Tree spatial pattern within the forest–tundra ecotone: a comparison of sites across Canada


Abstract: Although many studies have focused on factors influencing treeline advance with climate change, less consideration has been given to potential changes in tree spatial pattern across the forest–tundra ecotone. We investigated trends in spatial pattern across the forest–tundra ecotone and geographical variation in the Yukon, Manitoba, and Labrador, Canada. Tree cover was measured in contiguous quadrats along transects up to 100 m long located in Forest, Ecotone, and Tundra sections across the forest–tundra transition. Spatial patterns were analyzed using new local variance to estimate patch size and wavelet analysis to determine the scale and amount of aggregation. Compared with the Forest, tree cover in the Ecotone was less aggregated at most sites, with fewer smaller patches of trees. We found evidence that shorter trees may be clumped at some sites, perhaps due to shelter from the wind, and we found little support for regular spacing that would indicate competition. With climate change, trees in the Ecotone will likely become more aggregated as patches enlarge and new patches establish. However, results were site-specific, varying with aspect and the presence of krummholz (stunted trees); therefore, strategies for adaptation of communities to climate change in Canada’s subarctic forest would need to reflect these differences.

Résumé : Alors que plusieurs études ont mis l’accent sur les facteurs qui influencent la progression de la limite des arbres due aux changements climatiques, peu d’attention a été accordée aux changements potentiels du patron de répartition spatiale des arbres dans l’écotone entre la forêt et la toundra. Nous avons étudié les changements de la répartition spatiale dans l’écotone entre la forêt et la toundra de même que sa variation géographique au Yukon, au Manitoba et au Labrador, au Canada. Le couvert forestier a été mesuré dans des quadrats contigus établis le long de transects pouvant atteindre 100 m de longueur et situés dans les sections de forêt, d’écotone et de toundra dans la zone de transition entre la forêt et la toundra. Les patrons spatiaux ont été analysés avec les méthodes de la nouvelle variance locale pour estimer la taille des îlots de forêt et avec l’analyse par ondelettes pour déterminer l’échelle et le degré d’agrégation. Comparativement à la forêt, le couvert forestier de l’écotone était moins groupé dans la plupart des stations, ce qui s’est traduit par des îlots de forêt plus petits et moins nombreux. Nous avons trouvé des preuves que les petits arbres peuvent être regroupés dans certaines stations, probablement pour se protéger du vent, et nous avons trouvé peu de signes d’espacement régulier qui auraient indiqué la présence de compétition. Avec les changements climatiques, les arbres établis dans l’écotone se regrouperont probablement davantage par l’agrandissement des îlots et par l’établissement de nouveaux îlots. Cependant, ces résultats sont spécifiques aux stations puisqu’ils varient selon leur orientation et en fonction de la présence de krummholz (arbres prostrés). Ainsi, les stratégies d’adaptation des communautés aux changements climatiques dans la forêt subarctique canadienne devraient refléter ces différences.

[Traduit par la Rédaction]

Introduction

Increases in global temperature associated with climate change have caused range shifts in a wide array of taxa (Parmesan 2006; Woodall et al. 2009; Harsch et al. 2009). At the forest–tundra ecotone, tree range expansion is commonly cited as being constrained by temperature (Fang and Lechowicz 2006; Körner and Hoch 2006; MacDonald et al. 2009).
2008). We define the forest–tundra ecotone as the transition zone between forest and tundra at high elevation or latitude. Though the predicted poleward or altitudinal advance of treeline due to recent climate change has been observed in many regions, the rate and magnitude of response is highly variable (Harsch et al. 2009). This variability is related to site- and species-specific attributes limiting tree recruitment and growth (Lloyd and Fastie 2002; Danby and Hik 2007a), along with the magnitude of climate change (Intergovernmental Panel on Climate Change 2007). Site-specific differences may be the result of environmental influence or limitations in seed productivity or dispersal and other recruitment processes (e.g., Johnson 1975; Whipple 1978; Batllori et al. 2009; Aune et al. 2011).

Although much attention has focused on the factors influencing treeline advance, less has been given to the difference in tree spatial pattern across the forest–tundra ecotone, which may offer valuable insight into how a response to climate change is being initiated. The spatial configuration of the forest–tundra ecotone is dynamic, often in response to changes in climate (Szeicz and MacDonald 1995; Lescop-Sinclair and Payette 1995; Lloyd 2005). The spatial pattern of trees can be used to understand the biological, geographic, and environmental factors responsible for observed and future spatial configurations of the forest–tundra ecotone (Wiegand and Moloney 2004; Wiegand et al. 2006). Evidence suggests that changes in the spatial structure of the forest–tundra ecotone will be site-specific, with some sites experiencing advance and an increase in tree density and others experiencing only one of these changes or no change at all (Camarero and Gutiérrez 2004; Danby and Hik 2007a; Harsch et al. 2009). However, an assessment of the factors determining the site-specific responses needs further attention (Camarero et al. 2000; Wiegand et al. 2006).

Site-specific factors such as facilitative and competitive interactions among trees and shrubs, local disturbance regime, microtopography, wind, snow, and temperature may result in different spatial patterns (Wiegand et al. 2006; Resler 2006; McIntire and Fajardo 2009). For example, where trees are aggregated (or clumped), mutual benefit between neighbouring individuals could enhance their chance for successful establishment or survival. Conversely, a group of trees that is characterized by a regular spatial pattern may be influenced by competition for resources (Camarero et al. 2000; Camarero and Gutiérrez 2004). Aggregation could also arise from proximity to a seed source (McIntire and Fajardo 2009) or clustering in a favourable microtopographic site (Resler 2006). Seed productivity and dispersal are important but complex factors influencing the establishment of a tree seedling at higher elevation or latitude (Krugman et al. 1989; Batllori et al. 2009). Because the response of the forest–tundra ecotone to climate change will vary locally, it is important to understand the role of these site-specific factors.

We investigated the spatial pattern of trees across the forest–tundra ecotone at five sites across Canada as part of a larger research program (Hofgaard and Harper 2011). These sites encompass some of the variations in species composition and structure within the forest–tundra ecotone; these data are important for our understanding of how climate change will differentially affect spatial configuration of trees in the forest–tundra ecotone. Our objectives were (i) to describe and to compare the spatial pattern of tree cover in the forest, forest–tundra, and subtundra sections across the forest–tundra transition (hereafter referred to as Forest, Ecotone, and Tundra sections, respectively; we use forest–tundra ecotone to refer to the entire gradient), and (ii) to investigate differences among sites. We explored influences asserted by aspect, the presence of krummholz (stunted trees), and latitudinal vs. altitudinal gradient. We then used the gradient in spatial pattern to suggest how configuration of trees might change within the forest–tundra ecotone.

**Methods**

**Study areas**

In the summers of 2007 and 2008, we sampled representative locations across Canada to acquire information on spatial patterns within the forest–tundra ecotone (Fig. 1). From west to east, sites were established in the Kluane and Mt. Nansen regions of the Yukon Territory, near the town of Churchill, Manitoba, and in the Mealy Mountains of southern Labrador (hereafter referred to as Kluane, Nansen, Churchill, and the Mealy, respectively).

The Kluane region (Table 1; Fig. 1A) is located on the western flank of the Ruby Range Mountains of southwestern Yukon. The altitudinal limit of *Picea glauca* (Moench) Voss (white spruce) trees (>2 m tall) varies in elevation from 1275 to 1475 m, with south-facing slopes 50 to 100 m higher than north-facing slopes. Because aspect plays an important role, this site is divided into south-facing and north-facing sites (Kluane South and Kluane North, respectively). Annual, January, and July average temperatures of −3.1, −14.7, and 11.6 °C, respectively, have been recorded in this region from 1275 m elevation since 2003. Total annual precipitation at the nearest Environment Canada meteorological station (Burwash Landing, 38 km NW, 805 m) averages 280 mm, 35% of which falls as snow (Danby and Hik 2007b).

The Nansen site (Table 1; Fig. 1B) is located in the mountainous Yukon Plateau. Composed of primarily *P. glauca*, there is an abrupt and readily discernible transition in tree density at approximately 1340 m, with a scattering of higher elevation trees (>2 m tall) between 1340 and 1550 m. *Picea mariana* (Mill.) B.S.P. (black spruce) is uncommon at this site, occurring as single individuals or small patches within *P. glauca* stands. Annual, January, and July average temperatures of −3.5, −18.5, and 13.0 °C, respectively, were recorded on site in 2008–2009 at 1300 m. Total annual precipitation ranges between 300 and 400 mm, approximately 90% of which falls as snow or slush (R. Savidge, unpublished data).

The Churchill site (Table 1; Fig. 1C) is located within the broad boreal–tundra transition forest on the southwestern side of Hudson Bay. This area is located within the latitudinal forest–tundra ecotone and is composed of a mosaic of *P. glauca* and *P. mariana* forest and tundra, as well as wetlands in low-lying areas. Annual, January, and July average temperatures were −6.9, −26.7, and 12.0 °C, respectively, for the period 1971–2000 (Environment Canada 2009).
Annual precipitation was 431.6 mm, approximately 40% of which falls as snow (Environment Canada 2009).

The Mealys site (Table 1; Fig. 1D) is located within the Mealys site National Park and is described as southern mountainous outliers of the High Subarctic Tundra Ecoregion (Meades 1990). This altitudinal forest–tundra ecotone is composed of *Larix laricina* (Du Roi) K. Koch (eastern larch), *Abies balsamea* (L.) Mill. (balsam fir), *P. glauca*, and *P. mariana*, with trees (>2 m tall) extending up to 700 m in sheltered areas. Between approximately 600–700 m, these different species form extensive mats of stunted trees or krummholz with short, isolated, and shrubby trees up to 900 m. Annual, January, and July average temperatures were −1.6, −16.4, and 13.2 °C, respectively, for the period of 2002–2008 (John Jacobs, unpublished data). Annual precipitation is greater than 2000 mm, falling mostly as snow (John Jacobs, unpublished data).

**Table 1.** Location, tree species, and sampling design for each study site.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Location</th>
<th>Elevation (m)</th>
<th>Tree species</th>
<th>No. of transects</th>
<th>Transect length (m)</th>
<th>Quadrat size (m)</th>
<th>Cover classes (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kluane North</td>
<td>61.2°N,</td>
<td>1195–1355</td>
<td><em>Picea glauca</em></td>
<td>2</td>
<td>4</td>
<td>2</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>138.4°W</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0–1, 1–5, 5–10, 10–25, 25–50, 50–75, 75–100</td>
</tr>
<tr>
<td>Kluane South</td>
<td>61.2°N,</td>
<td>1265–1525</td>
<td><em>Picea glauca</em></td>
<td>2</td>
<td>4</td>
<td>3</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>138.4°W</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0–1, 1–5, 5–10, 10–25, 25–50, 50–75, 75–100</td>
</tr>
<tr>
<td>Nansen</td>
<td>62.1°N,</td>
<td>1283</td>
<td><em>Picea glauca, Picea mariana</em></td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>62</td>
</tr>
<tr>
<td></td>
<td>137.2°W</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1, 3, to the nearest 5% thereafter</td>
</tr>
<tr>
<td>Churchill</td>
<td>58.8°N,</td>
<td>22</td>
<td><em>Picea glauca, Picea mariana</em></td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>94.1°W</td>
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<td></td>
<td>0–1, 1–5, 5–10, 10–25, 25–50, 50–75, 75–100</td>
</tr>
<tr>
<td>Mealys</td>
<td>53.6°N,</td>
<td>517–819</td>
<td><em>Picea glauca, Picea mariana, Abies balsamea, Larix laricina</em></td>
<td>2</td>
<td>4</td>
<td>2</td>
<td>50, 100*</td>
</tr>
<tr>
<td></td>
<td>58.8°W</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0, 1, 2, 3, to the nearest 5% thereafter</td>
</tr>
</tbody>
</table>

**Note:** Transects are labeled as F (forest), E (ecotone), or T (tundra).

*Transect length was 50 m in half of the transects and 100 m in the other half.

Fig. 1. Map of Canada illustrating the location of the four study areas in relation to the forest–tundra ecotone. The position of the Arctic treeline, as mapped by Timoney et al. (1992), is indicated by the dotted black line. Boreal–tundra transition forests and subarctic alpine tundra, as mapped by Palko et al. (1996), are indicated by light gray and dark gray shading, respectively. Inset maps illustrate the configuration of transects in (A) Kluane, (B) Nansen, (C) Churchill, and (D) the Mealys in relation to the forest–tundra ecotone at each site. Arrows indicate the general progression of vegetation on the landscape from forest to tundra. Details on sampling design including transect lengths are provided in the text and in Table 1. Transects are labeled as F (forest), E (ecotone), or T (tundra) for each site. Scale varies for each inset map.

Sampling followed standard protocols developed by the International Polar Year research group on the forest–tundra ecotone (Hofgaard and Rees 2008). At each site, 50, 60, or 100 m long transects were located perpendicular to the main gradient from the forest to the tundra (Table 1; Fig. 1). Transects were shorter than 100 m at some sites due to time constraints or difficult terrain. The nature of this ecotone...
differed among sites, with shorter, sharper gradients in Churchill and Nansen, gradual gradients in Kluane North and Kluane South, and even more diffuse gradients in the Mealys, with gradient lengths (distance between the lowermost and uppermost transects) ranging from 75 m in Churchill to over 8.5 km in the Mealys. Only one gradient was used for the Mealys, Kluane North, and Kluane South. At the two other sites, separate gradients were sampled at different locations within each site. Replicate transects were used for the Forest, Ecotone, or Tundra sections across each gradient in all sites except Churchill. Distances between adjacent transects varied at each site, ranging from 10 m in Nansen to over 2 km in the Mealys, with averages of 80, 103, 10, 42, and 1071 m for Kluane North, Kluane South, Nansen, Churchill, and the Mealys, respectively. Although there were sometimes scattered trees in the Tundra section, trees may or may not have been present along the transects.

Percent tree cover was estimated in 1 × 1 or 2 × 2 m contiguous quadrats along the entire length of each transect (Table 1). Trees were subdivided by height class: seedlings (<15 cm), saplings and subbaroebent trees or krummholz (≥15 cm and <200 cm, hereafter referred to as short trees), and tall trees (≥200 cm); however, there were too few seedlings to analyze separately. Subbaroebent trees or krummholz (trees with a prostrate growth form) may be as old as taller trees but have been truncated or stunted by wind erosion (Peregr and Payette 1998) or thermally limited annual growth (Danby and Hik 2007b). Dead trees were rare and only sampled at Kluane North, Kluane South, and Churchill.

Analysis

New local variance (NLV) and wavelet analysis were used to estimate the patch size and scale of spatial pattern, respectively, for each transect using the free software program PASSAGE 2 (Rosenberg 2009). Patch size is the average width of clumps of high tree abundance, and scale is the distance between the patches. Wavelet analysis also provided a measure of aggregation or the contrast between patches and gaps. Together these three metrics provide standard characteristics of spatial patterns of the size, spacing, and intensity (amount of contrast) of patches of tree cover. Wavelet diagrams also allowed us to examine the distribution of patches visually along each transect. Spatial analysis was only performed if there were nonzero values in at least three quadrats along a transect. Some individual species found only in the Forest section on a given site were not analyzed separately (P. mariana in Nansen and P. glauca and L. laricina in the Mealys). Cover classes were converted to midpoint values. Total cover values were derived by summing midpoint cover values for all sizes and species; estimates were then rounded up to the nearest midpoint cover value.

The two-term version of NLV is recommended for estimating patch size (Dale 1999), whereas wavelet analysis is recommended for assessing the scale of the pattern (Dale and Mah 1998). The Mexican Hat wavelet, commonly used to detect patches (Dale and Mah 1998), was used for the longer transects. We used the French Top Hat wavelet for the Nansen and shorter Mealys transects (62 and 50 m, respectively) as it gave more detailed results that were more appropriate for the shorter transects. For both analyses, randomization tests were conducted using 999 iterations with a 95% confidence interval. Randomization tests for NLV could not be performed in the program for the shorter transects because of an inadequate number of contiguous quadrats. Maximum distances of 33% and 25%, respectively, were used for NLV and wavelet analysis.

NLV and wavelet scale diagrams were examined visually to estimate patch size and scale. For patch size, the distance of the first peak (high point in the graph) was selected; for a wide peak, the middle distance was chosen. Only peaks that were significantly greater than the 95% confidence interval derived from randomization tests were used; nearby peaks were considered if the first peak was not significant. Scale was estimated as the distance of the first significant peak of the wavelet scale diagram except a scale of one quadrant was not considered, as recommended by Campbell et al. (1998); however, these authors suggest that scales of two or three quadrats can be considered if multiple transects are used. We also summed the wavelet variance for the scales of 1–10 m to provide an estimate of aggregation at the same distances for each site; these scales were chosen arbitrarily to cover the range of scales possible for all sites. We then standardized the results by dividing wavelet variance by the sample variance (Rossi et al. 1992), which enabled comparisons of trends in pattern, irrespective of trends in abundance.

Results

The variation in tree abundance and species composition among different sites provides a context for the results of the spatial pattern analysis. Tree species richness increased from west to east, with all four conifer species present in the Mealys (Table 2). Picea glauca was the only species common to all sites and was found in all sections at all sites except the Tundra section in the Mealys, where it was only found outside the transects (L. Hermanutz and A. Trant, personal observation). Because there were very few differences in spatial patterns among species, results are only presented for all species combined. Total and tall tree cover were always greatest in the Forest section and lowest in the Tundra section, whereas short tree cover was greatest in the Ecotone section at all sites except Kluane North and Nansen (Fig. 2). Total and tall tree cover varied substantially among the five sites for all three sections. Short tree cover varied substantially among sites in the Ecotone (from 2% in Kluane North and Kluane South to 21% in the Mealys) and was only greater than 1% in the Tundra section in Kluane North.

Patch size varied among sites, as well as across the forest–tundra ecotone (Fig. 3). In Kluane North, Kluane South, and Nansen, patch sizes were mostly 2–4 m, with some larger 5 and 7 m patches in Kluane South and 8–18 m patches in Nansen (individual results not shown). NLV results for the Mealys and Churchill were more complex, often with multiple peaks on the NLV graphs and variable patch sizes ranging from 2 to 13 or 23 m, respectively, for the Mealys and Churchill. For total cover, patch size decreased from Forest to Tundra for most sites, but patches were larger in the Ecotone than in the Forest for the Mealys (Fig. 3a). Results were similar for tall and short
trees except in Churchill, which had larger patches of shorter trees in the Ecotone (Figs. 3b, 3c).

The scale (distance between patches) was generally 3–6 m, but ranged up to 11–17 m on all sites (individual results not shown). There were few significant peaks for Nansen, especially for total cover, indicating that there was no significant aggregation at any scale. Patches of short and tall trees were farther apart in the Forest than in the Ecotone for most sites (Fig. 4) as scale generally decreased from the Forest to the Tundra. Notable exceptions include the Tundra.

**Table 2.** Percentage of quadrats in which a given tree species was recorded in each section at each of the sites.

<table>
<thead>
<tr>
<th></th>
<th>Kluane North</th>
<th>Kluane South</th>
<th>Nansen</th>
<th>Churchill</th>
<th>Mealys</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>E</td>
<td>T</td>
<td>F</td>
<td>E</td>
</tr>
<tr>
<td>Picea glauca</td>
<td>44</td>
<td>32</td>
<td>8</td>
<td>35</td>
<td>17</td>
</tr>
<tr>
<td>Picea mariana</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Larix laricina</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Abies balsamea</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

**Note:** Transects are labeled as F (forest), E (ecotone), or T (tundra).
Fig. 4. Average (±SE) scale as estimated by the first peak in wavelet variance for the Forest, Ecotone, and Tundra sections of the forest–tundra ecotone at the study sites for (a) total, (b) tall tree, and (c) short tree cover. At Nansen, none of the peaks in scale was significant for total tree cover in the Ecotone, indicating that there was no significant aggregation for which scale could be determined. Sample sizes for Forest, Ecotone, and Tundra, respectively, are as follows: (a) Kluane North (N), 2, 3, 2; Kluane South (S), 2, 4, 2; Nansen, 4, 0, 0; Churchill, 3, 2, 0; Mealys, 2, 4, 0; (b) Kluane N, 2, 3, 0; Kluane S, 2, 4, 2; Nansen, 5, 0, 0; Churchill, 2, 2, 0; Mealys 2, 1, 0; (c) Kluane N, 2, 3, 2; Kluane S, 0, 2, 0; Nansen, 3, 1, 0; Churchhill, 1, 2, 1; Mealys 1, 2, 0.

Fig. 5. Average (±SE) standarized wavelet variance at scales of 1–10 m for the Forest, Ecotone, and Tundra sections of the forest–tundra ecotone at the study sites for (a) total, (b) tall, and (c) short tree cover. Sample sizes for Forest, Ecotone, and Tundra, respectively, are as follows: (a) Kluane North (N), 2, 4, 2; Kluane South (S), 2, 4, 2; Nansen, 8, 6, 1; Churchill, 3, 3, 2; Mealys, 2, 4, 0; (b) Kluane N, 2, 3, 0; Kluane S, 2, 4, 2; Nansen, 8, 5, 0; Churchill, 2, 2, 0; Mealys, 2, 1, 0; (c) Kluane N, 2, 4, 2; Kluane S, 0, 4, 0; Nansen, 6, 3, 1; Churchhill, 2, 2, 1; Mealys, 1, 4, 0.

A transect in Kluane South and an increase in scale from the Forest to the Ecotone for tall trees in Churchill and for total tree cover in the Mealys. The latter trend is different from both short and tall trees, likely because an increase in the frequency of quadrats resulted in a peak at a finer scale in the Forest that was significant only with both sizes of trees included.

Standardized aggregation (amount of clumping) for total cover decreased from the Forest to the Ecotone for all sites except Nansen and Churchill (Fig. 5a). Aggregation was also greater in the Forest than in the Ecotone for tall trees at all sites except Kluane South (Fig. 5b). However, intensity, measured as wavelet variance at the scale of the pattern, was greater in the Forest than in the Ecotone for tall trees at all sites including Kluane South (results not shown). Short trees were more aggregated in the Ecotone than in the Forest in Nansen and the Mealys (Fig. 5c).

Wavelet diagrams of position variance provide a detailed examination of the distribution of total tree cover along the transects at each site (Figs. 6–9). Overall, there were few patches of tree cover along transects in Tundra, although...
the position variance for these patches was generally significant. More patches, often clumped in groups, were evident along Forest transects, whereas there were only a few significant patches in the Ecotone. In Kluane, the North and South sites were very similar with perhaps slightly more significant patches in the Ecotone in the North than in the South, which had long sections of the transects with no patches. Transects in Nansen were mostly only long enough to detect one significant peak, although many other patches were evident, especially in the Forest. In Churchill, patches appeared to be evenly spaced with not much difference between the Forest and Ecotone. In the Mealys, there were more evenly spaced patches along the Forest transects than along the Ecotone transects, which had large gaps with no patches.

The two upper Ecotone transects also had many patches, but they were not significant.

**Discussion**

**Trends in spatial pattern across the forest–tundra ecotone**

There was substantial geographic variation in spatial pattern across our sites. Differences in the gradient of tree cover from the Forest section to the Tundra section among sites show that the relative position of the sections to the...

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Fig. 6. Position variance along the Tundra, Ecotone, and Forest transects in Kluane North and Kluane South. Transects are ordered with increasing elevation up the valley. Position variance is the wavelet variance summed across all scales for each distance. The thin line represents the results of the randomization test; peaks in the position variance (bold line) that are above the thin line are significant. Note the different scale for the y axis for the top five graphs.

Fig. 7. Position variance along the Ecotone and Forest transects in Nansen. Transects are ordered with increasing elevation up the valley. See the caption for Fig. 6 for details about interpreting position variance.
forest–tundra gradient was not the same. This variability could have contributed to the lack of a common pattern among sites. It is also important to acknowledge that we had few transects at each of only a few study areas within the vast forest–tundra ecotone across Canada. Thus, although our study design included a breadth of sites, it lacked depth at individual sites. However, some general trends across the forest–tundra ecotone were apparent. Compared with the Forest, tall tree cover in the Ecotone was less aggregated at most sites with fewer smaller patches of trees. Although trees were present along some Tundra transects, the spatial pattern of tree cover in Tundra was difficult to detect because of the low tree abundance; therefore, we focus our interpretation on the difference in spatial pattern between the Forest and the Ecotone.

Although patches of tree cover were generally smaller in the Ecotone than in the Forest, as expected with the difference in tree size, larger patches of shorter trees were observed in the Ecotone in Churchill and the Mealys. Larger patches may arise in the transition area where vegetative growth such as layering is more prominent, particularly in the Mealys where there are extensive mats of krummholz. In Kluane, localized permafrost, colder soil temperatures, and more abundant and longer-lasting snow cover on the North site (Danby and Hik 2007b) may have resulted in less vegetative growth, producing smaller patches that were more closely spaced than in the South site. In Churchill, our only latitudinal site, patches of tall trees were much farther apart in the Ecotone than in the Forest.

The decrease in aggregation of tall tree cover and patch size from the Forest to the Ecotone differed from other studies (Humphries et al. 2008; Lingua et al. 2008). The “swiss cheese” model of the forest–tundra ecotone (Payette et al. 2001) describes the transition as a gradual change from a forested landscape with patches of tundra to a tundra landscape with patches of forest. Greater patchiness is expected in the middle of the transition, but our sites (including our Forest transects) may have all been located in a tundra landscape with patches of forest (highest average tree cover < 40%). Therefore, the Forest transects would be located nearest the middle of the transition where we expect the greatest patchiness according to this model. An exception to this general trend was greater clumping in the Ecotone for short trees in Nansen, where saplings may have established in patches away from taller trees, and in the Mealys, where there were extensive dense mats of krummholz.

**Insight into factors affecting tree establishment in the forest–tundra ecotone**

Several factors could have affected tree establishment and growth that resulted in the observed spatial patterns. Processes such as facilitation through shelter from wind, seed dispersal, and factors such as an uneven microtopography can all act to generate a clumped spatial pattern (Humphries et al. 2008). Total tree cover may have been more clumped in the Ecotone than in the Forest due to the favourable effects of shelter from wind or snow abrasion. Wind is widely acknowledged to be an important influence on ecological pattern and process within the forest–tundra ecotone (see review by Holtmeier and Broll 2010). Research has demonstrated the role of wind in structuring the physiognomy of trees across the forest–tundra ecotone (e.g., Yoshino 1973), altering leaf physiology (e.g., Hadley and Smith 1986), and structuring vegetation pattern (e.g., Holtmeier 1982). Our results appear to support the body of literature demonstrating this latter category of wind-related effects. A concurrent increase in aggregation and reduction in tree cover from the Forest to the Ecotone could indicate an interaction between temperature and wind. If only wind was important, we would expect an increase in aggregation but similar tree cover. If only temperature was important, we would expect a reduction in tree cover but consistent measures of aggregation. Therefore, we suggest that at some sites, temperature may be a limiting factor, whereas wind may be a structuring...
factor for the spatial pattern of trees within the forest–tundra ecotone. This is analogous with the notion proposed by Holtmeier and Broll (2005) that temperature influences the forest–tundra ecotone at a coarser scale than wind. Although patch sizes were smaller in the Ecotone than in the Forest, aggregation was not greater in the Ecotone at all sites for all variables, indicating that wind as a structuring factor may not be universal. Tree species may be important; Picea glauca may exhibit less sheltering effects as this species tends to form tree islands rather than larger mats of krummholz. Greater clustering of short trees rather than tall trees in the Ecotone than in the Forest, also found in Kluane and the Mealys using mapped point patterns by De Fields (2009) and at a tropical treeline by Šrutek et al. (2002), was likely a result of layering followed by intraspecific resource competition (Pereg and Payette 1998; Holtmeier 2003). Tall trees may be robust enough to be able to withstand harsh conditions such as mechanical damage and desiccation during winter, whereas short trees may obtain greater benefit from being aggregated. In the Mealys, tree establishment in the Ecotone may be dependent on favourable microsites in a landscape with abundant exposed rock and glacial erratics, as observed elsewhere (see Holtmeier and Broll 2010). In Kluane South, greater aggregation but not patch size in the Ecotone than in the Forest for tall trees infers that patches were denser rather than larger. This provides support for wind shelter effects at higher elevations. Other factors such as microtopography and seed dispersal also contribute to aggregation (Resler 2006; McIntire and Fajardo 2009) and are therefore important to consider, but these factors would likely be similar across the forest–tundra ecotone. Alternatively, an even distribution of trees could indicate a greater influence of competition or regular microtopography as the forest develops. Because the spatial analysis that we used cannot test for a regular or even pattern, we can only assess the role of these factors by examining which transects had less aggregation or a greater scale indicating the absence of patches at short distances. Using these indirect measures, we found little evidence that trees were more evenly spaced in the Forest except in Kluane South where there was less aggregation of tall trees in the Forest than in the Ecotone. At this site, scale was much greater and more variable; De Fields (2009) found evidence of regular spacing of trees at this site using mapped point patterns that could indicate competition. In Churchill, patches of tall trees were much farther apart in the Ecotone than in the Forest in contrast to other sites, indicating an absence of clumping at short distances and perhaps an even distribution. The absence of significant aggregation for many transects also suggests an even distribution in Nansen.

Overall, our results of decreased clumping of smaller patches of tall trees that are further apart in the Ecotone than in the Forest suggest that trees are not spatially configured to provide shelter from the wind at most of our study sites. Conversely, aggregation in the Forest suggests that competition among trees is not a major limiting factor. Both of these inferences appear to contradict the stress-gradient hypothesis for interspecific interactions that facilitation increases and competition decreases with abiotic stress (Maestre et al. 2009) and thus warrants further investigation. However, intraspecific competition and wind shelter effects are likely important site-specific factors at some study sites.

Implications for climate change

Trends in tree spatial pattern across the forest–tundra ecotone provide some insight into how the configuration may change with a changing climate given the assumption that trees within this transition become more abundant. With climate warming, the spatial pattern in the Ecotone could transition to that in the Forest. Given this assumption, trees in the Ecotone that likely established as either isolated individ-

Fig. 9. Position variance along the Ecotone and Forest transects in the Mealys. Transects are ordered with increasing elevation up the valley. Note the different scale for the y axis for the shorter transects. See the caption for Fig. 6 for details about interpreting position variance.
tuals or in small dispersed patches will likely develop into forests through an enlargement of patches by either vegetative growth or new establishment. These patches would become denser and more aggregated, sometimes merging together. There may also be establishment of new patches as trees establish in forest openings (Weisberg and Baker 1995) that would lead to greater aggregation within the forest–tundra ecotone. This increase in the clumping of trees would result in ecosystem and habitat changes possibly affecting regional biodiversity (Gibson et al. 2009). If there was treeline advance or development of the Tundra into the Ecotone at the same time, the forest–tundra ecotone could shift without a change in spatial pattern. However, forest density could be increasing in the forest–tundra ecotone without a concurrent poleward or upward advance at some sites, which would lead to a change in spatial configuration.

Our results suggest that trends in spatial pattern and the potential factors affecting tree establishment within the forest–tundra ecotone are site-specific. Factors such as the width of the forest–tundra gradient, aspect, tree species, microclimate, microtopography, and the presence of krummholz likely affect the configuration of trees in the forest–tundra ecotone and the development of the pattern of the forest–tundra ecotone with climate change. In sites with a lot of krummholz, there may be an intermediate stage of large krummholz patches before the development of a more open forest. Because of this variation across Canada, there is little overall support for hypotheses concerning factors affecting tree abundance in the forest–tundra ecotone. Instead, we suggest that processes such as passive facilitation through sheltering from wind and intraspecific competition act differently at different sites, resulting in a highly variable configuration of the forest–tundra ecotone. Because response to change will vary across Canada, adaptation of northern communities to change must be tailored to individual sites.

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