



Leading-edge disequilibrium in alder and spruce populations across the forest–tundra ecotone

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Abstract. The distribution and composition of Arctic vegetation are expected to shift with ongoing climate change. Global models generally predict northward shifts in high-latitude ecotones, and analysis of remote sensing data shows widespread greening and changes in vegetation structure across the circumpolar Arctic. However, there are still uncertainties related to the timing of these shifts and variation among different plant functional types. In this paper, we investigate disequilibrium dynamics of green alder and white spruce in the Tuktoyaktuk Coastal Plain, NWT. We used high-resolution air photographs captured in the 1970s and 2000s to quantify changes in the distribution and abundance of alder and spruce near their northern limits. We found increases in alder and spruce stem density over time, but no change in their range limits, indicating that both species are affected by leading-edge disequilibrium. Low stand density and temperature limitation of reproduction along the northern margin likely contributed to observed disequilibrium in both species. We also observed the greatest change in species occupancy within a burned area, suggesting that the increased frequency of fire will play a significant role in the timing and magnitude of near-term vegetation change.

Key words: air photographs; range limits; shrubline; spatial pattern; sub-Arctic; treeline; tundra; climate change.

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INTRODUCTION

Climate change is altering the distribution and structure of global vegetation, and many species are exhibiting shifts toward higher elevations and latitudes (Hickling et al. 2006, Chen et al. 2011). Across the circumpolar Arctic, surface air temperatures are warming at twice the global average (Taylor et al. 2017), and trends in the Normalized Difference Vegetation Index (NDVI) indicate widespread increases in productivity (Karlsen et al. 2014, Pattison et al. 2015). These broadscale greening trends have been corroborated by analysis of repeat photography and vegetation surveys, which show increases in the cover and density of upright shrubs and

graminoids and decreases in moss and lichen (Elmendorf et al. 2012, Fraser et al. 2014, Myers-Smith et al. 2015, Moffat et al. 2016). Tree density in the sub-Arctic forest has also increased in some regions (Miller et al. 2017, Lantz et al. 2019), but many latitudinal treelines have been stable, exhibiting a slower climate response than other northern vegetation types (Payette and Filion 1985, Scott et al. 1987, Gamache and Payette 2005, Wilmking et al. 2012, Brown et al. 2018, Lantz et al. 2019).

Monitoring shifts in the structure and composition of northern plant communities is important because these changes are likely to drive climate feedbacks in association with decreased albedo and increased net solar radiation and

near-surface ground temperatures (McGuire et al. 2002). Differences in the magnitude of climate feedbacks among plant functional types highlight the need for fine-scale investigations (Chapin et al. 2005, Lorant et al. 2011). Global vegetation models often assume equilibrium between climatic conditions and vegetation distribution, generally forecasting northward shifts in vegetation in association with warming (Pearson et al. 2013, Paulson and Körner 2014). However, several lines of evidence suggest that the range of some sub-Arctic plant species have not shifted with recent climate change, and are thus exhibiting aspects of leading-edge disequilibrium (Kanbo and Danby 2017, Brown et al. 2018, Timoney et al. 2019, Lantz et al. 2019).

Leading-edge disequilibrium (LED) occurs when changes in the composition and distribution of vegetation communities lag behind changes in climate (Svenning and Sandel 2013). This process results in communities that contain only a fraction of the species that could be supported under the given climate conditions (Webb 1986). Disequilibrium can occur due to slow vegetation growth, low seedling survival, limited seed dispersal (Kanbo and Danby 2017, Brown et al. 2018, Kruse et al. 2019), herbivory (Jameson et al. 2015), and competition with established species (Urban et al. 2012). Variations in the timing of LED also differ according to plant functional type and terrain conditions (Bertrand et al. 2011). Understanding the duration and timing of lagged responses is therefore critical to accurately predict the timing and magnitude of near-term vegetation change.

In this paper, we evaluate the magnitude of LED in green alder (*Alnus viridis* subsp. *fruticosa* (Ruprecht) Nyman) and white spruce (*Picea glauca* (Moench) Voss) in the Tuktoyaktuk Coastal Plain by assessing changes in the distribution and abundance of these species across a latitudinal gradient. Recent studies indicate that these species are responding differently to regional climate change. While the growth of alder and other deciduous shrubs has increased rapidly within the past decade (Lantz et al. 2013, Myers-Smith et al. 2015, Moffat et al. 2016), the spruce treeline has not shown significant movement (Lantz et al. 2019). Specifically, we test whether alder and spruce stem density has increased since the 1970s and determine if the range of

both species has expanded. To accomplish this, we used high-resolution air photographs to model the probability of alder and spruce occurrence. We also used these data to compare dispersal limitation by quantifying spatial point patterns of alder and spruce recruits.

METHODS

Study area

Our study area in northwestern Canada (Fig. 1) is located within the Tuktoyaktuk Coastal Plain Ecoregion (ECG 2012). This region is characterized by gently rolling terrain dotted with thousands of small lakes (Burn and Kokelj 2009). Permafrost soils are ice-rich and thermokarst features including thermokarst lakes, pingos, thaw slumps, and ice wedge polygons are common (Burn and Kokelj 2009, ECG 2012). The Tuktoyaktuk Coastal Plain includes two ecotones: (1) the transition from a landscape dominated by spruce woodland to upright shrub tundra (Timoney et al. 1992) and (2) the transition from upright shrub tundra to tundra dominated by sedges or prostrate shrub and lichens (Lantz et al. 2010).

Climate

Across the study area, monthly average temperature is below 0°C for up to nine months of the year (Environment Canada 2019). Average annual temperature from 1970 to 2016 was −9.2°C and −8.6°C at Tuktoyaktuk (69°26′ N, 133°01′ W) and Inuvik (68°18′ N, 133°29′ W), respectively. During the short summer, there is a latitudinal temperature gradient across the study area decreasing at a rate of ~3.1°C per degree of latitude (Lantz et al. 2010). We used data from Inuvik and Aklavik (68°13′ N, 135°00′ W) to calculate regional trends in air temperature from 1926 to 2019. These data comprise the longest continuous monthly temperature record in the Beaufort Delta region. This analysis shows that mean annual air temperature and mean summer air temperature have warmed by 3.5° and 1.9°C, respectively (Fig. 2).

Data sources

Fine-scale air photographs.—Grayscale air photographs captured in July 1972 (1:12,000) and in

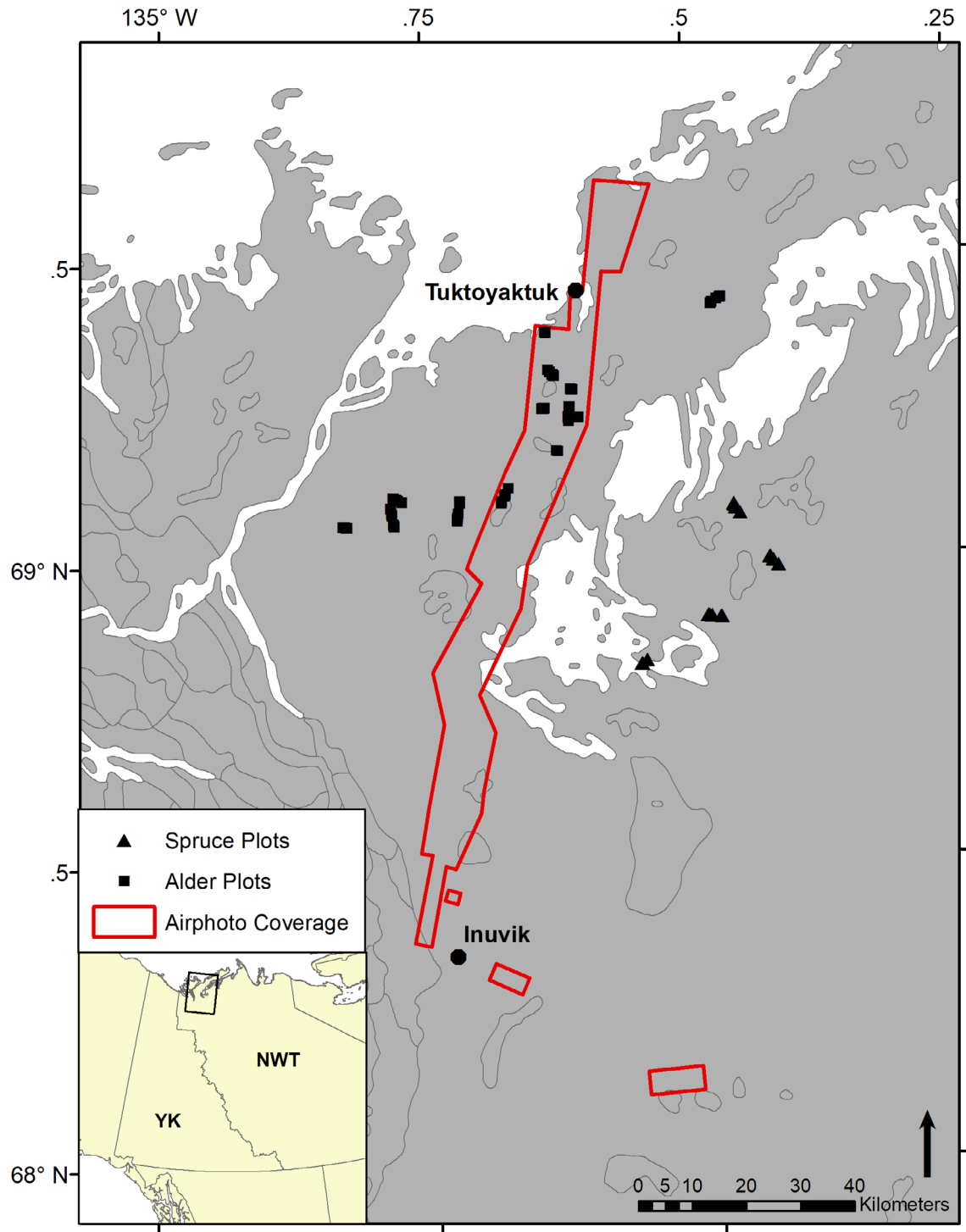


Fig. 1. Map showing the study area within the Tuktoyaktuk Coastal Plain. The boxes on the map show the extent of the fine-scale air photographs. Symbols indicate where ultra-high-resolution repeat photographs were used to estimate changes in spruce and alder stem density and to quantify spatial point patterns. The inset shows the study area within the Western Canadian Arctic.

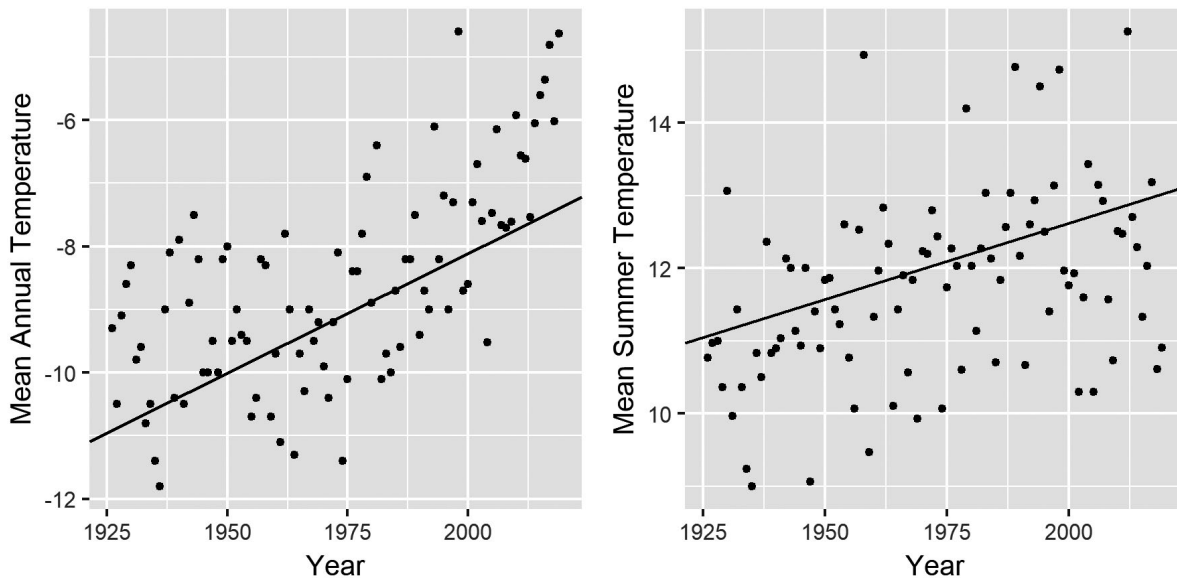


Fig. 2. Mean annual (left) and summer (right) air temperature records using Inuvik–Aklavik composite data from 1926 to 2019. The solid lines show the Theil–Sen regression slope. Mean annual temperature and mean summer temperature both show significant ($P < 0.05$) increasing trends. Temperature data are from Environment Canada and can be obtained at http://climate.weather.gc.ca/historical_data/search_historic_data_e.html.

July 1984 (1:20,000) were used to map the historic extent of spruce and alder across the study area. Images along five flight lines were acquired from the National Air Photo Library (NAPL), forming a 170-km transect stretching from approximately 68.1° N to 69.6° N (Fig. 1). The 1972 air photographs cover the majority of the study area from 68.1° N to 69.45° N, and images from 1984 covered a small zone in the northern part of the study area (~69.45–69.6 N). Air photographs were georeferenced in ArcMap 10.3.1 using first- and second-order polynomial transformations and 2004 color orthophotographs as a reference (1:30,000; Northwest Territories Centre for Geomatics). These color orthophotographs were also used to map the range of spruce and alder in 2004.

Ultra-high-resolution image pairs.—Ultra-high-resolution historic and modern air photographs were used to estimate changes in green alder and white spruce stem density and to quantify the spatial pattern of these populations. Historic air photographs were captured in false-color infrared between August 6th and 8th, 1980 using a Vinten 492 S/N camera (Sims 1983, Moffat et al. 2016). These images were recaptured using a Nikon D7000 camera mounted to a Bell 206 Long

Ranger helicopter (Fraser et al. 2014, Moffat et al. 2016). The modern images used to map spruce were acquired on 30 June 2015, while images used to map alder were recaptured between August 7th and 8th, 2013. The spatial resolution of the historic and modern image pairs was ~2–4 cm (Moffat et al. 2016). Average RMS error for photograph pairs used to map alder was 0.24 m (range 0.0062–0.74 m; Moffat et al. 2016), and RMS error for spruce photograph pairs was 0.52 m (range 0.08–1.22 m; Lantz et al. 2019).

Analysis

Fine-scale species distribution.—The distribution of spruce and alder across the study area was characterized by randomly selecting 1200 plots within the extent of the fine-scale air photographs (Fig. 1). These circular plots were 200 m in diameter and were separated by at least 100 m. We excluded plots that fell within lakes or streams or gaps in the air photographs (fiducial marks, etc.), and after deletions, 1012 plots remained. Each plot was visually inspected for the presence or absence of alder and spruce using photograph brightness, texture, context, and shadow. Alder was distinguished by its uniformly

dark, spherical crown, and short circular shadow, while spruce was identified by a lighter and more diffuse crown and a long pyramidal shadow (Fig. 3). Detectability was comparable between historic and modern images, and the resolution of the images allowed us to confidently identify large individuals. Detectable alder crowns were approximately 1 m across, and spruce shadows were approximately 10 m in length. This sampling was repeated within the same plots on both historic (1972 and 1984) and modern (2004) air photographs.

Data from both species and time periods were used to model the probability of species

occurrence as a function of latitude in R using logistic regression and the logit link function (R Core Team 2017). We excluded plots from the model that fell within an area impacted by a large fire that burned the vegetation in 1968 (Wein 1976, Landhäusser and Wein 1993), and only modeled alder above the forest–tundra boundary (68.45° N), as understory alder is obscured by forest cover. From the original 1200 plots, the spruce models used data from 934 plots, while the alder models used data from 853 plots. We used the likelihood ratio test to determine if the latitude variable improved model fit over an intercept-only model. We

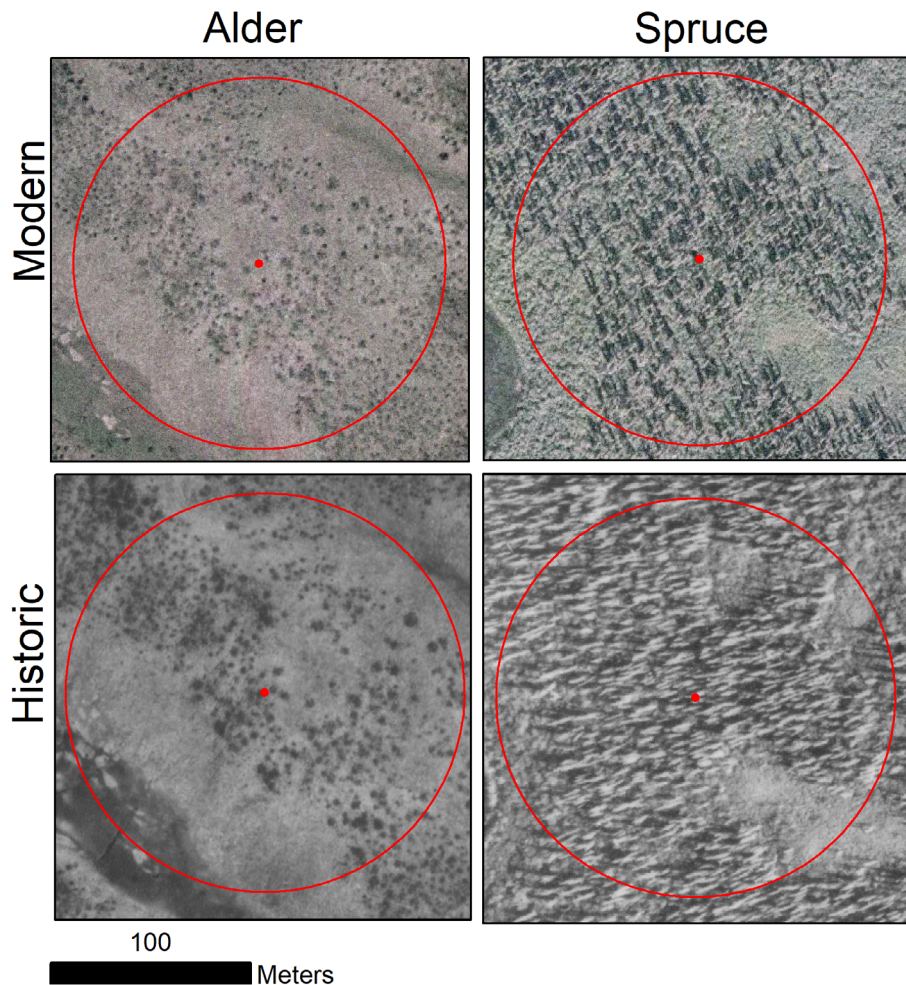


Fig. 3. Fine-scale air photographs from 2004 (top row) and 1972 (bottom row) used to assess the presence or absence of alder and spruce within 31415-m² plots. Alder (at left) was identified by its dark and spherical appearance, while spruce (at right) is distinguished by its light color and conical shadow.

assessed model fit using the standardized Pearson test for ungrouped data with the LogisticDx package in R (Dardis 2015). For each species, we also tested for significant differences between the slope and intercept parameters of historic and modern models.

Change in stem density.—Using the smaller dataset of ultra-high resolution image pairs we quantified changes in the density of alder and spruce by manually delineating the number of stems within circular plots with a 15 m radius (706 m²; Fig. 1). Alder stem density was mapped within 72 plots across three transects, and spruce density was mapped in 52 plots across four transects using the same criteria for mapping on the fine-scale air photographs (Fig. 3). Transects were organized by latitude, and plots were randomly located in areas that had either alder or spruce cover in 1980. Nonparametric Wilcoxon signed-rank tests were used to assess whether the median change in total stem count from 1980 to 2014 was significantly different from 0 for each transect (adjusting the *P*-value for multiple comparisons).

Accuracy assessment of ultra-high resolution mapping.—To assess the accuracy of fine-scale mapping using air photographs, we compared stem maps generated from the air photographs with field surveys. In 2016, we validated spruce mapping at eight sites using 706-m² plots. In 2019, we surveyed five alder sites using 314-m² plots. Smaller alder plots were used because the higher density of shrubs limited the extent of surveys we could complete at remote sites. Field surveys of alder were compared to photographs captured in 2015, which had the same spatial resolution as the 2013 images used in our analysis. Image quality and resolution were consistent between historic and modern images; thus, we are confident that the mapping error did not affect the overall direction of change. In each plot in the field, we mapped all visible alder and spruce crowns and recorded their height. Overall accuracy was calculated as the proportion of all plants correctly identified in the both the field and photographic mapping.

Spatial pattern and recruitment.—Ultra-high-resolution images also provided an opportunity to examine spatial point patterns, which can provide insight into the role of resource competition and seed dispersal (Chapin et al. 1989, Leps 1990,

Kruse et al. 2019). To quantify the spatial arrangement of spruce and alder stems, we calculated the Average Nearest Neighbor (ANN) index for each species using stem maps derived from ultra-fine-scale air photographs using Arc-Map 10.3.1. This index is based on the average distance between each point and its nearest neighboring point (Diggle 1983). We calculated the expected ANN index for each plot assuming a completely random pattern and compared this to the observed index assuming a standard normal distribution (Diggle 1983). To determine whether the point pattern within each plot was significantly dispersed, clustered, or random, a *z*-test was used to compare the observed and expected values of the ANN index at the *P* < 0.05 level for each plot, after controlling for the false discovery rate using the *fdr* method in R (Benjamini and Hochberg 1995). A nonsignificant result indicates a random pattern, while large values suggest spatial dispersion and small values indicate aggregation.

To test if spruce and alder recruits were aggregated around mature plants, we classified alder and spruce stems as mature if they were at least 33 yr old (i.e., were present in both historic and modern air photographs) and classified recruits as stems that were only present in the modern air photographs. We used this approach because we are confident that stems observed in the same location in both images are the same individual. Subsequently, we used the Multi-Type Nearest Neighbor (MNN) function to test for significant spatial dependence between mature stems and new recruits using the *Spatstat* package in R statistical software (Baddeley et al. 2015). The MNN function was calculated for the ten plots that showed the greatest increase in stem density for each species. This function quantifies the degree of spatial dependence between mature stems and new recruits by comparing the distance from each mature stem to the nearest recruit with an expected empty space value assuming no spatial relationship between points (Baddeley et al. 2015). Low values of this index indicate that the two datasets are spatially dispersed relative to each other, while higher observed values indicate aggregation (Diggle 1983, Baddeley et al. 2015). We computed observed and expected values of MNN as a function of distance to test if the spatial dependence of mature plants and recruits

varies with spatial scale. To summarize these data for each species, we plotted these data and a 95% CI and compared them to an expected curve representing no spatial dependence.

RESULTS

Fine-scale species distribution

Both spruce and alder showed an overall increase in the proportion of plots occupied over time. Alder was observed in 61% and 74% of historic and modern plots, respectively, representing an increase of 13% (Fig. 4). The largest increase occurred between 68.4° N and 68.5° N, in an area impacted by a severe fire that occurred in 1968 (Fig. 5). Additionally, there were increases of 6–12% in the middle of the study area (between 68.86° N and 69.35° N). Spruce was observed in 8% and 10% of historic and modern plots, respectively, and was restricted to latitudes south of 68.85° N (Fig. 5). In plots south of 68.85° N, spruce was observed in 21% of plots in historic images and 25% of the modern images. Similar to alder, change in spruce was greatest within the extent of the 1968 fire and no change occurred beyond 68.8° N (Fig. 5).

The distribution of alder and spruce showed marked differences across our study area. Alder was present along the entire latitudinal gradient and showed a gradual decrease in presence toward the northern limit. Changes in alder presence were also distributed evenly throughout the middle of its range. Spruce was restricted to lower latitudes, and species presence decreased rapidly approaching its northern limit. The logistic regression models of alder and spruce occurrence showed that both species declined with latitude, but the decline in spruce occurred much further south than alder. The probability of observing spruce decreased rapidly in both time periods, approaching 0% at approximately 68.9° N.

All models were significant ($P < 0.001$; Table 1), and the 95% confidence intervals of the historic and modern models for both species overlap across the study area, suggesting that no change in range limit has occurred (Fig. 6). Furthermore, the likelihood ratio test shows that the slope and intercept parameters were not significantly different between time-periods for either

species. Modeled alder occurrence also decreased with latitude (Fig. 5), but the change was more gradual compared to spruce. Unlike spruce, the probability of observing alder did not reach 0%, but remained at approximately 30% in the northernmost part of the study area. Goodness-of-fit tests in both time periods showed reduced fit for alder compared to spruce models (Table 1).

Change in stem density

Analysis of ultra-fine-scale photographs shows that the number of spruce and alder stems increased significantly between 1980 and 2013 ($P < 0.001$; Fig. 7), with increased stem density observed in 74% of alder plots and 58% of spruce plots. The mean increase with a 95% confidence interval for spruce was 43.80 ± 15.94 stems per hectare, and the mean increase in alder was 38.01 ± 12.61 stems per hectare. Increases in stem density were significantly different from zero in all alder transects and the two southernmost spruce transects.

Accuracy assessment

The overall mapping accuracy for alder and spruce stems was 64% (SD = 15.4%) and 80% (SD = 21.1%), respectively, indicating that the majority of plants were correctly identified in the sample plots (Table 2). Overall accuracy increased to 76% when limited to shrubs >1 m and 85% for spruce >1 m (Table 2), indicating that our estimates of alder and spruce recruitment are likely conservative.

Spatial point patterns and recruitment

Analysis of the Average Nearest Neighbor statistic shows that spruce stems were significantly clustered ($P < 0.05$) in approximately half of the plots, while the remainder exhibited a non-significant random pattern (Table 3). In contrast to spruce, alder exhibited a random spatial pattern within 87% of plots, while 10% of plots showed a significantly dispersed pattern, and 3% showed significant clustering (Table 3). For both species, the frequency of clustered, dispersed, and random plots was similar between the historic and modern air photographs. The spatial pattern of new recruits, quantified with the Multi-Type Nearest Neighbor statistic, followed a similar pattern to that observed for adult species. Spruce recruits showed more aggregation

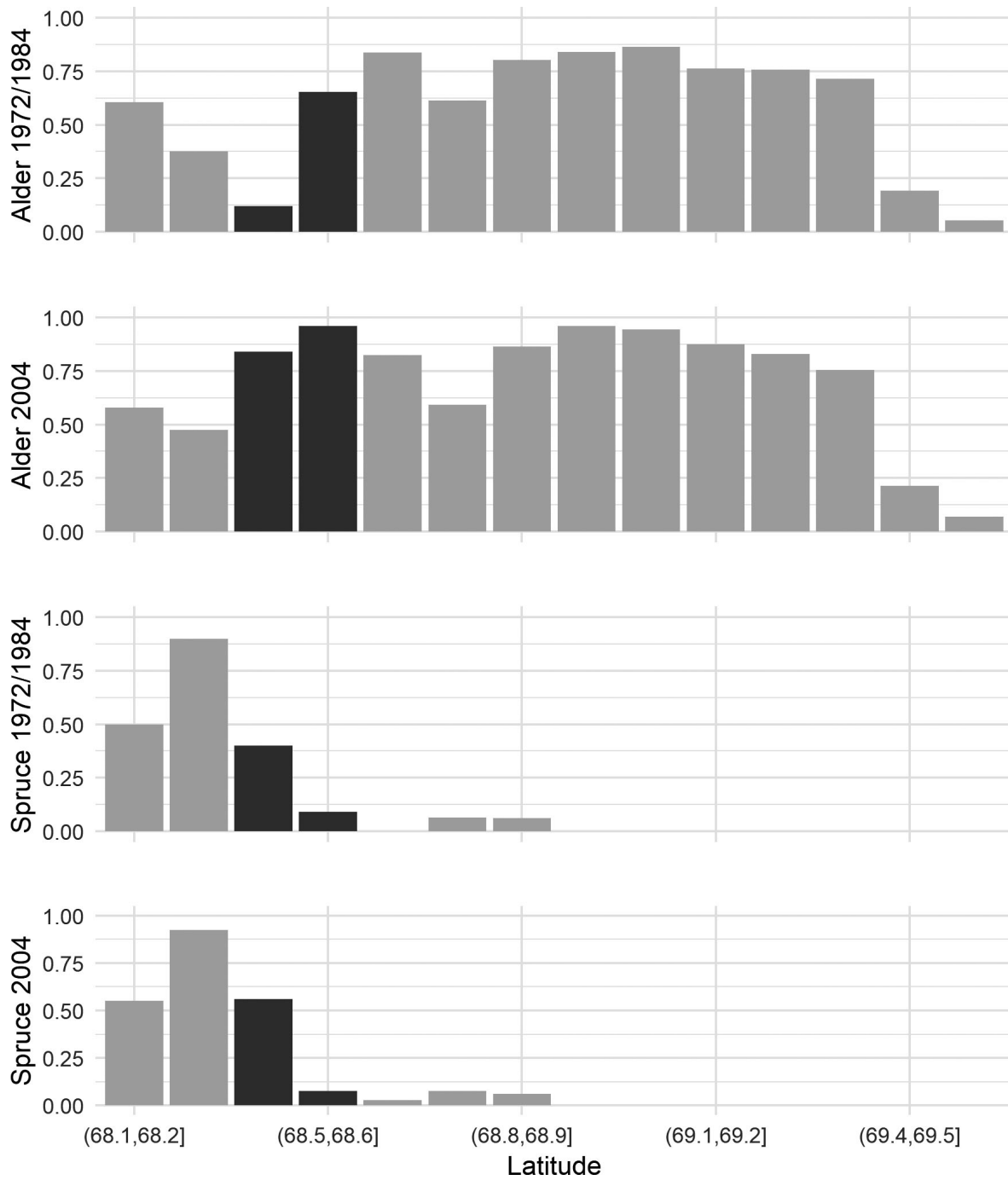


Fig. 4. Proportion of plots with alder in historic (1972/1984) and modern (2004) fine-scale air photographs (upper two plots). Proportion of plots with spruce in historic (1972/1984) and modern (2004) air photographs (lower two plots). Historic air photographs north of 69.4° N were captured in 1984, and the remainder were captured in 1972. The dark gray bars indicate the bins affected by fire; bin 68.45 N was 98% affected and bin 68.55 N was 42% affected by the 1968 fire.

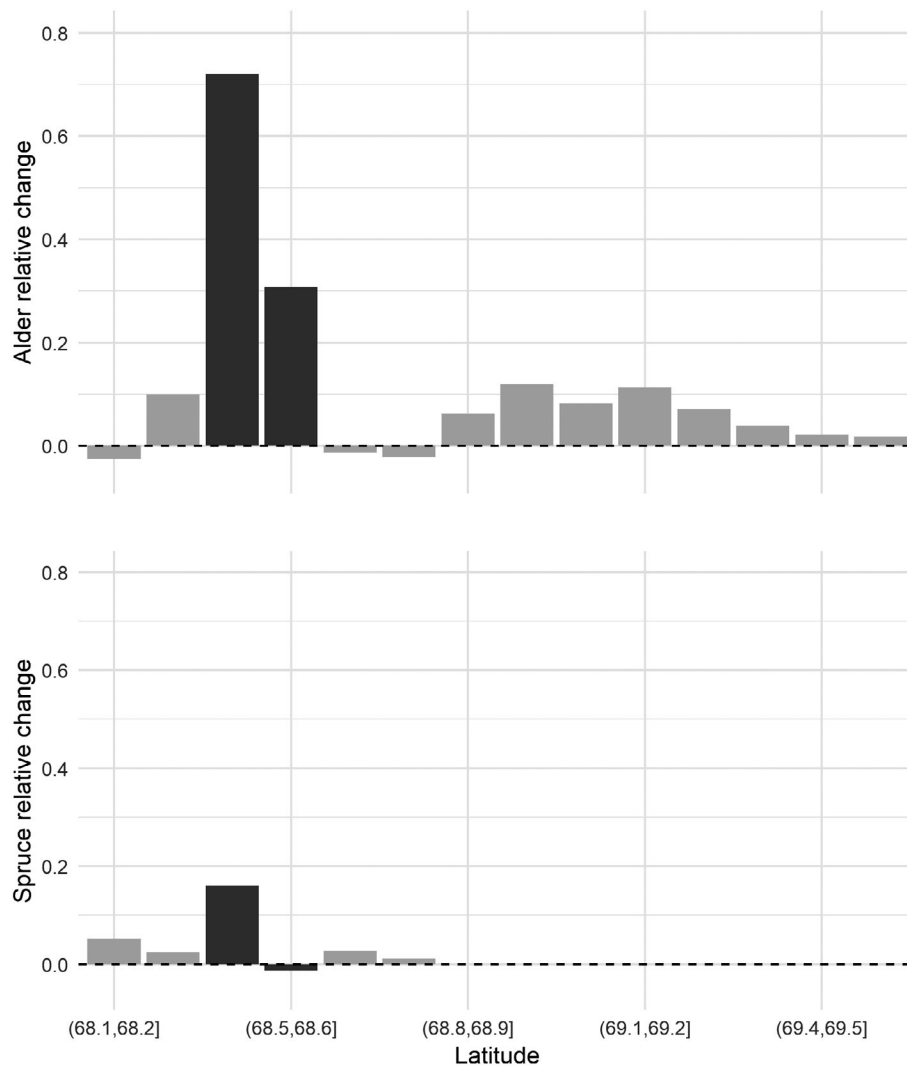


Fig. 5. Relative change in the proportion of plots containing spruce and alder. Positive values indicate increases in occurrence of these species between the historic and modern images. Areas affected by the 1968 fire located between 68.4° N and 68.5° N are shown as dark gray bars.

around mature stems, while alder recruits were distributed randomly in relation to mature stems at all spatial scales (Fig. 8).

DISCUSSION

Our analysis suggests that climate-driven changes in white spruce and green alder are limited at the range margin where both species are in disequilibrium with current climate conditions. Sites in the northern part of the study area showed little change in either species, and

models of species occurrence did not change significantly over time (Figs. 5 and 6). This provides evidence that both species exhibit leading-edge disequilibrium, contrary to regional and global models which generally predict a northward shifts in the range of Arctic shrubs and trees in association with warming (Kaplan and New 2006, Pearson et al. 2013, Paulson and Körner, 2014). Models that use the statistical relationships between climate conditions and vegetation composition to predict future vegetation change assume equilibrium and may not

Table 1. Coefficients from the logistic regression models of spruce and alder presence/absence as a function of latitude.

Species and year	Predictor	β	SE β	df	<i>P</i>	Residual deviance
Alder						
1972/1984	Intercept	175.4611	19.9845	851	<0.001	959.67
	Latitude	-2.5276	0.2891		<0.001	
	Null Model	0.83560	0.07454	852		1045.67
2004	Intercept	178.3877	21.2175	851	<0.001	886.19
	Latitude	-2.5660	0.3068		<0.001	
	Null Model	1.081	0.07847	852		965.34
Spruce						
1972/1984	Intercept	488.0790	44.5752	932	<0.001	260.22
	Latitude	-7.1436	0.6508		<0.001	
	Null Model	-2.4676	0.1219	933		512.30
2004	Intercept	491.3824	44.0472	932	<0.001	270.86
	Latitude	-7.1899	0.6429		<0.001	
	Null Model	-2.3956	0.1183	933		536.61

Notes: The null model was fit without latitude as an independent variable (i.e., intercept only). Latitude was found to be a significant predictor in all models, but the alder models in both time periods showed poorer fit than the spruce models.

accurately reflect the timing of these shifts under disequilibrium conditions (Svenning and Sandel 2013). These conclusions are corroborated by analyses of climate velocity showing that the rate of northward changes in vegetation productivity and species diversity is lower than the velocity of average temperature at high latitudes (Carroll et al. 2015, Huang et al. 2017). Fine-scale modeling of vegetation range shifts can account for these lags by incorporating data on growth, survival, and recruitment (Dormann et al. 2012, Kruse et al. 2019). Copenhagen-Parry et al. (2020) show that integrating seedling recruitment and survival data into species distribution models improves range predictions of alpine trees margins where recruitment is limited by low temperature. Taken together, this indicates that fine-scale investigations are required to characterize disequilibrium among different vegetation classes and improve projections of near-term vegetation change.

Observed stability in the position of the forest and upright shrub ecotones in our study area is likely the product of recruitment limitation driven by low stand density and reduced seed viability at the range edge. The northernmost spruce and alder stands we mapped had low stem densities that likely limit reproduction by restricting total seed availability and opportunities for long-range dispersal (Brown et al. 2018, Timoney et al. 2019, Kruse et al. 2019). Temperatures in our

study area decrease significantly with latitude (Lantz et al. 2019), and it is likely that low summer temperatures at the northern margin limit seed viability and range expansion. Seed viability and growth rates of several northern plant species, including white spruce, black spruce (*Picea mariana*), green alder, and larch (*Larix laricina*), have been shown to decrease with increasing latitude (Elliot 1979, Black and Bliss 1980, Lantz et al. 2010, 2019, Walker et al. 2012). For black spruce, Black and Bliss (1980) observed that successful seed germination required at least one day of mean air temperatures exceeding 15°C, and Lantz et al. (2019) show that no viable white spruce seed is produced when mean summer temperature is below 9°C. Previous research also shows that alder seed viability exhibits a logarithmic decline with summer temperature, and a minimum mean summer temperature of 7°C is required for viable seed production (Lantz et al. 2010). Taken together, these results suggest that low recruitment at the range limit of alder and spruce contributes to leading-edge disequilibrium observed in these species.

In our study area, alder may be less impacted by leading-edge disequilibrium than spruce because alder occurrence exhibits a gradual decline throughout the study area, while spruce exhibits an abrupt range edge. This is consistent with the hypothesis suggested by Epstein et al. (2004) that vegetation communities characterized

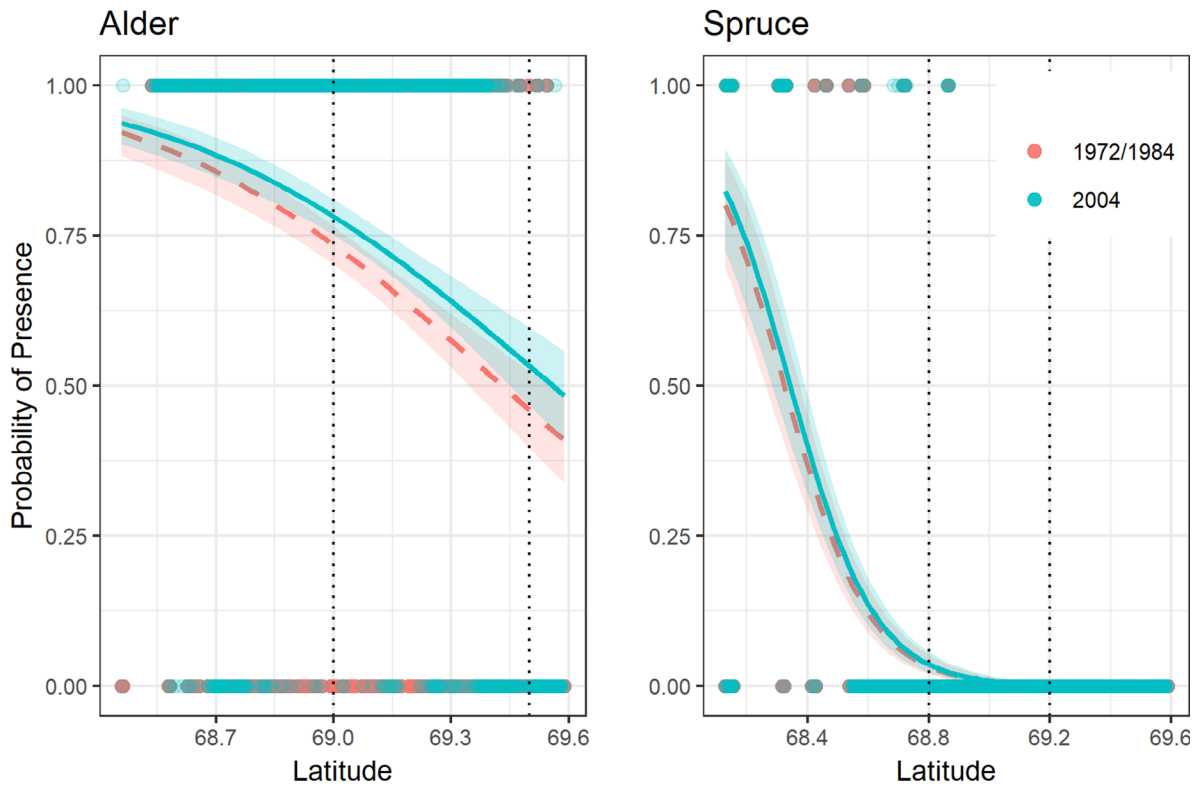


Fig. 6. Logistic regression models showing the predicted probability of observing spruce and alder by latitude in 1972/1984 (dashed red line) and 2004 (solid blue line). The shaded areas indicate the upper and lower bounds of the 95% confidence interval. Plots were excluded if they fell within the area of a 1968 fire, and alder was only modeled above the treeline (68.45° N). The dotted vertical lines indicate the latitudinal range of ultra-high-resolution plots used to assess change in stem density. In all models, latitude significantly reduced model deviance compared to an intercept-only model.

by gradual ecotones will be more sensitive to climate change. This conclusion is also supported by our observations that alder occupancy across the Tuktoyaktuk Coastal Plain is increasing more rapidly than spruce populations (Lantz et al. 2013, 2019, Fraser et al. 2014, Moffat et al. 2016). The abrupt range edge exhibited by spruce may also be related to greater dispersal limitation in this species. Spruce recruits were more clustered around mature individuals than alder, and spruce stems were more likely to exhibit clustering compared to alder stems, which tended to be random or dispersed. White spruce seed fall decreases dramatically with increasing distance from the stand (Dobbs 1976), while green alder seeds can likely be dispersed greater distances due to a papery membrane which can be caught by the wind (Fuller and del Moral 2003). Seed dispersal for

alder occurs from September to November (Matthews 1992), and in September for white spruce (Abrahamson 2015). Differences in weather conditions at these times may also explain the difference in seedling dispersal distance.

Our analysis also highlights the impact that fire and other disturbances have on northern vegetation dynamics. In 1968, a severe fire affected part of the southern extent of our study area. The fire burned for ten days and removed almost all vascular plant cover (Wein 1976, Landhäusser and Wein 1993). Five years after the fire, vascular plant cover had only recovered to 65%, and 17% of severely burned areas remained unvegetated (Landhäusser and Wein 1993). In our analysis, this burned area also contained the largest increases in spruce and alder occupancy (Fig. 5). These observations are consistent with

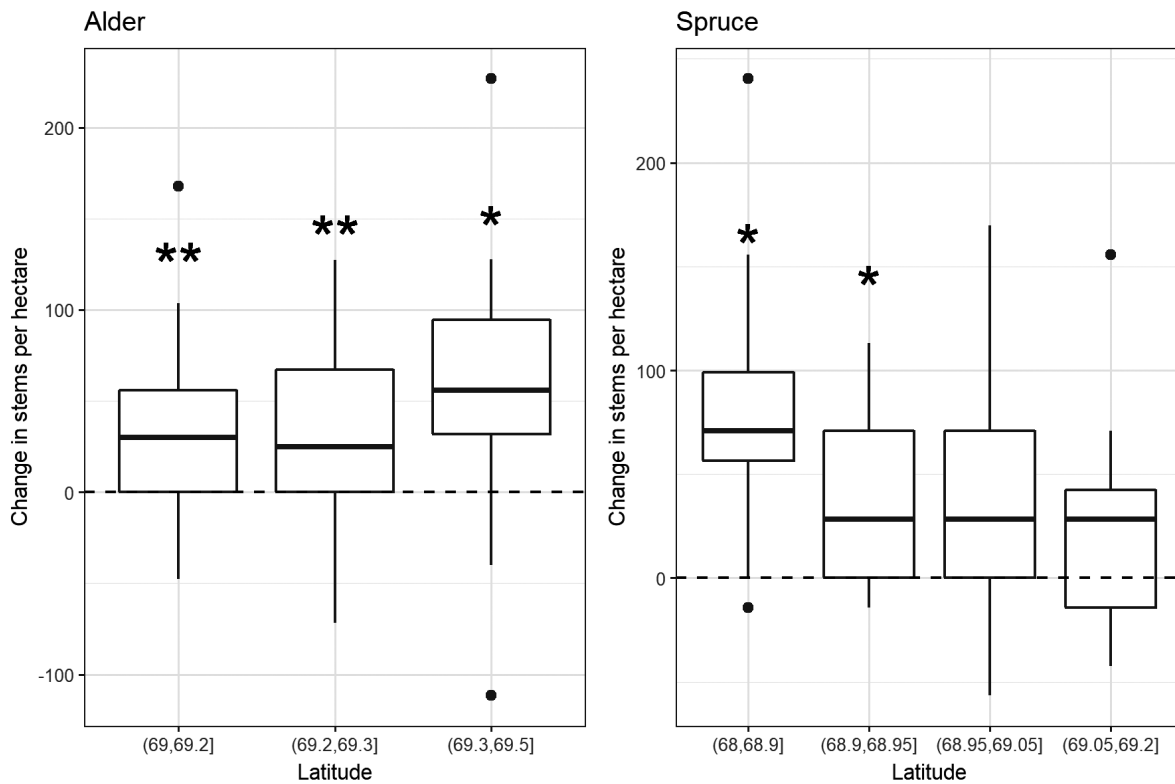


Fig. 7. Change in alder and spruce stem density by transect grouped by latitude. The solid black line in each box represents the mean value, and the ends of the boxes represent the 25th and 75th percentiles. The whiskers represent the 10th and 90th percentiles. Boxes marked with an asterisk have a median that is significantly different from zero, * indicates $P < 0.05$, and ** indicates $P < 0.01$. The dashed reference line shows no change in the number of stems.

Table 2. Accuracy of air photograph mapping estimated by comparison to field surveys.

Species	Plot	Overall accuracy (%)	Accuracy (%), >1 m only
Alder	1	41	60
	2	76	85
	3	60	71
	4	80	85
	5	65	80
Average		64	76
Spruce	1	92	92
	2	75	75
	3	92	100
	4	78	86
	5	40	49
	6	100	100
	7	100	100
	8	60	80
Average		80	85

previous work showing that disturbances can produce changes in vegetation growth and composition that outpace the near-term effects of climate change (Landhäusser and Wein 1993, Lantz et al. 2010, 2013, Brice et al. 2019). This suggests that increases in the rate and frequency of Arctic and sub-Arctic fires (Flannigan et al. 2006) will have a significant impact on the magnitude and timing in vegetation change for both spruce and alder.

CONCLUSIONS

This study used high-resolution air photographs to map the historical distribution and recruitment patterns of green alder and white spruce within the Tuktoyaktuk Coastal Plain. Based on the data presented, we draw the following conclusions:

Table 3. Results of the Average Nearest Neighbor analysis for alder and spruce showing the frequency of significantly clustered, dispersed, and random plots in both time periods as a percentage of the total number of plots.

Time period	Alder			Spruce		
	Clustered	Dispersed	Random	Clustered	Dispersed	Random
1980	3	8	88	56	2	41
2013/2015	0	13	87	57	0	43

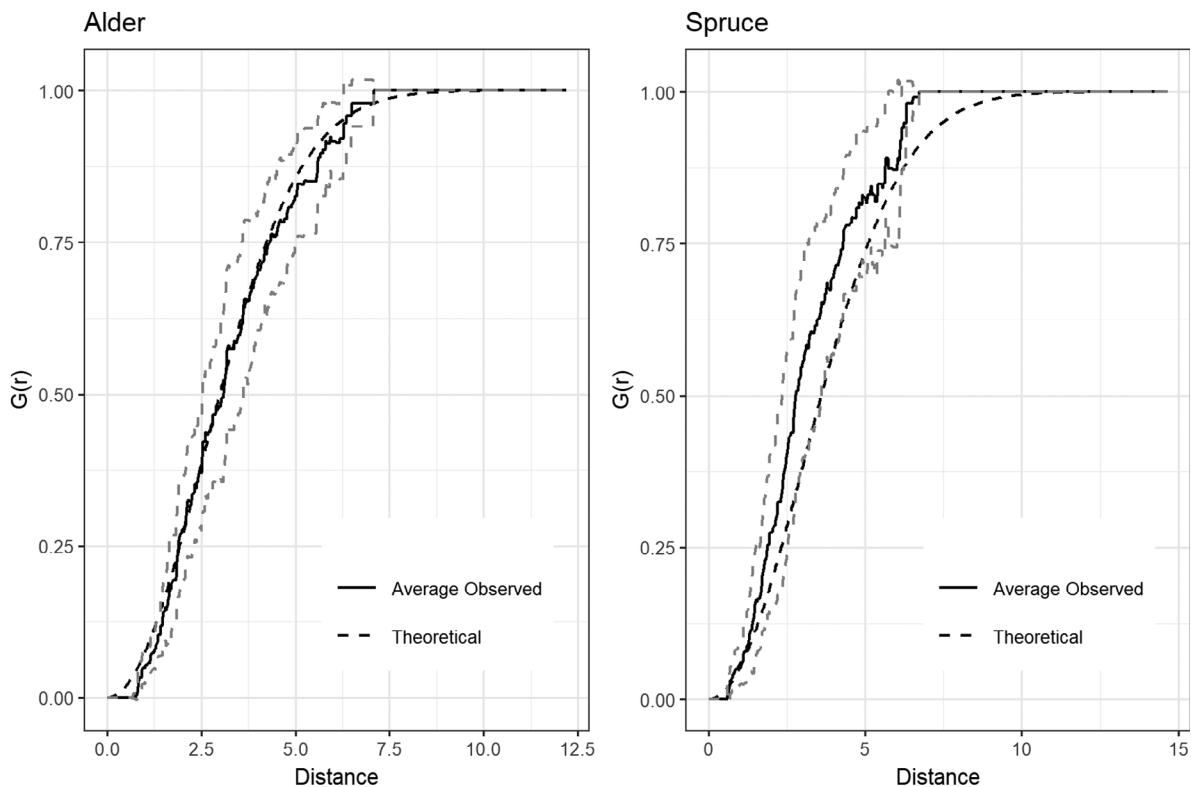


Fig. 8. Average Multi-Type Nearest Neighbor curve as a function of distance is shown as a solid black line. The dashed black line shows the theoretical empty space function, which represents no spatial dependence between mature stems and new recruits. An observed value greater than the theoretical line suggests new recruits are aggregated around mature stems, while a lower value suggests that new recruits are dispersed in relation to mature stems. The dashed grey show the upper and lower bounds of a 95% confidence interval for the average observed MNN statistic.

1. Stem density has increased for both spruce and alder, but the location of the tree and shrub ecotones has not changed significantly since the 1970s.
2. Vegetation change in the study area exhibits aspects of leading-edge disequilibrium, which is not adequately represented in climate-based projections of near-term vegetation change.
3. Disequilibrium in spruce and alder is likely driven by low stand density at the range margin as well as temperature limitations of vegetation growth and reproduction.
4. Alder is likely less impacted by leading-edge disequilibrium because it exhibits a gradual decline in occupancy across the study area, is generally more abundant than spruce, and is less limited by seed dispersal.

5. Burned areas exhibited the greatest change in spruce and alder occupancy, suggesting that fire and other disturbances will strongly influence the timing and magnitude of future vegetation shifts.

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