



Advancing towards novel tree lines? A multispecies approach to recent tree line dynamics in subarctic alpine Labrador, northern Canada

Andrew J. Trant^{1,2*} and Luise Hermanutz¹

¹Department of Biology, Memorial University, St John's, NL A1B 3X9, Canada, ²School of Environmental Studies, University of Victoria, Victoria, BC V8W 3R4, Canada

ABSTRACT

Aim Comparisons of how different species respond to changing climatic conditions offer insight into future community composition and the potential formation of novel communities. This study investigated changes at a subarctic forest–tundra ecotone, or ‘tree line’. Our objectives were: (1) to explore species-specific growth forms; (2) to identify temporal patterns of establishment and stand density; and (3) to explore relationships between climate and recruitment/survival amongst co-dominant tree species, with the expectation that climate change will affect species differentially.

Location The Mealy Mountains in the High Subarctic Tundra ecoregion in central Labrador, Canada.

Methods We examined tree line dynamics for four tree species over the past two centuries. Using ecological and age-structure data, we compared diameter/height relationships across the tree line and generated static age structures from which changes in stand density through time were compared. In addition, model residuals were used to quantify relationships between multi-decadal windows of temperature/palaeotemperature/Palmer Drought Severity Index and decadal tree recruitment.

Results Trees were more stunted as elevation increased, except for white spruce (*Picea glauca*) for which tree islands became the dominant growth form. The only tree seedlings found at the tree line were of larch (*Larix laricina*) and to a lesser extent black spruce (*Picea mariana*). From the age structure of trees (height > 2.0 m), only black spruce showed evidence of an advancing tree line. Larch and balsam fir (*Abies balsamea*) have become established at the tree line most recently and have undergone greater increases in density over the past few decades. Variability in recruitment increased with elevation: larch recruitment was positively correlated with temperature and negatively correlated with drought at low elevations but negatively correlated with temperature and positively correlated with drought at high elevations, whereas black spruce recruitment was consistently positively correlated with temperature and drought.

Main conclusions The multispecies approach provides evidence that species are responding differentially to climate. With continued climate change, we expect density increases and advances of larch and black spruce, giving rise to novel tree line communities.

Keywords

Abies balsamea, climate change, growth form, individualistic concept, *Larix laricina*, north-eastern Canada, novel vegetation communities, *Picea glauca*, *Picea mariana*, tree line advance.

*Correspondence and present address: Andrew J. Trant, School of Environmental Studies, PO Box 3060, STN CSC, University of Victoria, Victoria, BC, V8W 3R4, Canada.
E-mail: atrant@uvic.ca

INTRODUCTION

The boreal forest transitions to alpine tundra at the forest–tundra ecotone, or ‘tree line’ (Scott, 1995). At broad spatial scales, the positions of high-elevation tree lines consistently correlate with climate parameters such as mean annual soil temperature (Körner & Paulsen, 2004). At finer spatial scales, however, the relationship between temperature and tree line position is highly variable (Holtmeier & Broll, 2005). With substantial warming being observed in most subarctic and alpine regions (IPCC, 2013), forests are expected to encroach on alpine and tundra ecosystems (Kaplan & New, 2006). This increase in woody biomass will have important consequences for carbon dynamics (Cairns & Malanson, 1998; Wilmking *et al.*, 2006), albedo effects (Chapin *et al.*, 2005), and the fate of arctic–alpine species (Brandt *et al.*, 2013).

Changes in range limits, tree density, regeneration dynamics, and growth patterns have all been used to quantify subarctic tree line dynamics over the past few decades. At many sites, tree lines have advanced (e.g. Lescop-Sinclair & Payette, 1995; Lloyd *et al.*, 2002; Danby & Hik, 2007), although stable and retreating tree lines have also been documented (e.g. Szeicz & MacDonald, 1995). A meta-analysis by Harsch *et al.* (2009) suggests that changes in tree line position over the past century are related to the extent of regional winter warming and the type of tree line (i.e. diffuse, abrupt or krummholz). High levels of variability in the growth response of trees to climate suggest complex spatial and temporal interactions with temperature and precipitation (Wilmking *et al.*, 2004; D’Arriago *et al.*, 2007; Messaoud & Chen, 2011). The variability in tree line dynamics can partly be explained by the individualistic concept of the community (Gleason, 1926), which predicts that each species within a community will respond individually to changing climate over time. Tree lines with co-dominant tree species can thus be used to compare species-specific responses (Dufour-Tremblay *et al.*, 2012; Mamet & Kershaw, 2012) and to track the development of novel communities (Chapin & Starfield, 1997).

The response of tree lines to climate warming is dependent on many ecological processes. The production of viable seeds requires a minimum number of growing degree-days (Sirois, 2000). Establishment of seeds requires appropriate seedbeds, which are species-specific and which at tree lines may be less abundant than in a contiguous forest site where factors such as soil desiccation and temperature fluctuation are less pronounced (Germino *et al.*, 2002). Following establishment, the persistence of an individual requires a positive carbon balance (assimilation > respiration), which often depends on growing season length (Hoch & Körner, 2003). These species-specific characteristics are crucial for explaining the variability in responses observed in tree line environments.

This study investigated changes at a subarctic tree line. Its objectives were: (1) to explore differences in tree growth form among four co-dominant species; (2) to identify and compare temporal patterns of establishment and changes in stand density; and (3) to explore species-specific relationships between

climate and recruitment/survival. We expect tree line dynamics to vary substantially among species owing to species-specific trait and niche differences in response to climate.

MATERIALS AND METHODS

Study area

The dynamics of a multispecies tree line was studied in the north-central Mealy Mountains, Labrador, within the boundary of the proposed Akamiupishk^u/KakKasuak/Mealy Mountains National Park Reserve (53°36’6” N, 58°49’0” W; Fig. 1). Meades (2007) classifies the Mealy Mountains as being the southern outlier of the High Subarctic Tundra ecoregion. The tree line occurs along an elevational span of c. 600 m, which we classified into two zones based on the structural attributes of trees: (1) the ‘forest zone’ is dominated by trees with erect growth forms and has stands with the most closed canopies at the tree line, albeit with lower stem densities and less canopy structure than found in contiguous boreal or taiga forests (Scott, 1995); and (2) the ‘forest–tundra transition zone’ consists of trees with primarily erect growth forms, with some prostrate, or krummholz, growth forms, and less canopy structure than in the forest zone. The forest–tundra transition zone contains the tree limit (height > 2.0 m). The phrase ‘across the tree line’ is used herein to refer to an elevational transition, from the forest zone to the forest–tundra transition zone. The Mealy Mountains tree line is composed of four co-dominant tree species: balsam fir, *Abies balsamea* (L.) Mill.; larch, *Larix laricina* (Du Roi) K. Koch; black spruce, *Picea mariana* (Mill.)

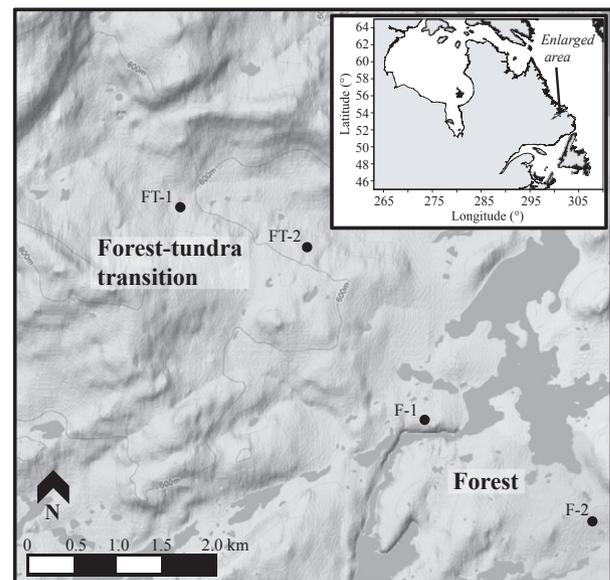


Figure 1 Map of eastern Canada, with the location of the study site in the Mealy Mountains, Labrador, Canada (53°36’6” N, 58°49’0” W; enlarged area). The enlarged area shows plots within the forest zone (F-1 and F-2) and forest–tundra transition zone (FT-1 and FT-2). Bodies of water and contour lines are in grey.

Britton, Sterns & Poggenb.; and white spruce, *Picea glauca* (Moench) Voss. Of these tree species, all are coniferous except for larch, which is deciduous. The age of reproduction for these species ranges from 4 to 15 years, with regular seed production after 20–30 years (Jameson, 2012), although this varies with local environmental conditions (Farmer, 1996). The majority of soils at the tree line are slightly acidic loamy sand (Sutton, 2008).

Summer temperatures for the first decade of the 21st century in central Labrador have increased by almost 1 °C compared with the period from 1970 to 2000 (Environment Canada, 2011). This warming trend is predicted to continue, resulting in temperature increases of 3 to 4 °C in the winter and of 2 to 3 °C in the summer by 2050 compared with the period from 1970 to 2000 (Lemmen *et al.*, 2008).

In the Mealy Mountains, there is a long-standing tradition of seasonal land use by Labrador Innu, with the majority of sustenance resource extraction being restricted to areas lower in elevation than our study sites (P. Armitage, Wolfverine & Associates Inc., St. John's, NL, pers. comm., 2012). Therefore, in the absence of human influence, differences in stand history and contemporary patterns can be attributed to climate, site characteristics, and ecological processes such as disturbance.

Field methods

All sampling was conducted in 2007 and 2008 within forest or the forest–tundra transition, within four plots with different aspects (F-1 and F-2, east; FT-1 and FT-2, north-east). Owing to high levels of landscape heterogeneity (e.g. forested, open water and exposed bedrock), plots were non-randomly selected to best represent the typical forest structure. Forest structure and stem density were measured by exhaustive sampling within plots (Table 1). Plot data for each zone [forest ($n = 2$) and forest–tundra transition ($n = 2$)] were combined when carrying out zonal comparisons. To estimate the age of establishment, basal increment cores were taken from all living and dead trees (height > 2.0 m). In both zones, regeneration was divided into small stems (height < 0.15 m), including both seedlings and vegetative reproduction, and

saplings (height between 0.15 and 1.99 m). Owing to the high densities of stems less than 2.0 m in height, regeneration was measured using five systematically located 2 m × 2 m subplots for each plot. The area sampled for saplings is small, because high levels of vegetative reproduction, especially in the forest zone, prevented exhaustive sampling at larger spatial scales. Within each subplot, a basal cross-section from each sapling and seedling was removed for age determination, wherein two radii per cross-section were counted. When seedlings were too small to remove a cross-section, a thin-section (using a scalpel blade) was removed and counted.

For each tree, height and diameter at breast height (d.b.h. = 1.4 m) were measured. Physical signs of damage (e.g. frost cracks, insect damage, porcupine scars) and whether individuals originated from seed or from vegetative reproduction (i.e. layering) were recorded. Individuals were considered to have arisen from layering if stems had the diagnostic J-shape at the litter/soil interface (Hofgaard & Rees, 2008).

Laboratory methods

Cores were glued into pre-grooved boards, and sanded and polished to increase the visibility of annual radial growth rings (Stokes & Smiley, 1996). All samples were counted using a Velmex[®] sliding stage micrometre (precision 0.005 mm) under a binocular microscope at 40× with a digital encoder. When the pith was missing from a sample, an adjustment was made to reflect this by estimating the age of the missing section based on the curvature of the innermost ring (Szeicz & MacDonald, 1995). Corrections were needed for 67% of samples, with the majority of corrections being of less than 10 years. Missing and false rings are uncommon at this study site (Trant, 2013).

DATA ANALYSIS

Growth form

To assess growth form, relationships were calculated by dividing tree height by d.b.h., meaning that taller, thinner

Table 1 Stand characteristics as classified by zone and species across the tree line in the Mealy Mountains, Labrador, Canada.

Zone	Area (ha)	Species	Tree density (stems ha ⁻¹)	Mean age (years) ± SE	Oldest tree (years)
Forest–tundra transition ($n = 2$)	0.10*	Balsam fir	110	79.1 ± 3.0	130
		Larch	75	107.9 ± 8.8	250
		White spruce	10	138.8 ± 17.1	210
		Black spruce	25	101.0 ± 12.1	180
Forest ($n = 2$)	0.10*	Balsam fir	199	62.5 ± 5.5	130
		Larch	380	57.0 ± 5.2	140
		White spruce	160	118.2 ± 19.1	340
		Black spruce	1550	78.3 ± 3.4	280

*Individual plot size was 0.05 ha.
SE, standard error.

trees have larger values than smaller, stunted trees. We explored these patterns across the tree line using general linear models for each species and all species combined. It was decided to examine tree growth form, rather than just height, in these analyses, in order to differentiate between younger and persistent trees.

Age structure, establishment and density

Stand dynamics were examined using the static age structures of living trees, saplings and seedlings, compiled by species, using decadal age-class frequency distributions to reduce error associated with age determination (Wong & Lertzman, 2001). For regeneration, data from subplots were scaled so that the survey areas matched those of trees (Table 1). Age structures were compared between the forest zone and the forest–tundra transition zone using three statistics as follows: (1) age-class distributions were compared using a nonparametric Kolmogorov–Smirnov test (K-S test); (2) median ages of individuals were compared using a nonparametric Mann–Whitney test (M-W test); and (3) establishment date was inferred using the five oldest individuals and compared using a M-W test. Frequency histograms of establishment dates were visually assessed to examine trends across the tree line and by species.

A further approach to examining stand dynamics involved reconstructing temporal changes in stand densities and recruitment across the tree line for each species. This approach incorporates establishment and mortality data to look at changes in the density of living trees at the decadal scale. From these data, changes in tree density can be compared between zones and among tree species. Furthermore, by comparing the relative patterns of reconstructed densities between zones, it is possible to infer rates of infilling and mortality (i.e. increases in local density), with steeper positive slopes corresponding to faster rates of infilling and/or lower rates of mortality. Extending tree density patterns enables coarse predictions to be made about future tree lines.

Recruitment and climate

The final approach used to understand recent tree line dynamics was to explore relationships between recruitment/survival and climate. Even for long-lived organisms, such as trees, it is expected that few individuals will survive to the older age classes, and therefore that they will decrease in abundance with increasing cohort age. Negative exponential function models are best suited for age structures with constant mortality rates and may be more suitable for clonal trees (Légère & Payette, 1981), whereas power function models are more appropriate for age structures that exhibit high mortality in younger age classes with survivorship increasing with age (Hett & Loucks, 1976). Recruitment periods and mortality were interpreted carefully so as not to overlook asymmetrical contributions of different cohorts through time

that are not explained by environmental conditions (Johnson *et al.*, 1994). Model selection of either negative exponential or power functions was based on significant *P*-values and by selecting the model with the largest r^2 -value. Significant models represent static age structures that follow the expected distribution, whereas non-significant models are either the result of limited sample size or of patterns that are not representative of naturally regenerated stands. The residuals from these models, calculated as the difference between the theoretical and observed values, provide valuable information about recruitment peaks (high levels of establishment and/or low levels of mortality) and recruitment troughs (low levels of establishment and/or high levels of mortality) over time (e.g. Daniels & Veblen, 2004).

To explore recruitment/survival and temperature patterns we used high-resolution gridded climate reanalysis data for summer temperature, with data coverage from 1901 to 2009 (CRU TS 3.1: University of East Anglia Climatic Research Unit, 2008). In order to extend the temporal coverage to 1800, we also used palaeotemperature data from Salt Water Pond (SWP), central Labrador (G.C. Jacoby & R.D. D'Arrigo, Lamont-Doherty Earth Observatory, Columbia University, unpublished data) and the Palmer Drought Severity Index (PDSI) for central Labrador (Cook *et al.*, 2004). The appropriateness of using palaeotemperature data was determined by running Pearson correlations for temperature and palaeotemperature data for the shared period (1901–1985; $r^2 = 0.76$, $P = 0.012$). The residuals from negative exponential and power function models at the decadal scale were analysed to test correlations with decadal mean summer temperatures (June, July, August), annual palaeotemperatures, and annual PDSI. Because recruitment can be influenced by climate at various temporal scales, decadal recruitment was correlated with multi-decadal windows of forward means, namely 10, 20, 30, 40 and 50 years following establishment (Szeicz & MacDonald, 1995; Danby & Hik, 2007; Mamet & Kershaw, 2012). Despite the limitations of using multi-decadal windows of forward means past 1960 (e.g. a 50-year forward mean is not possible after the decade of 1960), using this approach allows for the exploration of post-establishment influences of climate throughout the early life history stages of the trees. All statistical analyses were performed, and maps generated, in R 2.14 (R Development Core Team, 2006).

RESULTS

Growth form

For all species combined, trees were significantly more stunted in the forest–tundra transition zone than in the forest zone ($F = 19.65$, $P < 0.001$). When species were examined separately, this pattern held for balsam fir ($F = 29.14$, $P < 0.001$) and larch ($F = 19.02$, $P < 0.001$), but not for black spruce ($F = 3.33$, $P = 0.070$) or white spruce ($F = 0.71$, $P = 0.41$) (Fig. 2).

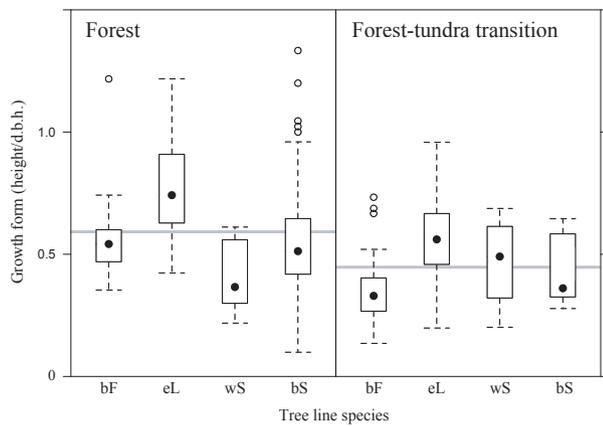


Figure 2 Box and whisker plots of tree growth form across the tree line in the Mealy Mountains, Labrador, Canada, for balsam fir: $F = 29.14$, $P < 0.001$; larch: $F = 19.02$, $P < 0.001$; white spruce: $F = 0.71$, $P = 0.41$; and black spruce: $F = 3.33$, $P = 0.070$. Grey lines correspond to significantly different mean values for each zone: $F = 19.65$, $P < 0.001$. Filled circles are median values, and open circles are data points that are beyond 1.5 times the size of the box (3rd to 1st quartiles). Species codes: bF, balsam fir; eL, larch; wS, white spruce; bS, black spruce. d.b.h., diameter at breast height.

Age structure, establishment and density

The number of small stems (height < 15 cm) varied across the tree line and by species, with the only substantial seedling densities observed in the forest zone for larch (9250 ± 2185 seedlings ha^{-1}). Moderate levels of vegetative reproduction were observed for balsam fir (1500 ± 474 small stems ha^{-1}) and black spruce (250 ± 79 small stems ha^{-1}). Only small numbers of black spruce seedlings (250 ± 79 seedlings ha^{-1}) and stems arising from vegetative reproduction (250 ± 79 seedlings ha^{-1}) were observed in the forest–tundra transition zone (Fig. 3).

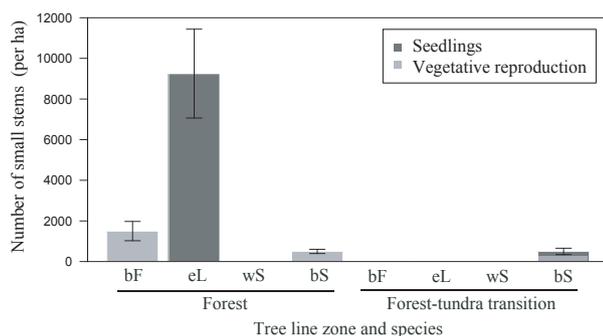


Figure 3 Small stem densities (< 15 cm in height) per hectare across the tree line in the Mealy Mountains, Labrador, Canada, according to species with error bars representing \pm standard error. Stems that were identified as being from sexual reproduction (i.e. seedlings) are shown in dark grey, and stems arising from vegetative reproduction are shown in light grey. Species codes: bF, balsam fir; eL, larch; wS, white spruce; bS, black spruce.

For trees, age-class distributions were significantly different for balsam fir and larch across the tree line (Table 2a). Based on median ages, trees of all species were older in the forest–tundra transition zone (85.0 years) than in the forest zone (70.5 years) (Table 2b). While this result seems counterintuitive when discussing advancing tree lines, it should be noted that the comparison of median values is a coarse metric that should be interpreted with other statistics that offer more insight into patterns of establishment and regeneration. For living trees, only black spruce had significant differences in establishment between zones, with stems in the forest zone establishing prior to those in the forest–tundra transition zone (Table 2c, Fig. 4). Establishment dates of living trees in the forest zone show an interesting pattern of black and white spruce establishing before balsam fir (Fig. 4), while in the forest–tundra transition zone, larch were older than the other species.

Within the forest zone, black spruce and to a lesser extent white spruce, had higher stem densities prior to 1900, when balsam fir and larch begin to show increased stem densities (Fig. 5). Within the forest–tundra transition zone, balsam fir and larch reached higher stem densities than white spruce and black spruce. By 2100, based on current regeneration trajectories, we predict the forest zone to have undergone dramatic increases in larch and black spruce, while the forest–tundra transition zone is predicted to show an increase in larch density only (grey curves, Fig. 5). Considering all trees sampled ($n = 367$), there were only six dead trees, giving a mortality rate lower than 2.0%, suggesting that all species are experiencing increases in density.

Recruitment and climate

For the forest zone, static age-structure models were significant for all species except white spruce, but for the forest–tundra transition zone this was the case only for larch and black spruce models (Fig. 6). In the forest–tundra transition zone, balsam fir had a pulse in recruitment (or reduced mortality) between 1940 and 1950, which resulted in non-significant age-structure models. The lack of significant age-structure models for white spruce may be a result of small sample sizes.

Recruitment residuals from the forest zone were positively correlated with summer temperature and palaeotemperature (CRU and SWP, respectively) with the exception of white spruce recruitment, which was negatively correlated (Table 3). In the forest zone, balsam fir and larch recruitment were negatively correlated with the PDSI, while the recruitment of both spruce species was positively correlated with the PDSI. For the forest–tundra transition zone, larch recruitment was negatively correlated with temperature, while black spruce recruitment was positively correlated. Both larch and white spruce recruitment was correlated positively with PDSI. Potential lag times for established seedlings to reach sexual maturity may differ across the tree line and should be considered when interpreting recruitment results.

Table 2 Results of statistical tests for differences in tree age structure across the tree line in the Mealy Mountains, Labrador, Canada, by: (a) distribution, (b) median age of all individuals, and (c) establishment date inferred from the five oldest individuals.

Species	(a) Age class distribution	(b) Median age	(c) Establishment date
Balsam fir	$D = 0.342, P = 0.050$	$W = 334, P = 0.004^{FT}$	$W = 5, P = 0.130^{FT}$
Larch	$D = 0.518, P < 0.001$	$W = 184, P < 0.001^{FT}$	$W = 5, P = 0.151^{FT}$
White spruce	$D = 0.588, P = 0.138$	$W = 26, P = 0.209^{FT}$	$W = 22, P = 0.056^F$
Black spruce	$D = 0.349, P = 0.166$	$W = 506, P = 0.034^{FT}$	$W = 25, P = 0.012^F$

^F or ^{FT} denotes a zone with an older median age or earlier establishment (F, forest; FT, forest–tundra transition). Values with $P < 0.05$ are in bold. The D -statistic corresponds to the maximum vertical deviation between the two distributions (Kolmogorov–Smirnov test), and the W -statistic reflects the difference between the two rank totals (Mann–Whitney test).

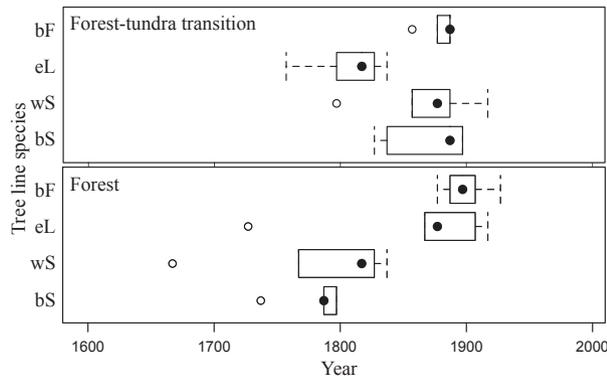


Figure 4 Box and whisker plots showing the establishment of trees across the tree line in the Mealy Mountains, Labrador, Canada, based on the establishment dates of the five oldest individuals in each zone, according to species. Filled circles are median values, and open circles are data points that are beyond 1.5 times the size of the box (3rd to 1st quartiles). Species codes: bF, balsam fir; eL, larch; wS, white spruce; bS, black spruce.

Age-structure models in the forest–tundra transition zone for balsam fir and in both zones for white spruce were not significant. No one window of forward means best explained correlations with temperature or drought indices.

DISCUSSION

Differences in how species respond to recent climate warming offer important insights into past and future changes at tree lines. Our results support the individualistic concept postulated by Gleason (1926), with interspecific variation in climate change responses. With this research, we have identified differences in growth form across the tree line and among species. Using a multispecies approach, we have highlighted species-specific responses at the tree line that may have been muted if species had been examined together or if only a single target species had been examined. We observed variability in the range expansion of tree line species, with multiple lines of evidence suggesting that larch and black spruce are responding to recent climate warming. Our results show that tree line advance over the past two centuries has

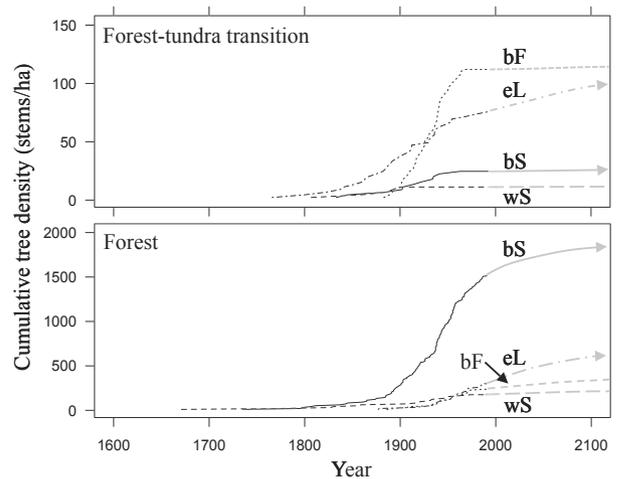


Figure 5 Reconstructed densities of living and dead trees (> 2 m in height) across the tree line in the Mealy Mountains, Labrador, Canada, according to species. Grey curves correspond to predictions of tree density until 2100 for the existing tree line zones. Grey lines terminating with arrows correspond to those species expected to lead tree line advance during the projected period. Species codes: bF, balsam fir; eL, larch; wS, white spruce; bS, black spruce.

been species-specific and that current climate warming will probably manifest in novel tree line communities (Mascaro *et al.*, 2013).

Shifts in tree growth form across tree lines can be used to explore plasticity and potential tolerance to climatic conditions. All tree species become more stunted across the tree line, coinciding with less tolerable climatic conditions, except for white spruce, which tends to form persistent and tall tree islands in marginal conditions. Larch showed the least stunted growth forms across the tree line, which may be best explained by the flexibility of larch stems and the ability of larch to tolerate more extreme conditions without stem damage (Sakai & Weiser, 1973). Less stem damage, in particular to the apical meristem, would result in less prostrate, horizontal growth in larch in contrast to balsam fir at our study site. The resilience of stems to damage may play an increasingly important role in relation to the expected increase in extreme weather, especially icing events, associated with

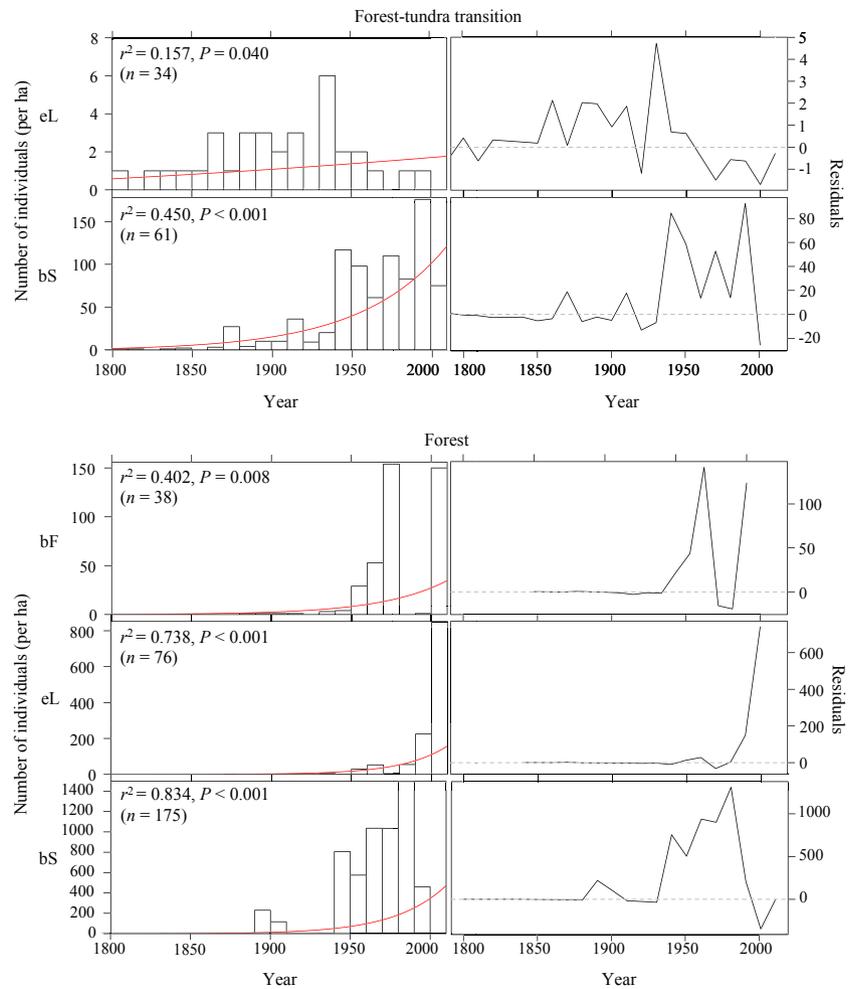


Figure 6 Age structure and residual plots across the tree line in the Mealy Mountains, Labrador, Canada, grouped into 10-year age classes for balsam fir (forest: $y = 2.92 \times 10^{-20} e^{0.024 \times \text{Year}}$), larch (forest: $y = 3.15 \times 10^{-30} \times e^{0.04 \times \text{Year}}$; forest-tundra transition: $y = 4.37 \times 10^{-17} \times \text{Year}^{5.09}$), and black spruce (forest: $y = 8.66 \times 10^{-15} e^{0.018 \times \text{Year}}$; forest-tundra transition: $y = 1.50 \times 10^{-203} \times \text{Year}^{62.21}$). Only significant models are presented. Red curves represent either negative exponential or power models, depending on which model had the highest r^2 -value. Species codes: bF, balsam fir; eL, larch; bS, black spruce.

climate change (IPCC, 2013). Unbroken, and thus taller, stems may give larch an advantage over other species with similar dispersal mechanisms.

There was a paucity of seedlings observed at the tree line, with the exception of larch and to a lesser extent black spruce, suggesting that a tree line advance has not been widely initiated over the last decade. Previous findings from this location show that trees are producing viable seed across the tree line (Jameson, 2012). Furthermore, seedling establishment does not appear to be limited by seedbed availability (Wheeler *et al.*, 2011). It has also been shown that black and white spruce planted as seeds or seedlings will establish and survive beyond the current tree line (Munier *et al.*, 2010). So why are seedlings not more common? Jameson (2012) found that pre-dispersal seed predation was high in the forest-tundra transition and krummholz zones, potentially limiting the abundance of seeds reaching the seedbed. This finding is supported by other studies that found that high levels of seed mortality via predation can constrain the position of tree lines (Payette *et al.*, 1982; Castro *et al.*, 1999). Another potential limitation for understanding regeneration dynamics is that, at our study site, knowledge of survivorship has been reported only for early life history stages, with no available data on sapling survival (e.g. Wheeler *et al.*, 2011).

While the presence of viable seeds indicates that the physiological requirements for seed production have been satisfied, tree line advance may require a large quantity of seeds (Danby & Hik, 2007; Holtmeier, 2009). Masting events, which may be needed to initiate substantial tree line change, have not been observed at our study site over the past decade.

Many studies have found increased vegetative reproduction at northern, compared with southern range limits (e.g. Black & Bliss, 1980; Szeicz & MacDonald, 1995; Pereg & Payette, 1998). In northern Quebec, Sirois (1997) documented a shift from sexual to vegetative reproduction in balsam fir and black spruce, starting in the late 19th century and becoming the dominant form of establishment of stems throughout the 20th century. These findings are consistent with regeneration patterns observed at our site. The prevalence of vegetative reproduction varies significantly among species and is dependent on environmental conditions (e.g. high humidity). At our study sites, we documented vegetative reproduction for three species, but not for larch. Vegetative reproduction will not enable the tree line to advance at the same rate that can be accomplished by seed dispersal, but vegetative processes may play a critical role in sustaining individuals through periods of less favourable climate, when the physiological requirements for seed production and

Table 3 Pearson correlations of recruitment/survival residuals of tree line species in the Mealy Mountains, Labrador, Canada, and temperature (1901–2009; CRU), palaeotemperature (1800–1985; SWP) and reconstructed Palmer Drought Severity Index (1800–1985; PDSI), with the size of multi-decadal window of forward means used in parentheses.

	Pearson correlation coefficient		
	CRU	SWP	PDSI
Forest–tundra transition			
Balsam fir	n.s.	n.s.	n.s.
Larch ($n = 34$)	−0.65 (30 years)	−0.42 (10 years)	0.42 (50 years)
White spruce	n.s.	n.s.	n.s.
Black spruce ($n = 61$)	0.55 (20 years)	0.54 (20 years)	0.47 (20 years)
Forest			
Balsam fir ($n = 38$)	0.78 (40 years)	0.58 (30 years)	−0.52 (50 years)
Larch ($n = 76$)	0.72 (10 years)	0.42 (30 years)	−0.67 (50 years)
White spruce ($n = 17$)	n.s.	n.s.	n.s.
Black spruce ($n = 175$)	0.81 (40 years)	0.58 (40 years)	0.48 (40 years)

Values with $P < 0.15$ are shown; values with $P < 0.05$ are in bold. Non-significant age structure models are denoted with n.s. CRU: mean monthly summer temperature data (CRU TS 3.1: University of East Anglia Climatic Research Unit, 2008); SWP: Salt Water Pond annual palaeotemperature data from central Labrador (G.C. Jacoby & R.D. D'Arrigo, Lamont-Doherty Earth Observatory, Columbia University, unpublished data); PDSI: annual Palmer Drought Severity Index for central Labrador (Cook *et al.*, 2004).

establishment are not satisfied. When climatic conditions become suitable, individuals that persisted via vegetative reproduction will be well positioned to initiate seed production and, theoretically, range expansion (Trant *et al.*, 2011).

An understanding of multispecies tree line dynamics requires an evaluation of individualistic responses, in order to anticipate changes in interactions and community structure. Our results document the adequate recruitment and possible upward migration of larch, as it is the only species with substantial seedling regeneration, partially climate-sensitive recruitment and physical characteristics well suited for the predicted future climate. The lack of climate-sensitive recruitment and seedling occurrence of larch in the forest–tundra transition zone suggests that a potential reproductive threshold has been surpassed in the forest zone, but not yet in the forest–tundra transition zone. That drier and warmer conditions correspond to larch recruitment in the forest zone, but not in the forest–tundra transition zone, suggest that soil moisture deficits may manifest differently across the tree line because seedbeds in the forest–tundra transition zone are exposed to higher levels of direct solar radiation (Holtmeier, 2009).

Across much of the circumpolar tree line, there has been a recent surge in larch (*Larix* spp.) recruitment (Devi *et al.*, 2008; MacDonald *et al.*, 2008; Mamet & Kershaw, 2012; Tremblay *et al.*, 2012), a pattern that we observed in Labrador, although perhaps to a lesser extent. The combination of high stem flexibility and the deciduous habit of larch makes them ideal species to thrive in winter environments where stochastic icing events are expected to be more common (Sakai & Weiser, 1973). Moreover, larch has an additional advantage over the evergreen tree line species because the shedding of needles prior to winter decreases the chances of their being adversely affected by winter drought (Berg & Chapin, 1994). Range expansions and increases in density for deciduous species, such as larch, will result in higher albedo

feedback processes compared with evergreen coniferous species (Bonan, 2008).

Because we have documented a range expansion over the past century, along with climate-sensitive recruitment, we expect black spruce to be an integral component of future tree lines. However, a recent gradual decrease in recruitment over the past 30 years that is otherwise linked to warmer and wetter climates is in agreement with the findings of Mamet & Kershaw (2012), who report a gradual decrease of black spruce recruitment at the tree line near Churchill, Manitoba. Although black spruce in northern Quebec has shown patterns of an increase in height over the past 20 years (Gamache & Payette, 2004), there has not been an observed increase in recruitment (Dufour-Tremblay *et al.*, 2012).

Less clear are the responses of the other co-dominant tree line species, white spruce and balsam fir, to recent climate warming. Despite having high stem densities and showing strongly climate-sensitive recruitment, similar to larch, balsam fir has shown poor regeneration by seed. Furthermore, the fragility of balsam fir stems may limit tree height and ultimately decrease dispersal potential owing to leader breakage. For white spruce, the fact that recruitment is negatively correlated with temperature over the past two centuries suggests that recent temperature increases may not yet be strong enough to promote white spruce regeneration (Payette, 2007), or that white spruce may be more susceptible to the summer moisture deficits that can accompany warmer summers (Barber *et al.*, 2000). Our results are concordant with work by Payette (2007), who also reported inland white spruce to have shown negative responses to climate warming in northern Labrador over the past 50 years, compared with coastal sites, which have shown a positive response. If future climatic conditions become favourable for white spruce, we expect that the other co-dominant tree line species will already have undergone a

range expansion. It will thus be more difficult for white spruce to advance, owing to inter-specific competition, meaning that it will become a sub-dominant species (Price & Kirkpatrick, 2009). While individualistic responses from our multispecies tree line are consistent with findings from other less diverse tree lines (e.g. Dufour-Tremblay *et al.*, 2012; Mamet & Kershaw, 2012), the potential for changes in inter-specific interactions should be the focus of future work.

Multispecies tree lines and the potential for novel communities

Although tree line responses to climate change are often discussed in the context of advance and the subsequent loss of alpine/tundra habitat, our work draws attention to the possibility of novel communities and ecosystems, forming as the result of non-uniform responses (Walther, 2010). Novel communities will probably be composed of individuals with traits favouring adaptability and dispersal (Lurgi *et al.*, 2012) and will be exposed to novel abiotic and biotic interactions (Hobbs *et al.*, 2009). Traits, such as persistence, which have played an important role in facilitating tree line advance over the past two centuries may be less relevant in the development of these novel tree line communities. Our work highlights the interspecific variation of plant communities exposed to the same changing climatic conditions. Based on predicted changes in densities and responses to climate, we expect novel tree lines to be composed of larch and black spruce. However, we also anticipate nonlinear responses of regeneration to changing climate, and therefore highlight the need to consider threshold responses from these and the other tree line species.

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BIOSKETCHES

Andrew Trant is a postdoctoral research fellow in the School of Environmental Studies at the University of Victoria. His research interests focus on how landscapes respond to climate change. Working with trees, shrubs and alpine plant communities, he is interested in how shifting climate means and variability can affect ecosystem function.

Luise Hermanutz is a professor of biology at Memorial University. Her research programme focuses on the conservation and ecology of northern ecosystems, looking at the impacts of climate change on tundra ecosystems, and the impacts of hyper-abundant herbivores on forest health and the conservation of rare plants.

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