Complex Changes in Plant Communities across a Subarctic Alpine Tree Line in Labrador, Canada

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ABSTRACT. As climate warms, abiotic factors, as well as plant community and biodiversity structure, may constrain or promote the movement of ecotone boundaries. Our study sought to examine how plant communities change across the tree-line ecotone of the Mealy Mountains in Labrador, Canada. We established eight transects (50–100 m in length) along an elevation gradient in three tree-line zones (forest, forest-tundra, and alpine-tundra) and recorded all species and cover of vegetation in contiguous 1 × 1 m quadrats. Companion abiotic parameters of nutrients and soil temperature were also measured. The absence of abrupt changes in important soil nutrients and growing season temperatures suggests that these factors do not limit tree species establishment beyond the current tree line. Vegetation cover and richness, however, were highly variable and in some cases changed non-linearly across the tree-line ecotone. Tree cover and species density generally decreased with elevation, while some field layer species (< 25 cm in height) increased; the latter change seems to be influenced by ground shrubs rather than herbaceous species. As expected, transects separated by the greatest difference in elevation were the least similar (higher beta diversity/species turnover); however, species turnover between the forest and forest-tundra transects was higher than it was between forest-tundra and alpine-tundra transects, even though the latter were separated by a greater elevation. Community structure and species turnover vary greatly across a tree line with the greatest differences between the forest and the forest-tundra, suggesting a biotic or abiotic barrier. While our ability to predict how the tree line will respond to continued climate change is complicated by these patterns in plant communities, the potential barriers investigated and others identified will be a useful focus for future studies.

Key words: climate change; forest-tundra ecotone; Labrador; Mealy Mountains; soil temperature; species turnover

RÉSUMÉ. Au fur et à mesure que le climat se réchauffe, les facteurs abiotiques de même que la structure des communautés végétales et de la biodiversité pourraient contraindre ou promouvoir le mouvement des délimitations des écotones. Notre étude cherche à examiner comment les communautés de plantes changent dans l'écotone de la limite forestière des montagnes Mealy au Labrador, Canada. Nous avons établi huit transects (de 50 à 100 m de longueur) le long d'un gradient d'altitude chevauchant trois zones de la limite forestière (forêt, toundra forestière et toundra alpine), puis répertorié toutes les espèces et la couverture végétale se trouvant dans des quadrats contigus d'un mètre sur un mètre. Nous avons également mesuré les paramètres abiotiques des éléments nutritifs et des températures du sol connexes. L'absence de changements abrupts en ce qui a trait aux importants éléments nutritifs du sol et aux températures de la période de croissance suggère que ces facteurs ne limitent pas l'établissement des espèces d'arbres au-delà de la limite forestière actuelle. Cependant, la couverture végétale et sa richesse variaient beaucoup et, dans certains cas, changeaient de façon non linéaire dans l'écotone de la limite forestière. De manière générale, le couvert arboré et la densité des espèces diminuaient avec l'altitude, tandis que certaines espèces de la couverture vivante au-dessus du sol (< 25 cm de hauteur) augmentaient. Ce dernier changement semble influencé par le couvert arbustif et non pas par les espèces herbacées. Comme nous nous y attendions, les transects qui étaient séparés par la plus grande différence d'altitude étaient les moins semblables (plus grande diversité bêta et plus grand renouvellement des espèces). Cependant, le renouvellement des espèces entre le transect de la forêt et le transect de la toundra forestière était plus grand qu'entre les transects de la toundra forestière et de la toundra alpine, même si ces derniers étaient séparés par de plus grandes élévations. La structure des communautés et le renouvellement des espèces varient beaucoup au sein d'une limite

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forestière, les plus grandes différences étant enregistrées entre la forêt et la toundra forestière, ce qui suggère une barrière biotique ou abiotique. Bien que notre aptitude à prévoir comment la limite forestière réagira au changement climatique continu soit embrouillée par les modèles de communautés végétales, les barrières potentielles faisant l'objet d'études et d'autres barrières joueront un rôle important dans des études ultérieures.

Mots clés : changement climatique; écotone de la toundra forestière; Labrador; montagnes Mealy; température du sol; renouvellement des espèces

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INTRODUCTION

Circumboreal ecosystems are experiencing significant environmental changes (IPCC, 2013). A key structural component of northern ecosystems is the tree line, a major transition between the forest and tundra and a significant habitat for numerous species, such as breeding birds (Lewis and Starzomski, 2015). The tree line is a complex ecotone that comprises not only tree species at the edge of their geographic distribution, but also a diverse assortment of understory plants and growth-forms (Körner, 2003). Relatively little is known about how non-tree community composition changes across elevation gradients (Hofgaard and Wilmann, 2002; Bruun et al., 2006).

Community similarity offers a means to examine the relationship between non-tree community composition and tree-line dynamics. Greater community similarity (or low beta diversity: less turnover in species across a gradient) across the tree line may result in increased potential for tree range expansion, as those communities are more likely to fulfill the biotic requirements of the dispersing tree species (e.g., the presence of dispersal agents, mycorrhizal mutualists, and suitable seedbed; Case et al., 2005). If plant species generally occurring in the forest ("supplying" environments) are also found across the ecotone (in "receiving" environments), even at low densities, their presence could signify a diffuse ecotone (Neilson, 1993), increasing the potential for related species to extend their altitudinal range. Thus, diffuse ecotones would have linear or gradual changes in diversity and species turnover. In contrast, more abrupt, or non-linear, patterns observed in plant communities—as would be the case if a boundary occurred across the ecotone where plant communities are not similar— could potentially indicate a biotic or abiotic barrier (e.g., temperature threshold or herbivory). Since different vegetation layers can respond differentially to climate change (Hofgaard and Wilmann, 2002; Pardo et al., 2013), observed patterns of plant communities across an ecotone are often complex and difficult to explain (Batllori et al., 2009).

To date, the focus of climate change research at the forest-tundra ecotone has been on trees (Harsch and Bader, 2011) and their responses to increased summer and winter temperatures, growing season length, and changes in duration of snow cover. At the tree line, relationships between temperature and range limits of tree species across gradients, both latitudinal (Payette and Filion, 1985; Hobbie and Chapin, 1998; MacDonald et al., 2000) and altitudinal

(Körner and Paulsen, 2004; Körner, 2012) are well known. How tree species are responding to recent global change (e.g., increased summer temperatures) is less clear. Numerous studies report a poleward or upward advance of the tree line at fine spatial scales (e.g., Lloyd et al., 2002; Danby and Hik, 2007; Pardo et al., 2013); however, responses at broad scales are more variable (e.g., Harsch et al., 2009; Harper et al., 2011; Callaghan et al., 2013). This variability may be due to regional climate patterns (IPCC, 2013), response potential of tree species (Trant and Hermanutz, 2014), low seed viability (Wilmking et al., 2012; Jameson et al., 2015), herbivory (Olofsson et al., 2009), local geomorphology and topography (Macias-Fauria and Johnson, 2013), disturbance regime (Brown and Johnstone, 2012), or the influence of seedbed and subcanopy species diversity (Wheeler et al., 2011; Cranston and Hermanutz, 2013). However, patterns of community structure are seldom considered as a means of understanding tree-line ecotone dynamics.

The distribution of plant species within the tree-line ecotone is in part related to local site characteristics that are linked to climate, either directly (e.g., air and soil temperature, frost damage, winter and summer precipitation, snow depth and duration, snowmelt timing) or indirectly (e.g., soil nutrients and seedbed composition; Hofgaard and Wilmann, 2002; Körner, 2003). Climate change is altering many of these local characteristics. For example, soil nutrient levels are higher because warmer temperatures accelerate rates of decomposition, though increased resource uptake by plants may offset these enhanced nutrient values (Davidson and Janssens, 2006). Climate-mediated disturbances may also increase or decrease the availability of seeds and seedbeds (Brown and Johnstone, 2012). Another important consequence of climate change for plants is the increased frequency of soil moisture deficits (i.e., drought) in summer (Vittoz et al., 2008). Earlier snowmelt could increase exposure of plants to early-season freezing events, particularly during vulnerable stages of early development (Inouye, 2008; Wheeler et al., 2014). Thus, multiple dynamic interactions control the distribution of plant species across the tree-line ecotone. Trees and understory respond differently to these interactions, and their responses are not linked (Pardo et al., 2013).

At our study site in the Mealy Mountains, the necessary ectomycorrhizal fungal communities (Reithmeier and Kernaghan, 2013), soil nutrients (Jacobs et al., 2014), and other requirements for seedling establishment and tree-line expansion (Munier et al., 2010) have been documented

beyond the current tree line. However, while minimum temperature requirements for seed production and germination have been satisfied in the Mealy Mountains, continued warming would likely have a positive effect on the current low seed viability (~5%; Jameson et al., 2015). Warming during the winter months could alleviate stress and mortality related to winter soil temperature minimums (Munier et al., 2010), though the resulting earlier snowmelt and increased vulnerability to late frosts might also lead to drought stress and mortality early in the growing season (Allen et al., 2010; Walker et al., 2015). However, evidence of tree-line advance in this system is limited and species-specific (Trant and Hermanutz, 2014). Current patterns of plant diversity, community structure, and abiotic conditions across the tree line are thus critical to a better understanding of the role that these components will ultimately play in mediating tree-line response (Camarero et al., 2006).

We characterized vegetation composition and structure across the tree line in the Mealy Mountains, using a community context to examine the supplying and receiving environments. Our objectives were to (1) describe changes in species composition and abundance of all vegetation layers (tree, shrub, field, ground) and functional types (tree, krummholz, tall shrub, medium shrub, small shrub, ground shrub, forest herb, moss, lichen, liverwort); and (2) characterize patterns in soil nutrients and temperature along an elevation gradient (i.e., temperature constraints, Körner and Paulsen, 2004; nitrogen deficiencies, Thébault et al., 2014). The overarching prediction is that diffuse tree lines will change gradually across the ecotone, with adjacent sites being more similar (i.e., less dissimilar) to each other than sites that are farther away. The results of this study will add to our understanding of community composition change across tree-line ecotones and provide information specific to this Labrador tree line that may help to predict the local ecosystem impacts of climate change.

METHODS

Study Site

The Mealy Mountains are the dominant highlands of southern Labrador, Canada (53°36′ N, 58°49′ W), occupying an area of approximately 2000 km^2 south of Lake Melville (Fig. 1A). Mountain summits are broad and rounded, with maximum elevations near 1100 m asl. The highlands (the area above 800 m) are dominated by alpine vegetation, bordered by boreal forest and wetlands at lower elevations, and have been described as southern mountainous outliers for the High Subarctic Tundra ecoregion (Meades, 1990). Local glacial and glaciofluvial deposits are conspicuous and important components of the physical landscape.

Our study site (Fig. 1A) is located approximately 20 km south of Lake Melville in an eastward trending valley south of an unnamed summit (1057 m; 53°36′ N, 58°50′ W). The site comprises approximately 63 km^2 at elevations of 500–1000 m and falls within the boundaries of the proposed Akami-uapishku/KakKasuak/Mealy Mountains National Park Reserve. We stratified our sampling of the tree line a priori by defining three tree-line zones (Fig. 1): forest (F), forest-tundra (FT), and alpine-tundra (AT). The F zone (~500 m elevation and lower) is a relatively closed-canopy forest dominated by black spruce (*Picea mariana*), white spruce (*P. glauca*), balsam fir (*Abies balsamea*) and eastern larch (*Larix laricina*), with a seedbed composed primarily of feathermosses (*Pleurozium schreberi* and *Hylocomium splendens*) under the shaded canopy cover and *Cladonia* lichens in unshaded gaps (Fig. 1B). The FT zone (550–650 m) is a complex of open-canopy habitat with black spruce krummholz patches and white spruce, balsam fir, and scattered eastern larch (Fig. 1C, D; Jameson et al., 2015). Other dominant FT zone species include Arctic dwarf birch (*Betula glandulosa*), northern bilberry (*Vaccinium uliginosum*), Labrador tea (*Rhododendron groenlandicum*), and black crowberry (*Empetrum nigrum*), with the seedbed composed of patchy lichens and feathermosses (Cranston and Hermanutz, 2013). The AT zone (~650 m and above) is dominated by low-lying shrubs such as northern bilberry, lingonberry (*Vaccinium vitis-idaea*) and mountain heath (*Phyllodoce caerulea*) with feathermoss and lichen seedbeds (Fig. 1E; Munier et al., 2010). Exposed rock, bedrock and small ponds are common throughout the FT and AT zones. A complete species list can be found in online Appendix 1.

Climate studies were conducted in the study area from July 2001 to October 2009, using automatic climate stations at three locations and short-term instrumentation at other locations along the elevation gradient. This region supports warm, moist summers and cold winters with more than 2.0 m of annual precipitation, much of which falls as snow. Late-winter snow cover was deeper and more uniform in the F zone (2.0 ± 0.3 m) than in the FT (1.4 ± 0.6 m) and AT (1.3 ± 0.5 m) zones. Average annual growing degree days (using a 5°C threshold) were 754, 694, and 455 in the F, FT, and AT zones, respectively, and the corresponding average growing season temperatures were 11°C, 10°C, and 8°C (Jacobs et al., 2014).

Field Methods

The method used in this study was modified from PPS Arctic Manual protocols (common protocols for field measurements and handling of collected materials for PPS Arctic, a core project under the International Polar Year: http://ppsarctic.nina.no; Hofgaard and Rees, 2008). Along an elevation gradient through the three zones (F, FT, and AT), we laid out eight transects perpendicular to that gradient (F-1 = 50 m, F-2 = 100 m, FT-1 = 100 m, FT-2 = 50 m, FT-3 = 50 m, FT-4 = 100 m, AT-1 = 100 m, AT-2 = 50 m). Specific locations were selected to capture vegetation representative of each zone and minimize non-vegetation features such as bare ground and open water. More transects were established in the FT zone to capture the apparent
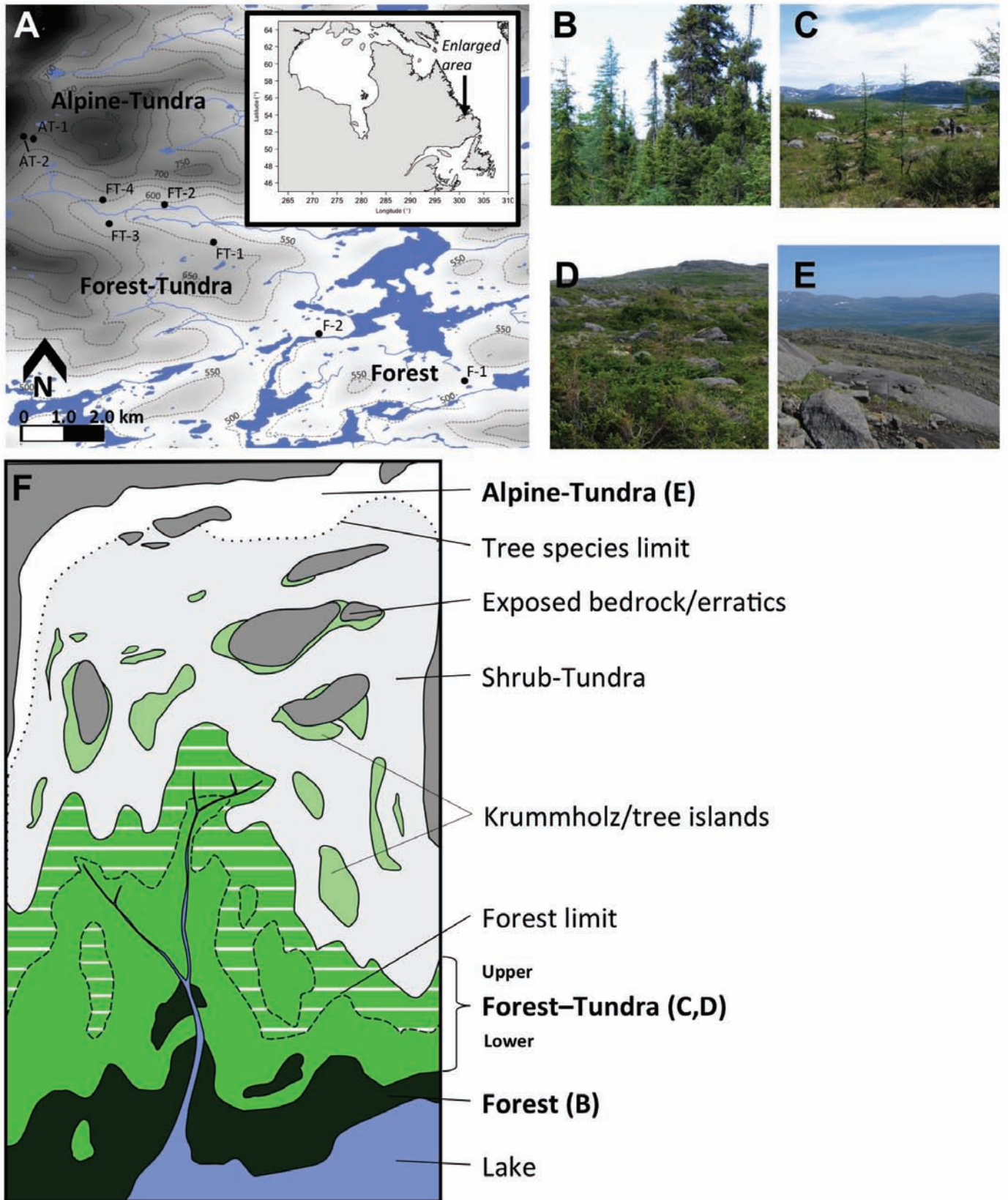
FIG. 1. A) Map of the study site in the Mealy Mountains, Labrador (Canada), with 50 m contour lines, and representative photos across the tree line for B) forest, C-D) forest-tundra, and E) alpine-tundra zones, and F) a stylized tree line illustrating the high level of heterogeneity and variability.

high levels of variability in this zone. Transect length was increased to 100 m when additional field time was available, though the number of quadrats used in subsequent analyzes was standardized to ensure equal sampling effort. While the purpose of this study was to investigate vegetation composition, encountering exposed rock and open water was unavoidable given the heterogeneity of the landscape, especially in the FT and AT zones. The location and length of transects therefore minimized those elements wherever possible (in a stratified random sampling framework; Diekmann, 2003). In zones with trees (F and FT), additional plots were established directly adjacent to transects for extensive sampling of the physical and age structure of trees (see Trant and Hermanutz, 2014).

Soil Nutrients and Temperature

Soil nutrients (N, NH_4-N, NO_3-N, Ca, Mg, K, P, Mn, S, and Al) were sampled in the summers of 2007 and 2008, using plant root simulator ion exchange membranes (PRS™ anion-cation pairs, Western Ag Innovations, Saskatoon, Saskatchewan). Probes were buried in soil at 10 cm depth along the elevation gradient (Fig. 1A) over periods of at least four weeks, from late June into July (F: $n = 66$, FT: $n = 113$, AT: $n = 42$). Soil temperature along the elevation gradient (Fig. 1A) was measured hourly over a full year (2008–09) using data loggers (Onset Inc.) placed at 10 cm depth away from large, statured vegetation or mounds and depressions (F: $n = 4$, FT: $n = 7$, AT: $n = 4$; Jacobs et al., 2014).

Vegetation Community Structure

We established contiguous 1×1 m quadrats along each transect, so that the number of quadrats was equal to the length (m) of each transect (F-1: $n = 50$, F-2: $n = 99$, FT-1: $n = 100$, FT-2: $n = 50$, FT-3: $n = 50$, FT-4: $n = 100$, AT-1: $n = 100$, AT-2: $n = 50$). To capture the spatial structure of the vegetation community, we estimated cover of vegetation by species (or in some cases by group) within each quadrat in each of the following predefined layers: tree (> 200 cm), shrub (> 25 cm tall), field/herbaceous (< 25 cm), and ground (mosses, lichens, bare ground, water, etc.), as well as by functional type: tree (> 200 cm), krummholz (mature tree < 200 cm), tall shrub (> 100 cm), medium shrub (50 to 100 cm), small shrub (25 to 50 cm), forest herb, and ground shrub (see Hofgaard and Rees, 2008 for details). We grouped plant species in each vegetation layer into six cover classes: 1: < 1%, 2: 1%–5%, 3: 6%–25%, 4: 26%–50%, 5: 51%–75%, 6: 76%–100%.

DATA ANALYSIS

Soil Nutrients and Temperature

Bioavailable soil nutrient fluxes over a four-week period during the growing season (June, July, and August) were compared among zones using ANOVA (F: $n = 66$, FT: $n = 113$ and AT: $n = 42$) and were later $\log_{10}$ transformed for better visualization of patterns in figures. Hourly soil temperature data were used to calculate daily averages and standard errors (Jacobs et al., 2014).

Vegetation Community Structure

The number of quadrats with vegetation community data varied between transects because a subset of quadrats contained only exposed rock or open water. As F-1 had the minimum number of vegetated quadrats ($n = 41$), we randomly selected the same number of quadrats ($n = 41$) from all other transects to ensure equal sampling intensity.

We explored mean cover (percent cover per m^2) and species richness (number of species per m^2) of evergreen versus deciduous species, as well as herbaceous versus woody species and the listed functional groups. Standard errors were used to depict differences among mean values of vegetation structure within transects.

Community Composition and Beta Diversity

To explore plant community structure and cover across the elevation gradient, and associate dominant vegetation to the tree-line zone, we used non-metric multidimensional scaling (NMDS) with fitted centroids to explore the relationships amongst the vegetation layers and zones (Zuur et al., 2007). This approach is more appropriate than a constrained ordination such as canonical correspondence analysis (CCA), which is best suited for testing specific hypotheses and also assumes a unimodal relationship (Oksanen et al., 2007; Zuur et al., 2007). Further, NMDS is a more appropriate method for data sets in which many observations are equal to zero (Zuur et al., 2007).

NMDS analyses were conducted using package vegan, function "metaMDS" (Oksanen et al., 2007) in the statistical software package R (R Development Core Team, 2012). To evaluate the relationship between vegetation composition along the elevation gradient, we used the "ordiellipse" function, which creates a dispersion ellipse using standard error of the weighted average of scores (Oksanen et al., 2007). Changes in cover and species composition are presented in two ways: as a biplot of the species scores and as 95% confidence ellipses of the transect centroids (site scores).

A Sørensen's Index of Dissimilarity (SID) was calculated from presence/absence matrices for each species. We then constructed a Euclidean elevation dissimilarity matrix and correlated it to the SID matrix using a Mantel Test (Zuur et al., 2007). To compare patterns of dissimilarity to the expected pattern of species turnover across a diffuse ecotone, we fit a linear model to Sørensen dissimilarity between unique combinations of transects and the corresponding difference in Euclidean elevation. A linear model was selected over non-linear models because it could be interpreted as diffuse (gradual) changes across the tree line. Non-linear models were difficult to interpret given
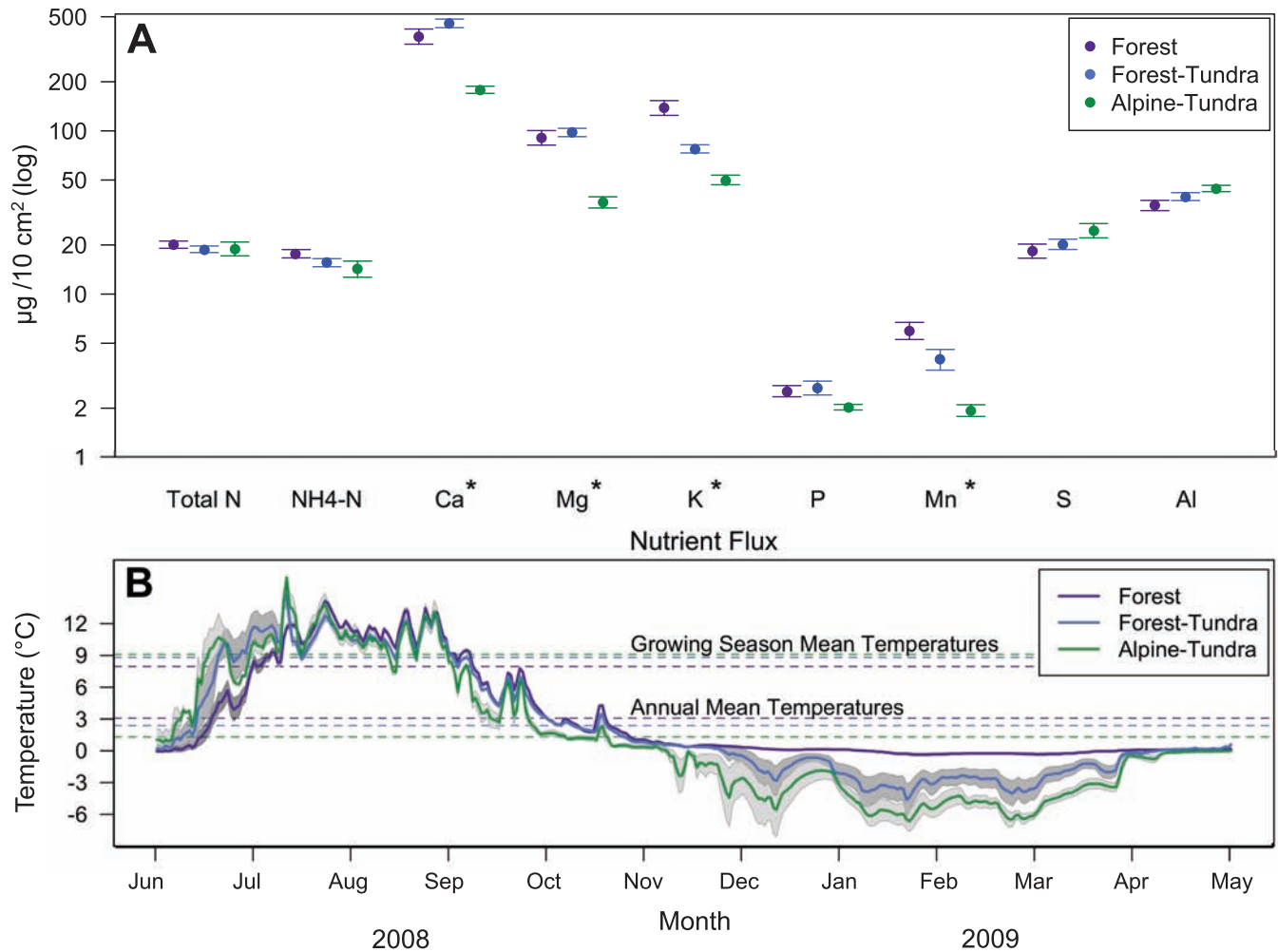
FIG. 2. Descriptive data across the tree line in the Mealy Mountains, Labrador (Canada). (A) nutrient fluxes (mean ± SE) over a four-week period. Asterisks (*) denote significant differences among tree-line zones. (B) daily averaged soil temperature at 10 cm depth. Shaded areas represent SD, and dashed lines corresponding to the growing season (June, July, August) and mean annual temperatures for each zone.

that we were examining transect similarity as a function of difference in elevation between transects.

In the regression between SID and Euclidean elevation dissimilarity, positive residuals indicate higher-than-average dissimilarity over the transects, whereas negative residuals indicate lower dissimilarity. For a diffuse tree line, sites separated by greater distances were expected to be more dissimilar (i.e., less similar). Analyses were performed using the statistical package R (R Development Core Team, 2012).

RESULTS

Soil Nutrients and Temperature

No significant differences among zones were found for total N, NH_4-N, P, S, and Al. Differences in Ca, Mg, K, and Mn were significant (t-test; $p < 0.01$), with the lowest levels in the AT. NO_3-N was often below the limit of detection

(< 2.0 µg/10 cm^2/burial time) and therefore was excluded from analyses (Fig. 2A). For annual soil temperature, F soils were on average nearly 2°C warmer (mean = 3.1°C) than AT soils (mean = 1.3°C) and 1°C warmer than FT soils (mean = 2.4°C); however, growing season soil temperatures were more similar across zones (Fig. 2B). Soil temperatures decreased with elevation in winter ($p < 0.01$), but no significant differences were observed throughout the growing season. The AT soils appear to warm more quickly in the spring and cool faster in the fall.

Vegetation Community Structure

Mean cover values of both evergreen and deciduous species were highly variable across the elevation gradient. As expected, the F zone had the highest mean cover of evergreen species in the tree layer (Fig. 3A). As a transition zone, the FT zone was very heterogeneous with the highest mean cover of evergreen and deciduous species in the shrub layer; of particular note are the high shrub cover values of
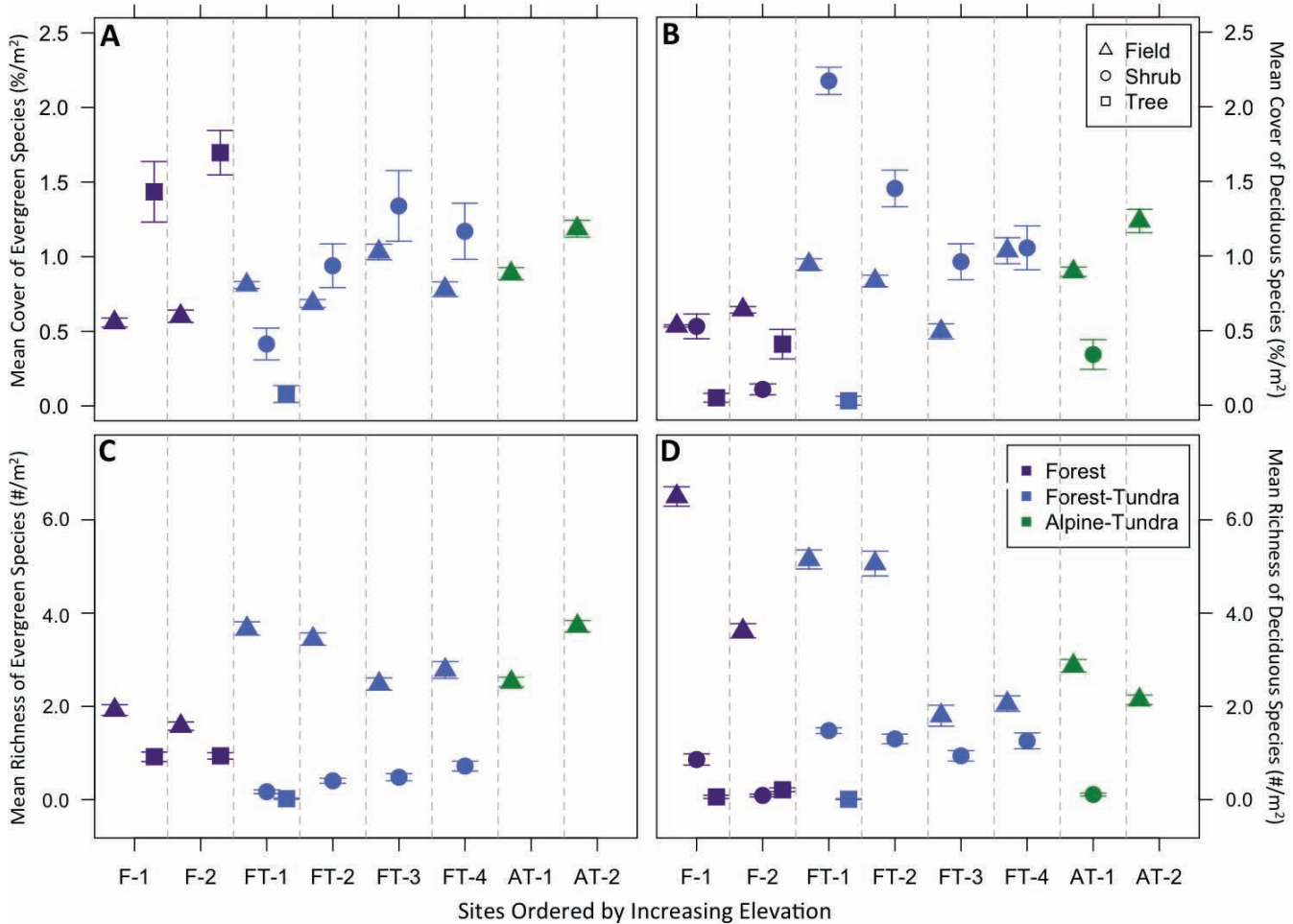
FIG. 3. Mean cover (± SE) of A) evergreen and B) deciduous species, and mean richness (± SE) of C) evergreen and D) deciduous species in field, shrub, and tree layers across an elevation gradient in the Mealy Mountains, Labrador (Canada).

black spruce krummholz and Arctic dwarf birch, northern bilberry, and Labrador tea in FT-4 (Fig. 3B). The AT zone was characterized by low deciduous shrub cover and was dominated by prostrate species that characterize the field layer, such as bearberry (*Arctostaphylos uva-ursi*) and Arctic dwarf birch (Fig. 3A, B). While field cover increased across the elevation gradient, tree density generally decreased. However, this decrease was species-dependent, with black spruce and eastern larch decreasing while white spruce and balsam fir were most dense in the FT zone.

Like cover values, species richness values for evergreen and deciduous species were highly variable across the elevation gradient. Evergreen shrubs did not occur in AT, which was dominated by field layer vegetation (Fig. 3A, C). Deciduous field richness decreased with elevation, while shrub richness was highest in the FT zone (Fig. 3D). From a functional group perspective, trees dominated the F zone and lowest part of the FT zone, with reduced cover and species richness in FT as the tree line becomes highly fragmented and patchy (Fig. 4). Krummholz occurred only in the FT zone and generally increased in both cover and species richness with elevation (Fig. 4). Tall shrubs such as alder were rare (see online Appendix 1) but were observed

on two transects (one in the F zone and one in FT). Medium shrubs such as Arctic dwarf birch were found in nearly all transects with relatively low cover and richness in the F zone. Medium shrubs represented the dominant functional group in both cover and richness in the FT zone; both cover and richness showed non-linear patterns across the elevation gradient (Fig. 4), and cover for evergreen and deciduous species had a similar pattern (Fig. 3A, B). Herbs were common and had similar coverage in all zones, though richness declined strongly with elevation (Fig. 4). Small shrubs such as Arctic dwarf birch and northern bilberry were also found in all zones, with relatively similar cover and species richness in all zones (Fig. 4). Generally, ground shrub cover and species richness increased with elevation (Fig. 4). While highly variable, functional group cover and richness showed variability patterns consistent with both a diffuse ecotone (linearly increasing or decreasing) and more complex ecotone dynamics (highest in FT zone).

Community Composition and Beta Diversity

The NMDS produced an adequate fit in two dimensions (Stress = 0.20). Confidence ellipses did not overlap within F
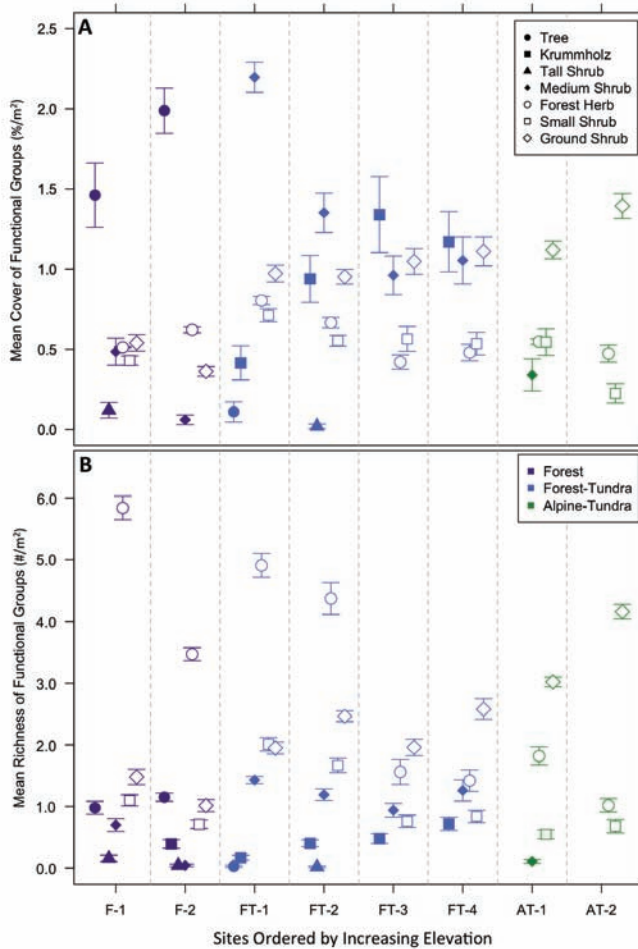
FIG. 4. Functional groups across an elevation gradient shown by A) mean cover and B) species richness (± SE) in the Mealy Mountains, Labrador (Canada).

FIG. 5. Non-metric multidimensional scaling (NMDS) ordination of species cover (Stress = 0.20) in the Mealy Mountains, Labrador (Canada). 'Ordiellipse' was used to create and overlay standard error ellipses around the centroids of each transect. Forest = purple, forest-tundra = blue, and alpine-tundra = green. Font size corresponds to vegetation layers with field = small, shrub = medium, and tree = large. See online Appendix 1 for list of species names.

described above (Fig. 5). The linear model (slope = 0.001 ± 0.0002, $p < 0.001$, R^2_{adj} = 0.520) describes the relationship between SID and difference in elevation. Transect comparisons showed that F and FT zones were more dissimilar than expected (with all comparisons falling above the modeled line), while FT and AT zones were more similar than expected (with all comparisons falling below the modeled line).

DISCUSSION

The complex change in vegetation communities across an elevation gradient is especially striking between plant communities in the forest and forest-tundra zones, suggesting that the "receiving" community of the forest-tundra zone is dissimilar, or non-diffuse, and there is potential for biotic and abiotic barriers to the establishment of forest species in the F-T zone. In our study, tree density changes were asymmetrical: some species (e.g., black spruce) decreased with elevation, while other species (e.g., balsam fir) had highest densities in the forest-tundra zone. As decreasing evergreen tree density is most often found across the forest-tundra zone (Takahashi et al., 2012), it is unusual to have greater densities in this zone. However, balsam fir is a poor disperser; the concentration of fir in the forest-tundra zone suggests that those trees are remnants from a period when the tree line was above its current elevation (Trant et al., 2011). In contrast, the plant communities in the forest-tundra and alpine-tundra zones were more similar than

or AT transects or most FT transects, nor did they overlap between AT and F transects or between F and FT transects. However, AT-1 slightly overlapped with FT-3 and FT-4, the most exposed of the FT transects. Site position along the elevation gradient appears to be the dominant driver of community differences, with much variability in community composition both within and among zones (Fig. 5).

The NMDS associates species with transects (Fig. 5). In particular, community differences between F and FT zones were associated with black spruce, Arctic dwarf birch, moss, lichen, and northern bilberry (field layer). Of these key species, black spruce was more characteristic of F transects, while Arctic dwarf birch dominated FT transects. Arctic dwarf birch and moss were both most abundant in FT transects. AT transects were characterized by lichen, Arctic dwarf birch (stunted and low-lying in the field layer), northern bilberry (field layer), and bearberry.

In general, transects separated by greater differences in elevation (F and AT) have a higher SID and greater beta diversity (r = 0.808, p = 0.002; Fig. 6). This turnover in community composition is driven by the loss of trees and mosses and the dominance of shrubs and lichens as
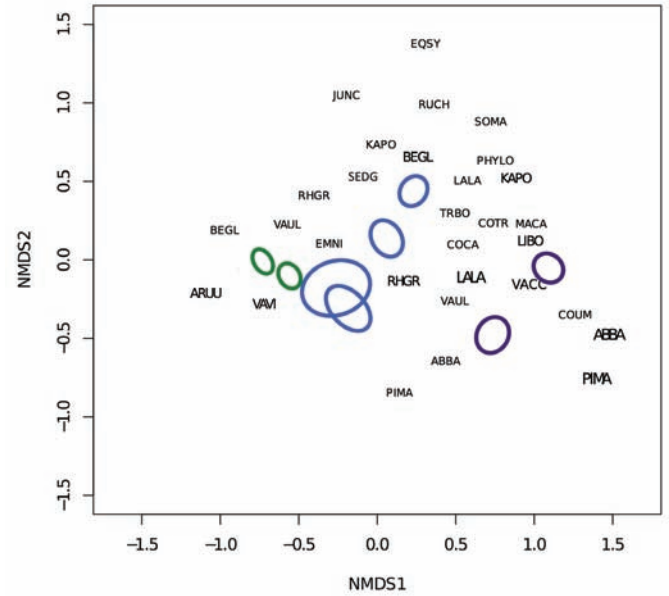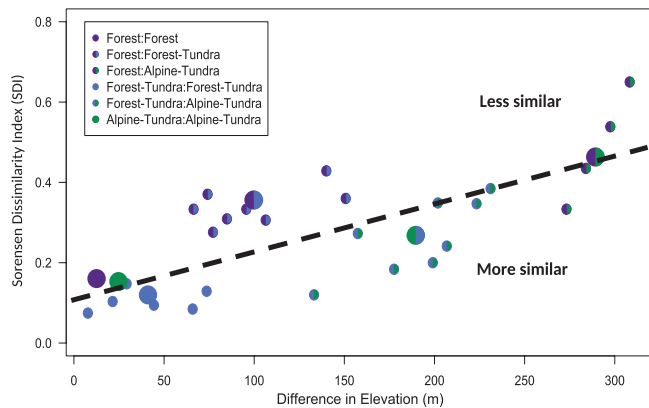
FIG. 6. Sørensen's Index of Dissimilarity and Euclidean elevation dissimilarity values in the Mealy Mountains, Labrador (Canada) shown with a modeled linear relationship. The large circles correspond to the mean of each unique transect comparison (e.g., all forest and forest-tundra comparisons). Transect comparisons between the forest and forest-tundra (purple:blue) are more dissimilar than predicted across a diffuse ecotone, suggesting a barrier, despite being approximately 100 m closer in elevation to each other than forest-tundra and alpine-tundra transect comparisons (green:blue). Transect comparisons located above the modeled line represent greater species turnover (i.e., less similarity) than predicted across a diffuse ecotone and may represent a dispersal, environmental or ecological barrier. Transect comparisons located below the modeled line represent less species turnover (i.e., greater similarity) than predicted across a diffuse ecotone and may represent little change in community structure despite the change in elevation.

expected, which we interpret as meaning there are fewer barriers to establishment between these zones and hence they are more diffuse than the lower edge of the tree line. These circumstances could result in more rapid changes as forest-tundra species benefit from warming temperatures associated with climate change.

All three zones had similar levels of the most important growth nutrients, N and P, suggesting that available nutrients are not limiting for plant species at our study site. This result contrasts with those of Thébault et al. (2014), who found that inorganic nitrogen deficiencies may limit tree-line expansion in southern Patagonia. However, alpine-tundra sites did have significantly lower levels of soil Ca, Mg, K, and Mn, which may have more subtle but still significant consequences for plant species that should be examined in future studies. When considered together, nutrients are unlikely to be driving the observed patterns of diversity and composition or constraining future changes across the elevation gradient.

During the growing season, soil temperatures across the ecotone were not significantly different, and all zones exceeded the season mean ground temperature range of 6°–7°C postulated by Körner and Paulsen (2004) as the limit of tree growth. However, in early spring, alpine-tundra and forest-tundra soils warmed more quickly than the forest soils, probably because solar radiation increases at higher elevations as forest canopy cover decreases. In the winter, this faster warming is best explained by examining the direct effects of abiotic conditions, such as the quality and quantity of snow that insulates against temperature

extremes, an important factor affecting vegetation dynamics (Myers-Smith et al., 2011). Snowpack demonstrates high spatial variability outside the forest zone, especially in the forest-tundra zone, where heterogeneity in snow-trapping shrubs and topography drive snow accumulation patterns. These landscape-scale snow patterns contribute to the variability (forest-tundra and alpine-tundra zones) and stability (forest zone) of soil temperatures (Jacobs et al., 2014). Wind transport of snow is expected to be greatly reduced in a warmer winter (as happened in this region in 2010), when wetter snowfall and more frequent icing occur, implying that snow distribution patterns could become more uniform at higher elevations under a warmer climate. More uniformity in snow distribution patterns could influence plant communities by favouring the establishment of individuals in exposed areas that would previously have been relatively snow-free throughout the winter and by potentially shifting away from species that benefited from long-lasting snow-cover in depressions or snow berms (Kreyling et al., 2012). Recent temperature increases, as drivers of snow pattern change as well as possible soil moisture deficits, are expected to have contrasting effects on the trajectories of plant communities (Crimmins et al., 2011). Jacobs et al. (2014) concluded that, while annual precipitation in the region increased in 2001–10 relative to 1971–2000, the growing season climate has become drier as a result of increased evapotranspiration driven by 40 years of substantial regional climate warming (Way and Viau, 2015). Such changes in water balance at our study site may result in growing season drought stress that could decrease species' response potential (Walker et al., 2015). These lines of evidence suggest that the lower edge of this ecotone is non-diffuse, with barriers potentially driven by abiotic factors (including snow cover and possibly early growing-season temperatures) that appear quite different in the forest-tundra and alpine-tundra zones. Other abiotic factors, such as geology, permafrost, and differing soil textures, could also result in a barrier and should be considered in future studies.

Complex changes in vegetation communities are also driven by interactions between biotic and abiotic factors. Shifts in community structure and abundance, interpreted through mean cover of different vegetation layers, were variable across the tree line ecotone. Decreased tree abundance was accompanied by an increase in the abundance of medium shrubs. High cover of medium shrub species in the forest-tundra zone is likely related to increased tree patchiness and heterogeneity, which allow more light to the shrub layer while trees are still abundant enough to offer winter protection to shrubs by trapping snow. This protection comes in the form of reduced abrasion from ice-scouring if individuals are under snow (Scott et al., 1993), as well as insulation of soils from extreme winter and spring freezing temperatures (Jacobs et al., 2014; Wheeler et al., 2014). Medium shrubs also trap snow, and once established, they too could enhance survivorship of lower-statured vegetation in the alpine-tundra zone (Myers-Smith et al., 2011).

Unimodal cover and species richness patterns observable in the medium shrub functional group have skewed distributions, with maximum values at lower elevations in the forest-tundra zone. These distributions demonstrate larger differences in abundance between the forest and forest-tundra zones than between the forest-tundra and alpine-tundra zones, suggesting that the upper edge of the tree line is more diffuse than the lower edge.

Patterns of decreases (Grabherr et al., 1995) and increases (Batllori et al., 2009) in overall plant species richness have been documented along elevation gradients, with ecotone transition areas sometimes representing zones of highest species richness (Gottfried et al., 1998). In our study, plant species richness varied and was dependent on the particular layer or functional group being examined. Our results are similar to those of Bruun et al. (2006), who show markedly different patterns of species richness across an alpine elevation gradient with decreasing herbaceous species richness. The pattern that we observed of highest richness of woody species halfway along the elevation gradient was also observed in tropical highlands by Desalegn and Beierkuhnlein (2010), though contrary to our findings, that study reported an increase in herbaceous species richness. Low statured and woody plants may be better able to persist in environments with more extreme temperatures; given that they are generally longer-lived than herbaceous species and more likely to reproduce clonally, they could potentially capitalize on years with more favourable growing conditions (Trant et al., 2011).

We have documented complex changes across the tree line in community structure, species richness, species composition, and species turnover, changes which are inconsistent with a diffuse ecotone. These patterns were especially evident between forest and forest-tundra zones. Abiotic differences between these zones exist for soil temperature, with minimum values in the forest zone remaining near 0°C because of persistent and even snow cover during cold periods (Jacobs et al., 2014). Differences in community structure and diversity, despite the obvious linkages to seed germination, establishment, and recruitment, are rarely discussed in the context of tree-line advance (Dufour-Tremblay et al., 2012). Non-diffuse tree lines could impede advance through negative interactions between ground vegetation, shrubs, and tree seedlings and the lack of suitable seedbeds (Wheeler et al., 2011; Dufour-Tremblay et al., 2012; Cranston and Hermanutz, 2013). Indeed, our results suggest that the advance of shrubs into the alpine zone is the more likely scenario. However, although shrub cover has been suggested to facilitate tree-line advance through enhanced seedling establishment and survivorship (Treberg and Turkington, 2010), we did not find evidence of shrub facilitation at our study site (Cranston and Hermanutz, 2013). Tree-line change likely depends on complex interactions with shrub and ground layers, as well as abiotic conditions: the sorts of interactions for which we currently have limited empirical data, and which are seldom incorporated into our projections of future northern habitats.

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APPENDIX 1

The following table is available as a supplementary file to the online version of this article at:
http://arctic.journalhosting.ucalgary.ca/arctic/index.php/arctic/rt/suppFiles/4528/0
TABLE S1. Species names, codes, and associated layer used in the analyses in the Mealy Mountains, Labrador (Canada).

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