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

Karen A. Harper, Ryan K. Danby*, Danielle L. De Fields*, Keith P. Lewis*, Andrew J. Trant*, Brian M. Starzomski, Rodney Savidge, Luise Hermanutz

* These authors contributed equally.

K.A. Harper[1], D.L. De Fields[2] and B.M. Starzomski[3]. School for Resource and Environmental Studies, Dalhousie University, Suite 5010, 6100 University Ave., Halifax, NS, B3H 3J5, Canada.

[1]Corresponding author (e-mail: Karen.Harper@Dal.ca). Phone: (902) 494-6355. Fax: (902) 494-3728.

R.K. Danby. Department of Geography and School of Environmental Studies, Queen's University, Kingston, ON, K7L 3N6, Canada, ryan.danby@queensu.ca

K. Lewis[4], A.J. Trant and L. Hermanutz. Dept of Biology, Memorial University, St. John's, NL, A1B 3X9, Canada, (keithl@mun.ca, atrant@mun.ca, lhermanu@mun.ca)

R. Savidge. Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, NB, E3B 6C2, Canada, savi@unb.ca

[2]D.L. De Fields. Present address: North Slave Metis Alliance, 32 Melville Drive, Box 2301, Yellowknife, NT, X1A 2P7, Canada, defields@dal.ca

[3]B.M. Starzomski. Present address: School of Environmental Studies, University of Victoria, 3800 Finnerty Road, Victoria, BC, V8P 5C2, Canada, starzom@uvic.ca

1   [4]K. Lewis. Present address: Sustainable Development and Strategic Science Branch,

2   Department of Environment and Education, P.O. Box 8700, St. John's, NL, A1B 4J6,

3   Canada

4

5

1 **Abstract:** While many studies have focused on factors influencing treeline advance with

2 climate change, less consideration has been given to potential changes in tree spatial

3 pattern across the forest-tundra ecotone. We investigated trends in spatial pattern across

4 the forest-tundra ecotone and investigated geographical variation in the Yukon, Manitoba

5 and Labrador, Canada. Tree cover was measured in contiguous quadrats along transects

6 up to 100 m long located in Forest, Ecotone and Tundra sections across the forest-tundra

7 transition. Spatial patterns were analyzed using New Local Variance to estimate patch

8 size, and wavelet analysis to determine the scale and amount of aggregation. Compared to

9 the Forest, tree cover in the Ecotone was less aggregated at most sites with fewer smaller

10 patches of trees. We found evidence that shorter trees may be clumped at some sites,

11 perhaps due to shelter from the wind, and we found little support for regular spacing that

12 would indicate competition. With climate change, trees in the Ecotone will likely become

13 more aggregated as patches enlarge and new patches establish. However, results were site

14 specific, varying with aspect and the presence of krummholz (stunted trees); therefore

15 strategies for adaptation of communities to climate change in Canada's subarctic forest

16 would need to reflect these differences.

17

1 Introduction

2   Increases in global temperature associated with climate change have caused range

3 shifts in a wide array of taxa (Parmesan 2006; Woodall et al. 2008; Harsch et al. 2009).

4 At the forest-tundra ecotone, tree range expansion is commonly cited as being

5 constrained by temperature (Fang and Lechowicz 2006; Körner and Hoch 2006;

6 MacDonald et al. 2008). We define the forest-tundra ecotone as the transition zone

7 between forest and tundra at high elevation or latitude. While the predicted poleward or

8 altitudinal advance of treeline due to recent climate change has been observed in many

9 regions, the rate and magnitude of response is highly variable (Harsch et al. 2009). This

10 variability is related to site and species-specific attributes limiting tree recruitment and

11 growth (Lloyd and Fastie 2002; Danby and Hik 2007a) along with the magnitude of

12 climate change (IPCC 2007). Site-specific differences may be the result of environmental

13 influence or limitations in seed productivity or dispersal and other recruitment processes

14 (e.g., Johnson 1975; Whipple 1978; Batllori et al. 2009; Aune et al. this issue).

15   While much attention has focused on the factors influencing treeline advance, less

16 has been given to the difference in tree spatial pattern across the forest-tundra ecotone,

17 which may offer valuable insight into how a response to climate change is being initiated.

18 The spatial configuration of the forest-tundra ecotone is dynamic, often in response to

19 changes in climate (Szeicz and MacDonald 1995; Lescop-Sinclair and Payette 1995;

20 Lloyd 2005). The spatial pattern of trees can be used to understand the biological,

21 geographic and environmental factors responsible for observed and future spatial

22 configurations of the forest-tundra ecotone (Wiegand and Moloney 2004; Wiegand et al.

23 2006). Evidence suggests that changes in the spatial structure of the forest-tundra ecotone

1   will be site-specific, with some sites experiencing advance and an increase in tree density

2   and others experiencing only one of these changes or no change at all (Camarero and

3   Gutierrez 2004; Danby and Hik 2007a, Harsch et al. 2009). However, an assessment of

4   the factors determining the site-specific responses needs further attention (Camarero et al.

5   2000; Wiegand et al. 2006).

6   Site-specific factors such as facilitative and competitive interactions among trees

7   and shrubs, local disturbance regime, microtopography, wind, snow and temperature may

8   result in different spatial patterns (Wiegand et al. 2006; Resler 2006; McIntire and

9   Fajardo 2009). For example, where trees are aggregated (or clumped), mutual benefit

10 between neighbouring individuals could enhance their chance for successful

11 establishment or survival. Conversely, a group of trees that is characterized by a regular

12 spatial pattern may be influenced by competition for resources (Camarero et al. 2000;

13 Camarero and Guiterrez 2004). Aggregation could also arise from proximity to a seed

14 source (McIntire and Fajardo 2009) or clustering in a favourable microtopographic site

15 (Resler 2006). Seed productivity and dispersal are important but complex factors

16 influencing the establishment of a tree seedling at higher elevation or latitude (Krugman

17 et al. 1989; Batllori et al. 2009). Since the response of the forest-tundra ecotone to

18 climate change will vary locally, it is important to understand the role of these site-

19 specific factors.

20   We investigated the spatial pattern of trees across the forest-tundra ecotone at five

21 sites across Canada as part of a larger research program (Hofgaard and Harper this issue).

22 These sites encompass some of the variation in species composition and structure within

23 the forest-tundra ecotone; these data are important for our understanding of how climate

1   change will differentially affect spatial configuration of trees in the forest-tundra ecotone.

2   Our objectives were: 1) to describe and to compare the spatial pattern of tree cover in the

3   forest, forest-tundra and sub-tundra sections across the forest-tundra transition (hereafter

4   referred to as Forest, Ecotone and Tundra sections, respectively; we use forest-tundra

5   ecotone to refer to the entire gradient) and 2) to investigate differences among sites. We

6   explored influences asserted by aspect, the presence of krummholz (stunted trees) and

7   latitudinal vs. altitudinal gradient. We then used the gradient in spatial pattern to suggest

8   how configuration of trees might change within the forest-tundra ecotone.

9

10   **Methods**

11

12   **Study areas**

13   In the summers of 2007 and 2008, we sampled representative locations across

14   Canada to acquire information on spatial pattern within the forest-tundra ecotone (Fig. 1).

15   From west to east, sites were established in the Kluane and Mt. Nansen regions of the

16   Yukon Territory, near the town of Churchill, Manitoba, and in the Mealy Mountains of

17   southern Labrador (hereafter referred to Kluane, Nansen, Churchill and the Mealys).

18   The Kluane region (Table 1, Fig.1a) is located on the west flank of the Ruby Range

19   Mountains of southwest Yukon. The altitudinal limit of *Picea glauca* (white spruce) trees

20   (>2 m tall) varies in elevation from 1275 to 1475 m, with south-facing slopes 50 to 100 m

21   higher than north-facing slopes. Since aspect plays an important role, this site is divided

22   into south-facing and north-facing sites (Kluane South and Kluane North, respectively).

23   Annual, January and July average temperatures of -3.1°C, -14.7°C and 11.6°C,

1   respectively, have been recorded in this region from 1275 m elevation since 2003. Total

2   annual precipitation at the nearest Environment Canada meteorological station (Burwash

3   Landing, 38 km NW, 805 m) averages 280 mm, 35 % of which falls as snow (Danby and

4   Hik 2007b).

5   The Nansen site (Table 1, Fig.1b) is located in the mountainous Yukon Plateau.

6   Composed of primarily *Picea glauca*, there is an abrupt and readily discernible transition

7   in tree density at approximately 1340 m with a scattering of higher elevation trees (>2 m

8   tall) between 1340 and 1550 m. *Picea mariana* (black spruce) is uncommon at this site,

9   occurring as single individuals or small patches within *P. glauca* stands. Annual, January

10   and July average temperatures of -3.5°C, -18.5°C and 13.0°C, respectively, were

11   recorded on site in 2008-2009 at 1300 m. Total annual precipitation ranges between 300

12   and 400 mm, approximately 90 % of which falls as snow or slush (R. Savidge,

13   unpublished data).

14   The Churchill site (Table 1, Fig.1c) is located within the broad boreal-tundra

15   transition forest on the southwest side of Hudson Bay. This area is located within the

16   latitudinal forest-tundra ecotone and is composed of a mosaic of *P. glauca* and *P.*

17   *mariana* forest and tundra, as well as wetlands in low-lying areas. Annual, January and

18   July average temperatures were -6.9°C, -26.7°C and 12.0°C, respectively for the period

19   1971-2000 (Environment Canada 2009). Total annual precipitation was 431.6 mm,

20   approx. 40 % of which falls as snow (Environment Canada 2009).

21   The Mealys site (Table 1, Fig.1d) is located within the Mealy Mountains National

22   Park and is described as southern mountainous outliers of the High Subarctic Tundra

23   Ecoregion (Meades 1990). This altitudinal forest-tundra ecotone is composed of *Larix*

1 *laricina* (eastern larch), *Abies balsamifera* (balsam fir), *P. glauca* and *P. mariana* with

2 trees (>2 m tall) extending up to 700 m in sheltered areas. Between approx. 600-700 m,

3 these different species form extensive mats of stunted trees or krummholz with short,

4 isolated and shrubby trees up to 900 m. Annual, January and July average temperatures

5 were -1.6°C, -16.4°C and 13.2°C, respectively, for the period of 2002-2008 (John Jacobs,

6 unpublished data). Annual precipitation is greater than 2000 mm, falling mostly as snow

7 (John Jacobs, unpublished data).

8

9 **Sampling design**

10   Sampling followed standard protocols developed by the International Polar Year

11 research group on the forest-tundra ecotone (Hofgaard and Rees 2008). At each site,

12 transects of 50, 60 or 100 m length were located perpendicular to the main gradient from

13 the forest to the tundra (Table 1, Fig. 1). Transects were shorter than 100 m at some sites

14 due to time constraints or difficult terrain. The nature of this ecotone differed among sites

15 with shorter, sharper gradients in Churchill and Nansen, gradual in Kluane North and

16 South and even more diffuse in the Mealys with gradient lengths (distance between the

17 lowermost and uppermost transects) ranging from 75 m in Churchilll to over 8.5 km in

18 the Mealys. Only one gradient was used for the Mealys, Kluane North and South. At the

19 other two sites, separate gradients were sampled at different locations within each site.

20 Replicate transects were used for the Forest, Ecotone or Tundra sections across each

21 gradient in all sites except Churchill. Distances between adjacent transects varied at each

22 site ranging from 10 m in Nansen to over 2 km in the Mealys with averages of 80, 103,

23 10, 42 and 1071 m for Kluane North, Kluane South, Nansen, Churchill and the Mealys,

1 respectively. Although there were sometimes scattered trees in the Tundra section, trees

2 may or may not have been present along the transects.

3   Percent tree cover was estimated in 1 x 1 or 2 x 2 m contiguous quadrats along the

4 entire length of each transect (Table 1). Trees were subdivided by height class: seedlings

5 (<15 cm), saplings and sub-arborescent trees or krummholz ($\geq$ 15 cm and < 200 cm,

6 hereafter referred to as short trees) and tall trees ($\geq$ 200 cm); however, there were too few

7 seedlings to analyze separately. Sub-arborescent trees or krummholz (trees with a

8 prostrate growth form) may be as old as taller trees, but have been truncated or stunted by

9 wind erosion (Pereg and Payette 1998) or thermally limited annual growth (Danby and

10 Hik 2007b). Dead trees were rare and only sampled at Kluane North, Kluane South and

11 Churchill.

12

13 **Analysis**

14   New Local Variance (NLV) and wavelet analysis were used to estimate the patch

15 size and scale of spatial pattern, respectively, for each transect using the free software

16 program PASSAGE 2 (Rosenberg 2009). Patch size is the average width of clumps of

17 high tree abundance and scale is the distance between the patches. Wavelet analysis also

18 provided a measure of aggregation or the contrast between patches and gaps. Together

19 these three metrics provide standard characteristics of spatial pattern of the size, spacing

20 and intensity (amount of contrast) of patches of tree cover. Wavelet diagrams also

21 allowed us to examine the distribution of patches visually along each transect. Spatial

22 analysis was only performed if there were non-zero values in at least 3 quadrats along a

23 transect. Some individual species found only in the Forest on a given site were not

1   analyzed separately (*P. mariana* in Nansen, *P. glauca* and *Larix laricina* in the Mealys).

2   Cover classes were converted to midpoint values. Total cover values were derived by

3   summing midpoint cover values for all sizes and species; estimates were then rounded up

4   to the nearest midpoint cover value.

5   The two-term version of NLV is recommended for estimating patch size (Dale

6   1999) whereas wavelet analysis is recommended for assessing the scale of the pattern

7   (Dale and Mah 1998). The Mexican Hat wavelet, commonly used to detect patches (Dale

8   and Mah 1998), was used for the longer transects. We used the French Top Hat wavelet

9   for the Nansen and shorter Mealys transects (60 and 50 m, respectively) since it gave

10   more detailed results that were more appropriate for the shorter transects. For both

11   analyses, randomization tests were conducted using 999 iterations with a 95 %

12   confidence interval. Randomization tests for NLV could not be performed in the program

13   for the shorter transects due to an inadequate number of contiguous quadrats. Maximum

14   distances of 33 % and 25 %, respectively, were used for NLV and wavelet analysis.

15   NLV and wavelet scale diagrams were examined visually to estimate patch size

16   and scale. For patch size, the distance of the first peak (high point in the graph) was

17   selected; for a wide peak the middle distance was chosen. Only peaks that were

18   significantly greater than the 95 % confidence interval derived from randomization tests

19   were used; nearby peaks were considered if the first peak was not significant. Scale was

20   estimated as the distance of the first significant peak of the wavelet scale diagram except

21   a scale of one quadrat was not considered, as recommended by Campbell et al. (1998);

22   however, these authors suggest that scales of two or three quadrats can be considered if

23   multiple transects are used. We also summed the wavelet variance for the scales of 1-10

1 m to provide an estimate of aggregation at the same distances for each site; these scales

2 were chosen arbitrarily to cover the range of scales possible for all sites. We then

3 standardized the results by dividing wavelet variance by the sample variance (Rossi et al.

4 1992), which enabled comparisons of trends in pattern, irrespective of trends in

5 abundance.

6

7 **Results**

8   The variation in tree abundance and species composition among different sites

9 provides a context for the results of the spatial pattern analysis. Tree species richness

10 increased from west to east, with all four conifer species present in the Mealys (Table 2).

11 *Picea glauca* was the only species common to all sites and was found in all sections at all

12 sites except for Tundra section in the Mealys, where it was only found outside the

13 transects (L. Hermanutz and A. Trant, pers. obs.). Since there were very few differences

14 in spatial pattern among species, results are only presented for all species combined.

15 Total and tall tree cover were always greatest in the Forest section and lowest in the

16 Tundra section, whereas short tree cover was greatest in the Ecotone section at all sites

17 except for Kluane North and Nansen (Fig. 2). Total and tall tree cover varied

18 substantially among the five sites for all three sections. Short tree cover varied

19 substantially among sites in the Ecotone (from 2 % in Kluane North and South to 21 % in

20 the Mealys) and was only greater than 1 % in the Tundra section in Kluane North.

21   Patch size varied among sites as well as across the forest-tundra ecotone (Fig. 3).

22 In Kluane North, Kluane South and Nansen, patch sizes were mostly 2-4 m with some

23 larger 5 and 7 m patches in Kluane South and 8-18 m patches in Nansen (individual

1   results not shown). NLV results for the Mealys and Churchill were more complex, often

2   with multiple peaks on the NLV graphs and variable patch sizes ranging from 2 to 13 or

3   23 m, respectively, for the Mealys and Churchill. For total cover, patch size decreased

4   from Forest to Tundra for most sites but patches were larger in the Ecotone compared to

5   the Forest for the Mealys (Fig. 3a). Results were similar for tall and short trees except for

6   Churchill which had a larger patch size of shorter trees in the Ecotone (Fig. 3b, c).

7   The scale (distance between patches) was generally 3-6 m, but ranged up to 11-17

8   m on all sites (individual results not shown). There were few significant peaks for

9   Nansen, especially for total cover, indicating there was no significant aggregation at any

10   scale. Patches of short and tall trees were farther apart in the Forest compared to the

11   Ecotone for most sites (Fig. 4) as scale generally decreased from the Forest to the Tundra.

12   Notable exceptions include the Tundra transect in Kluane South, and an increase in scale

13   from the Forest to the Ecotone for tall trees in Churchill and for total tree cover in the

14   Mealys. The latter trend is different from both short and tall trees, likely because an

15   increase in the frequency of quadrats resulted in a peak at a finer scale in the Forest that

16   was significant only with both sizes of trees included.

17   Standardized aggregation (amount of clumping) for total cover decreased from the

18   Forest to the Ecotone for all sites except for Nansen and Churchill (Fig. 5a). Aggregation

19   was also greater in the Forest compared to the Ecotone for tall trees at all sites except

20   Kluane South (Fig. 5b). However, intensity, measured as wavelet variance at the scale of

21   the pattern, was greater in the Forest compared to the Ecotone for tall trees at all sites

22   including Kluane South (results not shown). Short trees were more aggregated in the

23   Ecotone compared to the Forest in Nansen and the Mealys (Fig. 5c).

1   Wavelet diagrams of position variance provide a detailed examination of the

2   distribution of total tree cover along the transects at each site (Figs. 6-9). Overall, there

3   were few patches of tree cover along transects in Tundra, although the position variance

4   for these patches was generally significant. More patches, often clumped in groups, were

5   evident along Forest transects, whereas there were only a few significant patches in the

6   Ecotone. In Kluane, the North and South sites were very similar with perhaps slightly

7   more significant patches in the Ecotone in the North compared to the South which had

8   long sections of the transects with no patches. Transects in Nansen were mostly only long

9   enough to detect one significant peak, although many other patches were evident,

10   especially in the Forest. In Churchill, patches appeared to be evenly spaced with not

11   much difference between the Forest and Ecotone. In the Mealys there were more evenly

12   spaced patches along the Forest transects compared to the Ecotone transects which had

13   large gaps with no patches. The two upper Ecotone transects also had many patches but

14   they were not significant.

15

16   **Discussion**

17

18   **Trends in spatial pattern across the forest-tundra ecotone**

19   There was substantial geographic variation in spatial pattern across our sites.

20   Differences in the gradient of tree cover from the Forest section to the Tundra section

21   among sites shows that the relative position of the sections relative to the forest-tundra

22   gradient was not the same. This variability could have contributed to the lack of a

23   common pattern among sites. It is also important to acknowledge that we had few

1   transects at each of only a few study areas within the vast forest-tundra ecotone across

2   Canada. Thus, although our study design included a breadth of sites, it lacked depth at

3   individual sites. However, some general trends across the forest-tundra ecotone were

4   apparent. Compared to the Forest, tall tree cover in the Ecotone was less aggregated at

5   most sites with fewer smaller patches of trees. Although trees were present along some

6   Tundra transects, the spatial pattern of tree cover in Tundra was difficult to detect

7   because of the low tree abundance; therefore we focus our interpretion on the difference

8   in spatial pattern between the Forest and the Ecotone.

9   Although patches of tree cover were generally smaller in the Ecotone compared to

10   the Forest, as expected with the difference in tree size, larger patches of shorter trees were

11   observed in the Ecotone in Churchill and the Mealys. Larger patches may arise in the

12   transition area where vegetative growth such as layering is more prominent, particularly

13   in the Mealys where there are extensive mats of krummholz. In Kluane, localized

14   permafrost, colder soil temperatures, and more abundant and longer lasting snow cover

15   on the North site (Danby and Hik 2007b) may have resulted in less vegetative growth

16   producing smaller patches that were more closely spaced compared to South site. In

17   Churchill, our only latitudinal site, patches of tall trees were much farther apart in the

18   Ecotone compared to the Forest.

19   The decrease in aggregation of tall tree cover and patch size from the Forest to the

20   Ecotone differed from other studies (Humphries et al. 2007; Lingua et al. 2008). The

21   'swiss cheese' model of the forest-tundra ecotone (Payette et al. 2001) describes the

22   transition as a gradual change from a forested landscape with patches of tundra to a

23   tundra landscape with patches of forest. Greater patchiness is expected in the middle of

1   the transition but our sites (including our Forest transects) may have all been located in a

2   tundra landscape with patches of forest (highest average tree cover < 40 %). Therefore

3   the Forest transects would be located nearest the middle of the transition where we expect

4   the greatest patchiness according to this model. An exception to this general trend was

5   greater clumping in the Ecotone for short trees in Nansen where saplings may have

6   established in patches away from taller trees and in the Mealys where there were

7   extensive dense mats of krummholz.

8

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

10   Several factors could have affected tree establishment and growth that resulted in

11   the observed spatial patterns. Processes such as facilitation through shelter from wind,

12   seed dispersal and factors such as an uneven microtopography can all act to generate a

13   clumped spatial pattern (Humphries et al. 2008). Total tree cover may have been more

14   clumped in the Ecotone compared to the Forest due to the favourable effects of shelter

15   from wind or snow abrasion. Wind is widely acknowledged to be an important influence

16   on ecological pattern and process within the forest-tundra ecotone (see review by

17   Holtmeier and Broll 2010). Research has demonstrated the role of wind in structuring the

18   physiognomy of trees across the forest-tundra ecotone (e.g. Yoshino 1973), altering leaf

19   physiology (e.g. Hadley and Smith 1986) and structuring vegetation pattern (e.g.

20   Holtmeier 1982). Our results appear to support the body of literature demonstrating this

21   latter category of wind-related effects. A concurrent increase in aggregation and

22   reduction in tree cover from the Forest to the Ecotone could indicate an interaction

23   between temperature and wind. If only wind was important, we would expect an increase

1   in aggregation but similar tree cover. If only temperature was important, we would expect

2   a reduction in tree cover, but consistent measures of aggregation. Therefore, we suggest

3   that at some sites, temperature may be a limiting factor whereas wind may be a

4   structuring factor for the spatial pattern of trees within the forest-tundra ecotone. This is

5   analogous with the notion proposed by Holtmeier and Broll (2005) that temperature

6   influences the forest-tundra ecotone at a coarser scale than wind.

7   Although patch sizes were smaller in the Ecotone compared to the forest,

8   aggregation was not greater in the Ecotone at all sites for all variables indicating that

9   wind as a structuring factor may not be universal. Tree species may be important; *Picea*

10   *glauca* may exhibit less sheltering effects since this species tends to form tree islands

11   rather than larger mats of krummholz. Greater clustering of short trees rather than tall

12   trees in the Ecotone compared to the Forest, also found in Kluane and the Mealys using

13   mapped point patterns by De Fields (2009) and at a tropical treeline by Šrůtek et al.

14   (2002), was likely a result of layering followed by intraspecific resource competition

15   (Pereg and Payette 1998; Holtmeier 2003). Tall trees may be robust enough to be able to

16   withstand harsh conditions such as mechanical damage and desiccation during winter,

17   while short trees may obtain greater benefit from being aggregated. In the Mealys, tree

18   establishment in the Ecotone may be dependent on favourable microsites in a landscape

19   with abundant exposed rock and glacial erratics, as observed elsewhere (see Holtmeier

20   and Broll 2010). In Kluane South greater aggregation but not patch size in the Ecotone

21   compared to Forest for tall trees infers that patches were denser rather than larger. This

22   provides support for wind shelter effects at higher elevations. Other factors such as

23   microtopography and seed dispersal also contribute to aggregation (Resler 2006; McIntire

1 and Fajardo 2009) and are therefore important to consider, but these factors would likely

2 be similar across the forest-tundra ecotone.

3   Alternatively, an even distribution of trees could indicate a greater influence of

4 competition or regular microtopography as the forest develops. Since the spatial analysis

5 we used cannot test for a regular or even pattern, we can only assess the role of these

6 factors by examining which transects had less aggregation or a greater scale indicating

7 the absence of patches at short distances. Using these indirect measures, we found little

8 evidence that trees were more evenly spaced in the Forest except for Kluane South where

9 there was less aggregation of tall trees in the Forest compared to the Ecotone. At this site,

10 scale was much greater and more variable; De Fields (2009) found evidence of regular

11 spacing of trees at this site using mapped point patterns that could indicate competition.

12 In Churchill, patches of tall trees were much farther apart in the Ecotone compared to the

13 Forest in contrast to other sites, indicating an absence of clumping at short distances and

14 perhaps an even distribution. The absence of significant aggregation for many transects

15 also suggests an even distribution in Nansen.

16   Overall, our results of decreased clumping of smaller patches of tall trees that are

17 further apart in the Ecotone compared to the Forest suggests that trees are not spatially

18 configured to provide shelter from the wind at most of our study sites. Conversely,

19 aggregation in the Forest suggests that competition among trees is not a major limiting

20 factor. Both of these inferences appear to contradict the stress-gradient hypothesis for

21 interspecific interactions that facilitation increases and competition decreases with abiotic

22 stress (Maestre et al. 2009), and thus warrants further investigation. However,

1   intraspecific competition and wind shelter effects are likely important site-specific factors

2   at some study sites.

3

4   **Implications for climate change**

5   Trends in tree spatial pattern across the forest-tundra ecotone provide some

6   insight into how the configuration may change with a changing climate given the

7   assumption that trees within this transition become more abundant. With climate

8   warming, the spatial pattern in the Ecotone could transition to that in the Forest. Given

9   this assumption, trees in the Ecotone that likely established as either isolated individuals

10   or in small dispersed patches will likely develop into forests through an enlargement of

11   patches by either vegetative growth or new establishment. These patches would become

12   denser and more aggregated, sometimes merging together. There may also be

13   establishment of new patches as trees establish in forest openings (Weisberg and Baker

14   1995) that would lead to greater aggregation within the forest-tundra ecotone. This

15   increase in the clumping of trees would result in ecosystem and habitat changes possibly

16   affecting regional biodiversity (Gibson et al. 2009). If there was treeline advance or

17   development of the Tundra into Ecotone at the same time, the forest-tundra ecotone could

18   shift without a change in spatial pattern. However, forest density could be increasing in

19   the forest-tundra ecotone without a concurrent poleward or upward advance at some sites

20   which would lead to a change in spatial configuration.

21   Our results suggest that trends in spatial pattern and the potential factors affecting

22   tree establishment within the forest-tundra ecotone are site-specific. Factors such as the

23   width of the forest-tundra gradient, aspect, tree species, microclimate, microtopography

1   and the presence of krummholz likely affect the configuration of trees in the forest-tundra

2   ecotone and the development of the pattern of the forest-tundra ecotone with climate

3   change. In sites with a lot of krummholz, there may be an intermediate stage of large

4   krummholz patches before the development of a more open forest. Because of this

5   variation across Canada, there is little overall support for hypotheses concerning factors

6   affecting tree abundance in the forest-tundra ecotone. Instead, we suggest that processes

7   such as passive facilitation through sheltering from wind and intraspecific competition act

8   differently at different sites resulting in a highly variable configuration of the forest-

9   tundra ecotone. Since response to change will vary across Canada, adaptation of northern

10 communities to change must be tailored to individual sites.

11

References

Batllori, E., Camarero, J.J., Ninot, J.M., and Gutiérrez, E.. 2009. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. Global Ecol. Biogeo. **18**:460-472. doi: 10.1111/j.1466-8238.2009.00464.x.

Camarero, J.J., and Gutierrez, E. 2004. Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. Climatic Change. **63**: 181-200.

Camarero, J.J., Gutierrez, W., and Fortin, M.J. 2000. Spatial pattern of subalpine forest-alpine grassland ecotones in the Spanish Central Pyrenees. Forest Ecol Manag. **134**: 1-16.

Campbell, J.E., Franklin, S.B., Gibson, D.J., and Newman, J.A. 1998. Permutation of two-term local quadrat variance analysis: general concepts for interpretation of peaks. J. Veg. Sci. **9**: 41-44.

Dale, M.R.T. 1999. Spatial pattern analysis in plant ecology. Cambridge University Press, Cambridge, U.K.

Dale, M.R.T., and Mah, M. 1998. The use of wavelets for spatial pattern analysis in ecology. J. Veg. Sci. **9**: 805-814.

Danby, R.K., and Hik, D.S. 2007a. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. J. Ecol. **95**: 352-363.

Danby, R.K., and Hik, D.S. 2007b. Responses of white spruce (*Picea glauca*) to experimental warming at a subarctic alpine treeline. Global Change Biol. **13**: 437-451.

De Fields, D.L. 2009. Spatial pattern of trees and shrubs within the Canadian forest-tundra ecotone. M.E.S. thesis, School of Resource and Environmental Studies, Dalhousie University. Halifax, Nova Scotia, Canada.

Environment Canada. 2009. Canadian Climate Normals 1971-2000. [online] Available from http://www.climate.weatheroffice.ec.gc.ca/climate_normals/ [accessed 3 November, 2009]

Fang, J., and Lechowicz, M.J. 2006. Climatic limits for the present distribution of beech (Fagus L.) species in the world. J. Biogeogr. **33**: 1804-1819.

Gibson, S.Y., Van Der Marel, R.C., and Starzomski, B.M. 2009. Climate change and conservation of leading-edge peripheral populations. Cons. Biol. **23**: 1369-1373.

Hadley, J.L., and Smith, W.K. 1986. Wind effects on needles of timberline conifers: seasonal influences on mortality. Ecology. **67**: 12-19.

Harsch, M.A., Hulme, P.E., McGlone, M.S., Duncan, R. P., and Richard, P. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecol. Lett. **12**: 1040-1049.

Hofgaard, A. and Rees, G. 2008. PPS Arctic Manual. Available from: http://ppsarctic.nina.no/files/PPS%20Arctic%20Manual.pdf

Holtmeier, F.-K. 1982. 'Ribbon Forest' and 'Hedges.' Strip-like distribution patterns of trees at the upper timberline in the Rocky Mountains. Erdkunde**. 36**: 142–153.

Holtmeier, F.-K. 2003. Mountain Timberlines: Ecology, Patchiness, and Dynamics. Kluwer Academic, Dordrecht, Netherlands.

Holtmeier, F.-K. and Broll, G. 2005. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. Global Ecology and Biogeography **14**: 395-410.

Holtmeier, F.-K. and Broll, G. 2010. Wind as an ecological agent at treelines in North America, the Alps, and the European Subarctic. Physical Geography. **31**: 203-233.

Humphries, H.C., Bourgeron, P.S., and Mujica-Crapanzano, L.R. 2008. Tree spatial patterns and environmental relationships in the forest-alpine tundra ecotone at Niwot Ridge, Colorado, USA. Ecol. Res. **23**: 589-605.

IPCC. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, United Kingdom and New York.Edited by Soloman, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L Miller .

Johnson, E. A. 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. Can. J. Bot. **53:** 2933-2941.

Körner, C., and Hoch, G. 2006. A test of treeline theory on a montane permafrost island. Arct. Antarct. Alp. Res. **38**: 113-119.

Krugman, S.L., Stein, W.I. and Schmitt, D.M. 1989. Seed biology, In Seeds of Woody Plants in the United States, U. S. D. A., Agriculture Handbook 450, U. S. Gov't. Printing.

Lescop-Sinclair, K., and Payette, S. 1995. Recent advance of the arctic treeline along the eastern coast of the Hudson Bay. J. Ecol. **83**: 929-936.

Lingua, E., Cherubini, P., Motta, R. and Nola, P. 2008. Spatial structure along an altitudinal gradient in the Italian Central Alps suggests competition and facilitation among coniferous species. J. Veg. Sci. **19**: 425-436.

Lloyd, A. 2005. Ecological histories from Alaskan tree lines provide insight into future change. Ecology. **86**: 1687-1695.

Lloyd, A., and Fastie, C.L. 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. Climatic Change. **52**: 481-509.

MacDonald, G.M., Kremenetski, K.V., and Beilman, D.W. 2008. Climate change and the northern Russian treeline zone. Philos. Trans. R. Soc. Lond. B. Biol. Sci. **363**: 2285-2299.

Maestre, F.T., Callaway, R.M., Valladares, F., and Lortie, C.J. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. J. Ecol. **97**: 199-205.

McIntire, E., and Fajardo, A. 2009. Beyond description: the active and effective way to infer process from spatial patterns. Ecology. **90**: 46-56.

Meades, S.J. 1990. Natural regions of Newfoundland and Labrador. Protected Areas Association, St. John's NL, Canada.

Palko, S., St-Laurent, L., Huffman, T., and Unrau, E. 1996. Canadian vegetation and land cover: a raster and vector data set for GIS applications. *In* GIS Applications in Natural Resources 2. *Edited by* M. Heit, H.D. Parker & A. Shortreid. GIS World, Fort Collins, CO. pp. 185-19.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. S. **37**: 637-669.

Payette, S., Fortin, M.J. and Gamache, I. 2001. The subarctic forest-tundra: the structure of a biome in a changing climate. BioScience **51**: 709-718.

Pereg, D., and Payette, S. 1998. Development of black spruce growth forms at treeline. Plant Ecol. **138**: 137-147.

Resler, L. 2006. Geomorphic controls of spatial pattern and process at alpine treeline. Prof. Geogr. **58**: 124-138.

Rosenberg, M. S. 2009. Passage 2. Available from http://www.passagesoftware.net/

Šrůtek, M., Dolezal, J., and Hara, T. 2002. Spatial structure and associations in a *Pinus Canariensis* population at the treeline, Pico Del Teide, Tenerife, Canary Islands. Arctic, Ant. Alp. Res. **34**: 201-210.

Szeicz, J.M., and MacDonald, G.M. 1995. Recent white spruce dynamics at the subarctic alpine treeline of north-western Canada. J. Ecol. **83**: 873-833.

Timoney, K.P., La Roi, G.H., Zoltai, S.C., and Robinson, A.L. 1992. The high subarctic forest-tundra of northwestern Canada: Position, width, and vegetation gradients in relation to climate. Arctic. **45**: 1-9.

Weisberg, P.J., and Baker, W.L. 1995. Spatial variation in tree regeneration in the forest-tundra ecotone, Rocky-Mountain National Park, Colorado. Can. J. For. Res. **25**: 1326-1339.

Whipple, S. A. 1978. The relationship of buried, germinating seeds to vegetation in an old-growth Colorado subalpine forest. Can. J. Bot. **56**: 1505-1509.

Wiegand, T., and Moloney, K.A. 2004. Rings, circles and null-models for point pattern analysis in ecology. Oikos. **104**: 209-229.

Wiegand, T., Camarero, J. Ruger, N., and Gutierrez, E. 2006. Abrupt population changes in treeline ecotones along smooth gradients. J. Ecol. **94**: 880-892.

Woodall, C.W., Oswalt, C.M., Westfall, J.A., Perry, C.H., Nelson, M.D., and Finley, A.O. 2008. An indicator of tree migration in forests of the eastern United States. Forest Ecol. Manag. **257**: 1434-1444.

Yoshino, M.M. 1973. Wind-shaped trees in the subalpine zone in Japan. Arctic and Antarctic Research. **5**: A115-A126.

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

Study site	Location	Elevation	Tree species	# of transects			Transect length	Quadrat size	Cover classes (%)
				F*	E*	T*			
Kluane North	61.2N, 138.4W	1195-1355 m	*P. glauca*	2	4	2	100 m	1 x 1 m	0-1, 1-5, 5-10, 10-25, 25-50, 50-75, 75-100
Kluane South	61.2N, 138.4W	1265-1525 m	*P. glauca*	2	4	3	100 m	1 x 1 m	0-1, 1-5, 5-10, 10-25, 25-50, 50-75, 75-100
Nansen	62.1N, 137.2W	1283 m	*P. glauca, P. mariana*	6	6	6	62 m	2 x 2 m	1, 3, to the nearest 5 % thereafter
Churchill	58.8N, 94.1W	22 m	*P. glauca, P. mariana*	3	3	3	100 m	1 x 1m	0-1, 1-5, 5-10, 10-25, 25-50, 50-75, 75-100
Mealys	53.6N, 58.8W	517-819 m	*P. glauca, P. mariana, A. balsamea, L. laricina*	2	4	2	50, 100 m**	1 x 1m	0-5, 6-25, 25-50, 50-75, 75-100

* F = Forest, E = Ecotone, T = Tundra sections.

**Half of the transects in each section were 50 m and half were 100 m.

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

	Kluane North			Kluane South			Nansen			Churchill			Mealys		
	F*	E*	T*	F	E	T	F	E	T	F	E	T	F	E	T
Picea glauca	44	32	8	35	17	2	22	27	2	42	49	8	17	0.3	0
Picea mariana	0	0	0	0	0	0	18	0	0	13	17	0	60	21	0
Larix laricina	0	0	0	0	0	0	0	0	0	3	12	0.3	11	0.3	0
Abies balsamea	0	0	0	0	0	0	0	0	0	0	0	0	31	18	0

* F = Forest, E = Ecotone, T = Tundra sections.

Figure captions

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 Kluane (A), Nansen (B), Churchill (C), and the Mealys (D) 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.

Fig. 2. Average (± SE) cover of all trees combined (A), tall trees (B) and short trees (C) across the forest-tundra ecotone at the study sites. Sample sizes are the number of transects at each site as indicated in Table 1.

Fig. 3. Average (± SE) patch size 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. Sample sizes for Forest, Ecotone, Tundra, respectively, are: A) Kluane North 2, 4, 2, Kluane South 2, 4, 2, Nansen 8, 6, 1, Churchill 3, 3, 1, Mealys 2, 4, 0; B) Kluane North 2, 3, 0, Kluane South 2, 4, 2, Nansen 8, 5, 0, Churchill 2, 2, 0, Mealys 2, 1, 0; C) Kluane North 2, 4, 2, Kluane South 0, 4, 0, Nansen 6, 3, 1, Churchill 1, 2, 1, Mealys 1, 4, 0.

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 were significant for total tree cover in the Ecotone indicating there was no significant aggregation for which scale could be determined. Sample sizes for Forest, Ecotone, Tundra, respectively, are: A) Kluane North 2, 3, 2, Kluane South 2, 4, 2, Nansen 4, 0, 0, Churchill 3, 2, 0, Mealys 2, 4, 0; B) Kluane North 2, 3, 0, Kluane South 2, 4, 2, Nansen 5, 0, 0, Churchill 2, 2, 0, Mealys 2, 1, 0; C) Kluane North 2, 3, 2, Kluane South 0, 2, 0, Nansen 3, 1, 0, Churchill 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, Tundra, respectively, are: A) Kluane North 2, 4, 2, Kluane South 2, 4, 2, Nansen 8, 6, 1, Churchill 3, 3, 2, Mealys 2, 4, 0; B) Kluane North 2, 3, 0, Kluane South 2, 4, 2, Nansen 8, 5, 0, Churchill 2, 2, 0, Mealys 2, 1, 0; C) Kluane North 2, 4, 2, Kluane South 0, 4, 0, Nansen 6, 3, 1, Churchill 2, 2, 1, Mealys 1, 4, 0.

Fig. 6. Position variance along the Tundra, Ecotone and Forest transects in Kluane North and 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 Tundra, 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.

Fig. 8. Position variance along the Tundra, Ecotone and Forest transects in Churchill. Note the different scale for the y-axis for the Tundra transects. See the caption for Fig. 6 for details about interpreting position variance.

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.
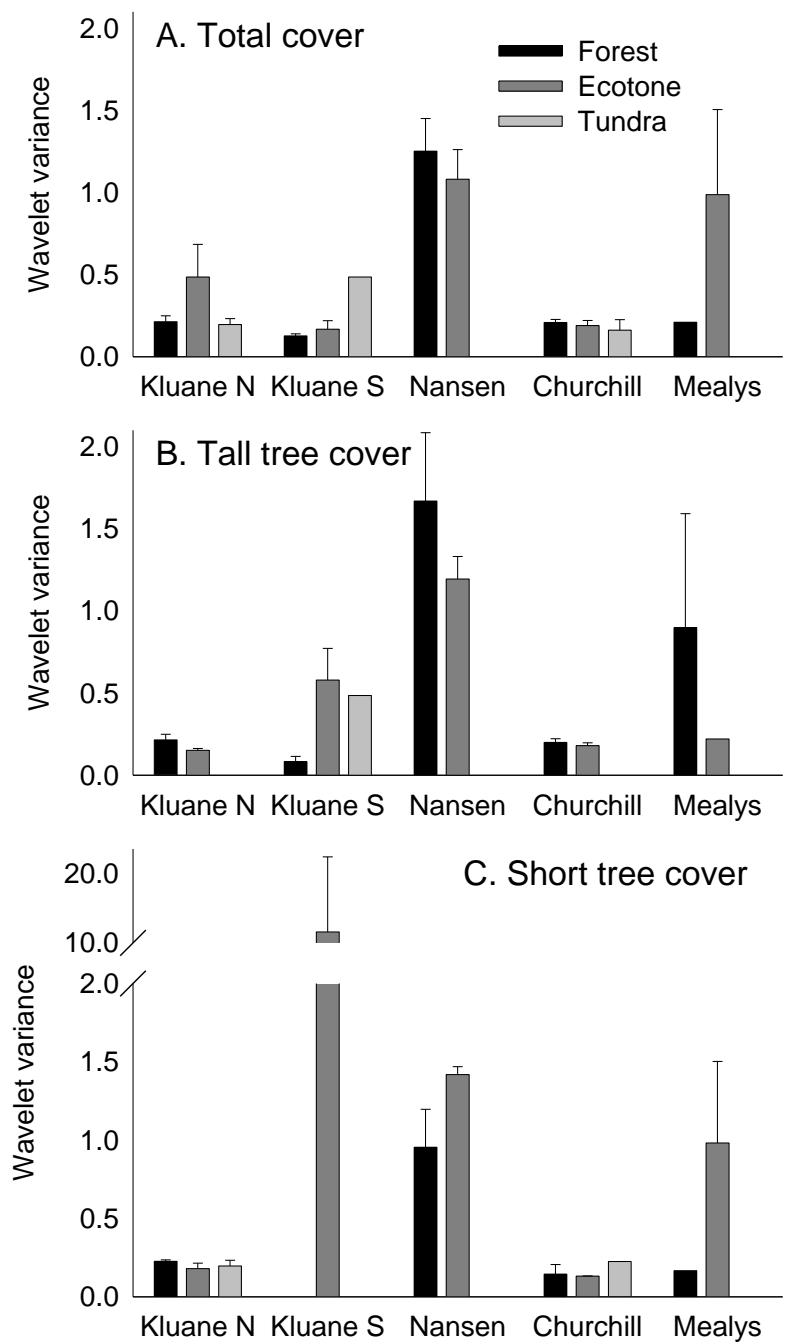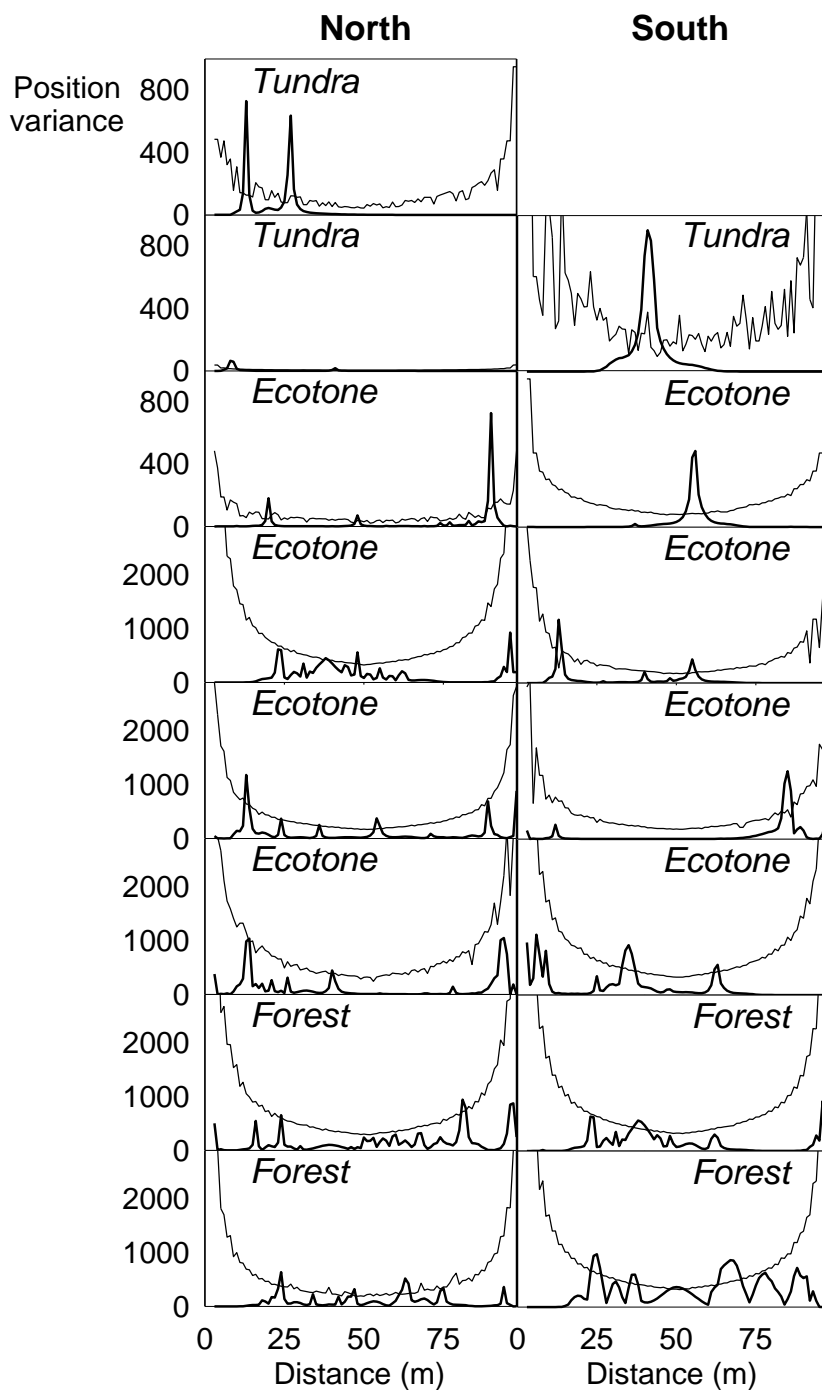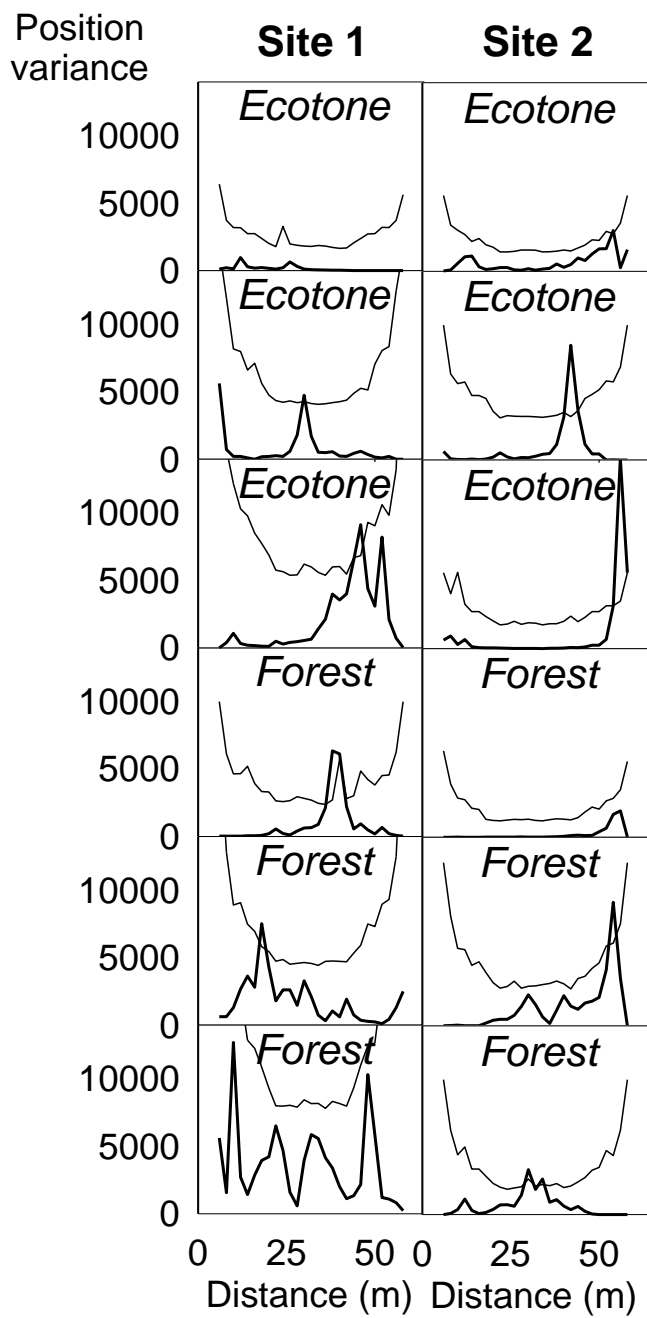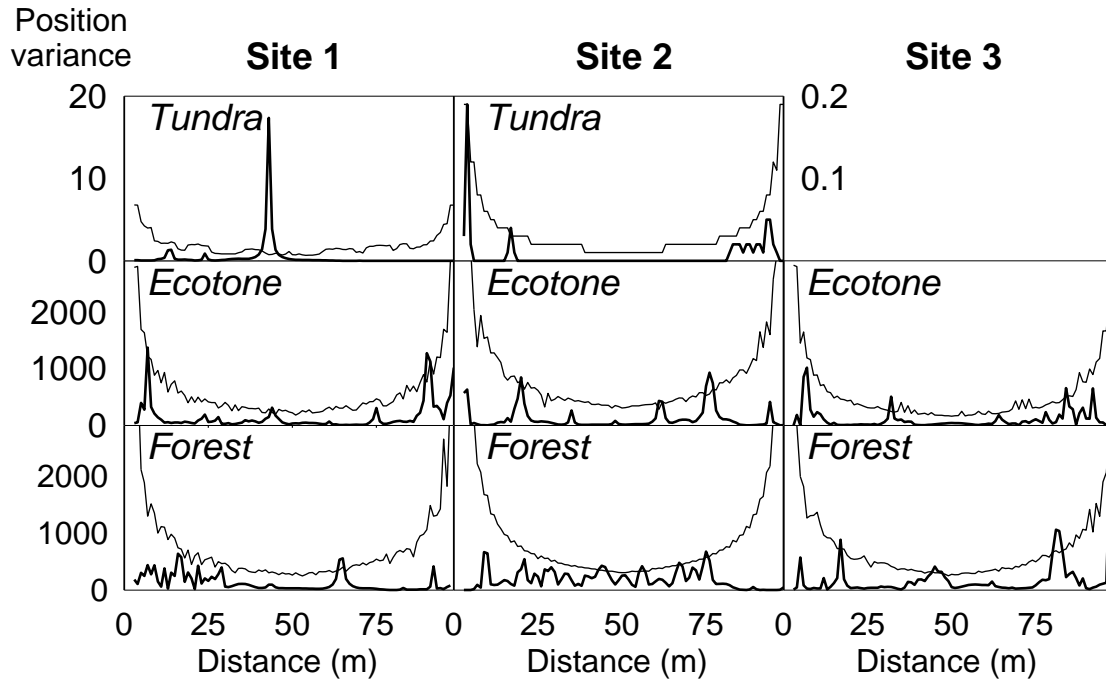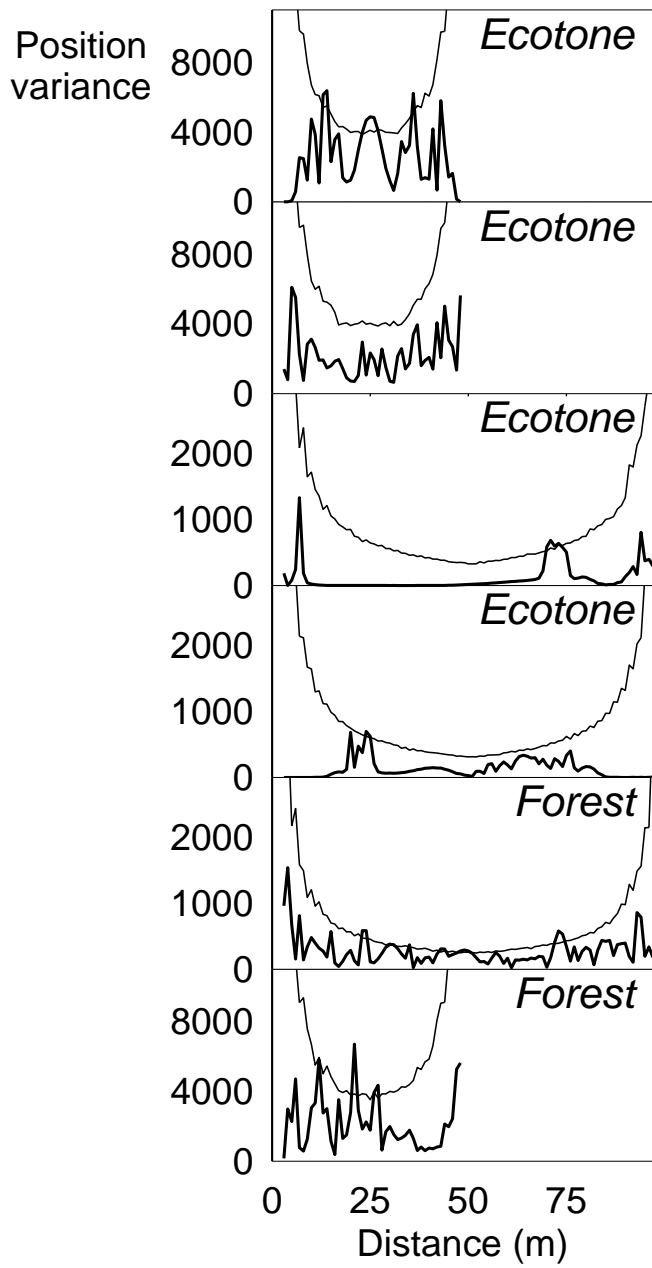
Figure 1
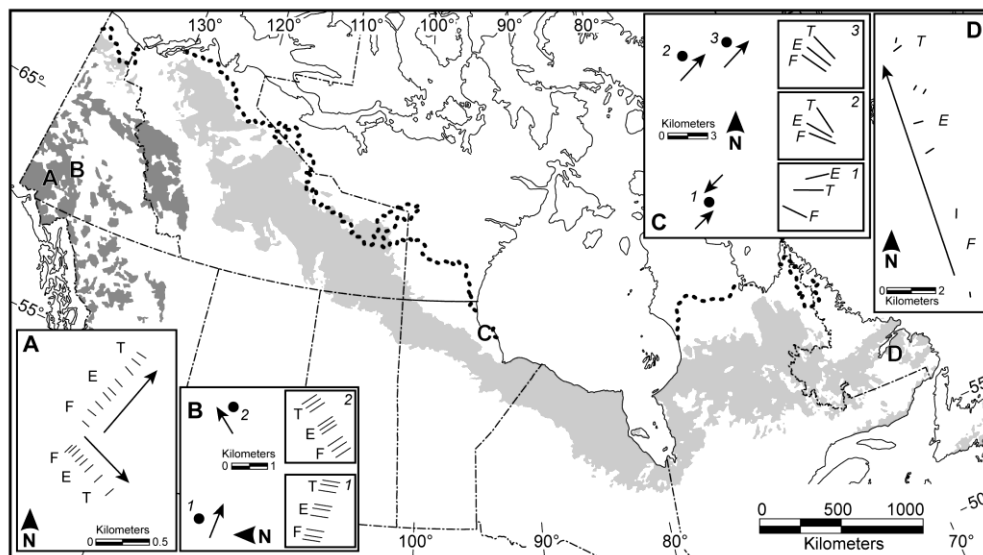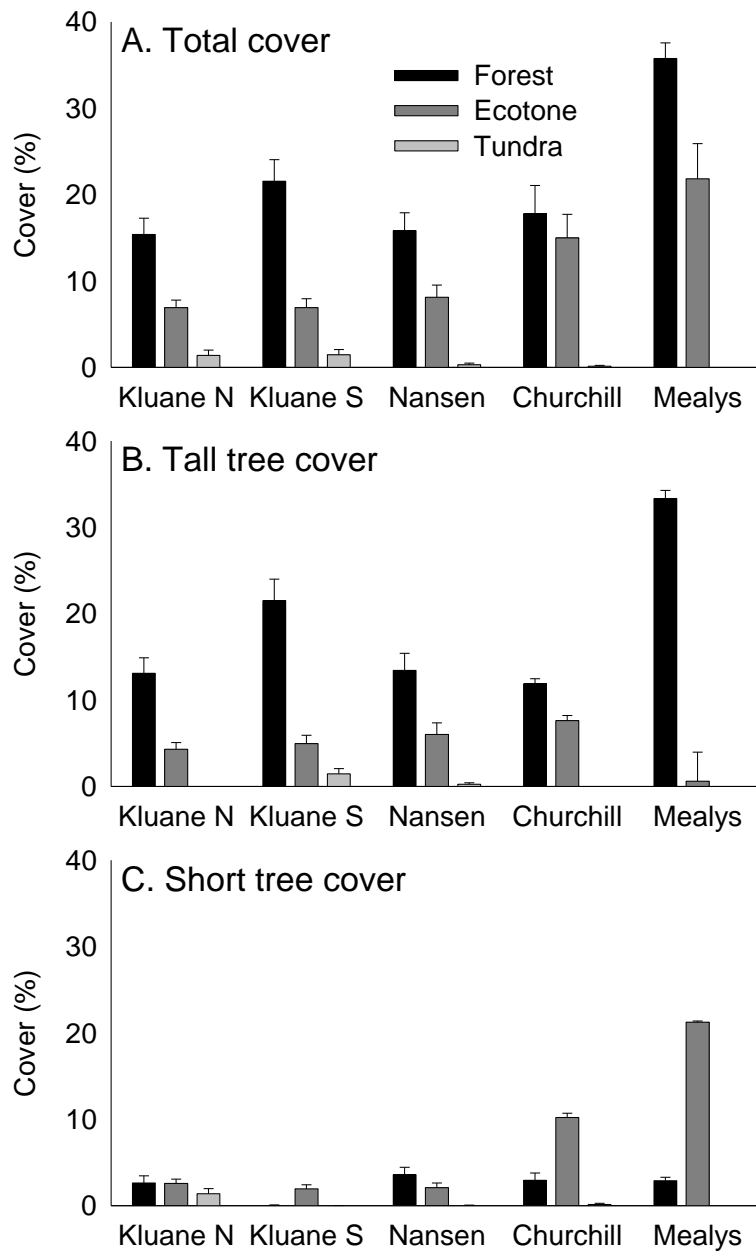
Figure 2
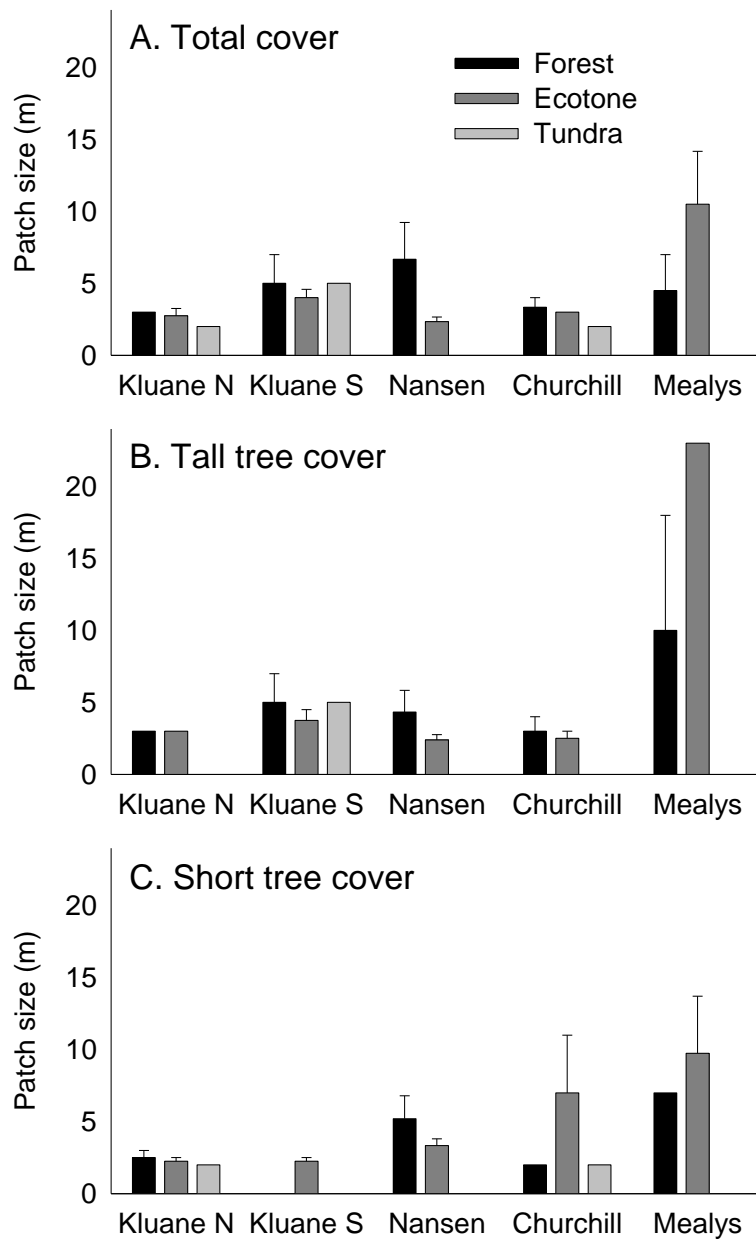
Figure 3
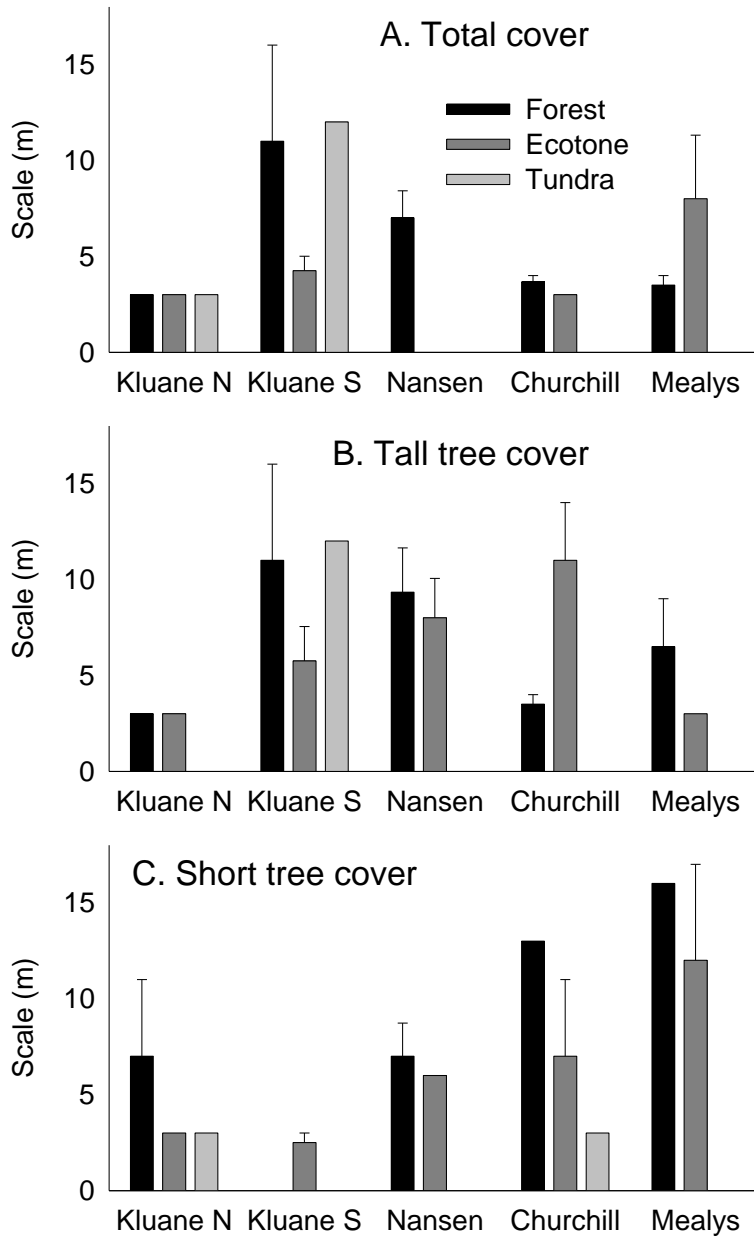
Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9