Canadian Journal of Forest Research
 Revue canadienne de recherche forestière

Spatial aspects of structural complexity in Sitka spruce-western hemlock forests, including evaluation of a new canopy gap delineation method

Journal:	<i>Canadian Journal of Forest Research</i>
Manuscript ID	cjfr-2017-0029.R1
Manuscript Type:	Article
Date Submitted by the Author:	12-Apr-2017
Complete List of Authors:	Schneider, Eryn; University of Montana, Forest Mangement Larson, Andrew; University of Montana, Department of Forest Management
Keyword:	spatial patterns, gap dynamics, old-growth, competition, canopy gap
Please Select from this Special Issues list if applicable:	N/A

SCHOLARONE™
 Manuscripts

**Spatial aspects of structural complexity in Sitka spruce-western hemlock forests, including
evaluation of a new canopy gap delineation method**

Eryn E. Schneider and Andrew J. Larson

Eryn E. Schneider (Corresponding Author); University of Montana W.A. Franke College of
Forestry & Conservation; 32 Campus Drive, Missoula, MT 59812; 605-212-5717;
eryn.schneider@umontana.edu

Andrew J. Larson; W.A. Franke College of Forestry & Conservation; 32 Campus Drive,
Missoula, MT 59812; 406-243-5532; a.larson@umontana.edu

Abstract

Structural complexity in long-lived forests where stand-replacing disturbances are rare is thought to emerge from chronic small scale disturbances and competitive interactions between trees. We analyzed tree size distributions, tree spatial patterns, and canopy gap attributes in ten, 1.42 ha stem mapped plots in old-growth Sitka spruce-western hemlock forests in southeast Alaska. Most plots had rotated sigmoid or reverse J-shaped diameter distributions. Overstory tree patterns were uniform at short distance (<5 m) and random or aggregated at larger distances (>5 m); understory trees were spatially random or aggregated at most scales. Tree patterns were highly variable across plots. Overstory and understory tree populations were spatially independent in most medium canopy cover (40%-70%) plots, but spatially repelled in most high canopy cover ($>70\%$) plots. Canopy gap delineation using a traditional geometric approach identified more gaps and greater forest area in gaps compared to a new method based on canopy tree shadow lengths. We recommend defining the lower limit of canopy gap size using overstory tree crown diameter; gap delineation based on overstory tree shadow length is overly conservative at higher latitude sites. Our analyses show that, despite their low species richness, the temperate rainforests of southeast Alaska are highly structurally diverse.

Key words: spatial patterns, gap dynamics, old-growth, competition, canopy gap

Introduction

Old-growth forests provide important ecosystem functions including wildlife habitat, regulation of energy and nutrient cycles, and long-term carbon sequestration unmet by younger forests (Spies 2004). Horizontal and vertical heterogeneity—structural complexity—are emergent properties of old-growth stands that directly influence their functional characteristics (Franklin and Van Pelt 2004). Structural complexity is the long-term result of disturbance history, competitive interactions, tree mortality and recruitment, and the edaphic mosaic (Lertzman et al. 1996; Franklin et al. 2002; Franklin and Van Pelt 2004, Larson et al. 2015).

In forests where stand replacing disturbances are rare, conceptual models of stand dynamics assume that small scale disturbances (i.e., wind, snow and ice, insects, disease) drive the development of structural and spatial heterogeneity in maturing forests (Nowacki and Kramer 1998, Franklin et al. 2002). As stands transition from mature to old-growth, the structural and compositional consequences of canopy gap formation obscures the imprint of earlier competition-driven self-thinning mortality (Lertzman et al. 1996; Franklin et al. 2002). Overstory tree mortality creates localized canopy gaps allowing light to reach the forest floor (Lertzman and Krebs 1991). Gap size and the architecture of surrounding canopy trees directly influence and alter the patterns of light, moisture, and nutrients available to the understory (Canham et al. 1990, Van Pelt and Franklin 1999, Van Pelt and Franklin 2000). Gap-associated microenvironments influence seedling performance, regeneration response, community composition, and productivity (Lertzman and Krebs 1991; McCarthy 2001, Coates 2002).

Gap patterns and dynamics have been investigated in the coastal temperate rainforests of southeast Alaska (Alaback 1988; Ott 1997; Ott and Juday 2002). However, it is not clear how well the canopy gap concept applies at higher latitudes, because light that penetrates the forest

canopy is increasingly displaced away (because of low sun angles) from the structural gap and associated soil resources with increasing latitude (Canham et al. 1990; Zhu et al. 2015, Kramer et al. 2001). An additional challenge is how to detect and classify canopy gaps in an objective, repeatable manner that is linked to ecosystem function and forest dynamics. Zhu et al. (2015) recently introduced a method to objectively define minimum gap size based on the shortest shadow length of canopy trees surrounding a gap and canopy tree crown diameter, which directly accounts for the influence of surrounding canopy trees to moderate the light regime and modify the within gap microclimate and associated processes. The applicability of this new method to other forest types, especially higher latitude forests requires evaluation.

Tree spatial patterns reflect both the disturbance regime and past species interactions. Distinct structural patterns can be detected from within a structurally complex forested matrix, which provide insight into the underlying ecological processes (McIntire and Fajardo 2009).

Competitive interactions are an additional mechanism driving structural change in long-lived and old-growth forests, and past competition may be detected in tree spatial patterns (Franklin et al. 2002; Parish and Antos 2004, Lutz et al. 2014, Larson et al. 2015). In temperate forests of the Pacific Northwest, the very shade-tolerant tree *Tsuga heterophylla* (western hemlock) is a strong competitor that may directly influence forest dynamics (Lutz et al. 2014). Competition theory predicts that large canopy trees will outcompete smaller understory trees for resources in their immediate environment, leading to a spatial segregation of the two populations at local scales (i.e., up to about 10 m) and a tendency towards a uniform distribution of overstory trees (Moeur 1997; Larson and Churchill 2008). Previous work has found spatial segregation between large overstory trees, particularly hemlock, and understory trees (i.e., ingrowth; Getzin

et al. 2006; Lutz et al. 2014). If present, strong competitive interaction suggests that the large overstory trees are strongly influencing the forest dynamics.

Northern coastal Sitka spruce (*Picea sitchensis*) – western hemlock (*Tsuga heterophylla*) forests form the largest expanse of intact old-growth temperate rainforest worldwide, providing a natural observatory in which to examine the structure and stand development of long-lived forests (Alaback 1988; McCarthy 2001). The objectives of this study were to characterize the structural and spatial attributes of unmanaged northern coastal spruce-hemlock forests, and to interpret this analysis of forest stand structure and spatial pattern in terms of past developmental processes, especially gap dynamics and competitive interactions between trees. We first report species composition and forest structure, including tree diameter distributions, providing context for our spatial analyses and interpretation of forest dynamics. Second, we investigate canopy gap attributes, including gap size distributions, total open space unoccupied by overstory tree crowns, and an assessment of the new Zhu et al. (2015) gap detection method. Third, we use spatial point pattern analysis to investigate past competitive interactions between tree populations, and to test the hypothesis of spatial segregation between overstory and understory tree populations (Lutz et al. 2014). These objectives require large plots (>1 ha) in which the locations of individual trees are mapped, a field sampling approach that complements traditional forest sampling with small (<1 ha) fixed area plots, but are better suited for different objectives (Lutz 2015).

Materials and methods

Study Area and Sampling Design

The data analyzed here were collected in 1964 as part of a forest inventory study designed, “To determine which basal area factor and point cluster pattern combinations would

provide acceptably accurate measurements of basal area per acre.” (LaBau 1967). The original study was motivated by a directive from the U.S. Forest Service Washington Office that instructed USFS Regional Offices to convert forest inventory field sampling from fixed radius plots to point (i.e., prism) sampling. The scope of the original study was old-growth spruce-hemlock forests (LaBau 1967).

Study sites were located in old-growth Sitka spruce-western hemlock forests within the Tongass National Forest around Juneau and Petersburg, Alaska in the summer of 1964 (Figure 1). Using a stratified random sampling design, plots were located using aerial photographs (1:15,840 scale; LaBau 1967). Plots were required to be: (1) accessible—less than a mile from a road or beach; (2) commercial forest land capable of producing at least 8,000 board feet per acre (actual gross Scribner board foot volume for sampled plots: 26,764 - 110,947 bd ft); (3) at least 150 years old; (4) a spruce and/or hemlock forest in which at least 50% of timber volume was either spruce or hemlock; and (5) covering at least 2.02 ha (5 acres). Twenty-six potential plot locations were identified and classified as medium density (canopy closure of 40-70%) or full density (70-100% canopy closure) stocking based on aerial photo interpretation. All five locations falling into the medium density category were selected for sampling. The remaining sites were in high density areas, of which five were randomly selected for sampling. A total of 10, 1.42 hectare (100.6×140.8 m; 5×7 chains) plots were located and sampled. Because the old-growth near Juneau tends to have lower timber volumes, two plots were located near Petersburg, Alaska. Plot elevations ranged between 10 m and 500 m above sea level. The climate of southeast Alaska is mild and maritime with summer and winter mean temperatures of 8°C and 1°C respectively; and mean annual precipitation is 145 cm and 266 cm for Juneau and Petersburg, respectively, occurring year-round, making prolonged drought rare (WRCC 2016).

Data Collection

Plot locations identified in aerial photographs were navigated to in the field and used as plot centers. Plot boundaries were laid out and corners staked using a staff compass, topographic chain, and relascope (LaBau 1967). Closure requirements for the primary plot boundary control traverse specified an allowable error of 1 in 300 (LaBau 1967). All live trees greater than 7.6 cm (3.0 in) in diameter at breast height (DBH, 1.37 m) were mapped in 20.12 m (66.0 ft) wide parallel columns within each 1.42 ha plot by making perpendicular side shots from a staked steel tape located in the center of each column. Each column was subdivided into 404.9 m² subplots (1/10th acre) to facilitate tree measurement and data recording. Within subplots, each tree was assigned a unique identifying number and species, DBH, and height in number of 4.9 m (16 ft) logs, as well as tree spatial coordinates were measured and recorded (LaBau 1967). Dead trees were not sampled.

To facilitate our study of gap attributes and tree spatial patterns, we designated three canopy strata based on tree height; overstory, midstory and understory (Larson and Franklin 2006). We designated trees ≥ 25 m tall as overstory trees, approximating the 75th percentile of tree heights which had a lower DBH limit of 38.5 cm, and consistent with past usage in this forest type (Hennon and McClellan 2003). Trees 10-25 m tall were termed midstory, and ≤ 10 m were designated as understory trees. To fully explore the analytical consequences of this definition of overstory trees we conducted a sensitivity analysis using overstory tree heights of 20, 25, and 30 m on gap parameters (see Table S2, S3).

Spatial Analysis

Gap analysis

Canopy openings are regions of the forest canopy unoccupied by overstory tree crowns. For this analysis, we define open areas as regions with no direct overhead overstory canopy cover, with no lower size limit. Canopy gaps (Figure 2) are defined as contiguous open areas of sufficient size to create forest understory conditions that are functionally different from smaller canopy openings, in terms of, for example, increased available light, nutrients, or soil moisture (Zhu et al. 2015). The classical definition of a canopy gap is an opening created by the death of a dominant overstory tree (Runkle 1982).

Open area and canopy gaps were identified and quantified using mapped tree locations, modeled tree heights, maximum crown dimensions, and tree shadow lengths. Tree heights were determined using estimated crown ratio values and a regionally parameterized height to diameter relationship (Keyser 2015). We used modeled total tree heights for gap delineation because the field-measured height in merchantable logs will always underestimate, sometimes severely, total tree height. Crown ratio values were determined using a set of Weibull-distribution based equations (Keyser 2015). Species specific maximum crown diameter estimates were determined using regionally parameterized relationships between tree diameter and maximum crown dimensions (Bechtold 2004; Keyser 2015).

We used a canopy opening detection algorithm developed by Churchill et al. (2017) for point pattern datasets. The opening algorithm determines the location and area of unoccupied space in a point pattern (i.e., a tree stem map) based on a user designated threshold distance from a fixed grid of points to the nearest tree. Polygons are then drawn in all unoccupied areas larger than the threshold distance from each of the surrounding tree boles. A tree crown buffer with a length equal to the average overstory tree crown radius is subtracted from the polygon so gaps extend from overstory tree crown edge to crown edge. All overlapping polygons are merged and

the area of each merged opening is calculated. This calculated gap area is the open area devoid of any overstory foliage, which is analytically equivalent to a canopy gap as defined by Runkle (1982). Eliminating the tree crown buffer is analytically equivalent to Runkle's (1982) expanded gap, where displaced light due to the canopy gap is still highly influential extending to the base of the boles of gap bordering trees (Runkle 1982). An edge correction buffer equal to the threshold distance was applied to the perimeter of each plot to ensure only complete canopy gaps would be calculated. Without this buffer, partial gaps on the plot edge would be calculated, potentially inflating total gap area since no information is available for trees beyond the sampling window.

Geometric gaps

We used the classic definition of a canopy gap (Runkle 1982) as a benchmark against which to evaluate the new method proposed by Zhu et al. (2015). Developmental canopy gaps result from the death of one or more canopy trees (Runkle 1982). The smallest functional gap would then be the open area caused by the death of a single overstory tree. We used this to define the lower limit of a functional "geometric gap" with a lower limit equal to the crown diameter of a single overstory tree (Figure 2B). A functional gap using this definition had a threshold distance of 8.88 m and tree crown buffer of 4.44 m. This value is consistent with the average size of a single tree canopy gap across forest types (Canham et al. 1990).

Shadow gaps

Using the methods of Zhu et al. (2015), we determined the lower limit of functional gap size using the shortest shadow length of an average overstory tree; gaps greater than or equal to this area are termed "shadow gaps". Shadow length was calculated using an overstory tree height of 25 meters, average plot latitude, and the solar angle at noon (1200 hrs) averaged over the

growing season (Figure 2A; Zhu et al. 2015). The average crown diameter of an overstory tree was subtracted from the shadow length to determine the lower limit of a functional shadow gap. Shadow gaps were quantified using the algorithm described above with a threshold distance of 11.78 m and tree crown buffer of 4.44 m.

Open area

Total open area in the plot devoid of overstory foliage was calculated using the same opening algorithm with a threshold distance of 4.44 m and tree crown buffer of 4.44 m. These values determined open area extending from the edge of all non-overlapping overstory tree crowns—the total area with no direct overhead overstory canopy coverage. Non-gap open area was calculated as the difference between total open area and functional gap area.

Stand level spatial analysis

We analyzed tree spatial patterns and interactions at the stand and within-stand scales using the statistical program R version 3.2.1 (R Core Team 2016) and functions in the spatstat library (Baddeley and Turner 2005). Stand level spatial patterns were evaluated using the pair correlation function with an isotropic edge correction and default distance range. The pair correlation function (g) is a normalized, non-cumulative density function that calculates the probability of finding the observed density of neighboring trees in a ring centered around each point in a given point pattern across a range of distances (Wiegand and Moloney 2004). Significance is assessed by comparing the empirical result to the density generated through a random point process at those same distances (Wiegand and Moloney 2004). The advantage of using a non-cumulative function is that spatial patterns can be detected at given inter-tree distances rather than up to a given distance. Observed values less than 1 indicated a uniform pattern and greater than 1 suggest aggregation. Significance was evaluated using a Monte Carlo

simulated 95% confidence envelope. A goodness of fit test was unnecessary since spatial analysis was exploratory. The pair correlation function was used to evaluate the spatial patterns of: (1) overstory trees of all species, (2) only western hemlock (i.e., *Tsuga*) overstory, and (3) understory trees of all species. Spatial patterns of overstory spruce only were not evaluated due to low sample size.

Within-stand level spatial analysis

By reducing the scale of observation to within the stand, patches of trees and individuals can be identified. These local spatial patterns were evaluated using a clustering algorithm that assigns each tree to a patch or as a widely spaced individual using an analytically determined fixed inter-tree distance (Plotkin et al. 2002; Larson and Churchill 2008). Inter-tree distance is measured from stem center to stem center. Trees are a member of the same patch if the inter-tree distance is less than the inter-tree distance from at least one other patch member. Individual trees have no neighbors within at least the inter-tree distance. Inter-tree distance was determined using percolation analysis, where the inflection point in distribution is used as the inter-tree distance (Plotkin et al. 2002). Analysis was conducted on all overstory trees.

Competition analysis

The bivariate pair correlation function ($g_{i,j}$) was used to examine competitive spatial relationships between overstory (i) and understory (j) populations. A null model of population independence was used to test the prediction of overstory-understory segregation, especially that driven by *Tsuga* (hemlock; Goreaud and Pelissier 2003). If overstory trees suppress ingrowth, then the observed $g_{\text{over,under}}(r) < 1$ where the sub-populations are repelled from each other. Competitive interactions between *Tsuga* overstory—all species understory and all species overstory—all species understory were evaluated.

To evaluate overall spatial patterns and relationships by canopy density type, all spatial analysis methods were also conducted using the pool function in the spatstat library in R paired with a Monte Carlo simulation envelope utilizing the respective null models (Baddeley et al. 2016). When overstory *Tsuga* populations were evaluated in a pooled framework, plot 104 was removed from the analysis in the medium density class due to an insufficient sample size of overstory *Tsuga* stems.

Results

Forest structure and composition

Western hemlock (*Tsuga heterophylla*) dominated overstory and understory species composition, accounting for over 90% of stems in medium density plots and 75% in full density plots (Table 1). However, the largest trees in terms of diameter were Sitka spruce (*Picea sitchensis*). Plot 104, a full density plot located in a riparian area, was a compositional outlier with Sitka spruce making up 75% of the species composition, and the only plot to have black cottonwood (*Populus trichocarpa*) (Table S1). Red alder (*Alnus rubra*) and yellow cedar (*Cupressus nootkatensis*) accounted for only 0.25% and 1.2% of total stems, respectively. When present, all non-dominant species were mostly confined to the midstory and understory positions.

Stem density ranged from 315-666 trees ha⁻¹ in medium and 246-664 trees ha⁻¹ in full density plots. Twenty-five percent and 46% of the trees were tall enough to be considered overstory trees, but accounted for 76% and 83% of the total plot basal area in medium and full density plots respectively. The two plots located near Petersberg (plots 143, 161) were not structurally different from the plots located near Juneau in any of our analysis.

Forests in the medium and full density strata exhibited different, recognizable patterns in their size distributions. Medium density plots exhibited reverse J-shaped diameter distributions,

except for plot 104 which had a rotated sigmoid distribution (Figure 3). Conversely, most full density plots exhibited rotated sigmoid distributions, with the exception of plot 76 which had a reverse J distribution, and plot 32 which exhibits a distribution transitional between unimodal and rotated sigmoid (Figure 4).

Gaps

Stand stem maps indicate that old-growth tree structure consists of varying sizes and numbers of canopy gaps, widely spaced individual trees, and tree patches (Figure 5, S1, S2). Medium density plots consistently had greater numbers of gaps accounting for more of the total open area in each plot (Table 2, Figure S3). The classical geometric gap definition (Runkle 1982) produced two to six times more area in functional gaps than gaps delineated using the Zhu et al. (2015) shadow method, and this difference held over a range of overstory tree heights (Figure S3, Table S2-S3). In both plot density strata, the distribution of geometric gaps followed a right skewed normal distribution covering the full range of gap size classes, while shadow derived gaps exhibited a flat distribution with a more restricted range of size classes, especially in full density plots (Figure 6, S4).

Spatial Patterns

Stand level

Stand level overstory tree spatial patterns exhibited a spatially random tree distribution across most distances, with significant aggregation observed across most distances for understory trees (Table 3). All full density overstory trees tended to exhibit significant uniformity, mostly at short distances (1-3 m), with medium density plots tending towards more random distributions across all distances (Figure S5, S6). *Tsuga* overstory trees in medium density plots were randomly arranged, but one plot indicated significant aggregation around 10

m and one plot exhibited significant uniformity around 4 m (Figure S7). Full density overstory *Tsuga* was uniformly distributed at short distances (1-4 m) in four of the five plots and aggregated at three different ranges (6-7 m, 13 m, and 17 m; Figure S8) in the other plot. Understory trees in all but one plot (plot 104) exhibited significant aggregation across most distances in both density classes, but was much stronger in full density plots (Figure S9, S10). Stand-level tree spatial patterns were random across all distances when plots were pooled by density class for all univariate overstory and understory tree analyses: the pooled analysis masked the substantial inter-plot variation.

Within stand spatial patterns

Within stand spatial patterns consisted of widely spaced individuals, tree patches with two or more individuals, and inter-tree percolation distances consistent with average tree crown diameter. Percolation analysis identified overstory, midstory, and understory inter-tree distances around 8, 6, and 4 m respectively which are consistent with the average maximum crown diameter for each subpopulation (Figure 7). Medium density overstory trees were evenly distributed among patch sizes in terms of percent density and basal area, while overstory trees in full density plots occurred mainly as two very large patches that accounted for 85% and 83% of the density and basal area (pooled by density) respectively, with little variation in patch distribution between plots (Table 4, Table S4).

Competition

Overstory hemlock and understory populations were spatially independent across most distances regardless of density class except two full density plots which indicated significant repulsion between the two populations across nearly all distances (Figure 8, 9). Medium density plots exhibit some small scale attraction (1-3 and 10 m), with one plot also indicating repulsion

around 11 m (Figure 8). Two of the full density plots indicate repulsion across all distances (1-25 m), with significant repulsion detected in the other three (Figure 9). Pooled analysis indicated that overstory hemlock and understory populations are spatially independent, again obscuring the between plot variation.

An examination of the spatial relationship between all overstory and all understory trees indicated significant repulsion, attraction, and independence across various differences between plots and within in density class. Most medium density plots showed significant attraction at short and middle distances, one plot indicating only independence, and one plot with repulsion around 11 m (Figure S11). High between plot variation was also apparent for full density plots, where one plot showed independence, three plots had significant repulsion anywhere from 3-25 m, and the last plot overstory and understory trees were spatially attracted from 2-12 m (Figure S12).

Discussion

Our analyses quantify for the first time spatial aspects of structural complexity in Sitka spruce-western hemlock forests, and provide a new line of evidence supporting a role for gap dynamics in this forest type. Large, stem mapped plots offer a means to investigate attributes of forest structure and dynamics that cannot be studied with traditional small fixed area plots (e.g., Lutz et al. 2014), an approach that has not previously been used in the temperate rainforests of southeast Alaska (but see Deal et al. 1991). Our analyses of tree spatial patterns, gap size distributions, and spatial relationships between overstory and understory trees show that, despite their low species richness, the temperate rainforests of southeast Alaska are highly structurally diverse.

The original sampling design for this study targeted old-growth forests, which at the time of sampling in 1964 were defined as sites with no evidence of past timber harvest in which at least 150 years had passed since stand-initiating disturbance (LaBau 1967). Previous work in old-growth spruce-hemlock forests of southeast Alaska showed that old-growth structural features do not become apparent until about 160-200 years after stand-initiating disturbance (Alaback 1984). Thus, our study sites likely include both true old-growth stands, as well as younger stands that might be better described as transitional (*sensu* Zenner 2005) or early old-growth (*sensu* Freund et al. 2015).

Forest structure

Tree diameter distributions provide insights into past forest development, and vary predictably along a forest age and structural development gradient (Alaback 1984, Zenner 2005). In wind-disturbed spruce-hemlock forests of southeast Alaska, young forests originating from stand-replacement disturbance characteristically exhibit a unimodal diameter distribution up to about stand age 160 years; at greater ages a reverse-J diameter distribution was most common (Alaback 1984). A rotated sigmoid diameter distribution is generally associated with stands that are transitional between the mature and old-growth structural stages (Zenner 2005, Freund et al. 2015). Sites with disturbance histories that include intermediate non-stand replacing disturbances typically exhibit more complex DBH distributions, including rotated sigmoid (Ott and Juday 2002, Zenner 2005) and bi- or multi-modal distributions (Deal et al. 1991, Kramer et al. 2001, Ott and Juday 2002, DeGayner et al. 2005).

All plots included trees >100 cm DBH (Table S1), and nine of 10 plots had either rotated sigmoid or reverse J-shaped diameter distributions (Figure 3, 4), evidence that these are late-successional stands that have either attained old-growth structure or are transitional between

mature and old-growth (c.f., Ott and Juday 2002). Plot 32 had a skewed normal distribution (Figure 4), indicating that this site may be just beginning to transition to old-growth structure (Alaback 1984). Reverse-J shaped DBH distributions were most common and most pronounced in the medium canopy density stratum (Figure 3), suggesting that these sites may have more highly developed old-growth attributes, and have developed for a longer time since the last stand-replacing disturbance than the full canopy density plots (Figure 4). However, a complete population age structures would be needed to definitively assess stand age and developmental histories (Deal et al. 1991).

Gap delineation, area, and size distributions

Two types of canopy gaps occur in the temperate rainforests of southeast Alaska: developmental gaps and edaphic gaps. Developmental canopy gaps are the result of individual tree mortality and small-scale, chronic disturbance. Most trees die standing or from bole breakage in temperate old-growth conifer forests of the Pacific Northwest, with only about 20 to 25% of trees uprooted (Spies et al. 1990, Hennon and McClellan 2003, Larson and Franklin 2010). Tree death and gap formation due to bole breakage is often associated with preexisting decay and prior wounding, which compromise tree structural integrity and predispose mortality (Hennon 1995, Hennon and McClellan 2003, Larson and Franklin 2010). Edaphic gaps are persistent canopy openings within the forest matrix associated with sites unsuitable for development of a closed canopy, such as stream courses, rock outcrops, or wetlands (Lertzman et al. 1996). Extreme structural variants of edaphic gaps also occur that prevent the development of a closed canopy. For example, low-productivity palustrine forested wetlands—sites that support development of spruce-hemlock forests but where a shallow depth to the water table limits productivity (Bisbing et al. 2015), sometimes preventing development of a closed canopy.

Another example is “priority” gaps (*sensu* Schmidt et al. 1998) where patches of dense mats of hardwood or shrub stems establish early in stand development and exclude conifer regeneration, preventing canopy closure. A strength of our analysis is that it provides an unbiased sample of forest gap structure and tree spatial patterns in coastal spruce-hemlock forests. However, we are not able to distinguish developmental gaps from edaphic gaps. Thus, our analysis of forest canopy gap structure represents the combined effects of site conditions (edaphic and priority gaps) and past tree mortality (developmental gaps).

Gap structure was present in both canopy density classes with an average of 34% and 20% of total medium and full density plot areas influenced to some degree by canopy openings (Table 2). These values are similar to the average of 30.2% found by Lertzman et al. (1996) for combined developmental and edaphic gap area in forests of coastal British Columbia. On average, 23.2% and 6.0% of plot area was in functional canopy gaps for medium and full density categories, respectively, using the geometric (Runkle 1982) gap delineation method. This range is consistent with previous estimates of the area in developmental canopy gaps, which range from 3.8% to 33.7% in old-growth Alaskan temperate forests (Nowacki and Kramer 1998, Ott and Juday 2002). We used mapped tree locations and modeled tree heights and crown widths to estimate area in canopy openings and gaps, while previous studies directly measured canopy gaps in the field. Although modeled tree crowns do not represent actual crown geometry with perfect fidelity, our results for gap size distributions and total area in openings or gaps agree with previous field-based gap delineation studies.

Our estimates of the functional gap size distribution using the geometric delineation approach are slightly different from previous studies, but our range of gap size values are consistent with other studies. Geometric gaps exhibited an approximately normal, right skewed

distribution, while canopy gap distributions in old-growth temperate forests in southeast Alaska and British Columbia consistently exhibit right skewed or negative exponential distributions suggesting the prevalence of many smaller gaps (Lertzman and Krebs 1991; Ott 1997; Nowacki and Kramer 1998, Bartemucci et al. 2002; Ott and Juday 2002). Our geometrically derived gaps spanned the range of size classes (1-600+ m²), with many mid-sized gaps (100-300 m²) and some large gaps (>600 m²) apparent in both density classes (Figure 6). In temperate forests in southeast Alaska canopy gaps have been found to range from 6-264 m² (Nowacki and Kramer 1998, Ott and Juday 2002), from 5-525 m² in southwest British Columbia (Lertzman and Krebs 1991), up to 1,253 m² on rare occasions in northern British Columbia (Bartemucci et al. 2002, and from 25.5-366 m² in more southern temperate forests (Van Pelt and Franklin 2000). Using field based methods, gaps >600 m² are rare usually only detected using Runkle's (1982) expanded gap definition, where the gap extends from tree bole to bole rather than the canopy edges (Bartemucci et al. 2002). However, in Chilean temperate rainforest average canopy gap size was 425 m² (Veblen 1985) and gaps as large as 739 m² were measured in the southern Sierra Nevada (Van Pelt and Franklin 2000).

We do not recommend using the Zhu et al. (2015) gap delineation method (i.e., shadow gaps, Figure 2A) in tall, higher latitude forests, such as the coastal spruce-hemlock forests studied here. At our study sites, the Zhu et al. (2015) method underestimated the number of and total area in canopy gaps (Figure 6, S3, Table 3, S2-S3) relative to the classical Runkle (1982) method because the Zhu et al. (2015) definition of a minimum functional gap size increases with decreasing sun angle. The Zhu et al. (2015) method is much more appropriate for lower latitude tropical and subtropical forests where the understory light regime is more directly regulated by overhead canopy cover and gaps (Canham et al. 1990). Canopy gaps regulate other

environmental variables in addition to light, such as precipitation throughfall rates and snow accumulation and persistence on the forest floor (Dickerson-Lange et al. 2017), and soil moisture (Gray et al. 2002). These important gap-influenced processes and environmental features are closely related to the actual geometry of canopy gaps, which is better represented using the Runkle (1982) geometric gap method.

Tree spatial patterns and evidence of past competition

Competitive interactions produced a much stronger spatial signal in full density than medium density plots. However, we did not observe what we expected in terms of spatial patterns and competitive interactions in the pooled analyses. Significant spatial patterns consistent with past competitive mortality were evident only in individual plot analyses. The pooled analyses masked significant spatial patterns due to alternate scales of significant patterns between plots within a density class, which may be due to a high degree of variation in edaphic and biophysical conditions in the region. The overall random distribution of canopy trees, and those in medium density stands was not consistent with our prediction of uniformity, but is consistent with the findings for canopy tree patterns in old-growth of similar forest types (Larson and Churchill 2008, Lutz et al. 2014). In contrast, most of the individual full density plots indicated significant uniform spatial patterns from 1-3 m suggesting that earlier self-thinning mortality was an important developmental process in those stands (Larson et al. 2015).

Site and species-specific factors may explain why we did not find the predicted spatial signature of strong competitive interactions between overstory and understory trees. First, the sampling design did not capture the smallest diameter trees (>7.6 cm DBH). The lack of significant aggregation in the understory trees may also be partially attributed to the missing smallest size classes, which typically show the strongest signal of spatial aggregation, with

midstory trees tending towards random distributions (Van Pelt and Franklin 2000, Parish et al. 1999, Lutz et al. 2014). In addition, the low solar angles in latitudes above 50° N displaces the available light in canopy gaps away from the gap into the forest matrix creating a spatial disconnect between the location of the gap and the regeneration response (Canham et al. 1990; Coates and Burton 1997; Kneeshaw and Bergeron 1998; Van Pelt and Franklin 2000). This displacement may contribute to the apparent attraction between overstory and understory trees at some sites, as seedlings and saplings have been found to be more or equally abundant on edges of gaps and into the forest matrix, where the competitive interactions with the overstory is inconsequential compared to the availability of light or the presence of suitable establishment sites (Ban et al. 1998, Van Pelt and Franklin 2000, Coates 2002).

Conclusions

This study provides two novel contributions towards objectively quantifying structural complexity in tall, higher latitude forests. We provide the first quantification of spatial aspects of structural complexity for higher latitude Sitka spruce-hemlock forests. Despite their low species richness, forest structure was highly heterogeneous, characterized by a forest mosaic of canopy gaps, tree patches, and a diverse range of tree sizes. These distinctive structural features contribute to the unique ecological functions of old-growth forests that are unmet by younger stands (Spies 2004; Franklin and Van Pelt 2004). However, the strong competition and spatial segregation signals observed in more southern temperate conifer forests were much weaker and only occasionally apparent in our data, likely due to low sun angles, lower site productivity, and greater edaphic heterogeneity in our higher latitude rainforest study sites

This study is the first to test Zhu et al.'s (2015) shadow gap delineation method in tall, higher latitude forests. We consider it an excellent method at lower latitudes, but because of the

singular emphasis on noon solar angles to define canopy gaps, the Zhu et al. (2015) approach underestimates total area and number of canopy gaps in higher latitude forests. Thus, we do not recommend using the Zhu et al. (2015) method at higher latitude sites. Objectively delineating canopy gaps using the traditional geometric gap (Runkle 1982) is more appropriate for higher latitude forests, including coastal Sitka spruce-western hemlock forests.

Acknowledgements

We are indebted to Mr. Vernon J. LaBau for providing the dataset for this analysis and the crew who assisted in collecting it. Three anonymous reviewers provided constructive suggestions that improved this manuscript.

Draft

References

- Alaback, P.B. 1984. A comparison of old-growth forest structure in the western hemlock–Sitka spruce forests of southeast Alaska. *In*: Proceedings of the Symposium: Fish and Wildlife Relationships in Old-Growth Forests, Juneau, AK, 12–15 April 1982. *Edited by* W.R. Meehan, T.R. Merrell Jr., and T.A. Hanley. American Institute of Fishery Research Biologists, Morehead City, NC. pp. 219–226.
- Alaback, P. B. 1988. Dynamics of old-growth temperate rainforests in southeast Alaska. *In* Proceedings of the 2nd Glacier Bay Science Symposium. *Edited by* A.M. Milner and J.D. Wood. Gustavus, AK. pp. 150-153.
- Alaback, P.B., and Juday, G.P. 1989. Structure and composition of low elevation old-growth forests in research natural areas of southeast Alaska. *Nat. Area J.* **9**(1): 27-39.
- Baddeley, A., Rubak, E., and Turner, R. 2016. Spatial point patterns: methodology and applications with R. CRC Press, Boca Raton, FL.
- Baddeley, A., and Turner, R. 2005. Spatstat: an R package for analyzing spatial point patterns. *J. Stat. Softw.* **12**(6):1–42.
- Ban, Y., Xu, H., Bergeron, Y., and Kneeshaw, D.D. 1998. Gap regeneration of shade intolerant *Larix gmelini* in old growth boreal forests of northeastern China. *J. Veg. Sci.* **9**(4): 529-536.
- Bisbing, S.M., Cooper, D.J., D'amore, D.V., and Marshall, K.N. 2015. Determinants of conifer distributions across peatland to forest gradients in the coastal temperate rainforest of Southeast Alaska. *Ecohydrology.* **9**(2): 354-367.

- Bartemucci, P., Coates, K.D., Harper, K.A., and Wright, E.F. 2002. Gap disturbance in northern old-growth forests of British Columbia, Canada. *J. Veg. Sci.* **13**(5): 685-696.
- Bechtold, W.A. 2004. Largest-crown-width prediction models for 53 species in the Western United States. *West. J. Appl. For.* **19**(4): 245-251.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* **20**(5): 620-631.
- Churchill, D.J., Carnwath, G.C., Larson, A.J., and Jeronimo, S.A. 2017. Historical forest structure, composition, and spatial pattern in dry conifer forests of the western Blue Mountains, Oregon. USDA For. Serv. Gen. Tech. Report PNW-GTR. *In press*.
- Coates, K.D. 2002. Tree recruitment in gaps of various size, clearcuts, and undisturbed mixed forest of interior British Columbia, Canada. *For. Ecol. Manag.* **115**(1): 387-398.
- Coates, K.D., and Burton, P.J. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *For. Ecol. Manag.* **99**(3): 337-354.
- Deal, R.L., Oliver, C.D., and Bormann, B.T. 1991. Reconstruction of mixed hemlock-spruce stands in coastal southeast Alaska. *Can. J. For. Res.* **21**(5): 643-654.
- DeGayner, E.J., Kramer M.G., Doerr, J.G., and Robertsen, M.J. 2005. Windstorm disturbance effects on forest structure and black bear dens in southeast Alaska. *Ecol. Appl.* **15**(4): 1306-1316.
- Dickerson-Lange, S.E., Gersonde, R.F., Hubbart, J.A., Link, T.E., Nolin, A.W., Perry, G.H., Roth, T.R., Wayand, N.E. and Lundquist, J.D. 2017. Snow disappearance timing is

- dominated by forest effects on snow accumulation in warm winter climates of the Pacific Northwest, USA. *Hydrological Processes*. DOI: 10.1002/hyp.11144
- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C. and Bible, K. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manag.* **155**(1): 399-423.
- Franklin, J.F., and Van Pelt, R. 2004. Spatial aspects of structural complexity in old-growth forests. *J. Forest.* **102**(3): 22-28.
- Freund, J.A., Franklin, J.F., and Lutz, J.A. 2015. Structure of early old-growth Douglas-fir forests in the Pacific Northwest. *For. Ecol. Manag.* **335**: 11-25.
- Getzin, S., Dean, C., He, F., Trofymow, J.A., Wiegand, K., and Wiegand, T. 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography* **29**(5): 671–682.
- Goreaud, F. and Pélissier, R. 2003. Avoiding misinterpretation of biotic interactions with the intertype K_{12} -function: population independence vs. random labelling hypotheses. *J. Veg. Sci.* **14**(5): 681-692.
- Gray, A.N., Spies, T.A., and Easter, M.J. 2002. Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. *Can. J. For. Res.* **32**(2): 332-343.
- Hennon, P.E. 1995. Are heart rot fungi major factors of disturbance in gap-dynamic forests? *Northwest Sci.* **69**(4): 284-293.

- Hennon, P.E., and McClellan M.H. 2003. Tree mortality and forest structure in the temperate rain forests of southeast Alaska. *Can. J. For. Res.* **33**(9): 1621-1634.
- Keyser, C. E. 2015. Southeast Alaska and Coastal British Columbia (AK) Variant Overview—Forest Vegetation Simulator. USDA For. Serv., Forest Management Service Center Internal Rep. Fort Collins, CO.
- Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology* **79**(3): 783-794.
- Kramer, M.G., Hansen, A.J., Taper, M.L., and Kissinger, E.J. 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. *Ecology* **82**(10): 2749-2768.
- LaBau, V.J. 1967. An analysis of design and technique of cluster point sampling in coastal Alaska old-growth forests. Thesis. Oregon State University.
- Larson, A. J., and Churchill, D. 2008. Spatial patterns of overstory trees in late-successional conifer forests. *Can. J. For. Res.* **38**(11): 2814–2825.
- Larson, J.A., and Franklin, F.J. 2006. Structural segregation and scales of spatial dependency in *Abies amabilis* forests. *J. Veg. Sci.* **17**(4): 489-498.
- Larson, J.A., and Franklin, F.J. 2010. The tree mortality regimen in temperate old-growth coniferous forests: the role of physical damage. *Can. J. For. Res.* **40**(11): 2091-2103.
- Larson, A.J., Lutz, J.A., Donato, D.C., Freund, J.A., Swanson, M.E., HilleRisLambers, J., Sprugel, D.G., and Franklin, J.F. 2015. Spatial aspects of tree mortality strongly differ between young and old-growth forests. *Ecology* **96**(11): 2855-2861.
- Lertzman, K.P., and Krebs, C.J. 1991. Gap-phase structure of a subalpine old-growth forest. *Can. J. For. Res.* **21**(12): 1730-1741.

- Lertzman, K.P., Sutherland, G.D., Inselberg, A., and Saunders, S.C. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecology* **77**(4): 1254-1270.
- Lutz, J.A., Larson, A.J., Furniss, T.J., Donato, D.C., Freund, J.A., Swanson, M.E., Bible, K.J., Chen, J., and Franklin, J.F. 2014. Spatially nonrandom tree mortality and ingrowth maintain equilibrium pattern in an old-growth *Pseudotsuga-Tsuga* forest. *Ecology* **95**(8): 2047-2054.
- Lutz, J.A. 2015. The evolution of long-term data for forestry: large temperate research plots in an era of global change. *Northwest Sci.* **89**(3): 255-269.
- McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environ. Rev.* **9**(1): 1-59.
- McIntire, E.J.B., and Fajardo, A. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology* **90**(1): 46-56.
- Moeur, M., 1997. Spatial models of competition and gap dynamics in old-growth *Tsuga heterophylla/Thuja plicata* forests. *For. Ecol. Manag.* **94**(1): 175-186.
- Nowacki, G.J., and Kramer, M.G. 1998. The effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska. USDA For. Serv. Pacific Northwest Research Station General Technical Report PNW-GTR-421.
- Ott, R.A. 1997. Natural disturbance at the site and landscape levels in temperate rainforest of southeast Alaska. PhD Thesis. University of Alaska, Fairbanks, AK.
- Ott, R.A., and Juday, G.P. 2002. Canopy gap characteristics and their implications for management in the temperate rainforests of southeast Alaska. *For. Ecol. Manag.* **159**(3): 271-291.

- Parish, R., and Antos, J.A. 2004. Structure and dynamics of an ancient montane forest in coastal British Columbia. *Oecologia* **141**(4): 562-576.
- Parish, R., Antos, J.A., and Fortin, M.J. 1999. Stand development in an old-growth subalpine forest in southern interior British Columbia. *Can. J. For. Res.* **29**(9): 1347-1356.
- Plotkin, J.B., Chave, J., and Ashton, P.S. 2002. Cluster analysis of spatial patterns in Malaysian tree species. *Am. Nat.* **160**(5): 629-644.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org>.
- Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* **63**(5): 1533-1546.
- Schmidt, M.G., Ogden, A.E., and Lertzman, K.P. 1998. Seasonal comparison of soil temperature and moisture in pits and mounds under vine maple gaps and conifer canopy in a coastal western hemlock forest. *Can. J. Soil Sci.* **78**(2): 291-300.
- Spies, T.A. 2004. Ecological concepts and diversity of old-growth forests. *J. For.* **102**(3): 14-20.
- Spies, T.A., Franklin, J.F., and Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can. J. For. Res.* **20**(5): 649-658.
- Van Pelt, R., and Franklin, J.F. 1999. Response of understory trees to experimental gaps in old-growth Douglas-fir forests. *Eco. Apps.* **9**(2): 504-512.
- Van Pelt, R., and Franklin, J.F. 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. *Can. J. For. Res.* **30**(8): 1231-1245.
- Veblen, T.T. 1985. Forest development in tree-fall gaps in the temperate rainforests of Chile. *Natl. Geogr. Res.* **1**(2): 162-183.

- Wiegand, T., and Moloney, K.A. 2004. Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* **104**(2): 209-229.
- Western Regional Climate Center (WRCC). 2016. Period of record general climate summary: Juneau, AK [online]. Available from <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?akjune>. [accessed 12 December 2016].
- Zenner, E.K. 2005. Development of tree size distributions in Douglas-fir forests under differing disturbance regimes. *Eco. Apps.* **15**(2): 701-714.
- Zhu, J., Zhang, G., Wang, G.G., Yan, Q., Lu, D., Li, X. and Zheng, X. 2015. On the size of forest gaps: Can their lower and upper limits be objectively defined? *Arg. Forest Meteorol.* **213**: 64-76.

Draft

Table 1. Stand structure and compositional attributes for old-growth Sitka spruce-western hemlock forest stands in southeast Alaska. Medium density represents forests with 40-60% canopy closure and full density is 70-100% canopy closure. Plus/minus values are the standard error of the mean. Overstory trees are ≥ 25 m in height, midstory is trees with heights of 10-25 m, and understory trees are all trees < 10 m tall.

Species	All				Overstory		Midstory		Understory	
	Density (TPH)	Basal area (m ² /ha)	DBH range (cm)	QMD (cm)	Density (TPH)	Basal area (m ² /ha)	Density (TPH)	Basal area (m ² /ha)	Density (TPH)	Basal area (m ² /ha)
Medium density										
PISI	89 ± 37	18.38 ± 9.37	7.6 - 177.5	41.9 ± 4.4	34 ± 9	16.05 ± 3.76	51 ± 8	2.30 ± 0.44	4 ± 1	0.07 ± 0.02
TSHE	425 ± 95	46.01 ± 10.85	7.6 - 132.6	30.2 ± 2.7	70 ± 7	33.23 ± 4.00	220 ± 20	11.36 ± 0.98	135 ± 16	1.40 ± 0.16
POTR	6 ± 6	0.80 ± 0.80	15.2 - 44.5	6.7 ± 6.7	2 ± 0	0.42 ± 0.00	3 ± 0	0.37 ± 0.00	1 ± 0	0.02 ± 0.00
ALRU	6 ± 5	0.44 ± 0.37	8.4 - 43.2	28.0 ± 2.7	1 ± 0.4	0.08 ± 0.05	4 ± 2	0.33 ± 0.18	3 ± 2	0.04 ± 0.02
<i>Total</i>	<i>518 ± 68</i>	<i>64.72 ± 4.28</i>	<i>7.6 - 177.5</i>	<i>34.44 ± 2.84</i>	<i>105 ± 2</i>	<i>49.40 ± 2.09</i>	<i>273 ± 17</i>	<i>13.87 ± 0.61</i>	<i>140 ± 16</i>	<i>1.45 ± 0.16</i>
Full density										
PISI	92 ± 12	37.70 ± 8.04	7.6 - 162.1	61.1 ± 8.6	67 ± 3	36.45 ± 3.77	24 ± 6	1.17 ± 0.28	2 ± 1	0.01 ± 0.004
TSHE	344 ± 78	55.60 ± 3.10	7.6 - 133.6	40.6 ± 3.6	111 ± 4	42.56 ± 0.74	171 ± 25	12.47 ± 1.99	62 ± 13	0.64 ± 0.13
CUNO	56 ± 56	4.82 ± 4.82	10.7 - 55.6	27.9 ± 0.0	0 ± 0	0.00 ± 0.00	50 ± 0	4.71 ± 0.00	6 ± 0	0.01 ± 0.00
<i>Total</i>	<i>448 ± 88</i>	<i>94.33 ± 5.78</i>	<i>7.6 - 162.1</i>	<i>46.44 ± 5.76</i>	<i>178 ± 5</i>	<i>79.08 ± 4.37</i>	<i>205 ± 31</i>	<i>14.58 ± 2.40</i>	<i>65 ± 13</i>	<i>0.67 ± 0.13</i>
All plots										
PISI	91 ± 20	28.0 ± 6.90	7.6 - 177.5	51.5 ± 5.7	51 ± 3	26.25 ± 2.07	37 ± 4	1.73 ± 0.18	3 ± 0.3	0.04 ± 0.01
TSHE	385 ± 60	50.8 ± 5.90	7.6 - 133.6	35.4 ± 2.7	90 ± 4	37.90 ± 1.44	196 ± 11	11.91 ± 0.74	99 ± 8	1.02 ± 0.08
CHNO	56 ± 56	4.82 ± 4.82	10.7 - 55.6	27.9 ± 0.0	0 ± 0	0.00 ± 0.00	50 ± 0	4.71 ± 0.00	6 ± 0	0.01 ± 0.00
POTR	6 ± 6	0.80 ± 0.80	15.2 - 44.5	6.7 ± 6.7	2 ± 0	0.42 ± 0.00	3 ± 0	0.37 ± 0.00	1 ± 0	0.02 ± 0.00
ALRU	6 ± 5	0.44 ± 0.37	8.4 - 43.2	28.0 ± 2.7	1 ± 0.4	0.08 ± 0.05	4 ± 2	0.33 ± 0.18	3 ± 2	0.04 ± 0.02
<i>Total</i>	<i>482 ± 54</i>	<i>79.53 ± 6.0</i>	<i>7.6 - 177.5</i>	<i>41.11 ± 3.15</i>	<i>141 ± 4</i>	<i>64.24 ± 2.25</i>	<i>239 ± 12</i>	<i>14.22 ± 0.83</i>	<i>103 ± 8</i>	<i>1.06 ± 0.08</i>

*PISI = Sitka spruce (*Picea sitchensis*); TSHE = western hemlock (*Tsuga heterophylla*); CHNO = yellow cedar (*Cupressus nootkatensis*); POTR = black cottonwood (*Populus trichocarpa*); ALRU = red alder (*Alnus rubra*). Note: The data do not include any records of *Tsuga mertensiana* which co-occurs with *Tsuga heterophylla* in many coastal forests in Southeast Alaska. Large individuals of these species can be difficult to differentiate. Thus, we acknowledge the potential for the TSHE category to include minor amounts of *Tsuga mertensiana*.

Table 2. Summary values for open areas for 10 Sitka-spruce western hemlock forests in southeast Alaska. Values in parentheses are percent of total plot area in functional canopy gaps per plot. Each plot occupies a total area of 14,164 m².

Plot	Total open area (m ²)	Area in shadow gap (m ²)	Area in geometric gap (m ²)
Medium density			
104	4754	1410 (9.9)	3009 (21.2)
130	5195	448 (3.2)	3699 (26.1)
132	4883	946 (6.7)	3432 (24.2)
141	4888	562 (4.0)	3133 (22.1)
220	4599	951 (6.7)	3177 (22.4)
All Plots	4864 ± 98	863 ± 170 (6.1)	3177 ± 123 (23.2)
Full density			
32	2364	207 (1.5)	378 (2.7)
76	3380	338 (2.4)	1766 (12.5)
111	2884	354 (2.5)	867 (6.1)
143	2509	0 (0.0)	400 (2.8)
161	3339	0 (0.0)	836 (5.9)
All Plots	2895 ± 208	180 ± 78 (1.3)	849 ± 251 (6.0)

Table 3. Pair correlation function spatial pattern summary values for overstory and understory trees by plot and pooled (“All”) for each density class by distance. The dataset used for overstory *Tsuga heterophylla* was reduced to four plots since plot 104 had an insufficient sample size. Spatial patterns are indicated by symbol type: + indicates aggregation, o is random, and – is uniform.

Distance (m)	0-5	5-10	10-15	15-20	20-25
All Overstory (≥ 25 m tall)					
Medium density					
104	+	o	o	o	o
130	o	o	o	o	o
132	o	o	o	o	o
141	-	o	o	o	o
220	o	o	o	-	o
All Medium	o	o	o	o	o
Full density					
32	-	o	o	o	o
76	-	o	o	o	o
111	-	o	+	o	o
143	-	o	o	o	o
161	-	o	o	+	o
All Full	o	o	o	o	o
Overstory <i>Tsuga heterophylla</i> (≥ 25 m tall)					
Medium density					
130	o	o	o	o	+
132	o	+	o	o	o
141	-	o	o	o	o
220	o	o	o	-	o
All Medium	o	o	o	o	o
Full density					
32	-	o	o	o	o
76	-	o	o	o	o
111	o	+	+	+	+
143	-	o	o	o	o
161	-	o	+	+	o
All Full	o	o	o	o	o
All Understory (≤ 10 m tall)					
Medium density					
104	o	o	o	o	o
130	+	+	+	o	+

132	+	+	+	+	+
141	+	0	0	0	0
220	+	+	0	0	0
All Medium	0	0	0	0	0
Full density					
32	+	+	+	+	+
76	+	+	+	+	0
111	+	+	+	+	0
143	+	+	0	0	+
161	+	+	+	+	0
All Full	0	0	+	0	0

Draft

Table 4. Summary statistics for within-stand spatial patterns of widely spaced individual trees (*i.e.* patch size = 1) and patches of trees. A fixed inter-tree distance of 8.88 m was used for overstory trees. BA is basal area in meters squared and SEM is standard error of the mean presented in parentheses.

Overstory						
<i>Patch size (number of trees)</i>						
Value (SEM)	1	2-4	5-7	8-10	11-15	16+
Medium density						
# Patches ha^{-1}	10 (2)	9 (2)	3 (0)	2 (0)	1 (0)	1 (0)
% Total density	9.6 (2.1)	21.3 (5.7)	16.4 (1.6)	14.2 (3.5)	13.3 (3.3)	18.2 (3.3)
%Total BA	10.5 (2.4)	24.1 (5.5)	16.7 (2.0)	11.5 (3.7)	15.3 (2.6)	21.1 (5.7)
Full density						
# Patches $ha^{-1} \pm SEM$	4 (1)	4 (0)	1(0)	0 (0)	0 (0)	2 (0)
% Total density	2.1 (0.5)	6.1 (1.2)	4.5 (1.5)	0.9 (0.9)	1.9 (1.9)	84.6 (3.1)
%Total BA	2.0 (0.6)	6.7 (0.9)	4.8 (1.5)	0.9 (0.9)	1.9 (1.9)	83.2 (3.0)

Figure captions

Figure 1. Plots were located in the Tongass National Forest in southeast Alaska. Eight plots were located immediately around Juneau and two were near Petersburg, Alaska. Plot locations indicated with a circle represent medium density plots and triangles show full density plots.

Figure 2. Sketch of lower limit of functional gap size. (A) Shadow gap method. SA_{noon} is the solar angle ($^{\circ}$) at noon local time; C_r is the crown radius (4.44 m); C_d is the crown diameter (8.88 m) which is equal to $2 \times C_r$; H is average overstory tree height (25 m); shadow length is the full shadow of a surrounding overstory tree at noon; $SG_{\text{lower limit}}$ is the lower limit of a functional shadow gap (m) and is equal to the shadow length – C_d . (adapted from Zhu et al. 2015). (B) Geometric gap method. $GG_{\text{lower limit}}$ is the lower limit of a functional geometric gap and is equal to C_d or $2 \times C_r$. Assumptions: (1) slope of the gap location is 0° on flat land; (2) H , height of surrounding trees is the same. Hemlock silhouette provided by Natural Resources Canada, <https://tidcf.nrcan.gc.ca/en/trees/factsheet/119>.

Figure 3. Diameter distribution in 10 cm diameter classes for five medium density (40-60% canopy cover) old-growth Sitka spruce-western hemlock forests in southeast Alaska. Labels are located at the center point of the 10 cm diameter classes. PISI: Sitka spruce (*Picea sitchensis*); TSHE: western hemlock (*Tsuga heterophylla*); OTHER includes: yellow cedar (*Cupressus nootkatensis*); black cottonwood (*Populus trichocarpa*); and red alder (*Alnus rubra*).

Figure 4. Diameter distribution in 10 cm diameter classes for five full density (70-100% canopy cover) old-growth Sitka spruce-western hemlock forests in southeast Alaska. Labels are located at the center point of the 10 cm diameter classes. PISI = Sitka spruce (*Picea sitchensis*); TSHE = western hemlock (*Tsuga heterophylla*); OTHER includes: yellow cedar (*Cupressus nootkatensis*); black cottonwood (*Populus trichocarpa*); and red alder (*Alnus rubra*).

Figure 5. Example stem maps for old-growth Sitka spruce – western hemlock forests in southeast Alaska. Tree boles are colored by species and point size represents overstory, midstory, and understory canopy position. A 4.44 m radius was used to project tree crowns on overstory trees to show patches calculated using a fixed inter-tree distance of 8.88 m. Patch size is on a color gradient following the number of trees in a patch. Gaps and associated buffer distances are shown with a solid or dashed line. Background coloration is a graphical display of open area where colors indicate the distance to the nearest overstory trees in meters. Panel A is a medium density plot. Panel B is a full density plot.

Figure 6. Gap size distribution pooled by density class for shadow (Zhu et al. 2015) and geometric (Runkle 1982) gaps. Size class is presented in 50-100 m² bins. Gap areas less than the threshold distance are artifacts of edge correction which quantifies the ‘in’ plot area of gaps bisected by the edge buffer.

Figure 7. Proportional patch size distribution for ten Sitka spruce western hemlock plots. A patch is considered any grouping of two or more trees within a fixed distance of each other. Each

line represents one plot. Overstory trees are defined as any tree greater than or equal to 25 m in height, midstory trees are 10-25 m tall, and understory trees are less than 10 m tall. Plots in full density areas are indicated in black and medium density plots in gray.

Figure 8. Spatial relationships between understory trees (< 25 m tall) and overstory trees (≥ 25 m tall) for the medium density class and pooled value using a replicated bivariate pair correlation function. The analysis was reduced to four plots since plot 104 did not have enough overstory hemlock to conduct the analysis. The black line is the observed pattern and the shaded regions are a simulated 95% confidence envelope. Observed values above (below) the envelope indicates attraction (repulsion) and within indicate independence.

Figure 9. Spatial relationships between understory trees (≤ 10 m tall) and overstory trees (≥ 25 m tall) for the full density class and pooled value using a replicated bivariate pair correlation function. The black line is the observed pattern and the shaded regions are a simulated 95% confidence envelope. Observed values above (below) the envelope indicates attraction (repulsion) and within indicate independence.

Draft

Figure 1

Figure 2

Figure 3

Figure 4

A

B

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Supplementary Material

Table S1: Stand structure and compositional attributes of 10 old-growth Sitka spruce-western hemlock forest stands. Medium density represents forests with 40-60% canopy closure and full density is 70-100% canopy closure. Overstory, midstory, and understory trees are ≥ 25 m, 10-25 m, and <10 m in height respectively. TPH is trees per hectare. PISI = Sitka spruce; TSHE = western hemlock; CHNO = yellow cedar; POTR = black cottonwood; ALRU = red alder.

All						Overstory		Midstory		Understory	
Species	Density (TPH)	Basal area (m ² /ha)	DBH range (cm)	QMD (cm)		Density (TPH)	Basal area (m ² /ha)	Density (TPH)	Basal area (m ² /ha)	Density (TPH)	Basal area (m ² /ha)
Medium density											
Plot 104	PISI	226	55.25	7.6 - 122.2	46.8	109	49.18	110	6.02	6	0.05
	TSHE	82	5.08	7.6 - 77.5	23.6	4	1.66	63	3.27	15	0.14
	POTR	6	0.80	15.2 - 44.5	33.7	2	0.42	3	0.37	1	0.02
	ALRU	> 1	0.07	30.7	30.7	0	0.00	1	0.07	0	0.00
	<i>Total</i>	315	61.20	7.6 - 122.2	41.8	115	51.26	177	9.73	22	0.21
Plot 130	PISI	42	4.28	7.6 - 97.0	30.1	6	3.26	33	1.00	4	0.20
	TSHE	623	59.40	7.6 - 132.6	29.2	86	42.33	323	14.84	213	2.22
	<i>Total</i>	665	63.67	7.6 - 132.6	29.3	92	45.59	356	15.84	217	2.24
Plot 132	PISI	33	10.98	7.9 - 177.5	54.5	11	9.77	21	1.20	1	0.01
	TSHE	379	67.56	7.6 - 123.2	40.0	90	55.95	191	10.54	98	1.06
	ALRU	11	0.81	8.4 - 43.2	25.3	1	0.15	6	0.59	5	0.07
	<i>Total</i>	423	79.34	7.6 - 177.5	41.0	102	65.87	218	12.33	104	1.14
Plot 141	PISI	32	7.04	7.9 - 101.3	44.1	13	6.27	17	0.76	2	0.02
	TSHE	487	46.00	7.6 - 95.3	29.1	84	31.19	234	13.03	169	1.76
	<i>Total</i>	519	53.03	7.6 - 101.3	30.3	97	37.46	251	13.80	171	1.78
Plot 220	PISI	113	14.37	7.6 - 100.6	33.8	33	11.79	72	2.53	8	0.06
	TSHE	553	52.00	7.6 - 109.0	29.0	85	35.02	289	15.12	179	1.84
	<i>Total</i>	666	66.37	7.6 - 109.0	29.9	118	46.81	361	17.65	187	1.90

Full density											
Plot 32	PISI	67	21.76	20.1 - 101.6	53.7	62	21.00	6	0.42	0	0.00
	TSHE	531	66.00	7.6 - 75.7	33.4	146	37.09	343	28.47	41	0.43
	CHNO	56	4.82	10.7 - 55.6	27.9	0	0.00	50	4.71	6	0.10
	Total	654	92.58	7.6 - 101.6	35.6	208	58.43	399	33.61	47	0.53
Plot 76	PISI	129	20.56	7.6 - 111.8	37.8	47	17.13	76	3.38	7	0.05
	TSHE	535	59.13	7.6 - 120.7	31.5	94	41.96	266	15.38	174	1.80
	Total	664	79.70	7.6 - 120.7	32.8	141	59.09	342	18.76	181	1.85
Plot 111	PISI	109	40.97	8.1 - 113.3	58.0	74	39.29	34	1.66	2	0.01
	TSHE	259	52.96	7.6 - 133.6	42.8	108	44.73	103	7.76	47	0.48
	Total	368	93.93	7.6 - 133.6	47.8	182	84.02	137	9.42	49	0.49
Plot 143	PISI	84	40.57	23.9 - 135.6	65.9	82	40.41	2	0.16	0	0.00
	TSHE	224	49.73	7.6 - 104.6	44.6	112	42.09	88	7.40	24	0.23
	Total	308	90.30	7.6 - 135.6	51.2	194	82.50	90	7.56	24	0.23
Plot 161	PISI	71	64.65	23.1 - 162.1	90.3	68	64.44	3	0.21	0	0.00
	TSHE	175	50.52	7.6 - 126.5	50.8	95	46.94	55	3.32	25	0.26
	Total	246	115.17	7.6 - 162.1	64.7	163	111.38	58	3.53	25	0.26

Table S2. Gap analysis summary statistics for 10 stem mapped plots in southeast Alaska. Gaps were calculated using no plot edge buffer. Height is a fixed value designating canopy tree threshold (i.e., 20, 25, 30 m); S and G indicate gap sampling method: S = shadow length, G = geometric. SEM is standard error of the sampling mean.

				Number of gaps in size class [proportion of total plot area] (m ²)							
Plot	Height-method	Gaps ha ⁻¹	Mean area ± SEM (m ²)	0-50	51-100	101-200	201-300	301-400	401-500	501-600	600+
Medium density											
104	20-S	8	242.4 ± 47.1	0 [0.00]	2 [0.01]	5 [0.06]	2 [0.04]	1 [0.02]	1 [0.03]	1 [0.04]	0 [0.00]
	20-G	13	264.7 ± 90.8	4 [0.01]	6 [0.03]	1 [0.01]	3 [0.06]	1 [0.03]	0 [0.00]	1 [0.04]	2 [0.17]
	25-S	7	274.2 ± 58.5	0 [0.00]	2 [0.01]	2 [0.01]	2 [0.04]	0 [0.00]	4 [0.13]	0 [0.00]	0 [0.00]
	25-G	11	302.0 ± 84.4	1 [0.0]	4 [0.02]	3 [0.03]	2 [0.03]	1 [0.03]	2 [0.06]	0 [0.00]	2 [0.14]
	30-S	5	404.7 ± 151.0	0 [0.00]	2 [0.01]	2 [0.02]	0 [0.00]	0 [0.00]	1 [0.03]	0 [0.00]	2 [0.13]
	30-G	4	710.5 ± 461.8	0 [0.00]	2 [0.01]	1 [0.01]	0 [0.00]	1 [0.03]	1 [0.04]	0 [0.00]	1 [0.21]
130	20-S	7	251.5 ± 43.0	0 [0.00]	1 [0.01]	4 [0.05]	2 [0.04]	2 [0.05]	0 [0.00]	1 [0.04]	0 [0.00]
	20-G	15	229.3 ± 60.6	6 [0.01]	5 [0.02]	5 [0.05]	0 [0.00]	0 [0.00]	1 [0.03]	3 [0.12]	2 [0.12]
	25-S	3	380.9 ± 68.9	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.02]	1 [0.02]	1 [0.03]	1 [0.04]	0 [0.00]
	25-G	13	271.0 ± 36.4	1 [0.00]	2 [0.01]	3 [0.03]	3 [0.10]	2 [0.05]	3 [0.09]	2 [0.08]	0 [0.00]
	30-S	4	412.9 ± 84.4	0 [0.00]	0 [0.00]	0 [0.00]	3 [0.06]	1 [0.02]	0 [0.00]	0 [0.00]	2 [0.10]
	30-G	8	559.3 ± 214.8	0 [0.00]	1 [0.01]	0 [0.00]	6 [0.11]	0 [0.00]	1 [0.03]	0 [0.00]	3 [0.29]
132	20-S	6	201.3 ± 54.9	0 [0.00]	2 [0.01]	3 [0.03]	1 [0.01]	1 [0.02]	0 [0.00]	1 [0.04]	0 [0.00]
	20-G	15	195.8 ± 39.3	3 [0.01]	4 [0.02]	8 [0.08]	2 [0.03]	1 [0.02]	1 [0.03]	0 [0.00]	2 [0.09]
	25-S	5	272.4 ± 67.7	0 [0.00]	0 [0.00]	3 [0.02]	1 [0.02]	1 [0.02]	1 [0.03]	1 [0.04]	0 [0.00]
	25-G	9	376.7 ± 87.0	1 [0.00]	0 [0.00]	3 [0.03]	3 [0.05]	1 [0.02]	1 [0.03]	3 [0.12]	1 [0.09]
	30-S	5	290.4 ± 54.5	0 [0.00]	0 [0.00]	2 [0.02]	3 [0.06]	1 [0.02]	0 [0.00]	1 [0.04]	0 [0.00]
	30-G	8	389.4 ± 100.3	0 [0.00]	1 [0.01]	2 [0.02]	4 [0.07]	2 [0.05]	0 [0.00]	1 [0.04]	2 [0.15]
141	20-S	6	186.2 ± 15.6	0 [0.00]	0 [0.00]	4 [0.04]	4 [0.06]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	17	176.2 ± 29.4	5 [0.01]	5 [0.03]	6 [0.06]	4 [0.07]	0 [0.00]	4 [0.13]	0 [0.00]	0 [0.00]
	25-S	5	213.4 ± 28.2	0 [0.00]	0 [0.00]	4 [0.04]	2 [0.04]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]
	25-G	16	209.4 ± 25.9	2 [0.01]	3 [0.02]	8 [0.09]	5 [0.09]	2 [0.05]	3 [0.09]	0 [0.00]	0 [0.00]
	30-S	3	1498.7 ± 784.6	0 [0.00]	0 [0.00]	1 [0.01]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	3 [0.41]
	30-G	3	2028.0 ± 1298.5	0 [0.00]	0 [0.00]	1 [0.01]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	3 [0.56]

220	20-S	5	146.1 ± 20.9	0 [0.00]	1 [0.01]	5 [0.05]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	16	149.4 ± 21.4	4 [0.01]	6 [0.03]	7 [0.07]	4 [0.07]	1 [0.03]	1 [0.03]	0 [0.00]	0 [0.00]
	25-S	4	281.3 ± 71.8	0 [0.00]	0 [0.00]	2 [0.01]	1 [0.02]	2 [0.05]	0 [0.00]	1 [0.04]	0 [0.00]
	25-G	13	251.5 ± 70.4	2 [0.01]	4 [0.02]	6 [0.06]	3 [0.05]	0 [0.00]	1 [0.03]	0 [0.00]	2 [0.14]
	30-S	4	880.4 ± 509.6	0 [0.00]	0 [0.00]	1 [0.01]	2 [0.03]	1 [0.02]	0 [0.00]	0 [0.00]	2 [0.31]
	30-G	4	1188.2 ± 712.3	0 [0.00]	1 [0.01]	1 [0.01]	0 [0.00]	0 [0.00]	2 [0.06]	0 [0.00]	2 [0.42]
Full density											
32	20-S	0	0.0 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	1	81.6 ± 0.0	0 [0.00]	1 [0.01]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	25-S	1	206.9 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.01]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	25-G	5	96.6 ± 34.7	1 [0.00]	5 [0.02]	0 [0.00]	0 [0.00]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]
	30-S	2	1570.8 ± 647.0	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	2 [0.31]
	30-G	4	1096.7 ± 551.6	0 [0.00]	0 [0.00]	2 [0.02]	0 [0.00]	2 [0.05]	0 [0.00]	0 [0.00]	2 [0.40]
76	20-S	5	160.6 ± 25.7	0 [0.00]	2 [0.01]	3 [0.03]	2 [0.03]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	11	135.6 ± 27.5	4 [0.01]	3 [0.01]	5 [0.04]	2 [0.03]	1 [0.02]	1 [0.03]	0 [0.00]	0 [0.00]
	25-S	4	211.2 ± 37.4	0 [0.00]	0 [0.00]	2 [0.02]	3 [0.05]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]
	25-G	11	199.9 ± 48.2	3 [0.01]	4 [0.02]	3 [0.03]	3 [0.05]	1 [0.03]	1 [0.03]	0 [0.00]	1 [0.05]
	30-S	5	412.8 ± 141.8	0 [0.00]	0 [0.00]	2 [0.02]	3 [0.05]	0 [0.00]	0 [0.00]	0 [0.00]	2 [0.13]
	30-G	6	533.3 ± 129.9	0 [0.00]	0 [0.00]	1 [0.01]	3 [0.05]	1 [0.02]	1 [0.03]	0 [0.00]	3 [0.22]
111	20-S	3	187.0 ± 61.8	0 [0.00]	2 [0.01]	0 [0.00]	1 [0.02]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	12	126.4 ± 10.8	2 [0.01]	3 [0.02]	12 [0.13]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	25-S	1	105.4 ± 0.0	0 [0.00]	0 [0.00]	1 [0.01]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	25-G	5	127.3 ± 26.5	0 [0.00]	4 [0.02]	1 [0.01]	2 [0.03]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	30-S	1	106.4 ± 7.0	0 [0.00]	1 [0.01]	1 [0.01]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	30-G	8	155.1 ± 29.9	0 [0.00]	4 [0.02]	4 [0.04]	2 [0.03]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]
143	20-S	3	107.4 ± 17.6	0 [0.00]	2 [0.01]	2 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	12	126.4 ± 10.8	2 [0.01]	3 [0.02]	12 [0.13]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	25-S	1	105.4 ± 0.0	0 [0.00]	0 [0.00]	1 [0.01]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	25-G	5	127.3 ± 26.5	0 [0.00]	4 [0.02]	1 [0.01]	2 [0.03]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	30-S	1	106.4 ± 7.0	0 [0.00]	1 [0.01]	1 [0.01]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	30-G	8	155.1 ± 29.9	0 [0.00]	4 [0.02]	4 [0.04]	2 [0.03]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]

161	20-S	4	167.8 ± 24.6	0 [0.00]	1 [0.01]	4 [0.05]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	17	133.0 ± 19.6	6 [0.02]	2 [0.01]	12 [0.12]	3 [0.05]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]
	25-S	1	151.2 ± 12.9	0 [0.00]	0 [0.00]	2 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	25-G	8	140.1 ± 23.0	2 [0.01]	3 [0.02]	3 [0.04]	3 [0.05]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]
	30-S	1	165.6 ± 23.4	0 [0.00]	0 [0.00]	2 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	30-G	5	146.8 ± 22.1	0 [0.00]	2 [0.01]	4 [0.04]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]

Draft

Table S3. Gap analysis summary statistics for 10 stem mapped plots in southeast Alaska. Gaps were calculated using an edge buffer equal to the lower limit gap size (i.e. threshold distance). Height is a fixed value designating canopy tree threshold (i.e. 20, 25, 30 m); S and G indicate gap sampling method: S = shadow length, G = geometric. SEM is standard error of the sampling mean.

Number of gaps in size class [proportion of total plot area] (m ²)											
	Height-method	Gaps ha ⁻¹	Mean area ± SEM (m ²)	0-50	51-100	101-200	201-300	301-400	401-500	501-600	600+
Medium density											
104	20-S	6	219.0 ± 34.3	0 [0.00]	1 [0.01]	5 [0.06]	1 [0.02]	2 [0.05]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	8	301.5 ± 116.1	2 [0.00]	4 [0.02]	0 [0.00]	3 [0.05]	0 [0.00]	1 [0.03]	0 [0.00]	2 [0.15]
	25-S	3	352.6 ± 78.0	0 [0.00]	0 [0.00]	1 [0.01]	1 [0.02]	0 [0.00]	2 [0.07]	0 [0.00]	0 [0.00]
	25-G	6	376.1 ± 121.7	0 [0.00]	1 [0.01]	2 [0.02]	2 [0.04]	1 [0.02]	0 [0.00]	0 [0.00]	2 [0.12]
	30-S	1	793.7 ± 133.3	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	2 [0.11]
	30-G	1	1216.4 ± 1119.9	0 [0.00]	1 [0.01]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.16]
130	20-S	6	204.8 ± 18.1	0 [0.00]	0 [0.00]	4 [0.05]	4 [0.07]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	8	313.7 ± 68.5	0 [0.00]	2 [0.01]	3 [0.03]	0 [0.00]	1 [0.03]	2 [0.07]	1 [0.04]	2 [0.09]
	25-S	1	223.8 ± 144.2	0 [0.00]	1 [0.01]	0 [0.00]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]	0 [0.00]
	25-G	10	264.2 ± 26.7	0 [0.00]	1 [0.01]	2 [0.02]	7 [0.12]	2 [0.05]	2 [0.06]	0 [0.00]	0 [0.00]
	30-S	2	293.4 ± 57.2	0 [0.00]	0 [0.00]	0 [0.00]	2 [0.03]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]
	30-G	6	473.7 ± 196.7	0 [0.00]	1 [0.00]	0 [0.00]	4 [0.07]	1 [0.02]	0 [0.00]	0 [0.00]	2 [0.17]
132	20-S	2	209.9 ± 55.1	0 [0.00]	0 [0.00]	1 [0.01]	1 [0.01]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	9	211.4 ± 50.2	2 [0.01]	2 [0.01]	3 [0.03]	3 [0.05]	2 [0.05]	1 [0.03]	0 [0.00]	1 [0.05]
	25-S	2	315.3 ± 82.7	0 [0.00]	0 [0.00]	1 [0.01]	1 [0.02]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]
	25-G	6	381.4 ± 104.8	0 [0.00]	0 [0.00]	4 [0.04]	1 [0.02]	0 [0.00]	1 [0.03]	2 [0.08]	1 [0.08]
	30-S	2	368.7 ± 75.0	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.02]	1 [0.02]	0 [0.00]	1 [0.04]	0 [0.00]
	30-G	5	412.6 ± 164.2	0 [0.00]	1 [0.01]	2 [0.02]	2 [0.03]	0 [0.00]	0 [0.00]	0 [0.00]	2 [0.14]
141	20-S	4	192.6 ± 11.9	0 [0.00]	0 [0.00]	3 [0.04]	3 [0.05]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	12	192.0 ± 39.2	2 [0.01]	6 [0.03]	3 [0.03]	2 [0.03]	0 [0.00]	4 [0.13]	0 [0.00]	0 [0.00]
	25-S	1	281.0 ± 44.3	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.02]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]
	25-G	11	208.9 ± 37.8	3 [0.01]	2 [0.01]	3 [0.03]	3 [0.06]	1 [0.02]	3 [0.09]	0 [0.00]	0 [0.00]
	30-S	3	657.4 ± 60.5	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	2 [0.08]	2 [0.11]
	30-G	4	928.2 ± 519.1	0 [0.00]	0 [0.00]	1 [0.01]	1 [0.01]	1 [0.03]	0 [0.00]	0 [0.00]	2 [0.27]
	20-S	1	150.7 ± 14.4	0 [0.00]	0 [0.00]	2 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]

220

	20-G	10	158.6 ± 28.8	3 [0.01]	2 [0.01]	5 [0.05]	3 [0.05]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]
	25-S	2	317.0 ± 119.4	0 [0.00]	0 [0.00]	1 [0.01]	1 [0.02]	0 [0.00]	0 [0.00]	1 [0.04]	0 [0.00]
	25-G	6	353.0 ± 102.2	0 [0.00]	1 [0.01]	2 [0.02]	4 [0.07]	0 [0.00]	0 [0.00]	0 [0.00]	2 [0.12]
	30-S	2	958.8 ± 481.6	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	2 [0.18]
	30-G	3	1037.9 ± 605.2	0 [0.00]	0 [0.00]	1 [0.01]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	2 [0.27]
Full density											
32	20-S	0	0.0 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	1	81.6 ± 0.0	0 [0.00]	1 [0.01]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	25-S	1	206.9 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.01]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	25-G	1	189.0 ± 112.4	0 [0.00]	1 [0.01]	0 [0.00]	0 [0.00]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]
	30-S	2	834.8 ± 623.4	0 [0.00]	1 [0.00]	0 [0.00]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]	1 [0.15]
	30-G	4	838.3 ± 524.9	0 [0.00]	0 [0.00]	1 [0.01]	1 [0.02]	1 [0.02]	0 [0.00]	1 [0.04]	1 [0.21]
76	20-S	1	207.9 ± 32.8	0 [0.00]	0 [0.00]	1 [0.01]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	8	121.0 ± 37.7	4 [0.01]	3 [0.01]	2 [0.02]	0 [0.00]	1 [0.02]	1 [0.03]	0 [0.00]	0 [0.00]
	25-S	1	338.2 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]
	25-G	6	196.3 ± 56.8	1 [0.00]	0 [0.00]	5 [0.05]	2 [0.03]	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.04]
	30-S	1	417.7 ± 64.7	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.02]	1 [0.03]	0 [0.00]	0 [0.00]
	30-G	4	414.9 ± 84.0	0 [0.00]	0 [0.00]	2 [0.03]	0 [0.00]	1 [0.02]	0 [0.00]	1 [0.04]	2 [0.09]
111	20-S	0	0.0 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	8	97.3 ± 24.9	2 [0.01]	8 [0.04]	1 [0.01]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]	0 [0.00]
	25-S	1	354.1 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]
	25-G	4	173.5 ± 67.1	0 [0.00]	1 [0.01]	3 [0.02]	0 [0.00]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]
	30-S	1	447.6 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]
	30-G	2	383.9 ± 221.9	0 [0.00]	0 [0.00]	2 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	1 [0.06]
143	20-S	0	0.0 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	20-G	10	88.9 ± 13.7	6 [0.02]	2 [0.01]	6 [0.06]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	25-S	0	0.0 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	25-G	2	133.3 ± 49.6	1 [0.00]	0 [0.00]	1 [0.01]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	30-S	0	0.0 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
	30-G	3	181.0 ± 15.7	0 [0.00]	0 [0.00]	2 [0.02]	2 [0.03]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
161	20-S	1	201.9 ± 65.6	0 [0.00]	0 [0.00]	1 [0.01]	1 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]

7

20-G	12	129.0 ± 26.5	5 [0.01]	2 [0.01]	7 [0.07]	2 [0.03]	0 [0.00]	1 [0.03]	0 [0.00]	0 [0.00]
25-S	0	0.0 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
25-G	4	167.3 ± 31.7	0 [0.00]	2 [0.01]	1 [0.01]	2 [0.03]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
30-S	0	0.0 ± 0.0	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]
30-G	1	151.7 ± 15.4	0 [0.00]	0 [0.00]	2 [0.02]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]	0 [0.00]

Draft

Table S4. Summary of within stand level spatial patterns of widely spaced individuals (i.e. patch size = 1) and patches of overstory trees for 10 Sitka spruce-western hemlock forests in SE Alaska. BA is basal area in meters squared and total density is per plot.

		Patch size (number of trees)					
Plot		1	2-4	5-7	8-10	11-15	16+
Medium density							
104	# Patches ha^{-1}	7	6	4	1	1	2
	% Total density	6.1	14.6	18.3	4.9	15.2	40.9
	%Total BA	6.5	16.6	15.1	4.9	15.2	41.4
130	# Patches ha^{-1}	14	14	3	1	1	1
	% Total density	14.5	38.9	16.8	6.1	10.7	13.0
	%Total BA	16.2	39.4	16.7	6.1	10.7	11.9
132	# Patches ha^{-1}	13	6	2	1	2	1
	% Total density	12.4	15.9	11.7	5.5	24.8	29.7
	%Total BA	14.0	16.5	10.7	5.5	24.8	24.0
141	# Patches ha^{-1}	12	12	3	2	1	1
	% Total density	11.6	29.0	17.4	19.6	10.9	11.6
	%Total BA	12.5	35.1	17.4	19.6	10.9	9.8
220	# Patches ha^{-1}	4	8	4	3	1	1
	% Total density	3.6	16.8	21.6	21.6	15.0	21.6
	%Total BA	3.2	12.8	23.4	21.6	15.0	18.5
Full density							
32	# Patches ha^{-1}	2	4	0	0	0	1
	% Total density	1.0	5.4	0.0	0.0	0.0	93.6
	%Total BA	1.4	5.8	0.0	0.0	0.0	92.8
76	# Patches ha^{-1}	4	4	2	1	0	2
	% Total density	3.0	7.5	8.0	4.5	0.0	77.0
	%Total BA	3.2	7.7	5.9	4.5	0.0	78.7
111	# Patches ha^{-1}	1	3	1	0	1	2
	% Total density	0.8	4.2	2.7	0.0	9.3	83.0
	%Total BA	0.4	4.9	5.2	0.0	9.3	77.9
143	# Patches ha^{-1}	6	3	1	0	0	3
	% Total density	2.9	3.3	4.0	0.0	0.0	89.9
	%Total BA	3.4	5.2	3.7	0.0	0.0	87.7
161	# Patches ha^{-1}	4	5	2	0	0	3
	% Total density	2.6	9.9	7.8	0.0	0.0	79.7
	%Total BA	1.8	9.8	9.4	0.0	0.0	79.0

Figure S1. Stem maps by plot for medium density Sitka spruce western hemlock forests in southeast Alaska. Tree boles are colored by species and size represents overstory, mid-story, and understory positions. A 4.44 m radius was used to project tree crowns on overstory trees to show patches at a fixed distance of 8.88 m. Patch size is the number of trees in a patch. Gaps and associated plot buffer distances are shown with a solid or dashed line. Background coloration is a graphical display of open area where colors indicate the distance to the nearest overstory trees in meters.

Figure S2. Stem maps by plot for full density Sitka spruce western hemlock forests in southeast Alaska. Tree boles are colored by species and size represents overstory, mid-story, and understory position. A 4.44 m radius was used to project tree crowns on overstory trees to show patches at a fixed distance of 8.88 m. Patch size is the number of trees in a patch. Gaps and associated plot buffer distances are shown with a solid or dashed line. Background coloration is a graphical display of open area where colors indicate the distance to the nearest overstory trees in meters.

Figure S3. Percentage of total open area which is devoid of overstory foliage, and the percentage of open area quantified as a functional gap delineated by the shadow or geometric gap definitions; pooled by density class.

Figure S4. Average number of edge buffered gaps on a per hectare basis by size class for 10 old-growth Sitka spruce-western hemlock forest in southeast Alaska pooled by canopy density. An edge buffer with a distance equal to the minimum gap distance was applied to the gap calculations. Error bars are one standard error of the mean. Shadow and geometric are the methods used to define a functional gap for the analysis. Minimum functional gap size is 42.3 m² and 15.5 m² for shadow and geometric gaps respectively.

Figure S5. Pair correlation function for all overstory trees (≥ 25 m tall) in medium density plots and for all plots pooled.

Figure S6. Pair correlation function for all overstory trees (≥ 25 m tall) in full density plots and for all plots pooled.

Figure S7. Pair correlation function for overstory western hemlock (TSHE) trees (≥ 25 m tall) in medium density plots and for all plots pooled. Plot 104 was eliminated from the analysis due to insufficient sample size of overstory hemlock.

Figure S8. Pair correlation function for overstory hemlock (TSHE) trees (≥ 25 m tall) in full density plots and for all plots pooled.

Figure S9. Pair correlation function for all understory trees (≤ 10 m tall) in medium density plots and for all plots pooled.

Figure S10. Pair correlation function for all understory trees (≤ 10 m tall) in full density plots and for all plots pooled.

Figure S11. Bivariate pair correlation function for medium density plots and for all plots pooled for all understory trees in relation to all overstory trees.

Figure S12. Bivariate pair correlation function for full density plots and for all plots pooled for all understory trees in relation to all overstory trees.