Variation in reproductive potential across a multi-species treeline
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ABSTRACT
Cone and seed production at the forest-tundra ecotone, or treeline, depend on species-specific tolerances to limiting abiotic and biotic factors. As range expansion via seed dispersal is needed to keep pace with climate change, reproductive limitations act as a bottleneck for treeline advance. The treeline in the Mealy Mountains, central Labrador, was comprised of four codominant species: black spruce (Picea mariana [Mill.] B.S.P.), white spruce (Picea glauca [Moench] Voss), eastern larch (Larix laricina [Du Roi] K. Koch), and balsam fir (Abies balsamea [L.] Mill.). Conifer stem surveys from three treeline zones (forest, forest-tundra transition, krummholz) were used to assess patterns of altitudinal distributions, tree densities, and cone production to provide insight into overall reproductive potential. The altitudinal limit of the spruce species was 39 m a.s.l. higher than the altitudinal limit of black spruce cone production. Black spruce had the highest densities of cone-bearing trees across treeline with eastern larch values being comparable in the forest-tundra transition zone, although overall cone production was low and highly variable in all species. Compared to the other treeline species, black spruce has the greatest reproductive potential for upslope advance.

Introduction
As northern and alpine climates continue to warm (IPCC 2014), thermal constraints on cone and seed production may become less limiting (Brown et al. 2018; Roland, Schmidt, and Johnstone 2014). Thus, a northward and upslope advance of seed-mediated conifer regeneration is expected (Grace, Berginger, and Nagy 2002; Körner and Paulsen 2004). This seed-mediated range expansion depends on the production, dispersal, and establishment of viable seeds within and beyond the current distribution of trees (Gamache and Payette 2005; Lescop-Sinclair and Payette 1995; Szeicz and MacDonald 1995). Yet, failure to produce viable seeds at high altitudes and latitudes has been widely reported (e.g., Elliott and Short 1979; Kroiss and HilleRisLambers 2015; Mencuccini, Piussi, and Zanzi Sulli 1995), and models suggest that limited seed production is a bottleneck to treeline advance (Chapin and Starfield 1997; Dullinger, Dinnbock, and Grabherr 2004; Greene et al. 2007; Kambo and Danby 2017). Cone and seed production requires the sequential completion of several biotic- and abiotic-influenced events: reproductive bud differentiation and maturation, pollination, fertilization, embryo development, and seed maturation (Farmer 1996). Interference with any stage of this process dramatically reduces viable seed production (Sveinbjörnsson, Hofgaard, and Lloyd 1995). Reproductive bud differentiation and flushing require minimum heat sums (Lindgren, Ekberg, and Eriksson 1977), and warm, dry summers and long growing seasons during bud initiation promote cone production (Despland and Houle 1997; Hofgaard 1993). Strong, icy winds and late-season frosts at treeline can cause extensive bud loss and impede future production by damaging the terminal leader (Krasowski and Simpson 2001). Because of these and other factors, including cone and seed predation (Jameson, Trant, and Hermanutz 2015), sexual...
regeneration is often absent at a species limit (Holtmeier 2009).

The current composition of treeline tree species and their respective life histories and ecological amplitudes provide insight into how the ecotone may shift with climate change. The majority of treeline studies focus on one or two conifer species because of limited conifer diversity or study design (e.g., Black and Bliss 1980; Danby and Hik 2007; Koshkina, Moiseev, and Goryaeva 2008; Lloyd and Fastie 2003; Miller and Cummins 1982; Siros 2000; Szeicz and MacDonald 1995); however, few studies address higher diversities of conifers at the treeline (Daly and Shankman 1985; Kroiss and Hillevil 2015). At treelines with high conifer diversity, the question of how each species will respond to climate change and contribute to advance is more complex and difficult to predict (Trant and Hermanutz 2014).

The treeline of Labrador’s Mealy Mountains is comprised of four conifer species: black spruce (Picea mariana [Mill.] B.S.P.), white spruce (Picea glauca [Moench] Voss), eastern larch (Larix laricina [Du Roi] K. Koch), and balsam fir (Abies balsamea [L.] Mill.). Remotely sensed data show an upslope movement of the treeline during 1983–2008 (Simms and Ward 2013), while age structure analyses show that this response is species specific (Trant and Hermanutz 2014). However, the species-specific reproductive mechanisms of this change are unknown. Previous studies at this field site found that black spruce and white spruce seedling emergence was enhanced with experimental warming combined with disturbance (Munier et al. 2010), and that seeds sown above the current treeline can germinate and survive for more than eight years (Cranston and Hermanutz 2013; Munier et al. 2010). Additionally, seedbed substrates favoring recruitment are not limiting for black spruce (Wheeler, Hermanutz, and Marino 2011). However, a key variable in treeline advance is viable seed production. Thus, understanding the current dynamics of cone and seed production throughout the ecotone is essential for predicting the pace and pattern of treeline advance as regional climate continues to warm.

To explore the treeline structure and composition of the Mealy Mountains and to compare seed availability for the upslope advance of four conifer species, this study addressed the following questions: (1) What are the species-specific altitudinal distributions and cone production limits at the treeline? (2) Does the structure and composition of trees and cone-bearing trees change across the treeline from the forest to krummholz zones? and (3) Is the production of viable seeds a limitation to the upslope advance of conifer species at this treeline?

Materials and methods

Study area

Survey sites were selected along the boreal treeline of an unnamed valley in the Mealy Mountains, Labrador, Canada (N 53° 37’ W 58° 49’; Figure 1), within the Akamiuapishkú/Mealy Mountains National Park Reserve. This area has no known history of forestry or other significant landscape modifications. The valley tends upslope from east to west over approximately 7 km (~500–1,060 m above sea level [a.s.l.]), with moraines and eskers alternately providing shelter or exposing vegetation to intense, predominantly south-west winds (Jacobs, Chan, and Sutton 2014). Automated climate stations (Campbell Scientific Inc.) at 570, 600, and 995 m a.s.l. monitored hourly surface air temperatures and precipitation in the valley between July 2001 and September 2009. Mean annual temperature ranged from −1.5°C at 570 m a.s.l. to −4.2°C at 995 m a.s.l. from 2001 to 2007. Altitude affects temperature at a mean annual lapse rate of approximately −0.7°C per 100 m elevation. Annual precipitation regularly exceeds 2,000 mm, with minimal summer moisture deficits (Jacobs, Chan, and Sutton 2014). Climate projections for 2038–2070 for this region of Labrador predict significant increases in summer (~2°C) and winter (~3°C) daily mean temperatures along with increases in mean daily precipitation values between 0.2 mm and 0.3 mm across all seasons (Finnis 2014).

Treeline zone description

Based on a landscape-scale vegetation map (Loader 2007), we stratified the treeline ecotone into three zones for sampling: forest, forest-tundra transition, and krummholz (sensu Scott 1995, Shrub Tundra). Field surveys were performed in these three zones to determine species-specific altitudinal distribution and cone production limits, and to track changes in species composition, stem density, and cone production across the treeline.

The forest zone comprises continuous boreal forest found in low-lying areas of the valley near 500 m a.s.l. Black spruce, white spruce, balsam fir, and eastern larch are less exposed and exhibit true arborescent growth. The forest understory is composed of woody shrubs (Betula spp., Alnus spp., Salix spp.). Lichens (Cladonia spp., Cladina spp., Cetraria spp.) dominate open areas while mosses dominate shaded, wet areas (Pleurozi um schreberi and Hylocomium splendens). The forest-tundra transition (henceforth, transition) zone is made up of distinct stands
of open canopy woodland between the continuous forest zone and the limit of arborescent growth form (i.e., the tree-form line). Stands in the transition zone grow where local topography and site conditions are favorable (e.g., the lee sides of moraines). Woody shrubs and vegetative layering conifers make up the transition understory. Black spruce, white spruce, and balsam fir tend to form so-called tree islands close to the tree-form line. Trees in these small, microhabitat-dependent islands form the upper elevational limit of true arborescent growth in the valley (Trant et al. 2015).

The krummholz zone begins at the tree-form line at approximately 600–620 m a.s.l. Increased exposure to icy wind abrasion, frost desiccation, and heavy snow packs results in conifers adopting suppressed, slow-growing, clonal krummholz growth forms (Pereg and Payette 1998; Trant, Jameson, and Hermanutz 2011). Krummholz-zone individuals range from stunted miniatures of the tree’s true growth form to prostrate, layering mats extending just below the average snow-pack level. Krummholz patches generally become smaller and more discrete toward the tundra. Beyond and among the krummholz patches are large areas dominated by dwarf birch (*Betula glandulosa* [Michx.]) and ericaceous vegetation. No vertebrate cone predation was observed during the June–September study period (2007–2008), nor were there signs of cone or seed caches in any of the treeline zones.

**Site selection**

A forest-zone site (F3), three transition-zone sites (T1–T3), and four krummholz-site transects (K1–K4) were surveyed during the 2007 and 2008 growing seasons. A different survey approach was required for the krummholz zone because of the physiognomic and spatial distribution differences of conifers below and above the tree-form line (i.e., tree density and height decreased significantly).

We established randomly directed transects in forest (F3) and transition-zone (T1–T3) sites in July 2007 (Table A1). Three 2 × 100 m transects were established per site (except at T1, where bisecting transects, 2 × 100 m and 2 × 120 m, were established to accommodate local topography and stand size) and 10 m survey intervals were marked using measuring tape. In total, 0.056 ha of the forest zone and 0.164 ha of the transition zone were surveyed. Two additional fixed-area forest sites were used.
(F1 and F2, Table A1) to calculate reproductive potential indices (see description in a later section). These sites were used rather than F3 because of logistical difficulties in returning to sample cones; however, these sites represent similar forest structure and composition to F3. To survey the discrete conifer patches across the krummholz zone, we established three transects (K1–K3) running perpendicular to the slope of the valley, with an additional krummholz transect (K4) established on the north-facing valley wall. Krummholz-zone transects ranged from 40 × 1,585 m at the valley’s highest elevations and low conifer density to 15 × 325 m in areas of higher conifer density near the transition zone (K1 and K4, respectively) for a total krummholz-zone survey area of 12.502 ha (Table A2).

**Altitudinal limits and treeline survey for stem densities and cone production**

All four conifer species can layer vegetatively, which makes distinguishing individuals from clones difficult without removing topsoil and investigating root patterns (Cooper 1911). Because this study addresses cone production, a widely used measure of potential seed productivity (e.g., Broome, Hendry, and Peace 2007; Kantorowicz 2000), the term stem was used to describe any upright leader supporting branches with the potential to yield reproductive buds, regardless of genetic origin. After extensive preliminary surveys in the forest and transition zones, no conifer stems less than 0.8 m in height were found bearing reproductive buds (Jameson 2012). Thus, only stems greater than 0.8 m tall were identified to species in each forest and transition-zone survey interval. Height class (0.8–2 m, 2–4 m, >4 m) of each stem and the presence or absence of seed cones were determined using 8 × 42 binoculars. Key differences that necessitated distinct surveying methods on krummholz-zone transects included patchy tree distribution, stem height and architecture, and the tendency of shorter, unshaded stems to produce reproductive buds. Height inclusion criterion was lowered to 0.5 m for the krummholz zone, and krummholz patches covering more than 1 m² in basal areas of foliage with at least one potentially reproductive stem were surveyed individually. A central waypoint was recorded for each patch and its relative area was estimated by measuring its longest and widest extents. Within each patch, species were identified and the height of the tallest stem, the number of upright stems, and the number of cone-bearing stems within the krummholz patch were recorded. Cone production was categorized for each stem at each surveyed site (0, 1–10, 11–50, 51–250, >250 cones) for all zones.

Given that our focus was to document the distribution of stems and reproductive structures across the treeline, survey intervals that did not contain at least one conifer stem were removed from the analysis. All forest-zone intervals contained conifer stems (twenty-eight intervals, treed area = 0.056 ha), whereas six treeless transition intervals were removed from the analysis (seventy-six intervals, treed area = 0.156 ha). Conifers were distributed sporadically throughout the krummholz zone, surrounded by rocky outcrops, small bodies of water, dwarf birch, and alpine vegetation. Treeless areas were removed from the analysis in order to more accurately assess true conifer density using ArcMap version 9.3 (ESRI Inc.). Krummholz-zone transects were plotted on a 1:50,000 digital elevation map (GeoBase®) using waypoints and field notes. Elevations reflect interpolated data extracted from the digital elevation map (±10 m elevation). Each krummholz patch position was mapped using a central way point and its maximum length and width. Krummholz survey intervals were identified as continuous sections of the transect where the extents of the longest lengths of krummholz patches were separated by less than 30 m for K1–K3, and by less than 10 m for the higher density, lower elevation K4 (Table A2). Interval areas were calculated using Hawths Analysis Tools for ArcGIS (Beyer 2004). Using ArcMap, thirty-four distinct krummholz-zone survey intervals were identified for a total of 2.627 ha of treed area. This represents 21 percent of the total area surveyed along the four krummholz-zone transects.

Overall conifer stem density (stems/ha), species-specific stem density, overall density of cone-bearing conifer stems (cone-bearing stems/ha), and the density of cone-bearing stems of each species were calculated for survey intervals and were compared among zones and then within zones among species using Mann-Whitney U tests (hereafter, MWU; Conover and Conover 1980) with Bonferroni corrections (p < α/[number of groups being compared], α = 0.05) to adjust for multiple comparisons. Statistical analyses and visualizations were performed using R version 2.12.0 (R Development Core Team 2016).

Spatial autocorrelation is a concern for tree-density studies because of spatial heterogeneity from variable topography and relatively localized regeneration patterns (Fortin, Drapeau, and Legendre 1989). To address this concern, spatial autocorrelation of conifer stem density was assessed for 10 m survey intervals in each forest and transition-zone site by calculating Moran’s I coefficients using SAM v. 3.1 (Rangel, Diniz-Filho, and Bini 2010). Moran’s I analysis calculates the risk of violating the assumption of sample independence (Legendre and Fortin 1989), which is required when...
using the MWU test to test for differences among zones and species.

**Reproductive potential**

For our study, reproductive potential was defined as a relative contribution for three important stages of reproduction by seed: (1) cone productivity index (summed seed cone survey category midpoints for each survey area, with 300 used for the > 250 seed cone category/total survey area), (2) seed productivity index (cone productivity index × mean number of seeds per cone for each treeline zone), and (3) viable seeds productivity index (cone productivity index × mean number of viable seeds per cone for each treeline zone).

Data for the number of seeds per cone and the number of viable seeds per cone were originally reported, with complete methodology, in Jameson, Trant, and Hermanutz (2015). Species-specific methodological differences for determining seed viability may have underestimated the viability of eastern larch and black spruce because they were not cold stratified, following the recommendation by the International Seed Testing Association (International Seed Testing Association 2009; Jameson, Trant, and Hermanutz 2015).

**Results**

**Altitudinal distribution and cone production limits**

All four conifer species were present and produced cones in the krummholz zone (Table 1). The two spruce species were found up to 804 m a.s.l., and balsam fir only 10 m lower. Eastern larch, although also present in the krummholz zone, had the lowest distribution limit, with one stem less than 1 m tall found at 691 m a.s.l. This individual and one eastern larch seedling found outside the survey area at 770 m a.s.l. were outliers; all other eastern larch stems were found below 625 m a.s.l.

Altitudinal cone-production limits differed among species by more than 150 m: black spruce, 766 m a.s.l.; balsam fir, 721 m a.s.l.; white spruce, 642 m a.s.l.; and eastern larch 613 m a.s.l. The limit of black spruce cone production lagged 39 m in elevation below the species' altitudinal distribution limit, compared to differences of 73 m and 162 m in balsam fir and white spruce, respectively. For eastern larch, the altitudinal distribution and cone-production limits were nearly equal (<10 m elevation difference).

**Structure and composition of trees across the treeline**

Conifer density was not spatially autocorrelated within the 10 m interval class (Moran’s I index, p > 0.05; Table A3) and no consistent trend of autocorrelation emerged when species were analyzed individually. The densities of the reproductive conifer stems sampled were highly variable within zones and across the treeline (Figure 2a). Transition-zone stem density was most variable where black spruce density ranged from 0 stems/ha to 22,500 stems/ha (site T3; forty-five black spruce stems within a 20 m² survey interval). Median conifer stem density decreased significantly between the forest and krummholz zone (MWU, p < Bonferroni-adjusted α: 0.016). Stem densities differed among tree species across the treeline zones. Black spruce had a significantly higher overall stem density and higher densities within zones than all other conifers (MWU, p < Bonferroni-adjusted α: 0.008) except for balsam fir in the transition zone (MWU, p = 0.009; Figure 2b). White spruce had the lowest overall median stem density and only in the forest, were its density was not significantly lower than that of either eastern larch or balsam fir. Eastern larch and balsam fir densities were higher than white spruce density in the transition zone.

| Altitudinal Limit | Species        | Elevation (m a.s.l.) | Height of Tallest Stem (m) | Basal Length × Width (m) | Number of Stems | Number of Stems Bearing Cones |
|-------------------|----------------|---------------------|---------------------------|-------------------------|-----------------|-----------------------------|
| Species limit     | Black spruce   | 805                 | 0.6                       | 1.3 × 1.0               | 5               | 0                           |
|                   | White spruce   | 804                 | 1.4                       | 2.2 × 2.2               | 7               | 0                           |
|                   | Eastern larch  | 690                 | 0.7                       | 1.5 × 1.2               | 1               | 0                           |
|                   | Balsam fir     | 794                 | 1.4                       | 4.9 × 3.0               | 3               | 0                           |
| Limit of cone production | Black spruce | 766                 | 1.3                       | 2.2 × 2.2               | 16              | 2                           |
|                   | White spruce   | 642                 | 2.3                       | 4.4 × 3.1               | 10              | 6                           |
|                   | Eastern larch  | 613                 | 3.7                       | 2.2 × 1.5               | 1               | 1                           |
|                   | Balsam fir     | 721                 | 1.6                       | 13.2 × 2.9              | 24              | 1                           |

Note. All distinct krummholz-zone stems greater than 0.5 m tall, covering more than 1 m² in basal area were surveyed in 12.5 ha of fixed-area transects, up to 830 m a.s.l. (see Table A1).
and krummholz zones. Eastern larch was largely absent from the krummholz zone, where only ten stems were observed, whereas balsam fir was the second-most dominant krummholz-zone conifer next to black spruce.

Relative composition of height classes differed between forest and transition zones (Table 2). Black spruce dominated the lower height classes, accounting for more than 65 percent each of forest and transition-zone stems 0.8–2 m and forest stems 2–4 m. Despite being present in relatively high densities, less than 1 percent of transition-zone black spruce stems grew more than 4 m in height. White spruce accounted for half of conifer stems greater than 4 m in the forest zone and 22 percent in the transition zone, but made up less than 10 percent of all other height classes. Eastern larch, the dominant canopy species in the transition zone, comprised more than 60 percent of stems in the more than 4 m height class.

Figure 2. Number of stems per hectare for (a) all conifers, (b) each codominant treeline species, and the number of cone-bearing stems for (c) all conifers and (d) each codominant treeline species in the forest, transition, and krummholz zones. Dashed horizontal lines show sample means. Box and whisker plots indicate tenth and ninetieth percentiles, and the first, second (median), and third quartiles. Crosshairs indicate the fifth and ninety-fifth percentiles. Uppercase letters (A, B, C) above each box indicate differences among zones (horizontally: Mann-Whitney U test with Bonferroni-adjusted $\alpha = 0.016$), while lowercase letters (a, b, c) to the left of each box indicate differences among species (vertically: Mann-Whitney U test with Bonferroni-adjusted $\alpha = 0.008$).
Table 2. Percent composition and cone production of black spruce, white spruce, eastern larch, and balsam fir stem height classes below tree-form line* (~600–620 m a.s.l.) in the Mealy Mountains, Labrador, Canada. Stem heights were classed as follows: H1 = 0.8–2 m, H2 = 2–4 m, H3 = > 4 m. Percentage of stems producing cones was calculated for each species in each height class. Krummholz-zone data are not included in this table because of differences in sampling methodology due to low overall stem densities.

| Zone         | Species         | Number of Stems | Percentage of Stems by Species | Percentage of Total Stems by Height Class | Percentage of Stems Producing Cones |
|--------------|-----------------|-----------------|-------------------------------|-----------------------------------------|-----------------------------------|
|              |                 |                 | H1     | H2     | H3     | H1     | H2     | H3     | H1     | H2     | H3     |
|              |                 |                 |       |       |       |       |       |       |       |       |       |
| Forest       | Black spruce    | 269             | 63.6  | 33.1  | 3.3   | 68.4  | 68.5  | 22.5  | 2.9   | 69.7  | 66.7  |
|              | White spruce    | 52              | 46.2  | 15.4  | 38.5  | 9.6   | 6.2   | 50.0  | 4.2   | 62.5  | 100   |
|              | Eastern larch   | 73              | 58.9  | 31.5  | 9.6   | 17.2  | 17.7  | 17.5  | 2.3   | 8.7   | 100   |
|              | Balsam fir      | 26              | 46.2  | 38.5  | 13.4  | 4.8   | 7.7   | 10    | 0     | 50.0  | 75.0  |
| Transition   | Black spruce    | 593             | 78.6  | 21.2  | 0.2   | 65.3  | 44.5  | 1.3   | 5.8   | 48.4  | 100   |
|              | White spruce    | 41              | 29.3  | 29.3  | 41.5  | 1.7   | 4.2   | 21.8  | 0     | 50.0  | 82.4  |
|              | Eastern larch   | 136             | 36.3  | 27.4  | 36.3  | 6.9   | 12.9  | 62.8  | 8.2   | 59.5  | 89.8  |
|              | Balsam fir      | 329             | 60.5  | 35.9  | 3.6   | 26.2  | 38.8  | 14.1  | 0     | 5.4   | 0     |

Note. *All stems greater than 0.8 m in height were surveyed in fixed survey intervals: 0.056 ha in the forest (n = 420 stems) and 0.164 ha in the transition zone (n = 1099 stems).

The density of conifer stems that produced cones was variable and low across the treeline (Figure 2a). Forest-zone black spruce had the highest variation in cone production and highest cone-bearing stem density (median, 5,000 stems/ha; range, 0–6,000 stems/ha). Overall, cone-bearing conifer stem densities decreased significantly between the forest and krummholz zones (MWU, p < Bonferroni-adjusted α: 0.016). This significant decrease in cone production was observed in the two spruce species, but not in eastern larch or balsam fir (Figure 2b).

In contrast to black spruce stem density dominance across the treeline, zone-specific co-dominances in cone-bearing stem density were observed between black spruce and other conifers (Figure 2c, Figure 2d). Overall cone-bearing black spruce stem density was not significantly different from eastern larch, nor was it different from forest white spruce, transition-zone eastern larch, or krummholz-zone balsam fir within zones (MWU, p > Bonferroni-adjusted α: 0.008). Few cone-bearing white spruce stems were found in the transition zone (median, <1 cone-bearing stem/ha), and no white spruce cone production was observed on krummholz-zone transects.

Eastern larch had significantly higher densities of cone-bearing stems within the transition zone than either white spruce or balsam fir (MWU, p < Bonferroni-adjusted α: 0.008) and across all zones combined. In contrast to the spruce species, significantly more cone-bearing eastern larch stems were found in the transition than in the forest (MWU, p < 0.008); however, only 1 out of 10 krummholz-zone eastern larch stems had recently produced cones. Balsam fir had among the lowest cone-bearing stem densities overall and within the forest and transition zones. Balsam fir, however, was the only conifer besides black spruce to produce cones above 642 m a.s.l. (Table 1). There were no significant differences among zones in the density of cone-bearing balsam fir stems (MWU, p > Bonferroni-adjusted α: 0.016).

The percentage of stems producing cones generally increased with increasing height class (Table 2), particularly between the 0.8–2 m and 2–4 m categories. More than 65 percent of stems greater than 4 m in height produced cones in the forest and transition zones in each species except balsam fir. No balsam fir less than 2 m in height produced cones in either zone.

Reproductive potential

Overall, viable seed productivity decreased substantially between the forest and krummholz zones (Figure 3), a pattern also observed for seed productivity and both strongly influenced by cone productivity (Appendix Figure A1). However, all eastern larch productivity indices were higher in the transition than in the forest zone. Forest-zone black spruce had the highest cone, seed, and viable seed productivity indices. Balsam fir produced cones, seeds, and viable seeds in the transition and krummholz zones, but its productivity was negligible compared to the other species. White spruce cone productivity was low at all sites except for one (T3), where it was higher than black spruce and balsam fir. White spruce seed and viable seed productivity were very low in the transition zone and could not be calculated for the forest because no white spruce trees were sampled in that zone.

Discussion

The presence of four conifer species at the Mealy Mountains treeline, including tree and krummholz growth forms, exemplifies the complex vegetation dynamics and mosaic nature inherent to alpine tree-lines worldwide (Holtmeier 2009). The multispecies
treeline varied substantially in species composition, density, height structure, and cone production across the treeline. Such variability has not to date been incorporated into models of treeline change, and may partially explain the wide variability encountered in treeline response to climate warming (e.g., Harsch et al. 2009).

**Altitudinal distribution and cone production limits**

Black spruce, white spruce, and balsam fir reach their altitudinal limits at approximately 800 m a.s.l. in the Mealy Mountains. The spruce species were expected to grow at the highest altitudes because both are stress and cold tolerant, forming the leading edges of several North American treelines (Elliott-Fisk 1983). The more southerly distributed balsam fir, absent from the latitudinal treeline (Hustich 1953), was not expected to reach similar altitudes. At its northern limit in western Québec (~53°N, 200 m a.s.l.), balsam fir has an arborescent growth form because its northward expansion is limited by fire frequency because it acts as a late successional species, following black spruce (Sirois 1997). By contrast, the central coast of Labrador has a much lower fire frequency than western Québec (~500 vs. 100 years; Foster 1983; Payette et al. 1982) and dendrochronological research found no evidence of fire in the Mealy Mountains (Trant 2013; Trindade 2009). With infrequent fires, balsam fir established beyond the treeline in favorable microsites, and persists near its thermal limit by means of clonal layering. Balsam fir is not a common treeline species in Canada; its presence in krummholz form is more consistent with Appalachian mountain ranges (e.g., Reiners and Lang 1979; Sprugel 1976) and along the Labrador coast (Hustich 1953).

Eastern larch had the lowest altitudinal limit with all but one stem found below 625 m a.s.l.—the approximate Mealy Mountains tree-form line. Although eastern larch can occasionally layer, it does not have the growth plasticity of either black spruce or balsam fir to form krummholz; sexual reproduction is by far its dominant regenerative strategy (Elliott and Short 1979; Hustich 1953; Payette, Deshaye, and Gilbert 1982). With outlying stems at 691 m and 770 m a.s.l., eastern larch’s threshold of tolerance appears to lie beyond the current Mealy Mountains treeline. These individuals, up to 2.2 km in distance from the closest cone-bearing eastern larch stem, highlight the ability of wind-dispersed conifer seeds to travel significant distances and establish in favorable microsites.

In contrast to the species’ similar altitudinal distribution limits in the Mealy Mountains, a clear hierarchy of altitudinal limits to cone production was found among species. Black spruce produced cones approximately 45 m higher in elevation than the other species and, unexpectedly, balsam fir produced cones at higher elevations than white spruce. This was surprising, because balsam fir reaches its distribution limit at 58°N (Bakuzis and Hansen 1965), while cone-bearing white spruce have been reported beyond the arctic circle in Alaska, at elevations greater than 700 m (Cooper 1986; Roland, Schmidt, and Johnstone 2014). Eastern larch did not produce cones above 613 m a.s.l., the lowest limit of cone production among the four species. Eastern larch had the smallest difference between altitudinal limits of distribution and cone production. The coincidence of these limits in

![Figure 3. Viable seed productivity index across the treeline from the forest, transition, to krummholz zones shown for all conifers and for each tree species by treeline zone. This index was calculated by multiplying the cone productivity by the mean number of viable seeds per cone for each treeline zone. Error bars represent standard error. Tree species are BS (black spruce), WS (white spruce), EL (eastern larch), and BF (balsam fir).](image-url)
eastern larch was also found at the treeline in northern Québec (Payette and Gagnon 1979) and supports the prevailing idea that eastern larch is in equilibrium with current climatic conditions and has high potential for advance if temperature is the limiting factor (Payette 1993; Tremblay, Lévesque, and Boudreau 2012).

**Structure and composition of trees across the treeline**

Black spruce is the dominant conifer of the Mealy Mountains, representing 67 percent of the stems surveyed, while white spruce had the fewest stems. This composition is consistent with post-glacial vegetation history and interior Labrador’s forests (Lamb 1980; Roberts, Simons, and Deering 2006). Regional palynological records indicate that post-glacial forests dominated by white spruce (~6,000 yr BP) were gradually replaced by competitively superior balsam fir and, finally, by black spruce (Lamb 1980) as organic matter accumulated, impeding drainage and raising soil acidity (see Viereck 1970). Eastern larch, although not considered in Lamb’s (1980) analysis, are also strong competitors in the wet, acidic soils characteristic of the region (Duncan 1954; Sutton 2008).

Black spruce dominance in the Mealy Mountains can be explained by its use of both seed and clonal regeneration (Black and Bliss 1980). Clonal layering is less influenced by climatic conditions than sexual reproduction, and allows for population maintenance and localized expansion when conditions do not favor seed production (Laberge, Payette, and Bousquet 2000; Trant, Jameson, and Hermanutz 2011). White spruce and eastern larch show lower prevalence of clonal layering and rely heavily on regeneration from seed (Elliott and Short 1979; Hustich 1953). In the Mealy Mountains, most survey intervals contained single white spruce or eastern larch stems (46% and 35%, respectively). Isolated from conspecifics, these individuals were likely derived from seed. By contrast, 20 percent and 6 percent of intervals contained single balsam fir or black spruce stems, which indicates that layering is an important strategy in the Mealy Mountains and may explain the prevalence of black spruce and balsam fir, particularly beyond the forest zone.

Black spruce may also dominate the treeline zone as a consequence of its production of semi-serotinous cones. These cones disseminate seeds gradually for months and years after maturity, creating an aerial seed bank in the absence of fire (Black and Bliss 1980). Seeds of the other species are released on maturity with highly variable viability. Balsam fir is viable for only a single season. With high annual variation in growing-season length and mean summer temperatures in the Mealy Mountains (Jacobs, Chan, and Sutton 2014), it is highly advantageous for black spruce to retain seed reserves for multiple years, thus increasing the likelihood of having climatic conditions suitable for germination (Black and Bliss 1980; Messaoud, Bergeron, and Asselin 2007), because once seeds make contact with the ground, viability decreases significantly after the first year (Fraser 1976).

Climate may exert more control over cone production near the species’ limit than endogenous factors, resulting in the variable, low annual cone production observed in the Mealy Mountains. Overall, the proportion of conifer stems producing cones was 13 percent and cone-bearing stem density was highly variable, ranging from 0 to 7,000 stems/ha. Larger scale climate effects on cone production are evident across the range of these species. For example, cone production by black spruce in northern Yukon (Brown et al. 2018) and white spruce near Churchill, Manitoba (Mamet and Kershaw 2012), and Alaska (Roland, Schmidt, and Johnstone 2014) decreased along the treeline. Siros (2000) did not find a significant relationship between black spruce cone production and latitude in western Québec, but production dropped significantly at the treeline compared to the southern forest–tundra transition. Declining black and white spruce cone production toward the Mealy Mountains alpine tundra is comparable to observations at other Canadian treeline (Brown et al. 2018; Mamet and Kershaw 2012).

Masting was not observed in any of the four species during surveys, nor were any mast years apparent between 2001 and 2010 (L. Hermanutz, unpublished data). Cone production by the four species is generally biennial in the optimal regions of their distributions (Powell 1977); alternate bearing cycles are controlled by poorly understood endogenous factors, but can be modified by extrinsic factors such as climate (Farmer 1996). Most stems surveyed in the Mealy Mountains were less than 4 m tall with limited crown development to produce the numbers of cones typical of resource-draining mast years found at lower elevations (>1,000 cones/tree; Powell 2009). Also, the average summer lapse rate creates a strong elevation gradient of more than 2°C between forest trees and the species limit (Jacobs, Chan, and Sutton 2014). This temperature gradient may explain in part the significantly higher cone production by forest trees compared to krummholz trees.

Although black spruce was the most consistent cone producer among zones, its cone production did not differ significantly from eastern larch overall. White
spruce rarely produced cones beyond the forest zone and balsam fir had few cone-bearing stems throughout the treeline. White spruce and balsam fir are more constrained than black spruce by lower growing season heat sums, and as a result they produce fewer cones and have longer intervals between good cone crop years (Messaoud, Bergeron, and Asselin 2007). The reproductive buds of white spruce and balsam fir are also especially susceptible to damage from spring frosts (Nienstaedt 1985). Below-freezing temperatures are common during the Mealy Mountains growing season, where between May and July an average of twenty-nine days with temperature lows less than 0°C were recorded (2002–2007, J. Jacobs, unpublished data). Such temperatures can damage reproductive buds and may be a source of cone loss, particularly for white spruce and balsam fir. Black spruce may be less affected by frost damage, as bud flushing was found to occur approximately two weeks after white spruce (Zasada, Sharik, and Nygren 2002). Further study during late spring is required to quantify bud loss to frost.

Reproductive potential

Cone production, although useful as a measure for potential seed production, is not a reliable proxy of viable seed production near the treeline (Elliott and Short 1979). Consequently, seed viability for all four species was examined and, despite insect-induced mortality (affecting 85% of trees sampled), all species were found to produce some viable seeds in 2008 (Jameson, Trant, and Hermanutz 2015). However, seedling surveys suggest that germination is limited despite viable seed production by all species in each zone, with only two black spruce seedlings found across the treeline (Jameson 2012). Both were found in the warmest, least exposed area of the treeline at 512 m a.s.l. Variable climatic and biotic factors limit viable seed availability prior to dispersal (Jameson, Trant, and Hermanutz 2015) and species-specific requirements must be met before germination can occur (e.g., Black and Bliss 1980). Thus, the presence of viable seeds does not guarantee successful regeneration via seed, given that viable seeds must disperse to suitable seedbeds, germinate, and survive before tree establishment can occur (Brown et al. 2018). Our results are discussed in the context of where the potential for regeneration via seed is possible, but not necessarily where it will occur.

Although cone-bearing stem density in the Mealy Mountains is relatively low and variable, of the four conifers black spruce is in the best position to advance via seed (Figure 3). Black spruce is currently the most abundant and most consistent cone producer in the treeline. This current positioning combined with dominance conferred by clonal and seed regeneration, aerial seed banks, high physiognomic plasticity, and frost resistance suggests that black spruce is most likely to lead an upslope treeline advance. The krummholz zone, however, has low levels of cone and seed production for all species, which may slow the initial rate of treeline advance. Thus, infilling of the krummholz zone, with seeds dispersing from the transition and forest zones, seems a likely precursor to treeline advance.

Approximately 63 percent and 79 percent of potentially reproductive forest and transition-zone black spruce stems are between 0.8 m and 2 m tall. Taller black spruce trees produced more cones, with a sharp increase in cone production between the 0.8–2 m height class and the 2–4 m height class. Because warming at the treeline can elicit leader growth and crown ramification (Gamache and Payette 2004), cone-bearing capacity may increase and these smaller stems could eventually compete with or supplant established canopy trees, leading to increased dispersal ability (Nathan and Muller-Landau 2000; Payette et al. 1985). However, many important factors regulating tree growth at the treeline, such as wind and ice abrasion (e.g., Scott, Hansell, and Erickson 1993), may impede the advantages reaped from warmer temperatures.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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### Table A1. Central locations, elevations, and survey areas of forest and transition-zone sites within the Mealy Mountains, Labrador, Canada. Intervals surveyed were considered treed if they contained at least one tree and, thus, non-treed areas were removed from analyses. Locations are given in UTMs. Stem density is given for trees more than 5 cm in diameter at 1.3 m, while basal area includes all stems greater than 0.8 m in height of any diameter at 1.3 m.

| Zone | Site | Elevation (m a.s.l.) | Total Surveyed Area (ha) | Treed Surveyed Area (ha) | Number of Trees Sampled | Dominant Species | Stem Density (stems/ha) | Basal Area (m²/ha) |
|------|------|----------------------|--------------------------|--------------------------|-------------------------|------------------|-----------------------|------------------|
| Forest | F1  | 381285 5939244 | 0.052 | 0.052 | NA | 108 | P. mariana | 1,558 | 0.70 |
| | F2  | 383309 5938048 | 0.052 | 0.052 | NA | 142 | P. mariana | 1,365 | 0.75 |
| | F3  | 382195 5938985 | 0.056 | 0.056 | n = 28 | 420 | P. mariana | 1,536 | 1.38 |
| | Forest total | | 0.160 | 0.056 | n = 28 | | | |
| Transition | T1  | 379894 5941798 | 0.044 | 0.038 | n = 19 | 166 | P. mariana | 659 | 0.46 |
| | T2  | 379766 5941596 | 0.060 | 0.054 | n = 27 | 328 | P. mariana | 1,450 | 1.10 |
| | T3  | 380586 5944330 | 0.060 | 0.060 | n = 30 | 605 | P. mariana | 1,333 | 1.65 |
| | Transition total | | 0.164 | 0.152 | n = 76 | | | |

### Table A2. Krummholz transect characteristics and location, elevation, and area of krummholz-zone survey intervals within the Mealy Mountains, Labrador, Canada. Interval locations are given in UTMs.

| Transect (Intervals) | Transect Dimensions (m) | Total Transect Area (ha) | Total Treed Interval Area (ha) | Treed Interval Dimensions (m) | Number of Trees Sampled | Elevation (m a.s.l.) | Interval Area (ha) |
|----------------------|-------------------------|--------------------------|-------------------------------|-----------------------------|-------------------------|----------------------|------------------|
| K1 (n = 9) | 40 × 1,585 | 6.344 | 0.525 | 1 | 1 | 376948 | 5,943,076 | 776 | 0.031 |
| | 4 | 376877 | 5942952 | 762 | 0.020 |
| | 3 | 376791 | 5942803 | 759 | 0.024 |
| | 5 | 376511 | 5942417 | 755 | 0.027 |
| | 7 | 376477 | 5942370 | 753 | 0.026 |
| | 1 | 376394 | 5942255 | 752 | 0.113 |
| | 4 | 376334 | 5942165 | 768 | 0.041 |
| | 9 | 376227 | 5942005 | 803 | 0.005 |
| | 2 | 376138 | 5941928 | 786 | 0.075 |
| K2 (n = 13) | 20 × 1,545 | 3.089 | 1.283 | 2 | 3 | 376346 | 5941889 | 795 | 0.022 |
| | 3 | 376395 | 5941925 | 786 | 0.075 |
| | 4 | 376518 | 5942052 | 753 | 0.323 |
| | 5 | 376732 | 5942287 | 733 | 0.100 |
| | 6 | 376831 | 5942346 | 724 | 0.072 |
| | 7 | 376918 | 5942389 | 721 | 0.177 |
| | 9 | 376992 | 5942427 | 717 | 0.004 |
| | 2 | 377048 | 5942467 | 709 | 0.062 |
| | 10 | 377119 | 5942517 | 700 | 0.121 |
| | 11 | 377201 | 5942609 | 692 | 0.040 |
| | 12 | 377249 | 5942667 | 690 | 0.088 |
| | 13 | 377414 | 5942827 | 687 | 0.198 |
| K3 (n = 6) | 20 × 1,290 | 2.580 | 0.506 | 1 | 4 | 377927 | 5942741 | 679 | 0.049 |
| | 2 | 377768 | 5942543 | 661 | 0.115 |
| | 3 | 377608 | 5942328 | 668 | 0.207 |
| | 4 | 377555 | 5942225 | 683 | 0.009 |
| | 5 | 377358 | 5942006 | 714 | 0.001 |
| | 6 | 377165 | 5941767 | 738 | 0.124 |
| K4 (n = 6) | 15 × 325 | 0.488 | 0.313 | 1 | 1 | 378433 | 5931800 | 624 | 0.008 |
| | 2 | 378444 | 5931846 | 619 | 0.094 |
| | 3 | 378461 | 5941914 | 613 | 0.086 |
| | 4 | 378485 | 5942007 | 604 | 0.070 |
| | 5 | 378496 | 5942050 | 603 | 0.004 |
| | 6 | 378508 | 5942096 | 601 | 0.052 |
| Krummholz total (n = 34) | | 12.502 | 2.627 | | | | | |
Figure A1. Cone productivity index (a) and seed productivity index (b) across the treeline from the forest, transition, to krummholz zones shown for all conifers and for each tree species by treeline zone. The cone productivity index was calculated by summing the seed cone survey category midpoints and dividing by the survey area for each treeline zone. The seed productivity index was calculated by multiplying the cone productivity index by the mean number of seeds per cone for each treeline zone. Error bars represent standard error. Tree species are BS (black spruce), WS (white spruce), EL (eastern larch), and BF (balsam fir).

Table A3. Moran’s I analysis assessing spatial autocorrelation of overall conifer stem density at survey intervals 10, 20, 30, 40, and 50 m apart in one forest site (F3) and three transition-zone sites (T1–T3). No significant autocorrelation was found (α = 0.005).

| Site | Distance Class | Number of Pairs | Moran’s I | p Value | I(max) | I/I(max) | I/I(max) |
|------|----------------|-----------------|-----------|---------|--------|----------|----------|
| F3   | 1              | 25              | -0.043    | 0.794   | 0.794  | -0.067   |
|      | 2              | 25              | -0.176    | 0.347   | 0.347  | -0.265   |
|      | 3              | 25              | 0.051     | 0.819   | 0.819  | 0.074    |
|      | 4              | 27              | -0.144    | 0.432   | 0.432  | -0.248   |
|      | 5              | 26              | -0.143    | 0.427   | 0.427  | -0.199   |
| T1   | 1              | 17              | -0.098    | 0.598   | 0.598  | -0.138   |
|      | 2              | 24              | -0.199    | 0.322   | 0.322  | -0.378   |
|      | 3              | 20              | -0.117    | 0.588   | 0.588  | -0.225   |
|      | 4              | 23              | 0.199     | 0.307   | 0.307  | 0.462    |
|      | 5              | 28              | -0.121    | 0.497   | 0.497  | -0.226   |
| T2   | 1              | 24              | 0.211     | 0.256   | 0.256  | 0.242    |
|      | 2              | 28              | 0.301     | 0.121   | 0.121  | 0.416    |
|      | 3              | 26              | 0.081     | 0.663   | 0.663  | 0.108    |
|      | 4              | 27              | -0.066    | 0.698   | 0.698  | -0.110   |
|      | 5              | 28              | -0.152    | 0.387   | 0.387  | -0.234   |
| T3   | 1              | 25              | 0.158     | 0.452   | 0.452  | 0.215    |
|      | 2              | 27              | -0.087    | 0.628   | 0.628  | -0.117   |
|      | 3              | 29              | 0.258     | 0.101   | 0.101  | 0.366    |
|      | 4              | 27              | -0.1200   | 0.528   | 0.528  | -0.144   |
|      | 5              | 30              | -0.284    | 0.065   | 0.065  | -0.363   |