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**OVERSTORY STRUCTURE DRIVES FINE-SCALE COUPLING
OF UNDERSTORY LIGHT AND VEGETATION IN TWO
TEMPERATE RAINFOREST FLOODPLAINS**

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Abstract

Riparian ecosystems – particularly floodplains – of temperate rainforest regions are productive, diverse, functionally important and socially valued, yet we lack key information about their structure and function to guide conservation and management. In two one-hectare floodplain sites in coastal British Columbia, we mapped tree locations, classified gap processes, and described understory vegetation and light transmission on a systematic grid. We used hemispheric photography and spatial interpolation to map understory light and we examined how environmental heterogeneity affects understory vegetation. Understory light levels are high (overall median 18% full sun) but vary appreciably over short distances (0.5% to 19% full sun over 14 m). Understory composition varies in relation to light transmission, indicating that overstory structure drives fine-scale spatial structure in the understory plant community. Overstory trees appear to create “shade refuges” from competition with dominant shrubs. Shrub cover increases with light and may also play a role in maintaining persistent canopy openings by slowing conifer recruitment. Despite substantial differences in age and development history, each stand exhibits fine-scale spatial coupling of understory light and vegetation. Management practices encouraging structural complexity may accelerate development of similar processes and patterns to restore floodplain function in high-density second growth stands.

Keywords: riparian forest; canopy gaps; light transmission; understory vegetation; coastal temperate rainforest.

41 Introduction

42 Understanding how disturbance and other stand development processes shape overstory and
43 understory vegetation is central to forest ecology (Watt 1947, Brokaw 1985, Franklin et al.
44 2002). As a stand matures, small-scale canopy disturbances and tree growth generate complex
45 horizontal and vertical structure (Spies and Franklin 1988, Lertzman et al. 1996, Franklin et al.
46 2002). Such small-scale canopy disturbances increase the availability and heterogeneity of
47 understory resources such as light (Runkle 1984, Canham et al. 1990), with consequences for the
48 productivity, composition, and diversity of understory vegetation (Denslow 1985, Mladenoff
49 1990, McCarthy 2000). Conversely, understory vegetation may influence tree recruitment, gap
50 filling, and stand dynamics (Spies and Franklin 1989, Royo and Carson 2006). For example, in
51 some forests *Rubus spectabilis* Pursh invades forest openings, inhibits conifer regeneration, and
52 may be able to maintain persistent canopy openings (Henderson 1978, Minore and Weatherly
53 1994, Tappeiner et al. 2001). Similar processes have been observed with *Acer circinatum* Pursh
54 (McGhee 1996) among other understory plants (Royo and Carson 2006) – hereafter referred to as
55 the persistent gap hypothesis.

56 Dividing the forest into coarse classes of gap and closed canopy provides a first approximation
57 of canopy openness and within-stand resource heterogeneity. However, despite the sometimes
58 stark differences in canopy openness between gaps and closed canopy patches (e.g., Levey
59 1988), the fine-scale patterns and processes of light transmission are often more complex than
60 can be adequately described by this dichotomy (Lieberman et al. 1989). This is particularly true
61 in higher latitude temperate forests where the ubiquitous effects of topography (Canham et al.
62 1990) are accentuated by tall canopies and sub-canopy layers, resulting in the footprint of light

transmission sometimes being displaced substantially from the actual canopy opening (Van Pelt and Franklin 2000). The original binary gap concepts and methods also begin to break down for large openings (e.g., 1000 m² according to Schliemann and Bockheim 2011) and very open forests (Zhu et al. 2015). Treating the distribution of understory light as a continuous variable increases our ability to resolve and interpret the spatial patterns of light and potential drivers of understory vegetation (Lieberman et al. 1989, Frelich et al. 2003).

Riparian forests of the Coastal Temperate Rainforest (CTR) of North America (Schoonmaker et al. 1997) are among the most productive forests on the continent, with mature floodplain stands attaining among the highest canopy volumes on earth (Van Pelt et al. 2006). These forests support high understory vegetation biomass, tend to have higher plant species diversity than upland forests (Gregory et al. 1991; Pabst and Spies 1998), and support vigorous populations of culturally-important plant species (Turner 1998). Floodplain forests in the CTR also provide valuable habitat for a diversity of terrestrial wildlife, and interact with river systems in ways that create and maintain salmon habitat and linkages between terrestrial and marine ecosystems (Naiman et al. 2010). Floodplain forests also have significant timber value. In the CTR of British Columbia, floodplain forests have been preferentially harvested compared to upland forests (Pearson 2010) due to their productivity, timber quality, and accessibility. The BC Conservation Data Centre has assigned a conservation status of *imperiled* or higher to most coniferous floodplain communities in the CTR (BC CDC 2017). Despite the ecological significance and conservation status of these forests, we know little about the details of canopy structure and fine-scale interactions with understory light and vegetation, especially in the more Northerly portions of the CTR in BC and Alaska.

In this paper, we examined two large (1 ha), intensively surveyed forest plots in conifer-dominated floodplain stands of the CTR along the BC coast to characterize stand structure, assess the spatial heterogeneity of understory light regimes, and analyze the role of light and other environmental variables in driving within-stand vegetation patterns and processes.

Materials and Methods

Site descriptions

We studied two sites in the submontane variant of the very wet maritime subzone of the Coastal Western Hemlock zone (CWHvm1) of the British Columbia coast (Meidinger and Pojar 1991) (Figure 1 and Table 1). Mean annual precipitation for the CWHvm1 is 2682 (1555-4387) mm, mean temperature of the warmest month is 16.3 (13.8-18.8) °C, and growing degree-days average 1633 (1313-2011) days (Green and Klinka 1994) (Table 1). These sites were selected as representative examples of floodplain forests in the CTR as part of a larger network of long-term old-growth monitoring plots (MacKinnon et al. 2010).

The Kitlope site is located near the outlet in a 2758 km² unlogged watershed on the North Coast of British Columbia at the head of the Gardner Canal. The Carmanah site is on the Southwest coast of Vancouver Island and located more centrally within a 68 km² watershed. Both the Kitlope and Carmanah stands are in relatively flat valley-bottom sites classified as high bench floodplains with the corresponding *Picea sitchensis* – *Rubus spectabilis* Plant Association (Green and Klinka 1994). Typical high bench floodplains are classified as infrequently flooded sites (return interval >5 yr) (Green and Klinka 1994). Soils at the two sites are derived from fine textured alluvium (>70 cm depth) with varying degrees of humus development. Across the Kitlope site there was evidence of a recent low energy flood: during sampling there were silt

lines up to 1 m on tree boles and ~ 1 cm of fresh silty alluvium over most of the forest floor, under only ~ 0.5 cm of organic litter. Understory vegetation in each site is characterized by high total shrub layer cover (median >75%) dominated by *Rubus spectabilis* (median $\geq 55\%$). In each stand, the largest overstory trees are *Picea sitchensis* (Bong.) Carr., with several individuals taller than 60 m in height (max 62 to 93 m). Based on coring a sample of main canopy trees, stand age at Kitlope is at least 95 years. Stand age at Carmanah is at least 350 years, based on a core from a 50 m tall *P. sitchensis* (the largest trees could not be cored with the available increment borer). Floodplain forests in the CTR can develop a degree of old-growth character much earlier than upland forests (Van Pelt et al. 2006), and despite differences in age, both the Kitlope and Carmanah stands exhibit attributes of “old-growthness” (Wells et al. 1998, Franklin et al. 2002) including very large trees, open and structurally diverse canopies, and productive understory vegetation.

Sampling

Each site consists of a 100 m x 100 m (1 ha) plot in which all trees ≥ 5 cm diameter at breast height were mapped and measured (Figure S1, Supplementary material¹). We sampled understory vegetation in 25 subplots (2 m x 2 m) systematically distributed on a regular grid in each site and took hemispheric canopy photographs at 50 points on a regular grid, including in all vegetation subplots. Subplots had a minimum separation of 20 m and canopy photos had a minimum separation of 14 m. In subplots, we estimated percent foliar cover of all shrubs and herbs by species, based on a vertical projection to the ground.

¹Supplementary material for this article is available through the journal Web site.

127 We recorded canopy cover class (closed canopy, expanded gap, canopy gap) following the
128 methods of Lertzman and Krebs (1991). Using this method allowed us to compare our sites to
129 other CTR forests in the literature. An opening in the forest canopy was defined as a *canopy gap*
130 if it exceeded $\frac{1}{2}$ an average tree crown width in diameter. *Expanded gap* refers to the region
131 from a canopy gap boundary (crown margins) to a line connecting the boles of trees whose
132 canopies define the canopy gap. *Closed canopy* refers to the area beyond the boundary of an
133 expanded gap. Trees ≥ 10 m tall, with DBH ≥ 22 cm, were considered canopy trees, following
134 Lertzman and Krebs (1991). More recent methods for defining canopy gaps – particularly
135 minimum and maximum gap sizes – depend on the height of canopy trees surrounding a gap
136 (Zhu et al. 2015). However, these more complex techniques still result in a dichotomous
137 characterization of canopy openness and would prevent direct comparison of our results to
138 earlier studies in the region.

139 We defined gap origin (developmental, edaphic, unknown origin) following the methods of
140 Lertzman et al. (1996). Gaps of developmental origin have evidence of a gapmaker: a tree that
141 died to create the gap. Edaphic origin gaps are openings associated with edaphic conditions (e.g.,
142 stream channel, rock outcrop, or thin soil); gapmakers may be present but cannot, on their own,
143 explain the opening (Lertzman et al. 1996). Gaps of unknown origin are openings not obviously
144 associated with tree mortality or edaphic conditions.

145 To estimate light transmission to the understory as a continuous variable, we took hemispheric
146 canopy photographs above the shrub layer at each photo point, using a Cannon 5D digital SLR
147 camera and a Sigma 8-mm fisheye lens. Photos were taken above the shrub layer to ensure a
148 clear view of the overstory (lens height 180 ± 5 cm at Carmanah; 195 ± 5 cm at Kitlope). The
149 lens was leveled and oriented north. We registered the north position in the image with a small

LED light mounted on a lens plate. Shrub foliage above the lens was pulled away from the field of view. Auto exposure bracketing was generally used to record images at three exposures – we selected the highest contrast image that still maintained small gaps near the horizons (Frazer et al. 2000a).

We recorded additional environmental characteristics that might influence plants in each vegetation subplot. We visually estimated percentage ground covered by organic forest floor (≥ 1 cm organic layer), mineral soil (<1 cm organic layer), coarse woody debris, and other substrates. We recorded the thickness of organic horizons (L, F, and H) and the Ah layer (mineral soil enriched in humified organic matter). Substrate, soil horizon, and textural classes (by hand texturing) were defined following BC Ministry of Forests and BC Ministry of Environment Lands and Parks (1998).

Data preparation and processing

We used Gap Light Analyzer Version 2.0 (GLA 2.0) (Frazer et al. 2000a) to estimate light transmission, canopy openness, and leaf area index from canopy photographs. Site-specific configurations were used for elevation, latitude, longitude, and growing season, and subplot specific configurations for slope, aspect, and topographic shading. To increase the accuracy of light estimates, we calculated monthly cloudiness index, spectral fraction, and beam fraction based on solar radiation data collected at the most representative coastal meteorological station with solar radiation data (Port Hardy) using equations provided with GLA (Frazer et al. 1999). Growing season start and end dates were inferred from a combination of expert opinion (K. Lertzman and A. MacKinnon) and local climate normals for growing degree-days (degree-days above 5°C) and the frost-free period. Finally, we calibrated GLA for the Sigma 8-mm F3.5

172 fisheye lens by using 24 calibration data points provided by Sigma Corporation to define a
173 custom projection transformation in GLA (Frazer et al. 1999).
174 GLA requires a manual image thresholding procedure to designate each pixel as sky or non-sky.
175 We used two thresholding rules. First, even the lightest vegetation tones were designated as non-
176 sky. Second, we used regional thresholding (Frazer et al. 1999) to avoid loss of smaller gaps near
177 the horizon, or conversely, loss of fine foliage adjacent to open sky. To provide an indication of
178 precision with light transmission estimates, we re-processed GLA estimates from nine
179 photographs. Differences in percentage full sun estimates between runs were 0.31% full sun on
180 average and were never more than 3% full sun.

181 As measures of subplot species diversity, we calculated richness (S), evenness (E), and
182 dominance (Ls) using PC-ORD 5 (McCune and Mefford 2006). Species richness is the number
183 of species. Evenness – how evenly cover is distributed among species – is calculated as $E = H / \ln(S)$ (Pielou 1969) where H is Shannon diversity index $H = -\sum(p_i \ln(p_i))$ and p_i is the proportion
184 of cover in the i th species ($p_i = n_i/N$) (Gurevitch et al. 2002). Dominance expresses the probability
185 that two randomly chosen individuals belong to the same species, calculated as $Ls = D-1$
186 (Gurevitch et al. 2002) where D is Simpson's diversity index $D = 1/\sum(p_i^2)$.

188 We calculated derived measures of edaphic conditions for each subplot. Distance to the nearest
189 waterbody (small channels) was estimated from a fine-scale field-drawn map of waterbodies. We
190 used the SPAW Model with Soil Water Characteristics program (available online:
191 <http://hydrolab.arsusda.gov/SPAW/SPAWDownload.html>) to estimate percentage clay,
192 percentage sand, saturated hydraulic conductivity (Ks: cm/hr) and Plant Available Water (PAW:
193 cm³ water/cm³ soil) from field estimates of soil textural class and coarse fragment content. The
194 SPAW model uses the empirical equations of Saxton and Rawls (2006).

Some of the systematically sampled locations were not included in the analysis because they were rare (undersampled) and distinct microsites or were topographically elevated above the floodplain. At Carmanah, this included three subplots (eight photo points) on an elevated terrace landform, with different edaphic conditions than the floodplain; and two subplots in a fluvial channel lacking soil or vegetation. For vegetation analyses, we also omitted a subplot where the herbaceous layer and forest floor had been almost entirely buried by recent flood sediments. Furthermore, a recent wind disturbance at Carmanah substantially affected three subplots via the direct influence of overstory removal and slash accumulation. These subplots were subjected to a sensitivity analysis and removed from subsequent vegetation analysis – an effort to control for the temporal lag of understory vegetation response to canopy disturbance (e.g., Nicotra et al. 1999). At Kitlope, one subplot was omitted because it was in a small waterbody.

Analysis

We used ESRI's ArcGIS to generate maps of the spatial distribution of understory light and overstory trees. We used a tension spline interpolation to visualize light gradients between sample points. This interpolation method creates a smooth, minimum curvature surface that passes exactly through the data points.

We used linear correlation analysis to examine relationships among measures of light transmission, vegetation structure, and diversity. Because a number of the vegetation and environment variables in the dataset show positive spatial autocorrelation at 20 m (Giesbrecht 2010), potentially inflating Type I error rate for the correlation analysis (Legendre and Legendre 1998), we used Dutilleul's procedure in PASSaGE v2 (Rosenberg 2009) to correct for the effect of spatial autocorrelation on *t*-tests of correlation significance (Dutilleul 1993).

Non-metric multidimensional scaling (NMS) (Mather 1976, Kruskal 1964) was used to describe variation in species composition on multivariate axes. We conducted the NMS with the Sørensen (Bray-Curtis) distance measure, using the autopilot mode in PC-ORD 5 (McCune and Mefford 2006) with the “slow and thorough” setting. To aid interpretation, we rotated the resulting ordination graphs to maximize the correlation of Axis 1 with percentage full sun (McCune and Grace 2002). Axes 2 and 3 thus describe compositional variation that is virtually independent of light. After applying the rotations, we used correlation coefficients and ordination diagrams to describe the compositional axes in terms of species abundances and to examine relationships between compositional axes and environmental variables. We assessed the quality of the NMS solution, based on the proportion of variance in the original data represented by each axis and the three axes cumulatively. This proportion was computed using the Sørensen (Bray-Curtis) distance measure.

Prior to conducting the NMS ordination, we prepared the community dataset following McCune and Grace (2002). We deleted rare species: those with less than five occurrences. We applied a relativization to species abundances because our interest is more in compositional than structural changes. Specifically, we relativized by species maximum, which balances the emphasis on dominant species and species with lower abundances. Finally, we applied an arcsine square root transformation to all species to reduce the positive skew that characterizes community data.

Results

Stand composition and development

Both stands have a small number of large to very large *Picea sitchensis* trees – presumably the pioneer cohort (Figure 2). Both stands have a larger number of small to intermediate sized trees,

including some shade intolerant deciduous trees in the smaller (<50 cm) size classes. However, understory tree densities are very low compared to mature and old-growth forests in upland (zonal) sites of the same biogeoclimatic variant in BC (BC Ministry of Forests 2001), which have respectively 301 and 414 mean stems per hectare in the 7.5-17.5 cm diameter classes. By contrast, Kitlope has 27 stems and Carmanah has 55 stems, in this size range. Overall stem densities (117 at Kitlope; 241 at Carmanah) are also low compared to zonal forests of this subzone (720 and 790 for old-growth and mature stands respectively).

Despite these broad similarities of Kitlope and Carmanah, the two stands differ substantially in other aspects of composition and tree size structure, suggesting different developmental histories. The diameter distribution of live trees at Carmanah follows an approximate negative exponential distribution as expected for an old-growth forest, with shade tolerant *Tsuga heterophylla* abundant in most size classes <100 cm diameter and *Picea sitchensis* virtually absent below 100 cm. At Kitlope, tree densities are much lower in the small to intermediate (<90 cm) size classes, *Picea sitchensis* is present in the broad range of size classes and other conifers are nearly absent, suggesting a stand with less understory reinitiation of shade tolerant conifers than evident at Carmanah. Snags are abundant at Carmanah, including some very large (>100cm diameter) individuals (Figure S2, Supplementary material), which are mostly *Tsuga heterophylla* or unknown conifers, indicating main canopy tree mortality events that would have meaningfully increased light transmission to the understory. By contrast, there is little evidence of canopy tree mortality at Kitlope, with few snags >50 cm diameter.

Gap structure and light transmission

Closed canopy microsites are rare at both Kitlope (8%, of $n=50$) and Carmanah (2%, of $n=42$). At least 92% of each site is in expanded gap or canopy gap (Figure 3). At Carmanah, 27% of

canopy gap microsites and 12% of expanded gap microsites are located in an area of recent windthrow (presumably the winter before sampling, when extensive wind disturbance occurred across the BC south coast). Overall, most gap areas at Carmanah are developmental in origin (83%) – clearly associated with a dead tree – while the remainder (17%) have edaphic origins (Figure 3**Error! Reference source not found.**). By contrast, few gap microsites at Kitlope are clearly associated with tree mortality (2%) or edaphic factors (9% of gaps).

Kitlope and Carmanah each have median 18% of the PAR that would be available under an unobstructed view of the sky (hereafter “% full sun”) (Table 2). At Kitlope, mean light transmission is $18.8 \pm 4.8\%$ full sun, ranging from 10.0 to 33.9%. At Carmanah, mean light transmission is $17.9 \pm 5.7\%$, and varies from 9.0 to 28.3% (Figure 4). Carmanah has more microsites with $<12.5\%$ full sun and a bi-modal distribution of light availability, which taken together result in greater variation among microsites than at Kitlope (Figure 4). Light transmission at Kitlope is unimodal and more strongly concentrated around the mean.

Understory light is spatially variable within each one-hectare site. Light transmission estimates at adjacent sample points (14 m separation) range from very similar ($\pm 0.5\%$ full sun) to very different ($\pm 19\%$ full sun). These spatial gradients are also visually represented with the contour shading in Figure 5, based on interpolated light values between photo locations. Our understory light maps show the end result of solar radiation passing through the overstory filter. The vertical and horizontal distribution of forest biomass (represented in a basic way by mapped tree locations, tree diameters, and canopy cover classes) interacts with directional incoming radiation to produce the observed spatial pattern of light transmission.

Species composition in relation to environmental heterogeneity

At both sites, fine-scale spatial variation of the understory plant community is organized along recognizable compositional gradients. The autopilot NMS procedures recommended three compositional axes for each site. At Kitlope, the three axis solution represents 79% of variance in the original data, has a final stress of 14.05, final instability <0.00001 , and is significantly stronger than expected by chance ($P=0.004$). At Carmanah, the three axis solution represents 90% of variance in the original data, has a final stress of 8.32, final instability <0.00001 , and is significantly stronger than expected by chance ($P=0.004$). The NMS method produces axes defined by vegetation composition alone, without direct incorporation of environmental variables.

The strongest compositional axis at Kitlope (Axis 1) is best related to light transmission, with a strong linear correlation ($r=0.72$; Table 3 and Figure 6). There is only evidence of weak associations between Axis 1 and the edaphic properties we measured such as forest floor thickness or mineral soil texture (all $|r|<0.33$). Axis 1 represents 41% of the variance in the original data and describes a compositional gradient exemplified by *Oplopanax horridus*, *Dryopteris expansa*, and *Osmorhiza berteroi* associated with lower light levels and *Ribes bracteosum* and *Circaea alpina* associated with higher light levels. See Supplementary material S3 for a more complete examination of species associated with light. Axis 2 and Axis 3 represent 17% and 21% of the variance in the original data, respectively, and are unrelated to measured edaphic variables (Table 3 and Figure 6).

The strongest compositional axis at Carmanah (Axis 1) is also best related to light transmission ($r=0.57$), with only weak correlations with the edaphic properties we measured (all $|r|<0.35$) (Table 4 and Figure 6). Axis 1 at Carmanah represents 34% of variance in the original data and

describes a compositional gradient characterized by increasing cover of *Rubus spectabilis* and *Ribes bracteosum* with increasing light availability, with decreasing cover of *Blechnum spicant* among other species (Supplementary material S3) as light increases.

Axis 2 at Carmanah represents 27% of variance in the original data and is most strongly correlated with substrate properties, particularly clay content ($r=0.67$) and humus thickness ($r=-0.56$), independent of light ($r=-0.01$). Axis 3 at Carmanah represents 28% of variance in the original data and is not meaningfully correlated with the edaphic variables we measured (Table 4).

Cover of understory layers and species diversity in relation to light

The covers of herb and shrub layers show differing degrees of correlation with light transmission through the canopy. As expected, shrub cover is positively correlated with light transmission at both sites ($r=0.48$, $P_{Dut}=0.02$ Kitlope; $r=0.63$, $P_{Dut}=0.008$ Carmanah) (Table 5) after stratifying to exclude the recent windthrow. This is consistent with a hypothesis of light-limited shrub biomass. Herb cover, by contrast, is not significantly correlated with light, in either site, suggesting that shrubs play an important role in mediating herb response to overstory light transmission. Indeed, herb cover decreases significantly with *Rubus spectabilis* cover at Kitlope ($r=-0.41$, $P_{Dut}=0.04$).

Rubus spectabilis cover shows a strong and significant positive correlation with light transmission at Carmanah ($r=0.79$, $P_{Dut}=0.001$) but, surprisingly, not at Kitlope ($r=0.24$, $P_{Dut}=0.25$) (Table 5). However, *R. spectabilis* cover is positively correlated with light at Kitlope after controlling for the cover of other shrubs using partial correlation (Legendre and Legendre 1998) ($r=0.52$, $P=0.011$). Thus, at Kitlope, *R. spectabilis* response to abundant light may be

mediated by other factors such as competition with other shrub species. Indeed, further examination reveals that *Ribes bracteosum*, and sometimes also *Sambucus racemosa*, are more abundant than *R. spectabilis* in five of the six subplots that are bright yet have low *R. spectabilis* cover. In all other subplots, *R. spectabilis* is the most abundant of the three species. Furthermore, *R. spectabilis* was not completely absent from any subplot at Kitlope, suggesting that even in the darkest microsites in this stand, light may not be limited enough to exclude this plant.

Point level species diversity varies inversely with *Rubus spectabilis* cover. Increasing cover of *R. spectabilis* is positively correlated with dominance (Ls) at both Kitlope ($r = 0.71$, $P_{Dut} < 0.001$) and Carmanah ($r = 0.73$, $P_{Dut} = 0.002$). Correspondingly, *R. spectabilis* cover is negatively correlated with species evenness (E) at both sites (Table 5). At Carmanah, Ls has a strong positive correlation with light ($r = 0.72$, $P_{Dut} = 0.004$) and E has a negative correlation with light ($r = -0.64$, $P_{Dut} = 0.01$). Point diversity is not directly related to light transmission at Kitlope. Species richness does not show strong correlations with light or *R. spectabilis* in either site.

Recent conifer regeneration is limited at both sites. At Kitlope, no conifers were observed in the low shrub layer (<2 m) of subplots, and seedlings (all *Picea sitchensis*) were reported in only 5 subplots (21%). At Carmanah, no seedlings and only one conifer <2 m were observed across all subplots and most of the understory *Tsuga heterophylla* outside of subplots are found growing on logs.

Discussion

Openness: canopy openness and light transmission in context

Canopy structure in these floodplain forests is characterized by a high degree of canopy openness and light transmission compared to a broad range of tropical to temperate forests (Supplementary

material S4). Both Kitlope and Carmanah have high overall light transmission rate (median 18% full sun) and canopy openness (11.0 to 11.6%) compared to a range of other riparian and upland sites in the CTR (Frazer et al. 2000b, Sarr and Hibbs 2007a), although similar openness estimates have been reported for some drier (rainshadow), non-riparian forests of the CTR on eastern Vancouver Island (Frazer et al. 2000b). Similarly, our study sites have very high incidence of locations classed as canopy gap and expanded gap (92% at Kitlope, 98% at Carmanah) compared to the Tofino Creek watershed on West Vancouver Island (56%; Lertzman et al. 1996) and snowy subalpine rainforests on the BC south coastal mainland (70%; Lertzman and Krebs 1991). By contrast, mean light transmission at Carmanah and Kitlope is markedly lower than reported for a number of old-growth boreal forests in Quebec (27%; Bartemucci et al. 2006) and northern BC (26.7%; Bartemucci et al. 2002).

Such comparison of floodplain canopy openness and light transmission to a broader range of forests is complicated by methodological limitations. For example, the classic canopy gap definition we used includes some openings that are small compared to the height of surrounding trees, and may not meet recent recommendations for minimum size criteria (Zhu et al. 2015). This underscores the merits of using approaches such as hemispheric photography for global comparisons of canopy openness and light transmission. However, practical constraints dictate that hemispheric photographs can only be used to sample a small proportion of a landscape. By contrast, emerging applications of airborne laser scanning promise unprecedented capacity to compare hemispheric measures of canopy openness over large areas and at multiple scales (e.g., Moeser et al. 2014).

Origins of openness and sources of shade: processes leading to open and variable canopies

The origins of canopy openness – and sources of shade – differ between the two sites we studied, reflecting differing processes of stand development and of developmental stages. Carmanah has a bi-modal distribution of light (Figure 4) likely associated with the higher density and irregular spatial distribution of shade-casting conifers (Figure 5). At Kitlope there are few small and intermediate sized conifers to create deep shade microsites (Figure 2). In terms of gap origins, most gap microsites at Carmanah arise from the mortality of trees (Figure 3), and snags are common in a range of size classes, as expected for an old-growth forest driven by gap-phase processes. At Kitlope, by contrast, most gaps do not clearly have an associated gap-maker and few large snags were observed. Many of the ‘gaps’ at Kitlope may be legacy openings that have never been occupied by conifers. Very few of these legacy openings had obvious edaphic origins (Figure 3). Potential causes of such low initial densities and persistent legacy openings include frequent flooding and intense competition with shrubs/herbs, beginning early in stand development (Van Pelt et al. 2006).

Patterns of openness: spatial heterogeneity of understory light transmission

Within these two stands, light levels vary substantially over short distances, producing complex spatial patterns of light within each one-hectare site (Figure 5). Contour maps of light at the top of the shrub layer provide a visual representation of the spatial rate of change in the abiotic environment as a result of variable shading from trees. Our results show that light transmission can both vary substantially over short distances (e.g., a change of 19% full sun over 14 m) and more gradually over longer distances (e.g., <1% full sun over 20 m), depending on location within the stand. Such spatial variation in light has implications for fine-scale patterns of

microclimate, animal habitat, and silvicultural opportunities, in addition to the vegetation attributes examined in this study.

In many forests, the processes of mortality, recruitment and growth result in increasing levels of structural and environmental heterogeneity over time (Franklin et al. 2002). We find that fine scale mapping provides a compelling visual synthesis of the within-stand spatial heterogeneity of canopy structure (canopy openness, canopy cover class, tree locations and sizes) and environmental conditions (understory light) created by stand development and disturbance (Figure 5). Despite differences in stand age and development history, both the Kitlope and Carmanah stands have developed substantial spatial heterogeneity in the overstory and understory. These spatial patterns are clearly related to gap-phase processes in the Carmanah stand. At Kitlope, by contrast, there is little evidence of gap-phase dynamics suggesting other processes must account for the observed spatial heterogeneity. Regardless of the explanation (discussed further below), the younger Kitlope site provides an example of relatively rapid development of a degree of old-growth character by floodplain forests (Van Pelt et al. 2006). Our study, however, examined only a few of the characteristics that might differentiate old-growth from younger (or managed) floodplain stands.

Understory response to openness: light transmission shapes understory vegetation

We observed fine-scale spatial variation of understory vegetation composition that is strongly influenced by light transmission (or shading) by the overstory. At each site, the strongest compositional gradient is correlated with light transmission, largely independent of edaphic measures. However, the relationship between light and understory vegetation composition is weaker at Carmanah, potentially due to a temporal lag in vegetation response to recent canopy disturbance: the understory vegetation has not yet responded to the new resource distribution

created by that disturbance. The influence of light could also be weaker at Carmanah because more of the plant community is organized along a soil gradient. Here we observed that an additional component of understory vegetation composition (Axis 2) was correlated with edaphic conditions (soil organics and mineral texture). It is not surprising that there are more complex interacting drivers of the understory plant community in the stand exhibiting both more complex soils (e.g., a more developed forest floor; Table 2) and more recent canopy disturbance.

Species positively associated with light may have evolved strategies to exploit and dominate higher light microsites. *Ribes bracteosum* and *Rubus spectabilis*, tall shrubs associated with light in both our sites, are dominant in the understory of many open riparian areas across the CTR (Pabst and Spies 1998, Sarr and Hibbs 2007b, Hocking and Reynolds 2011). The mechanisms of *R. spectabilis* dominance have been well studied. This plant species utilizes rapid rhizome extension and stem growth to colonize openings, overtop other plants, and maintain high abundance (Tappeiner et al. 1991, Tappeiner et al. 2001). As a consequence, point level species diversity in our study decreased with increasing cover of *R. spectabilis*. However, despite the adaptations of *R. spectabilis*, our results suggest that its dominance of bright patches is not a foregone conclusion in the presence of *R. bracteosum* and *Sambucas racemosa*.

While some species thrive in the brightest microsites, others reach greatest abundance in the shade of overstory trees (e.g., *Oplopanax horridus*, *Dryopteris expansa*, *Blechnum spicant*, and *Osmorhiza berteroi*). *O. horridus* increases abruptly in shadier microsites at Kitlope and is never abundant above about 20% light transmission - despite the fact that *O. horridus* can be observed thriving in much brighter environments elsewhere (Burton 1998). At Carmanah, shadier microsites also have higher evenness and lower dominance. In these open floodplain forests, shady microsites may provide refuges from competition with dominant shrubs, such as *Ribes*

439 *bracteosum* and *Rubus spectabilis*. These “shade refuges” contribute to greater community
440 diversity by allowing poorer light competitors to reach relative abundance somewhere in the
441 stand. We suggest that a shade refuge is an example of the broader phenomenon of spatial
442 refuges for diversity. Keppel et al. (2012) define *refuges* as “places that through structures or
443 processes provide shelter from disturbances, predation, herbivory or competition.” Examples of
444 spatial refuges for plants include rock-outcrops functioning as refuges from herbivores (Chollet
445 et al. 2013) and hummocks functioning as refuges from invasive plant competitors in serpentine
446 grasslands (Gram et al. 2004).

447 Analysis of the Kitlope and Carmanah floodplain plots supports the assertion of Pabst and Spies
448 (1998) that overstory structure and light transmission are important drivers of understory
449 composition within riparian stands. In their study, overstory structural measures were correlated
450 with understory vegetation composition along streamside-to-hillslope topographic gradients and
451 were interpreted as proxies for light. Our results build on this idea by confirming that when
452 floodplains are examined independent of hillslope sites, light transmission is still correlated with
453 understory composition patterns at a fine scale within stands.

454 Despite the strong environmental correlates of understory composition, much variation in
455 understory composition remains unexplained. This is common for studies that examine
456 environment-composition relationships within forest understories (Frelich et al. 2003, Chávez
457 and Macdonald 2010). It is also not surprising that plant communities are not in equilibrium with
458 their (light) environments within dynamic, fluvially influenced stands. Other than the light,
459 edaphic, and vegetation properties we measured, processes that could play a role in structuring
460 floodplain plant communities at this spatial scale include chance colonization events, disturbance
461 (e.g., wind and tree-fall), the interaction of topography and flooding (Menges and Waller 1983,

Little et al. 2013), ungulate herbivory (Woodward et al. 1994, Stockton et al. 2005), ground water upwelling (Mouw et al. 2009), salmon derived nutrients (Hocking and Reynolds 2011), overstory composition (Pabst and Spies 1998), and below-ground interaction with trees (e.g., Lindh et al. 2003).

Persistent patterns of openness: feedbacks on stand dynamics and canopy structure

The dominance of light-associated understory shrubs may also play a role in shaping the patterns and dynamics of stand structure. At both Kitlope and Carmanah, shrubs are abundant, but regenerating conifers are sparse – despite light transmission levels more than sufficient for growth of at least some of the conifers present in the stand (Wright et al. 1998, Drever and Lertzman 2001). Our observations are consistent with the “persistent gap” hypothesis, which – in combination with canopy disturbance and perhaps flooding – could explain why Kitlope and Carmanah both have very open canopies – and low tree densities – compared to many forests, despite their different developmental stages. The phenomenon of understory plants influencing gap-phase stand dynamics has been described for a wide range of forests (Royo and Carson 2006). At the scale of the CTR region, the importance of persistent shrub gaps might vary with the intensity of herbivory, as high densities of ungulates have dramatically altered understory vegetation at some locations (e.g., Woodward et al. 1994, Stockton et al. 2005).

Typical gap-phase processes are said to promote a spatially and temporally “moving window of light availability” (Nicotra et al. 1999). Our results suggest an alternative process: hyper-competitive shrubs can exclude conifer establishment and hold that window open and stationary for some period of time. By invading and dominating openings, shrubs could increase the persistence of the spatial patterns of openness created by canopy tree mortality – or by patterns of initial site colonization. However, observations of conifer regeneration on logs (e.g., Harmon

and Franklin 1989) suggest that the presence of logs in such settings could facilitate eventual recruitment of canopy trees even in the presence of intense competition from a productive, dominant shrub understory.

Conclusions

Convergent patterns of openness and overstory-understory interactions

Our analyses at Kitlope and Carmanah, suggest concepts of stand development and within-stand interactions that may have broader applicability to coastal temperate rainforests. Across a range of ages and developmental processes, these forests can attain very open canopies, resulting in abundant understory light and vegetation development. Horizontal and vertical variation in forest canopy structure results in complex spatial patterns of light and shade in the understory. The resulting gradients of understory light in turn structure the understory community at fine scales, with potential feedbacks on patterns of tree recruitment and overall stand density. This suggests that different developmental processes and time-scales can result in stands of similar structure, with open canopies, productive and diverse understories, and coupling of overstory and understory plant layers. This conclusion has interesting implications for management practices intended to restore or accelerate the presence of old forest characteristics in younger or managed stands, particularly on floodplains. It is important to note in a management context, that it is as much the variability in openness as openness itself that is an attribute of such older stands (Frazer et al. 2000b).

In our data, open canopies allowed vigorous growth of dominant shrubs while tree canopies created “shade refuges” where less competitive understory species persisted. The mix of both bright and dark locations was an important factor underlying the distribution of diversity within

the stands. Our results suggest that in the many high-density second-growth conifer forests on similar sites, stand management that encourages canopy openness and heterogeneity (e.g., spatially variable thinning) may accelerate the development of processes and patterns seen at Kitlope and Carmanah. This supports a model of functional openness in stands that reflects various interacting sources – stand developmental processes and small-scale disturbances, edaphic variability, and persistent occupancy of sites by shrubs. Landscape scale analyses – such as those possible with airborne laser scanning – have the potential to characterize canopy openness and understory interactions more comprehensively across a broad range of forest conditions and environmental settings.

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References

- Bartemucci, P., D.K. Coates, K.A. Harper, and E.F. Wright. 2002. Gap disturbances in northern old-growth forests of British Columbia, Canada. *J. Veg. Sci.* **13**: 685-696.
- Bartemucci, P., C. Messier, and C.D. Canham. 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. *Can. J. For. Res.* **36**: 2065-2079.
- B.C. Conservation Data Centre. 2017. BC Species and Ecosystems Explorer. B.C. Minist. of Environ. Victoria, B.C. Available: <http://a100.gov.bc.ca/pub/eswp/> (accessed Apr 5, 2017).
- BC Ministry of Forests and BC Ministry of Environment Lands and Parks. 1998. Field manual for describing terrestrial ecosystems: Land Management Handbook Number 25. BC Ministry of Forests and BC Ministry of Environment Lands and Parks.
- BC Ministry of Forests. 2001. Mensuration data from the provincial ecology program. *For. Sci. Prog.*, B.C. Min. For., Victoria, B.C. Work. Pap. 62/2001. <http://www.for.gov.bc.ca/hfd/pubs/Docs/Wp/Wp62.htm>
- Brokaw, N.V.L. 1985. Treefalls, regrowth, and community structure in tropical forests. *In* The ecology of natural disturbance and patch dynamics. *Edited by* Pickett, S.T.A., and P.S. White. Academic Press, Orlando, FL. pp. 53-69.
- Burton, P.J. 1998. Inferring the response of berry-producing shrubs to partial cutting in the ICHmc. Unpublished final report to Forest Renewal BC Research Program. Symbiosis Research and Restoration, Smithers, BC.
- Canham, C.D., J.S. Denslow, W.J. Platt, J.R. Runkle, T.A. Spies, and P.S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* **20**: 620-631.
- Chávez, V. and S.E. Macdonald. 2010. The influence of canopy patch mosaics on understory plant community composition in boreal mixedwood forest. *For. Ecol. Manage.* **259**: 1067-1075.
- Chollet, S., C. Baltzinger, L. Ostermann, F. Saint-André, and J-L. Martin. 2013. Importance for forest plant communities of refuges protecting from deer browsing. *For. Ecol. Manage.* **289**: 470-477.
- Denslow, J.S. 1985. Disturbance-mediated coexistence of species. *In* The ecology of natural disturbance and patch dynamics. *Edited by* Pickett, S.T.A., and P.S. White. Academic Press, Orlando, FL. pp. 307-323.
- Drever, R.C. and K.P. Lertzman. 2001. Light-growth response of coastal Douglas-fir and western redcedar saplings under different regimes of soil moisture and nutrients. *Can. J. For. Res.* **31**: 2124-2133.

- Dutilleul, P. 1993. Modifying the t test for assessing the correlation between two spatial processes. *Biometrics*, **49**: 305-314.
- Franklin, J.F., T.A. Spies, R. Van Pelt, A.B. Carey, D.A. Thornburgh, D.R. Berg, D.B. Lindenmayer, M.E. Harmon, W.S. Keeton, D.C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* **155**: 399-423.
- Frazer, G.W., C.D. Canham, and K.P. Lertzman. 1999. Gap Light Analyzer (GLA) Version 2.0: Imaging software to extract forest canopy structure and gap light transmission indices from true-colour hemispherical (fisheye) photographs. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.
- Frazer, G.W., C.D. Canham, and K.P. Lertzman. 2000a. Gap Light Analyzer Version 2.0. *Bull. Ecol. Soc. Amer.* **81**: 191-197.
- Frazer, G.W., J.A. Trofymow, and K.P. Lertzman. 2000b. Canopy openness and leaf area in chronosequences of coastal temperate rainforests. *Can. J. For. Res.* **30**: 239-256.
- Frelich, L.E., J. Machado, and P.B. Reich. 2003. Fine-scale environmental variation and structure of understory plant communities in two old-growth pine forests. *J. Ecol.* **91**: 283-293.
- Giesbrecht, I.J.W. 2010. Understory light and vegetation in two floodplain forests in coastal British Columbia. MRM research project, Simon Fraser University, Burnaby, BC. Report No. 508.
- Gram, W.K., E.T. Borer, K.L. Cottingham, E.W. Seabloom, V.L. Boucher, L. Goldwasser, F. Micheli, B.E. Kendall, and R.S. Burton. 2004. Distribution of plants in a California serpentine grassland: are rocky hummocks spatial refuges for native species? *Plant Ecol.* **172**: 159-171.
- Green, R.N. and K. Klinka. 1994. A field guide to site identification and interpretation for the Vancouver Forest Region. British Columbia Ministry of Forests, Research Branch.
- Gregory, S.V., F.J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. *BioScience*, **41**: 540-551.
- Gurevitch, J., S.M. Scheiner, and G.A. Fox. 2002. The ecology of plants. Sinauer Associates, Inc., Sunderland, MA.
- Harmon, M.E. and J.F. Franklin. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology*, **70**: 48-59.
- Henderson, J.A. 1978. Plant succession on the *Alnus rubra/Rubus spectabilis* habitat type in western Oregon. *Northwest Sci.* **52**: 156-167.
- Hocking, M.D. and J.D. Reynolds. 2011. Impacts of salmon on riparian plant diversity. *Science*, **331**: 1609-1612.

- Keppel, G. and G.W. Wardell-Johnson. 2012. Refugia: keys to climate change management. *Global Change Biol.* **18**: 2389-2391.
- Kruskal, J.B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika*, **29**: 115-129.
- Legendre, P. and L. Legendre. 1998. Numerical ecology. 2nd edition. Elsevier, Amsterdam.
- Lertzman, K.P. and C.J. Krebs. 1991. Gap-phase structure of a subalpine, old-growth forest. *Can. J. For. Res.* **21**: 1730-1741.
- Lertzman, K.P., G.D. Sutherland, A. Inselberg, and S.C. Saunders. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecology*, **77**: 1254-1270.
- Levey, D.J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology*, **69**: 1076-1089.
- Lieberman, M., D. Lieberman, and R. Peralta. 1989. Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology*, **70**: 550-555.
- Lindh, B.C., A.N. Gray, and T.A. Spies. 2003. Responses of herbs and shrubs to reduced root competition under canopies and in gaps: a trenching experiment in old-growth Douglas-fir forests. *Can. J. For. Res.* **33**: 2052-2057.
- Little, P.J., J.S. Richardson, and Y. Alila. 2013. Channel and landscape dynamics in the alluvial forest mosaic of the Carmanah River valley, British Columbia, Canada. *Geomorphology*, **202**: 86-100.
- MacKinnon, A., S.C. Saunders, and H. Klassen. 2010. Coast forest region old growth dynamics (OGD) project [online]. Available from www.for.gov.bc.ca/rco/research/eco/oldgrowthforests/oldgrowthdynamics/index.htm [accessed 1 Dec 2010].
- Mather, P.M. 1976. Computational methods of multivariate analysis in physical geography. J. Wiley & Sons, London. 532pp.
- McCarthy, J. 2000. Gap dynamics of forest trees: a review with particular attention to boreal forests. *Envir. Rev.* **9**: 1-59.
- McCune, B. and J.B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.
- McCune, B. and M.J. Mefford. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5.19. MjM Software, Gleneden Beach, Oregon, U.S.A.
- McGhee, R.A. 1996. Ecology and management of hardwoods in coniferous forests: a case study of vine maple persistence. MRM research project, Simon Fraser University, Burnaby, BC. Report No 189.
- Meidinger, D. and J. Pojar. 1991. Ecosystem of British Columbia. Province of British Columbia, Ministry of Forests, Research Branch, Victoria.

- Meidinger, D., T. Lee, G. Douglas, W. George, G. Britton, W. MacKenzie, and H. Qian. 2009. British Columbia plant species codes and selected attributes. Version 6 Database. Research Branch. B.C. Ministry of Forests.
- Menges, E.S. and D.M. Waller. 1983. Plant strategies in relation to elevation and light in floodplain herbs. *Amer. Nat.* **122**: 454-473.
- Minore, D. and H.G. Weatherly. 1994. Riparian trees, shrubs, and forest regeneration in the coastal mountains of Oregon. *New For.* **8**: 249-263.
- Mladenoff, D. 1990. The relationship of the soil seed bank and understory vegetation in old-growth northern hardwood-hemlock treefall gaps. *Can. J. Bot.* **68**: 2714-2721.
- Moeser, D., J. Roubinek, P. Schleppi, F. Morsdorf, and T. Jonas. 2014. Canopy closure, LAI and radiation transfer from airborne LiDAR synthetic images. *Agric. For. Meteorol.* **197**: 158-168.
- Mouw, J.E.B., J.A. Stanford, and P.B. Alaback. 2009. Influences of flooding and hyporheic exchange on floodplain plant richness and productivity. *Riv. Res. Appl.* **25**: 929-945.
- Naiman, R.J., J.S. Bechtold, T.J. Beechie, J.J. Latterell, and R. Van Pelt. 2010. A process-based view of floodplain forest patterns in coastal river valleys of the Pacific Northwest. *Ecosystems*, **13**: 1-31.
- Nicotra, A.B., R.L. Chazdon, and S.V.B. Iriarte. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology*, **80**: 1908-1926.
- Pabst, R.J. and T.A. Spies. 1998. Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests in coastal Oregon. *Can. J. Bot.* **76**: 298-315.
- Pabst, R.J. and T.A. Spies. 1999. Structure and composition of unmanaged riparian forests in the coastal mountains of Oregon, U.S.A. *Can. J. For. Res.* **29**: 1557-1573.
- Pearson, A.F. 2010. Natural and logging disturbances in the temperate rain forests of the Central Coast, British Columbia. *Can. J. For. Res.* **40**: 1970-1984.
- Pielou, E.C. 1969. An introduction to mathematical ecology. John Wiley and Sons, New York.
- Rosenberg, M.S. 2009. PASSaGE 2: Pattern Analysis, Spatial Statistics and Geographic Exegesis. Software available online: <http://www.passagesoftware.net/index.php>
- Royo, A.A. and W.P. Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. For. Res.* **36**: 1345-1362.
- Runkle, J.R. 1984. Development of woody vegetation in treefall gaps in a beech-sugar maple forest. *Holarct. Ecol.* **7**: 157-164.
- Sarr, D.A. and D.E. Hibbs. 2007a. Multiscale controls on woody plant diversity in western Oregon riparian forests. *Ecol. Mono.* **77**: 179-201.

- Sarr, D.A. and D.E. Hibbs. 2007b. Woody riparian plant distributions in western Oregon, USA: comparing landscape and local scale factors. *Plant Ecol.* **190**: 291-311.
- Saxton, K.E. and W.J. Rawls. 2006. Soil water characteristic estimate by texture and organic matter for hydrologic solutions. *Soil Sci. Am. J.* **70**: 1569-1578.
- Schoonmaker, P.K., B. von Hagen, and E.C. Wolf. 1997. Introduction. *In* The rainforests of home: profile of a North American bioregion. *Edited by* P.K. Schoonmaker, B. von Hagen, and E.C. Wolf. Island Press, Washington, DC. pp. 1-6.
- Schliemann, S.A. and J.C. Bockheim. 2011. Methods for studying treefall gaps: a review. *For. Ecol. Manage.* **261**: 1143-1151.
- Soil Classification Working Group. 1998. The Canadian System of Soil Classification (third edition). Agriculture and Agri-Food Canada Publication 1646, pp. 187.
- Spies, T.A. and J.F. Franklin. 1988. Old growth and forest dynamics in the Douglas-fir region of Western Oregon and Washington. *Nat. A. J.* **8**: 190-201.
- Spies, T.A. and J.F. Franklin. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. *Ecology*, **70**: 543-545.
- Stockton, S.A., S. Allombert, A.J. Gaston, and J.-L. Martin. 2005. A natural experiment on the effects of high deer densities on the native flora of coastal temperate rain forests. *Biol. Cons.* **126**: 118-128.
- Tappeiner, J., J. Zasada, P. Ryan, and M. Newton. 1991. Salmonberry clonal and population structure: the basis for a persistent cover. *Ecology*, **72**: 609-618.
- Tappeiner, J.C. II, J.C. Zasada, D.W. Huffman, and L.M. Ganio. 2001. Salmonberry and salal annual aerial stem production: the maintenance of shrub cover in forest stands. *Can. J. For. Res.* **31**: 1629-1638.
- Turner, N.J. 1998. Plant technology of First Peoples in British Columbia. Royal British Columbia Museum Handbook. UBC Press, Vancouver.
- Van Pelt, R. and J.F. Franklin. 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. *Can. J. For. Res.* **30**: 1231-1245.
- Van Pelt, R., T.C. O'Keefe, J.J. Latterell, and R.J. Naiman. 2006. Riparian forest stand development along the Queets River in Olympic National Park, Washington. *Ecol. Mono.* **76**: 227-298.
- Watt, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* **35**: 1-22.
- Wells, R., K.P. Lertzman, and S.C. Saunders. 1998. Old-growth definitions for the forests of British Columbia, Canada. *Nat. Areas J.* **18**: 279-292.
- Woodward, A., E.G. Schreiner, D.B. Houston, and B.B. Moorhead. 1994. Ungulate-forest relationships in Olympic National Park: retrospective exclosure studies. *Northwest Sci.* **68**: 97-110.

- Wright, E.F., K.D. Coates, C.D. Canham, and P. Bartemucci. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. *Can. J. For. Res.* **28**: 871-886.
- Zhu, J., G. Zhang, G.G. Wang, Q. Yan, D. Lu, X. Li, and X. Zheng. 2015. On the size of forest gaps: Can their lower and upper limits be objectively defined? *Agric. For. Meteorol.* **213**: 64–76.

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Tables and Figures

Tables

Table 1. Geographic and growing season characteristics for Kitlope and Carmanah.

	Kitlope	Carmanah
Location		
Latitude (N)	53°12'10.0"	48°40'07.6"
Longitude (W)	127°49'35.9"	124°41'10.8"
Elevation (m)	8	138
Growing season start and end		
DD5-100 (date of budburst for most plants)	May 9	April 5
bFFP: (beginning of the frost free period)	May 18	April 11
eFFP: (end of the frost free period)	Oct 3	Nov 2
Inferred start of growing season	May 9	April 5
Inferred end of growing season	Sept 12	Oct 12

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Table 2. Descriptive statistics for environment variables at each site. Organic and mineral horizon descriptors (LFH, Ah) follow the Canadian System of Soil Classification (Soil Classification Working Group 1998).

Variable	Kitlope					Carmanah				
	<i>n</i>	Median	Mean	SD	CV (%)	<i>n</i>	Median	Mean	SD	CV (%)
Substrate and Forest Floor										
Forest Floor (% cover)	24	3	6	14	223	16	85	81	21	26
CWD (% cover)	24	0	5	9	193	16	15	18	21	115
Mineral Soil (% cover)	24	96	87	22	25	16	0	1	2	400
Humus thickness (cm)	24	0.0	0.0	0.0	490	16	2.5	2.6	1.7	66
LFH thickness (cm)	24	0.5	0.6	0.5	89	16	3.5	4.0	2.3	58
Ah thickness (cm)	24	4.1	4.9	2.7	55	16	1.3	1.5	1.2	80
Dead Wood in LFH (% vol.)	24	0	1	3	237	16	0	6	12	193
Soil Texture and Water Properties										
% Clay	24	20	21	11	53	16	10	11	8	72
% Silt	24	56	53	20	37	16	25	32	28	88
% Sand	24	20	26	23	89	16	65	58	31	54
% Coarse Fragments	24	0	0	0	na	16	3	26	34	133
Plant Available Water (cm ³ water/cm ³ soil)	24	17	17	5	29	16	8	10	8	77
Hydraulic conductivity (cm/hr)	24	12	21	22	106	16	33	38	26	68
Overstory Structure and Light Transmission										
<i>Omitting terrace and fluvial channel microsites</i>										
% Site openness	49	11.6	11.5	2.6	22.9	39	11.0	11.1	3.3	30.1
LAI 4 (Leaf Area Index 4)	49	2.5	2.5	0.2	9.6	39	2.5	2.5	0.4	15.4
LAI 5 (Leaf Area Index 5)	49	2.5	2.5	0.2	8.9	39	2.7	2.7	0.3	11.5
Direct PAR (mol/m ² /d)	49	0.6	0.7	0.3	46.1	39	0.6	0.6	0.3	40.6
Diffuse PAR (mol/m ² /d)	49	3.8	3.8	1.0	26.1	39	3.5	3.4	1.1	32.1
Total PAR (mol/m ² /d)	49	4.3	4.5	1.1	25.4	39	4.1	4.1	1.3	31.9
% Direct PAR	49	14.8	17.2	8.0	46.2	39	17.6	17.6	7.1	40.5
% Diffuse PAR	49	18.7	19.1	5.0	26.1	39	18.0	17.9	5.8	32.1
% PAR (aka. % full sun)	49	17.7	18.8	4.8	25.3	39	17.9	17.9	5.7	31.9

CWD is coarse woody debris; LFH is the sum of all soil organic horizons; Ah is an organic rich mineral soil layer; and PAR is photosynthetically active radiation.

Table 3. Summary statistics for ordination results at Kitlope ($n=24$). The cumulative proportion of variation represented by the three axes (R^2) is 0.79 before and after rotation. Bold font identifies correlations with $r^2 \geq 0.3$. Species names follow Meidinger et al. (2009).

		Axis 1	Axis 2	Axis 3
% represented after rotation				
Species Name	Species Code	<i>r</i>	<i>r</i>	<i>r</i>
<i>Oplopanax horridus</i> (Smith) Miq.	OPLOHOR	-0.659	0.542	-0.348
<i>Ribes bracteosum</i> Dougl. ex Hook.	RIBEBRA	0.642	0.154	-0.093
<i>Rubus spectabilis</i> Pursh	RUBUSPE	0.334	-0.318	0.632
<i>Sambucus racemosa</i> ssp. <i>pubens</i> (Michx.) House	SAMBRAC	0.374	0.085	-0.515
<i>Athyrium filix-femina</i> (L.) Roth	ATHYFIL	-0.340	0.481	-0.107
<i>Circaea alpina</i> L.	CIRCALP	0.462	-0.390	-0.352
<i>Dryopteris expansa</i> (K.B. Presl) Fraser-Jenkins & Jermy	DRYOEXP	-0.613	-0.153	-0.294
<i>Galium triflorum</i> Michx.	GALITRI	-0.432	-0.226	-0.437
Poaceae sp.	GRASS	0.136	0.368	-0.153
<i>Lysichiton americanus</i> Hult. & St. John	LYSIAME	-0.027	-0.192	-0.357
<i>Maianthemum dilatatum</i> (A. Wood) Nels. & J.F. Macbr.	MAIADIL	-0.334	0.391	-0.407
<i>Osmorhiza berteroi</i> DC.	OSMOBER	-0.560	0.319	0.062
<i>Osmorhiza purpurea</i> (Coult. & Rose) Suksd.	OSMOPUR	-0.252	0.111	0.511
<i>Polystichum braunii</i> (Spenner) Fée	POLYBRA	0.336	0.262	-0.153
<i>Stellaria crispa</i> Cham. & Schlecht.	STELCRI	0.321	-0.410	-0.390
<i>Streptopus amplexifolius</i> (L.) DC.	STREAMP	-0.157	-0.141	-0.501
<i>Streptopus lanceolatus</i> var. <i>curvipes</i> (Vail) Reveal	STRELAN1	-0.237	0.674	0.432
<i>Tiarella trifoliata</i> L.	TIARTRI	-0.430	0.241	-0.347
<i>Trautvetteria caroliniensis</i> (Walt.) Vail	TRAUCAR	-0.317	-0.115	0.053
Environment				
LF Thickness ^a (LnLFwtPls1)		-0.259	-0.011	0.052
Ah+H Thickness ^b (AhHwt)		-0.321	0.229	-0.026
% Sand ^c (LnSand)		-0.168	-0.113	-0.067
% Clay ^c (LnClay)		-0.301	-0.023	-0.101
% Silt (Silt)		0.311	0.131	0.113
Distance to Water (DistW)		0.327	-0.059	0.207
% Full Sun		0.722	0.020	-0.034

Note: For brevity and to avoid use of collinear explanatory variables, we have not presented results for PAW or Ks. Both variables are functionally associated with soil texture. Similarly, from the canopy photo analyses we use only % Full Sun.

^a weighted by the % of the subplot covered by organic matter substrate type and transformed as natural log of (X+1).

^b weighted by the % of the subplot covered by organic matter substrate type.

^c natural log transformed.

Table 4. Summary statistics for ordination results at Carmanah ($n=16$). The cumulative proportion of variation represented by the three axes (R^2) is 0.90 before and after rotation. Bold font identifies correlations with $r^2 \geq 0.3$.

		Axis 1	Axis 2	Axis 3
% represented after rotation		<i>r</i>	<i>r</i>	<i>r</i>
Species Name	Species Code			
<i>Ribes bracteosum</i>	RIBEBRA	0.669	0.061	0.216
<i>Rubus spectabilis</i>	RUBUSPE	0.730	0.109	0.009
<i>Vaccinium parvifolium</i> Sm.	VACCPAR	-0.514	0.393	0.149
<i>Athyrium filix-femina</i>	ATHYFIL	-0.246	0.349	0.462
<i>Blechnum spicant</i> (L.) Roth	BLECSPI	-0.656	0.736	0.194
<i>Boykinia occidentalis</i> T. & G.	BOYKELA	-0.273	-0.174	0.687
<i>Claytonia sibirica</i> L.	CLAYSIB	-0.043	-0.541	0.712
<i>Prosartes smithii</i> (Hook.) Utech, Shinwari & Kawano	DISPSMI	-0.364	-0.571	-0.121
<i>Dryopteris expansa</i>	DRYOEXP	-0.257	0.743	-0.164
<i>Galium triflorum</i>	GALITRF	-0.290	-0.203	0.743
<i>Maianthemum dilatatum</i>	MAIADIL	-0.506	0.354	0.213
<i>Mitella ovalis</i> Greene	MITEOVA	-0.282	-0.095	0.733
<i>Polystichum munitum</i> (Kaulf.) K.B. Presl	POLYMUN	-0.370	-0.385	-0.295
<i>Tiarella trifoliata</i>	TIARTRI	0.092	-0.194	0.549
<i>Trautvetteria caroliniensis</i>	TRAUCAR	0.192	-0.211	0.183
Environment				
Forest Floor Thickness (FF)		0.002	-0.507	0.138
LF Thickness ^a (LnLFwtPls1)		0.292	-0.343	-0.280
H Thickness ^b (Hwt)		-0.205	-0.559	0.143
Ah+H Thickness ^b (AhHwt)		-0.034	-0.523	-0.013
% Sand (Sand)		0.341	-0.244	0.089
% Clay ^c (LnClay)		-0.242	0.673	-0.009
% Silt (Silt)		-0.345	0.111	-0.115
% Full Sun		0.571	-0.014	-0.001

Note: For brevity and to avoid use of collinear explanatory variables, we have not presented results for PAW or Ks. Both variables are functionally associated with soil texture. Similarly, from the canopy photo analyses we use only % Full Sun.

^a weighted by the % of the subplot covered by organic matter substrate type and transformed as natural log of (X+1).

^b weighted by the % of the subplot covered by organic matter substrate type.

^c natural log transformed.

Table 5. Correlation analysis of: a. understory vegetation layers in relation to light; b. total herb cover in relation to the shrub layer; c. diversity in relation to light; d. diversity in relation to *Rubus spectabilis* cover. Bold coefficients are significant at the 0.05 level according to Dutilleul corrected *P* values.

Variable 1	Variable 2	Kitlope					Carmanah (all)					Carmanah (no windthrow)				
		<i>n</i> =24					<i>n</i> =19 ^a					<i>n</i> =16 ^a				
		<i>r</i>	<i>P</i>	<i>P</i> _{Dut}	<i>n_e</i>	GL	<i>r</i>	<i>P</i>	<i>P</i> _{Dut}	<i>n_e</i>	GL	<i>r</i>	<i>P</i>	<i>P</i> _{Dut}	<i>n_e</i>	GL
a. Layer vs. Light																
Shrub	% Full Sun	0.48	0.017	0.023	22		0.34	0.161	0.155	19		0.63	0.008	0.008	16	
Herb	% Full Sun	-0.33	0.110	0.112	24		-0.05	0.849	0.886	12		-0.01	0.957	0.959	15	
Vascular	% Full Sun	0.29	0.167	0.167	24		0.30	0.214	0.139	26		0.59	0.017	0.029	14	
sRUBUSPE	% Full Sun	0.24	0.260	0.248	25		0.45	0.052	0.052	19		0.79	0.000	0.001	13	
b. Herb Layer vs. Shrubs																
Herb	Shrub	-0.12	0.587	0.574	26		-0.24	0.314	0.336	18		-0.22	0.422	0.482	13	
Herb	sRUBUSPE	-0.41	0.044	0.040	25		-0.08	0.730	0.705	22		-0.01	0.964	0.965	15	
c. Diversity vs. Light																
S	% Full Sun	-0.22	0.292	0.336	20		-0.43	0.067	0.138	13		-0.47	0.065	0.077	15	
E	% Full Sun	-0.09	0.668	0.640	28		-0.53	0.021	0.063	13	-	-0.64	0.008	0.010	15	
Ls ^b	% Full Sun	0.13	0.537	0.511	27		0.63	0.004	0.032	12		0.72	0.002	0.004	14	
d. Diversity vs. <i>Rubus spectabilis</i>																
S	sRUBUSPE	-0.16	0.456	0.436	26		-0.31	0.196	0.137	24		-0.43	0.095	0.091	16	
E	sRUBUSPE	-0.67	0.000	0.001	23		-0.67	0.002	0.002	18		-0.65	0.006	0.008	15	
Ls ^b	sRUBUSPE	0.71	0.000	0.000	23		0.70	0.001	0.000	21		0.73	0.001	0.002	15	

r: Pearson correlation coefficient. This estimate is not adjusted by the Dutilleul procedure.

n_e: effective sample size, after Dutilleul correction.

P: the *P*-value from a conventional t-test, not corrected for spatial autocorrelation.

*P*_{Dut}: the *P*-value from a Dutilleul corrected t-test, which accounts for spatial autocorrelation of each variable.

GL: Gain “+” or Loss “-” of statistical significance (at the 0.05 level) after applying the Dutilleul correction.

sRUBUSPE: summed cover of *Rubus spectabilis* in all layers.

S: species richness.

E: species evenness.

Ls: species dominance.

^a correlations were examined with (*n*=19) and without (*n*=16) recent windthrow disturbance subplots.

^bLs was square root transformed for the Kitlope analysis and for Carmanah *n*=19 analysis.

Figures

Figure 1. Map of Kitlope and Carmanah study locations in coastal British Columbia, Canada.

Figure 2. Diameter (DBH) distributions of live trees within the Kitlope and Carmanah plots. Colours are used to differentiate species.

Figure 3. Frequency of three canopy cover types at each site. Closed canopy (CC), expanded gap (EG), and canopy gap (CG). Figures are based on $n=42$ at Carmanah, after omitting terrace microsites, and $n=50$ at Kitlope.

Figure 4. Frequency distribution of % full sun. Fluvial channel and terrace microsites were omitted: $n=49$ at Kitlope, $n=39$ at Carmanah.

Figure 5. Maps of understory light (% full sun) in relation to overstory tree size and location. Light values between sample locations were estimated and mapped using a tension spline interpolation.

Figure 6. NMS ordination diagrams and joint-plots for the two primary axes at Kitlope ($n=24$) and Carmanah ($n=16$). The angle of the arrow represents the direction of correlation between ordination scores and light transmission. The length of the arrow represents correlation strength. Only correlations with $r^2 > 0.3$ are shown.

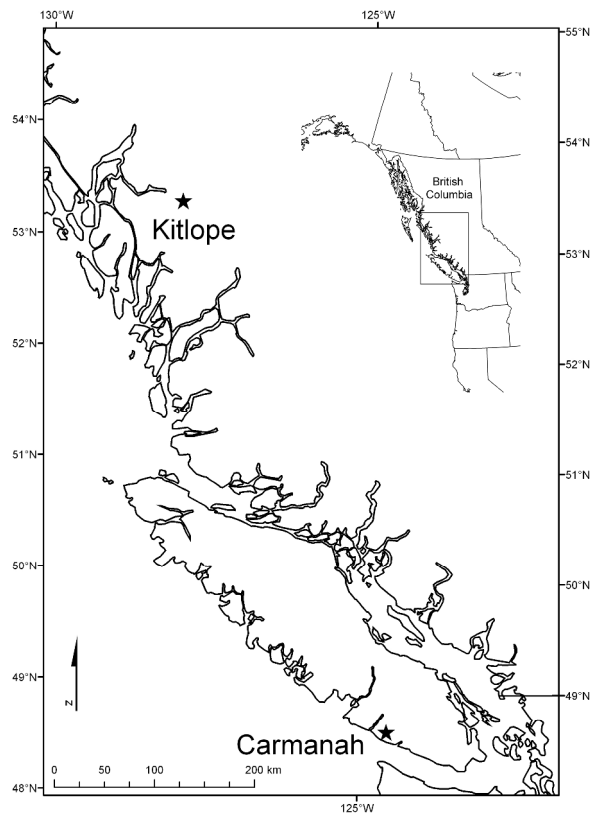


Figure 1.

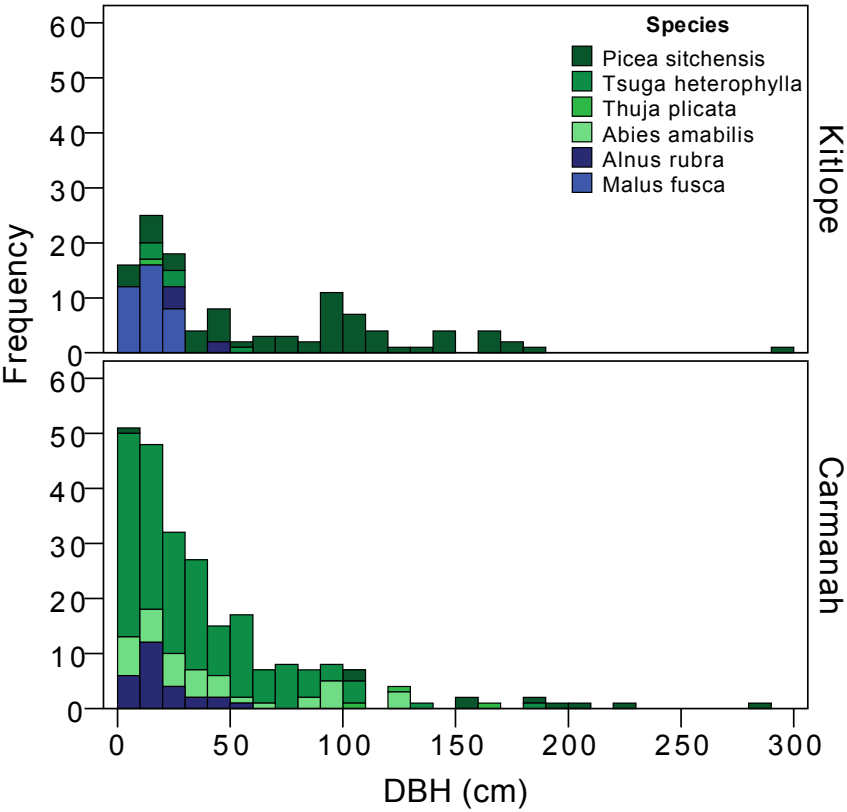


Figure 2

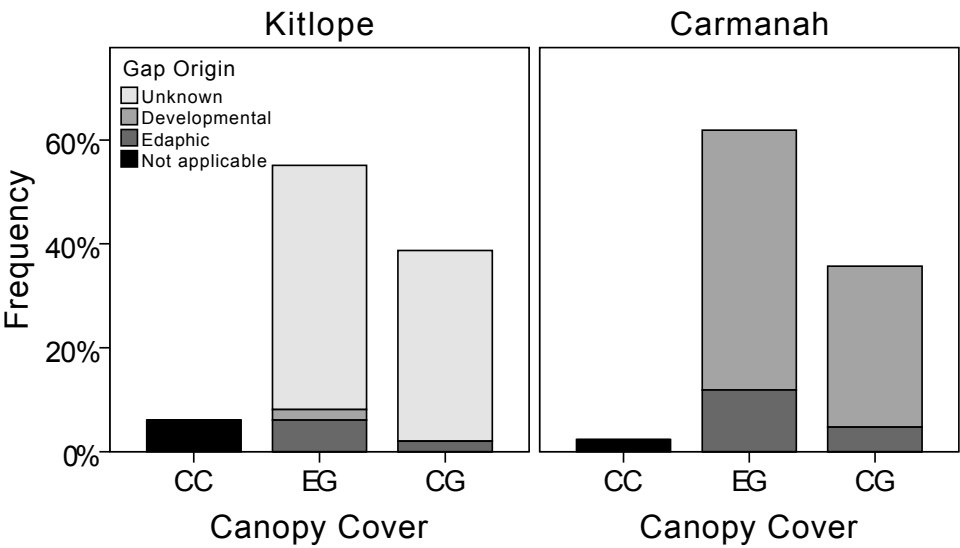


Figure 3

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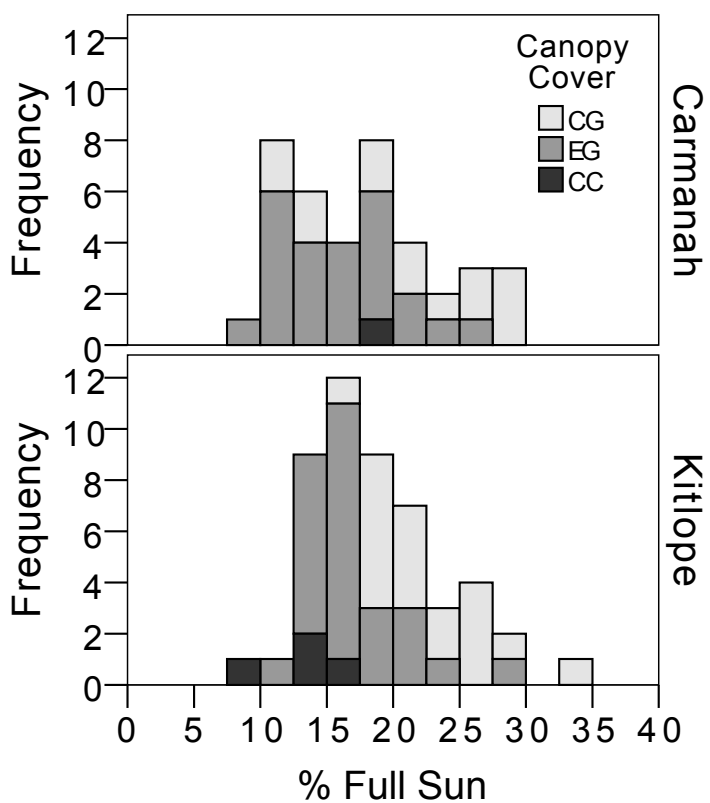


Figure 4.

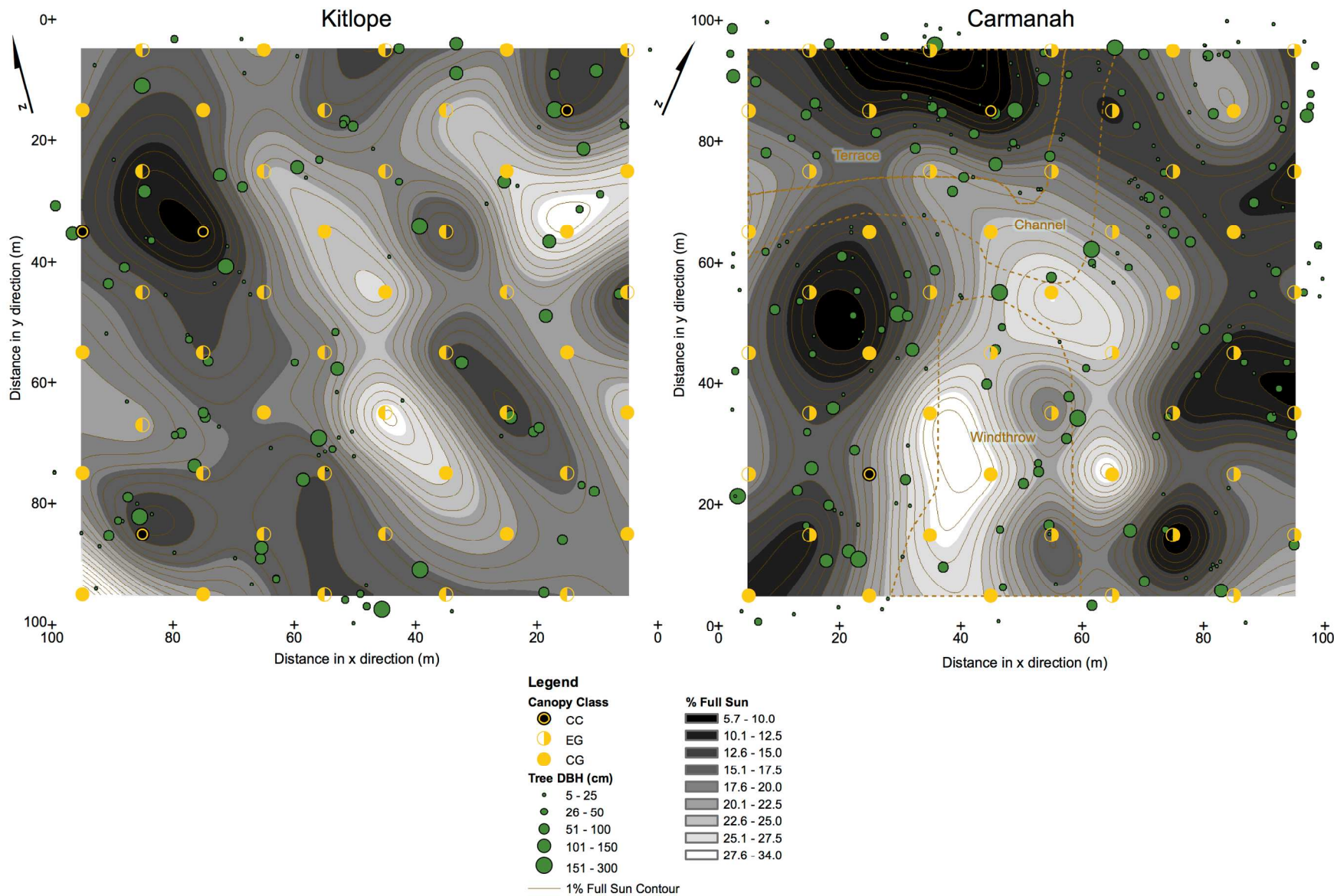


Figure 5.

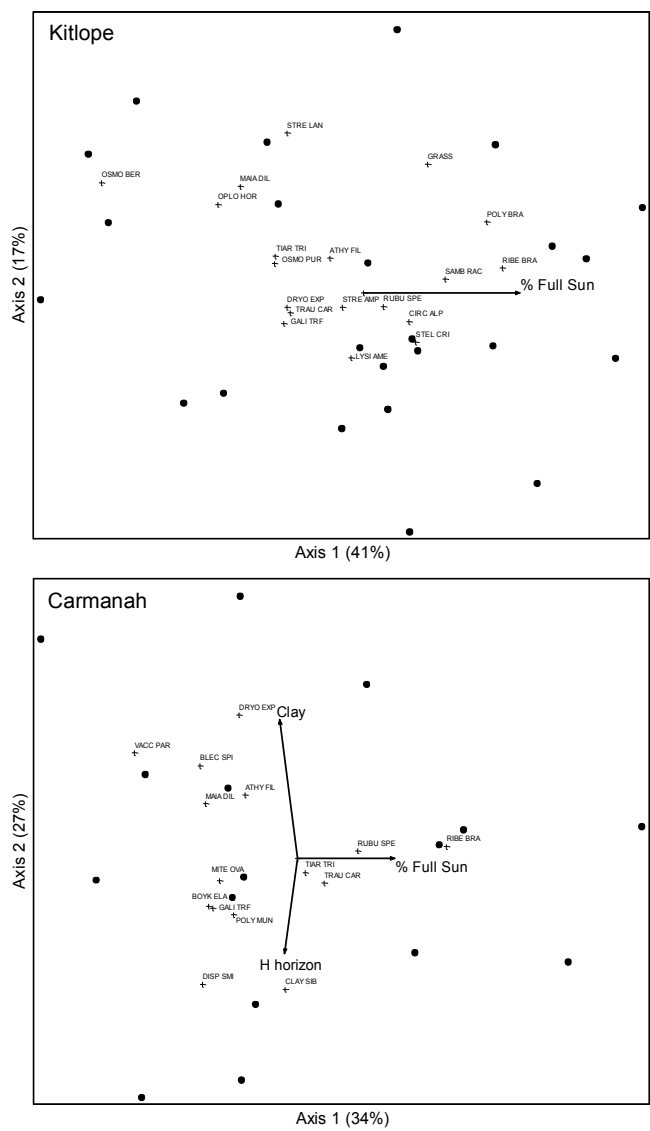


Figure 6.

Supplementary Material

Giesbrecht et al. 2017. Overstory structure drives fine-scale coupling of understory light and vegetation in two temperate rainforest floodplains. Canadian Journal of Forest Research. DOI: 10.1139/cjfr-2016-0466

S1. Sampling design

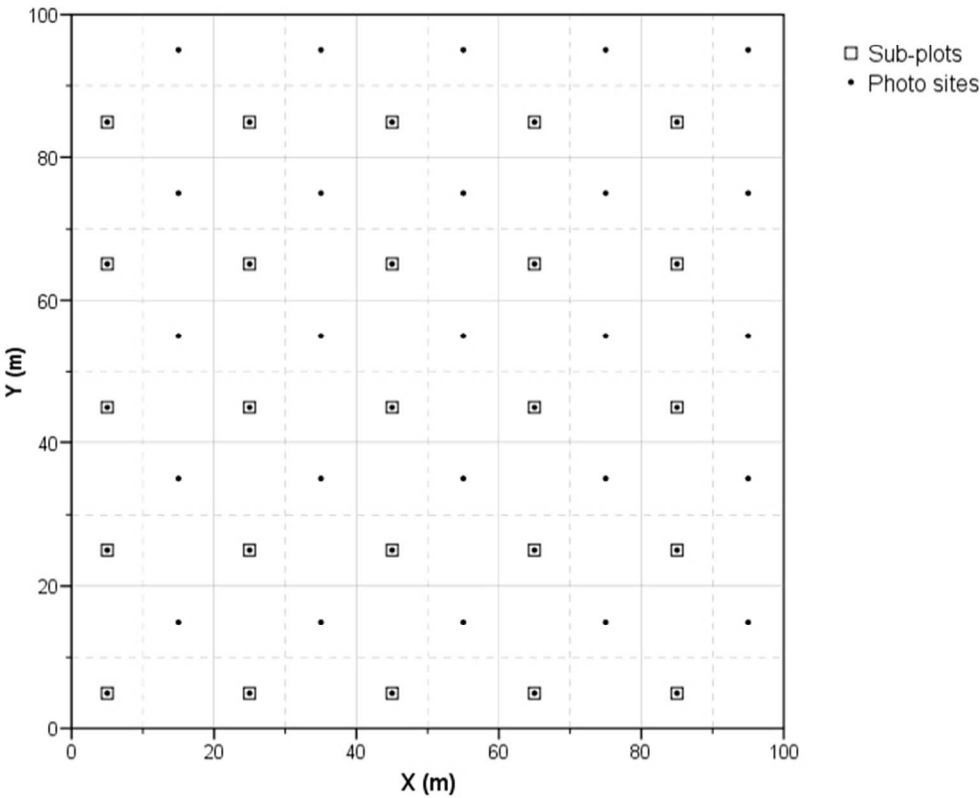


Figure S1. Plan view of sampling layout for subplots and photo sites in the one-hectare macroplots.

S2. Snag diameter distributions

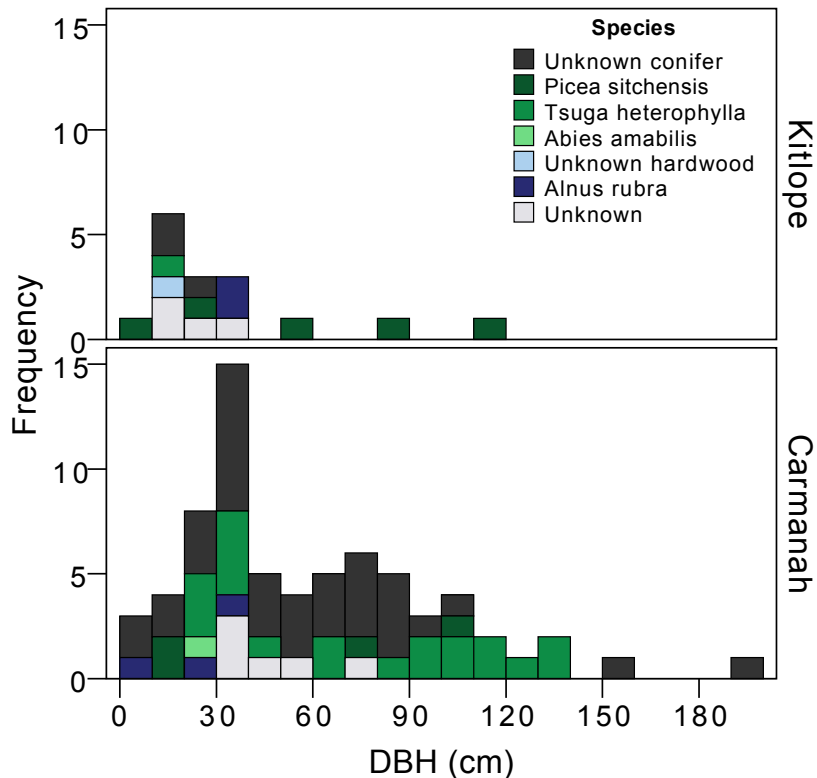


Figure S2. Diameter (DBH) distributions for snags at Kitlope and Carmanah.

S3. Species cover variations along ordination axes

In some circumstances, it can be misleading to interpret a linear correlation coefficient of species abundance over a compositional or environmental gradient, particularly in the absence of a scatterplot (McCune and Grace 2002). A number of features common to community datasets can make a linear correlation coefficient misleading either by under-representing a relationship that exists (nonlinear response, solid response curve, and outliers) or over-representing one that does or does not exist (zero truncation and outliers). We have attempted to avoid such interpretation

errors by examining overlays and scatter plots for each species and environmental variable on the ordination axes.

For Kitlope, examination of overlay-scatter plot graphs in PC-ORD revealed that several additional species increase (*Sambucus racemosa* ssp. *pubens*, *Polystichum braunii*, *Rubus spectabilis*, and *Stellaria crispa*) or decrease (*Galium triflorum*, *Osmorhiza berteroi*, *Tiarella trifoliata*) along axis 1, but their responses are nonlinear or obscured by outliers, hence the rather low r values for linear correlations. *Oplopanax horridus* shows signs of a threshold along axis 1 (in addition to the fairly strong linear correlation) with most occurrences and higher abundances in the lower two thirds of the axis.

At Carmanah, a few species show relationships with axis 1 that are not well captured by the linear correlation coefficients, either due to nonlinearities or outliers. For example, *Galium triflorum* and *Mitella ovalis* are only – but not always – present in the darker half of the axis 1 distribution.

S4. Canopy openness and light transmission compared to other forests

Median site openness (highly correlated with light transmission) at Kitlope and Carmanah (~11%) appears to be higher than the median openness of upland old-growth on the wetter west side of Vancouver Island (~7.5%) and similar to the median openness on the drier east side of Vancouver Island (by visual comparison to boxplots of Frazer et al. 2000). Median percentage light transmission at Kitlope and Carmanah is higher than reported for most streamside, midslope or hillslope forests sampled in Oregon by Sarr and Hibbs (2007). Roburn (2003) reported mean 5% full sun transmission in each of two *Picea sitchensis* floodplain forests in the Seymour

Valley of southwest British Columbia – substantially less than we have reported for Kitlope or Carmanah, potentially reflecting differences in stand development stage and the volume of subcanopy trees. Mean percentage full sun transmission (18-19%) in our study is greater than reported for a range of temperate and tropical forest studies (Canham et al. 1990, Nicotra et al. 1999, Lhotka and Loewenstein 2006), which have mean values between 0.5 and 7.0% total transmission. Mean percentage full sun is similar to the sub-boreal (18.0%), sub-alpine (19.0%), and northern temperate (16.0%) stands of old-growth in northern British Columbia (Bartemucci et al. 2002). By contrast, mean light transmission at Carmanah and Kitlope is markedly lower than reported for a number of old-growth boreal forests in Quebec (27%; Bartemucci et al. 2006) and northern BC (26.7%; Bartemucci et al. 2002).

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References for Supplementary Material

- Bartemucci, P., D.K. Coates, K.A. Harper, and E.F. Wright. 2002. Gap disturbances in northern old-growth forests of British Columbia, Canada. *J. Veg. Sci.* **13**: 685-696.
- Bartemucci, P., C. Messier, and C. Canham. 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. *Can. J. For. Res.* **36**: 2065-2079.
- Canham, C.D., J.S. Denslow, W.J. Platt, J.R. Runkle, T.A. Spies, and P.S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* **20**: 620-631.
- Frazer, G.W., J.A. Trofymow, and K.P. Lertzman. 2000. Canopy openness and leaf area in chronosequences of coastal temperate rainforests. *Can. J. For. Res.* **30**: 239-256.
- Lhotka, J.M. and E.F. Loewenstein. 2006. Indirect measures for characterizing light along a gradient of mixed-hardwood riparian forest canopy structures. *For. Ecol. Manage.* **226**: 310-318.
- McCune, B., and J.B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.
- Nicotra, A.B., R.L. Chazdon, and S.V.B. Iriarte. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology*, **80**: 1908-1926.
- Roburn, A. 2003. Light transmission and understory vegetation in two old-growth riparian stands: a study in spatial pattern. MRM research project, Simon Fraser University, Burnaby, BC. Report No. 331.
- Sarr, D.A. and D.E. Hibbs. 2007. Multiscale controls on woody plant diversity in western Oregon riparian forests. *Ecol. Mono.* **77**: 179-201.