

# Patterns of shrub abundance and relationships with other plant types within the forest–tundra ecotone in northern Canada

Karen A. Harper, Amanda A. Lavallee, and Pavel Dodonov

**Abstract:** Throughout the forest–tundra ecotone where trees and tall shrubs are becoming more abundant, knowledge of associations between shrubs and surrounding vegetation could inform predictions of their changing relationships. We assessed shrubs in 1 m × 1 m contiguous quadrats along two ~450 m transects across tundra and ecotone landscapes near Churchill, Canada to determine patterns in relation to lakeshore edges, soil pH, microtopography, and other plant groups. We used wavelet analysis to assess patterns and generalized least squares for relationships with environmental variables. Shrubs were taller and more diverse at edges, particularly in tundra. The ecotone was more complex than tundra with greater variation in tall shrub and tree cover, shrub height, and microtopography. Shrub richness was positively correlated with microtopography but exhibited no relationship with pH. Bivariate relationships of shrubs with other plant groups varied for different scales. In tundra, shrub richness was negatively correlated with graminoids, forbs, and moss, but positively correlated with lichens within 1 m; opposite relationships were found at 4–60 m scales. Relationships in the ecotone were reversed and more complex at different scales. As trees encroach in the tundra, the spatial pattern of shrubs will become more complex at a variety of scales, likely with cascading effects on other plant types.

**Key words:** forest–tundra ecotone, heterogeneous landscapes, shrub expansion, spatial pattern, wavelet analysis.

**Résumé :** À travers l'écotone forêt–toundra où les arbres et grands arbustes deviennent plus abondants, la connaissance des associations entre les arbustes et la végétation environnante pourrait renseigner les prévisions sur l'évolution de leurs relations. Nous avons étudié des arbustes en cadrats contigus de 1 m × 1 m, le long de deux transects d'environ 450 m traversant les paysages de toundra et d'écotone proches de Churchill au Canada, afin de déterminer les configurations relatives aux berges de lac, au pH du sol, à la microtopographie, et aux autres groupes de plantes. Nous avons utilisé l'analyse par ondelettes pour établir des modèles et nous avons appliqué la méthode des moindres carrés généralisée pour l'étude des relations avec les variables environnementales. Les arbustes étaient plus grands et plus diversifiés sur les berges, particulièrement dans la toundra. L'écotone était plus complexe que la toundra avec une plus grande variation au niveau du couvert de grands arbustes et d'arbres, de la hauteur d'arbuste, et de la microtopographie. La richesse arbustive montre une corrélation positive avec la microtopographie, mais ne présente pas de relation avec le pH. Les relations à deux variables des arbustes

Received 29 June 2017. Accepted 13 June 2018.

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avec les autres groupes de plantes varient à différentes échelles. Dans la toundra, la richesse arbustive montre une corrélation négative avec les graminées, les herbes non graminéennes et la mousse, mais est positivement corrélée avec les lichens dans un rayon de 1 m; des rapports opposés ont été constatés à des échelles de 4–60 m. Les rapports dans l'écotone étaient inversés et plus complexes à différentes échelles. À mesure que les arbres empiètent sur la toundra, la configuration spatiale des arbustes deviendra plus complexe à des échelles variées, possiblement avec des effets en cascade sur d'autres types de plantes. [Traduit par la Rédaction]

*Mots-clés* : écotone forêt–toundra, paysages hétérogènes, expansion arbustive, configuration spatiale, analyse par ondelettes.

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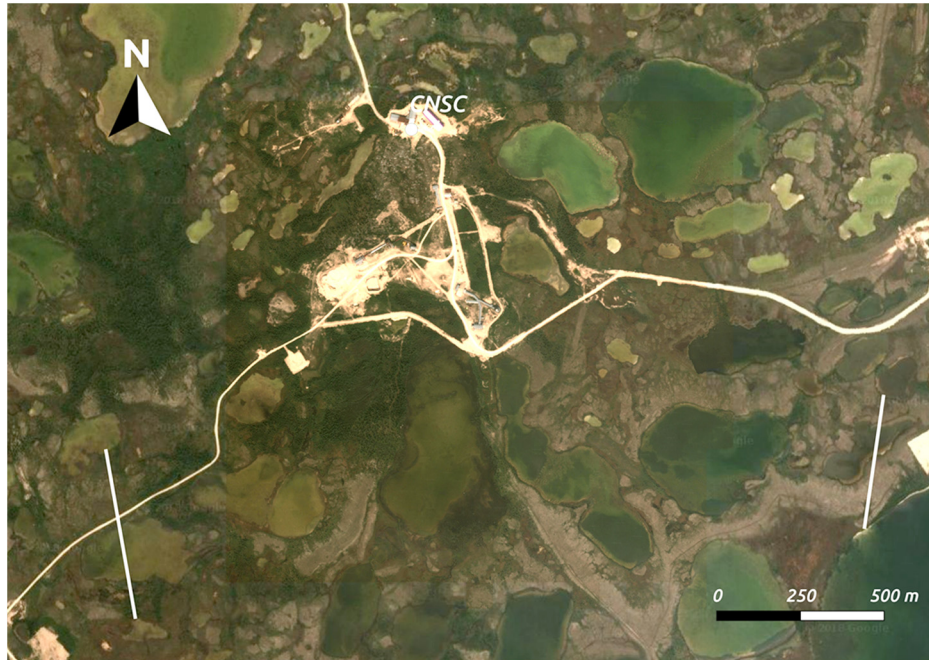
## Introduction

Landscapes at the southern edge of Arctic regions are heterogeneous mosaics of different vegetation types with potential for dramatic change as plant communities shift northward due to climate change (Serreze et al. 2000; Bret-Harte et al. 2002; Danby and Hik 2007). Within many sites in the forest–tundra ecotone, an advancing treeline has been accompanied by increasing abundance of trees (Danby and Hik 2007; Harsch et al. 2009) and shrubs (Frost and Epstein 2014). Shrub densification has also been occurring at many different sites across the Arctic biome (Chapin et al. 2005; Myers-Smith 2007; Blok et al. 2011; Hallinger and Wilmking 2011; Myers-Smith et al. 2011). Shrub expansion may cause physical and biological changes to the subarctic landscape by modifying microclimate (temperature, shade, and soil moisture), microtopography, and biodiversity (Sturm et al. 2005; Hallinger et al. 2010; Myers-Smith et al. 2011). The shrub layer, often the tallest vegetation in low Arctic landscapes, affects the surrounding shorter vegetation and plays a crucial role as a source of shelter and habitat; e.g., many bird species were found to be more abundant in riparian shrub patches than in the surrounding shorter vegetation (Henden et al. 2013). Shrub species exhibit different patterns, particularly around water systems, which reflect their wide tolerances to environmental conditions (Swanson 2015). Shrub dynamics may not be homogeneous across subarctic/Arctic landscapes; shrubs in more moist areas such as at the edges of water bodies may be more sensitive to climate change (Myers-Smith et al. 2015; but see Fraser et al. 2014).

As a heterogeneous array of habitat types (Payette et al. 2001; Harper et al. 2011; Ropars and Boudreau 2012), the forest–tundra ecotone has a high frequency of natural edges or transitions. Although many studies have focused on the patterns of vegetation across anthropogenic forest edges in managed landscapes at lower latitudes, few have focused on natural edges and transitions, particularly in northern heterogeneous landscapes. Edges and transition zones may substantially affect the spatial pattern of vegetation and habitat throughout subarctic landscapes. For example, the heterogeneous mosaic of shorter vegetation and taller dense patches of *Salix* and *Betula* shrubs can result in productive riparian biodiversity hotspots (Henden et al. 2013). Understanding the spatial pattern of the shrub layer within the forest–tundra ecotone will be useful for inferring relationships between shrub distributions and environmental factors that facilitate shrub growth and affect other plant types.

We examined the role of distance to edges of water bodies and environmental factors (microtopography, pH) in determining the spatial pattern of the shrub layer, and the relationship of shrubs with trees and shorter plant types at different scales. We considered tall and prostrate shrubs in the shrub layer across two subarctic/Arctic landscapes in central Canada: tundra and forest–tundra ecotone. Our specific objectives for shrubs were (1) to determine patterns across edges of water bodies, (2) to relate their abundance to pH and

**Fig. 1.** Location of the Churchill Northern Studies Centre near the western shore of Hudson Bay, and the locations of the tundra (right) and forest–tundra ecotone (left) transects. The Churchill Northern Studies Centre is approximately 20 km east of the town of Churchill, MB, Canada. The background image (©2018, CNES/Airbus, DigitalGlobe) was obtained from Google via the OpenLayers Plugin (Kalberer and Walker 2017) in QGIS (QGIS Development Team 2017).



microtopography, and (3) to assess relationships with other plant types (trees, herbs, graminoids, bryophytes, and ground cover lichens) at different scales. We compared our results between Arctic tundra and forest–tundra ecotone landscapes because we were particularly interested in determining the effect of tree cover in the forest–tundra ecotone on the relationships between shrubs and other plant types. These results will help inform predictions of the changing relationships between shrubs and surrounding vegetation as trees are expected to invade tundra landscapes at the southern edge of Arctic regions due to climate change. In particular, we provide insight into how the abundance and spatial pattern of different shrubs will be altered by encroaching trees at fine to intermediate scales and how these changes might affect other life forms.

## Methods

### Study area

We conducted our study near the town of Churchill, MB, Canada, along the western side of Hudson Bay (Fig. 1). The subarctic Churchill area is considered to be an area of transition between boreal forest and Arctic tundra. The vegetation is a mosaic of *Picea glauca* and *P. mariana* with patches of wetlands and dense shrubs. The shrub layer is composed of taller shrubs at least 40 cm in height with bases containing multiple stems and shoots (e.g., *Salix*, *Betula*, and *Alnus*), and erect dwarf shrubs of intermediate 10–40 cm height, which dominate in ecotone areas and pockets of tundra (e.g., *Vaccinium*, shorter *Salix*, *Arctostaphylos*, and *Rhododendron*). In open tundra, there are prostrate dwarf shrubs between 0 and 10 cm tall, which include *Empetrum nigrum*, *Dryas integrifolia*, *Andromeda*

*polifolia*, *S. reticulata*, and *Vaccinium vitis-idaea* (see Supplementary Material 1<sup>1</sup>). The average temperature of Churchill is 12 °C in July and −26.7 °C in January and the average annual precipitation is 430 mm, of which approximately 40% is snowfall (Environment Canada 2009).

### Sampling design

We placed one transect 1.8 km southeast of the Churchill Northern Studies Centre in open tundra habitat, and another 1.5 km southwest of the Centre in forest–tundra ecotone habitat with a mixture of tree-covered and tundra areas (Fig. 1). We located the transects according to the following criteria: (1) end points at the edge of water bodies free from any shrub cover because our main interest was on edges and to avoid boundary effects in the analyses (caused when zero-values are artificially added to replace the unsampled vegetation outside the transects' limits; by ending the transects at water body edges, we ensured that the zero-value quadrats were actually there); (2) an additional water body along the transects to increase the number of edges; (3) reasonably homogeneous in either tundra or ecotone vegetation along the entire length of the transect; (4) easy access from the road for safety reasons due to the presence of polar bears in the area; and (5) a length of at least 300 m excluding water bodies. We placed our transects at the two sites that best satisfied these criteria based on examination of satellite imagery and field exploration. Transect lengths were 412 and 460 m for the tundra and ecotone, respectively. Lakes along the transects were 110–120 m wide, and the ecotone transect also crossed three smaller water bodies, at most 16 m wide with some plant cover, and a 9 m wide gravel road. We sampled shrubs (both erect and prostrate) and environmental variables within contiguous 1 m × 1 m quadrats along each transect. Our sampling was similar to the extensive sampling along a very long transect across a forested landscape used in Brososke et al. (1999). However, we used spatially contiguous sampling because of the heterogeneity of the Churchill landscape, and as recommended by Dale (1999) to study the spatial pattern of vegetation.

In each quadrat, we estimated the cover (classes: 0%–10%, 10%–25%, 25%–50%, 50%–75%, and 75%–100%) and height (classes: 0–10, 10–40, 40–100, and 100–160 m) of each shrub species. We also sampled the total cover of graminoids, forbs, lichens, *Sphagnum* moss, other moss, and trees (tree species ≥40 cm tall) using the same cover classes. We measured soil pH at a depth of 5 cm using a pH meter (model pH-707 from Tecpel), performing two measurements per plot and sampling every other quadrat.

To assess microtopography, we estimated the proportion of the quadrat occupied by hummocks ( $P_h$ ) and measured the maximum hummock height ( $H_h$ ). In quadrats with more complex topography, we also estimated the proportion occupied by lower ground ( $P_l$ , small depressions in the soil), and measured the maximum depth of the lower ground in relation to the quadrat base level ( $H_l$ , negative value). We calculated the proportion of the quadrat base level as  $P_b = 1 - P_h - P_l$ . We quantified microtopography as the variance in height weighted by the proportion of high, medium, and low ground in each quadrat  $= \sqrt{P_b \times H_a^2 + P_h(H_h - H_a)^2 + P_l(H_l - H_a)^2}$  with the weighted average of the height as  $H_a = H_h \times P_h + H_l \times P_l$ .

### Data analysis

We used the following response variables for the analyses: shrub richness (number of species per plot), maximum shrub height per quadrat, total cover of short (<40 cm tall)

<sup>1</sup>Supplementary material is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/as-2017-0028>. Data are stored in the Polar Data Catalogue, doi:<https://doi.org/10.21963/12947> (Harper et al. 2018).



and medium-height (between 40 cm and 1 m tall) shrubs, cover of the two tallest shrub species (*Salix planifolia* and *Betula glandulosa*), and cover of individual shrub species (see Supplementary Materials 1<sup>1</sup>). Although we also calculated species diversity using the Shannon index, results were very similar to species richness per quadrat, therefore we only present results for species richness. As explanatory variables, we used pH, microtopography variance, and six structural variables: cover of trees, graminoids, forbs, lichens, *Sphagnum*, and other moss. We calculated pH as the mean of the pH measurements per quadrat (for every second quadrat). In all analyses, we only used species and structural elements that were present in at least 10% of the nonwater quadrats for each transect. This criterion excluded *S. planifolia* and *S. candida* in the tundra; and *Myrica gale*, *Rhododendron groenlandicum*, *S. candida*, and *Shepherdia canadensis* in the ecotone. Mid-points were used for the cover and height classes.

We used wavelet analysis to assess the spatial pattern of shrub response variables along the two transects for scales up to 75 m. The highly redundant transformation of the data shows how similar the data are to a wavelet template at contiguous scales of 1, 2, . . . ,  $j$  meters, where  $j$  is the maximum scale of variation in the response variable examined, at each position along the transect (Percival and Walden 2000; Dong et al. 2008; Rouyer et al. 2008; Dodonov 2015). The amount of variation at each scale is calculated by averaging the squared continuous wavelet transform coefficients across all positions for a given scale, resulting in a measure called scale variance (Dale and Mah 1998). Similarly, the amount of variation at each position considering all scales, or position variance, is calculated by averaging the squared coefficients across all scales for a given position. We used the Mexican Hat wavelet, a second derivative of a Gaussian function (Percival and Walden 2000), for scale variance and the Haar wavelet for position variance. The Mexican hat wavelet is symmetric and shows areas with large values (peaks) surrounded by areas with small values, whereas the Haar wavelet is asymmetric and responds better to abrupt transitions (Dale and Mah 1998). Wavelet results are generally unreliable at the limits of the transects because the wavelet template extends outside the transect length. Because of this transects are often artificially extended by adding zeroes to their extremities (Percival and Walden 2000). However, we avoided this issue because the transects began and ended at water bodies and were therefore naturally bounded by zeroes on both sides.

We used generalized least squares to assess whether and how pH and microtopography affect shrub variables; this analysis is similar to linear regression, but accounts for nonindependence among sampling units (Zuur et al. 2009). We used only the quadrats for which we had measured both pH and microtopography. We then adjusted three linear models for each response variable: a null (intercept-only) model, one containing pH and another containing microtopography. All models included a term for spatial autocorrelation, modelled as a first-order autoregressive process, to account for the spatial dependence between nearby quadrats (Zuur et al. 2009). We assessed the significance of each explanatory variable by comparing the corresponding model to the null model (Zuur et al. 2009). We calculated McFadden's pseudo- $R^2$  statistic as  $1 - \log\text{-likelihood (full model)}/\log\text{-likelihood (null model)}$  as well as Pearson's  $R^2$ ; the difference between these two is that Pearson's  $R^2$  does not account for spatial autocorrelation in the response variables.

We used bivariate wavelet analysis with the Mexican hat wavelet to assess the relationship between pairs of variables. In this analysis, the continuous wavelet transform coefficients calculated for two variables are multiplied by one another (Hudgins and Huang 1996). Bivariate wavelet scale covariance is then calculated by averaging the resultant matrix for each scale across all positions (Rosenberg and Anderson 2011). High positive and negative covariance values indicate that two variables have similar and opposite patterns, respectively, at the corresponding scales or positions.

**Table 1.** Location and characteristics (averages  $\pm$  SD) of the tundra and forest–tundra ecotone transects.

	Tundra	Ecotone
Latitude and longitude		
Start	58°43'36.38"N, 93°47'46.45"W	58°43'27.99"N, 93°49'59.83"W
End	58°43'49.32"N, 93°47'41.86"W	58°43'43.94"N, 93°50'5.28"W
Shrub species richness		
Total (No. of species per transect)	15	21
Per quadrat (No. of species)	6.6 $\pm$ 2.07	5.65 $\pm$ 2.94
Maximum shrub height (cm)	16.44 $\pm$ 16.99	47.94 $\pm$ 40.61
Shrub cover (%)		
Short shrubs	43.89 $\pm$ 20.81	63.10 $\pm$ 43.58
Medium-tall shrubs	18.95 $\pm$ 14.86	31.30 $\pm$ 28.25
<i>Betula glandulosa</i>	4.71 $\pm$ 11.50	8.97 $\pm$ 14.79
<i>Salix planifolia</i>	0.61 $\pm$ 5.65	8.00 $\pm$ 16.75
Cover (%) of other plants		
Grasses	15.48 $\pm$ 21.85	21.49 $\pm$ 17.65
Forbs	1.38 $\pm$ 2.60	2.60 $\pm$ 6.38
Lichens	40.12 $\pm$ 30.44	4.75 $\pm$ 10.64
<i>Sphagnum</i>	10.04 $\pm$ 12.94	7.75 $\pm$ 14.13
Other mosses	10.43 $\pm$ 18.94	23.21 $\pm$ 27.45
Trees	0 $\pm$ 0	5.50 $\pm$ 16.04
Range in microtopography (cm)	5.85 $\pm$ 3.01 <sup>a</sup>	5.74 $\pm$ 3.78
Soil pH	6.32 $\pm$ 0.38	6.20 $\pm$ 0.30

Note: Values are for all quadrats along each transect (except for latitude, longitude, and total richness).

<sup>a</sup>Excluding an outlier; the range with the outlier was 6.18 ( $\pm$ 4.09) cm.

We calculated wavelet scale and position variance for the response variables mentioned above (six main ones plus cover of individual species presented in Supplementary Material 1<sup>1</sup>), and scale and position covariance between the response variables and the six structural variables. We used restricted randomizations (Manly 2007) to assess significance under the null hypothesis of random distribution of quadrats throughout our transects. For each transect, we generated 999 random datasets by randomizing the order of the quadrats corresponding to vegetated areas. This differs from full randomizations because we did not randomize between vegetated areas, lakes and ponds, and roads, as such randomizations would not be ecologically meaningful. We calculated one-tailed 95% confidence intervals for wavelet variance and two-tailed 95% confidence intervals for wavelet covariance from the 999 random datasets and the original data (i.e., using a total of 1000 datasets) (Manly 2007; Ruxton and Neuhäuser 2013). Afterwards, we assessed the significant scales of spatial pattern for the different response variables and relationships, and visually related wavelet position variance to the locations of significant landscape features such as lakes or roads.

All analyses were performed in R 3.2.3 (R Core Team 2015) with the nlme package (Pinheiro et al. 2017) for generalized least squares analysis and the wmtsa package (Constantine and Percival 2016) for wavelet analyses. Functions for calculating wavelet position and scale variance and covariance are available at <https://github.com/pdodonov/TimeSeRies>. The full R code and the datasets used for the analyses are available as Supplementary Materials 2 and 3,<sup>1</sup> respectively.

## Results

The tundra transect had a total of 15 shrub species and was characterized by a lack of trees, an average maximum shrub height of only 16 cm, low cover of mosses and shrubs in all height classes, and very high cover of lichens (Table 1; Supplementary Material 1<sup>1</sup> for results for individual species). The ecotone, with a total of 21 shrub species, had a more complex vegetation structure with greater average and variation of cover of the two tallest

shrub species (*B. glandulosa* and *S. planifolia*), tree cover, and maximum shrub height. Soil pH was very similar along both transects. Fine-scale variation in microtopography in the tundra was more consistent compared with the ecotone, with peat mounds (hummocks) uniformly distributed throughout the transect.

#### Spatial pattern of shrubs and other plant types

In the tundra, patches of greater shrub species richness, taller shrubs, short shrub cover, and cover of the two tallest shrub species were prominent next to lakes, whereas patterns for shrub richness and the cover of medium tall shrubs were not consistent (Fig. 2). In the ecotone, patches of greater species richness were often located away from water bodies and there was no apparent pattern in shrub height. Patches of high cover of short and medium-tall shrubs were generally away from water bodies and at the edges of the road. Patches of the tallest shrubs, *B. glandulosa* and *S. planifolia*, were found throughout the transect, including at some but not all lakeshore edges.

Along the tundra transect, abrupt transitions in shrub richness, short shrubs, and *B. glandulosa*, as shown by wavelet position variance, were found next to lakes and between them, but transitions in shrub height and medium-height shrubs were centered between the lakes (Fig. 3). Along the ecotone transect, most variables had abrupt transitions near the ponds and on one side of the lake, but these transitions extended away from the water bodies as well. Overall, in contrast with the tundra, the ecotone was very heterogeneous, with many transitions and changes in shrub species (Supplementary Material 1<sup>1</sup>).

All shrub variables and individual shrub species were clustered at a wide variety of scales in both the ecotone and tundra, up to the maximum scale assessed (results not presented). Significant scales from the wavelet analysis spanned large ranges from <5 m to over 50 m.

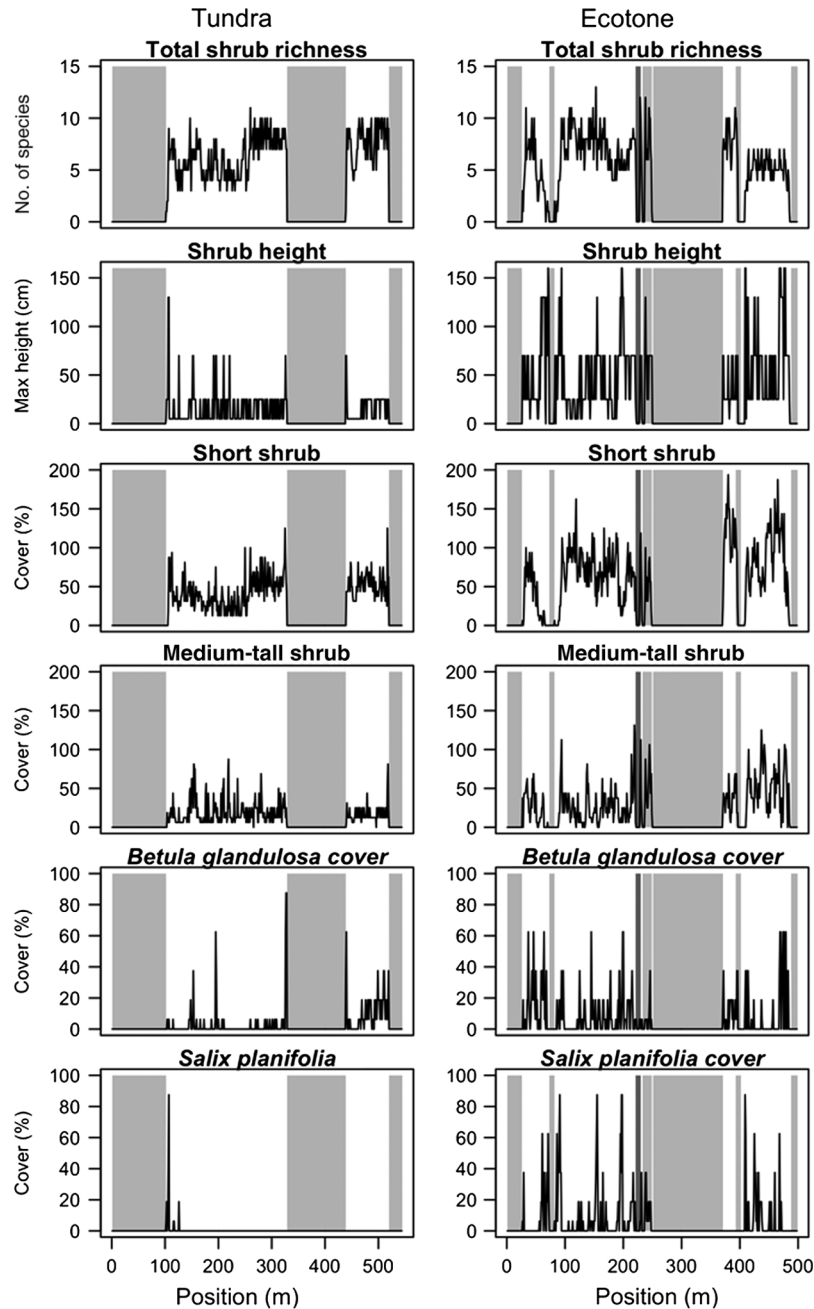
Plant groups also displayed distinct patterns that differed between the tundra and the ecotone (Figs. 4, 5). Moss and sparse tree cover characterized the ecotone transect. Forbs had greater cover and transitions near water bodies along both transects, whereas lichens dominated most of the tundra transect except near the lakes. For the other groups, relationships with edges are not clear; there was much spatial variation in all structural variables, with transitions both near and far from the edges of water bodies.

#### Bivariate relationships between shrubs and explanatory variables

There were very few significant relationships between pH or microtopography and any of the main shrub response variables (Table 2; Table S2 in Supplementary Material 1<sup>1</sup>). For pH, the only significant correlation was with the cover of medium-tall shrubs in tundra with a pseudo- $R^2$  of 0.001. Microtopography was significantly positively correlated with species richness in both the tundra and ecotone with Pearson's  $R^2$  values above 0.1, suggesting that species richness benefits slightly from greater variation in microtopography at the quadrat level. There was also significant positive correlation of short shrubs and microtopography in the tundra.

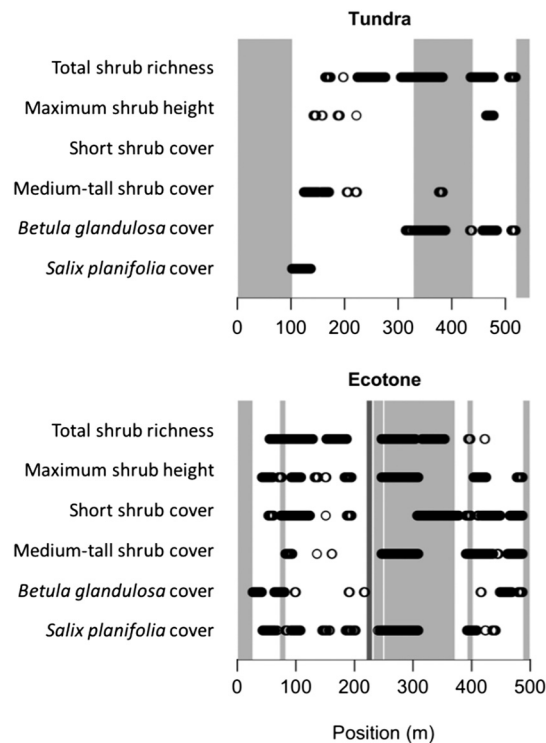
Correlations with other plant groups at different scales, as revealed by bivariate wavelet scale variance, often differed between the tundra and the ecotone (Fig. 6). In the tundra, at very fine scales of 1–2 m, shrub richness was negatively correlated with the cover of graminoids, forbs, and non-*Sphagnum* moss, but positively correlated with lichens. However, broader patches (approximately 4–63 m wide) of high shrub richness also had abundant graminoids, forbs, *Sphagnum*, and other moss (positive bivariate scale covariance), but less lichen cover (negative covariance). Therefore, it appears that in tundra areas with abundant graminoids, forbs, and moss, more shrub species occur in areas with lichens at a fine scale. This trend is reversed again at the greatest scales measured of up to 75 m, with greater richness in broad areas with more lichen.

**Fig. 2.** Trends along the tundra and ecotone transects for shrub species richness, maximum shrub height and cover of short shrubs (species <40 cm height), medium-tall shrubs (species >40 cm and <1 m height), *Betula glandulosa*, and *Salix planifolia*. Grey shading represents locations of water bodies (all lakes in the tundra; lakes: 1–25, 249–370 m, ponds: 71–79, 221–225, 232–234, 397–408, and 485–495 m in the ecotone) and the darker grey shading represents the location of a road. Cover is often >100% because cover of individual species was summed to calculate total amounts for short and medium-tall shrub cover.





**Fig. 3.** Locations of significant transitions as measured by wavelet position variance along the tundra and ecotone transects for shrub species richness, maximum shrub height and cover of short shrubs (species <40 cm height), medium-tall shrubs (species >40 cm and <1 m height), *Betula glandulosa*, and *Salix planifolia*. Grey shading represents locations of water bodies (all lakes in the tundra; lakes: 1–25, 249–370 m, ponds: 71–79, 221–225, 232–234, 397–408, and 485–495 m in the ecotone) and the black line represents the location of a road. Significant change in a variable may occur within a lake when it marks the difference in the values of the variable on both sides of that position at fine or broad scales.

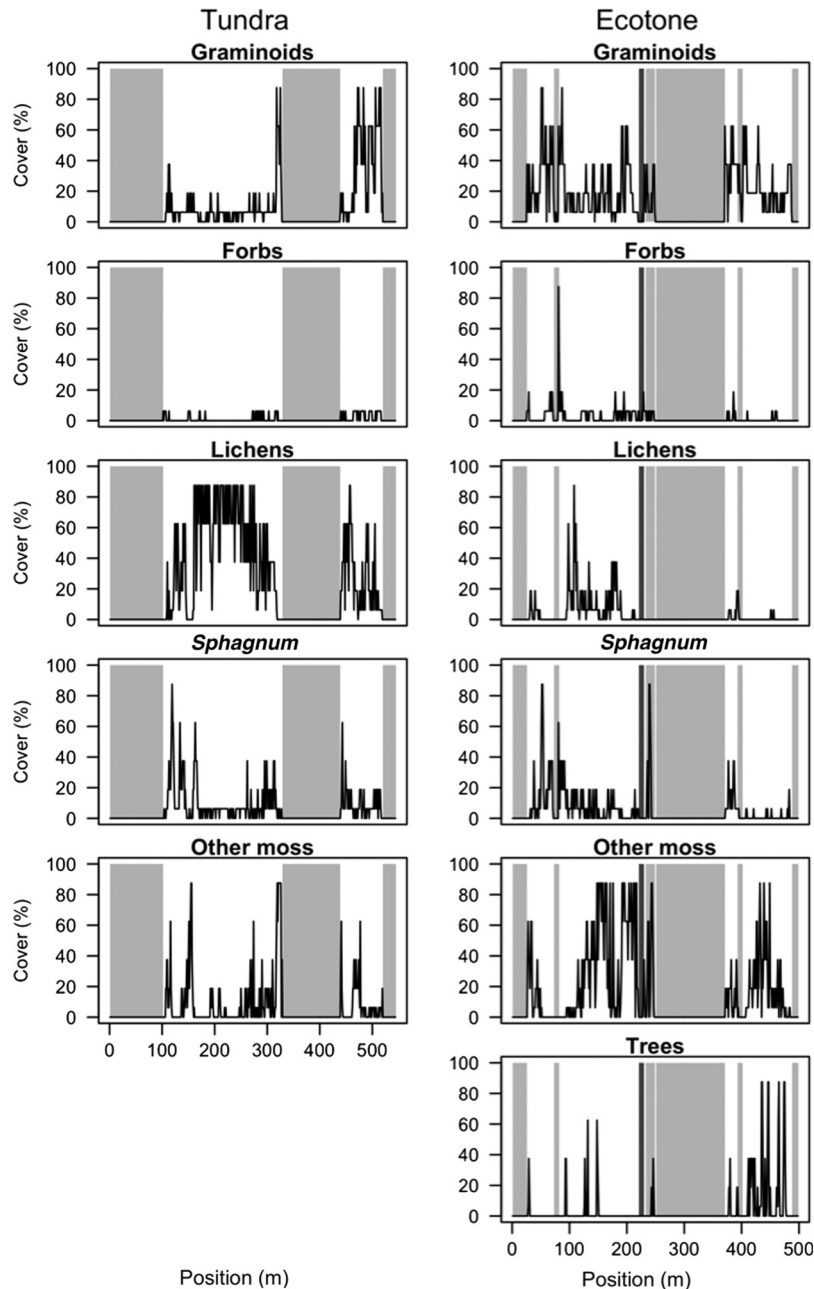


The relationship of shrub richness with other plant groups was quite different in the ecotone. There were more shrub species in areas with more graminoids and forbs but less lichen, *Sphagnum*, and moss within 1–2 m, but with more lichen, moss, and trees and fewer forbs at scales of around 10 m. The correlations of richness with graminoids, forbs, and lichens were reversed in the ecotone compared with the tundra.

Correlations between shrub height and plant groups were more similar between the tundra and the ecotone (Fig. 6). At the quadrat level, taller shrubs were found with greater cover of lichen and *Sphagnum* (tundra only) and lower cover of other moss. Graminoids and forbs were positively correlated and lichens were negatively correlated with shrub height at moderate scales. Some of these trends were reversed at broader scales of over 50 m. The main difference between tundra and ecotone was the relationship with tree cover in the ecotone, which was negatively associated with shrub height at a scale of 1 m, but positively associated at slightly greater distances.

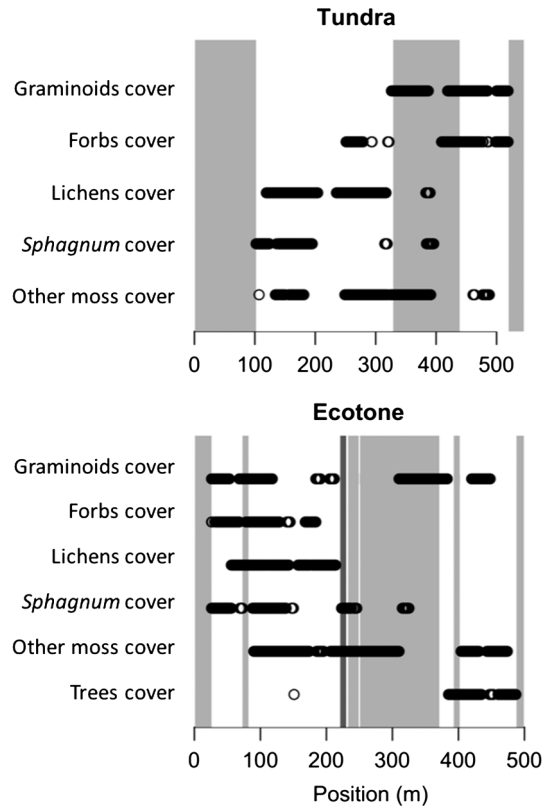
The results of bivariate scale variance for short and medium-height shrubs illustrate complex relationships at more scales in the ecotone (Fig. 6). In the tundra, at very fine scales of 1–3 m, short shrubs were negatively correlated with graminoids, forbs, *Sphagnum*, and other moss but positively correlated with lichens, whereas medium-tall shrubs were positively correlated with both lichens and *Sphagnum*, and negatively correlated with other

**Fig. 4.** Trends along the tundra and ecotone transects for the cover of plant functional types including graminoids, forbs, lichens, *Sphagnum*, other moss, and trees. Grey shading represents locations of water bodies (all lakes in the tundra; lakes: 1–25, 249–370 m, ponds: 71–79, 221–225, 232–234, 397–408, and 485–495 m in the ecotone) and the black line represents the location of a road.



moss. All of the correlations were reversed for moderate scales with the additional negative correlations between medium-tall shrubs and graminoids and forbs. Results were surprisingly different in the ecotone with positive correlations of short and medium-tall shrubs with graminoids, forbs, and *Sphagnum*, and negative correlations with lichens, other moss,

**Fig. 5.** Locations of significant transitions as measured by wavelet position variance along the tundra and ecotone transects for the cover of plant functional types including graminoids, forbs, lichens, *Sphagnum*, other moss, and trees. Grey shading represents locations of water bodies (all lakes in the tundra; lakes: 1–25, 249–370 m, ponds: 71–79, 221–225, 232–234, 397–408, and 485–495 m in the ecotone) and the black line represents the location of a road. Significant change in a variable may occur within a lake when it marks the difference in the values of the variable on both sides of that position at fine or broad scales.



and trees (only with trees for medium-tall shrubs) at very fine scales. Opposite correlations occurred at broader scales but these started at 4–23 m and often reversed again such that correlations were different at 4–10, 10–25, and 25–50 m in the ecotone, indicating complex interactions at multiple scales.

Correlations of structural variables with the two tallest shrubs, *B. glandulosa* and *S. planifolia*, were also more complex at multiple scales in the ecotone compared with the tundra (Fig. 6). In the tundra, *B. glandulosa* was generally found in quadrats with more lichen and *Sphagnum*, and fewer graminoids, forbs, and other mosses. These correlations were reversed at more moderate scales except for *Sphagnum*. Correlations with both taller shrubs were complex in the ecotone and difficult to summarize concisely because they differed at several scales. One notable feature for *B. glandulosa* was the lack of significant correlations at the quadrat level. Both taller shrubs had correlations at different ranges of scales, which often differed from the tundra.

## Discussion

The forest–tundra ecotone landscape mosaic near Churchill was dominated by a heterogeneous shrub layer, which exhibited spatial variation at different scales. At a fine scale

**Table 2.** Results with  $p$ -values for correlations (Pearson's  $R^2$ /McFadden's pseudo  $R^2$ ) of microtopography and pH with shrub species richness, maximum shrub height and cover of short shrubs (species <40 cm height), medium-tall shrubs (species >40 cm and <1 m height), *Betula glandulosa*, and *Salix planifolia* for the tundra and ecotone transects.

	Tundra		Ecotone	
	Microtopography	pH	Microtopography	pH
Shrub species richness	0.1090/0.0009*	0.0323/0.0051	0.1630/0.0025*	0.0436/0.0019
	$p = 0.02$	$p = 0.10$	$p = 0.04$	$p = 0.68$
Maximum shrub height	0.0001/0.0002	0.0263/0.0058	0.0021/0.0010	0.0094/0.0047
	$p = 0.82$	$p = 0.10$	$p = 0.79$	$p = 0.41$
Short shrubs	0.1120/0.0106*	0.0002/0.0435	0.0220/0.1391	0.0002/0.0470
	$p = 0.004$	$p = 0.79$	$p = 0.71$	$p = 0.94$
Medium-tall shrubs	0.0081/0.0622	0.0371/0.0008*	0.0014/0.2481	0.0119/0.0905
	$p = 0.53$	$p = 0.03$	$p = 0.34$	$p = 0.64$
<i>Betula glandulosa</i>	0.0000/0.0337	0.0079/0.0202	0.0003/0.0588	0.0023/0.0250
	$p = 0.27$	$p = 0.67$	$p = 0.83$	$p = 0.58$
<i>Salix planifolia</i>	N/A	N/A	0.0009/0.0635	0.0251/0.0087
			$p = 0.55$	$p = 0.09$

\*Significant correlations at  $\alpha = 0.05$ .

**Table 3.** Summary of results organized by objective.

	Tundra	Ecotone
Patterns across edges of water bodies	<ul style="list-style-type: none"> <li>• Peaks in shrub richness, tall shrubs, short shrubs next to lakes; inconsistent patterns for shrub richness, medium shrubs</li> <li>• Abrupt transitions in richness, short shrubs, <i>Betula glandulosa</i> next to and between lakes, in height and medium shrubs between lakes</li> </ul>	<ul style="list-style-type: none"> <li>• Peaks in species richness, short and medium shrubs away from water bodies; inconsistent patterns for height; peaks in tall shrubs throughout the transect</li> <li>• Abrupt transitions near water bodies</li> <li>• Greater heterogeneity than in the tundra with significant patterns at a variety of scales</li> </ul>
Relationships with pH and microtopography	<ul style="list-style-type: none"> <li>• pH only significant for medium shrubs with extremely low <math>R^2</math></li> <li>• Microtopography positively correlated with species richness and short shrubs</li> </ul>	<ul style="list-style-type: none"> <li>• No relationships with pH</li> <li>• Microtopography positively correlated with species richness</li> </ul>
Relationships of shrubs with other plant types at different scales	<ul style="list-style-type: none"> <li>• Mostly negative relationships with lichens (except for large scales)</li> <li>• Mostly positive relationships with forbs and graminoids</li> <li>• Various scale-dependent relations with <i>Sphagnum</i> and other moss</li> </ul>	<ul style="list-style-type: none"> <li>• Various scale-dependent relationships with graminoids, forbs, lichens, and <i>Sphagnum</i></li> <li>• Mostly positive relationships with other moss and trees</li> </ul>

(i.e., within 1 m quadrats), shrubs were correlated with most other plant types but showed little relationship with pH or microtopography. At a slightly greater scale (approximately 4–10 m), shrubs often exhibited the opposite correlations with other plant types, and were affected by proximity to water bodies. Different relationships at different scales suggest complex relationships between shrubs and other plant types, leading to a more heterogeneous landscape, which could then result in more microhabitats for other organisms. We found differences in patterns of shrubs and especially in relationships with other plant types between the tundra and the ecotone (Table 3). Herein, we discuss patterns of shrubs at edges, effects of pH and microtopography, relationships with other groups of plants, and differences between tundra and ecotone shrub communities to infer potential changes caused by shrub encroachment in a warming environment.





The advantage of the wavelet analysis approach is that it assesses scales of pattern and detects locations at which species vary and are positively or negatively associated with other species (or other variables). However, we acknowledge the obvious limitations of sampling only one transect each in the tundra and ecotone. Intensive sampling along one or a few transects is inherent to the wavelet analysis approach and to spatial pattern analysis in general (e.g., [Brosofske et al. 1999](#); [Keitt and Urban 2005](#); [James et al. 2010](#); but see [Bradshaw and Spies 1992](#)). However, a very small sample size is unavoidable with this type of sampling, making it difficult to generalize; indeed we know of few studies that use transects as replicates for spatial pattern analysis (but see [Harper et al. 2006](#)). Although our transect locations matched a priori criteria and are representative of some of the variation in the landscape, it is difficult to find any location that could be considered truly representative because of the heterogeneity at multiple scales. Therefore, it should be noted that our results and their interpretation should be considered as more of an inductive approach to generate hypotheses rather than a deductive approach to test hypotheses that could be applied to a broader area.

Some of the patterns indicated by the raw data were not detected in the univariate wavelet analysis. For example, wavelet analysis detected visible peaks in shrub species richness and shrub height bordering lakes in the tundra at only one lake for species richness and none for shrub height. Still, this analysis demonstrated more heterogeneous shrub cover in the ecotone than in the tundra. The most informative results, however, come from bivariate scale variance, which provided insight into the relationships between shrubs and other plant groups at different scales, including differences between the tundra and ecotone transects.

#### **Patterns of shrubs in the forest–tundra ecotone**

We found greater shrub species richness at the edges of all lakes in the tundra, similar to previous studies ([Ehrich et al. 2012](#); [Henden et al. 2013](#)), but at the edges of only some water bodies in the ecotone. Flat open landscapes in the Arctic and subarctic regions have lower plant species richness because of harsher environmental conditions such as increased wind exposure and soil erosion ([Britton 1966](#)). Proximity to edges of water bodies may serve as a proxy variable for soil moisture level, which might explain greater shrub species richness in those areas if water is a limiting resource ([Valentin et al. 1999](#)), as increased moisture may lead to greater productivity and consequently greater cover and height of shrubs at lakeshore edges ([Ehrich et al. 2012](#); [Henden et al. 2013](#)). The transition between lakeshore and upland habitats may also offer more microhabitats, with different levels of moisture or nutrient availability, for a greater number of shrub species.

The pattern of most shrub variables did not seem to be affected by the presence of the road in the ecotone except for greater cover of medium-tall shrubs, particularly *S. lanata*. Increased soil moisture due to soil compaction from vehicle disturbance in the linear corridor could affect shrub spatial patterns in a similar manner as near the edges of water bodies. However, the road was on higher ground so was probably drier than the surrounding vegetation and the proximity of the road to water bodies would have masked edge influence from the created edge. Further study focusing on created edges from linear corridors could examine possible effects in more detail. For example, [Gill et al. \(2014\)](#) found increased growth of *Alnus* next to gravel roads on tundra sites in the Northwest Territories accompanied by less understorey and higher nutrient availability.

#### **Relationships of shrubs with pH, microtopography, and other plant types**

We found virtually no effect of pH on shrubs and only a slight effect of microtopography on shrub richness. The range in pH might have been too small to detect significant effects

on shrubs. However, it is interesting to note that the highest value in the ecotone (6.8) was at the road edge, likely due to limestone gravel. pH has been found to be an important factor in determining species richness of vascular plants, bryophytes, and lichens in dwarf shrub-dominated tundra (Gough et al. 2000), and in a dry grassland in Sweden (Löbel et al. 2006). Löbel et al. (2006) also found greater vascular plant species richness in plots with more microtopographic variation, similar to our results. Greater microtopographic variation, caused by low depressions and hummocks, allows for a variety of shrub species to colonize and grow as some species prefer to grow on the drier hummocks, whereas others prefer lower wetter areas (Bergkamp 1998). In regions of low microtopographic variation with flat ground, water infiltration into the soil is uniform and fewer species occupy the landscape (Bergkamp 1998). In Churchill, Gamon et al. (2012) found that elevation on a slightly greater scale affected the pattern of vegetation cover on a high-centered polygon.

Plant–plant interactions are important in determining species distributions and biodiversity in Arctic ecosystems (le Roux et al. 2013) but effects differ among taxa (Mod et al. 2016). At the finest 1 m scale, we found evidence of competition in the tundra shown by negative correlations of shrub richness, short shrubs, and *B. glandulosa* with graminoids, forbs, and moss. In contrast, more shrub species, taller shrubs, and greater cover of shrubs of all heights were often found in quadrats with more lichen and sometimes *Sphagnum*, suggesting a facilitative effect of shrubs on lichens, perhaps by outcompeting grass, forbs, and moss. These results are surprising and may reveal novel interactions between shrubs and other plant types at finer scales than assessed in previous studies. In other ecotone and tundra landscapes, shrubs have been found to shelter other vascular plants such as forbs and shade out lichens (Pajunen et al. 2011, 2012; Fraser et al. 2014; Mod et al. 2016). In the absence of trees, shrubs may facilitate lichens at very fine scales because of greater soil moisture with shading; alternatively, cause and effect may also be reversed with an increase in shrub cover because of water retention from *Sphagnum* and lichens. It is important to note that most shrubs in the tundra were either prostrate or short shrubs (generally up to 40 cm in height). Although we did not measure soil moisture, about half of the tundra transect and most of the ecotone transect was wet. Further research at fine scales would determine if this effect is site-specific or more widespread and would be able to address the discrepancies in results among studies.

Our results from the ecotone, where there are patches of trees and taller shrubs, are more consistent with results from other studies. More shrub species and greater shorter shrub cover were associated with greater cover of graminoids and forbs but lower cover of lichens and non-*Sphagnum* mosses at a fine scale. Shrub expansion has been linked to declines in lichen abundance with warming or nutrient addition, although not consistently (Chapin et al. 1995; Elmendorf et al. 2012; Fraser et al. 2014). The reversal from a positive association between shrubs and lichens in the tundra to a negative association in the ecotone provides additional evidence for the hypothesis that shrubs will outcompete lichens with warming (Fraser et al. 2014), as the landscape changes from tundra to ecotone and as taller shrubs replace shorter prostrate ones.

In the ecotone, negative correlations of trees with shrub height and short and medium-tall shrubs at a fine scale indicate that trees likely outcompeted shorter shrubs through shading. This interaction appears to have a cascading effect on correlations of shrubs with other plant types, which were often opposite to the patterns observed in the tundra. There may also be an effect of trees outcompeting graminoids and forbs as shrubs were more commonly found with graminoids and forbs.

Bivariate relationships at broader scales likely indicate mutual or opposite optimal environmental conditions. At scales of approximately 4–50 m in the tundra, more shrub species, taller shrubs, and greater cover of shrubs of all sizes were associated with areas of

greater cover of most plant groups except for lichens. Fewer shrub species and shorter shrubs were found in lichen-dominated tundra areas away from lakes, perhaps because conditions that favour shrubs at lake edges also inhibit lichens. These broader scale relationships, which were also detected by [Mod et al. \(2016\)](#), appear to be more important for general trends in tundra such as decreases in lichen cover that sometimes accompany increases in shrub cover in the western Canadian Arctic ([Fraser et al. 2014](#)).

In the ecotone, reversals in bivariate correlations occurred at multiple scales. For example, greater shrub species richness was associated with greater cover of most plant groups except for forbs at scales of approximately 4–15 m, but only with greater moss cover at a scale of approximately 25 m. It is difficult to interpret relationships at these different scales, but we believe that the complexity at multiple scales is due to the addition of trees in the ecotone, which appears to greatly affect relationships between shrubs and other plant groups. Trees positively affected the number and height of shrub species in nearby areas (approximately 4–10 m), perhaps due to protection from wind and snow.

#### Differences in patterns and relationships between the tundra and ecotone

Differences between the tundra and the ecotone transects can provide some insight into changes that will occur with climate warming. In Churchill, many tree seedlings in the forest–tundra ecotone landscape have the potential to change the vegetation ([Mamet and Kershaw 2012](#)), which may be mediated through effects on shrubs. As trees encroach into shrub-dominated tundra, they may facilitate shrub growth by alleviating stress from wind, increasing habitat complexity, and providing novel microhabitats ([McIntire and Fajardo 2014](#)), leading to a more complex shrub layer with variable height and greater species richness. However, such facilitative effects may be accompanied by competition from trees in small patches, which will depend on the life history of shrub species including shade tolerance. Less harsh conditions in the ecotone appear to favour not only the establishment of patches of trees, but also the dominance of tall shrubs in all microhabitats. *Betula glandulosa* was found in only scattered patches in lakeshore and upland areas in the tundra, but both tall shrubs (*B. glandulosa* and *S. planifolia*) were prevalent throughout the ecotone.

The presence of clumps of trees led to differences in shrub patterns between the tundra and ecotone. At a broad scale, shrub richness and composition were more homogeneous across the tundra with less variation in shrub cover and height compared with the ecotone. Tundra vegetation is evenly distributed at predictable scales, such as in a repeated pattern of hummocks of similar size and height that we observed, unless affected by proximity to edges or disturbance. The more heterogeneous shrub layer in the ecotone may be due to the more complex vegetation structure with patches of trees and tall shrubs. The pattern of shrubs at lakeshore edges may be changed by the presence of trees and taller shrubs near the edges of some water bodies in the ecotone, which likely prevented the establishment of numerous shrub species and kept shrubs shorter.

One of our key findings is the dramatic contrast in the results of the bivariate relationships of shrubs and other groups of plants between the tundra and the ecotone. Positive correlations of shrub richness, productivity, and abundance at fine scales with lichens in the tundra but with graminoids and forbs in the ecotone, and the reversal of these trends for moderate scales, are likely due to the presence of trees. Clumps of trees in the ecotone may replace shrubs as the dominant vegetation that outcompete other groups of plants. Scattered trees increase heterogeneity in the ecotone, leading to more complex relationships of shrubs with other plant groups at multiple scales.

Shrub species with heterogeneous patterns of patches in a variety of environmental conditions may be more adaptable to further environmental changes associated with climate change in the subarctic. Taller shrub species such as *Betula* and *Salix* are predicted to expand

into most tundra regions (Blok et al. 2011). Expansion of these tall shrubs in addition to the establishment of trees will then lead to competitive or facilitative interactions with shorter shrubs and other plant types at a fine scale, modifying the spatial structure.

Our study of a single long transect in each of the tundra and ecotone landscapes was designed to elucidate differences in shrub patterns and therefore changes that might occur with climate warming. From our results, we hypothesize that as trees encroach into tundra habitat in Churchill with climate warming, shrubs will (1) become taller and form a dominant layer with more species, (2) develop a more complex pattern with transitions in all parts of the landscape and not just at lakeshore edges, and (3) have more complex relationships with other plant groups at multiple scales. The end result will be more complex vegetation structure in the ecotone as the landscape changes from tundra to forest; however, the dynamic nature of the transition may result in lag and other transient effects. This increase in heterogeneity could be beneficial for diversity and habitat, but may be short lived with increased shrub densification (Ropars et al. 2015). Patterns of shrub distributions appear to be influenced by proximity to water bodies and by microtopography in both habitats, and by tall shrub cover in the tundra and tree cover in the ecotone. It is important to understand the role of these biotic interactions for modelling impacts to climate change (Mod et al. 2016). Our study reveals differences between tundra and ecotone landscapes at different scales, factors which may contribute to our understanding of adaptations of plants to climate change. Further study on the change in shrub patterns over time using long-term monitoring would be beneficial for understanding ongoing changes to Canadian subarctic landscapes as tree density increases in the forest–tundra ecotone.

### Conflicts of interest

The authors have no conflicts of interest to report.

### Acknowledgements

We would like to thank Danielle St. Louis for her field assistance, LeeAnn Fishback and other staff members of the Churchill Northern Studies Centre for their assistance, Peter Kershaw for advice on sampling design and the study site, and Natasha Dazé-Querry for her assistance preparing the manuscript. Funding and logistical support were provided by the Churchill Northern Studies Centre, the Strategic Cooperative Education Incentive, Natural Sciences and Engineering Research Council of Canada, and the Northern Scientific Training Program in Canada; the Emerging Leaders in the Americas Program; and the Coordination for Improvement of Higher Education Personnel in Brazil.

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