Sub-Regional Variation in the Structure, Composition and Ecology of Old-Growth Floodplain Forests in the Pacific Coastal Temperate Rainforest

by
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Abstract

A strong understanding of regional variation in structure and composition of old-growth floodplain forests and ecosystem drivers is critical for improving riparian old-growth management. We reviewed the literature to develop a framework to evaluate these and the relative roles of climate, disturbance, other drivers and their interactions. We then examined forest structure from 17 plots across ~11° of latitude along the northern Pacific Coastal Temperate Rainforest (PCTR). Mean annual temperature and precipitation were the most influential drivers of stand structure. Several flood proxies correlated with structural attributes suggesting that hydrological disturbance is a key driver of structure, likely driving greater variability among floodplain stands than upland stands. Northern plots showed slower stand development compared to southern plots, differences in structure suggest a need to re-evaluate sub-regional boundaries of the PCTR. Delineating sub-regional boundaries are important for monitoring and predicting how climate change will affect these forests and their disturbance regimes.

Keywords: old-growth; floodplain; Sitka spruce; developmental trends; riparian forest; forest structure

Dedication

This thesis is dedicated to all the countless amazing people that have gone out of their way in my life to help me succeed. I am ever grateful for the small, the random, and the unimaginable acts of kindness that you have bestowed upon me. You all inspire me. Because of you this thesis was possible. Thank-you.

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List of Acronyms

BA	Basal Area
BEC	Biogeoclimatic Ecosystem Classification
DBH	Diameter at Breast Height
DD>5	Growing degree days greater than 5ºC
ENSO	El Niño Southern Oscillation
CWD	Coarse Woody Debris
MAP	Mean Annual Precipitation
MAT	Mean Annual Temperature
NPG	Nivo-Pluvial-Glacial
PAS	Precipitation as Snow
PCTR	Pacific Coastal Temperate Rainforest
PDH	Pluvial Dominant Hybrid
PDO	Pacific Decadal Oscillation
SD of DBH	Standard Deviation of Diameter at Breast Height

Chapter 1. Old-growth floodplain forests in the Pacific Coastal Temperate Rainforest of North America: a review and analytical framework

1.1. Introduction

Riparian corridors, particularly floodplains, are a critical component of the Pacific Coastal Temperate Rainforest's landscapes, ecologically, economically, and culturally. Riparian forests are considered the most structurally and floristically diverse forests in the PCTR (Naiman and Bilby, 1998). Floodplains, ecosystems that extend from the active channel to valley slopes and receive inundation by via flooding, are composed of riparian forest patches and landforms which form a diverse and dynamic heterogeneous network. In the PCTR, this network consists of valuable aquatic and terrestrial habitat (Naiman et al., 2005b) that supports high-value timber production, carbon storage, and harbours high plant species diversity including culturally important species (Naiman et al., 2010; Sutherland et al., 2016). These ecologically diverse (*sensu* Naiman et al., 1993) floodplains are important for maintaining landscape scale species diversity. At the patch scale they supply economically and culturally valued large old trees (Sutherland et al., 2016) which are integral to floodplain processes (Latterell and Naiman, 2007; Latterell et al., 2006) and ecosystem function (Naiman et al., 2010).

The mild, warm and moist climate of the PCTR region is a significant factor in the development of massive conifers in coastal forests including floodplain stands (Waring and Franklin, 1979). Orographic precipitation and mountainous topography create climatic gradients west to east, with wetter coastal climates and drier eastern slopes. North to south, the PCTR region is divided into four sub-regions, the sub-polar (61ºN-59ºN), perhumid (59ºN-50ºN), seasonal (49ºN-43ºN), and warm (43ºN-38ºN), which are delineated by seasonal variation of precipitation (Alaback, 1991, 1996). This latitudinal span covers southeast Alaska, south to northern California (Alaback, 1996; DellaSala et al., 2011; Wolf et al., 1995) along the Insular, Coastal, and Olympic mountain ranges and parts of the western Cascades. Sub-regional boundaries are not confirmed, currently there are two very similar sets of sub-regions (i.e., DellaSala et al., 2011; Wolf et al., 1995), the sub-polar region extending farther south in DellaSala et al. (2011).

Climate change will inevitably shift climate envelopes and potentially create novel ecosystems (Mahony et al., 2018). Accurate delineation of sub-regional boundaries is important for monitoring and predicting how climate change will affect these forests and their disturbance regimes. Historically, Mean Annual Temperature (MAT) for each sub-region was 4ºC, 7ºC, 10ºC, and 12ºC, respectively (Alaback, 1996). A significant amount of precipitation occurs year-round in the subpolar and perhumid zones, Mean Annual Precipitation (MAP) ranges from 1000 – 7000 mm across the PCTR (Naiman and Anderson, 1997). Although the subpolar and perhumid regions receive more precipitation during the summer months (>20% and >10%, respectively) compared to the seasonal and warm regions, which receive less precipitation as snow in winter months (<10% and <5%, respectively) (Alaback, 1991, 1996). In the seasonal and warm temperate zones the lower amounts of summer rainfall can lead to annual droughts (Alaback, 1991, 1996).

Floodplain terraces in the PCTR support extraordinary examples of old-growth Sitka spruce forests (Peterson et al., 1997; Pojar et al., 2004) which are of special management concern throughout the region. In coastal British Columbia, all floodplain ecological communities are listed provincially and globally as either critically imperiled, of special concern, or vulnerable to extinction or extirpation[1] (B.C. Conservation Data Centre, 2018). In Alaska, these ecosystems are considered rare and are listed as of special concern. They are also home to several species that are listed as imperiled (Boggs et al., 2016). Beyond the forest, these rare ecosystems are important because they provide valuable instream habitat including side channel habitat important for Pacific salmon species (*Onchorhynchus* spp.). Salmon in turn provide nutrient subsides to the forests (Naiman et al., 2010). Further, floodplain forests are known for their floristic richness (Naiman et al., 2000). Floodplain ecosystems are also socially important, people culturally value large old trees (Blicharska and Mikusiński, 2014) which are ubiquitous in these ecosystems. Moreover, floodplain tree species are culturally important for coastal First Nations (e.g., monumental western redcedar; *Thuja plicata* Donn ex D. Don) (Hebda and Mathewes, 1984; Mobley and Lewis, 2009).

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[1] All BC low, medium, and high bench floodplain ecological communities are listed provincially as either critically imperiled, imperiled, of special concern, and/or vulnerable to extirpation or extinction. Their BC List Status is either Red (Extirpated, Endangered, or Threatened) or Blue (of Special Concern). Their Global Conservation Status is either critically imperiled, vulnerable to extirpation or extinction, or their Global Rank is not assessed yet (B.C. Conservation Data Centre, 2018).

Understanding the characteristics of old-growth floodplain forests is important for practitioners and policy makers so that they can create management plans that address societal and ecological needs. Old-growth characteristics have been described for coastal temperate upland forests (e.g., Franklin and Spies, 1991a, 1991b; Spies and Franklin, 1991; Van Pelt, 2007; Wells et al., 1998). Some work has been done in specific floodplain systems to characterize old-growth, though no comprehensive evaluation has been done to date across the extent of the PCTR to assess variability, structural and compositional drivers, and the relevance of variability for defining old-growth and informing management practices. Currently no trend with latitude has been identified in floodplain forest structure across the PCTR's climatic or latitudinal gradients (Naiman and Bilby, 1998).

Interactions between old-growth stand structure and the biophysical components of floodplains are significant for ecological function (*sensu* Franklin et al., 2002) and the formation of landscape level heterogeneity. These interactions drive patch creation, destruction, soil formation, and species composition through flood disturbance and lateral river movements (Pabst and Spies, 1998; Van Pelt et al., 2006). In the PCTR, several studies have examined these interactions and proposed developmental pathways for landforms and their successive forest types (i.e., Latterell et al., 2006; Little et al., 2013; Van Pelt et al., 2006). Though these studies use old-growth attributes to interpret floodplain dynamics and development, analyzing old-growth forest structure and composition was not their main focus, leaving some old-growth characteristics unanalyzed or under analyzed. Further, the hydrological disturbance regimes tied to these forests are projected to shift because of climate change (Schnorbus et al., 2014; Shanley et al., 2015). Forest structure and composition are likely to change as a result, changing the amount of old-growth forest at the landscape scale (Little et al., 2013; Whited et al., 2007). Despite knowing how landscape composition may be affected by climate change, we still know little about flood disturbance and potential changes at the stand level and how these will in turn affect floodplain dynamics at the landscape level.

An effective research programme that includes a structured analytical framework is required to provide a comprehensive understanding of old-growth floodplain forest ecosystems to create informed approaches for riparian old-growth management. Previous literature reviews have focused on PCTR floodplain ecology, drivers, and processes throughout floodplain development at multiple scales (i.e., Naiman et al., 2010; 2000). Here, we focus on old-growth floodplain forests and their drivers at the patch scale. We aim to: 1) synthesize the current understanding of old-growth floodplain forest structure, composition, and drivers of these characteristics; 2) compare floodplain and upland old-growth structure and composition; 3) discuss current knowledge gaps relevant to floodplain management to maintain ecological function at stand and landscape scales; and 4) provide a research framework for addressing these key knowledge gaps.

1.2. Drivers of Change in the Northern PCTR and Floodplain Forests

Riparian zones are transitional, bridging aquatic and terrestrial ecosystems, they extend from the active channel edge to upland areas and span from headwater streams to ocean's edge (Naiman et al., 2005b). Therefore, all floodplain forests are riparian, however not all riparian forests are floodplain forests. Here we focus on floodplain forests and treat riparian and floodplain as synonymous, though they are not functionally interchangeable. Floodplain forests border alluvial rivers. They are highly diverse due to the biophysical processes and feedbacks that form a complex mosaic of channels, pioneer bars, floodplains, terraces, and forest successional stages (Little et al., 2013; Naiman et al., 2010; Van Pelt et al., 2006). Alluvial rivers have low transport capacity which cause the accretion of stratified fine sediments (alluvium) in the valley bottom and prevents the river from scouring the valley bottom to bedrock, therefore differing them from bedrock valleys (Naiman et al., 2005b). Geomorphic processes typical of alluvial rivers include lateral movements (avulsion, incision, and deposition) which erode channels, deposit large wood into channels, and shape new floodplain landforms (Beechie et al., 2006; Little et al., 2013).

Large wood is a key ecological driver in patch formation (Naiman et al., 2000), playing a functional role in geomorphic processes by slowing water movement and trapping sediment. In turn, this generates terrestrial habitat (Latterell and Naiman, 2007; Latterell et al., 2006; Naiman et al., 2000). This is an example of biogeomorphic processes, where biota, in this case large trees, interact with geomorphic processes to influence floodplain development (Naylor et al., 2002). Thus, large wood and the old-growth forests that supply it are critical in maintaining biogeomorphic processes (Latterell and Naiman, 2007; Latterell et al., 2006; Naiman et al., 2010). Moreover, maintaining these processes is essential for conserving in stream biocomplexity (Latterell and Naiman, 2007) as well as landscape heterogeneity.

The amount of old forest present in the riparian mosaic depends on the residence time of alluvial landforms, or terraces. The proportion of young to old forest is dependent on the magnitude and frequency of hydrological disturbance; smaller rivers with less erosive power and therefore less severe disturbance regimes have a higher proportion of old forest (Acker et al., 2003; Little et al., 2013; Whited et al., 2007). The older a landform is the less likely erosion becomes from peak flows or disturbance events. Therefore, mature terraces have larger half-lives than pioneer bars and transitional terraces (Little 2013). On the Flathead River in Montana, landform erosion rates were associated with climate, flood regime, floodplain size, and the spatial arrangement and composition of patch types (Whited et al., 2007). Research on the Carmanah River in coastal BC supports the findings from the Flathead River. However, the Carmanah River's smaller drainage area and lower mean annual flood equate to less floodplain restructuring and consequently more old forest (Little et al., 2013). In Washington State, the Queets River's high mean peak flows decrease the half-life of mature terraces. Therefore, in comparison to Carmanah, the Queets has a higher rate of floodplain restructuring and less old forest (see Table 1.1) (Latterell et al., 2006). On four rivers, similar in character and geographical location to the Carmanah River in catchments that had a history of logging, conversion of vegetation by the active channel to non-vegetated land cover over a 5-year period (2006-2011) was 11.9%, 5.1%, 9.7%, and 7.6% (Talomey, Sheemahat, Machmell, and Bella Coola Rivers, respectively; MFLNRO, 2012, unpublished data).These conversion rates when broken down by yearly average are higher than those of the Queets, Carmanah, and Flathead. These differences may be caused by differences in catchment size, flood regime, shorter sampling time frames, human disturbance, or a combination of these. Overall, at a watershed scale, forest developmental stages appear to be in a dynamic equilibrium, as the percents of mature and old forest on the landscape shift yearly from geomorphic disturbances though over decades (Little et al., 2013).

Table 1.1 Hydrological characteristics and mature fluvial terrace information for examples of alluvial rivers in the Pacific Northwest. Percent mean mature forest is actual forest, not terrace. Floodplains were analyzed during similar time periods (1937-2007 and 1939-2002; Carmanah and Queets, respectively)(Latterell et al., 2006; Little et al., 2013).

Study Area	Drainage Area (km^2)	Mean annual flood (m^3/s)	Time Span (Years)	Mature Terrace half-life (Years)	Mean Mature Forest (%)	Floodplain restructured (%)
Carmanah	67	~100-200	70	360-1500	65	30
Queets	1153	2100	68	401	48	81

Climate mediated changes in flood regime can precipitate changes in forest structure and composition. Not only can changes in flood characteristics augment floodplain structure and species zonation (e.g., a young colonizing deciduous replacing old-growth after an intense flood event), but lower magnitude floods with higher frequencies can determine seedling success and establishment (Hughes, 1997). Further, in North America, changes in climate are linked to increases in fire, pathogens, and wind (Seidl et al., 2017; Shanley et al., 2015). The effects of climate change will vary spatially throughout the PCTR. In the coastal Pacific Northwest, the area burnt by wildfire is projected to increase between 160-1177%, there is high variability between models used to predict this increase yet it is still important to consider the role that these carbon dense forests play as sinks may be reversed (Rogers et al., 2011). Even though riparian areas are not usually characterized as at high risk for forest fires, these forests may be at increased risk with projected climate change (Mckenzie et al., 2004). As well, global scale climatic cycles, such as El Niño Southern Oscillation (ENSO) or the Pacific Decadal Oscillation (PDO), influence the age-class composition of riparian forests at the landscape scale. For instance, the PDO cool phase significantly increased the frequency, duration, and magnitude of peak flows on the Flathead River compared to the warming phase and subsequently the changes in flood regime shifted the ratio of young to mature forests (Whited 2007). Little et al. (2013) caution that the predicted flood regime shifts associated with climate change can have a similar effect. Change in disturbance regime will inevitably result in compositional change (Frelich and Reich, 1998). Thus, research is needed to explore the relation between flood disturbance and old-growth forest structure and composition. We understand that climate will impact the proportions of old forest on valley bottoms and that the area covered by old forest may decrease, therefore it is important to examine how changes in climate and disturbance patterns will influence stand structure and composition.

At the stand level, climate directly affects tree morality rates, productivity, and regeneration in forests as well as indirectly affecting forest health via pathogens and insects (Daniels et al., 2011). Conifers which dominate the overstory species composition in the PCTR are able to capitalize on the cool wet winters by photosynthesizing when hardwoods are dormant, as well as regulate water loss storage more effectively in summers (Franklin and Waring 1980). Yet, throughout the seasonal zone climate change has increased tree mortality in old-growth forests (van Mantgem et al., 2009). In coastal BC, average temperatures are 0.6ºC higher than at the beginning of the 20th century, with precipitation increasing 2-4% each decade mostly during winter (Boisvenue and Running, 2006). Windthrow events are predicted to increase particularly in wetter regions, as well as pathogens (Seidl et al., 2017). Further, climate affects decomposition rates (Naiman et al., 2005a), precipitation, and flood regimes. Predicted increases in precipitation in the PCTR and the runoff amount and timing are projected to impact peak flow frequency and magnitude (Schnorbus et al., 2014; Shanley et al., 2015).

Currently, in the PCTR, fire is not a dominant driver in floodplain forests (Pettit and Naiman, 2007). If fire becomes more prevalent in the seasonal and perhumid sub-regions of the PCTR as the climate warms, floodplain ecosystems will be at relatively high risk of damage or death as most floodplain species lack fire-tolerant adaptive traits. Dominant floodplain overstory species such as Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) have thin bark and are fire intolerant. In some catchments, fire-tolerant Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is present, typically in areas guarded from inundation (Collins et al., 2012). Still, Douglas-fir can be a leading overstory species on floodplains, for example along the Tahsish-Kwois River (see Chapter 2, Table 2.4). However, fire tolerant Douglas-fir is more common as a floodplain species in southern, more fire-prone areas of the seasonal sub-region. Floodplain topography, microclimate, and vegetation type restrict fuels from drying and in turn fire igniting and spreading (Gavin et al., 2003; Pettit and Naiman, 2007). In the wetter upland regions of the PCTR (e.g. west coast maritime influenced areas that receive orographic precipitation), fire is not a major disturbance agent in contrast to rainshadow areas in the seasonal and warm sub-regions where

Douglas-fir is the dominant overstory species (Daniels and Gray, 2006; Gavin et al., 2003; Hoffman et al., 2016; Lertzman et al., 2002). Fire intensity may be lessened on floodplains because of higher humidity and moisture levels in vegetation and soil, and dense vegetation resulting in decreased winds speeds (Pettit and Naiman, 2007). Lower elevation forests in valley bottoms in the northern PCTR can have a fire return interval > 6000 years (Gavin et al., 2003). In areas where First Nations historically practiced burning, fire return intervals were relatively frequent, even in wetter forest types that would otherwise have much longer return intervals (Hoffman et al., 2016). In drier regions such as Oregon, where fire disturbance is more frequent, no difference in fire return interval between upland and riparian zones was seen, though fire frequency may decrease as stream size increases (Pettit and Naiman, 2007).

Old-growth floodplain forests are distinguished from younger stands (e.g., on low or medium-bench sites) by a shift from flood disturbance to gap-phase dynamics as the main influence on stand structure (Hughes, 1997; Latterell et al., 2006). Gap-phase dynamics occur when one to a few standing trees dies slowly or in a small scale wind disturbance, creating a small gap in the forest canopy under which shade tolerant understory tree species can exploit the newly available resources (Lertzman and Krebs, 1991). This process generates fine scale heterogeneity by maintaining uneven-age stands (Lertzman et al., 1996). Riparian forests can be susceptible to windthrow due to shallow rooting depths compared to upland forests, particularly on topographically exposed sites (Moore and Richardson, 2012). These windthrow events and gap-phase processes produce large dead wood which is important for both terrestrial and aquatic habitat (Naiman et al., 2000).

1.3. Floodplain Forests - Character and Composition

Floodplain forests receive periodic inundation and typically consist of flood tolerant vegetation (MacKenzie and Moran, 2004). They are differentiated by the flood return interval and length of growing season inundation (MacKenzie and Moran, 2004). Old-growth floodplain forests on terraces receive less inundation than younger stands which reside on developing floodplains. Developing floodplains and floodplains transitioning to terraces are more frequently flooded for longer inundation periods than terraces. Language categorizing floodplain landforms (e.g., pioneer bar, developing floodplain, established floodplain, transitional fluvial terrace, mature terrace and old-growth terrace; Figure 1.2) reflects the landform toposequence and riparian forest succession. However, this language is more descriptive and informative for landforms than for forests. For instance, old-growth forests of similar age, composition, and structure can have different landform classifications (e.g., McKee et al. 1982).

Old growth terraces or mature terraces are termed “high-bench” sites in some classifications (see Figure 1.2). High bench sites are the least frequently flooded landforms (> 5-year return interval) with stands that are conifer dominated, though they may have a minor deciduous component (Green and Klinka, 1994; MacKenzie and Moran, 2004). However, high bench sites are not the only landforms to support old-growth stands. Since forests and landforms develop on a continuum, some medium bench sites also support old-growth. Medium bench (mid-bench) sites, or transitional terraces, have a more frequent (< 5-year) flood return interval that lasts around 10-25 days during freshet. Conifers are often present on raised microsites (Green and Klinka, 1994; MacKenzie and Moran, 2004). Leading conifer species on floodplains transition from fire adapted species in the southern seasonal subzone such as coastal redwoods (*Sequoia sempervirens* (D.Don) Endlicher) and Douglas-fir to Sitka spruce and western hemlock in the wetter, hypermaritime and maritime climates of the seasonal subzone and north throughout the perhumid subzone. In the seasonal and perhumid zones western hemlock is usually co-dominant with minor components of western redcedar, alder (*Alnus rubra* Bong.), black cottonwood (*Populus balsamifera spp. trichocarpa* L. (Torr. & A. Gray ex Hook.)) and big leaf maple (*Acer macrophyllum* Pursh). Low bench sites roughly encompass Latterell et al.’s (2006) developing and established floodplain classifications (see Figure 1.2). These experience annual flooding of up to 40 days (MacKenzie and Moran, 2004). This flooding restricts conifer development, allowing red alder, black cottonwood, and willow (*Salix)* to dominate (Green and Klinka, 1994; MacKenzie and Moran, 2004).

1.3.1. Structure and Composition

The vertical and horizontal complexity of old-growth floodplain forests arises in part from gap-phase processes which create multi-layered canopies of dominant, co-dominant trees and regeneration with openings that fill with Sitka spruce’s large volume crowns (Giesbrecht et al., 2017; Van Pelt et al., 2006). The large crowns are supported by towering large diameter trees, which are some of the tallest conifer species globally.

For example, Sitka spruce stand as tall as 93 m on the Queets River floodplain and 92 m on the Carmanah River (Pojar et al., 2004; Van Pelt et al., 2006). Floodplain productivity and Sitka spruce's fast growth rates help these stands develop their old-growth characteristics faster than upland forests (Van Pelt et al., 2006).

Old-growth floodplain tree species are adapted to survive inundation. Sitka spruce and western redcedar both have shallow root systems that allow them to endure periodic flooding (Naiman et al., 2010). Western redcedar is also capable of vegetative reproduction (Antos et al., 2016) which may help the species maintain its presence after flood events. Further, Sitka spruce, western redcedar, and western hemlock are able to establish on decomposed logs and stumps as well as mineral soil (Antos et al., 2016; Naiman et al., 2010).

Compared to old-growth upland forests, floodplain forest structure can be exceptionally complex (Van Pelt et al., 2006). Like upland forests, old-growth floodplain stands have lower densities of trees and higher numbers of diameter large trees than younger stands. However, there appears to be greater variability in tree size for floodplain stands (Figure 1.1). Figure 1.1 and Table 1.2 compare floodplain stand attributes to upland stands from published literature that included research on old-growth floodplain or upland stands in the PCTR (see Chapter 2, 2.2.2 for methods). Mean diameter can be larger for floodplain than upland stands, though few upland studies examined reported mean diameter (see Table 1.2). More data are needed for an accurate comparison. The standard deviation of diameter (SD of DBH), a measure of tree size variability, increases proportionally to mean diameter (Gerzon et al., 2011; Van Pelt et al., 2006) and can be larger and increase faster for floodplain stands than upland forests (Table 1.2) (Van Pelt et al., 2006). We see higher variability in floodplain attributes than upland stands. However, literature values for old-growth attributes, upland and floodplain, are sparse. Inconsistent reporting of old-growth attributes across studies reduced the amount of data available for comparison (see Chapter 2) (Burrascano et al., 2013) and consequently our ability to draw more meaningful conclusions. More research with consistent standardized reporting can facilitate cross-study comparison throughout the PCTR and help elucidate the drivers of structural variability (see Chapter 2).

Variability in stand structure arises in part from the climatic gradients spanning the PCTR. Site factors also introduce considerable variability in stand productivity (Balian and Naiman, 2005). Due to the amount of variability in stand structure, more data spanning the range of the PCTR are required to conduct a thorough analysis comparing upland and floodplain sites. Further, more consistent reporting of structural variables is needed for researchers, managers and planners to compare and draw accurate conclusions.

Table 1.2. Tree size diversity compared by mean Diamerter at Breast Height (DBH) and standard deviation of diameter (SD of DBH). Values were gathered from published peer-reviewed literature that reported old-growth stand attributes from upland and floodplain stands in the PCTR (see Chapter 2 for methods and criteria). DBH = Diameter at Breast Height. SD of DBH = Standard Deviation of DBH.

Study	Mean DBH (cm)	SD of DBH (cm)
Floodplain		
Queets River, WA		
Van Pelt et al. 2006	59.8	36.7
Van Pelt et al. 2006	55.2	38
Van Pelt et al. 2006	60.5	38.9
Van Pelt et al. 2006	42.2	50.3
Van Pelt et al. 2006	35.1	50.5
Carbon River, WA		
Van Pelt and Nadkarni 2004	44.1	52.7
Upland		
British Columbia		
Gerzon et al., 2011	-	27.4
Wells, 1996	50.44	37.7
Wind River Canopy R.F., WA		
North et al., 2004	33.9	33.8
Washington/Oregon		
Spies and Franklin, 1991	31	32.0
Freund et al., 2015	-	36.4

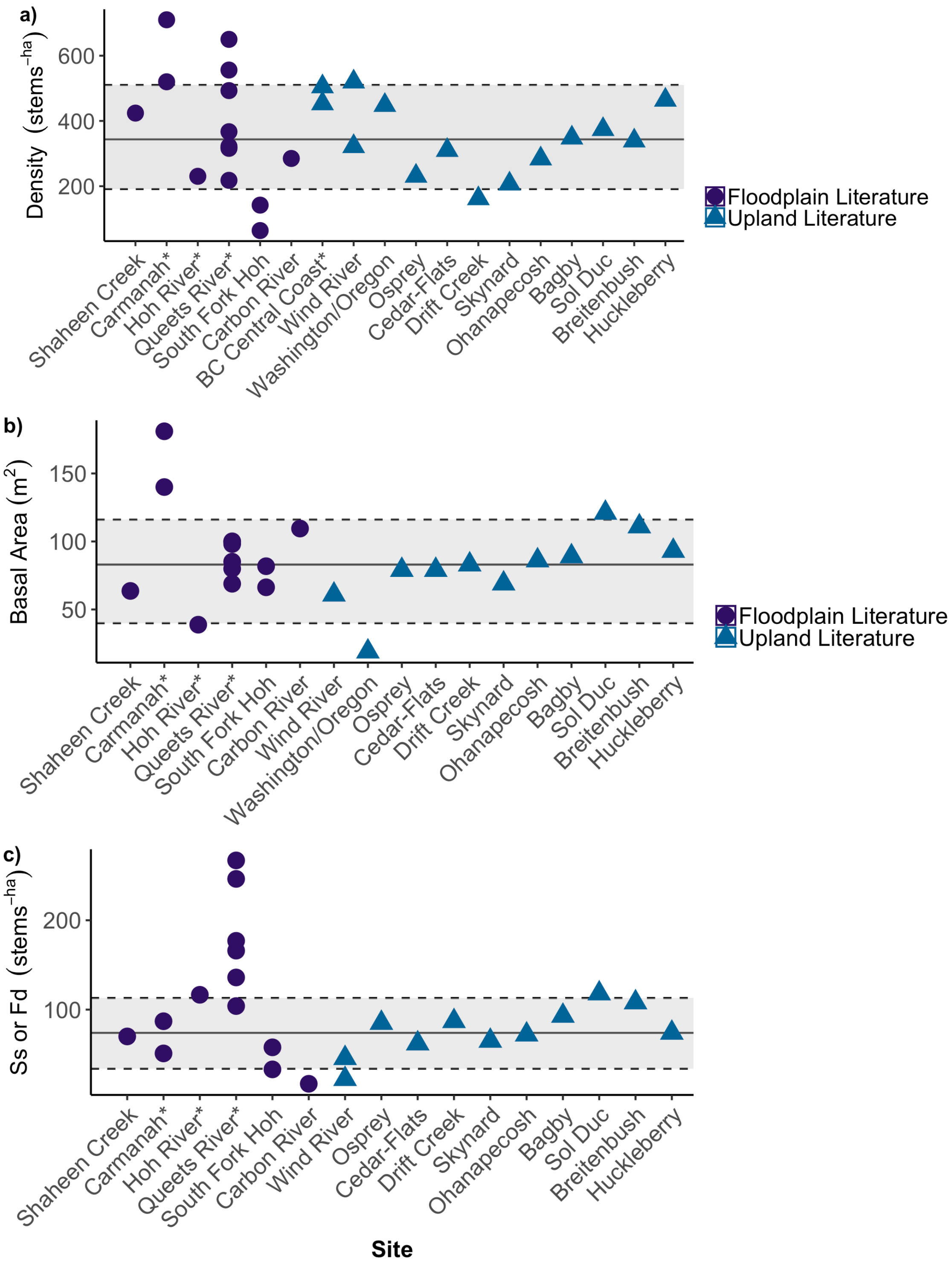

a)
Density (stems^-ha)
600
400
200
b)
Basal Area (m^2)
150
100
50
c)
Ss or Fd (stems^-ha)
200
100
Shaheen Creek
Carmanah*
Hoh River*
Queets River*
South Fork Hoh
Carbon River
BC Central Coast*
Wind River
Washington/Oregon
Osprey
Cedar-Flats
Drift Creek
Skynard
Ohanapecosh
Bagby
Sol Duc
Breitenbush
Huckleberry
● Floodplain Literature
▲ Upland Literature
Site

Figure 1.1 **Comparison of floodplain and upland old-growth structure: a) stems per hectare; b) basal area; and c) stems per hectare of the leading shade intolerant species (Ss is Sitka spruce and Fd is Douglas-fir). The horizontal dashed lines are the 5th and 95th quantiles and the black horizontal solid line is the median of the upland data. Sites with * have differing sampling methods (Carmanah = live stems > 3 cm DBH; Hoh River = live stems > 4 cm DBH; one Queets River plot = live stems > 1 cm DBH = 493 stems/ha). Data are from reported liturature values (see Table 2.10 and Table 2.11 for more information and citations). Several sites are reported in this figure and not in Table 1.2, this is because Osprey, Cedar-Flats, Drift Creek, Skynard, Ohanapecosh, Bagby, Sol Duc, Breitenbush, and Huckleberry are all from one study which only reported the study SD of DBH rather than for each site (Freund et al., 2015).**

1.3.2. Productivity

Floodplain forests are more productive than many uplands stands indicated by their early development of old-growth characteristics (Van Pelt et al., 2006). However, there is a paucity of research on riparian forest productivity in the PCTR. This makes it difficult to make comparisons among floodplain, non-floodplain riparian, and upland forests. On the Queets river, an increased contribution of Sitka spruce to stem density and basal area on mature terraces and lower basal area and stem density of western hemlock resulted in lower mean standing biomass than upland stands (Balian and Naiman, 2005), thus larger tree sizes do not compensate for reduced density in these stands. Sitka spruce made up a considerable proportion of the stand productivity (72-86%) with old-growth stands having the highest productivity among riparian stands (7.8-17.2 Mg/ha/year of biomass) (Balian and Naiman, 2005). For example, the South Fork Hoh's standing biomass (572.8 Mg/ha; McKee et al., 1982) was comparable to the Queets (541 Mg/ha; Balian and Naiman, 2005). Nonetheless, reported values for floodplain forests were similar to those of uplands forests (Balian and Naiman, 2005). However, in southeast Alaska, low elevation floodplain stands had more biomass than non-riparian stands which was attributed to better drainage by alluvial soils (Buma et al., 2016). Similarity in biomass between upland and riparian forests in the southern PCTR (e.g., Balian and Naiman, 2005; McKee et al., 1982) in contrast to riparian stands having more biomass in southeast Alaska (e.g., Buma et al., 2016) may be due to the exclusion of CWD in the southern studies. Flood disturbance may reduce the amount of CWD, though this is relative to the intensity and frequency of flooding as well as timing of data collection in relation to the last flood event.

1.3.3. Soil Nutrient and Moisture Availability

Productivity on floodplains is a result of nutrient and water availability from sediment fluxes from flood disturbance, soil texture, red alder nitrogen (N) fixation, and marine derived N from salmon (Naiman et al., 2010). Floodplain soils can also be characterized by their rapid soil organic matter (SOM) turnover rate (e.g. 10-years on the Queets River) (Bechtold and Naiman, 2009). Nutrient and moisture availability are higher on mature floodplain soils than young floodplain soils. Young terraces with more red alder have higher N availability than mature terrace soils because red alder fixes N. However, mature terrace soils are more capable of holding alder fixed N compared to younger floodplain soils which leach N readily (Bechtold et al., 2003). Alluvial, fine textured soils are critical in increasing and retaining soil organic matter (Bechtold and Naiman, 2009). Additionally, mature terrace soils have higher C:N ratios, total C, and total N than younger landforms (Balian and Naiman, 2005). Roots in mature riparian forests do not typically infiltrate cobbles: the buried, coarse fluvial material can act as a barrier between the rooting zone and hyporheic water (Naiman et al., 2010). However, water holding capacity via capillary movement facilitates water availability throughout the summer months thanks to fine textured alluvial soils, fine roots, and high SOM (Balian and Naiman, 2005). Water availability increases as landforms progress from pioneer bars to mature terraces, as do clay and soil organic matter (Fonda, 1974). Therefore, the willow and red alder stands typically located on early floodplain landforms have less water availability than the old-growth Sitka spruce stands found on more developed landforms.

Anadromous Pacific salmon returning to rivers to spawn from the ocean bring in marine derived nitrogen (MDN). When they die their carcasses can fertilize up to 200 m from the active channel (Helfield and Naiman, 2001). MDN increases forest productivity, contributing to Sitka spruce’s rapid growth (Helfield and Naiman, 2001, 2002). In northwestern Alaska, growth of Sitka spruce was triple on sites with salmon nutrient subsides to those inaccessible by salmon. However, if N from alder is present, it is taken up more than MDN (Helfield and Naiman, 2001). A proposed positive feedback stemming from amplified productivity in salmon bearing streams is that the large trees produced eventually become large instream wood creating instream habitat heterogeneity and ameliorating spawning habitat (Helfield and Naiman, 2001).

1.3.4. Biodiversity

The floodplain forest mosaic encompasses a variety of habitats; this heterogeneity fosters high levels of regional, or gamma, diversity across PCTR landscapes. Riparian forests are generally accepted as being higher in species diversity, or alpha diversity, than upland forests (Naiman, R.J., Bilby, R.E., Bisson, 2000; Naiman et al., 1993; Naiman and Decamps, 1997). Higher species diversity on floodplains is attributed to flood disturbance since light and mineral soil (establishment sites) become available for new seedlings after a large flood event (Acker et al., 2003). Understory light availability affects species diversity as well (Giesbrecht et al., 2017). However, whether species richness is higher in riparian zones *versus* upland forests is specific to the sub-region of the PCTR and to some extent the catchment. The difference between upland and riparian species diversity tends not to be species richness but to a greater extent, different sets of species residing in riparian *versus* upland forest ecosystems (Sabo et al., 2005).

Few studies contrast measures of species richness and diversity in upland and riparian forests in the PCTR. Of those, two indicate higher plant diversity in riparian forests (Acker et al., 2003; Gregory et al., 1991). One found species evenness values for small mammals to be higher in riparian areas (McComb et al., 1993). Another study found higher amphibian abundance (Gomez, 1992) in riparian forests. These studies were all conducted in Oregon, the majority on lower order streams that were not floodplain stands. This limits our ability to extrapolate beyond the study sites to the entire PCTR, including floodplain forests. Further research is needed to assess species diversity and differences between floodplain and upland stands.

1.4. Discussion

1.4.1. Key Knowledge Gaps

Our understanding of old-growth PCTR floodplain forest structure, composition, and their drivers is limited. These limitations stem from several different factors, foremost of which is that the majority of research has been restricted to a few catchments on the Olympic Peninsula. This research provides an excellent knowledge base but is regionally restricted. We need to evaluate the extent to which their results transfer to other systems (Latterell et al., 2006). Expanding floodplain research to unharvested areas in Alaska and BC will help put previous research in context (Latterell et al., 2006) and clarify how the structure and dynamics of old-growth floodplain forests differ with changes in climate, latitude, or hydrological regime. Some research has been conducted recently in British Columbia (e.g., Giesbrecht et al., 2017; Little et al., 2013), but there are still large portions of the PCTR for which there are limited data. Exacerbating the issue of poor geographical representation in floodplain research, historical forest harvest occurred disproportionately at lower elevations, often targeting floodplains (Pearson, 2010). This and other human impacts (e.g., agriculture, urban and rural development, industry) have decreased the number of catchments that remain in a natural state (Burnett et al., 2007; Naiman and Bilby, 1998) reducing the options for representative, accessible, reference stands to study.

To date, studies have focused largely on biogeomorphical processes and developmental pathways where old-growth forest structure is a secondary focus or parameter used to decipher the mechanisms that lead to landform development. Consequently, floodplain terminology relates more to toposequence than forest development, particularly in older stands. Further, terminology and available data impede direct comparison to other old-growth floodplain and upland stands. Floodplain terminology differs from study to study as does the information reported (Figure 1.2). As a result, not all information that is pertinent to elucidating forest structure and composition is presented. For example, many structural attributes (e.g., mean DBH, SD of DBH, stems/ha) which are valuable in characterizing old forest are not published. This is not just an issue for old-growth floodplain forest research but also for upland forests. The limitations above have contributed to four key knowledge gaps pertaining to old-growth floodplain forests, leading to minimal understanding on: 1) the structural and compositional variability among these stands; 2) key metrics or attributes for describing their structure and composition; 3) what drives their variability; and 4) how structure and composition may change due to management practices or climate change.

1.4.2. Data Availability and Terminology

Going forward, consistent reporting of relevant old-growth stand structural attributes is necessary to facilitate accurate comparison across studies. This is simple since supplementary data are publishable online for attributes that are not directly required for the publishing study. Some of the most important attributes for characterizing old-growth forest structure are being measured in the field and calculated, or are easily calculated, but not reported (e.g., mean DBH, SD of DBH, number of stems > 100 cm) (e.g., Freund et al., 2015; Hanley and Hoel, 1996; LePage and Banner, 2014; Little et al., 2013). The PCTR is a massive area making it a significant undertaking to understand variation in old-growth forest structure over the whole region. We need standardized reporting of structural variables to aid in piecing together a comprehensive understanding of old-growth forests over this large region. This is a problem for the PCTR and globally, as studies are lacking a sufficient suite of attributes that can adequately provide a complete sense of old-growth structure and dynamics (Burrascano et al., 2013). At minimum, research in old-growth forests should report mean DBH, total density of trees and snags, density of dominant canopy tree species, density of large trees > 100 cm DBH, density of dominant large trees > 100 cm, standard deviation of DBH, and basal area (e.g., Van Pelt et al., 2006). Currently this is a *de facto* standard and is therefore not always followed. Having an agreed upon minimum standard for old-growth metrics that includes variables important for characterizing old-growth stand structure, productivity, disturbance, and successional drivers would be a helpful contribution to old-growth research. Ideally, reporting would include more comprehensive data such as dead wood (snags and CWD), overstory diversity, indices of the spatial arrangement of trees, and canopy gaps (Burrascano et al., 2013). This would help in cross study comparisons where similar floodplain forest types are categorized with different terminology, such as mature or old-growth terrace (e.g., Figure 1.2).

It is logical that landform toposequences and forest successional stages have analogous terminology as their development coincides. However, landform and forest development are not entirely congruent and thus analogous terminology can mislead a reader, particularly concerning later forest developmental stages. Inconsistent naming conventions for landforms across studies hampers direct comparison among studies (Figure 1.2). To facilitate better cross study comparisons, separate, consistent, and clear terminology describing landforms and forests should be used. Perhaps using high bench instead of old growth terrace for landform and adding further forest qualifiers to describe stand type can relate forest character. Biophysical templates (e.g., floodplains, terraces, benches, etc.) are characterized by their geomorphology (Balian and Naiman, 2005). It is important to recognize that each floodplain study that we reviewed used a slightly different naming convention for their biophysical templates, which made direct comparisons challenging. Mature and old-growth terrace terminology can be misleading, these terms are intended to distinguish landforms, however old-growth forests can span several landform classes. For instance, forests on mature terraces have well developed old-growth structural and compositional characteristics and are considered old-growth. Yet the landform name, mature terrace, does not reflect the forest’s developmental stage. Even some transitional terraces can support developing old-growth forests. Because of this, we prefer to use broader classifications, such as medium and high bench to identify landforms (Green and Klinka, 1994; MacKenzie and Moran, 2004). Further classification of forest type beyond landform can be done using stand development stages (Franklin et al., 2002) and systems such as the Biogeoclimatic Ecosystem Classification (BEC) system which uses site soil moisture and nutrient regimes, slope position, and species cover (Green and Klinka, 1994). This method allows for a more accurate reporting of forest type and therefore better comparison across study sites.

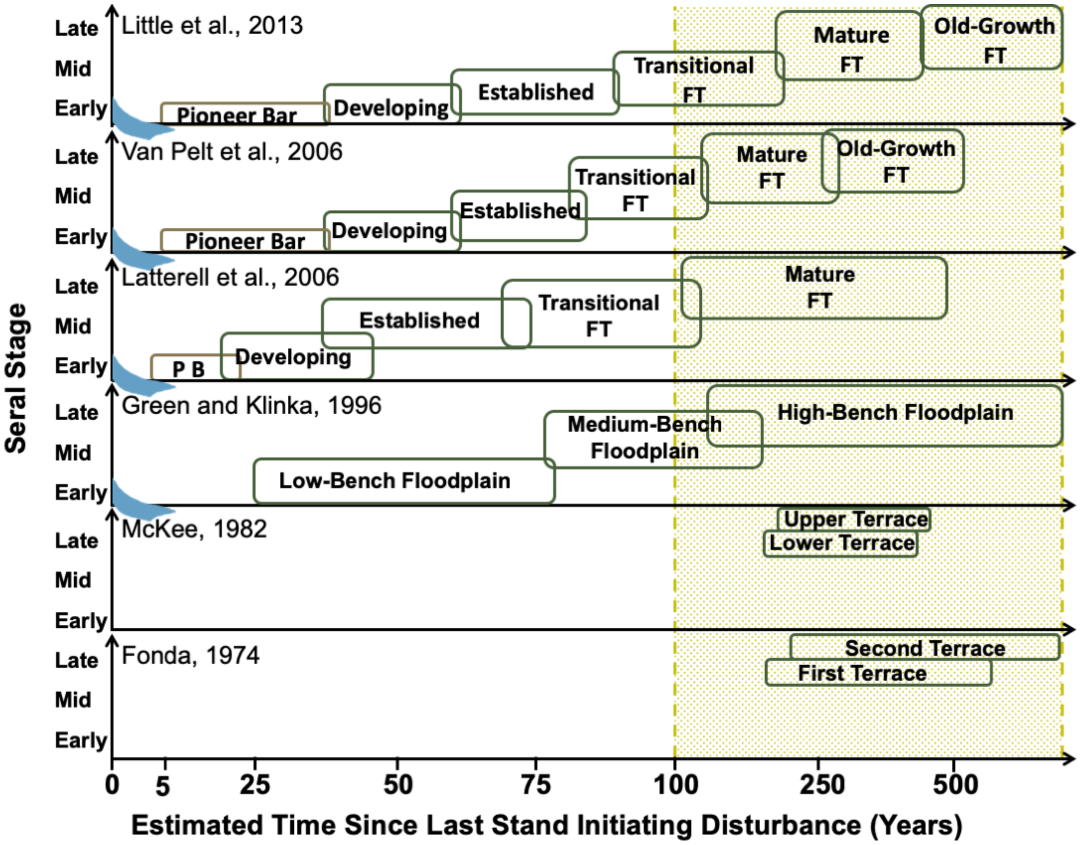


Figure 1.2 **Landform toposequences and their classification from previous studies in relation to each other. This also depicts the time frame that floodplain stands show old-growth characteristics (yellow shaded area between the yellow dashed lines). Some boxes may span greater timeframes (e.g., old-growth fluvial terrace), however the age range indicated in their particular study is drawn. Developing and Established are Developing Floodplain and Established Floodplain classifications. FT = Fluvial Terrace.**

1.4.3. Management Concerns

What are the consequences of not fully understanding the structure and composition of these old growth forests? Without having the necessary knowledge to draw on from a particular sub-region, managers and planners are forced to extrapolate from other studied sub-regions. This can cause policies and management practices to be implemented that are inappropriate for the sub-region in question. For instance, the wetter cedar-hemlock forests on the west coast of BC were thought to have a similar fire regime, low frequency large stand-replacing fires, as the adjacent drier coastal Douglas-fir forests (Lertzman et al., 2002). This resulted in even-aged management of large cutblocks intended to reflect the assumed disturbance regime, but did not reflect the actual disturbance regime (i.e., fine-scale gap-phase dynamics) (Lertzman et al., 2002; 1996). In addition, without adequate records of forest structure and composition and further monitoring, the opportunity for shifting baselines exists (Soga and Gaston, 2018). Managers are missing information on how these forests are responding to climate change and the impacts on ecological diversity, forest inventory, and conservation planning. In the same way, reference conditions for silviculture and restoration are insufficient. Current buffer zones do not fully protect the area in which a river can laterally move, and therefore forest harvest can result in changes to biogeomorphic processes due to a reduction in large wood (Latterell et al., 2006) and cause river simplification (e.g. less lateral movement, braided channels, less diverse habitat) (Gurnell et al., 2005; Latterell and Naiman, 2007).

Implementing appropriate management in floodplain forests is important because there is no substitution for large trees. An absence of coarse woody debris can cause channel simplification and decreased stream habitat (Collins et al., 2012). Large trees within the floodplain but up to several hundred meters from the active channel can be eventual sources of large wood (Latterell and Naiman, 2007). However, buffer widths can be insufficient to protect alluvial processes (Richardson et al., 2012). On the Queets River, half of the instream wood within a 63 year period was from ≥ 92 m from the channel, 95% within 265 m (Latterell and Naiman, 2007). Therefore, current minimum buffer widths may not be enough to ensure sufficient old-growth is present on the valley bottoms to maintain large wood needed for biogeomorphic processes. The new Great Bear Rainforest Land Use Order (B.C. Ministry of Forests Lands Natural Resource Operations and Rural Development, 2016) for the central and north coast of BC now protects 1.5 tree lengths from the active channel and all active fluvial units, which includes low and medium benches. A significant part of the PCTR has much smaller mandatory buffer widths, ~30 m in southeast Alaska (USDA Forest Service Alaska Region, 2016) and up to 50 m reserve zones with additional 20 m management areas that allows some harvest on the south coast of BC, though large rivers (>100 m) need no buffer (Forest Planning and Practices Regulation, 2016). Considering trees in the PCTR require approximately > 100 years to grow large enough to be effective instream wood, some rivers require much larger buffers to provide a continued supply of large wood than what is currently required.

1.5. Conclusions and Future Directions

Our ability to implement policy and manage ecosystems competently depends on our understanding of the system and our goals. We can further our collective knowledge and improve our ability to manage these ecosystems by addressing the proposed key knowledge gaps. Below we discuss these knowledge gaps jointly with a proposed research agenda, which itemizes steps for future research in old-growth floodplain forests (Table 1.3).

1.5.1. Structural and Compositional Variability among Floodplain Stands

A logical starting point for future work is to describe old-growth floodplain forest stand structure and composition across the PCTR's range (see Chapter 2). Stand structural characteristics are influenced by climate, disturbance, as well as ecological drivers (Figure 1.3). Elucidating forest structure and composition should be done in parallel with assessing the affect climatic gradients have on structure and composition since these are likely to change along gradients (Table 1.3, steps a-i &1-i) (see Chapter 2). From here we can expand our understanding on productivity, biomass accumulation, and carbon dynamics for which there is little information (Balian and Naiman, 2005). Additionally, we can explore how these characteristics change by catchment, climate and/or species composition. This will also help provide a more accurate timescale on the recruitment of large wood for restoring biogeomorphological processes in harvested catchments. Data collection during this process can also be extended to include assessing causes of tree mortality and used to derive background mortality rates (Table 1.3, steps b-ii & 3-iii). Repeat sampling of stand structure for these objectives will also provide insight into forest structural and compositional changes during stand development and those caused by climate change (Lutz, 2015). Recent research on tree productivity has shown that old trees continue to increase biomass proportionate to tree size (Stephenson et al., 2014). However traditional diameter based allometric growth equations fail to capture this growth (Stephenson et al., 2014). Here is an excellent opportunity to develop new growth equations for old-growth trees in floodplain stands while studying productivity and biomass.

Extending research beyond previously studied areas to investigate similarities and differences in stand structure, composition, and their drivers along the coast of BC and Alaska can be done using existing data from previously established permanent plots (e.g., Coast Forest Region Old Growth Dynamics Project and Research Natural Areas Network; see Chapter 2) (MacKinnon et al., 2010; USDA Forest Service Alaska Region, 2016). However, this is still a limited number of plots. Plot size also needs to be considered, smaller plot sizes (0.25 ha) are sufficient for describing structural attributes such as mean diameter, basal area, and density, but are not as good at capturing old-growth structural attributes (e.g., large diameter trees) or spatial structural complexity metrics (Zenner and Peck, 2009). Plots 0.5-1.0 ha better capture these metrics (Zenner and Peck, 2009). Expanding the permanent sample plot network to include more plots and larger plots is, however, logistically complicated and demands more financial resources, time, and personnel, particularly in the coastal region where floodplain forests can be difficult to access. However, the alternative is to risk losing our opportunity to properly understand these forests and how to manage them.

1.5.2. Key Metrics for Describing Structure and Composition

Old-growth floodplain forests are distinct from upland forests because of their species composition, disturbance regime, and productivity. However, old-growth metrics are largely based on upland Douglas-fir forests (e.g. Franklin and Spies, 1991a) and so is the majority of recent old-growth research (e.g., Freund et al., 2015; Reilly and Spies, 2015). Still, ecological attributes of old-growth forests are qualitatively comparable across forest types (e.g. large trees for the species, multi-layered canopies, canopy gaps) (Wells et al., 1998). Looking to old-growth literature based on Douglas-fir ecosystems is not unreasonable for Sitka spruce forests as parallels are easily drawn between the two forest types. For example, both leading species are shade-intolerant, long-lived, grow to great sizes, and initiate following a stand-replacing disturbance (e.g., flood or fire). Because of these similarities, it is valuable to compare these forest types to assess where our current knowledge of old-growth is applicable to Sitka spruce floodplain forests and where further research is needed. Further, this can help elucidate similarities and differences pertaining to management and restoration and how these change from near the active channel to several hundred metres away adjacent to upland stands. Detecting these patterns in structure and composition can inform floodplain management and rehabilitation efforts (Table 1.3, steps d-iv e-v).

1.5.3. Drivers

The most salient knowledge gaps pertaining to floodplain forests are centered on drivers of forest structure and composition. Discerning what differentiates stand structure and composition from site to site and sub-region to sub-region is fundamental in providing insight on the effects of forest management and climate change. To do this and to sufficiently describe structure and composition, we need to establish how these forests change along climatic gradients (e.g. MAP, MAT) which coincide with the PCTR's latitudinal gradient. Climate is known to affect composition (Waring and Franklin, 1979). Further, composition is recognized as changing with latitude (Whittaker, 1967). Yet even though the PCTR spans 23 degrees of latitude we currently treat these floodplain forests as comparable across the gradient without fully recognizing their differences.

At the stand level, the relative role that different disturbance agents play changes along the PCTR's climatic gradient. Acquiring data on hydrological regimes, windthrow, fire, insects, and pathogens will establish the relative roles of different disturbances on stand structure and composition. This will provide information on background mortality rates and density-dependent mortality (e.g., Lutz, 2014). Assessing how flood disturbance changes at a site over time can give insight into how flood regime differs from early old-growth to well-developed old-growth, as found in stands on the Carmanah and Kitlope Rivers (Giesbrecht et al., 2017). This will provide a baseline to assess future changes related to climate change as well as understand how these systems may change between sub-regions and disturbance regimes (Reilly and Spies, 2016).

Structure and composition in floodplain forests are driven by physical and ecological drivers. Determining the relative roles of disturbance and ecological characteristics such as understory light availability and tree mortality rates can help us create harvest and management actions that are more complimentary to natural processes and predict changes in structure and composition over time. This includes establishing natural disturbance regimes and their comparative role (Table 1.3, steps c-iii, 2-ii & 3-iii).

Determining how hydrological disturbance regimes relate to stand development including on-going structural and compositional changes, spatial and non-spatial, in old-growth forests can elucidate how significant a driver flood disturbance is at the stand level. Understanding these disturbance events and consequential ecological responses can identify links between forest development and dynamics and determine their relations to floodplain developmental pathways (e.g., Little et al., 2013; Van Pelt et al., 2006). Further, this can help recognize flood influence on overstory spatial heterogeneity, the resultant effect of understory light availability and its influence on composition (Giesbrecht et al., 2017), and the recruitment of large wood to maintain biogeomorphic processes (Naiman et al., 2010).

Table 1.3. Proposed research agenda pertaining to old-growth floodplain forests in the PCTR and proposed steps to address key knowledge gaps.

Research Topics	Research Actions
Forest Structure	
a) Stand structure and composition including habitat features (e.g. LW, snags, overstory diversity, understory species, etc.).	i. Collate and analyze existing permanent sample plot data (see Chapter 2).
b) Productivity, biomass, and carbon storage capacity.	ii. Resample permanent sample plot plots, determine species and site specific methods for assessing growth and production (see Balian and Naiman, 2005) and analyze.
c) Ecological drivers (e.g., overstory and understory competition, spatial relationships, heterogeneity and complexity) and interactions with physical drivers.	iii. Expand permanent sample plot plots to one hectare, assess overstory and understory interactions (see Giesbrecht et al., 2017), and determine horizontal and vertical heterogeneity (Zenner and Hibbs, 2000; Zenner and Peck, 2009).
d) Upland vs floodplain comparison, overstory and understory species.	iv. Conduct a meta-analysis assessing floodplain forests and how their structure and composition differ from upland forests, address any needed management adjustments.
e) Floodplain to upland transition – including plant species diversity and structural characteristics.	v. Run transects from old-growth riparian stream edge to upland old-growth, assess the transition of forest structure and composition, spatial variability, and implications for management (see Pabst and Spies, 1998; 1999).
Physical Drivers	
1) Climatic gradients and their influence on structure, composition, and drivers.	i. Use collated permanent sample plot and climatic data to assess the role climate plays on stand structure and composition. Use proxies to assess hydrological influences on stand structure and assess if further exploration is warranted.
2) Hydrological disturbance regimes	ii. If flood disturbance proves to have an effect on stand structure, determine flood disturbance regime using sediment core samples and tree cores (see Brown and Schoups, 2015; Lara et al., 2008).
3) Relative influence of disturbance agents and background mortality rates	iii. Use data from productivity analysis (b) and determine tree mortality rates and assess potential impacts of climate change (see Reilly and Spies, 2016).

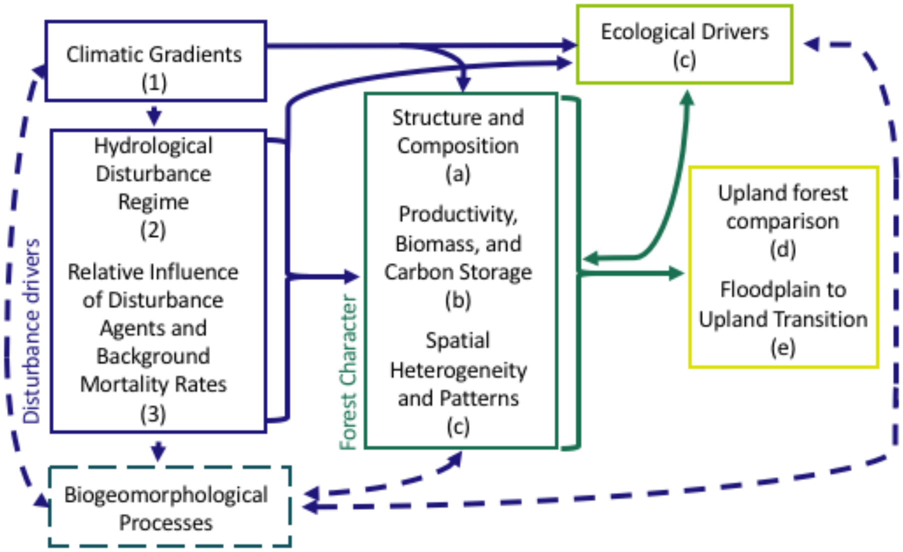


Figure 1.3 **Old-growth floodplain ecosystem knowledge gaps and interactions among knowledge gaps. The interconnected knowledge gaps related to old-growth floodplain forest components and influences associated with Table 1.3 are shown here. Understanding stand structure and composition (a) along the PCTR's latitudinal gradient will help provide insight into how climatic gradients and climate change can affect structure and composition. The structural and compositional data can be used as a baseline to examine productivity, biomass accumulation, and carbon storage (b). Spatial heterogeneity and complexity (a/c) can also be mapped and integrated into our understanding of forest function and the feedbacks that exist among structure, composition, and ecological drivers such as understory light availability caused by canopy gaps (c). The hydrological disturbance regime (2) also shapes these stands, we need to examine its relative role compared to other disturbances such as windthrow or fire (3). Understanding these ecosystem components can help us relate old-growth floodplain stands to upland forests (d)(e) and therefore better inform conservation planning and management decisions. The solid lines represent connections that can be explored through addressing these key knowledge gaps, the dashed lines signify connections that exist at a landscape or regional scale that require recognition but are beyond the scope of our research agenda.**

1.5.4. Beyond the Stand – Importance of Scale

Variability may be a key attribute of floodplain forests. The variability in stand structural attributes seen in Figure 1.1 among floodplain stands compared to upland stands demonstrates how different old-growth floodplain attributes can be, even within the same catchment (e.g., Queets River in Figure 1.1). Further, there is substantial variability among catchments and disturbance drivers, leading to variability in landforms and researchers trying to classify these landforms with a variety of terms (Figure 1.2). The interplay among climate, disturbance regimes, geographical location (e.g., proximity to stream and longitudinal position along stream), composition, and productivity all contribute to landform development and stand structure. Thus, these complex biophysical interactions create a heterogeneous forest mosaic at the landscape scale and variability in structural attributes when comparing among old-growth forest stands.

Recognizing the linkages among stand, landscape, and regional scales is important. There is no one explanation or driver of forest structure and composition. Rather different drivers act on differing spatial and temporal scales creating heterogeneity on the landscape and in turn, differing homogeneous study units (Lertzman and Fall, 1998). Our focus in this paper is on the patch scale; nevertheless, a holistic understanding of the riparian corridor is necessary to successfully manage ecological diversity. Often research is focused on a single forest type, or homogeneous unit such as we are (e.g., old-growth floodplain forests), however it is important to consider forest structure, composition, and function across multiple temporal (Buma et al., 2018) and spatial scales and how they are impacted by the cumulative effects of different natural drivers and management actions (Lertzman and Fall, 1998). Monitoring the amount of old forest present in valley bottoms and how this proportion shifts with changes to the hydrological regime is an import component in building our understanding of old-growth forests across multiple spatial and temporal scales. Establishing average proportions of old-growth patches relative to younger forest patches on the landscape (e.g., the average proportion of old-growth forest compared to young forest historically over time) and their turnover rates are also important in understanding changes in the proportion of old-growth forest on a floodplain caused by climate change (Little et al., 2013; Whited et al., 2007). Extending the study of relative amounts of old-growth patches to harvested watersheds (e.g., research led by MFLNRO on the Talomey, Sheemahat, Machmell, and Bella Coola rivers; MFLNRO, 2012, unpublished data) to understand turnover rates and how they differ to natural catchments will help with restoration efforts and forest planning. Moreover, this can help monitor the supply of CWD from old-growth forests on floodplains in the PCTR and CWD’s critical role in maintaining biogeomorphic processes. Patch diversity and biogeomorphic processes benefit both terrestrial and aquatic species and can subsequently benefit our fisheries, forestry, and tourism industries throughout the PCTR.

Chapter 2. Structure and composition of old-growth floodplain forests in the North Pacific Coastal Temperate Rainforest

2.1. Introduction

Old-growth forests dominated much of the pre-industrial landscape and are an important component of the Pacific Coastal Temperate Rainforest (PCTR). They play a distinct role ecologically, hydrologically, in terms of habitat (Franklin and Spies, 1991b; Spies et al., 1988), and are iconic in their social and cultural contexts (Blicharska and Mikusiński, 2014). In many ways, old growth floodplain forests epitomize these phenomena (Naiman et al., 2000, 2010). They illustrate extremes of size, diversity, dynamism (Van Pelt et al., 2006), and exhibit complex interactions within their hydrological and geomorphic context (Latterell et al., 2006; Little et al., 2013; Van Pelt et al., 2006). Yet despite a substantial amount of research on old-growth floodplain forests of the PCTR, we know little about regional variation in their structural characteristics and composition, or the environmental factors that drive those features.

Old-growth forest structure in the PCTR is renowned for large diameter trees, as are its floodplain forests. Large diameter trees are a key component of old-growth forest structure in the PCTR (Franklin and Spies, 1991b; Franklin et al., 2002; Lutz et al., 2018, 2013; Spies and Franklin, 1991; Wells et al., 1998), not only do they influence vertical and horizontal complexity but become important habitat components such as snags and coarse woody debris (CWD). Old-growth floodplain forests also consist of large, high volume, open canopies (Giesbrecht et al., 2017; Van Pelt et al., 2006), in part due to the large Sitka spruce (*Picea sitchensis*) that dominate the first 4-8 centuries of stand development. Large pieces of CWD are a particularly important structural attribute of floodplain forests. They interact with geomorphic processes by altering river movements and catching sediments, which create and destroy landforms over time generating a dynamic mosaic of multi-aged forest patches on the floodplain (Latterell et al., 2006).

There are considerable geographic gaps in our understanding of floodplain forest structure and composition in the PCTR. Significant efforts have gone into studying the interactions between large wood input from old-growth forests and geomorphologic processes on floodplains (e.g., Beechie et al., 2006; Latterell and Naiman, 2007;

Latterell et al., 2006; Little et al., 2013; Van Pelt et al., 2006). Processes such as bank erosion, stabilization, sediment mobilization and deposition, and development of pool-riffle sequences all depend strongly on structure provided by live and dead trees. As our insight into the ecology and function of floodplain systems in the PCTR has grown in recent decades, researchers have examined species composition, structure and succession (e.g. Fonda, 1974; Hanley and Hoel, 1996; McKee et al., 1982; Pabst and Spies, 1999), successional dynamics and pathways (e.g. Latterell et al., 2006; Little et al., 2013; Naiman et al., 2010; Van Pelt et al., 2006) and forest productivity relating to alluvial formations (e.g. Balian and Naiman, 2005). Although the breadth of research on floodplains in the PCTR is quite large, except for the for two studies in Alaska and British Columbia (Hanely and Hoel 1996 and Little et al. 2013, respectively), the geographic focus has been predominantly restricted to Washington State's Queets, Hoh and South Fork Hoh River valleys. Further, few studies have examined compositional drivers in floodplain forests (e.g. Giesbrecht et al., 2017; Pabst and Spies, 1998), structural drivers or how structure changes with latitude in the PCTR ecoregion.

The PCTR covers approximately 23º of latitude, which encompass roughly an 8ºC gradient in Mean Annual Temperature (MAT) (Alaback, 1996) and a 6000 mm gradient in Mean Annual Precipitation (MAP) (Naiman and Anderson, 1997). Compositional change along latitudinal gradients is a well-established pattern in ecology (Pielou, 1967; Whittaker, 1967; Willig et al., 2003). We might also expect the structure of alluvial forests to differ with latitude. Environmental gradients, such as precipitation, temperature, and photoperiod, all coincide with the PCTR's latitudinal gradient (Alaback, 1996). Environmental variables influence species composition, stand productivity, stand structure, and disturbance regime (Daniels et al., 2011; Major, 1951; Pojar et al., 1987). Moreover, floodplains are subject to hydrological gradients such as increases in precipitation affecting mean annual runoff and the seasonal proportion of annual discharge (Naiman et al., 2000). Precipitation is thought to be the main driver shaping regional variation in riparian forest ecosystems (Benda et al., 1998). As well, the amount of summer precipitation is used to delineate sub-regions of the PCTR (Alaback, 1996; DellaSala et al., 2011).

In upland forests of the PCTR, changes in forest structure are associated with latitude. Stem density proved to increase with latitude in coastal western hemlock forests (Wells, 1996). In contrast to Wells (1996), a meta-analysis of global temperate old-growth forests showed that stem density decreased as latitude increased, as did basal area. However stem density and basal area were found to increase with precipitation (Burrascano et al., 2013). Further, productivity, which influences structural development (Larson et al., 2008), and latitude were negatively correlated in Sitka spruce forests (Farr and Harris, 1979). Though latitude *per se* is not the driving force for structure and composition in floodplain forests, associated climatic gradients are thought to be important drivers, particularly precipitation. We expect structure in upland and alluvial forests to differ because of differences in disturbance regimes, soil formation (Bechtold and Naiman, 2009), and species composition. However, we expect floodplain forests to follow similar patterns as upland stands in relation to latitude, such as declines in mean diameter and basal area and increases in stem density at higher latitudes.

Language used to describe concurrent forest succession (e.g., young, mature, and old-growth forest) and developing landform toposequences (e.g., transitional, mature, and old-growth terraces) consists of interchangeable though not synonymous terms. This impedes direct comparison of floodplain forests across the PCTR (Chapter 1, 1.4.2). Research on floodplain forest structure and composition in the PCTR stems from two fields of study, forest ecology and geomorphology. The terminology delineating landforms and landform succession is inextricably linked to forest succession (Figure 2.1, from Chapter 1). Landforms evolve through geomorphological processes from pioneer bars, which can receive up to 40 days of flooding a year (Latterell et al., 2006), to fluvial terraces whose flood frequency can range from several times annually to less than or equal to once every 5 years (Green and Klinka, 1994). Forest succession progresses as landforms develop. For example, pioneer species such as red alder (*Alnus rubra* Bong.) establish on pioneer bars and transition to Sitka spruce dominated stands on transitional terraces. These transition to old-growth stands on mature terraces with western hemlock (*Tsuga heterophylla*) becoming a significant component. Transitional terraces support forests that are transitioning from disturbance regimes dominated by flood pulses to gap-phase dynamics dominated disturbance regimes, meaning transitional terraces can support forests with well-developed old-growth characteristics. Thus transitional, mature, and old-growth terraces can all support old-growth forests creating ambiguity in floodplain terminology and limiting our ability to compare accurately across stages of forest development (Chapter 1, 1.4.2).

Consistent and clear terminology is needed to describe equivalent landforms and forest successional stages. For the purposes of this study, we use the Biogeoclimatic Ecological Classification (BEC) system's method of categorizing floodplain forests (Banner et al., 2014; Green and Klinka, 1994; Pojar et al., 1987). The BEC classification's terminology avoids using analogous terms for landforms and forests. The classification is largely based on flood return interval and species composition. Our study focuses on old-growth forests on high bench and medium-high bench floodplains, transitioning along the continuum from medium to high bench floodplains. Medium bench sites have a frequent flood return interval (< 5 years), where high bench sites experience an infrequent flood return interval (> 5 years) (Green and Klinka, 1994; MacKenzie and Moran, 2004).

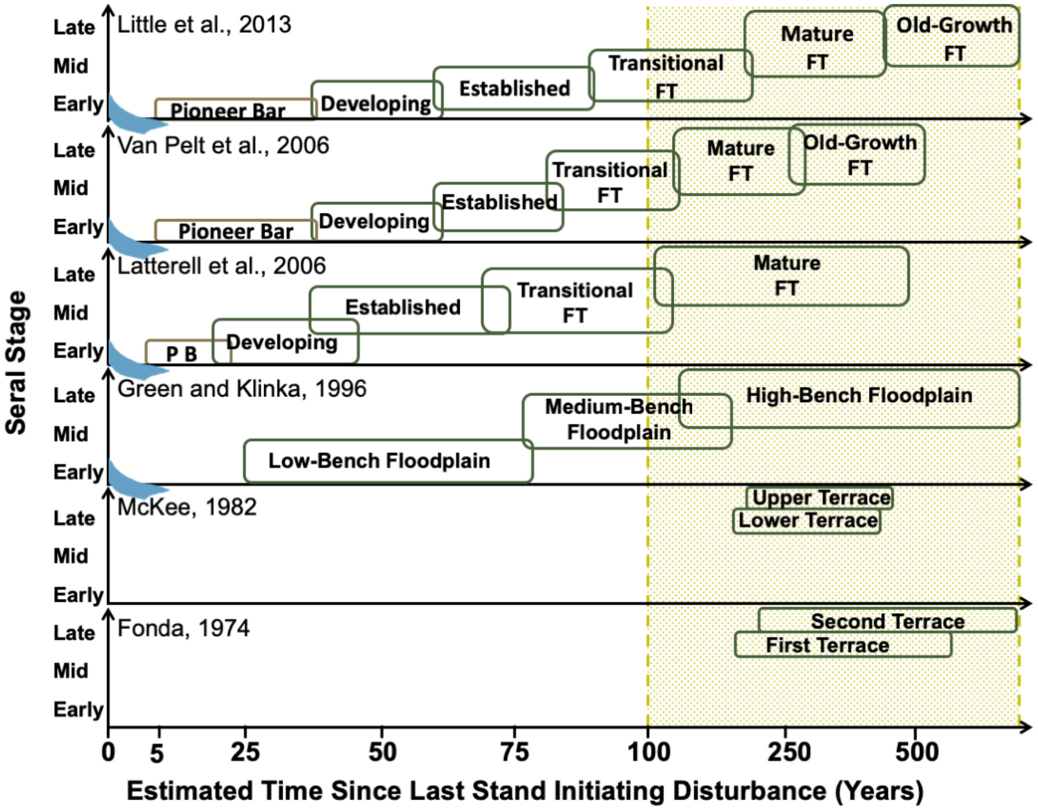


Figure 2.1 **Landform toposequences and their classification from previous studies in relation to each other. The time frame that floodplain stands show old-growth characteristics is in the shaded area between the yellow dashed lines. Some boxes may span greater timeframes (e.g., old-growth fluvial terrace), however the age range indicated in their particular study is drawn. Data from the upper and lower terrace plots (i.e., South Fork Hoh 1 and 2; McKee, 1982) are included in this study. Developing and Established are Developing Floodplain and Established Floodplain classifications. FT = Fluvial Terrace. PB = Pioneer Bar. This figure is from chapter 1.**

To address knowledge gaps relevant to structure and composition of floodplain forests (see Chapter 1) for the PCTR ecoregion we collated historical plot data spanning 11º degrees of latitude (between southeast Alaska and Washington State's Olympic Peninsula). Using these data, we: 1) describe structure and composition of floodplain old-growth forests; 2) establish how climatic gradients associated with latitude affect structure and composition; 3) explore flood disturbance as driver of variation in forest structure and composition; and 4) compare alluvial and upland old-growth forests to asses if forest structure is similar between forest types and if old-growth metrics used to describe upland forest types are applicable to the PCTR's floodplain forests.

2.2. Methods

2.2.1. Study sites

We examined sixteen old-growth floodplain forest stands in the perhumid (59°N - 50°N) and seasonal (49°N - 43°N) sub-regions of the PCTR (Figure 2.2). The sites are located across ~11° of latitude from Washington State, USA through British Columbia (BC), Canada, to southeast Alaska, USA. Those in Washington are located in Olympic National Park. Plots in BC are part of a network of old-growth permanent sample plots (MacKinnon et al., 2010) and those in Alaska were identified as Research Natural Areas (RNAs) monitoring sites.

Our old-growth floodplain forests are on high bench floodplains (> 5-year flood return), though some are thought to be transitioning along the continuum from medium (< 5-year flood return) to high bench floodplains, and one is on a medium bench site (Tahsish-Kwois Active; Table 2.1). Soils are layered alluvium, consisting of sand, clay, and silt with thin organic horizons (<5cm). Sites are dominated by Sitka spruce and western hemlock. Minor overstory species include red alder (*Alnus rubra*), western redcedar (*Thuja plicata*), and several others that only appear at single sites (*Pseudotsuga menziesii, Acer macrophyllum, Acer glabrum, Malus fusca, Pinus contorta, Tsuga mertensiana*, and *Populus trichocarpa*).

Gradients of mean annual temperature (MAT) and precipitation (MAP) coincide with the PCTR's latitudinal gradient. MAT averages 7°C and 10°C in the perhumid zone and seasonal zone, respectively (Alaback, 1996). MAP ranges from 1000 – 7000 mm across the PCTR (Naiman and Anderson, 1997), though the perhumid region receives more precipitation during the summer months (>10%) compared to the seasonal region (<10%) (Alaback, 1996). At our sites, MAT ranges from 3.9 - 9°C and MAP from 1685 to 3867 mm (Table 2.2). Our plots are located within watersheds with different streamflow regimes: Pluvial, Pluvial Dominant Hybrid (PDH), Nivo-Pluvial Glacial (NPG), and icefield. These streamflow regimes refer to the timing of low and high flows tied to seasonal runoff events and a catchment's potential for water storage in different forms. A pluvial, or rain dominated, streamflow regime is closely tied to precipitation (Pike et al., 2010). PHD streamflow regimes can receive snow at higher elevations, changing timing of seasonal runoff to later in the summer since precipitation is stored as snow and snow melt and rain contribute to runoff (Pike et al., 2010). Nivo-Pluvial Glacial (snow-rain-glacier) and Icefield streamflow regimes have later seasonal runoff than PDHs which occur around September due to the delayed snowmelt. The watershed containing the northern most plot (LaBau) is classified as an Icefield streamflow regime type. The majority of sites are Pluvial Dominant Hybrid and Pluvial types, with exception to the Kitlope River site which is Nivo-Pluvial-Glacial.

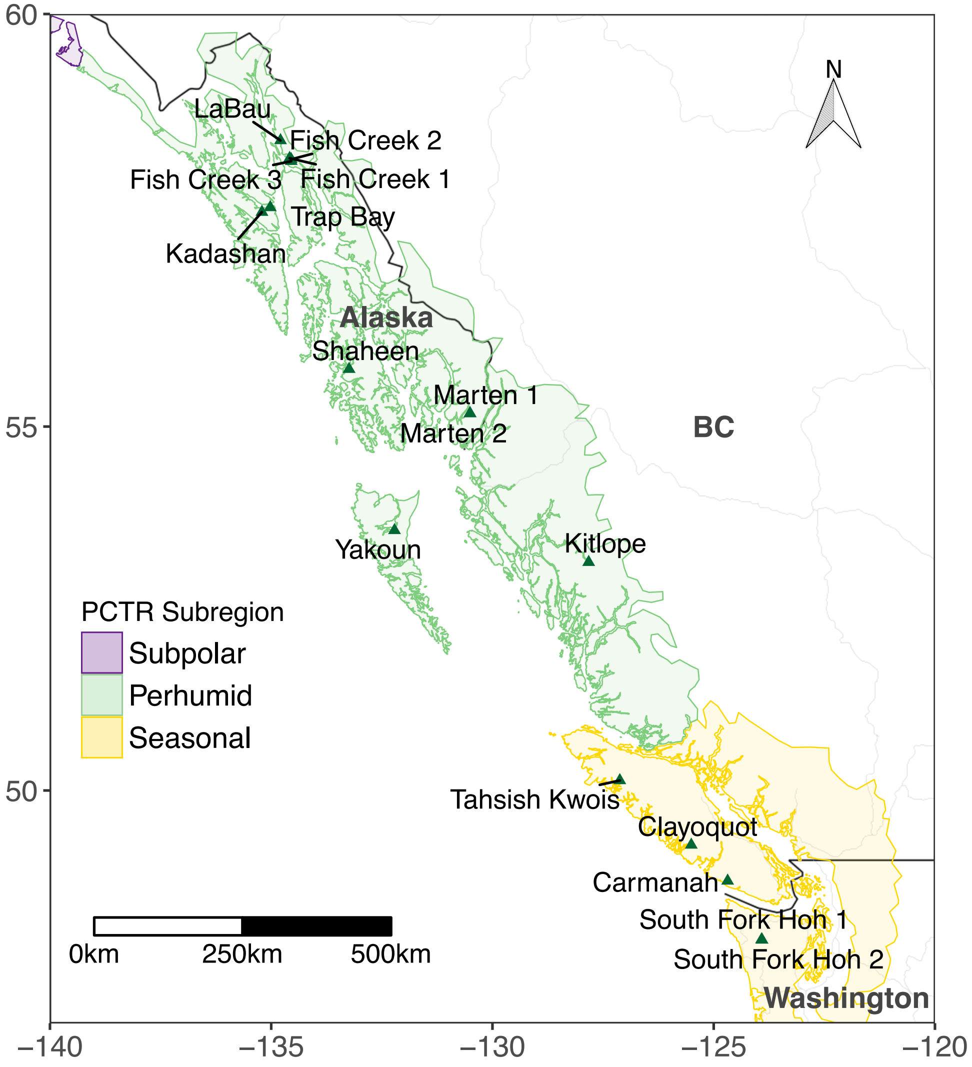


Figure 2.2 **Map of study area and sites and PCTR sub-regions (subregion boundaries are adapted from Wolf et al. (1995) by Holmes (Hakai I., 2016).**

2.2.2. Data collection

We collated data for live trees, snags and coarse woody debris (CWD) from existing unanalyzed data. Plots were established between 1964 and 1993, except for the Yakoun River site in 2017 (see Table 2.1). Sampling at each location followed similar methods though snags and CWD were not sampled at all plots (n=16 for live trees, n=13 for snags, and n=7 for CWD). Plot sizes vary from 0.25 hectares (ha) to 2.0 ha (see Table 2.1). Plots 0.5 ha in size were originally meant to be separate 0.25 ha plots, but they were functionally similar and spatially correlated so we combined them. Tahsish-Kwois and Tahsish-Kwois Active are adjacent to each other but are functionally different stands, one is a high-bench site and the latter is a medium bench site. Diameters of all live trees and snags >7.5 cm DBH were measured (DBH = 1.3 m for all plots except South Fork Hoh which used 1.37 m) and species recorded. The field crews measured and recorded diameters of all CWD ≥ 10 cm DBH. The crews allocated snags to one of eight decay classes and CWD to one of five decay classes (B.C. Ministry of Forests and Range and B.C. Ministry of Environment, 2010), recording species identification if possible, otherwise species were recorded as ‘unknown’. CWD debris lengths were also measured. For the Clayoquot site, CWD was measured using a 0.1 ha plot and a 0.15 ha plot within each 0.25 ha. These plots were combined because they were adjacent and similar forest type. Using historical data is a source of error in our analysis as we do not have exact co-ordinates for some sites or site information that one would typically collect establishing a plot today for a study of this nature (e.g. soils, stand age, site index, tree heights, and canopy volumes).

We derived environmental variables for each plot using ClimateNA version 5.50 including climate estimates for the climatic normal from 1961-1990 (Wang et al., 2016) (Table 2.2). We used the hydrology tools from ArcMAP (version 10.5) to calculate the flood disturbance proxies: catchment area to pour point, average gradient of the catchment area, and hypsometric integral. We acquired void-filled digital elevation models (DEMs) from Hydrosheds.org (2018). To find the point of highest flow accumulation adjacent to the plots to determine catchment area to pour point we used ArcMap’s Snap to Pour Point tool and the DEMs. We derived the average gradient from the calculated catchment area. Hypsometric Integral (HI; Strahler 1952), otherwise known as the elevation-relief ratio (Wood and Snell 1960), indicates the stage of geomorphic maturity, or erosion rate, and helps to characterize the catchment (Strahler

1954; Fenta 2017). We calculated HI by subtracting the minimum elevation from mean elevation and dividing by max elevation minus the mean (Pike and Wilson 1971; Brocklehurst and Whipple 2004). Catchment area, erosion rate, and streamflow regime are all thought to contribute to the hydrological disturbance regime and forest composition at the landscape scale (Little, 2011). Thus, we chose our flood proxies to assess if these also affect forest structure and composition at the stand scale.

Table 2.1. **Plot information. Geographic coordinates are in decimal degrees. "Established by" column indicates the lead researcher(s) that established the plot; however many more field staff were involved.**

Site	Year Sampled	Established By	Latitude	Longitude	Plot Size (ha)	Landform Type
LaBau	1964	LaBau, J.	N 58.540	E -134.791	1.42	H
Fish Creek 1	1987	Alaback	N 58.329	E -134.583	0.25	H
Fish Creek 2	1988	Alaback	N 58.317	E -134.549	0.25	H
Fish Creek 3	1988	Alaback	N 58.294	E -134.549	0.25	H
Trap Bay	1983	Alaback	N 57.741	E -135.023	0.25	H
Kadashan	1978	Alaback	N 57.685	E -135.211	0.25	H
Shaheen	1978	Alaback.	N 55.737	E -133.239	0.5	H
Marten 1	1991	Alaback	N 55.169	E -130.504	0.25	H
Marten 2	1991	Alaback	N 55.169	E -130.508	0.25	H
Yakoun	2017	Girard	N 53.632	E -132.215	0.25	H
Kitlope	1993	Nuszdorfer and Alaback	N 53.203	E -127.827	0.25	M-H
Tahsish Kwois	1992	Nuszdorfer and Alaback	N 50.146	E -127.121	0.25	H
Tahsish Kwois Active	1992	Nuszdorfer and Alaback	N 50.146	E -127.121	0.25	M
Clayoquot	1992	Pearson	N 49.203	E -125.508	0.5	H
Carmanah	1993	Nuszdorfer and Alaback	N 48.669	E -124.686	0.25	H
South Fork Hoh 1	1989	Franklin et al.[1]	N 47.785	E -123.918	2.0	H
South Fork Hoh 2	1989	Franklin et al.[1]	N 47.780	E -123.906	2.0	M-H

Note: landform type: H = high bench; M = medium bench; M-H = transitioning from M to H.

1 – The South Fork Hoh plots were established by a multitude of researchers and agencies including the National Park Service, USDA Forest Service, Oregon State University, Weyerhaeuser Company, University of Washington, Washington Department of Natural Resources, University of Alberta, University of Edinburgh, U.S. Geological Survey, and U.S. Fish and Wildlife Service (Franklin, 1979).

Table 2.2. Climatic variables for floodplain plots north to south. Climate data (MAT, MAP, PAS, and DD>5ºC) are from ClimateNA version 5.50 (Wang et al., 2016) and stream flow regime was provided by the BC government (Bill Floyd, BC FLNRO).

Site	Streamflow regime	MAT (°C)	MAP (mm)	PAS (cm)	DD>5°C
LaBau	Ice field	5	1692	389	1130
Fish Creek 1	PDH	4.4	1916	485	1017
Fish Creek 2	PDH	4.2	1908	531	982
Fish Creek 3	PDH	3.9	2029	610	924
Trap Bay	PDH	5	1896	425	1094
Kadashan	PDH	5.2	2028	439	1115
Shaheen	Pluvial	6.3	2553	323	1202
Marten 1	PDH	6.1	3567	648	1320
Marten 2	PDH	6.1	3522	636	1318
Yakoun	Pluvial	7.5	1685	123	1410
Kitlope	NPG	7	2140	443	1591
Tahsish Kwois	Pluvial	8.9	3824	149	1706
Clayoquot	Pluvial	9	3867	187	1807
Carmanah	Pluvial	8.4	3379	169	1599
South Fork Hoh 1	PDH	9	3687	185	1801
South Fork Hoh 2	PDH	8.9	3737	196	1779

Note: MAT = Mean Annual Temperature; MAP = Mean Annual Precipitation, PAS = Precipitation as Snow; DD>5 = Degree Days > 5°C; PDH = Pluvial Dominant Hybrid; and NPG = Nivo-Pluvial-Glacial.

Table 2.3 **Catchment data used in NMDS analysis; elevation data were used to calculate the hypsometric integral and not used in the analysis directly.**

Site	Mean Slope	Elevation			Hypsometric Integral	Catchment Area (km²)
		Min	Max	Mean		
LaBau	19.8	14	1907	902.64	0.469	112.10
Fish Creek 1	18.89	41	1039	407.68	0.367	9.94
Fish Creek 2	20.7	165	1038	546.20	0.437	21.05
Fish Creek 3	22.5	248	1024	658.09	0.528	3.06
Trap Bay	21.3	10	1017	370.65	0.358	11.70
Kadashan	18.3	30	783	328.48	0.396	46.39
Shaheen	13.9	23	849	254.84	0.281	40.48
Marten 1	27.6	4	1494	645.42	0.430	354.10
Marten 2	27.6	4	1494	644.91	0.430	354.62
Yakoun	9.3	9	1064	211.34	0.192	476.57
Kitlope	27.1	-2	2305	989.75	0.430	2,600.98
Tahsish Kwois	22.3	3	1439	529.55	0.367	314.34
Clayoquot	28.1	25	1439	652.69	0.444	58.21
Carmanah	22.0	151	1047	506.11	0.396	48.26
South Fork Hoh 1	26.7	226	2364	949.59	0.338	100.45
South Fork Hoh 2	27.0	234	2369	977.62	0.348	92.11

Note: catchment area = catchment area to pour point.

Literature Search

We collated structural attribute data from studies that focused on floodplain and upland old-growth forests in the PCTR. The following methods were used for the analysis in Chapter 1 and for comparison of literature values to data analyzed in this chapter. We used separate search criteria for floodplain and upland forests. In 2016 and 2017 we used the Web of Science database to find applicable peer-reviewed articles. For floodplain forests we searched: "old-growth" AND "floodplain" AND ("Pacific Northwest" OR "British Columbia" OR "Oregon" OR "Washington" OR “Alaska”). For upland forests we used: "old-growth" AND “structur*” AND ("Pacific Northwest" OR "British Columbia" OR "Oregon" OR "Washington" OR “Alaska”). To ensure we were not limited by our search criteria, we expanded our search to include articles cited from obtained literature and recommended by colleagues.

The research topics of studies with floodplain forest data were broad in comparison to upland sites, which tended to focus on forest structure, succession, and differences between old-growth and mature forests. In contrast, floodplain forest structural data were typically part of larger analyses related to river movements and landform changes. Therefore, floodplain research usually included geomorphic components as well as forest structure and succession. Inclusion criteria included: gap-dynamics as a primary disturbance, forests > 250 years old or specified to have comparable old-growth structure, low to moderate elevation and Douglas-fir, Sitka spruce, western redcedar, or western hemlock as a leading species (see Chapter 1).

To be included in our analysis, studies required at least one relevant and comparable variable for live tree structure, meaning a variable needed to be useful in characterizing old-growth and it had to be present in more than one study. The compiled dataset represents a thorough search, though the data available for such a meta-analysis are limited. Though a significant amount of effort has gone into studying old-growth forests in the PCTR over the last several decades, the body of literature for our analysis is still comparatively small. Not all studies reported data relevant to this study, nor were they consistent.

Stand structural variables included live stem and dead standing and downed wood. Live tree variables collected were: mean DBH, standard deviation (SD) of DBH, total stem density (minimum DBH varied from ≥ 1 cm to ≥ 12.5 cm; see Table 2.10 and Table 2.11 notes for more information), large tree (>100 cm DBH) density, basal area, basal area of leading species, leading species density, density of leading species >100 cm DBH and medium tree (>50 cm DBH) density. Snag structural variables are: density of leading species > 50 cm, snags density, snag DBH, density of snags >100 cm, density of snags >50 cm and snag volume. CWD (CWD; > 10 cm diameter) variables include: CWD mean diameter, CWD density, density of CWD > 100 cm diameter, CWD > 50 cm diameter, CWD volume, and leading species CWD volume. We also included site location and minimum age. In total, eight old-growth floodplain studies with 14 sites and six old-growth upland studies with 15 sites were included in our analysis.

We did not exclude studies for differences in sampling methods. Allowable differences included plot establishment procedures and minimum size requirements for trees, snags, and CWD. Plot establishment procedures varied by size and shape, though some studies used transects. Minimum DBH was typically greater than or equal to five centimetres, however some studies used ten, four, or one centimetre as a minimum (see Table 2.10, Table 2.11, Table 2.12, and Table 2.13 for information on particular studies). We were not able to use differences in minimums as exclusion factors as there would not be enough data to compile an adequate dataset. Although sampling methods and minimums differed, we made an effort to ensure that studies were comparable across sites including considering other site descriptors provided such as understory vegetation, density of tall shrubs, landform and disturbance regimes.

2.2.3. Analysis

We compiled summary statistics of stand-level attributes for live trees, snags, and CWD. Stand-level attributes for live trees, snags, and CWD included mean DBH, standard deviation of DBH (SD of DBH), basal area, and density. For live stems, we calculated density of large trees (≥ 100 cm DBH), density of *Picea*, density of *Picea* ≥ 100 cm, as well as density of all medium stems and *Picea* (≥ 50 cm and < 100 cm). Likewise, density was summed for large and medium snags as well as for each decay class. Other attributes summarized for CWD were volume, volume by decay class, density of large and medium CWD, and density by decay class. Species abundance and species richness were calculated for each plot. Species diversity was determined by the Shannon Index (H’) using the vegan package (Oksanen et al. 2017) in R (version 3.4.2). The mean and standard deviation were calculated using all plots for stems/ha and large trees as well.

After compiling the summary statistics for stand level attributes of dead wood components, we saw that there were noticeably more snags in more northern stands. We used a one-tailed t-test to assess if northern and southern plots differed significantly in snag density by decay class using the stats package in R (R Core Team, 2017). Northern and southern plots were grouped using the post-hoc cluster analysis described below. We used a two-tailed t-test to determine if the same northern and southern plot groups differed in overall snag density (R Core Team, 2017).

The non-parametric Spearman's rho (ρ) test for correlation (R version 3.4.2) was used to assess relationships between environmental variables, climate and flood disturbance proxies, and forest structure and composition, due to the non-normal distribution of the data. Environmental variables included MAT, MAP, PAS, mean slope, catchment area, and hypsometric integral. Variables were first standardized by their maximum.

We used Non-Metric Dimensional Scaling (NMDS) to examine stand structure and composition of floodplain forests in the PCTR, how these vary along climatic gradients, and possible drivers influencing structure and composition. Summary statistics of stand-level live tree and snag attributes for each plot (see Table 2.4 and 2.5) were standardized by dividing by the maximum for each variable (Legendre and Legendre, 1998) prior to calculating the dissimilarity matrix. We applied the Gower index, using the cluster package in R (version 3.4.2), as it can calculate the dissimilarity between quantitative values and factors (Borcard et al., 2011; Legendre and Legendre, 1998; Maechler et al., 2017). We ran separate NMDS ordinations for live and dead structure (see Figure 2.10; Figure 2.11; and Figure 2.12) as snag data was not collected at all sites creating missing values which prevented completing a single analysis with live and dead stand structural variables. As with snags, CWD was not sampled at all plots thus there was not a sufficient sample size for an NMDS ordination. Environmental gradient variables (Table 2.3) were linearly fit to the ordinations to help discern drivers of stand structure. We tested the significance of each fitted vector using a permutation test and ran 999 permutations. We plotted the fitted vectors with a p-value < 0.05 with the NMDS ordinations using the vegan package (Oksanen et al. 2017) in R (version 3.4.2). Preliminary analysis showed growing degree days to be highly correlated with MAT, thus we excluded it from the analysis to simplify the results and ordination plot.

We performed a post-hoc cluster analysis using live-tree stand summary data after relationships among sites displayed differently than anticipated in the NMDS ordinations. Using Ward's clustering method (Maechler et al., 2017; Murtagh and Legendre, 2014) with a Gower dissimilarity matrix, we assessed if there were other groupings suggested by the data that might show a need for further study on the characterization of sub-regions across the PCTR.

Data from our literature search on old-growth structural attributes were collated into summary tables (see Table 2.10; Table 2.11; Table 2.12; and Table 2.13). We plotted floodplain and upland data for mean DBH, stems/ha, basal area, and stems/ha of the leading shade intolerant species (i.e., Sitka spruce or Douglas-fir) with the median, 5^{th} and 95^{th} percentiles of the upland data for comparison (Figure 2.14).

2.3. Results

2.3.1. Stand Structure and Composition

Sitka spruce and western hemlock are the most prevalent tree species throughout our study sites representing 30.7% and 60.4% of overall individuals. Though western hemlock's density can be higher than Sitka spruce (16-500 compared to 4-228 stems/ha, respectively), higher densities of hemlock tend to reflect an abundance of smaller trees whereas spruce is the dominant canopy species in these stands. Sitka spruce are typically the largest trees (39.9-207.8 cm mean DBH) where western hemlock is smaller (13.8-68.3 cm mean DBH; see Table 2.4). Deciduous species tend to be a relatively minor component of these stands. Red alder (*Alnus rubra*) is the most common throughout the plots and though other species do occur there are typically few stems unless they replace alder as the main deciduous species.

There were substantial differences in stand structure across the region with mean diameter ranging from 29.1 to 85.5 cm (standard deviations from 23.2 to 68.4) and stems per hectare from 104 to 600 stems/ha (see Table 2.4). Stands in the north tended to have lower mean diameters compared to southern stands, leading to higher densities in higher latitude sites (Figure 2.3). Large stems (≥ 100 cm DBH) were more prevalent at lower latitudes (mean = 26.6 ± 16.6 stems/ha). We noted a more defined reverse J-shaped diameter distribution, typical of old-growth forests, in southern plots (Figure 2.5) compared to northern plots. In contrast, the more northern plots with higher densities of smaller stems displayed a reverse J-shaped distribution with a truncated tail. Sitka spruce was present in the sub-canopy in some of these stands, indicating the species may be able to maintain its presence through time, however some plots had few or no small diameter spruce (i.e. Shaheen, Clayoquot, Carmanah). Pulses of Sitka spruce are observable in some plots which may be related to Sitka spruce re-establishment after flood events. There was no discernable trend in overstory species richness along the latitudinal gradient, however there were more deciduous species overall in the south, though not all present in a single plot.

Characteristics of snags and CWD structure (size and density) were consistent with those of live structure. Stands with larger mean live stem diameters tended to have larger snags and pieces of CWD where stands with higher live tree densities tended to have higher proportions of dead standing and fallen trees (Table 2.5; Table 2.6). Plots located in Southeast Alaska consistently had more snags than BC and Washington plots and smaller mean diameters and SD of DBH (Figure 2.6). Overall, Alaska had more dead structure than lower latitude sites. Northern plots had significantly higher snag density than southern plots overall, however when compared by decay class only decay class IV was significantly different (Figure 2.8). The one southeast Alaska plot with a low number of snags, Marten 1 (with 16 snags/ha) had one of the higher CWD densities in our study area. Snags were more prevalent in lower decay classes throughout the study area (Figure 2.7). CWD was more abundant in the mid-decay classes, in volume and density (Figure 2.9).

Table 2.4 **Old-growth floodplain forest structural variables and overstory composition for stems ≥ 7.6 cm DBH. SD of DBH = Standard deviation of Diameter at Breast Height.**

Site and Species	Mean DBH (cm)	SD of DBH	Site BA (m^2)	Stems/ha	Stems ≥100 cm DBH/ha	Stems 50-100 cm DBH/ha
LaBau						
Picea sitchensis	39.9	24.5	38.9	226.1	2.1	72.5
Tsuga heterophylla	20.6	11.6	3.6	81.7	-	2.1
Alnus rubra	30.7	-	0.1	0.7	-	-
Populus tremuloides	32.1	11.1	0.6	6.3	-	-
Stand	**34.7**	**23.2**	**43.1**	**314.8**	**2.1**	**74.6**
Fish Creek 1						
Picea sitchensis	51.6	33.2	21.8	76	8.0	20.0
Tsuga heterophylla	27.7	16.1	23.3	272	4.0	16.0
Stand	**33.3**	**23.4**	**45.0**	**348**	**12.0**	**36.0**
Fish Creek 2						
Picea sitchensis	55.9	40.4	29.3	80	12.0	32.0
Tsuga heterophylla	24.2	19.6	38.0	500	4.0	44.0
Tsuga mertensiana	80.7	-	2.0	4	-	-
Unknown spp.	36.7	41.5	3.3	16	-	4.0
Stand	**29.2**	**26.4**	**72.7**	**600**	**16.0**	**84.0**
Fish Creek 3						
Picea sitchensis	51.3	34.3	32	108	8.0	44.0
Tsuga heterophylla	22.7	16.9	29	464	4.0	28.0
Stand	**28.1**	**23.9**	**61.0**	**572**	**12.0**	**72.0**
Trap Bay						
Picea sitchensis	54.4	27.6	66.4	228	16.0	100.0
Tsuga heterophylla	28.6	18.8	21.6	236	-	36.0
Pinus contorta	80.4	-	2	4	-	4.0
Alnus rubra	10.9	3.2	0.2	16	-	-
Stand	**40.6**	**27.0**	**90.2**	**484**	**16.0**	**140.0**
Kadashan						
Picea sitchensis	58.8	33.3	11.1	32	4.0	16.0
Tsuga heterophylla	33.9	23.5	7.8	60	-	12.0
Alnus rubra	27.0	9.8	0.7	12	-	-
Stand	**40.7**	**27.9**	**19.7**	**104**	**4.0**	**28.0**
Shaheen						
Picea sitchensis	150.0	33.9	7.2	4	4.0	-
Tsuga heterophylla	34.3	25.1	59.2	418	4.0	100.0
Stand	**35.4**	**27.5**	**66.5**	**422**	**8.0**	**100.0**
Marten 1						
Picea sitchensis	80.6	46.1	72.6	108	28.0	56.0
Tsuga heterophylla	33.3	26.4	19.0	136	8.0	20.0
Alnus rubra	30.9	-	0.3	4	-	-
Stand	**53.9**	**43.0**	**91.9**	**248**	**36.0**	**76.0**

Site and Species	Mean DBH (cm)	SD of DBH	Site BA (m^2)	Stems/ha	Stems ≥100 cm DBH/ha	Stems 50-100 cm DBH/ha
Marten 2						
Picea sitchensis	90.2	43.1	65.4	84.0	32.0	32.0
Tsuga heterophylla	26.0	10.2	1.4	24.0	-	-
Alnus rubra	43.2	0.8	1.2	8.0	-	-
Stand	**73.7**	**45.9**	**68.0**	**116.0**	**32.0**	**32.0**
Yakoun						
Picea sitchensis	89.4	70.0	63.2	64.0	32.0	4.0
Tsuga heterophylla	37.2	37.7	35.6	164.0	12.0	36.0
Alnus rubra	43.7	58.4	3.9	12.0	4.0	-
Stand	**51.4**	**53.5**	**102.8**	**240.0**	**48.0**	**40.0**
Kitlope						
Picea sitchensis	81.0	63.6	68.8	84.0	24.0	32.0
Tsuga heterophylla	13.8	4.1	0.3	16.0	-	-
Thuja plicata	14.1	-	0.1	4.0	-	-
Malus fucus	16.2	63.6	0.9	36.0	-	-
Stand	**54.8**	**58.8**	**70.0**	**140.0**	**24.0**	**32.0**
Tahsish Kwois						
Picea sitchensis	143.6	44.9	91.9	52.0	44.0	8.0
Tsuga heterophylla	68.3	58.3	34.4	56.0	12.0	16.0
Acer glabrum	11.9	1.8	0.3	28.0	-	-
Stand	**85.5**	**68.4**	**126.6**	**136.0**	**56.0**	**24.0**
Tahsish Kwois Active (KA)						
Picea sitchensis	83.30	39.1	28.7	44.0	16.0	16.0
Pseudotsuga menzisii	104.9	16.6	28.3	32.0	20.0	12.0
Alnus rubra	22.4	10.0	5.3	112.0	-	-
Acer glabrum	21.2	8.6	1.8	44.0	-	-
Stand	**45.1**	**38.8**	**64.0**	**232.0**	**36.0**	**28.0**
Clayoquot						
Picea sitchensis	137.5	52.7	50.7	30.0	22.0	6.0
Tsuga heterophylla	42.0	33.6	28.0	124.0	12.0	26.0
Thuja plicata	148.2	78.7	21.1	10.0	8.0	2.0
Acer macrophyllum	34.0	24.9	2.7	20.0	-	4.0
Alnus rubra	18.6	6.9	1.2	40.0	-	-
Stand	**54.6**	**54.2**	**103.7**	**224.0**	**42.0**	**38.0**
Carmanah						
Picea sitchensis	207.8	39.6	41.7	12.0	12.0	-
Tsuga heterophylla	41.5	31.4	37.2	176.0	20.0	36.0
Thuja plicata	117.2	31.8	22.8	20.0	16.0	4.0
Stand	**58.4**	**53.6**	**101.7**	**208.0**	**48.0**	**40.0**
South Fork Hoh 1						
Picea sitchensis	64.7	73.1	69.4	93.0	32.5	2.0
Tsuga heterophylla	49.0	20.8	16.0	72.0	1.5	27.5
Thuja plicata	77.2	27.6	0.5	1.0	-	1.0
Pseudotsuga menzisii	143.8	11.5	1.6	1.0	1.0	-
Stand	**58.5**	**57.1**	**87.5**	**167.0**	**35.0**	**30.5**

Site and Species	Mean DBH (cm)	SD of DBH	Site BA (m^2)	Stems/ha	Stems ≥100 cm DBH/ha	Stems 50-100 cm DBH/ha
South Fork Hoh 2						
Picea sitchensis	37.8	62.5	47.0	112.5	16.0	2.0
Tsuga heterophylla	61.9	32.1	12.9	34.0	4.5	15.5
Thuja plicata	175.0	-	1.2	0.5	0.5	-
Alnus rubra	38.5	31.3	0.5	3.0	-	1.5
Stand	**43.8**	**57.7**	**61.7**	**150.0**	**21.0**	**19.0**

Note: DBH is measured at 1.3 m for all plots except South Fork Hoh which used 1.37 m. Standard deviation (SD of DBH) increases as latitude decreases. Unknown species in the Fish Creek 2 plot are due to missing data.

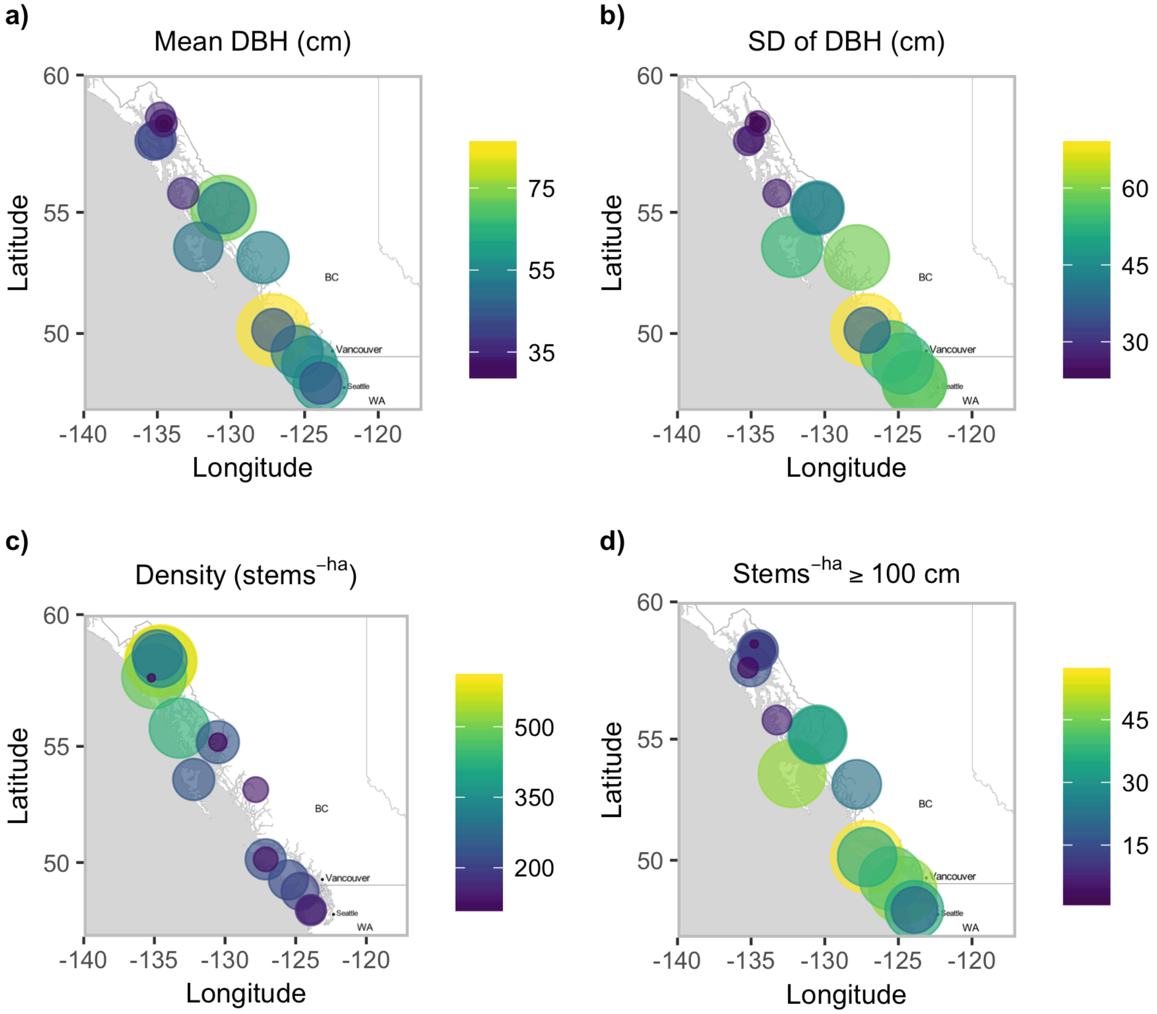


Figure 2.3 Stand structural attributes plotted along the PCTR's latitudinal gradient: a) mean diameter; b) standard deviation of diameter; c) density of live stems per hectare; and d) live stems larger than 100 cm diameter. The size and colour of the marker both indicate the variable's value.

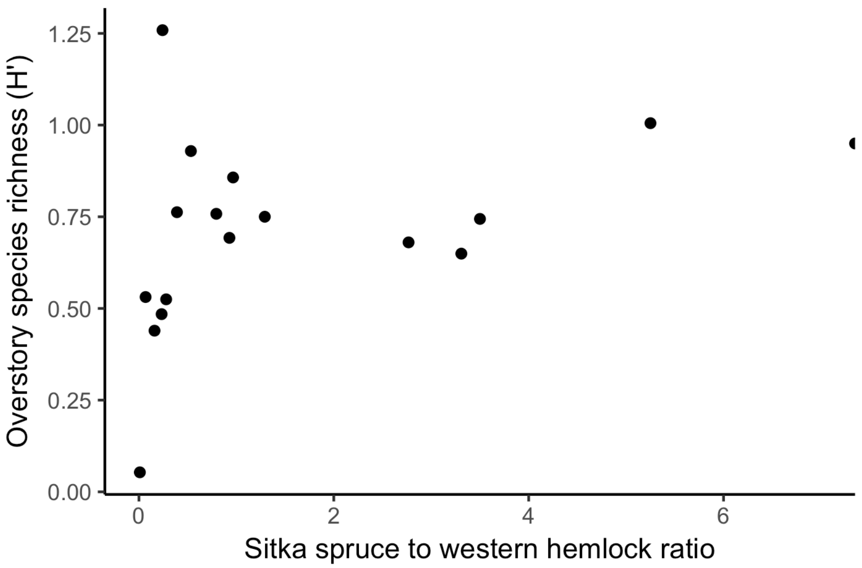


Figure 2.4 Species diversity (H') and ratio of Sitka spruce to shade tolerant western hemlock. There are no hemlock at the Tahsish Kwois Active plot, therefore the far right point which represents this plot is plotted as having an infinite ratio of Sitka spruce to western hemlock.

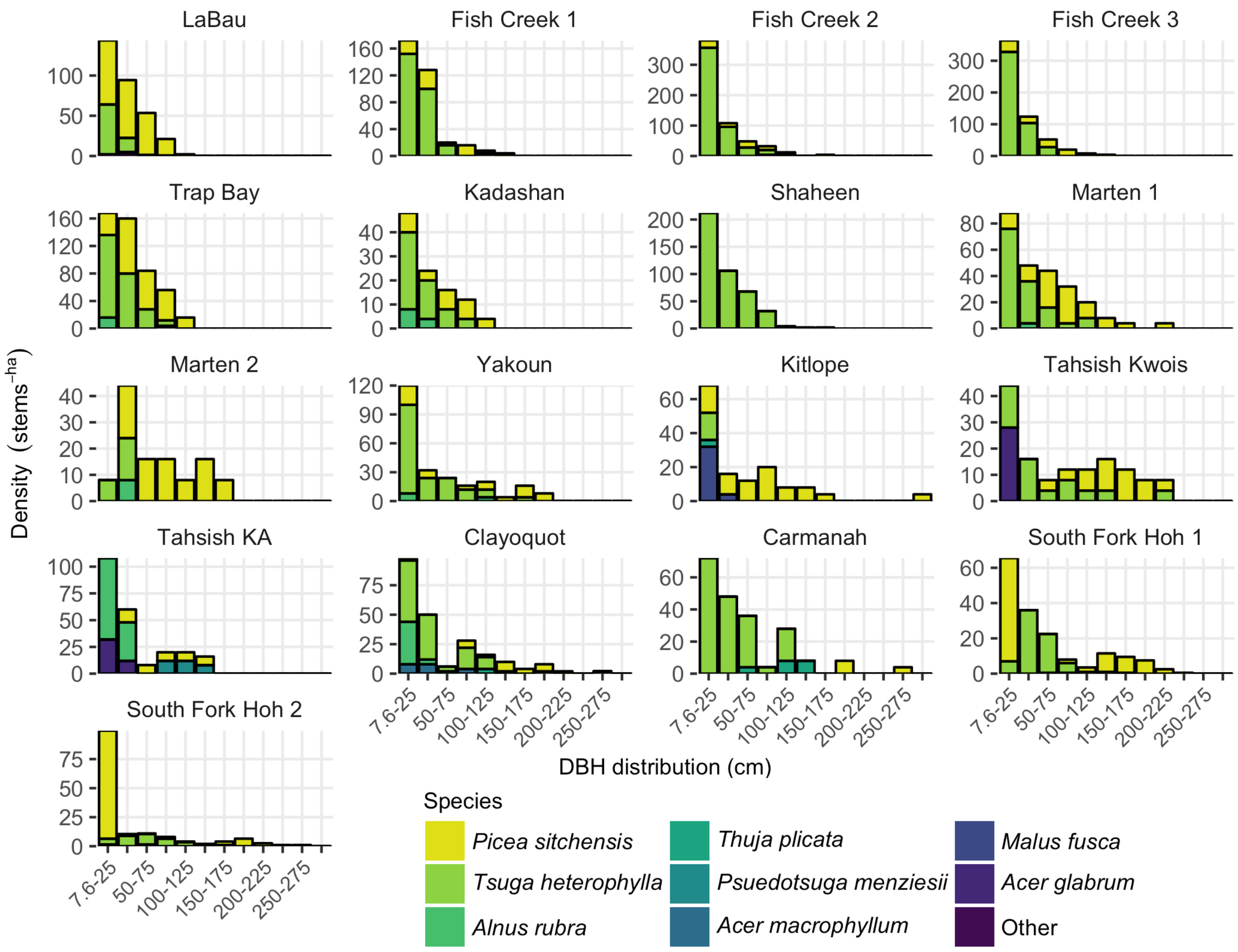


Figure 2.5 **Diameter distributions in 25 cm bins, upper left corner is the most northern plot and goes south to the right and down, ending on the southern most plot. Other species include black cottonwood, Douglas-fir, lodgepole pine, and mountain hemlock.**

Table 2.5. Snag structural characteristics of floodplain forests from southeast Alaska to southern BC.

Site	Mean DBH (cm)	SD of DBH	Site BA (m^2)	Snags/ha	Snags ≥100 cm DBH/ha	Snags 50-100 cm DBH/ha
Fish Creek 1	17.3	12.8	4.5	124	-	8
Fish Creek 2	34.8	30.8	24.2	144	8	32
Fish Creek 3	25.5	24.0	12.5	132	4	12
Trap Bay	33.3	26.6	12.9	92	4	16
Kadashan	45.5	37.5	60.7	224	28	36
Shaheen	46.2	35.7	43.2	162	8	66
Marten 1	72.5	67.5	10.9	16	4	4
Marten 2	68.0	46.9	100.0	188	56	36
Yakoun	96.1	58.3	46.6	48	16	16
Kitlope	30.9	9.8	3.0	36	-	-
Tahsish-Kwois	83.0	14.7	6.6	12	-	12
Tahsish KA	17.6	12.0	0.5	16	-	-
Clayoquot	78.9	62.5	18.5	24	6	10
Carmanah	54.6	34.1	21.8	68	12	28

Table 2.6. Coarse woody debris characteristics in PCTR floodplain forests. All pieces of CWD were ≥ 10 cm diameter.

Site	Mean DBH (cm)	SD of DBH	Stems/ha	Volume (m^3)	CWD ≥ 100 cm DBH	CWD 50-100 cm DBH
Kadashan	35.2	19.1	184	108.9	4	36
Marten 1	36.2	21.0	160	54.1	4	32
Marten 2	27.7	11.5	24	3.1	-	4
Kitlope	23.3	7.1	88	14.7	-	-
Tahsish-Kwois	41.6	16.8	68	32.1	-	16
Tahsish KA	37.2	33.1	92	21.5	8	8
Clayoquot	53.8	46.5	367	432.2	67	118
Carmanah	41.1	31.4	436	190.3	20	92

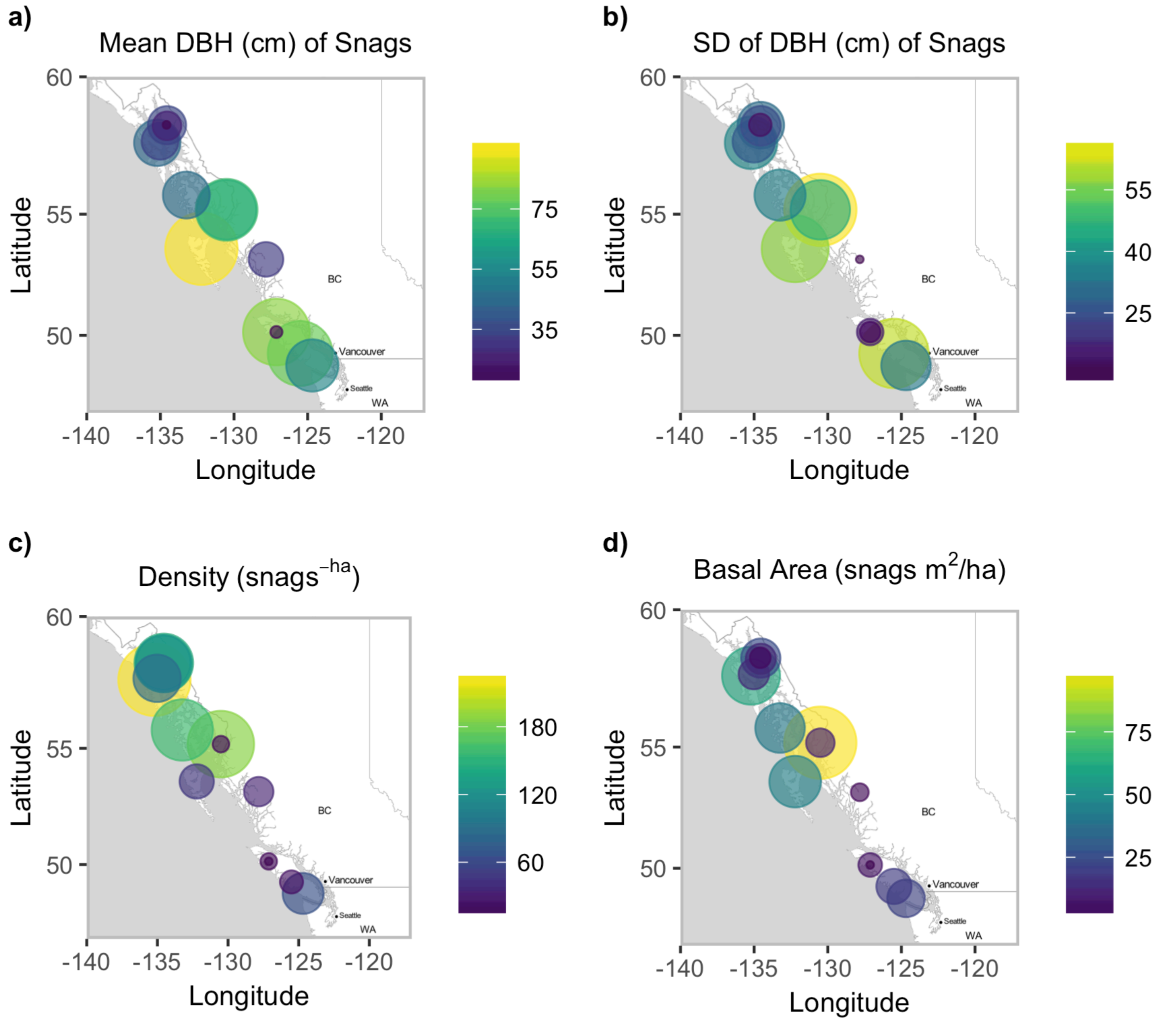


Figure 2.6 **Snag stand attributes plotted along a latitudinal gradient: a) mean diameter; b) standard deviation of diameter (SD of DBH); c) density of snags per hectare; and d) number of snags larger than 100 cm plotted along the PCTR's latitudinal gradient. The size of the point and the colour both indicate the variable's value.**

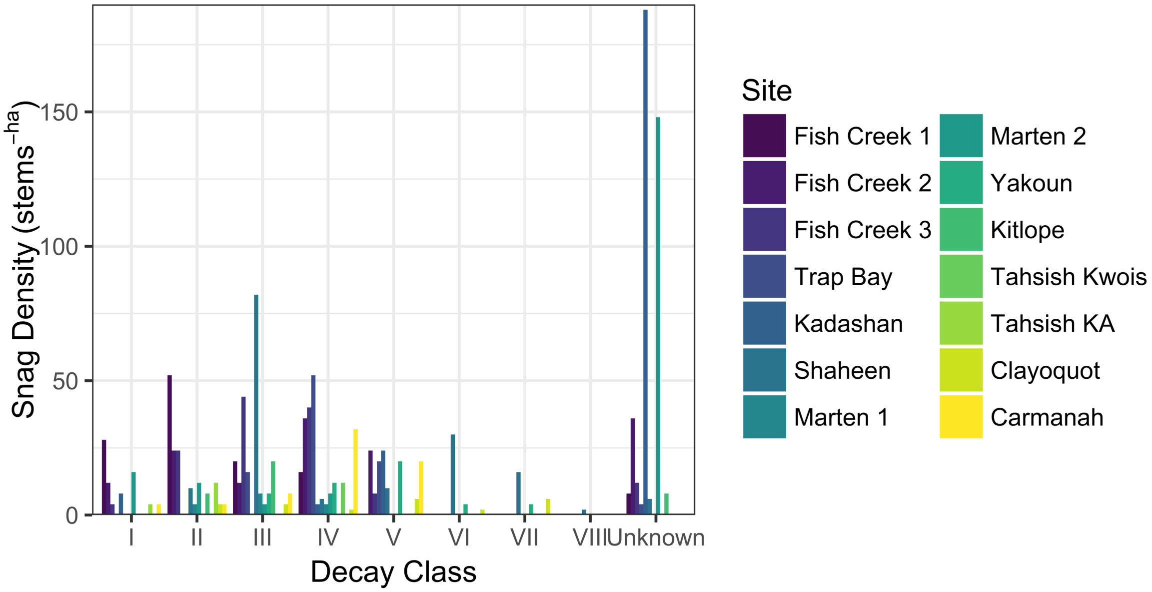


Figure 2.7 **Snag density by decay class. Some historical data were unrecorded or missing, composing the unknown decay class.**

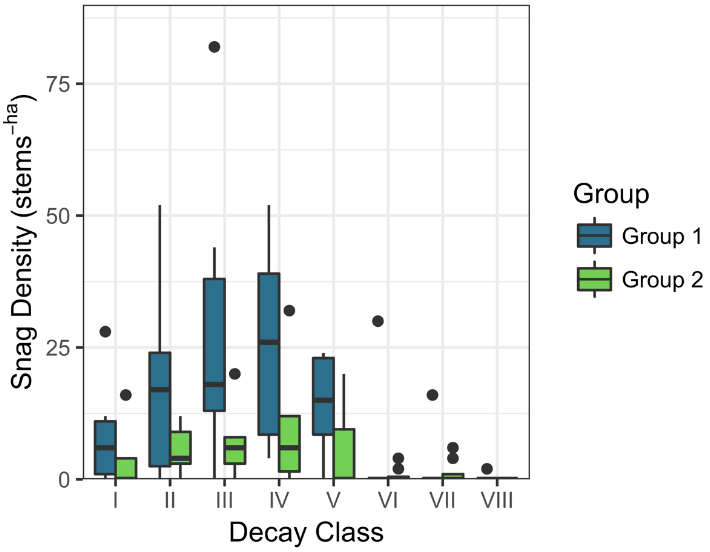


Figure 2.8 **Boxplot of group 1 (northern sites distinguished in the cluster analysis) and group 2 (southern sites) shows that snag density was higher northern plots (one-tailed t-test, t = 3.3445, df=56.189, $p < 0.01$), however not significantly for individual decay classes I to VII, except for decay class IV (one-tailed t-test, t =-1.9012, df = 7.1419, $p < 0.05$). The Unknown decay class was omitted.**

Table 2.7 **Results of a one-tailed student's t-test that assessed if snag density for Group 1 (northern sites) was greater than Group 2 (southern sites).**

Decay Class	Mean		t	Degrees of Freedom	p-value
	Group 1	Group 2			
I	8.67	3.0	-1.20	7.07	0.1351
II	18.33	5.5	-1.56	5.44	0.0871
III	29.00	6.5	-1.82	5.35	0.0620
IV	25.67	8.75	-1.90	7.14	0.0491*
V	14.33	5.75	-1.67	10.37	0.0621
VI	5.00	0.75	-0.85	5.12	0.2179
VII	2.67	1.25	-0.51	6.00	0.3152
VIII	0.33	0.00	-1.00	5.00	0.1816
All	**13.00**	**3.9375**	**3.34**	**56.189**	**0.0015****

Note: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

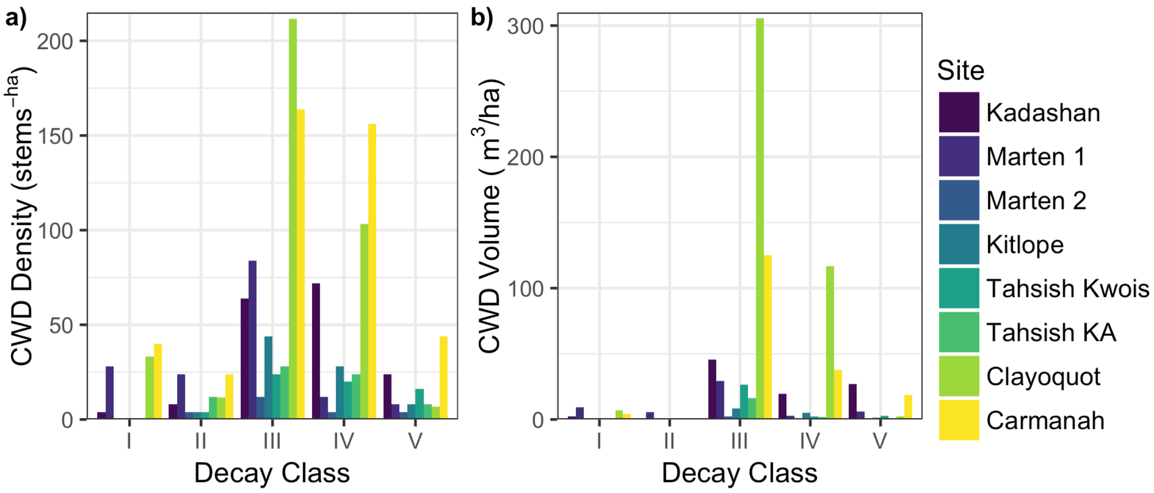


Figure 2.9 **a) Coarse Woody Debris (CWD) density and b) CWD volume (m^3) by decay class show that the majority of CWD was moderately decomposed and that volume does not necessarily reflect density. Tahsish KA = Tahsish Kwois Active.**

2.3.2. Climatic gradients and flood disturbance influence on stand structure and composition

Mean annual temperature (MAT) was the strongest of the environmental factors associated with forest structure and composition. The NMDS ordinations for live structure are shown in Figure 2.10 and Figure 2.11 displaying sites and attributes, respectively. The stress was 0.044 for the NMDS indicating that the ordination is a good representation of the sites in ordination space. Table 2.8 provides the r^2 and p-values for the fitted vectors of environmental gradient variables, MAT (r^2 = 0.7020 and p-value < 0.001) and MAP (r^2 = 0.4869 and p-value < 0.05) were the only significant explanatory variables, with MAT being more influential than MAP. The NMDS ordination showed a gradient in structure similar to those seen in Figure 2.3, with larger mean diameters and lower densities associated with southern sites and smaller stems at higher densities typically in more northern sites. MAT was significantly correlated with all variables for live stand structure and composition variables except for Sitka spruce density (see Table 2.8). MAT was only negatively correlated with snag density (ρ = -0.65; p-value < 0.05; Table 2.9). MAP shows a positive relationship with mean tree diameter, diameter diversity, and large stems (stems ≥ 100 cm DBH) (ρ = 0.59, ρ = 0.64, and ρ = 0.53 with p-values <0.05, 0.01, and 0.05, respectively). Negatively correlated with MAP were density of medium stems (50 cm ≥ stems ≤ 100 cm) and density of western hemlock (ρ = -0.56 and ρ = -0.51, respectively, with p-values <0.05) (Table 2.8). PAS was negatively correlated with SD of DBH and positively correlated with medium stem density (ρ = -0.51 and ρ = 0.28, respectively; p-values < 0.05) There were no visible patterns in relationships of streamflow regime type with structural attributes.

We expected sites would group among the *a priori* designations (e.g., Alaback, 1996; Wolf et al., 1995) of perhumid (59°N - 50°N) and seasonal (50°N - 43°N) sub-regions. However, instead they separated into two groups, north and south of approximately 57° latitude. This led us to run a *post-hoc* hierarchical cluster analysis (Figure 2.13) to assess further trends and potentially provide an alternative definition of the PCTR sub-regions. The first branches from the cluster analysis are plotted in the NMDS ordinations using 95% confidence ellipses. As seen in the NMDS ordination (Figure 2.10), sites north and south of ~ 57° latitude separated into two distinct groups. Plots north of ~57° latitude are located in the northern part of the Alaskan pan-handle, this area is cooler and has lower MAP than the Alaskan plots that grouped with the southern plots (Marten 1 and 2). In Figure 2.13 different dashed lines indicate possible hypotheses for secondary branching in the cluster analysis such as more or less MAP, more PAS, higher elevations, and differences in hydrological disturbance regime.

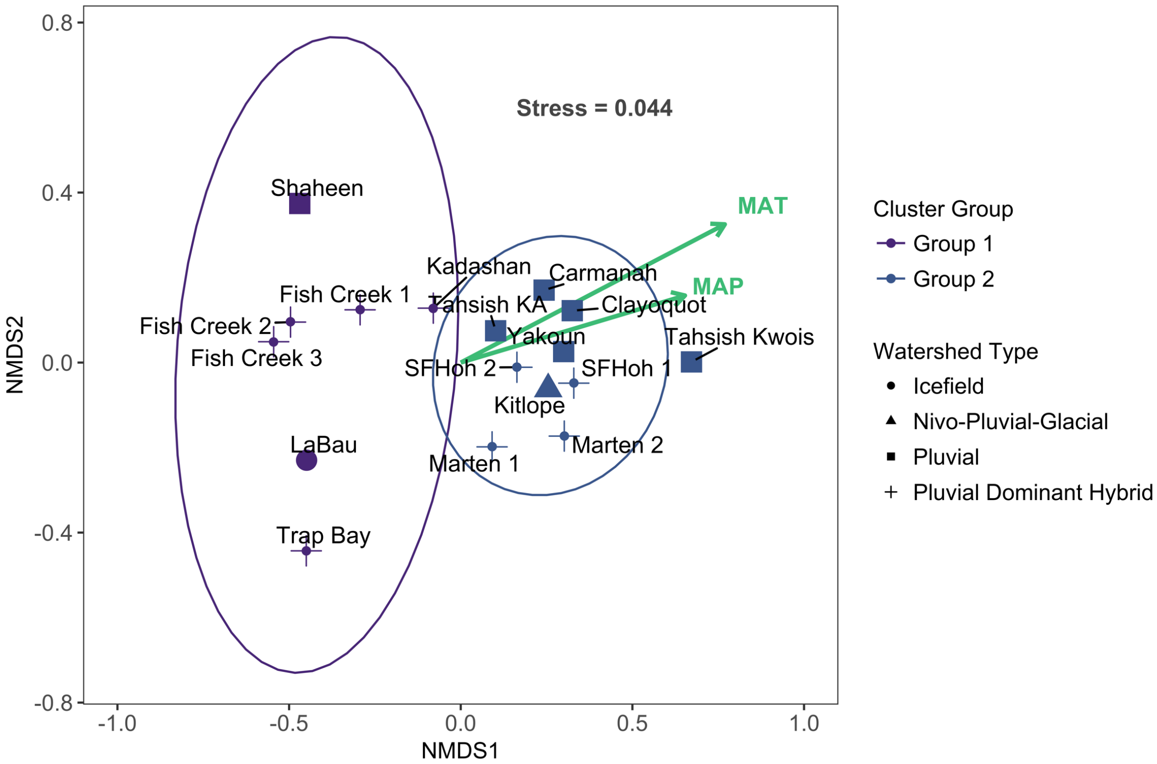


Figure 2.10 NMDS ordination displaying fitted vectors of environmental variables with a p-value < 0.05. Cluster groups from the hierarchical cluster analysis (Figure 2.13) are shown with 95% confidence ellipses, groups are north (purple; above 57° latitude) to south (blue; below above 57° latitude). Note: MAT is mean annual temperature and MAP is Mean Annual Precipitation.

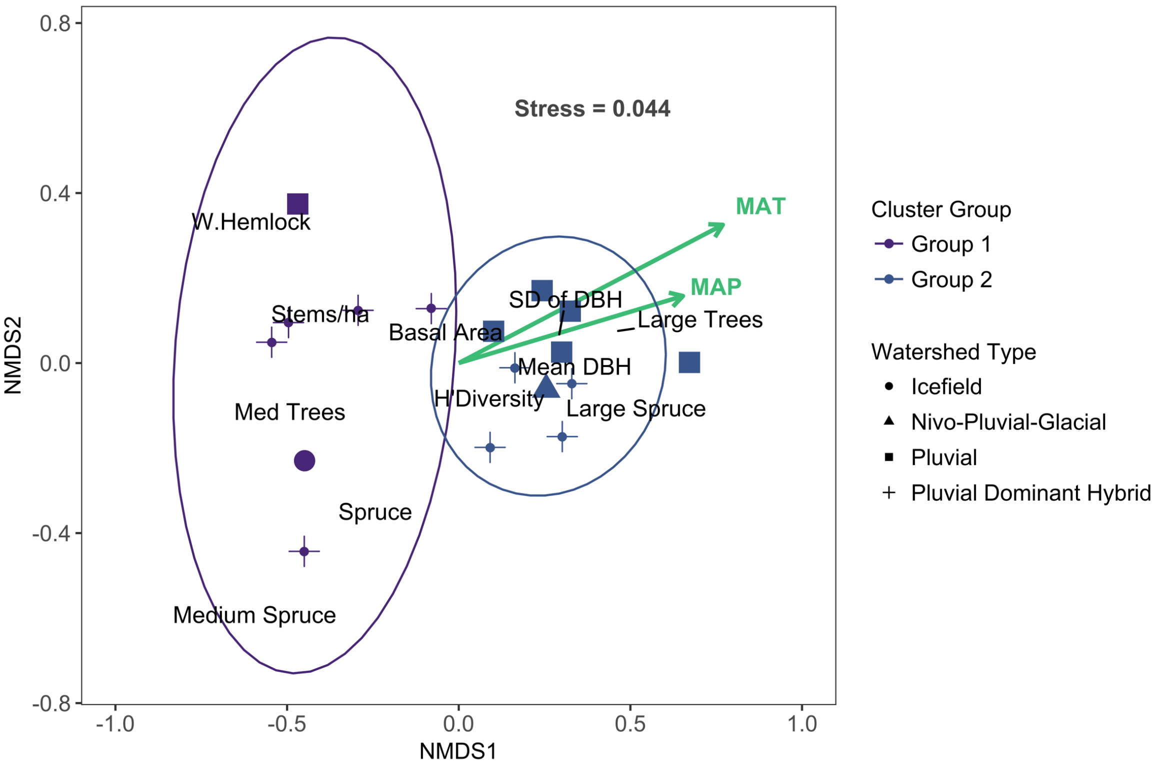


Figure 2.11 **NMDS ordination displaying stand structure and composition variables, points are sites (see Table 2.8). Fitted vectors are shown for environmental variables with a p-value < 0.05. Cluster groups from the hierarchical cluster analysis (Figure 2.13) are shown with 95% confidence ellipses, groups are (purple; above 57° latitude) to south (blue; below above 57° latitude). Note: Large stems are ≥ 100 cm; medium stems are ≥ 50 cm and < 100 cm; Large spruce are Sitka spruce ≥ 100 cm; med. spruce is spruce ≥ 50 cm and < 100 cm. All are in stems per hectare. MAT is Mean Annual Temperature and MAP is Mean Annual Precipitation.**

The structural and compositional gradients associated with snags reflected those of live structure (Figure 2.6). Figure 2.12 shows the ordination of snag structural variables with stress equal to 0.024. There were no significant vectors of environmental gradients corresponding to snags (Table 2.9).

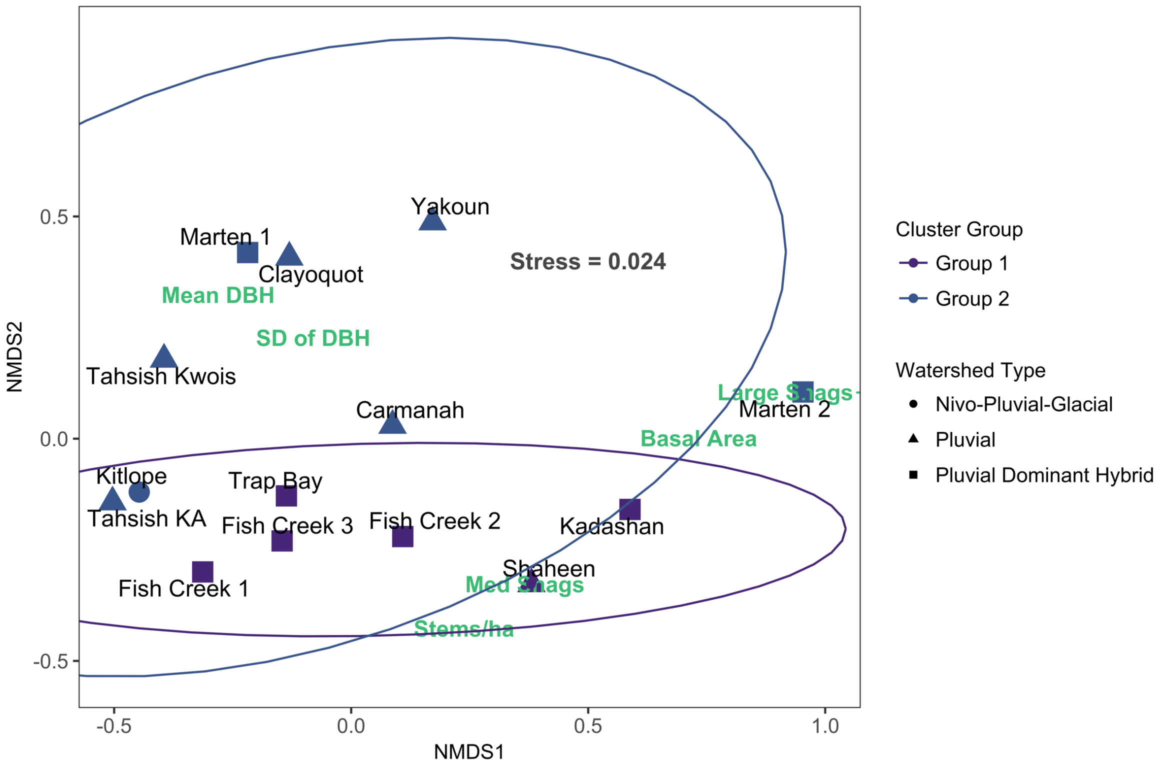


Figure 2.12 NMDS with sites plotted. Snag structure and composition variables (green) and site names (black) are labelled. Groups from the cluster analysis (Figure 2.13) are shown with 95% confidence ellipses. Group 1 is purple (above ~ N57° latitude), group 2 is blue (south of ~ N57°). Large snags are ≥ 100 cm DBH; medium snags are ≥ 50 cm and < 100 cm DBH. MAT and MAP are Mean Annual Temperature and Precipitation.

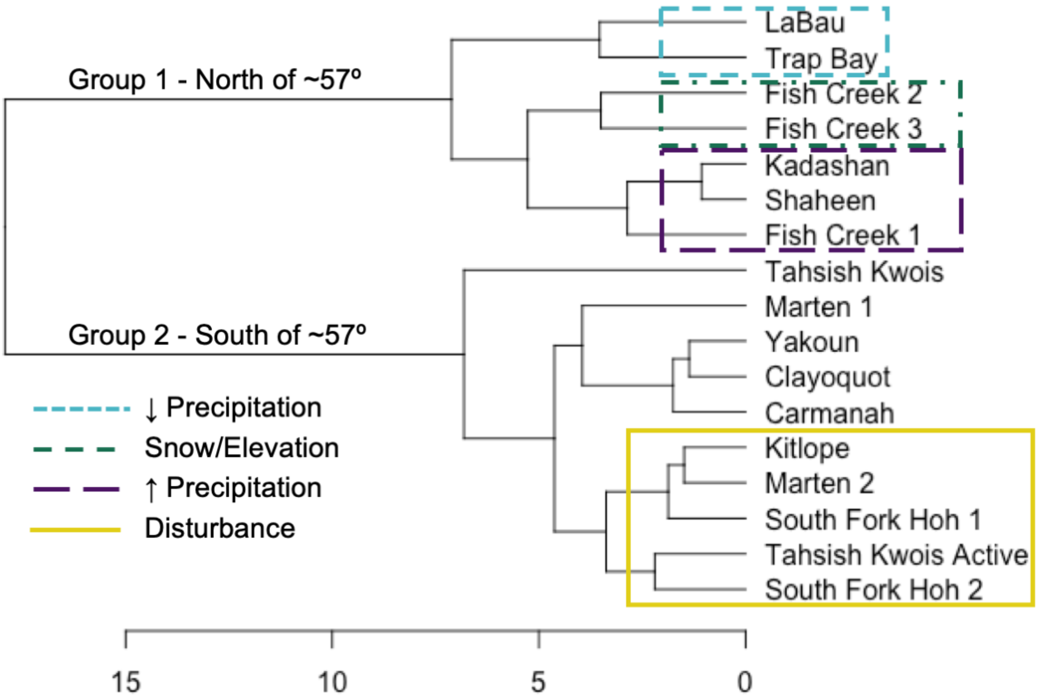


Figure 2.13 **Post-hoc heirarchical cluster analysis. Cluster groups 1 and 2 are noted on the primary branches and are shown in the NMDS plots (Figure 2.10; Figure 2.11; Figure 2.12). Each colour and dash combination represents a hypothesis for subsequent branching (e.g., the green dashed box around Fish Creek 2 and 3 indicates that we hypothesized that these were different than other plots north of ~57°N because of more mean annual precipitation as snow and/or their higher elevations than other sites). Flood disturbance (yellow box) is thought to be influencing the tertiary branching pattern seen within the southern plots, group 2. Tahsish-Kwois is an outlier due to its stand development stage.**

Correlation between stand structure and composition variables and flood proxies varied. MAP as discussed above, shows a positive relationship with mean tree diameter, diameter diversity and large stems (stems ≥ 100 cm DBH) ($\rho = 0.59$, $\rho = 0.64$, and $\rho = 0.53$ with p-values <0.05, 0.01, and 0.05, respectively). Negatively correlated with MAP were density of medium stems (50 cm ≥ stems ≤ 100 cm) and density of western hemlock ($\rho = -0.56$ and $\rho = -0.51$, respectively, with p-values < 0.05). Flood proxies were significantly correlated with several stand attributes (Table 2.8). Mean diameter, SD of DBH, large stems, large Sitka spruce, and overstory species diversity (H') exhibited significant positive relationships with catchment area ($\rho = 0.69$, $\rho = 0.58$, $\rho = 0.52$, $\rho = 0.63$ and $\rho = 0.5$ with p-values < 0.01, 0.05, 0.05, 0.01, and 0.05 respectively). Catchment area was negatively correlated with stem density ($\rho = -0.59$ and p-value <

0.05) and density of western hemlock ($\rho = -0.73$ and p-value <0.001). Mean slope was positively correlated to mean diameter, SD of DBH, and large Sitka spruce ($\rho = 0.51$, $\rho = 0.51$ and $\rho = 0.52$, respectively, with p-values < 0.05). Additionally, Hypsometric Integral (HI) showed a positive association with medium Sitka spruce density ($\rho = 0.59$ and p-value < 0.05).

Table 2.8 The results of the Spearman's rank correlation test and the NMDS analysis for live structure.

	Spearman's Rank Correlation Coefficients (ρ)						
Stand Attributes	**MAT**	**MAP**	**PAS**	**Mean Slope**	**Catchment Area**	**Hypsometric Integral**	**Watershed Type**
Mean DBH	0.74***	0.59*	-0.37	0.51*	0.69**	-0.35	-
SD of DBH	0.83***	0.64**	-0.46	0.51*	0.58*	-0.46	-
Basal Area	0.51*	0.31	-0.40	0.29	0.29	-0.32	-
Stem Density	-0.58*	-0.48	0.24	-0.33	-0.59*	0.24	-
Large stems	0.69**	0.53*	-0.52*	0.40	0.52*	-0.32	-
Med. stems	-0.56*	-0.56*	0.35	-0.27	-0.40	0.18	-
Sitka spruce	-0.35	-0.28	0.42	0.27	0.00	0.20	-
Large Sitka spruce	0.58*	0.45	-0.25	0.52*	0.63**	-0.37	-
Med. Sitka spruce	-0.69**	-0.42	0.66*	0.14	-0.06	0.59*	-
Western hemlock	-0.57*	-0.51*	0.26	-0.44	-0.73***	0.20	-
Species Diversity (H')	0.44*	0.24	-0.22	0.36	0.50*	-0.12	-
Squared correlation coefficient (r^2)	0.7020***	0.4869*	0.3595	0.2493	0.1527	0.1459	0.2723

Note: MAP, catchment area, hypsometric integral and mean slope are considered flood proxy variables.
*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Table 2.9 The results of the Spearman's rank correlation test and the NMDS analysis for snag structure.

Stand Attributes	Spearman's Rank Correlation Coefficients (ρ) MAT	MAP	PAS	Mean Slope	Catchment Area	Hypsometric Integral	Watershed Type
Mean DBH	0.51	0.27	-0.30	0.10	0.48	-0.36	-
SD of DBH	0.10	0.09	0.12	0.09	0.18	-0.09	-
Basal Area	-0.16	-0.29	0.06	-0.34	-0.05	-0.22	-
Stem Density	-0.65*	-0.51	0.42	-0.43	-0.45	0.13	-
Large stems	-0.10	-0.23	0.06	-0.26	0.04	-0.18	-
Med. stems	-0.26	-0.31	0.03	-0.50	-0.31	-0.29	-
Squared correlation coefficient (r^2)	0.3569	0.2106	0.1504	0.0652	0.0882	0.1032	0.136

Note: MAP, catchment area, hypsometric integral and mean slope are considered flood proxy variables.
*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

2.3.3. Comparison of Floodplain and Upland Old-Growth Forests

We added our data here to the comparison from Chapter 1 of structural variables between upland and riparian old-growth stands (Chapter 1, Figure 1.1). As in Chapter 1 we see more variability in stand structural variables among the riparian sites than in the upland sites (Figure 2.14). Adding additional data to the previous analysis shows that the variability seen in the few previously studied catchments carries throughout the PCTR. Several floodplain stands were above or below the 5th and 95th quantiles of mean DBH, stems/ha, basal area and stems/ha of the leading species (i.e., Sitka spruce or Douglas-fir) from upland stands. Tree size diversity was more comparable for floodplain and upland stands at lower latitudes, than across the PCTR. SD of DBH was more variable in floodplain forests (23.23 to 68.42; see Table 2.4 and 2.11) than values reported for upland stands (32 to 37.7; Table 2.11). SD of DBH variability is reduced for floodplains when we consider comparing stands in the same geographic range as the upland stands. Floodplain stands in the northern part of the PCTR, or group one from our cluster analysis, is lower (23.23 to 27.95) than group two (42.96 to 68.42), and floodplain literature values (36.7 to 50.5). Few upland studies report SD of DBH or mean diameter, so the lower values may be due to lack of reporting or be influenced by site selection.

The dead wood components of floodplain stands were comparable to upland stands, although there are more extreme values for floodplain stands. Upland stands had higher snag densities than southern floodplain sites (34 - 112 and 12 – 67 stems/ha, (respectively). However, the northern floodplain sites tend to have more than upland sites (16-224 snags/ha; Table 2.5; Table 2.12). Coarse woody debris on floodplains was highly variable; this may be related to flood regime and dependent on timing of sampling.

Table 2.10. **Structural characteristics of live trees from alluvial old-growth forests in the PCTR. Trees were ≥ 5cm DBH unless noted below.**

Location Study – Plot	**Leading Species**	**Plots**	**Est. Stand Age**	**Mean DBH (cm)**	**SD of DBH**	**Stems/ha**	**Stems/ha >100 cm**	**BA (m^2/ha)**	**BA Picea (m^2/ha)**	**Picea Stems/ha**
Shaheen Creek, AK (Alaback and Juday, 1989)	Picea/Tsuga	n = 1	500 - 750	-	-	424	-	63.6[1]	13.7	70
Carmanah River, BC[8] (Little et al., 2013)	Picea/Tsuga									
Transitional Terrace		n= 6	129 - 216	37	-	710	-	140	28	87
Mature Terrace		n = 7	330 - 595	45	-	520	-	181	109	51
Old Growth Terrace		n = 5	378 - 676	18	-	1115	-	68	0	13
Hoh River[2]**, WA** (Fonda, 1974)	Picea/Tsuga	n = 1	> 500 - 600	-	-	230.3	11.9/9.9[3]	38.8	15.6	116.6
Queets River, WA (Van Pelt et al. 2006)	Picea/Tsuga									
Plot K10		n = 1	130	59.8	36.7	316	45.5	100.1	49.9	136
Plot K04		n = 1	165	55.2	38	367	32.7	85.1	40.3	166
Plot K22		n = 1	185	60.5	38.9	218	29.2	80	46.1	104
Plot K16		n = 1	265	42.2	50.3	650	28.9	99.8	70.1	267
Plot K21		n = 1	330	35.1	50.5	556	29.2	98.1	59.5	177
Queets River, WA (Latterall, 2006)	Picea/Tsuga									
Mature Fluvial Terrace		n = 6	100 - 300	50.7	-	322	-	-	-	-
Queets River, WA[5] (Balian and Naiman 2005)	Picea/Tsuga		103 - 351	-	-	493[5]	-	68.9	44.5	246.3
S.Fork Hoh River, WA[6] (McKee et al. 1982)	Picea/Tsuga		266	65.6	-	142	-	81.8	61.9	57.8

Location Study – Plot	**Leading Species**	**Plots**	**Est. Stand Age**	**Mean DBH (cm)**	**SD of DBH**	**Stems/ha**	**Stems/ha >100 cm**	**BA (m^2/ha)**	**BA Picea (m^2/ha)**	**Picea Stems/ha**
Carbon River, WA (Van Pelt and Nadkarni 2004)	Pseudotsuga/ Tsuga		500	44.1	52.7	285	-	109.5	45.0	17

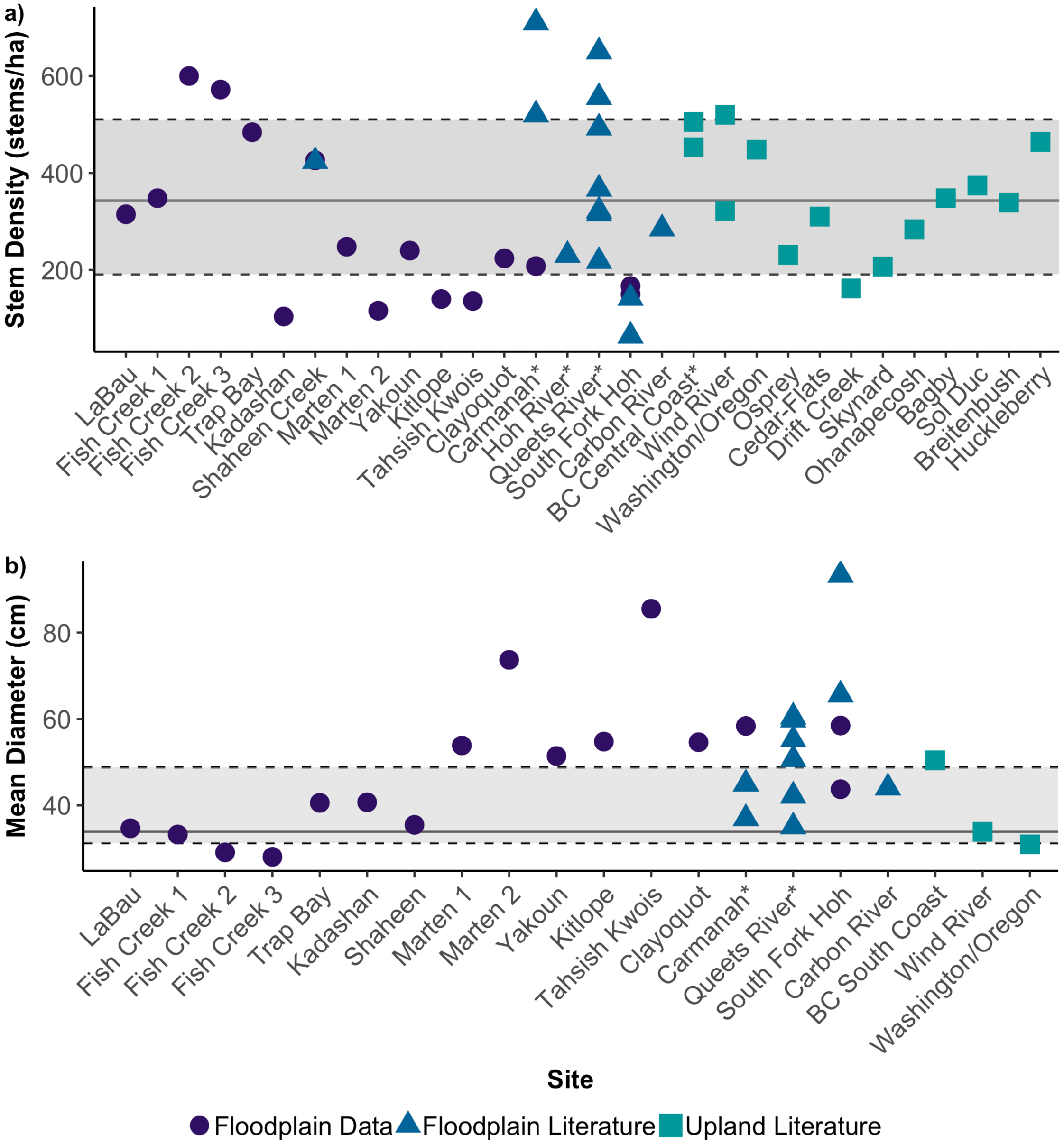
[1] Low due to recent Sitka spruce mortality.
[2] Stems >4 cm DBH.
[3] Stems per size class, 91-120 cm and 120+cm DBH.
[5] Stems ≥ 1 cm diameter live stems measured. Mature forest plots (2, 4, 6, 7, 10, 11, and 16).
[6] Upper terraces reported, similar to Fonda's (1974) second terrace, which is equivalent to a medium bench site. Four 1-ha plots were established, though how many for each forest type (low and high terraces) in the study is not mentioned.
[7] *Pseudotsuga* instead of *Picea*.
[8] Stems ≥ 3 cm DBH and ≥ 130 cm tall. Old-growth terrace plot was omitted from Figure 2.14 because it has no Sitka spruce > 5 cm DBH and is not comparable to the other stands.

Table 2.11. Structural attributes of live trees from upland sites in the PCTR. All trees were ≥ 5cm DBH unless noted below.

Location Study – Plot	**Leading species**	**Plots**	**Est. Stand Age**	**Mean DBH (cm)**	**SD of DBH**	**Stems/ha**	**Stems/ha >100 cm**	**BA (m^2/ha)**	**BA Picea (m^2/ha)**	**Picea (Stems/ha)**
Central coast, BC (LePage and Banner, 2014)[1]	*Thuja/Tsuga/ Picea*									
			>250			453				
			>250			505				
BC South Coast Wells, 1996	*Tsuga/Thuja*		>200	50.44	37.7	-	-		-	-
Wind River Canopy R.F., WA (North et al., 2004)	*Pseudotsuga/ Tsuga*		450	33.9	33.8	519.8	-	93.75	45.65	62.7
Washington/Oregon (Spies and Franklin, 1991)	*Pseudotsuga/ Tsuga*		>195	31	32	448	19	69	-	63[2]
Washington/Oregon (Freund et al., 2015)	*Pseudotsuga/ Tsuga*									
Osprey		n = 1	190	-	-	231	-	79	-	-
Cedar Flats		n = 1	191	-		310	-	79	-	-
Drift Creek		n = 1	193	-		162	-	83	-	-
Skynard		n = 1	193	-		207	-	69	-	-
Ohanapecosh		n = 1	296	-		284	-	86	-	-
Bagby		n = 1	297	-		348	-	89	-	-
Sol Duc		n = 1	317	-		374	-	121	-	-
Breitenbush		n = 1	326	-		339	-	111	-	-
Huckleberry		n = 1	328	-		464	-	93	-	-
Study Mean		n = 9	-	-	36.4	302	34	90	-	-

1 Stems ≥ 12.5 cm DBH.

2 Pseudotsuga instead of Picea


a)
Stem Density (stems/ha)
600
400
200
LaBau
Fish Creek 1
Fish Creek 2
Fish Creek 3
Trap Bay
Kadashan
Shaheen Creek
Marten 1
Marten 2
Yakoun
Kitlope
Tahsish Kwois
Clayoquot
Carmanah*
Hoh River*
Queets River*
South Fork Hoh
Carbon River
BC Central Coast*
Wind River
Washington/Oregon
Osprey
Cedar-Flats
Drift Creek
Skynard
Ohanapecosh
Bagby
Sol Duc
Breitenbush
Hucklebery
b)
Mean Diameter (cm)
80
60
40
LaBau
Fish Creek 1
Fish Creek 2
Fish Creek 3
Trap Bay
Kadashan
Shaheen
Marten 1
Marten 2
Yakoun
Kitlope
Tahsish Kwois
Clayoquot
Carmanah*
Queets River*
South Fork Hoh
Carbon River
BC South Coast
Wind River
Washington/Oregon
Site
● Floodplain Data
▲ Floodplain Literature
■ Upland Literature

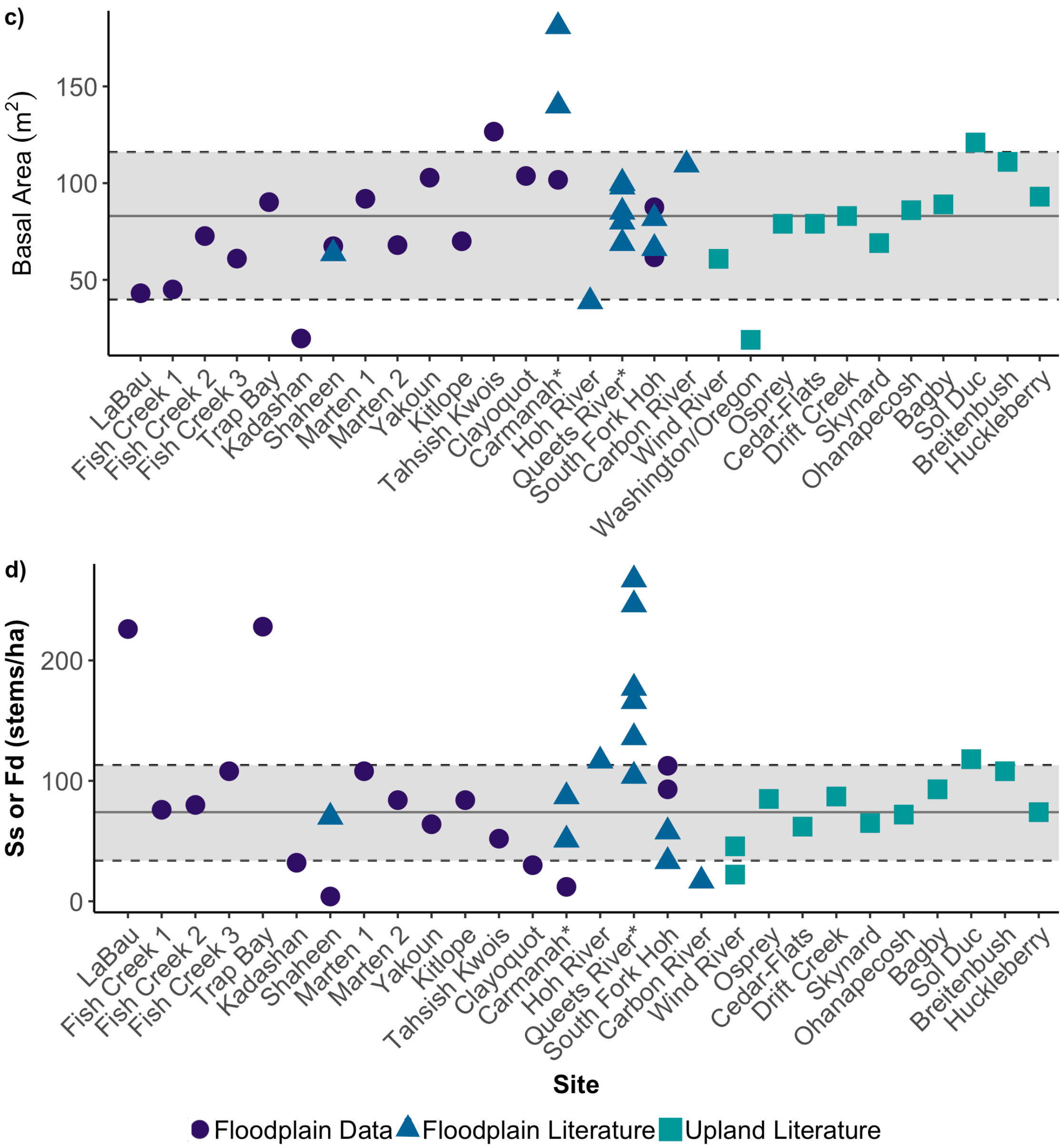


Figure 2.14 Comparison of floodplain and upland old-growth structure: a) stems per hectare; b) mean diameters; c) basal area; and d) stems per hectare of the leading shade intolerant species (Ss is Sitka spruce and Fd is Douglas-fir). Floodplain *data* are data from this study, floodplain and upland *literature* are from the PCTR. All floodplain points are arranged north to south, from left to right. Upland stands are plotted north to south after floodplain stands. The shaded horizontal bar represents the range of variability in upland stands, plotted between the dashed lines which are the 5th and 95th quantiles of each upland attribute for upland data (e.g., stems/ha of upland stands). The solid horizontal line is the median of the upland data. Sites with * have differing sampling methods from the rest, see Table 2.10 and Table 2.11. South Fork Hoh data, this study and from the literature are from the same plots, different sample years.

Table 2.12 Snag structural characteristics from upland and alluvial forests in the PCTR. All snags were ≥ 5 cm DBH unless noted below.

Location Study – Plot	**Leading species**	**Plots**	**Est. Stand Age**	**Mean DBH (cm)**	**Snags/ha**	**Snags/ha ≥ 100 cm**	**Snags/ha ≥ 50 cm (range)**	**Snag Volume (m^3) (range)**
Alluvial sites								
Queets River, WA (Van Pelt et al. 2006)	*Picea/Tsuga*							
Plot K10		n = 1	130	57.8	18.2	0	11.4	45.9
Plot K04		n = 1	165	36.9	30.8	0	7.7	29.9
Plot K22		n = 1	185	59.3	20.0	3.1	9.2	59.9
Plot K16		n = 1	265	28.1	16.7	1.1	2.2	11.3
Plot K21		n = 1	330	59.5	17.7	4.2	6.3	86.4
Carbon River, WA[1] (Van Pelt and Nadkarni, 2004)	*Pseudotsuga/ Tsuga*		500	83.9	66.7	13	18	526.9
Non-alluvial sites								
Washington/Oregon[1] (Spies and Franklin, 1991)	*Pseudotsuga/ Tsuga*			-	-	-	24 (20-28)	159 (128-199)
Washington/Oregon (Spies and Franklin, 1988)	*Pseudotsuga/ Tsuga*	n/a	200 - 525	51	41	-	17	148
Washington/Oregon[2] (Freund et al., 2015)	*Pseudotsuga/ Tsuga*							
Osprey		n = 1	190	-	74	-	-	140.2
Cedar Flats		n = 1	191	-	60	-	-	66.5
Drift Creek		n = 1	193	-	34	-	-	42.6
Skynard		n = 1	193	-	92	-	-	46.3
Ohanapecosh		n = 1	296	-	89	-	-	129.7
Bagby		n = 1	297	-	112	-	-	86.4
Sol Duc		n = 1	317	-	85	-	-	95.7
Breitenbush		n = 1	326	-	39	-	-	46.9
Huckleberry		n = 1	328	-	100	-	-	49.4

1 Coast range old-growth plot.

2 Snags ≥ 10 cm DBH.

Table 2.13 Coarse woody debris characteristics from upland and alluvial forests in the PCTR. All CWD pieces were ≥ 10 cm diameter.

Location Study – Plot	**Leading species**	**Mean DBH (cm)**	**CWD density (pieces/ha)**	**Logs ≥ 100 cm DBH**	**Logs ≥ 50 cm DBH**	**LW Volume (m³)**	**Spruce Volume (m³)**
Queets River, WA (Van Pelt et al. 2006)	*Picea/ Tsuga*						
Plot K10		57.8	18.2	0	11.4	128	3.1
Plot K04		36.9	30.8	0	23.1	97	0.1
Plot K22		59.3	20.0	0	4.6	298	18.8
Plot K16		28.1	16.7	2.2	11.1	241	5.5
Plot K21		59.5	17.7	5.2	14.6	654	28.9
Carbon River, WA[1] (Van Pelt and Nadkarni 2004)	*Pseudotsuga/ Tsuga*	46.5	-	-	-	1171	416[2]
Non-alluvial sites							
Washington/Oregon (Spies and Franklin, 1991)	*Pseudotsuga/ Tsuga*	-	-	-	-	266 (219-324)	-
Washington/Oregon (Spies and Franklin, 1988)	*Pseudotsuga/ Tsuga*		317	-	36[2]	228	-
Washington/Oregon (Freund et al., 2015)	*Pseudotsuga/ Tsuga*						
Osprey		36.9	20	-	-	356.7	-
Cedar Flats		42.4	99	-	-	584.3	-
Drift Creek		38.6	61	-	-	236.0	-
Skynard		30.1	117	-	-	280.9	-
Ohanapecosh		36.1	78	-	-	240.5	-
Bagby		34.6	108	-	-	294.1	-
Sol Duc		25.0	98	-	-	186.1	-
Breitenbush		34.3	57	-	-	172.3	-
Huckleberry		28.1	-	-	-	182.3	-

[1] *Pseudotsuga* instead of *Picea*. All logs counted and measured.

[2] > 60 cm diameter.

2.4. Discussion

Along the climatic gradients of the northern Pacific Coastal Temperate Rainforest we found considerable structural differences between stands from the northern and southern sub-regions of our study area. Variation in stand structure and composition of old-growth floodplain forests are the result of multiple drivers acting either as top-down or bottom-up controls (Gavin et al., 2003; Heyerdahl et al., 2001; Lertzman and Fall, 1998). Bottom-up controls (e.g., a stands longitudinal position along the stream and lateral position away from the stream) interact with top-down controls (e.g., climate) influencing hydrological disturbance regimes and driving forest structure. The significance of these controls is scale dependant though they can act across multiple scales. Climate was the overarching driver of species composition in these data (Ohmann and Spies, 1998) and stand structure as well. Mean annual temperature was the strongest gradient influencing structure and composition. Flood disturbance proxies also exhibit relationships with stand structure and composition suggesting that flood regime significantly contributes to the ongoing development of within-stand old-growth floodplain forest structure. This may explain why we see more variation in old-growth floodplain structure than in upland forests.

2.4.1. Structure, Composition, and Climate

Climate is a top-down driver of stand structure and composition (Lertzman and Fall, 1998) and can be the most influential driver of structure and composition (Ohmann and Spies, 1998). This is true for the northern PCTR's floodplain forests as both Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) were significantly correlated with structure and composition. Warmer MATs are associated with larger diameter growth, tree size diversity, and higher species richness in old-growth floodplain stands. Sitka spruce is known to exhibit adaptive traits to sub-regional climate along the PCTR's latitudinal gradient (Mimura and Aitken, 2007), which our data support. Sitka spruce's productivity and height have also been negatively correlated with latitude and growing degree days (Farr and Harris, 1979). Growing degree days were highly correlated with temperature and strongly influenced stand structure in our preliminary NMDS analysis, displaying a strong top-down control on structure and composition.

Cooler MATs were associated with higher stem densities and higher ratios of western hemlock to Sitka spruce (Table 2.8; Figure 2.3). Higher latitudes have been correlated with higher stem densities in upland forests in the PCTR and delayed stand development (Wells, 1996). However, this does not explain the higher proportions of shade-tolerant western hemlock which established after the Sitka spruce pioneer cohort. Though higher abundance of western hemlock can somewhat be explained by a lack of other overstory species as tree diversity decreases at higher latitudes (Alaback, 1991). Northern sites tended to have truncated reverse-J tree diameter distributions indicative of old-growth forests (Freund et al., 2015), where southern sites were more representative of the characteristic reverse-J distribution (Figure 2.5). Like Douglas-fir in old-growth stands (e.g., Freund et al., 2015), Sitka spruce typically populates the tail of the diameter distribution displaying a pulse of establishment that took place post-disturbance. Interestingly, we see second pulses of Sitka spruce in our plots, indicating that moderate disturbance may be enabling re-establishment of spruce at some sites (e.g., South Fork Hoh 1 and 2) and that stand-replacing disturbance is not always necessary for spruce regeneration.

Dead standing and downed wood paralleled live structure in that size and density differed with latitude and MAT. Larger mean diameters and SD of DBH occurred in southern sites (Figure 2.5; Table 2.5 and Table 2.6). Clayoquot and Carmanah sites had high densities of CWD in decay classes III and IV compared to other sites in our study, their overall volume (432.2 m^3 and 190.3 m^3) is comparable to CWD volumes in the Queets River valley which ranged from 128 – 654 m^3 (Table 2.13) (Van Pelt et al., 2006). Snag and CWD volumes in the mid to upper decay classes in Clayoquot and Carmanah are likely influenced by a large episodic disturbance event that took place on the south west coast of Vancouver Island long enough ago for the mortality caused to reach later decay classes at the time data was collected (Figure 2.7 and Figure 2.9). Most sites appear to have more than ongoing low-level mortality, some sites exhibit ongoing discrete mortality (i.e., Fish Creek 1, 2, and 3) where other sites have episodic disturbances like Clayoquot and Carmanah (i.e., Trap Bay, Marten 1, Kitlope, and Tahsish-Kwois). Additionally, Clayoquot's CWD is composed of larger pieces which subsequently contribute to a higher volume and lower density than the Carmanah site. Carmanah has a substantially higher CWD density and relatively lower CWD volume (Table 2.6).

Snag density was not correlated with PAS as we anticipated but was negatively correlated with MAT (Table 2.9). Although, we may not have found PAS to be significantly correlated because of low sample size, we see in Figure 2.6 and Figure 2.7 that higher snag densities were associated with higher latitude sites. Since snag densities are higher among the southeastern Alaska sites, we suggest further exploration into the contrast seen between northern and southern latitudes. Extending future analysis to include wind exposure as a disturbance agent may lend further insight. Southeast Alaska experiences periodic large scale wind disturbance, especially on exposed locations on the landscape (Kramer et al., 2001) and is more prone to wind disturbance than BC's central coast (Pearson, 2010). Interactions between wind and decay fungi are also prominent in southeast Alaska (Hennon and McClellan, 2003) which may account for higher snag densities.

Overstory species abundance did not vary appreciably, though sites in southern BC tended to have a greater abundance of deciduous trees. Overstory species diversity (H') increased with higher ratios of Sitka spruce to western hemlock to a point (Figure 2.4). However, for plots with deciduous species as sub-dominant and co-dominant overstory species the ratio of spruce to hemlock was not important. It is important to note that species composition in our study was limited by plot location and a lack of replicates. Other species such as western redcedar were present in some stands but because of random plot placement western redcedar was excluded (i.e., Yakoun).

Climate's significance when comparing structure and composition across sites is scale dependent; when the climatic gradient decreases, site conditions become more important for determining forest structure. Ohmann and Spies (1998) determined macroclimate to be the ultimate driver of community composition in a gradient analysis spanning the extent of Oregon with site conditions secondary (i.e., geology, disturbance and topography). Across a portion of our study area in southeast Alaska, Alaback and Juday (1989) observed that soil conditions were more important than climatic gradients in influencing stand structure. Considering these previous studies and our analyses, climate is a key regional driver of structure and composition in the PCTR though at finer spatial scales its importance becomes secondary to bottom-up drivers (e.g., soil type or topography).

2.4.2. Flood Proxies and Disturbance

Flood disturbance plays a key role in floodplain species composition (Pabst and Spies, 1998) and, as we hypothesized, our flood proxies correlate to several stand structural attributes indicating that stand structure is partially driven by flood disturbance (Table 2.8). The flood proxies used to examine the potential relationships between flood disturbance and stand structure and composition were selected with the reasoning that they each contribute to a catchment's hydrological regime, so cumulatively these variables would better correlate to stand structure and composition than we see in our analysis. The flood proxies that are indicators of more intense flood regimes, such as steep slopes and high rainfall, compound to indicate a higher potential for more frequent and severe flood events. Cumulatively, the flood proxies' correlations with stand structural attributes suggested that flood disturbance supports the growth of large diameter trees as well as a diversity of tree sizes (Table 2.8). Additionally, flood proxies indicated areas that have a higher potential for flood disturbance are more likely to have lower stem densities and less western hemlock. The correlation of flood proxies with these stand attributes indicates that flood disturbance can foster productivity and consequently the development of old-growth characteristics (e.g. large diameter trees and diversity of stem sizes). At the regional scale, flood disturbance is a secondary driver to climate, this is consistent with Ohmann and Spies (1998) study in Oregon's forests which also found disturbance to be a secondary driver to climate along with soils and topography.

Hydrological disturbance regimes are projected to change because of warmer temperatures associated with climate change (Schnorbus et al., 2014; Shanley et al., 2015) which will lead to shifts in streamflow regimes including changes in frequency, duration, and intensity of flood events. It is reasonable to connect these hydrological changes with the potential for forest structure and composition to change as well. Swanson and Lienkaemper (1980) found that forests on older terraces, where trees were > 250 years, were still affected by flooding and resulted in multi-aged stands not originating from a single flood event. The Kitlope plot's diameter distribution shows an indication of this with a single large Sitka spruce (DBH = 284 cm, Figure 2.5) which is likely from a previous cohort since the next largest tree is over a metre in diameter smaller (DBH = 168.4 cm). Changes in hydrological regime may therefore negatively impact old-growth forest structural complexity at the stand level.

2.4.3. Comparison to upland old-growth forests

The most obvious difference in attributes of floodplain *versus* upland stands in our study is that floodplain stands are more variable than uplands stands (Figure 2.14). This may be due to better selection of comparable sites by upland researchers or because floodplain sites and their processes are inherently more variable. Further, the geographical range we examined is much broader for floodplain forests than upland old-growth studies. We were restricted from completing a more comprehensive comparison because of inconsistent reporting of stand attributes in the literature and differences in sampling methods. However, for stem density, mean diameter, basal area, and density of shade-intolerant leading species we see floodplain values from our study and previous studies, above and below the 5th and 95th quantiles of upland data.

Our approach to characterizing old-growth in floodplain forests should be similar to upland stands. However, when defining old-growth on floodplains, flood-regime should be considered as CWD is highly variable and thus not an effective attribute to include in old-growth quantitative definitions. Further, quantitative old-growth definitions should reflect latitude or sub-region. Floodplain stands north of ~ 57° latitude met all dead wood criteria of the upland old-growth definition proposed for Douglas-fir stands by Franklin and Spies (1991a). However, some sites lacked large diameter live trees (>100 cm DBH) and those that made the threshold had markedly fewer large trees than southern sites (Table 2.4). Floodplain stands south of ~57° latitude, including from other studies, surpassed Franklin and Spies' (1991a) quantitative old-growth thresholds easily except for the three least developed stands in our study (Marten 2, Kitlope, and Tahsish-Kwois Active). Located on medium and medium bench transitioning to high-bench terraces, these plots lacked sufficient shade tolerant stems (≥ 10 shade tolerant trees ≥ 40 cm DBH) likely due to the more frequent and longer inundations on the lower landform position. Additionally, Kitlope does not have enough snags (≥ 4 snags ≥ 50cm DBH) or CWD to meet Franklin and Spies' (1991a) old-growth thresholds.

Interestingly, all sites that we know to have a more volatile flood regime do not make the CWD threshold proposed by Franklin and Spies' (1991a) (Marten 1 and 2, Kitlope, Tahsish-Kwois, and Tahsish-Kwois Active). When establishing the Kitlope plot, silt was found up to one metre on trees. CWD was found partially buried or washed away. Lower densities of dead wood may also be attributed to their developmental stage as they're transitioning to old-growth forest or are young old growth (e.g., vertical diversification stage; Franklin et al., 2002). However, Marten 1 is a well-developed old-growth stand and is still deficient in CWD according to Franklin and Spies' (1991a) old-growth definition. Floodplain forests' CWD volumes vary considerably. CWD volumes range less in our study (3.1 – 432.2 m^3/ha; Table 2.6) than in the Queets valley (97 - 654 m^3/ha; Table 2.13). Sutherland et al. (2016) also found CWD to be highly variable in coastal BC, though there was no significant difference between riparian and upland plots.

2.4.4. Stand development and structure

The variability in stand structure among old-growth floodplain forests is associated with variability in stand development and interacting drivers. Stands with higher MAT and MAP had more developed old-growth structure, including larger mean diameters and lower stem density. During stand development mean diameter increases over time following a sigmoidal curve (Franklin and Spies, 1991a, 1991b; Wells, 1996) and stem density inversely decreases (Acker et al., 1998; Spies and Franklin, 1991). However, stand development across our study area, with an array of physical, ecological and climatic drivers acting at different levels, is likely to vary from stand to stand and so should the shape of the curve. In Figure 2.15, each site in our study is plotted along theoretical curves, first proposed by Franklin and Spies (1991b) for old-growth Douglas-fir and adapted here for Sitka spruce floodplain stands.

Time since last stand replacing disturbance (stand age) may explain some differences in stand structure that are not readily explained by the climatic and disturbance drivers we've discussed. Shaheen and Tahsish-Kwois were two sites whose unique stand structure required further explanation beyond these drivers. Since we used historical data, we were unable to include stand age in our analysis as this information was not originally collected at all sites. However, using site descriptions, stand attributes, disturbance regime, and stand age when possible, we were able to place these stands along the hypothetical developmental curves.

We hypothesize that the Shaheen stand is substantially older than other sites and has undergone pioneer cohort loss, using Franklin et al.'s (2002) stand development stages. The Shaheen plot was predominantly western hemlock with a relatively small mean diameter and high stem density. Other sites in our study were in the vertical or horizontal diversification stages (Franklin et al., 2002). Longer intervals without stand replacing flood disturbance are responsible for the stand to last long enough to undergo pioneer cohort loss. However, because of flood disturbance this was thought to be rare, along with western hemlock becoming the leading overstory species (Balian and Naiman, 2005). The longevity of Sitka spruce in these stands has been questioned in the Queets Valley, where it was estimated that they last in good health no longer than 400 years on alluvial sites (Van Pelt et al., 2006). The Shaheen stand is probably > 500 years old with only a few large Sitka spruce left. In contrast, another alluvial plot established along Shaheen Creek by Alaback and Juday (1989) had several large diameter Sitka spruce (maximum diameter for Sitka spruce was 208 cm) and was between 500-750 years old without pioneer cohort loss (Table 2.10). Thus, stands along the same river can have much different developmental trajectories, or in our Shaheen case a shorter sigmoidal curve compared to Alaback and Juday's stand that would have a more elongated sigmoidal curve for mean diameter.

Developmental trajectories can be shifted up or down depending on the ecosystem's properties. Stands in the northern range of our study have trajectories that are elevated for curve 1 and depressed for curve 2 (Figure 2.15). The Tahsish-Kwois plot has exceptional stand attributes such as numerous large live trees (56 ≥ 100 cm/ha) and an 85.5 cm mean diameter which sets it apart from other stands in this study. This stand's developmental trajectory (i.e., curve 2) is much steeper than other stands that we examined. We see from Tahsish-Kwois' diameter distribution which has a developing reverse-J distribution, that this site hasn't started losing its initial pulse of Sitka spruce (Table 2.4; Figure 2.5). This lends reason to why the mean diameter and basal area are so high at this site. Given these attributes, it is reasonable to conclude that Tahsish-Kwois is younger than stands with similar climate. Differences in site index may also contribute to higher values though because site index was not included in our historical data, we were unable to asses this.

We illustrate in Figure 2.15 a reduction in biomass in very old to ancient floodplain stands occurring earlier than in upland stands indicated by the sigmoidal curves (curve 2) for upland and floodplain forests crossing. We see that over centuries mortality of large diameter Sitka spruce can shift the species composition to being dominated by smaller western hemlock stems as seen in our Shaheen plot and by Little et al. (2013) in their old-growth terrace plots in the Carmanah River valley (Table 2.10).

Little et al. (2013) also saw much higher stem densities (mature and old growth terraces had 520 stems/ha and 1115 stems/ha, respectively). Thus, smaller mean diameters and higher stem densities can be attributed to younger stands (Spies and Franklin, 1991), stands with shifted developmental trajectories (e.g., our northern plots), and stands where Sitka spruce were unable to re-establish throughout stand development creating a higher density stand largely of smaller hemlock.

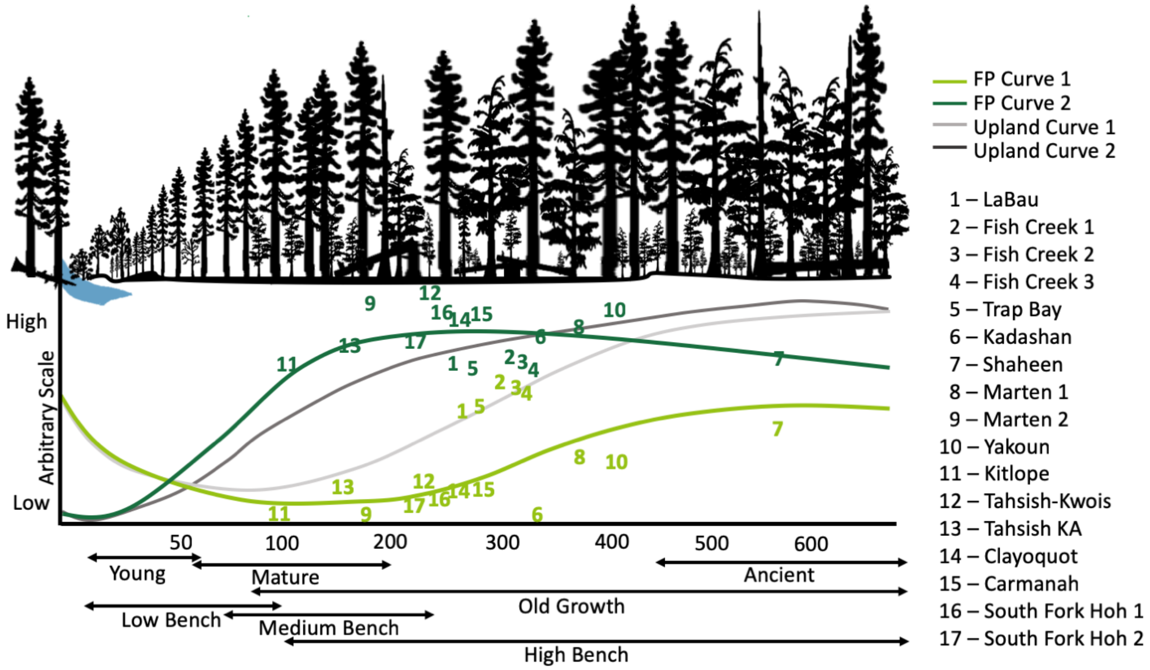


Figure 2.15 **Theoretical curves of structural attributes highlighting developmental trends in Sitka spruce floodplain forests. Curve 1 illustrates the progression of attributes such as stems/ha and dead wood density that follow as sigmoidal type curve. Curve 2 shows the development of attributes such as mean DBH and basal area. As an example, plots are positioned in terms of where they are along these curves using stems/ha (curve 1) and mean DBH (curve 2) (Graphic adapted from: Franklin and Spies, 1991a; Spies et al., 1988; Wells, 1996). FP = floodplain.**

2.4.5. Re-thinking the PCTR Sub-zones

The structural and compositional differences we see along the PCTR's climatic gradients can help us to refine our understanding of how we stratify sub-regions. As we noticed in the NMDS ordinations and the hierarchical clustering analysis, site groupings diverged from their current sub-regional classifications, the perhumid and seasonal temperate rainforest zones. Two main groups emerged. The first branch of the cluster analysis includes all sites north of Fredrick Sound, Alaska, or ~57° latitude. The second is south of this parallel (Figure 2.13). We had anticipated that the division among plots would likely relate to the PCTR's perhumid and seasonal sub-regions prior to running the initial NMDS analysis. Though we expected that there would be a gradient in structure north to south, with smaller, higher density trees in the more northern sites and more large diameter trees in the south, we did not expect such a clear distinction. We expected site conditions to exert enough bottom-up control over productivity that these rich, fast-growing sites would still achieve similar complex structure. This separation urges the question, are these forests located in a transitional zone between the perhumid and subpolar sub-regions and therefore deserving of a new classification, or do sites north of ~57° latitude have more in common with the subpolar sub-region and thus should the subpolar sub-region be extended south? If this region is deserving of its own sub-region, what are the extents? Currently there are two sets of sub-regional boundaries for the PCTR (i.e., DellaSala et al., 2011; Wolf et al., 1995). They are comparable, except for the boundary between the sub-polar and perhumid sub-regions, which shifts slightly. Thus, this northern perhumid – sub-polar boundary was already in question and our data encourage further examination.

Mean annual temperature and precipitation gradients are top-down controls affecting stand structure and separating the first branches of the cluster analysis. We reason that subsequent branching is related to interactions between climate, disturbance, elevation and developmental stage. For example, high elevation sites in southeast Alaska grouped together (Figure 2.13). Elevation gradients have been used as analogous gradients to latitude, such as in northern California where an increase in roughly 140-300 m can equate to an increase in one degree of latitude (Parker, 1994). Considering this, it makes sense that the higher elevation sites grouped together (e.g., Fish Creek 2 and 3) as climate is driving, or limiting, stand structural development in these plots. Climatic gradients associated with elevation are likely affecting sites south of ~ 57° latitude as well. The South Fork Hoh sites are much further south than other sites they grouped with and were expected to have more in common with sites in closer proximity. However, they are higher in elevation (> 200 m above sea level) than all sites south of ~ 57° latitude (around sea level for all but Carmanah which is ~ 150), likely contributing to their similarity in stand structure to sites more north in latitude than expected (i.e., Marten 1 and 2, Kitlope, Tahsish-Kwois Active). Elevation is a significant variable for explaining total variation (Ohmann and Spies, 1998) and predicting biomass (Buma et al., 2016). Our analysis suggests that elevation can also be used to explain stand structure in floodplain forests, as with upland forest in the PCTR (Wells, 1996).

Over elevation, hydrological disturbance is seen as the key reason for the tertiary branching of sites south of ~57° latitude in the cluster analysis (Figure 2.13). Sites with more severe flood regimes clustered together (i.e., Kitlope, Marten 2, South Fork Hoh 1 and 2, and Tahsish Kwois Active). Some catchments in our study area had two plots, of those, the plots that were medium-bench transitioning to high-bench were the plots that are found in this group, likely because these sites see more inundation than their high-bench counterparts. This illustrates that at the catchment scale disturbance is a more important driver than climate. Here, topography, or landform, is acting as a bottom-up control and driving stand structure at the site level. Otherwise, medium-high bench sites should group with their adjacent high-bench plot (i.e., Tahsish-Kwois plots and Marten 1 and 2). We see that controlling for disturbance in old-growth forests can help us elucidate sub-regional differences when re-evaluating the PCTR's sub-regional boundaries if stand structure is used to help evaluate potential boundaries.

Climatic gradients and disturbance regimes were unable to explain all the branching in the cluster analysis. The Shaheen plot (~ 55.7° latitude) was similar climatically to the Yakoun stand (~ 53.6° latitude) though exhibited far different structure. Another alluvial plot established along Shaheen Creek (Alaback and Juday, 1989) was also much different that the plot from our study, though similar to the Yakoun site. The Shaheen plot from our study, being further along in its developmental curve (Figure 2.15), has lost its pioneer cohort and therefore clusters with the higher density, smaller mean diameter, north of ~57° latitude sites rather than with sites to the south that are more climatically similar. It's reasonable to think that it would have stand characteristics more similar to our Yakoun, since it is relatively warm in comparison to sites to the north and receives significantly less precipitation than the Marten sites which are of similar MAT (~2550 mm compared to ~3500). Therefore, if reconsidering boundaries for the PCTR's sub-regions, focusing research efforts between ~ 55° and ~ 57° degrees would be a logical place to start for the northern perhumid sub-region.

Our findings encourage the refinement of the current sub-regional classifications of the PCTR. Reassessment and refinement of coastal BC BEC zones is in progress (Saunders pers. comm.); reviewing the PCTR classifications would complement the BEC revisions. Differences in stand structure and composition seen between the northern and southern zones of the perhumid sub-region were sizeable. Evaluating the PCTR's climatic gradients and how they drive forest structure can help monitor how climatic envelopes are shifting in the PCTR. Our understanding of climate change and its influence on floodplain forest disturbance regimes is in its infancy. At the landscape level, we know that warmer phases of large scale climatic patterns (e.g., El Niño Southern Oscillation or the Pacific Decadal Oscillation) can increase the severity of hydrological disturbances, which can decrease the proportion of older forest on the floodplain (Little et al., 2013; Whited et al., 2007). This creates some urgency as our time available to study these systems and implement adapted management plans and policies is limited. On average, temperatures in coastal BC are already 0.6ºC higher than at the beginning of the 20th century and each decade precipitation is increasing 2-4% (Boisvenue and Running, 2006). Landscape managers should plan for shifts in forest composition and decreased old-growth on the landscape, thus implementing the precautionary principle and conserving more old-growth and transitioning old-growth to maintain ecosystem resilience and habitat. Further, we are unfamiliar with how flood events with increased severity will interact with other disturbance events (e.g., windthrow, fire, insects, or harvest). Cumulative disturbances can cause unpredictable, non-linear, responses (Buma and Wessman, 2011). Examining how climate change will affect disturbances and floodplain forests' resilience mechanisms (*sensu* Buma and Wessman, 2011), their ability to recover after more severe disturbances, and how interactions with multiple severe disturbances is imperative for effective forest management and to maintain forest productivity and biodiversity.

2.5. Conclusions

Riparian areas are vital components of the Pacific Coastal Temperate Rainforest. Their ability to provide habitat for aquatic and terrestrial species and forest productivity is essential. Though riparian areas are significant elements of the ecosystem, they are also thought to be the most susceptible to environmental change (Naiman et al., 1993). However, we still know little regarding their natural disturbance regimes and how disturbance events affect forest structure, species composition, and ecosystem function. Our research highlights how variable structure and composition can be in floodplain forests of the PCTR, not only at sub-regional scales driven by climate, but also local scales driven by natural disturbance regimes.

Our data describes forest structure at the stand level and how it varies across the PCTR region. Though this is useful, we can only hint toward the complex interactions between disturbance regimes, climate, and structure as it's missing the power to elucidate the effect of differing disturbance regimes on stand structure. Consequently, our study is unable to predict the effects of climate change and its potential positive feedback-loops effecting disturbance regimes, stand structure, and ecosystem function. However, this is growing in importance for managing these forests for the multiple ecosystem services that they provide. Because of the distinctness of each stand and catchment's flood regime we suggest three connected actions to address these limitations. The first is to spatially analyze available historical stand maps of trees, snags, and logs for our sites and compare these to current stand conditions. This will help to determine background mortality and the relative roles of hydrological disturbance and wind, which are probable drivers of gap-phase dynamics in these forests. The second is to incorporate paleo-ecological methods, such as sediment cores and tree rings (e.g., Brown and Schoups, 2015; Lara et al., 2008) (Chapter 1, 1.4.1) to obtain the historical range of variation to use as a reference in monitoring flood regime changes and subsequent stand structural changes due to climate change in catchments with plot data. Lastly, we can expand the current network of plots to areas of the PCTR that are missing data points to ameliorate our latitudinal analysis, establish replicates in catchments with plots, and re-measure them on a time interval that will effectively capture stand dynamics (e.g., five years).

These actions will enable us to control for factors such as streamflow regime or site index to determine the effect of flood disturbance on stand structure. Linking paleo-ecology to current plot data allows us to establish a range of historical variation for flood regimes and compare them to current flood regime data, thus providing a better temporal perspective on disturbance regimes in these systems and their resilience to climate change (Buma et al., 2018). Our study area has relatively few data points compared to other large scale latitudinal studies (e.g., Ohmann and Spies, 1998; Schietti et al., 2016). British Columbia's coastal area is a significant part of the PCTR and there are still catchments unaffected by forest harvest, but the BC coast is underrepresented in the dataset relative to its geographical coverage. There is an important opportunity for the province to contribute research efforts to the old-growth floodplain plot network beyond maintaining established plots.

How we classify floodplain forest types and landforms affects a researcher's ability to compare across studies. Looking at Figure 2.1 (Chapter 1, Figure 1.2), we see different terms applied to similar floodplain landforms that support old-growth stand structure. Perhaps the reason that each study has a slightly different naming convention or applies a convention differently is that every catchment is different, as are their hydrological disturbance regimes. Currently the standard measure for illustrating the co-evolution of toposequence and forest succession, or biogeomorphic succession and the developmental pathways and processes, only includes time since disturbance (e.g., Little et al., 2013; Naiman et al., 2010; Van Pelt et al., 2006). However, frequency, intensity, and duration of flood events are also important in distinguishing landform development. In a catchment, two sites with similar times since stand initiating disturbance may be at different stages of landform and forest development. This can be because their developmental trajectories may differ due to differences in topography and flood regime, even without having one or several stand re-initiating flood events. Further, climatic gradients also affect forest development and structure. Thus, forests at different latitudes or elevations but on similar aged landforms may exhibit differing stages of forest development. Perhaps it's time for a paradigm shift in how we relate forests and landforms on floodplains so that we're not solely relying on time since last stand re-initiating disturbance to establish landform age and subsequently evaluate forest types.

To help researchers identify and control for differences among hydrological disturbance regimes that affect forest development, we suggest including flood frequency and severity as site descriptors. Frequency is already included in the BEC classification system (i.e., low, medium, and high-bench classifications; Green and Klinka, 1994; MacKenzie and Moran, 2004) though further refinement would help cross study comparison. Using frequency and severity of flood events, along with time since last stand replacing disturbance, to communicate the differences among landforms and catchments can help to identify what drives differences among old-growth floodplain stands. If possible, including time since last major non-stand reinitiating flood event can help bring some context to differences is stand structure (e.g. CWD volume and density) for stands with similar disturbance regimes and landform positions. Similarly, we must not ignore the fact that rare stand replacing events can occur without reducing the landform to active channel. Thus, landform and forest disturbance cycles may be asynchronous. Lastly, we must also recognize the important role that small, frequent, gap creating events have in generating differences among stands as rare stand replacing flood events are not the only disturbance mechanism affecting stand structure.

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Appendix.

Supplemental Tables and Figures

Table A1. Stand structural attributes for stems ≥ 5 cm DBH.

Site	Mean DBH (cm)	SD of DBH	Site BA (m^2)	Stems/ha	Stems ≥100 cm DBH/ha	Stems 50-100 cm DBH/ha	Sitka spruce/ha	Spruce ≥100 cm DBH/ha
LaBau	34.7	23.2	43.1	315	2	75	226	2
Fish Creek 1	33.0	23.4	45.1	352	12	36	80	8
Fish Creek 2	25.0	25.5	73.1	732	16	84	80	12
Fish Creek 3	24.6	23.4	61.3	680	12	72	108	8
Trap Bay	37.0	27.7	90.3	540	16	140	236	16
Kadashan	37.1	28.5	19.7	116	4	28	36	4
Shaheen	26.8	26.7	67.0	596	8	100	4	4
Marten 1	51.0	43.2	92.0	264	36	76	108	28
Marten 2	71.4	46.8	68.0	120	32	32	84	32
Yakoun	34.3	47.6	103.2	384	48	40	104	32
Kitlope	52.1	58.3	70.0	148	24	32	84	24
Tahsish-Kwois	85.5	68.4	126.6	136	56	24	52	44
Tahsish-Kwois Active	41.4	38.7	64.1	256	36	28	44	16
Clayoquot	49.9	53.5	103.8	248	42	38	30	22
Carmanah	57.4	53.5	101.7	212	48	40	12	12
South Fork Hoh 1	47.5	55.1	87.7	211.5	35	30.5	137.5	32.5
South Fork Hoh 2	34.6	52.6	61.8	199	21	19	160	16

SD of DBH = Standard Deviation of Diameter at Breast Height.

Table A2. Height of tallest dominant and co-dominant trees in metres (m).

Site	Sitka Spruce	Western Hemlock	Western Redcedar	Big Leaf Maple
Fish Creek 1	48.3	45.6	-	-
Fish Creek 2	49.9	33.8	-	-
Fish Creek 3	44.6	44.8	-	-
Marten 1	63.6	35.6	-	-
Marten 2	62.8	23.1	-	-
Yakoun	59.1	60,6	-	-
Kitlope	-		-	-
Tahsish-Kwois	60.7	38.5	-	-
Tahsish-Kwois Active	-		-	-
Clayoquot	75.8	25.2	40.2	32.7
Carmanah	-	-	57.3	-

Table A3. Snag density by decay class.

	Snags/ha by Decay Class								
Site	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**Unknown**
Fish Creek 1	28	52	20	16	-	-	-	-	8
Fish Creek 2	12	24	12	36	24	-	-	-	36
Fish Creek 3	4	24	44	40	8	-	-	-	12
Trap Bay	-	-	16	52	20	-	-	-	4
Kadashan	8	-	-	4	24	-	-	-	188
Shaheen	-	10	82	6	10	30	16	2	6
Marten 1	-	4	8	4	-	-	-	-	-
Marten 2	16	12	4	8	-	-	-	-	148
Yakoun	-	-	8	12	20	4	4	-	-
Kitlope	-	8	20	-	-	-	-	-	8
Tahsish-Kwois	-	-	-	12	-	-	-	-	-
Tahsish-KA	4	12	-	-	-	-	-	-	-
Clayoquot	-	4	4	2	6	2	6	-	-
Carmanah	4	4	8	32	20	-	-	-	-

Note: Data from some plots were missing decay class notes and original notes were not available, these snags were placed in the unknown class.

Table A4. Snag density by species. Unknown represents snags that were not identifiable.

Site	Sitka Spruce	W. Hemlock	W. Redcedar	Red Alder	Douglas maple	Pacific Crabapple	Unknown
Fish Creek 1	60	56	-	-	-	-	8
Fish Creek 2	-	144	-	-	-	-	-
Fish Creek 3	4	128	-	-	-	-	-
Trap Bay	64	28	-	-	-	-	-
Kadashan	52	104	-	24	-	-	44
Shaheen	-	162	-	-	-	-	-
Marten 1	12	-	-	-	-	-	4
Marten 2	128	44	-	8	-	-	8
Yakoun	20	28	-	-	-	-	-
Kitlope	4	-	-	20	-	4	8
Tahsish-Kwois	-	-	-	-	-	-	12
Tahsish-KA	-	-		12	4	-	-
Clayoquot	4	8	2	6	-	-	4
Carmanah	28	28	4	-	-	-	8