorders and internal injuries (Compton, 1993; Gunther, 1973; Sprague & Walker, 1980; Turner, 1973). Pacific yew has therefore been critical to the survival and culture of many Indigenous Peoples throughout the Northwest Coast and continues to be sought after as a carving material and medicine today (Pojar & MacKinnon, 2014; Turner, 1998).

Given the long-standing relationships between the Heiltsuk First Nation and Pacific yew (W. Housty, personal communication, July 28, 2020), its growth and patterns of abundance may be linked to eco-cultural legacies in ways that have not yet been investigated. In collaboration with the Heiltsuk First Nation, this research examines the size and abundance of Pacific yew on ancestral habitation sites and on control sites without intensive habitation histories around Calvert and Hecate Islands, British Columbia. I tested three hypotheses. First, I expected that the height and diameter at breast height (DBH) of Pacific yew would be higher on habitation sites than on control sites because soil nutrient subsidies from middens and historic fires have been shown to increase tree productivity and size of other conifers (Schang, 2020; Trant et al.,

2016). Second, I predicted that the abundance of Pacific yew would be higher on habitation sites than on control sites, due to nutrient subsidies and in alignment with general trends of higher abundances of culturally important species on habitation sites (Fisher et al., 2019; Hoffman et al., 2017; Hunter, 2021). Finally, I expected that foliage of Pacific yew growing on habitation sites would have higher nutrient contents, especially higher foliar calcium, potassium, nitrogen, phosphorus, and sodium content, than the foliage of Pacific yew on control sites. These elements can be found in higher concentrations on habitation sites because of anthropogenic inputs including fires, food preparation, and discarded bones and shells, though they linger in soils for different periods of time (Fisher et al., 2019; Holliday & Gartner, 2007; Trant et al., 2016). Higher soil nutrient concentrations should lead to greater foliar nutrient uptake by Pacific yew, as with other species examined on habitation sites (Fisher et al., 2019; Hunter, 2021; Trant et al., 2016).

This study improves our understanding of the habitat and populations of Pacific yew in old-growth forests at higher latitude, where they have not been investigated in detail. The results may also shed light on the long-term impacts of First Nations landscape modification on the growth of Pacific yew.

### **3.3. Methods**

#### **3.3.1 Site Selection**

I conducted fieldwork in July and August of 2020 on Calvert and Hecate Islands on the Central Coast of British Columbia (Fig. 1). Most of the study sites are located within Kwakshua and Meay Channels, protected channels between Calvert and Hecate Islands. This area is classified within the central variant of the Coastal Western Hemlock biogeoclimatic zone

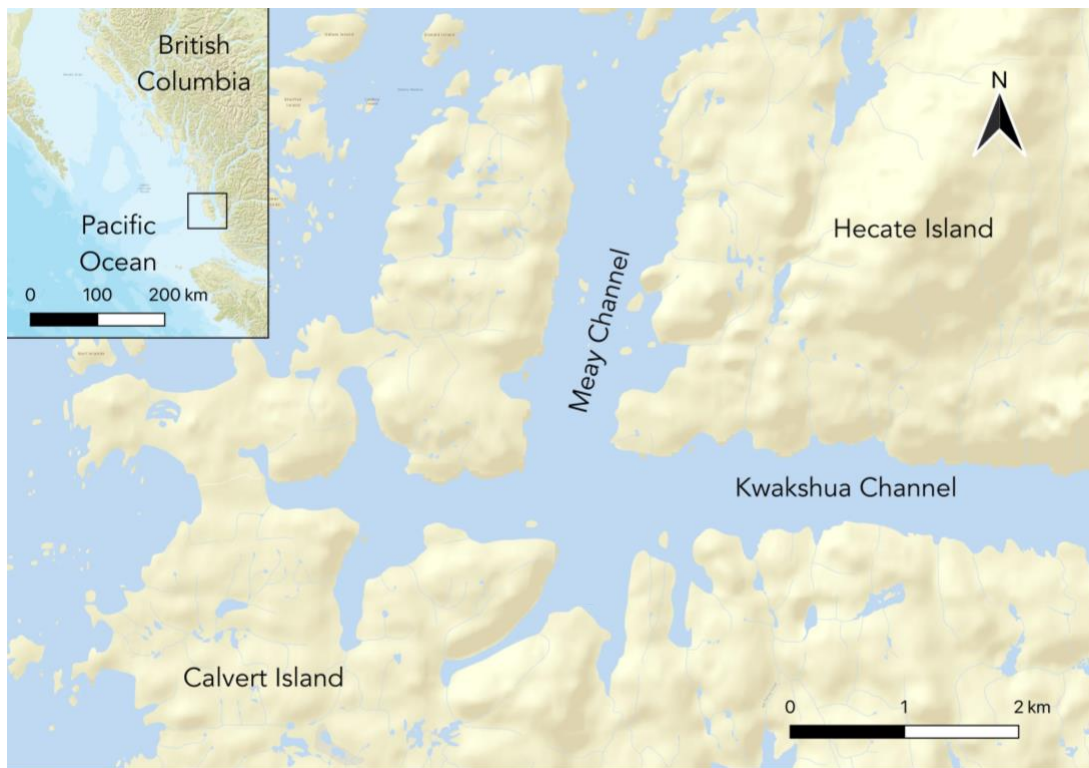
(CWHvh2), which is in the very wet hypermaritime subzone (Klinka et al., 1996). The mean annual temperature in this region is 8.2°C, with mean annual precipitation of 2,230 mm (Klinka et al., 1991). Dominant species in this zone include western redcedar, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), salal (*Gaultheria shallon* Pursh), false azalea (*Menziesia ferruginea* Hook.), lanky moss (*Rhytidiadelphus loreus* Hedw.), and step moss (*Hylocomium splendens* Hedw.) (Fisher et al., 2019).

In this region, habitation sites are defined as areas with a long-term history of repeated habitation by First Nations, as established through oral histories, archaeological research, and prior ethnoecological research (Trant et al., 2016). The presence of eco-cultural legacies on habitation sites, such as shell middens, berry gardens, and fire histories, is my experimental “treatment”. Each of seven habitation sites included in this study was paired with a nearby control site, established by Trant et al. (2016; see for further details on site selection). These control sites have similar forest productivity, environmental characteristics, and forest structure as the habitation sites they are paired with (Fig. 1). They are defined as areas with no known history of long-term inhabitation and associated landscape modification by First Nations. While these areas may have been used by First Nations for low-intensity purposes, any landscape impacts present in these areas are diffuse enough to be undetectable with current methods. This allows for comparison between habitation sites that experienced high-intensity use and control sites that have not had substantial human modification.

### **3.3.2 Data Collection**

At each study site, I collected data on Pacific yew along 70 m belt transects in the forest perpendicular to shore. This distance was chosen to capture the full extent of middens at

habitation sites and the landscape gradient between shoreline forests and deeper forests (British Columbia Archaeological Branch, 2019). I counted Pacific yew in a 10 m boundary on each side of the transect. Transects were spaced 30 m apart to achieve approximately 50% coverage of each site. The number of transects differed between sites ( $n = 3 - 8$ ) to account for varying site sizes, but each habitation and control pair had the same number of transects. I recorded each tree's UTM coordinates, distance from shore (near shore = 0 m - 23 m, mid



**Figure 1:** The study region on Calvert and Hecate Islands.

forest = 23.1 m - 47 m, deep forest = 47.1 m - 70 m), dbh in cm, and tree height in m using a Laser Tech TruPulse 200 laser rangefinder (error  $\pm 0.2$  m). I estimated canopy openness with a densiometer every 7 m along each transect and averaged the values to produce estimated transect canopy openness.

Soil moisture was measured every 7 m along each transect with a Fieldscout TDR Soil Moisture Meter. To account for variation in moisture in the active layer of the soil, which would affect the accuracy of measurements, I collected control moisture measurements. I did this by measuring soil moisture every morning in the same location to record moisture variation from day to day. I divided the moisture measurements obtained in the field by the control measurement from that morning to calculate the normalized percent soil moisture.

I also gathered samples of new growth of yew needles to analyze foliar calcium, phosphorus, nitrogen, sodium, and potassium content. Trees were chosen based on accessibility of needles for collection. Most were within 1 m to 5 m in height because smaller trees had insufficient needles for collection and needles on many taller trees were out of reach. The needles gathered from each tree were pooled for analysis. Nutrient content analysis was conducted by the Analytical Chemistry Services Laboratory in Victoria, BC.

High-resolution LIDAR (2 m pixel size) covering the study area was gathered in August 2012 by Terra Remote Sensing Inc. From LIDAR data I used the zonal statistics tool in QGIS (QGIS.org, 2022) to derive the mean aspect (degrees, categorized as North, South, East, and West for analysis) and slope (degrees) of each site. I also derived the mean slope (degrees) in a 7 m zone around each tree to account for GPS error. The site-level slope values were used for abundance analysis and the tree-level slope values were used for height and DBH analysis.

### **3.3.3 Statistical Analysis**

I recorded size and location data for 208 Pacific yew trees on 70 transects. Trees with DBH <5 cm or NA values (e.g., no height recorded for living trees growing horizontally on forest floor) for some measurements were excluded from the analysis for a final sample size of 133

trees. I used R 4.1.2 (R Core Team, 2021) to build linear models representing hypotheses about factors affecting the height and log-transformed DBH of Pacific yew trees. I conducted model checking by plotting residuals against model predicted values and by examining the normality of residuals with Q-Q plots. I conducted model selection on models that met linear model assumptions with the Akaike Information Criterion corrected for small sample sizes (AICc) (Bolker, 2008). Models were considered equivalent in terms of support if they were within 2 delta AICc units of each other (Bolker, 2008). Variables used were: site type (habitation/control); distance from shore (near shore/mid forest/deep forest); aspect (north/south/east/west); mean transect canopy openness (%); normalized transect soil moisture; and mean site-level and tree-level slope (degrees). Canopy openness, soil moisture, and slope values were standardized prior to analysis by subtracting the mean and dividing by the standard deviation.

I analyzed tree abundance as number of trees per transect to account for differing numbers of transects placed at each site pair. I repeated the model building and selection process above but ran generalized linear models (GLMs) with a negative binomial distribution and log-link function to account for overdispersion of the data (Faraway, 2016; Zuur et al., 2013). I used the “gam” function from the MGCV package to create the models (Wood, 2011) and the “gam.check” function to check model diagnostics.

To compare concentrations of calcium, phosphorus, nitrogen, sodium, and potassium in trees growing on habitation sites and control sites, I collected foliage samples from 27 Pacific yew trees (19 from habitation sites, 8 from control sites). I then conducted Welch’s two-sample

*t*-tests with data pooled by site type to determine if there is a difference in these target elements between the habitation and control sites.

### 3.4 Results

#### 3.4.1 Tree Height

There were no differences in tree height between habitation and control sites. Canopy openness and distance from shore best explain variation in yew height (Table 3), though with such a low  $R^2$  value (adjusted  $R^2 = 0.07$ ,  $df = 123$ ), much variation remains unexplained. Canopy openness has a strong negative effect on tree height, distance from shore has a moderate effect, and site type has a weak effect (Fig. 2a). There was likewise some support for another model with aspect, canopy openness, and distance from shore (Table 3; adjusted  $R^2 = 0.07$ ,  $df = 122$ ).

**Table 3:** AICc outputs for model selection of tree abundance, tree height, and log-transformed DBH. Df = degrees of freedom.

<i>Response Variable</i>	<i>Model</i>	$\Delta AICc$	<i>df</i>	<i>weight</i>
Tree height (m)	~ type + canopy + distance	0.0	6	0.44
	~ aspect + canopy + distance	0.7	7	0.31
	~ type + aspect + canopy + distance	2.6	8	0.12
	~ 1	4.7	2	0.04
	~ distance	5.8	4	0.02
	~ type	6.6	3	0.02
	~ soil	6.7	3	0.02
	~ slope	6.8	3	0.01
	~ aspect	7.8	4	0.01
	~ type + slope + distance	10.2	6	<0.01
	~ type + soil + distance	10.2	6	<0.01

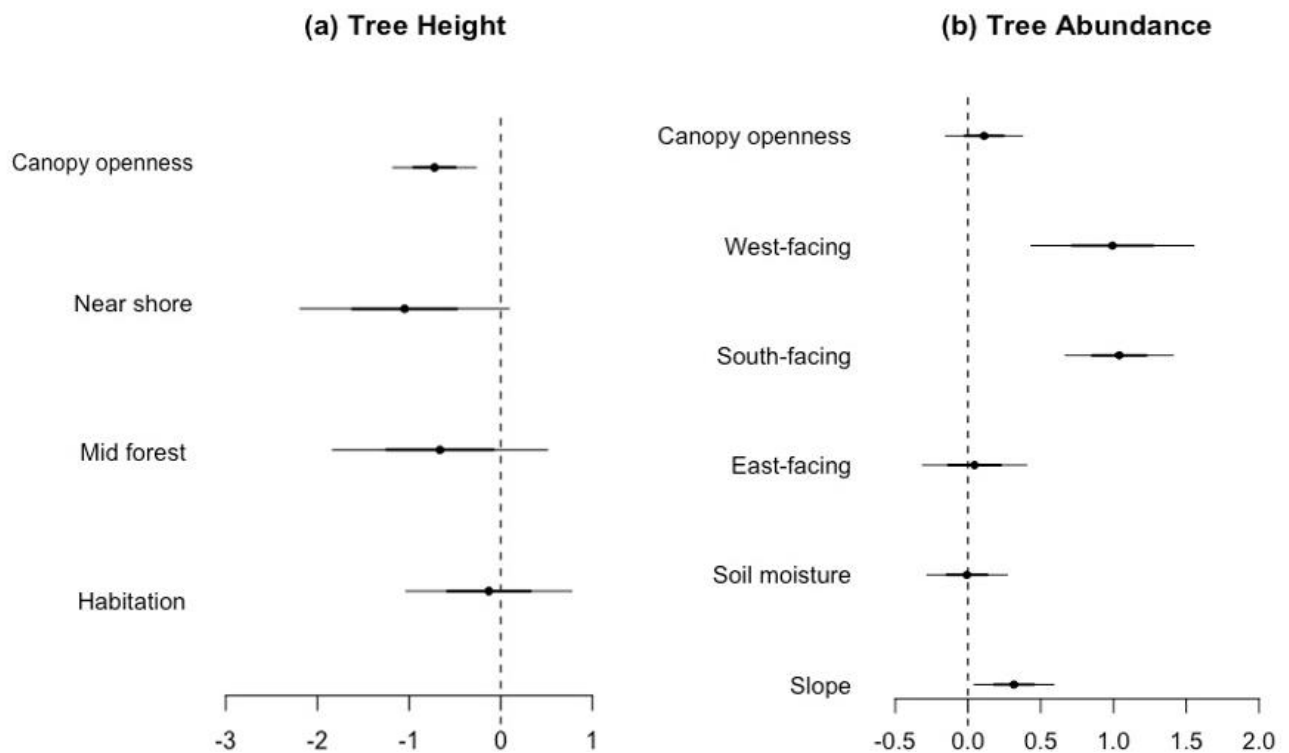
	~ soil + slope + distance	10.2	6	<0.01
	~ type + aspect + distance	10.4	7	<0.01
	~ type + soil + slope + distance	12.2	7	<0.01
Log-transformed DBH	~ <b>1</b>	0.0	2	0.38
	~ type	1.2	3	0.21
	~ soil	2.0	3	0.14
	~ slope	2.1	3	0.14
	~ aspect	4.1	4	0.05
	~ distance	4.1	4	0.05
	~ type + canopy + distance	5.9	6	0.02
	~ type + slope + distance	7.6	6	0.01
	~ soil + slope + distance	8.4	6	0.01
	~ type + aspect + canopy + distance	8.6	8	0.01
	~ type + aspect + distance	9.2	7	<0.01
	~ soil + slope + aspect + canopy + distance	12.7	9	<0.01
	~ type + soil + slope + aspect + canopy + distance	13	10	<0.01
		~ <b>soil + slope + aspect + canopy</b>	0.0	7
Tree abundance (trees/tract)	~ type + soil + slope + aspect + canopy	2.1	8	0.28
	~ slope	11.0	3	<0.01
	~ type + slope	12.9	4	<0.01
	~ soil + slope	13.2	4	<0.01
	~ <b>1</b>	14.9	2	<0.01
	~ type + soil + slope	15.3	5	<0.01
	~ soil	16.2	3	<0.01
	~ type + canopy	18.2	4	<0.01

### 3.4.2 DBH

The null model best explains variation in tree DBH (Table 3; df = 127), indicating that no variables included in modeling have strong influences on variation in DBH.

### 3.4.3 Abundance

There were no differences in Pacific yew abundance between habitation and control sites. Soil moisture, slope, aspect, and canopy openness best explain variation in tree abundance (Table 3; adjusted  $R^2 = 0.27$ ,  $df = 63$ ), with south- and west-facing aspects and site slope having strong positive effects on abundance (Fig. 2b). Canopy openness and soil moisture have weak effects.

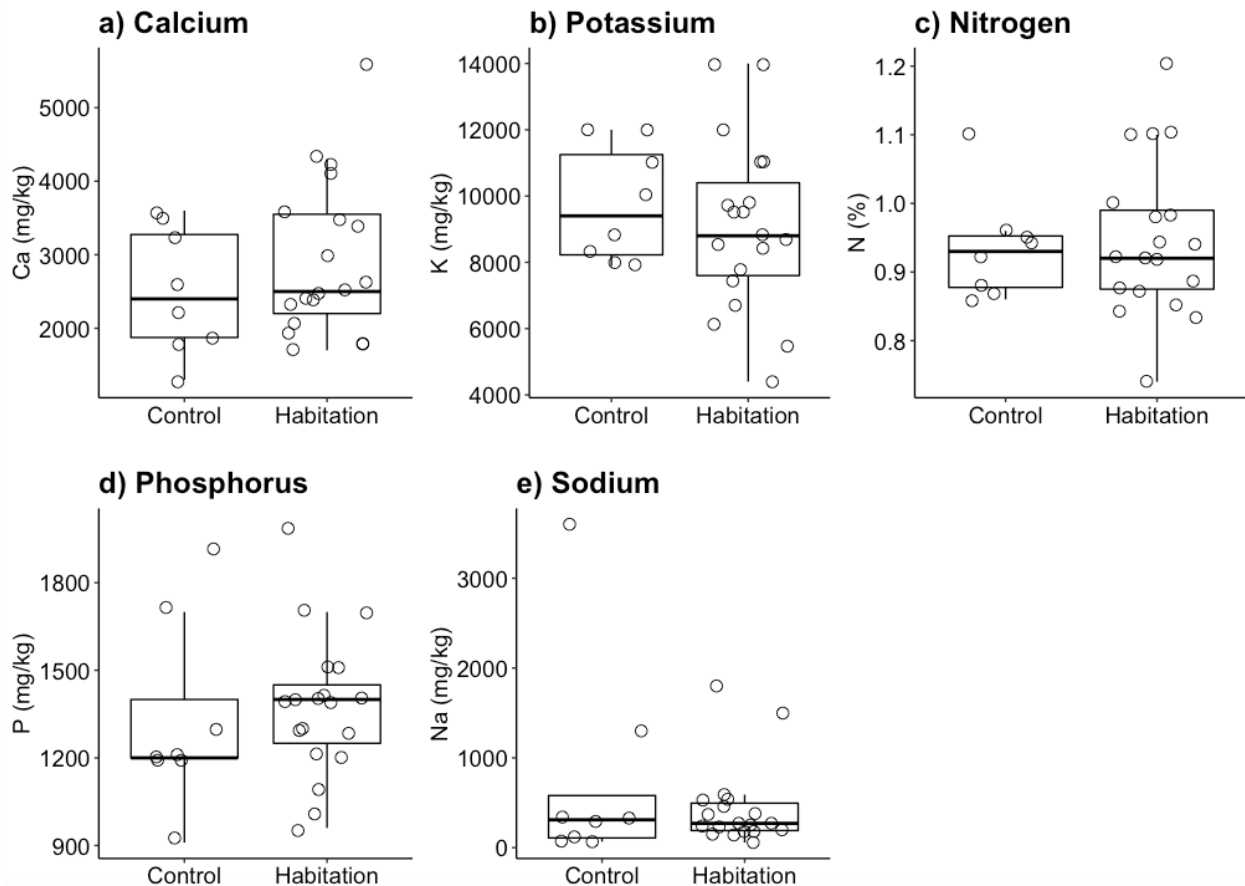


**Figure 2:** Model results for Pacific yew height (a) and abundance (b). Continuous predictors have been standardized.

### 3.4.4 Foliar Nutrient Content

There were no differences in foliar calcium ( $t = -1.08$ ,  $df = 16.39$ ,  $P = 0.23$ , Fig. 3a), potassium ( $t = -0.77$ ,  $df = 19.5$ ,  $P = 0.45$ , Fig. 3b), nitrogen ( $t = 0.33$ ,  $df = 19.46$ ,  $P = 0.75$ , Fig. 3c),

phosphorus ( $t = 0.40$ ,  $df = 10.76$ ,  $P = 0.70$ , Fig. 3d), or sodium levels ( $t = -0.74$ ,  $df = 7.84$ ,  $P = 0.48$ , Fig. 3e) between trees on habitation sites and on control sites.



**Figure 3:** Nutrient content in Pacific yew foliage at habitation and control sites. Upper whiskers extend to highest value within 1.5 times the inter-quartile range, lower whiskers extend to lowest value within 1.5 times the inter-quartile range, upper and lower box limits are first and third quantiles, inner lines are medians, and circles are data points. Calcium and phosphorus levels are slightly higher on habitation sites and potassium levels are slightly lower.

### 3.5 Discussion

Site type, canopy openness, and distance from shore influence Pacific yew height to some extent, with canopy openness and distance from shore exerting the strongest effects (Fig. 2a). Most variation in tree height is not explained by this model, however, which may be linked

to Pacific yew's broad environmental tolerances within old forests (Bolsinger & Jaramillo, 1990; Campbell & Nicholson, 1995). No variables tested seem to influence the DBH of Pacific yew (Table 3), which can most likely be explained by tree age. Tree abundance is influenced by soil moisture, site slope, aspect, and canopy openness, with aspect and slope exerting the strongest influences (Fig. 2b). This can likely be explained by the positive influences of light availability on Pacific yew reproduction demonstrated elsewhere in its range (Anderson, 2001; DiFazio, 1995; DiFazio et al., 1997). Foliar nutrient levels do not differ between habitation and control sites (Fig. 3), in contrast with other plant species that have higher foliar nutrient levels on habitation sites (Hunter, 2021; Trant et al., 2016). Unlike other studies conducted on the Central Coast, habitation histories do not seem to exert strong effects on Pacific yew size and abundance, demonstrating that more nuance is needed in the way that ecological ideas are applied to eco-cultural systems.

### **3.5.1 Tree Height and DBH**

Pacific yew height is affected to some extent by canopy openness, distance from shore, and site type (Table 3). Canopy openness exerts a negative effect on tree height, in contrast with other studies that have found that light availability increases Pacific yew productivity and can lead to growth releases (Bailey & Liegel, 1997; DiFazio, 1995). The effect sizes for this model are small, however, and must be interpreted with caution. The DBH of Pacific yew is not well explained by any variables included in this study (Table 3) and may be a function of tree age and disturbance histories (Bailey & Liegel, 1997; Minore & Weatherly, 1994a; Service, 1908), which could not be sampled in this study. These findings regarding tree size contrast with prior research on canopy species like Western hemlock and Western redcedar on habitation sites.

Trant et al. (2016) used many of the same site pairs and found that forests growing on habitation sites were taller than forests on control sites. They found aspect, distance from habitation site, and slope to be the most important variables in explaining forest height, but my results suggest that these variables do not exert a large effect on the size of Pacific yew. Pacific yew does not appear to respond to environmental conditions and the legacies of human habitation in the same manner as tree species that form most tree cover on the Central Coast.

Prior literature on Pacific yew at lower latitudes indicates that the species is a generalist, able to grow under a variety of environmental conditions (Bolsinger & Jaramillo, 1990; Busing et al., 1995b; Campbell & Nicholson, 1995). The species is known to tolerate wide ranges of canopy openness, soil types and drainage, and is found in a variety of forest types (Bolsinger & Jaramillo, 1990; Campbell & Nicholson, 1995; DiFazio et al., 1997). My findings regarding tree height and DBH support this hypothesis, even in very different ecosystems and at much higher latitudes than where Pacific yew has been studied previously. This suggests that environmental differences between habitation and control sites may not have been large enough to produce differences in the growth of Pacific yew. Additionally, variation in slope, canopy openness, and soil moisture was likely within the ranges tolerated by the species, and thus did not produce substantial differences in tree height and DBH.

### **3.5.2 Abundance**

Soil moisture, slope, aspect, and canopy openness affect the abundance of Pacific yew (Table 3). More yew trees grow on south- and west-facing sites than on east-facing sites, though the response of yew trees to north-facing sites is not known because none were available for inclusion in this study. These findings are in line with prior research that has found

aspect to be an important determinant of many components of forest productivity on the Central Coast (Banner et al., 2005; Trant et al., 2016). Aspect has also been found to impact Pacific yew productivity and seed production in Oregon, with south-facing areas showing greater tree productivity and light availability increasing strobilus production (Anderson, 2001; DiFazio, 1995; DiFazio et al., 1997). Aspect therefore likely plays an important role in Pacific yew reproduction and impacts its distribution on landscapes. Site slope has a moderate effect on yew abundance. This may be linked to prior ecological observations that the species prefers slopes (Bolsinger & Jaramillo, 1990; Campbell & Nicholson, 1995; Scher & Jimerson, 1989; Service, 1908), though further research is needed to investigate this relationship empirically. In addition, an equal number of habitation sites are located on south- and east-facing sites with fewer found on west-facing sites and habitation sites tend to be flatter than control sites. This indicates that the ideal locations for habitation site placement and the growth of Pacific yew may not entirely overlap. Although soil moisture is in the top-performing model, its small coefficient estimate indicates that it likely does not play a large role in explaining variation in Pacific yew abundance.

### **3.5.3 Foliar Nutrient Content**

There were no detectable differences in foliar nutrient content between yew trees growing on habitation sites and control sites. Other culturally important species have increased foliar nutrient levels as a result of soil enhancement by anthropogenic activity (Hoffman et al., 2017; Hunter, 2021; Trant et al., 2016), but Pacific yew does not appear to respond to increased nutrient levels in the same way. Prior research in Montana has suggested that Pacific yew can be more abundant on sites with higher soil nitrogen levels (McCune & Allen, 1985), but

nitrogen levels did not differ between habitation and control sites (Fig. 2c) due to limited residence time of human-derived nitrogen in soils without continual inputs (Johnson, 1992).

Interpretation of this finding is limited by both the lack of research into Pacific yew's nutrient requirements and by the small sample size used in this analysis. A more thorough investigation of foliar nutrient content with a larger sample size may shed light on the species' responses to anthropogenic soil modification.

#### **3.5.4 Impacts of First Nations Cultivation on Pacific Yew**

The size and abundance of Pacific yew are not explained well by site type, unlike findings of similar research that has found higher densities of culturally important species on or near habitation sites on the Central Coast (Fisher et al., 2019; Hoffman et al., 2017; Hunter, 2021). Species such as salmonberry (*Rubus spectabilis*) and huckleberry (*Vaccinium parvifolium*) were tended by First Nations on habitation sites to increase their productivity (Fisher et al., 2019). They have remained relatively abundant as a result, despite regular inhabitation of the sites ending over 100 years ago due to colonization (Fisher et al., 2019). Pacific yew does not follow this pattern, potentially because its cultivation occurred in different areas of the forest (see Turner et al., 2021 for examples of this practice applied to other species). There is some evidence that the Heiltsuk Nation cultivated and harvested Pacific yew in clusters near village sites, and not on the sites themselves (W. Housty, personal communication, July 28, 2020). Since this study only surveyed habitation sites directly and did not focus on the surrounding forests, the survey methods employed likely did not detect this potential abundance pattern and therefore the impacts of First Nations management on Pacific yew. This suggests that attempting to identify the legacies of First Nations landscape management through

examination of habitation and control sites, though very successful in other studies (Fisher et al., 2019; Hunter, 2021; Trant et al., 2016) and a useful method, is not applicable to every culturally important plant species due to their varying stewardship histories. Future research could shed light on patterns of Pacific yew growth and abundance linked to First Nations management by examining the species over a broader geographic area and employing community knowledge concerning site contexts and yew stewardship.

Although eco-cultural legacies do not appear to affect the growth and abundance of Pacific yew on formerly inhabited sites, these findings do not discount the importance of First Nations management and stewardship to the ecology of the Central Coast. Instead, they point to the need for a nuanced understanding of the diversity of management strategies employed by First Nations and the variety of eco-cultural legacies they can leave behind. While prior studies have had success in detecting eco-cultural legacies through the comparison of habitation and control sites (Fisher et al., 2019; Hunter, 2021; Trant et al., 2016), the case of Pacific yew demonstrates that there is not a one-size-fits-all method for studying eco-cultural legacies. Not all culturally important plant species were cultivated directly on habitation sites, and habitation sites are not the only locations of landscape modification by First Nations (see Armstrong et al., 2021 for examples of forest gardens and Hoffman et al., 2017, 2018 for legacies of anthropogenic burning on the Central Coast). These complex realities must be integrated into studies of Indigenous stewardship legacies to fully detect and explain patterns of anthropogenic ecological change. This means that to study eco-cultural legacies effectively, the use of scientific methods must be guided by traditional knowledge of the strategies employed to cultivate the species in question.

### **3.6 Conclusion**

I investigated the impacts of environmental conditions and ecological legacies of First Nations habitation on Pacific yew on the Central Coast of British Columbia. I found that, in contrast to other species investigated in the region, the size and foliar nutrient content of yew trees are not influenced by differences in conditions between habitation and control sites. This is likely due to the species' broad environmental tolerances, though further investigations of Pacific yew's responses to soil nutrients are needed. Pacific yew abundance is somewhat influenced by site aspect, which is likely an important factor in tree reproduction. Unlike some other species of cultural importance in the region, the abundance of Pacific yew does not differ between habitation and control sites. This may be due to the potential lack of intensive cultivation of yew on habitation sites, since the Heiltsuk Nation had dedicated cultivation areas near, but not necessarily on, habitation sites. This research fills an important knowledge gap about the ecology of Pacific yew on the Central Coast of BC and points to the need for more nuanced understanding of the diversity and scope of First Nations landscape management in ecological studies.

## Chapter 4: General Discussion

### 4.1 Overview of Results

My research explores the influences of Indigenous landscape management on ecological study and the interactions between human modification and habitat in explaining the ecology of Pacific yew. This contributes to a broader re-evaluation of the role of humans in shaping terrestrial ecosystems and of the paradigms used when conducting ecological research on intensively managed landscapes (Boivin et al., 2016; Ellis et al., 2021; Turner, 2020b).

In Chapter 2, I examined prior ethnobotanical and ecological research discussing Pacific yew, since the species has received little attention in over 20 years. I found that while current knowledge on the ecology of Pacific yew is likely sufficient to draw broad-scale conclusions, many important gaps exist that may affect the efficacy of conservation and management initiatives. Aside from its role as food and habitat for large mammals (Jenkins & Starkey, 1993; Korfhage et al., 1980; Pierce & Peek, 1984; Pierce, 1984), the ecosystem functions of Pacific yew are virtually unknown. Its habitat selection mechanisms and response to different forms of disturbance are also largely uninvestigated, which may have unknown consequences if the species' range shifts in the coming decades (Case & Lawler, 2017). These knowledge gaps may be attributed to past research priorities, since the high demand for Pacific yew for taxol at the time led to questions about its harvesting and regeneration potential (Campbell & Nicholson, 1995). Indigenous stewardship of Pacific yew was not widely documented in the ethnobotanical literature, nor did it feature in ecological explanations of study results. Although in line with the dominant ideas of natural areas as "wilderness" of the time (Ellis et al., 2021; Turner et al., 2021), changing conceptions of the depth of landscape modification brought about by humans

means that these studies may overlook key human aspects of Pacific yew ecology. This chapter therefore demonstrates the value in re-examining old research with new paradigms and highlights the importance of acknowledging and integrating Indigenous landscape histories into ecology.

In Chapter 3, I investigated the factors affecting the growth and distribution of Pacific yew on habitation sites on the Central Coast of BC. I hypothesized that thousands of years of intensive inhabitation and landscape modification at habitation sites (McLaren et al., 2015) would affect the height, diameter, abundance, and nutrient content of Pacific yew, as has been demonstrated in studies of other culturally important species at the same sites (Fisher et al., 2019; Hunter, 2021; Trant et al., 2016). I found that canopy openness, distance from shore, and weak effects of site type (habitation or control) best explain patterns in tree height and that no variables tested explain patterns of tree diameter. The abundance of Pacific yew was strongly influenced by site aspect and slope and I found no difference in foliar nutrient concentrations between habitation and control sites. My results differ from prior studies, which may be due to Pacific yew's broad environmental tolerances (Bolsinger & Jaramillo, 1990; Busing, Halpern, et al., 1995a) or active management of Pacific yew not occurring directly on habitation sites. These results explore the habitat of Pacific yew in a region where it has received little prior study and highlight the need for nuanced understandings of the diversity of plant management strategies and eco-cultural legacies on the Central Coast.

## 4.2 Challenges and Limitations

Although I gathered all information accessible, Chapter 2 was somewhat limited by the availability of past research. Some government reports and studies from the United States that may have had relevant information were unavailable, so their findings could not be integrated into this analysis. In addition, it is possible that older ethnobotanical and ecological papers relevant to the subject matter have not been digitized or were not present in physical collections consulted during the research process, and therefore could not be found.

Some methodological and logistical limitations affected data collection and interpretation in Chapter 3. Some habitation and control site pairs differ somewhat in environmental conditions such as slope and aspect, which may affect the identification of human-driven and landscape-driven variability in the paired site framework. The habitation sites also differ in size and intensity of use (McLaren et al., 2015), which may have impacted the strength of habitation signal I was able to detect. Although this variability between sites may have affected the interpretation of the study's results, the site pairs established by Trant et al. (2016) and Fisher et al. (2019) are the best options available for study in this region.

Field sampling was impacted by time and people power. Working within a tight data collection timeframe and with limited field assistance due to the COVID-19 pandemic, I could only sample habitation sites and not the areas surrounding the sites, as had been originally planned. I chose to limit my focus to habitation sites due to prior research indicating strong human-driven effects at the sites (Fisher et al., 2019; Hunter, 2021; Trant et al., 2016) and due to the methodological rigour of the paired site framework. Expanding sampling to include a buffer zone outside of the habitation site boundaries may have deepened the study results but

was not logistically feasible. Time and assistance limitations also meant that I could not take cores to assess tree ages, which would have contributed to my interpretation of the site histories.

Lastly, the COVID-19 pandemic also affected the level of community engagement possible in this study. I had hoped to visit Bella Bella during the course of this study to consult with collaborators and community members in person, but COVID-19 travel restrictions and safety concerns prevented these visits. Although collaboration opportunities were limited by the pandemic, I still worked with the Heiltsuk Integrated Resource Management Department (HIRMD) to develop my research questions, methodology, and received their input regarding cultural knowledge and connections to Pacific yew. Field data collected will be used by HIRMD to help guide future decisions about the management of Pacific yew.

### **4.3 Future Directions**

This research contributes valuable information about the ecology of Pacific yew and revisits the study of a species that has received little attention in over 20 years. My findings shed light on the factors affecting the growth and distribution of Pacific yew on the Central Coast and illustrate the need for greater understanding of the diversity of landscape management practices undertaken by Central Coast First Nations. Further questions remain, however, and the study of Pacific yew could be advanced in several ways. Expanding future studies to examine the distribution of Pacific yew over a broader geographic area would generate deeper insights into the relationships between Pacific yew and habitation sites and would address some of the habitat selection knowledge gaps I identified in Chapter 2. Including community knowledge on cultivation and harvesting sites would also be very valuable in

understanding the diversity of eco-cultural legacies present in the region. Examining cultural modifications to yew trees, if present, would also shed light on patterns of landscape modification and harvesting other than on habitation sites, which may be of use to the Central Coast First Nations. Including more variables in future studies, such as tree age, midden age and depth, and expanding investigations of foliar nutrient concentrations would likewise expand understandings of the relationships between First Nations landscape histories and Pacific yew.

More broadly, this work is part of a larger attempt to recognize and incorporate Indigenous Peoples and histories into ecological studies. Despite widespread and continuing landscape management and stewardship by Indigenous Peoples (Schuster et al., 2019; Turner, 2020a), most ecological studies fail to recognize this history or consider that it may impact study results (Boivin et al., 2016; Schang et al., 2020). Landscape management by Indigenous Peoples is linked to increased biodiversity and ecosystem resilience in the face of habitat loss and climate change (Ogar et al., 2020; Schuster et al., 2019) and collaborative efforts between Indigenous knowledge holders, researchers, and conservation practitioners are key to solving environmental challenges (Garnett et al., 2018; Ogar et al., 2020). In the face of unprecedented global change, the understandings of ecology and conservation needed to solve biodiversity and climate crises can only be achieved by including the perspectives of Indigenous Peoples, who have been stewards of their homelands and seas for millennia.

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## Appendix

**Table A1:** Full list of models fit for each response variable. Models highlighted in grey did not fit the assumptions of the data distribution and were not included in the AICc.

<i>Response Variable</i>	<i>Model</i>
Tree height (m)	~ type
	~ aspect
	~ canopy
	~ slope
	~ soil
	~ distance
	~ 1
	~ type + soil + slope + distance
	~ type + soil + distance
	~ type + slope + distance
	~ soil + slope + distance
	~ type + aspect + canopy + distance
	~ type + aspect + distance
	~ type + canopy + distance
	~ aspect + canopy + distance
	~ type + soil + slope + aspect + canopy + distance
	~ soil + slope + aspect + canopy + distance
DBH	~ type
	~ aspect
	~ canopy
	~ slope
	~ soil
	~ distance
	~ 1
	~ type + soil + slope + distance
	~ type + soil + distance
	~ type + slope + distance
	~ soil + slope + distance
	~ type + aspect + canopy + distance
	~ type + aspect + distance
	~ type + canopy + distance
~ aspect + canopy + distance	

	~ type + soil + slope + aspect + canopy + distance
	~ soil + slope + aspect + canopy + distance
	~ type
	~ aspect
	~ canopy
	~ slope
	~ soil
	~ 1
	~ type + soil + slope
	~ type + soil
Tree abundance (# of trees/transect)	~ type + slope
	~ soil + slope
	~ type + aspect + canopy
	~ type + aspect
	~ type + canopy
	~ aspect + canopy
	~ type + soil + slope + aspect + canopy
	~ soil + slope + aspect + canopy



**Figure A 1:** Examples of habitation sites sampled on Calvert Island, British Columbia.



**Figure A 2:** Examples of Pacific yew sampled on Calvert & Hecate Islands, British Columbia.