

Proliferating poplars: the leading edge of landscape change in an Alaskan subalpine chronosequence

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Abstract. We remeasured a classic chronosequence study in the subalpine zone of the Alaska Range to evaluate how plant community attributes have changed across a set of different-aged terraces over a 54-yr period (1958–2012). Our work focused on whether the tempo and trajectory of successional development described in the original study have changed over this period during which summer temperatures warmed by approximately 2°C. Our work revealed a rapid increase in the distribution, stature, and abundance of balsam poplar trees that was unanticipated in the original successional model alongside evidence that established late-successional plant communities have changed relatively little over the same time period. The spatial distribution of poplar expansion was both directional and highly variable, with greater expansion occurring in sites that were young surfaces in 1958, or else were disturbed during the intervening period. We present evidence that early successional environments in this region may be particularly susceptible to rapid alteration stimulated by climate warming that has allowed tree establishment and growth in subalpine areas. Sparsely vegetated sites allow for invasion or expansion of some species to be quickly realized because there is less resistance from competition with established vegetation, including mosses that insulate and paludify the soil. We suggest that established vegetation communities may have physical characteristics (such as cold and/or acidic soil profiles) that are inimical to the establishment of balsam poplar and may also be a source of competitive inertia, conferring a measure of resistance to directional changes in the landscape mosaic. However, when an early successional species has traits that allow it to persist and fundamentally alter the vegetation mosaic over time, as is the case with balsam poplar, it may serve as the leading edge of compositional changes with profound consequences. Our results highlight the capacity of a single species to catalyze the changes that may eventually lead to the altering of an entire landscape mosaic.

Key words: Alaska; climate change; Denali National Park; ecological succession; *Populus balsamifera*; shrub tundra; soil temperature; Special Feature: Science for Our National Parks' Second Century; vegetation change.

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INTRODUCTION

Vegetation change in response to a warming climate may transform large areas of Alaska in the coming decades (e.g., Chapin et al. 2010, Barrett et al. 2011), and some suggest that a “biome

shift” is currently underway in the region (Beck et al. 2011). However, Alaska supports a mosaic of vegetation types and plant communities that differ with respect to their resistance to changes in composition or process (Chapin et al. 2010). As a result, the rate of change in response to variation

in climate conditions will differ across the landscape based upon site and community-specific attributes (e.g., Johnstone et al. 2010a). Ground disturbance can accelerate vegetation change in response to warming in the far north and alpine areas (Lantz et al. 2009, Munier et al. 2010) and open sites early in primary succession may be more susceptible to rapid directional change. In contrast, sites supporting well-established vegetation and increased competition change less rapidly (Davis et al. 2000).

Increasing human populations and accelerated climate change have the potential to increase levels of disturbance. Thus, understanding changing successional dynamics is crucial for predicting changes in the pattern and process of Alaska's ecosystems into the future. Substantial research has already focused on changes in postfire secondary succession in the subarctic as climate and fire regimes shift (e.g., Johnstone and Chapin 2006a, b, Johnstone et al. 2010a, b, Kasischke et al. 2010). However, a less-studied dimension of successional change in the region is changing primary successional trajectories following geomorphic disturbance, which is our focus here. In the far north, plant communities early in primary succession generally exhibit faster rates of compositional change than communities late in a successional sequence because competition is reduced. Indeed, decreased competition early in primary succession may present fewer impediments to invasions of species into ecosystems. In some cases, early successional communities may harbor higher numbers of exotic species than later seres (Bellingham et al. 2005).

We expect, then, that plant community changes in response to climate shifts might manifest themselves first and most rapidly in early phases of primary succession as compared to well-established standing vegetation which could have greater resistance to change. This is important because relatively small changes that occur early in succession may have large consequences in shaping the ultimate successional trajectory and tempo. A gain or loss of even a single functionally distinct species early on can affect the fundamental trajectory of ecosystem development (St. John et al. 2012).

To investigate how a changing climate may be affecting primary successional trajectories in Alaska, we revisited a classic study of primary

succession (Viereck 1966). We anticipated that repeating this study would provide a unique perspective because the original fieldwork occurred before a pronounced trend of warming summer temperatures began in the 1970s. In addition, very few studies have directly assessed fine-scale plant community dynamics over half-century or greater spans of time based upon repeated field observations of specific study areas in the far north (but see Danby et al. 2011).

The original study was conducted on the outflow terraces of the Muldrow Glacier in Denali National Park and Preserve (then Mt. McKinley National Park, henceforth "Denali") in 1958 (Viereck 1966). Viereck's study described soil and vegetation development on a geomorphic chronosequence spanning different-aged landscape surfaces that he used to develop a model of soil and plant community succession. His hypothesized trajectory spanned sites occurring on recently colonized alluvium supporting a seral herb community he called the "pioneer stage" (stand 1; 25–30 yr old), through a "meadow stage" (stand 2; 100 yr old). He suggested that with the expansion of dwarf birch (*Betula nana*) and willow shrubs, the meadow stage would succeed to the "early shrub stage" supporting an open, low shrub canopy (stand 3; 150–200 yr old). He posited that the early shrub stage would succeed, through a deepening of the moss layer and a closing of the shrub canopy into a "late shrub stage" (stand 4; 250–300 yr old). Viereck used a much older upland surface north of the river for his representation of a "climax" stage of low shrub sedge, tussock-moss tundra (stand 5; 5000–9000 yr old).

Viereck described how the vegetation occurring on alluvium would develop and culminate (without further disturbance) into a low shrub, tussock-moss tundra community on wet, acidic, and organic-rich soils underlain by shallow permafrost, a common and widespread vegetation type in this region. He hypothesized that the physical changes associated with a deepening of the insulating moss mat, along with the progressive accumulation of organic matter with time, were the primary mechanisms driving the changes in soil attributes and plant community composition from seral herbs on barren silt to low shrub sedge, tussock-moss tundra. Central to Viereck's model of plant community change in this area was his hypothesis that soils progressively

cool over time, ultimately causing permafrost to develop, an assertion that relied both on his results and on other studies (Bliss and Cantlon 1957). In addition, Viereck (1966) cited the capacity of winter winds to injure exposed plant tissues and redistribute the snowpack as important factors regulating community structure in the area.

We used data from Viereck's (1966) study and a 2012 resurvey of the study area to evaluate the magnitude of plant species and community changes that have occurred across the Muldrow Glacier chronosequence over the last 54 yr. We also assessed the spatial variation in summer surface soil temperatures and spring snow depths relative to the successional sequence. This data set provided us with a unique opportunity to assess the predictions of successional change from the original study (Viereck 1966) in light of a changed climate, while also providing insights into how various plant communities may respond to continued climate warming in the future. Our primary objectives were to:

1. Reevaluate the successional trajectory proposed by Viereck (1966), to determine the degree to which observed changes matched the original successional model, while examining fine-scale changes at the species and plant community level over a period during which considerable climatic warming has occurred.
2. Investigate the patterns in two physical attributes of the successional stands that Viereck (1966) proposed as important, but did not quantify: variation in growing season soil temperatures and patterns in snow depth.
3. Quantify the apparent increase in abundance and distribution of trees (primarily *Populus balsamifera*) in the study area and investigate the possible consequences of this change for succession and plant community composition and distribution.

MATERIALS AND METHODS

Study area

The study area is located on the north slope of the Alaska Range in Denali at approximately 63°25' N, 150°35' W (Fig. 1) and is described by Viereck (1966). Here, the McKinley River

flows west out of the terminal moraine of the Muldrow Glacier, forming an outwash plain of coarse gravel approximately 1 km wide by 15 km long. The study area encompasses a set of five distinct, "stepped" outflow terrace surfaces, separated by obvious several-meter breaks in elevation (the entire study area lies between 730 and 760 m). The youngest terrace surfaces are adjacent to the McKinley River and the oldest increasingly farther away to the north. The terminal moraine on the eastern boundary of the study area has a minimum stabilization age of 1300 yr (late Holocene; Dortch et al. 2010). Viereck (1966) identified this set of terraces as a chronosequence, which he used to gain insights into how vegetation changes through time may occur. To assist in visualizing spatial variation of the primary vegetation structure, we created a vegetation map of the study area based on a supervised classification of 2010 SPOT5 satellite imagery (Appendix S1: Table S1, Fig. S1, Data S1). A representative photograph of each stand from 2012 is shown in Fig. 2.

The study area has a subalpine, continental climate with long, cold, dry winters and short, warm summers. The mean annual temperature at the headquarters of Denali (628 m elevation) was -3°C , with a mean high of 20°C in July and a mean low of -22°C in January, and a mean annual precipitation was 381 mm (1971–2000; Shulski and Wendler 2007). The majority of the annual precipitation in Denali falls during the summer (June through August). We used a 1-km spatial resolution PRISM (parameter-elevation regressions on independent slopes model) downscaled version of the Climatic Research Unit 3.1 gridded monthly temperature and precipitation data (Mitchell and Jones 2005, Simpson et al. 2005, available at <http://www.snap.uaf.edu/data.php>) to calculate the mean monthly summer (May through August) temperature and precipitation sums for the period 1901–2009 (the entire period for which these data were available). Estimated average monthly temperature during the May–August growing season significantly increased from a mean of approximately 9.5°C at mid-century to a mean of about 11.5°C in 2009 (adjusted R^2 : 0.40; $F = 36.62$, $df = 2, 106$; $P < 0.00001$). The temperature trend through time was curvilinear with significant linear and quadratic terms and the majority of this temperature increase

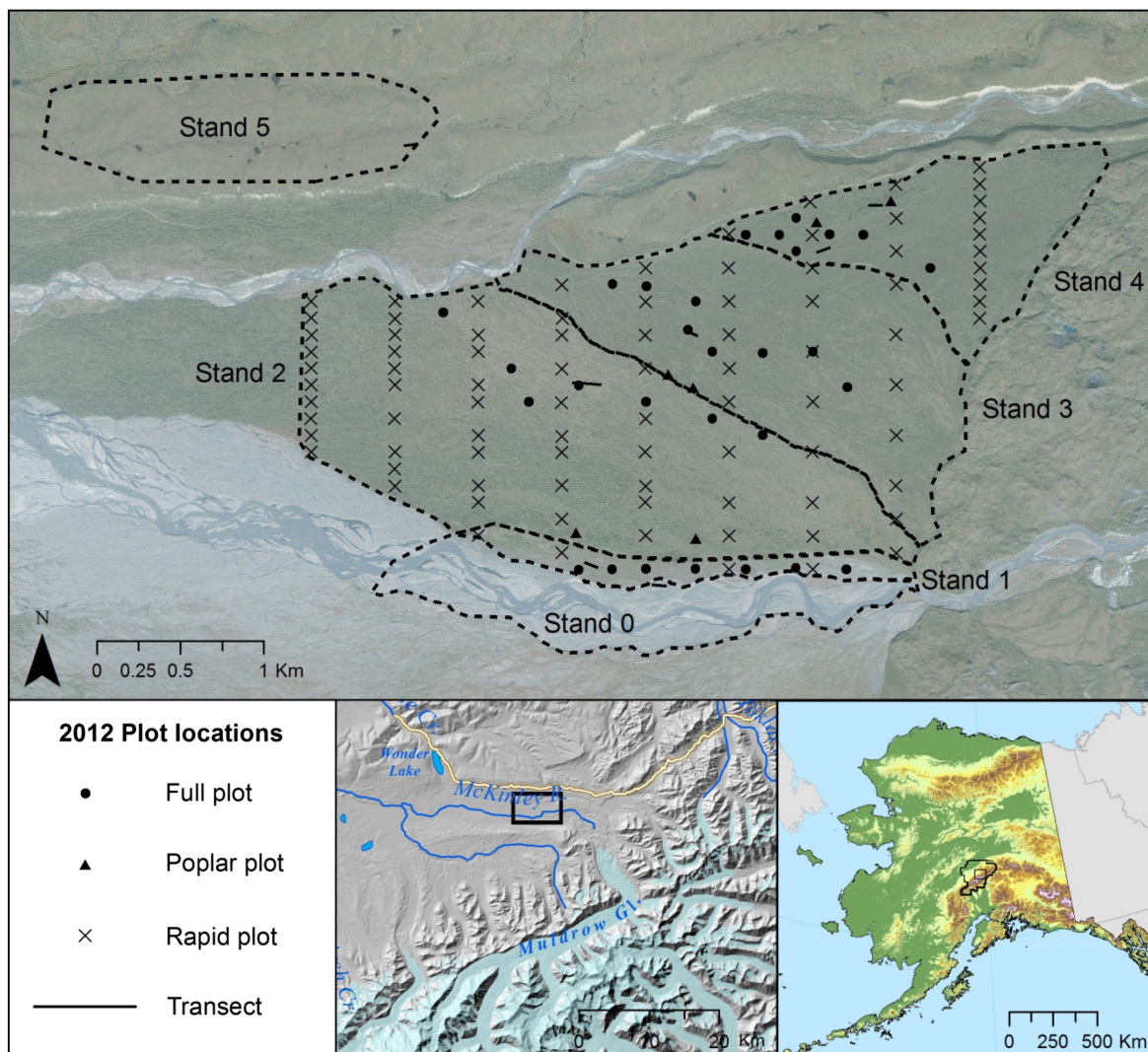


Fig. 1. Map of the study area showing 2012 plot locations and types and an IKONOS image of the study area. The position of the study area on the landscape is shown in the lower center, and the position of Denali National Park and Preserve in Alaska in the lower right. Stand 0 outlines the newest deposited surfaces nearest to active channels of the McKinley River and is utilized in this study to approximate the successional position of stand 1 in 1958. Stands 1–5 are outlined here as identified and described by Viereck (1966) in 1958. See *Methods* for plot type descriptions and selection methods.

occurred between the mid-1970s and 2009 (Fig. 3). There was no trend in summer precipitation for the study area over the period 1901–2009.

Sampling design

Our sampling plan integrated the remeasurement of plots sampled during previous visits to the study area (1958, 1975, and 2000), and a new set of observations to expand the spatial

coverage for the study area (Table 1, Fig. 1). Both the remeasured plots and new observations were made to compare with two legacy data sets: (1) the original 1958 field observations using a circular, variable-sized nested-plot design (Viereck 1966), henceforth “full plots,” and (2) a set of 90-m transects with 1- and 4-m² quadrats systematically located at 10-m intervals, henceforth “transects,” established in either

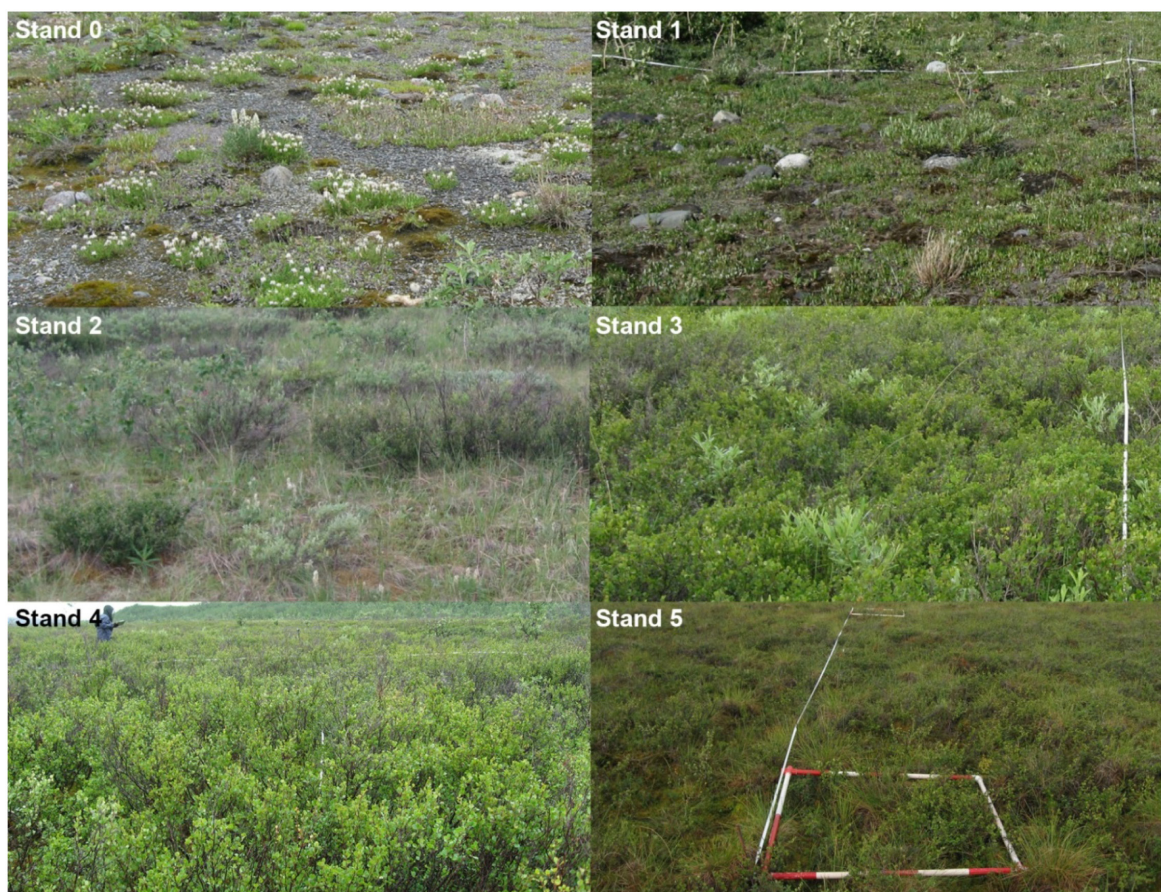


Fig. 2. Photographs showing a representative view of vegetation in each successional stand of the Muldrow Glacier study area as viewed in 2012.

1975 (D. Densmore, *unpublished data*) or 2000 (C. A. Roland, *unpublished data*).

Two of the original full plots were permanently marked and thus relocated and remeasured in place (PQ1 and PQ6). The remaining original full plots (33) were not marked. We estimated their location using Viereck's original field notes, and established our plot at the nearest point in a 100-m systematic grid (with random start) in a geographic information system (GIS). This yielded a set of plot locations possessing a broad similarity to the layout of the original study, while avoiding selection bias. We performed full plot sampling only in the first four successional stands (29 plots), because field investigation (C. A. Roland, *unpublished data*) revealed that successional change had not occurred in the "climax" tundra stand on permafrost between 1958 and 2012.

We remeasured two of the original 1975 transects (stands 1 and 5) and an original 2000 transect (stand 0) based on the relocation of original markers and photographs. However, the four remaining transects did not have permanent markers (installed in 1975: stands 2, 3, and 4; installed in 2000: stand 2). For these, we navigated to the estimated original transect end location in consultation with field notes and photographs, and used a random bearing and distance (≤ 20 m) to select the site for a new transect end nearby, installing new transects along the same bearing as the original transects.

In addition to resampling the two legacy data sets, we established a new set of plots and one transect to better quantify the spatial variation of woody vegetation and plant community composition throughout the study area. Eighty-nine 200-m² circular plots, henceforth "rapid

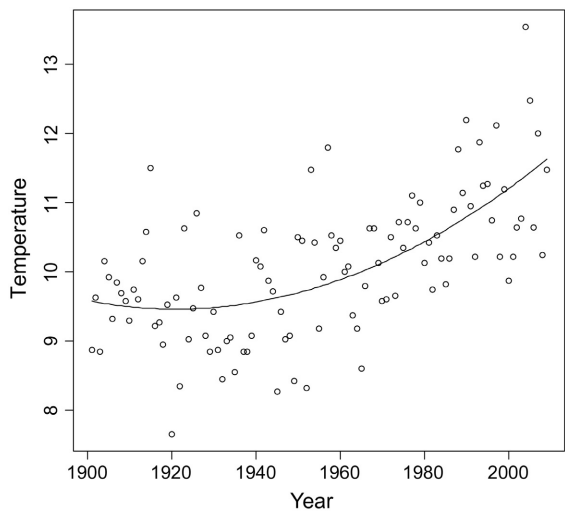


Fig. 3. Estimated mean monthly summer temperatures (°C) for the study area derived from climate data for each year (1901–2009) (available at <http://www.snap.uaf.edu/data.php>). The line illustrates a significant increasing curvilinear trend in mean monthly temperature over the 109 yr shown (adjusted $R^2 = 0.3974$, $F = 36.62$, $df = 2, 106$, $P < 0.00001$).

plots,” were distributed along nine north–south transects (Fig. 1) using a GIS to choose the nearest corresponding point in the same 100-m systematic grid used to re-establish the original full plot locations. One additional 90-m transect (in stand 4) and six additional full plots (two each in stands 2, 3, and 4) were installed within areas of balsam poplar woodland, henceforth “poplar transect” and “poplar full plots” (Table 1). The transect endpoint or full plot center was chosen via GIS, selecting the nearest corresponding point in the 100-m systematic grid that would allow for

a 90-m line or 16 m diameter circle of relatively homogeneous overstory cover as determined by high-resolution Ikonos satellite imagery for the study area (Fig. 1).

Field methods

Photography.—The legacy data sets we queried (1958, 1975, 2000) included numerous photographs of the study area, both at plot and transect locations and at points of interest throughout the stands. We relocated original photograph locations, where possible, to take repeated photographs, matching the frame and direction of view to that of the originals as closely as possible. We compared these photographs to help visualize any changes in vegetation structure between the sample iterations for each stand type, and to illustrate noteworthy ecological dynamics in the area.

Vegetation surveys.—We used three sets of field methods to examine the variation in plant communities across the study area, each equating to one of the data sets described above. Unknown plant specimens were collected from the field and identified in the laboratory by the first (vascular plants) and second (mosses and lichens) authors. Nomenclature for vascular plants followed Hultén (1968), the Flora of North America (1993+), and Cody (1996). Nomenclature for nonvascular plants followed the Flora of North America (1993+) for mosses and Esslinger (2015) for lichens. Viereck also made a comprehensive set of voucher specimens during the original sample, allowing us to establish a rigorous synonymy across the sample iterations and improve our confidence in the comparability of our results.

In the 35 full plots (including poplar full plots), we employed the original vegetation sampling

Table 1. Data sets used/plot types installed in the Muldrow Glacier study area of Denali National Park and Preserve, Alaska.

Plot type	Stand 0		Stand 1		Stand 2		Stand 3		Stand 4		Stand 5	
Year	1958	2012	1958	2012	1958	2012	1958	2012	1958	2012	1958	2012
Full plots	0	0	8	7	10	10†	10	9†	6	9†	5	0
Transects‡	0	1	0	1	0	(1)	0	1	0	2§	0	1
Rapid plots	0	0	0	4	0	41	0	28	0	16	0	0

Note: Value listed is the number of 200-m² plots or 90-m transects sampled in each visit year.

† Including two poplar full plots.

‡ Installed in 1975, except for stand 0 that was installed in 2000.

§ Including one poplar transect.

methods published in Viereck (1966). Starting at the plot center, we searched a series of concentric circular plots (0.01, 0.05, 0.1, 0.25, 0.5, 1, 2, 5, 10, 20, 50, 100, and 200 m²) for all vascular species. Non-vascular species were recorded up to the 20-m² plot size due to the smaller size and the pattern of variation in these taxa. We visually estimated percent cover of each species for the 200-m² plot size, regardless of which nested plot it was observed in. However, the cover estimation technique varied somewhat between iterations. Viereck (1966) relied upon a modified Hult-Sernander system to estimate the cover using of the following categories: “r” —erratic occurrence, usually only one or a few plants in the plot (0.1%); “+” —occasional, but less than 5% of the total plot (1%); “1” —abundant or common, but insignificant in cover, less than 5% cover of the entire plot (2.5%); “2” —very abundant or common, but low in cover, 5–25% of the total plot area (15%); “3” —25% to 50% cover, irrespective of the numbers of individuals (38%); “4” —50% to 75% cover (62%); “5” —75% to 100% cover (88%). In 2012, we estimated the cover, by species, using continuous cover percentages of all integers between 1% and 100%. To make comparisons between sample iterations, we used the midpoint percentage for Viereck’s original class estimates (given in parentheses above) and the continuous percentage estimates that we made in 2012. We measured diameter at breast height (1.37 m) of all live and dead trees ≥ 1.37 m in height and tallied live and dead seedlings (tree species ≤ 1.37 m in height) within a 20-m² circular subplot (2.52 m radius from plot center).

We employed the original methods for sampling the 90-m transects (including the poplar transect; D. Densmore, *unpublished data*), based on Ohmann and Ream (1971). We placed a 1-m² quadrat at 10-m intervals along a 100-m tape in which the cover of all vascular (excluding tall shrubs and trees) and nonvascular species was estimated. Where available, we used photographs taken in 1975 to ensure that quadrat placement was accurate. Using the corner of the 1-m² quadrat as the center point, we estimated the cover and density (in 1 cm diameter size classes) of tall shrubs and trees in a 4-m² circular plot (114 cm radius).

For the eighty-nine 200-m² rapid plots, we recorded the percent cover and the mean and maximum height of a set of woody species selected based on their commonness within

the study area and importance in one or more successional stages: *Picea glauca*, *Populus balsamifera*, *Betula nana*, *Potentilla fruticosa*, *Salix alaxensis*, *Shepherdia canadensis*, and *Vaccinium uliginosum*, as well as the genera *Dryas*, *Ledum*, and *Salix*. To quantify the density and basal area of tree species, we employed the same methods as for the full plots listed above.

Physical covariate measurements.—We measured soil attributes, surface strata depths, and temperature in small (30–40 cm) soil pits at four points on the outer boundary of each full and poplar plot (described in Roland et al. 2013). We did not dig soil pits in the rapid plots due to time constraints. At each pit, we measured surface layer horizon depths, depth to restrictive feature (using metal probe), and soil temperature (at a depth of 10 cm into the mineral soil). We also measured probe depth and soil temperature on all seven transects (stands 0–5 and poplar), probing at the two corners of each 1-m² quadrat that intercepted the transect, where quadrats were located at 10-m intervals.

We measured snow depths at the center of all full plots (including poplar full plots) and rapid plots and at an additional 261 points on a 100-m systematic grid over the period 20–23 March 2014, around the peak of annual snowpack depth for this area. During this time, the weather was stable and winds calm, with daily mean temperatures of approximately -3.8°C . We accessed locations by skis and used an avalanche rescue probe marked with 1-cm gradations to measure depths.

Analytical methods

Comparing vegetation and physical covariates among stands and between sample iterations.—We compared the variation in physical and plant cover values among stands, and between sample iterations in the same stand, using the Kruskal–Wallis nonparametric test to compare medians, treating full plots as replicates within each stand and each sampling year. We tested for the differences among stands using the pairwise Mann–Whitney *U*-test and the Benjamini–Hochberg adjustment method for multiple comparisons (McDonald 2014). Because full plot data for both sample iterations only included stands 1–4, we used transect data to compare means of physical values across all stands (0–5). We did not use statistical tests on these

comparisons because individual quadrats on a transect were not independent.

We used data from the 1958 and 2012 full plot data set (including poplar plots) to compile species lists by stand and year. We calculated the mean cover by stand and sample iteration for 17 taxa that occurred with at least 5% mean cover across one of the stands in either sample iteration (the equivalent of cover-abundance category 2 in Viereck 1966, Table 1) and determined the net change in mean cover over the period. We concluded that change was significant if an exact or asymptotic permutation test for differences in means revealed a P -value < 0.05 . We excluded stand 5 full plots (1958; $n = 6$) from these analyses because we did not remeasure this stand in 2012. Total sampled area was then equal between sampling iterations ($n = 35$, area sampled = 7000 m², in both 1958 and 2012). Because some sampling variation among iterations was to be expected, we considered plant species either “gained” or “lost” from the two 35 plot samples from stands 1–4 if only they occurred in at least four plots in one sample iteration and were absent from the other sample. We compiled the minimum and mean elevational range of these species in Denali, as quantified by a randomized landscape-scale systematic plot vegetation data set (Roland et al. 2004, Roland and Schmidt 2015) to investigate the elevational distribution of vascular plant species lost from the 1958 sample or gained in the 2012 sample.

Ordination of plant community data.—We used a nonmetric multidimensional scaling (NMS) ordination (PC-Ord version 5.33; McCune and Mefford 2006) to visualize the variation in community composition among stands and between sample iterations. We ran the NMS ordination analysis on AutoPilot mode, slow and thorough, with a random starting configuration and the Sorenson's distance measure selected. These settings choose a final dimensionality by comparing final stress values, and the best solution must be less than 95% of the randomized runs for that dimensionality (see McCune and Mefford 2006). Our main matrix consisted of estimated plot cover values of all species that occurred on three or more plots in 1958 and/or 2012 ($n = 113$ species; plot n , not including poplar plots, = 64). Our secondary matrix consisted of categorical variables that described plot status (sample iteration, stand, poplar presence/absence) and a set of covariates describing vegetation

character. Included in this matrix were measures of vascular plant, shrub, dwarf shrub, forb, and graminoid diversity; vascular plant richness; feathermoss, poplar, dwarf birch, and mineral soil cover; and living density and basal area of poplar.

We used NMS scores of selected species and all full plots (including poplar plots, whose scores were assigned post hoc) to plot their location in the existing ordination model. We rigidly rotated the ordination axes to align Axis 1 with stand number (116°), also displaying selected covariates of interest. To approximate the successional trajectory and compare the change in the vegetation community of each stand between sampling iterations, we calculated and plotted within-stand averages for each iteration, separating the 2012 poplar full plots as a separate sample iteration.

Poplar occurrence model.—We used logistic regression to model the probability of occurrence of poplar (any size class) and poplar seedlings (individuals < 1.37 m tall). We used stand number, distance to terrace edge, distance from the western edge of the study area (westernmost row of plots), and elevation as covariates in our models. Only the full plots and rapid plots measured in 2012 ($n = 118$) were included in this analysis, whereas the poplar plots were excluded because they were purposely selected. Distance from the western edge of the study area was included to test for a hypothesized west-to-east cline in occurrence of the species in the study area. Continuous covariates were standardized to have a mean of 0 and a SD of 1. Our model set included all possible combinations of these covariates, without interactions, and we used the Akaike information criterion (AIC) to select the most parsimonious model. Models were fit using program R 2.14.2 (R Development Core Team 2012) and the package “glmulti” (Calcagno 2012), which uses automated model selection to select among competing models. We also calculated the proportional reduction in deviance between the selected model and the null model to help assess fit.

Spatial variation in snow depth.—We created a contour map from a raster representing interpolated estimated snow depth across the study area using the Empirical Bayesian Kriging module in the ArcGIS Geostatistical Analyst, which accounts for the error in estimating the underlying semi-variogram by using repeated simulations (default

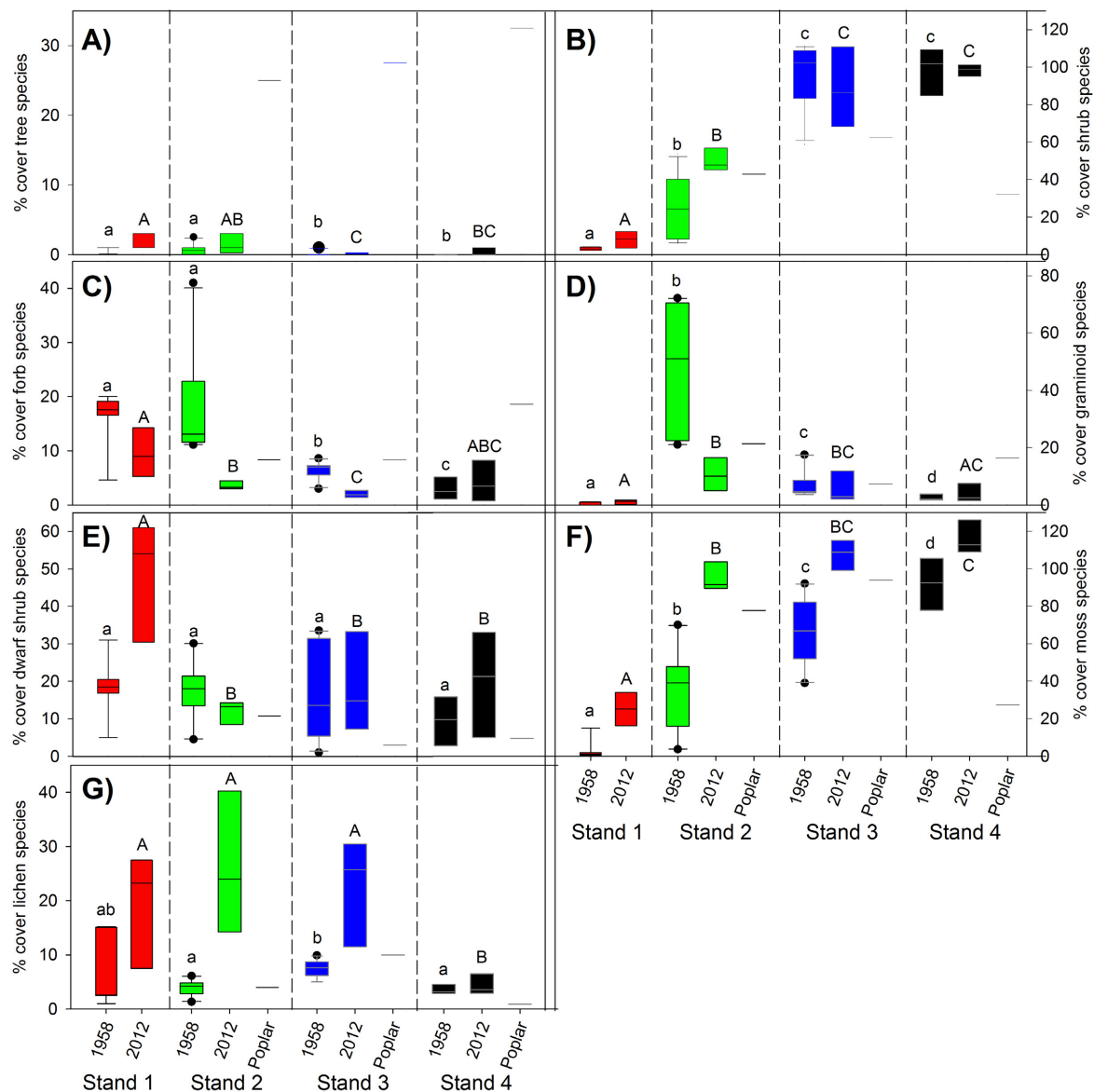


Fig. 4. The variation in species group cover percentages for (A) trees, (B) shrubs, (C) forbs, (D) graminoids, (E) dwarf shrubs, (F) mosses, and (G) lichens among the sets of full plots measured in stands 1–4 during two sampling iterations (1958 and 2012) and in the 2012 poplar plots (stands 2–4). Percent cover shown is a summation of individual species cover for all species in that group; thus, cover sometimes exceeded 100%; note varied axis lengths. Lower case letters annotate significant differences among stands in the 1958 sampling iteration. Upper case letters annotate significant differences among stands in the 2012 sampling iteration. Shaded stands indicate that we detected a significant difference over the sampling period (1958–2012) in that stand.

settings; ESRI 2001). Measured snow depths and their associated coordinate locations ($n = 385$) were the input data for the model, which portrays the estimated variation in snow depth across the study area.

RESULTS

Variation in cover by growth form

We detected several significant trends in species cover in seven growth forms across the

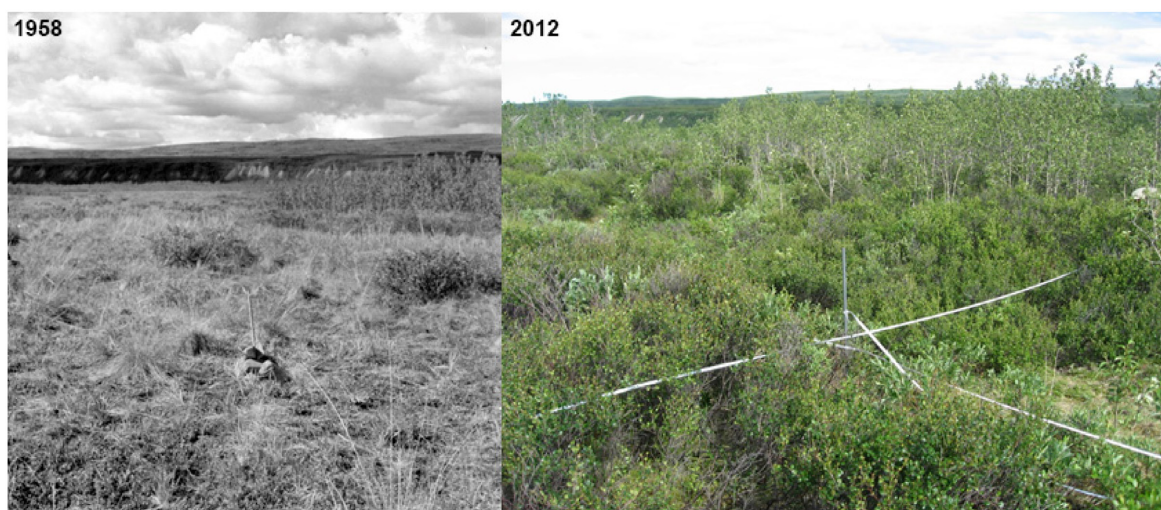


Fig. 5. Two photographs of Permanent Quadrat 1 in stand 2 of the Muldrow Glacier study area of Denali National Park and Preserve showing essentially the same view (the conduit marking plot center has not been moved). Over the intervening period, the vegetation of the plot has transformed from a graminoid-herbaceous floodplain meadow with two small clumps of *Betula nana* and a small stand of *Populus balsamifera* saplings in the background to a rather dense shrubland surrounded by patchy *P. balsamifera* woodland, with numerous tree saplings invading from the plot perimeter.

successional stands and the sample interval in the full plot data (Fig. 4). In stand 1, cover of mosses, lichens, dwarf shrubs, shrubs, and trees increased significantly from 1958 to 2012, along with a concurrent decrease in mineral cover (bare soil, rock). In stand 2, significant increases in moss, lichen, shrub, and tree cover, coupled with decreasing cover of graminoid and forb species, marked the widespread transition of much of this stand from the “meadow” stage to the “early shrub” stage or to poplar woodland, depending on the site (e.g., Fig. 5). By comparison, changes in cover by growth form in older stands 3 and 4 were less evident (e.g., Fig. 4), although significant increases in moss, lichen, and tree cover and concomitant decreases in forb cover were observed in stand 3 (Fig. 4). Cover percentages of growth forms measured in poplar plots (stands 2 through 4) showed substantial differences from the values observed in full plots within the same stand from either sample iteration (Fig. 4). These plots had higher cover of forbs and graminoids, and lower cover of mosses, lichens, and dwarf shrubs along with high tree cover (25–30%), as compared to corresponding full plots from the same stand in 2012.

Variation in dominant species cover

In general, the observed changes in dominant species cover follow the original model based on the successional position of species enumerated by Viereck (see Viereck 1966, Table 1). For example, the dominant pioneer species *Dryas drummondii* and *Astragalus adsurgens* declined in stand 1 over the sample interval, while cover of the dwarf shrub *Dryas integrifolia* expanded (Table 2). The largest simultaneous species-level cover changes occurred in stands 2 and 3. In stand 2, major decreases in *Leymus innovatus* cover occurred contemporaneously with large increases in *Betula nana* and the moss *Hylocomium splendens* cover (Table 2). In stand 3, *Pleurozium schreberi* cover exhibited the greatest mean percent cover change of any species in the full plot sample, as it increased by 39.5–61.9% mean cover in stand 3 over the sample interval. Cover of *D. integrifolia* and *Salix barratiana* decreased over the same period. Late-successional species such as *Empetrum nigrum*, *Vaccinium vitis-idaea*, and the moss *Ptilium crista-castrensis* also increased in cover in stands 3 and 4, although the changes were not always significant (Table 2).

Table 2. Estimated cover percentages for the 17 dominant species across stands 1–4 in two sampling iterations (1958 and 2012) and the difference in average cover between iterations in the Muldrow Glacier study area of Denali National Park and Preserve, Alaska.

Species	Form	Stand 1			Stand 2			Stand 3			Stand 4		
		1958	2012	Δ	1958	2012	Δ	1958	2012	Δ	1958	2012	Δ
<i>Dryas drummondii</i>	f	10.8	3.5	–7.3	0	0	0	0	0	0	0	0	0
<i>Astragalus adsurgens</i>	f	12.2	7.2	–5	0	0	0	0	0	0	0	0	0
<i>Dryas integrifolia</i>	ds	6.3	40.1	34	5.7	2	–3.6	6.8	0.3	–6.5	0	0	0
<i>Ditrichum flexicaule</i>	m	5.1	13.6	8.5	1	0	–1	0	0	0	0	0	0
<i>Stereocaulon paschale</i>	l	6.5	8	1.5	0.1	3.3	3.2	1	4.8	3.8	0.1	0	–0.1
<i>Populus balsamifera</i>	t	0.9	2.5	1.6	0.9	6.6	5.7	0	9.3	9.3	0	12.3	12.3
<i>Leymus innovatus</i>	g	1	0.95	–0.05	30	2.3	–27.6	1.5	0.7	–0.8	1.2	0.3	–0.9
<i>Arctostaphylos uva-ursi</i>	ds	1	5.2	4.2	11.3	8.3	–2.9	6.7	2.4	–4.2	0	0.3	0.3
<i>Festuca altaica</i>	g	0	0.3	0.3	12.7	9.7	–3.0	5.0	4.2	–0.8	1.3	1.4	0.1
<i>Betula nana</i>	s	0	0	0	8	30	22	62.2	59.7	–2.5	71	54.7	–16.3
<i>Hylocomium splendens</i>	m	0.1	1.4	1.3	31	65.8	34.8	43.1	35	–8	38.2	32.1	–6.1
<i>Salix barrattiana</i>	s	0	0	0	8.6	8.9	0.4	24.2	3.6	–20.6	1.6	0.6	–1.0
<i>Pleurozium schreberi</i>	m	0	0	0	0	18.3	18.3	22.4	61.9	39.5	50.2	47.6	–2.5
<i>Vaccinium uliginosum</i>	s	0	0	0	1.8	1.6	–0.2	2.3	13	10.7	19.6	13.3	–6.3
<i>Empetrum nigrum</i>	ds	0	0	0	1.8	1.0	–0.8	3.9	7.1	3.2	6.9	14.2	7.3
<i>Vaccinium vitis-idaea</i>	ds	0	0	0	0	1.6	1.6	5.7	12	6.3	5.4	8.6	3.2
<i>Ptilium crista-castrensis</i>	m	0	0	0	0	3.0	3.0	0	4.7	4.7	2.5	15.3	12.8

Notes: Taxa reported had $\geq 5\%$ cover in at least one stand and iteration and are sorted according to their original successional position with early successional taxa listed first and those associated with late succession listed last (see Viereck 1966, Table 1). Italicized values indicate significant decreases (using an exact or asymptotic permutation test for differences in means, $P < 0.05$), and boldface values indicate significant increases, in average cover of that species between the 1958 and 2012 sampling iterations. Form abbreviations are as follows: f, forb; ds, dwarf shrub; m, moss; l, lichen; t, tree; g, graminoid; s, shrub.

Changes in *P. balsamifera* occurrence and abundance

In a major change relative to the 1958 sample when balsam poplar was documented only in stands 1 and 2, balsam poplar trees occurred across the study area in 2012 (Fig. 6), with patches of high poplar abundance occurring in stands 1 through 4 (Appendix S1: Fig. S1). This species increased in density and/or frequency in full plots measured in all stands in 2012 relative to its frequency in 1958 (Fig. 6). Indeed, balsam poplar showed a unique pattern among all species observed in this data set: increasing frequencies into the smallest nested plot sizes in the 2012

sample relative to 1958 sample across all of the successional stands measured. For example, poplars were not observed within any of the 5-m² plots in any stand in 1958, but occurred in 71% and 14% of the 5-m² plots measured in stands 1 and 2, respectively, in 2012, indicating increases in the density of this species within these areas, and a conspicuous dynamic of *P. balsamifera* establishment at fine grain size within the study area over the sample interval.

The larger data set formed by combining the full and rapid plots confirms that balsam poplar occurred widely across all of the successional stands of the study area in 2012, although its

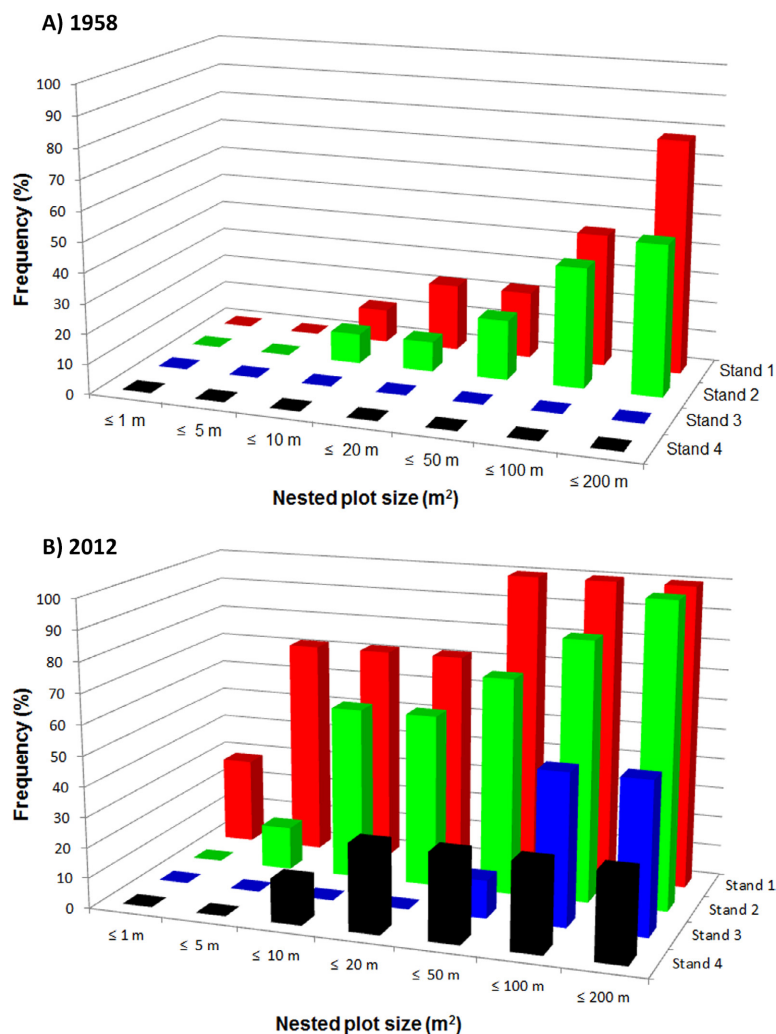


Fig. 6. Three-dimensional histogram showing the frequency of occurrence of *Populus balsamifera* in nested full plots measured in (A) 1958 and (B) 2012 across stands 1–4 in the Muldrow Glacier study area of Denali.

abundance (cover, density, and basal area) varied considerably among sites (Table 3). Although abundance of this species was also spatially variable, it attained high abundance and tall canopies in patches across all of the stands by 2012. Individual trees reached at least 5 m in height in plots in each stand, with the tallest trees in stands 2, 3, and 4 reaching 9.5 m, 8.25 m, and 12 m tall, respectively (Table 3).

Our logistic regression models for overall poplar and seedling occurrence revealed significant relationships between occurrence and characteristics of the study area. Occurrence probability of *P. balsamifera* overall declined significantly from west to east across the study

area and increased with increasing proximity to terrace edges. Additionally, stand 3 had significantly lower probability of poplar occurrence than stand 1, 2, or 4, which had occurrence probabilities that were not statistically different (Table 4). Stands 1 and 2 had significantly higher seedling occurrence probabilities than stands 3 and 4 (Table 4).

Variation in species composition and richness

Comparison of the overall vascular flora of the study area across the two sample iterations yielded similar overall species lists in stands 1–4. A total of 113 vascular plant species were observed across both iterations of full plots

Table 3. Mean values ($\pm$ SD) for balsam poplar (*Populus balsamifera*) attributes (and height of tallest tree) in stands 1–4 of the Muldrow Glacier study area of Denali National Park and Preserve.

Stand	Sample size	Frequency (%)	Average cover (%)	Live basal area (m ² /ha)	Density (no. of stems/ha)	Seedling density (no. of stems/ha)	Average height (cm)	Maximum height (cm)	Tallest individual (cm)
1	11	100	9.1 (17.4)	0.9 (2.7)	509 (1138)	29,227 (26,628)	107.8 (121.2)	198.5 (149.4)	500
2	48	89.6	13.9 (17.2)	2.6 (3.9)	1151 (1215)	4458 (8134)	278.3 (206.7)	403.6 (262.3)	950
3	36	61.1	5.2 (12.2)	1.3 (3.8)	543 (1236)	513 (1018)	124.2 (131.4)	182.8 (228.9)	825
4	23	65.2	7.3 (10.8)	1.9 (3.1)	1046 (1551)	457 (1107)	172.1 (202.9)	260.4 (309.0)	1200

Notes: Data come from full and rapid plots measured in 2012, excluding the poplar plots, which were selected for the presence of high poplar abundance ($n = 118$). Data for average height, maximum height, and tallest individual come only from rapid plots ($n = 89$). Maximum height is the average of the tallest individual in each plot across stands.

sampled in 1958 and 2012. Seventy-two of the 113 plant species (or 63%) were observed in one or more full plots in both 1958 and 2012. Only two species were present in four or more plots in 1958, but absent from the sample in 2012 (species “lost”; Table 5), whereas eight species that occurred in four or more of the 35 full plots measured in 2012 were not observed in the 1958 full plots (species “gained”; Table 6). The two species lost from the sample are alpine taxa, whose minimum elevations in the Denali systematic sample (Roland and Schmidt 2015) were higher than the study area and mean elevations were much higher (Table 5). In contrast, the eight species that were new to the sample in 2012 all had

minimum elevations more than 300 m below the elevation of our study area in the same systematic plot data set (Table 6). The species additions with highest frequency in 2012 were the xerophytic shrub *Juniperus communis* and the evergreen herb *Pyrola grandiflora*, which both occurred in nine 2012 plots. Perhaps the most noteworthy difference between the species lists compiled for the two sample iterations was the addition of a suite of mesophytic vascular plant taxa observed in plots in stand 4 in 2012 that were not recorded in 1958 (Table 6). Specifically, *Calamagrostis canadensis*, *Polemonium acutiflorum*, and *Valeriana capitata*, among others, are common species frequently observed in moist meadows and riparian habitats in Denali.

The mean number of vascular plant species per full plot averaged across all full plots and stands ($n=70$) was significantly higher in 2012 as compared to 1958 (27.5 vs. 21.2; adjusted $P = 0.017$; Fig. 7). At the stand level, only stand 1 showed a significant increase in richness when comparing the median values between iterations (Fig. 7). A pairwise Wilcoxon test showed significant differences among stands in median plot species richness in both years, with species richness in stand 1 lower as compared to the other stands (Fig. 7).

Small sample sizes prohibited the statistical evaluation of vascular plant species richness differences in the poplar full plots ($n = 2$ per stand) vs. full plots in the same stand. However, we found conspicuously higher vascular plant species richness in the poplar plots as compared to full plots. Indeed, plot species richness values in the poplar full plots were beyond the range of

Table 4. Results of generalized linear model analysis of *Populus balsamifera* occurrence in the Muldrow Glacier study area of Denali National Park and Preserve, Alaska ($n = 118$; model proportional reduction in deviance 0.27 for overall occurrence and 0.15 for seedling occurrence).

Predictor	Estimate	z
Overall <i>P. balsamifera</i> occurrence		
Intercept	2.46	0.0001
Stand 3	−2.38	0.0055
Distance from western edge of study area	−1	0.05
Distance to terrace edge	−0.86	0.0413
<i>P. balsamifera</i> seedling occurrence (stems < 1.37 m in height)		
Intercept	0.54	0.0497
Stand 3	−1.59	0.0022
Stand 4	−1.58	0.004

Table 5. The elevational distribution ($\pm$ SD) of two species that occurred in four or more plots in the 1958 sample, but were absent from the 2012 sample in the Muldrow Glacier study area. Elevation distribution based on landscape-scale systematic vegetation plot data set†.

Species found in 1958 only	Form	Frequency in study area (%)	No. of plots in systematic sample	Elevation (m)	
				Minimum†	Mean†
<i>Astragalus nutzotiniensis</i>	Forb	22.9	10	761	1045 $\pm$ 192
<i>Carex lachenalii</i>	Graminoid	11.4	24	969	1219 $\pm$ 147

† C. A. Roland (*unpublished data*); see Roland and Schmidt (2015).

variation observed in the other full plots for the same stand (Fig. 7).

Repeated measurements of two permanently marked quadrats—PQ1 and PQ6

Data from direct re-measurements of two permanently marked full plots were included in stand-level summaries presented above. Examining these data in detail increased our confidence that the observed trends at the stand level were not a sampling phenomenon, as all of the major changes observed paralleled those trends observed at the stand level in stands 2 and 3, and allowed us to directly compare cover by specific taxa. The vegetation in PQ1 changed dramatically between 1958 and 2012, with an increase in *Betula nana* cover from 1% to 58% and decreases in *Leymus innovatus* cover from 15% to 1% and *Salix barrattiana* cover from 15% to 0%. PQ1 also experienced a notable proliferation in poplar saplings, and repeat photographs of the plot vicinity revealed a major increase in abundance and stature of poplar trees in the area surrounding this plot (Fig. 5).

PQ6 was located in the northern part of stand 3 and was considered to be in the “early shrub stage” in 1958 (Viereck 1966). In PQ6, in contrast to PQ1 in stand 2, *Betula nana* cover remained mostly unchanged, with 62% cover in 1958 and 58% cover in 2012 (see Fig. 8). In this plot, the late-successional ericaceous species *Vaccinium uliginosum* and *Empetrum nigrum* increased from 3% to 14% and from 1% to 4% cover, respectively. Among the mosses, *Hylocomium splendens* cover decreased in both plots over the period (from 38% to 28% in PQ1 and from 38% to 15% in PQ6), whereas *Pleurozium schreberi* cover increased dramatically (from 0% to 63% in PQ1 and from 38% to 97% in PQ6). Additionally, cover of the moss *Ptilium crista-castrensis* increased from 0% to 7% in PQ6.

Spatial variation in surface soil attributes

Surface soil temperatures differed significantly across the successional gradient ($H = 17.818$, $P < 0.0001$ based on stands 1–4 full plot data; Table 7). Temperatures were warmest in the early successional stands and declined with increasing

Table 6. The elevational distribution ($\pm$ SD) of eight species that were new to the sample in 2012 and occurred in at least four full plots in the Muldrow Glacier study area based on landscape-scale systematic vegetation plot data set†.

Species found in 2012 only (in ≥ 3 plots)	Form	Frequency in study area (%)	No. of plots in systematic sample†	Elevation (m)	
				Minimum†	Mean†
<i>Juniperus communis</i>	Shrub	26	59	305	760 $\pm$ 281
<i>Pyrola grandiflora</i>	Forb	25.7	98	310	898 $\pm$ 288
<i>Calamagrostis canadensis</i>	Graminoid	22.9	370	153	625 $\pm$ 297
<i>Moehringia lateriflora</i>	Forb	22.9	95	188	802 $\pm$ 263
<i>Valeriana capitata</i>	Forb	22.9	198	211	954 $\pm$ 217
<i>Carex concinna</i>	Graminoid	17	28	305	604 $\pm$ 261
<i>Eurybia sibirica</i>	Forb	14.3	94	211	911 $\pm$ 309
<i>Polemonium acutiflorum</i>	Forb	11.4	184	211	927 $\pm$ 226

† See Roland and Schmidt (2015).

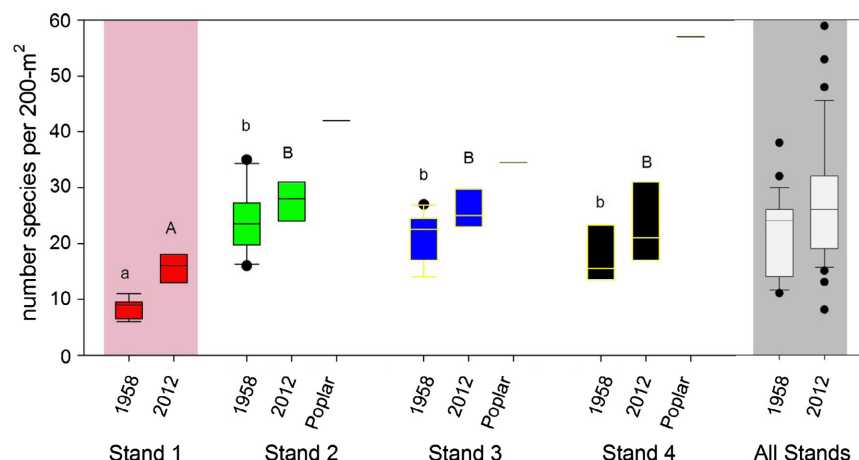


Fig. 7. The variation in vascular plant species richness observed among the sets of full plots measured in stands 1–4 during two sampling iterations (1958 and 2012) and in the poplar plots measured in 2012 in the Muldrow Glacier outflow terraces study area in Denali National Park and Preserve, Alaska. Lowercase letters indicate significant differences among stands in the 1958 sampling iteration. Uppercase letters indicate significant differences among stands in the 2012 sampling iteration. Shaded couplets indicate that we detected a significant difference over the sampling period (1958–2012) for this comparison. “All Stands” here includes the 2012 poplar plots ($n = 70$). Poplar plot values represent the mean value across two poplar plots per stand.

surface age, reaching below-zero mean values in the permafrost-influenced stand 5 (Table 7, Fig. 9). The depth of the living moss mat and the surface organic horizon increased across the successional sequence, with thin layers in stand 1 and deep layers in stand 4 (Table 7). Surface horizon depth (combined thickness of the living and organic mats) was negatively correlated with soil temperatures; thus with increasing surface horizon depth, soil temperatures decrease (Fig. 10). Poplar plots had consistently thinner living mat and organic horizon depths with consequently warmer soil temperatures as compared to full plots or transects from the same stand (note the particularly conspicuous differences in stand 4 soil temperatures between poplar and full plots and the stand 4 transect and poplar transect [located within stand 4; Figs. 9 and 10]).

Spatial variation in snow depth

Median snow depth measured across the study area in March 2014 was significantly lower in stand 1 relative to stands 2 through 4 ($H = 16.216$, $P = 0.001$) and trended higher within the poplar plots than within the full plots for the corresponding stand (Fig. 11). Our spatial analysis identified polygons with deeper snow in the western part of the study area (stand 2;

Fig. 12) and particularly thin snow cover in the windblown southern part of the study area (stand 1; Fig. 12). Low snow depth also occurred in an area that corresponded to conspicuous meadow features occupying the southeast corners of stand 2 and stand 3 (Fig. 12). Our analysis also identified polygons of deep snow in the northern part of the study area, in the immediate vicinity of a steep bluff (Fig. 12). The polygons of deep snow largely correspond to areas with particularly high density of *P. balsamifera* (compare vegetation map and snow depth layers in Appendix S1: Fig. S1, Data S1), which accords with our snow depth results.

Ordination of plant community structure relative to successional stand

Our NMS ordination (which included both 1958 and 2012 sample iterations but omitted the poplar plots) produced a stable two-dimensional solution exhibiting a stress of 9.7 and instability of 0.0 over 65 iterations representing 89.2% of the variance in the original Sorenson distance matrix. Full plots within each successional stand and sampling iteration clustered together and were arrayed along a successional trajectory of increasing stand age (Fig. 13; Appendix S2: Fig. S1, Data S1). Environmental and vegetation

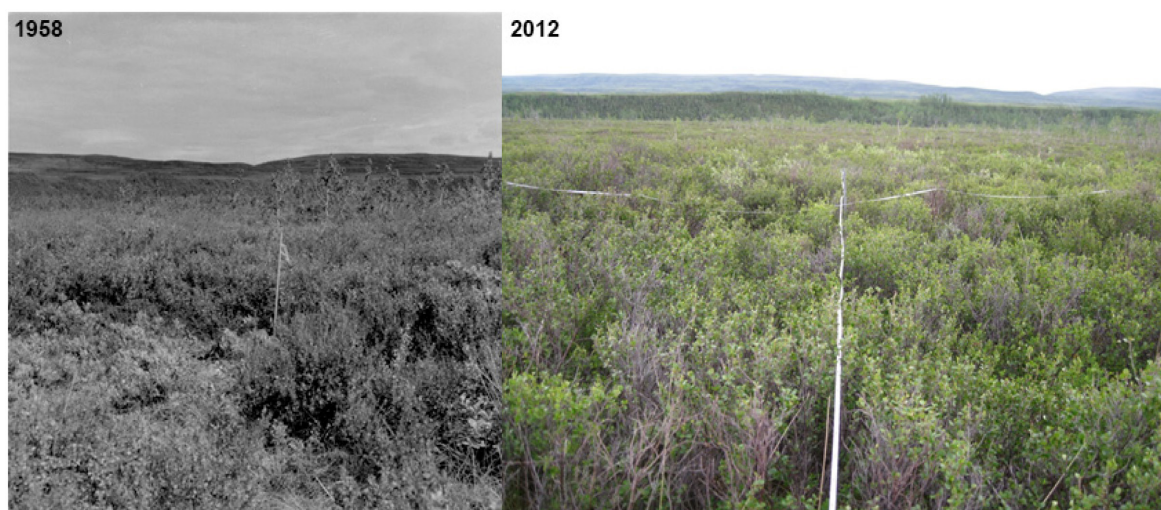


Fig. 8. Two photographs of Permanent Quadrat 6 in stand 3 of the Muldrow Glacier study area of Denali National Park and Preserve showing essentially the same view (the conduit marking plot center has not been moved); however, note that the “notch” in the ridge in the background is in the center of the frame in the photograph on the right and is closer to the right edge of the frame in photograph at left. Over the intervening period, the vegetation of the plot has remained relatively constant.

covariates plotted on these axes approximated this trajectory of stand age, with young surfaces in stand 1 associated with high mineral soil cover and high vascular plant diversity and older surfaces in stands 3 and 4 correlated with high feathermoss and *Betula nana* cover (Fig. 13; Appendix S2: Fig. S1, Data S1).

Vectors connecting the within-stand averages of each sampling iteration (1958 and 2012) confirmed

both the general diagonal orientation of the successional trajectory and that the distance between centroids from the two iterations decreased with increasing stand age (as indicated by the length of the stand centroid vectors in Fig. 13; Appendix S2: Fig. S1, Data S1). A slight arch to the successional trajectory of increasing stand age accommodates the general alignment of Axis 2 with measures of diversity. Vectors connecting the within-stand

Table 7. Summary of mean values ($\pm$ SD) for selected soil characteristics organized by successional stand in 2012.

Stand	Plot type	<i>n</i>	Soil temperature (°C)	Soil probe depth (cm)	Living mat depth (cm)	Organic mat depth (cm)
0	Transect	10	12.8 $\pm$ 0.6	14.7 $\pm$ 3.7	n/a	n/a
1	Transect	10	7.9 $\pm$ 0.5	11.8 $\pm$ 5.0	n/a	n/a
	Full plots	7	12.5 $\pm$ 3.1 ^a	8.5 $\pm$ 2.0 ^a	3.2 $\pm$ 1.1 ^a	0.9 $\pm$ 0.6 ^a
2	Transect	20	6.9 $\pm$ 1.5	10.8 $\pm$ 3.4	n/a	n/a
	Full plots	7	6.3 $\pm$ 0.8 ^b	12.5 $\pm$ 1.4 ^a	7.0 $\pm$ 1.4 ^b	7.3 $\pm$ 1.1 ^b
	<i>Poplar plots</i>	2	6.6 $\pm$ 0.02	23.7 $\pm$ 3.3	2.8 $\pm$ 0.0	10.8 $\pm$ 3.2
3	Transect	10	4.3 $\pm$ 1.1	11.9 $\pm$ 3.1	n/a	n/a
	Full plots	8	4.2 $\pm$ 1.0 ^c	18.2 $\pm$ 2.2 ^b	8.9 $\pm$ 1.9 ^{b,c}	11.7 $\pm$ 1.8 ^c
	<i>Poplar plots</i>	2	8.3 $\pm$ 0.7	16.6 $\pm$ 2.4	4.1 $\pm$ 1.9	10.3 $\pm$ 2.5
4	Transect	10	2.6 $\pm$ 0.8	21.4 $\pm$ 6.9	n/a	n/a
	Full plots	7	2.25 $\pm$ 0.7 ^d	26.3 $\pm$ 3.4 ^b	9.6 $\pm$ 1.0 ^c	11.5 $\pm$ 2.4 ^c
	<i>Poplar plots</i>	2	6.9 $\pm$ 1.0	86.9 $\pm$ 15.3	2.1 $\pm$ 2.3	10.8 $\pm$ 0.7
	<i>Poplar transect</i>	10	6.8 $\pm$ 1.4	78.3 $\pm$ 24.6	n/a	n/a
5	Transect	10	-0.3 $\pm$ 0.2	21.9 $\pm$ 4.4	n/a	n/a

Notes: Significantly different median values ($P \leq 0.001$) for full plots in stands have different letter superscripts when reading down the column. Poplar plots (italicized rows) were excluded from analysis due to the low sample size.

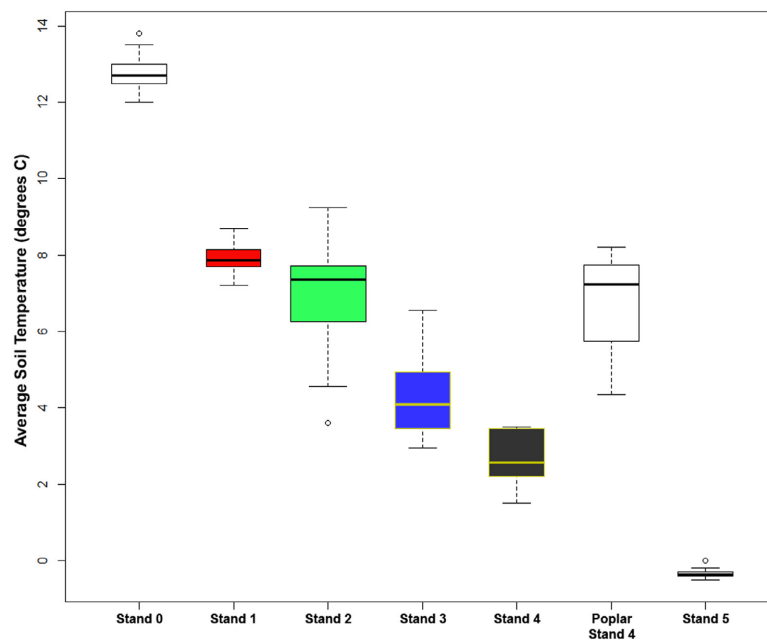


Fig. 9. Variation in mean soil temperature measured in 2012 among 1-m² quadrats on transects in stands 0–5 of the Muldrow Glacier outflow terraces study area in Denali National Park and Preserve, Alaska.

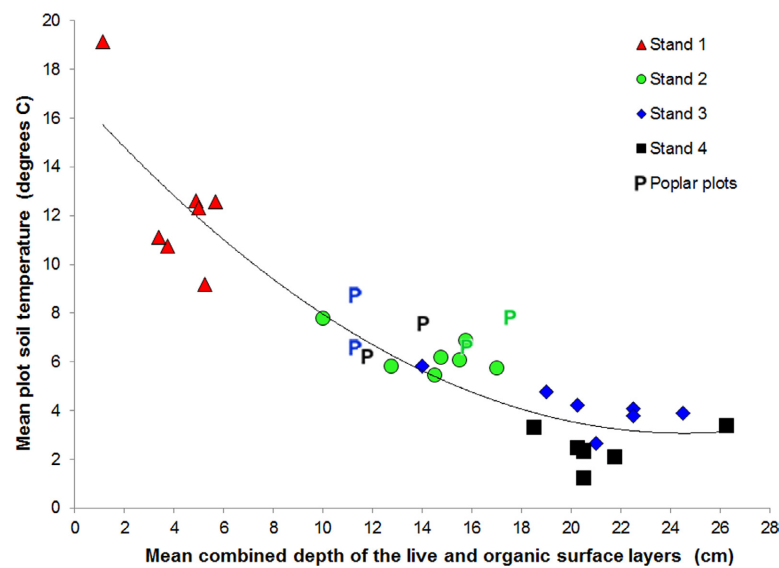


Fig. 10. The relationship between the combined depths of the moss and organic horizon and soil temperature in 35 full and poplar plots in the Muldrow Glacier study area of Denali National Park and Preserve, Alaska, in 2012. Note that successional stands sort out along this axis of variation with early stands having relatively thin soil surface horizons and warm soil temperatures, with soil temperatures diminishing with time through this successional sequence with the development of increasingly deep and insulating moss and organic horizons. Also note the relatively high temperatures of the poplar plots (from stands 2–4) relative to the cluster of points from the full plots in the same stand. The regression fit line shown is included for visual display purposes.

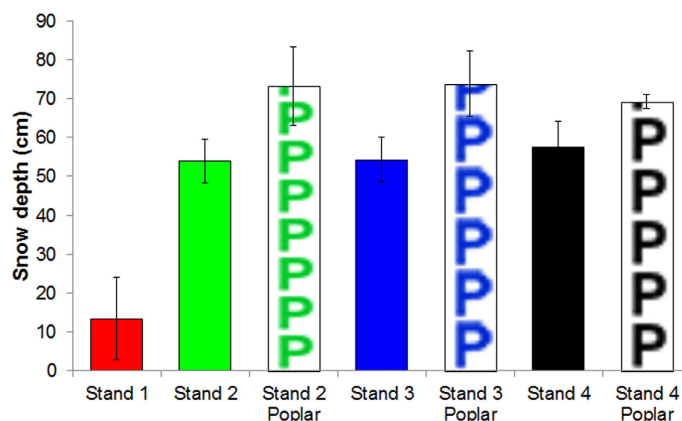


Fig. 11. Variation in the mean snow depth recorded in March 2014 for full plots (colored bars) and poplar plots (bars with Ps) in stands 1–4 of the Muldrow Glacier study area of Denali National Park and Preserve, Alaska.

averages of the 1958 full plots to the 2012 poplar full plots were oriented at increasingly greater angles to the vectors connecting the 1958–2012 (nonpoplar) full plot means, highlighting the increasingly

sharp differences in community composition in sites where high poplar cover has developed vs. the general vegetation mosaic of each stand. These poplar full plots clustered separately from the

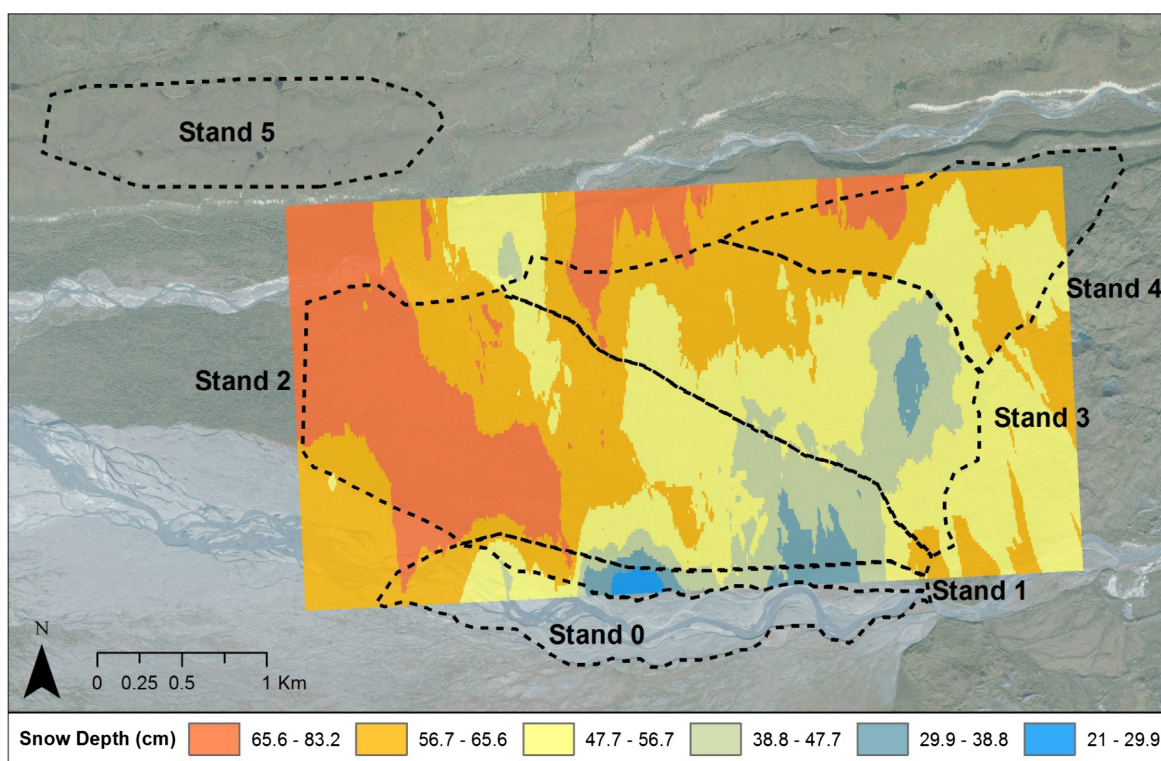


Fig. 12. A graphical representation of the snow depth model depicting the spatial variation in estimated snow depth (cm) based on an Empirical Bayesian Kriging analysis of 385 snow depth measurements recorded in the study area in Denali National Park and Preserve, Alaska, during March 2014. (An interactive version of this figure is provided in Appendix S1: Fig. S1.)

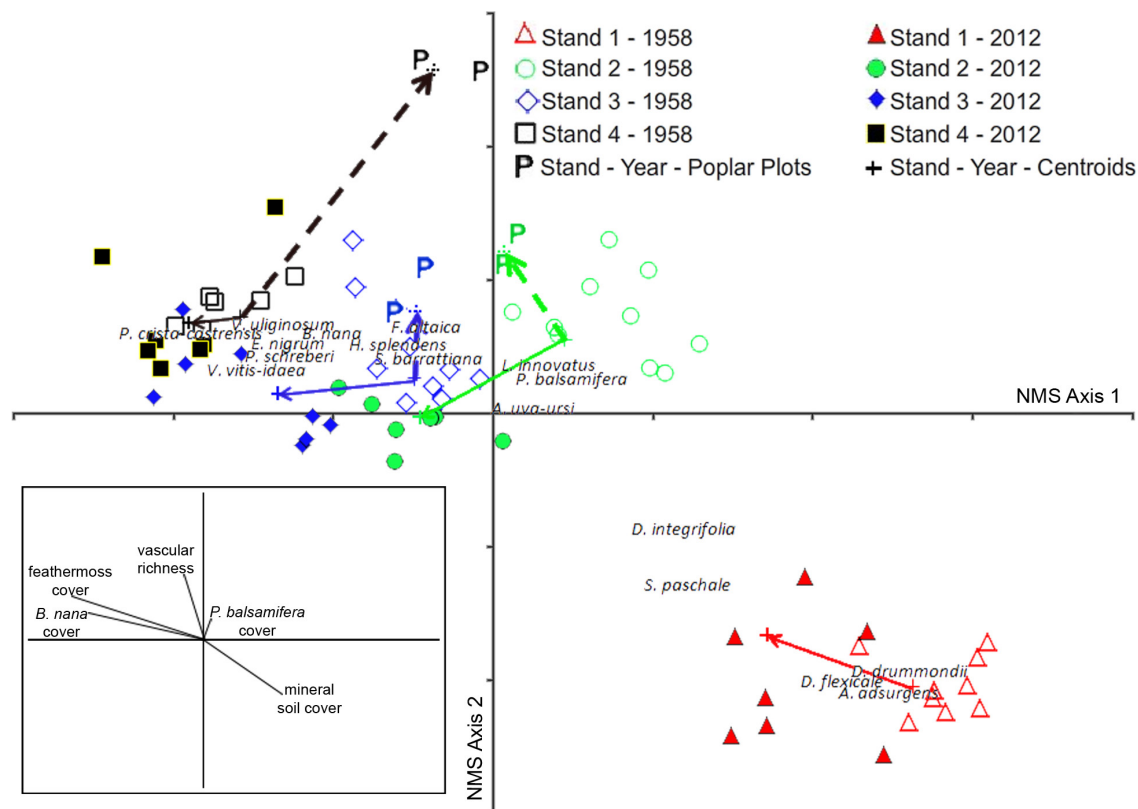


Fig. 13. A graphical presentation of the results of a nonmetric multidimensional scaling ordination analysis showing the location of full plots in species space. Open symbols represent the plots measured in 1958; filled symbols are those plots measured in 2012. Red triangles represent stand 1 plots, green circles stand 2 plots, blue diamonds stand 3 plots, and black squares stand 4 plots. "P" symbols represent poplar plots (with corresponding stand color). Solid arrows connect the within-stand averages for 1958 and 2012 sample years and thus illustrate successional progression. Dashed arrows connect within-stand averages for 1958 plot data and 2012 poplar plot data within those stands, illustrating a potential alternate successional trajectory. Locations of selected dominant species from each stand are shown (see Table 4 for species names). Covariate vectors of interest are plotted ($r^2 > 0.1$), with their length and direction representing the strength of their relationship with ordination scores. (An interactive version of this figure is provided in Appendix S2: Fig. S1.)

other plots in ordination space, skewed lower in Axis 1 (stands 2, 3, and 4) and higher on Axis 2 (stands 3 and 4) than the full plot scores in their respective stands measured in either 1958 or 2012. Interestingly, the vector connecting the centroid position for the two iterations of sampling in stand 1 full plots is oriented similarly to the vector between stand 4 full plots and stand 4 poplar plots, and orthogonally to the overall successional trajectory for the full plots in the other three stands. The environmental covariate vectors for vascular plant species richness, forb and graminoid diversity, and *P. balsamifera* cover align with the location

of poplar plots in the ordination space (Fig. 13; Appendix S2: Fig. S1, Data S1).

Photographs

Qualitative comparisons of repeated photographs visually confirmed the evidence for both the dramatic changes and relative stasis within the study area revealed in our field data, suggesting spatially variable patterns of vegetation change between our sampling iterations. Particularly conspicuous changes were the transformation of stand 1 from a very open, discontinuous vegetation mosaic in 1958 into a well-vegetated

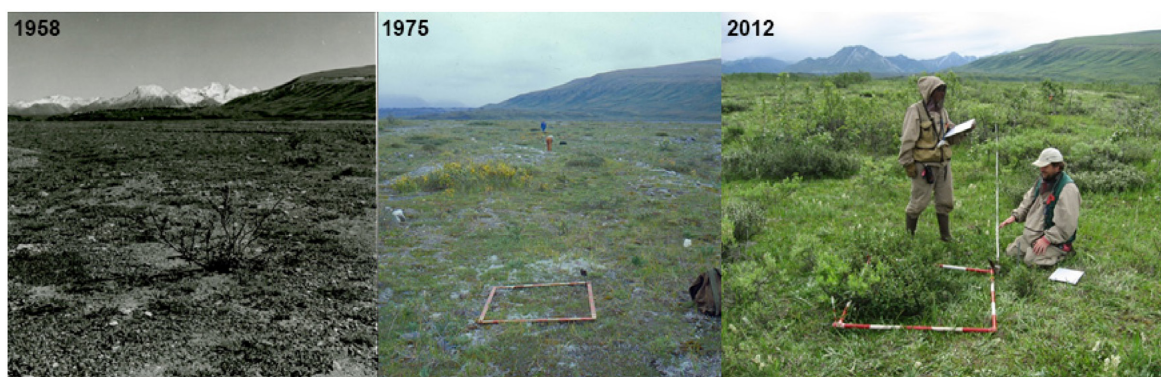


Fig. 14. A series of three photographs that show the changing vegetation mosaic in stand 1 of the Muldrow Glacier study area in Denali National Park and Preserve over the period 1958–2012. Vegetation has succeeded from a sparse early seral community with very scattered shrubs and considerable bare ground (at far left), to the mosaic of scattered, low patches of *Salix* spp. and *Shepherdia canadensis* (middle), to a continuously vegetated area with substantial patches of *Populus balsamifera* saplings and an interrupted shrub canopy (at right). These photographs show the west end of the stand 1 transect established in 1975 and resampled in 2012.

area supporting patches of poplars and tall shrubs in 2012 (Fig. 14), as well as the general spread and increase in stature of poplar stands throughout the study area (i.e., Figs. 5 and 14). Furthermore, photographs taken in the region of transect 0 (stand 0) show early-successional areas that are apparently being colonized by much larger-statured woody vegetation than was previously the case (Fig. 15). In contrast to these early successional changes, photograph pairs taken in stand 3, where the vegetation was early shrub stage, showed relatively little structural change between 1958 and 2012 (Fig. 8). Furthermore, photographs and field observations from stand 5 show no changes in gross structure of the vegetation mosaic (Fig. 16). Additional photographs provided documentation of the importance of wind in the distribution of vegetation in the area. For example, occasional *Picea glauca* trees occurring in the study area showed obvious evidence of winter dieback above the shrub/snow line (Fig. 17A), but under the protection of a *P. balsamifera* canopy, the species appears to be capable of growing tall and thriving in this area (Fig. 17B).

DISCUSSION

Our resampling of the Muldrow Glacier chronosequence provides a unique perspective on plant community succession and directional

change over a 54-yr period in a subalpine area where summer temperatures have warmed by about 2°C in recent decades. In some respects, our data confirm the original successional



Fig. 15. Photograph of a newly established terrace in the vicinity of transect 0, stand 0, that was established in 2000. The nature of the vegetation that is becoming established on this young surface is of a very different character and stature from the vegetation that developed in stand 1 prior to the initial measurements made in 1958 (see the left-most photograph in Fig. 14 for comparison). Specifically, erect shrubs (*Shepherdia canadensis* and *Salix* spp.) as well as *Populus balsamifera* saplings appear to be establishing earlier, with less of an herbaceous meadow phase in evidence between barren gravel and the “early shrub” phase described by Viereck (1966).

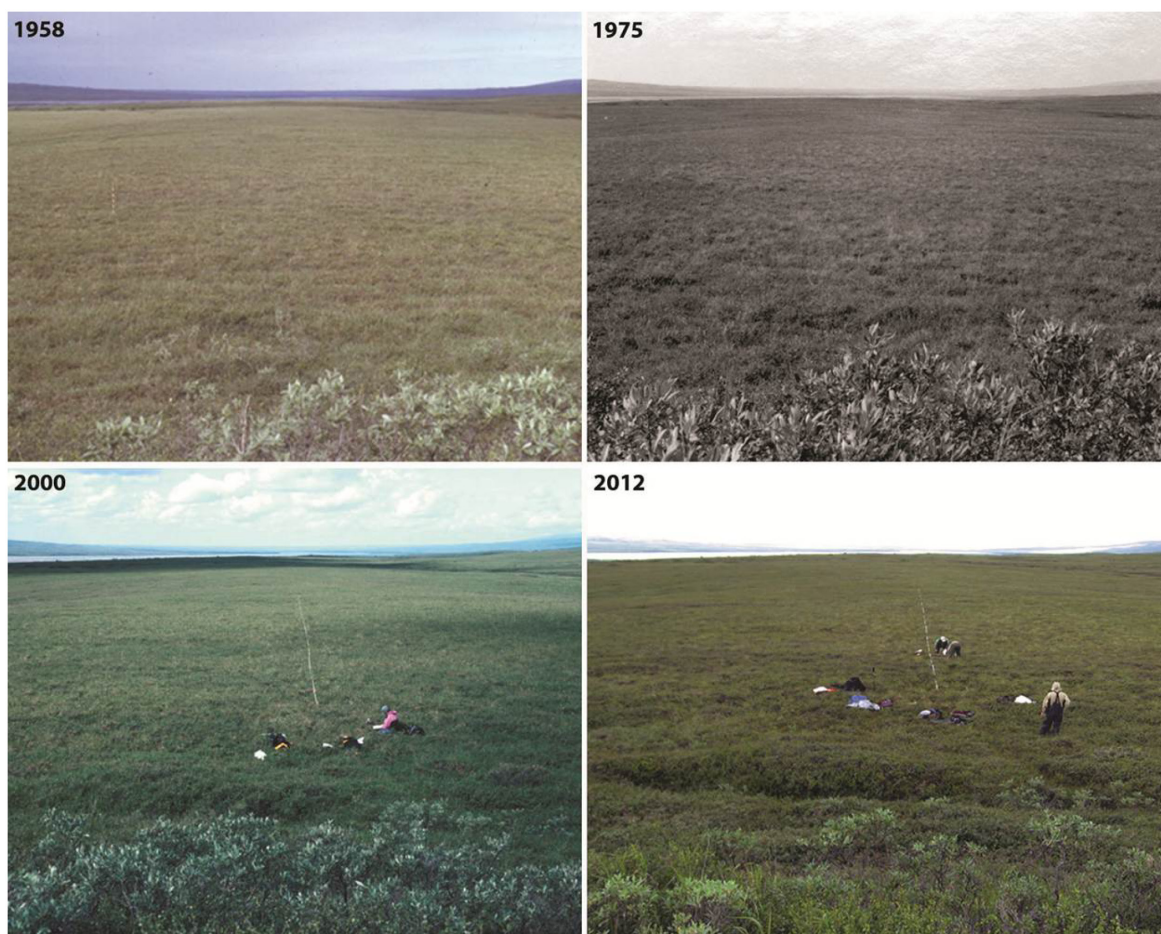


Fig. 16. Four identical views of Viereck's stand 5 underlain by shallow permafrost from 1958 through 2012. The photograph was taken from atop a hillock and the apparent depression seen in 2000 and 2012 photographs is the result of a slightly different angle of view. Essentially no change in the structure of the vegetation has occurred in this segment of the landscape (C. A. Roland, *unpublished data*).

trajectory posited by Viereck (1966), particularly in mid- to late-successional stands 3 and 4 where undisturbed patches of scrub tundra remained largely unchanged across the sample interval. However, our work also shows that the direction and tempo of primary succession in this area may have fundamentally changed over the interval separating the sample iterations. Specifically, we documented an increase in balsam poplar occurrence and abundance across the area and development of high-cover, relatively large-statured poplar woodlands in all four successional stands. Poplar thus appears to have “captured” the original successional trajectory (see Fig. 18), likely (at least in part) in response to recent climate warming and

amelioration of growing season conditions. This development was unforeseen in the original study and may ultimately facilitate the conversion of this region from one dominated by shrub tundra ecosystems to a boreal forest mosaic over time.

Evaluation of the original successional trajectory

Stand 1 exhibited the greatest departure from the original successional trajectory. The expected increase in herbaceous cover indicating a transition into the “meadow stage” did not occur. Instead, poplar increased substantially in stand 1 and the xerophytic dwarf shrub *Dryas integrifolia* reached much higher mean cover than was observed in 1958. This may

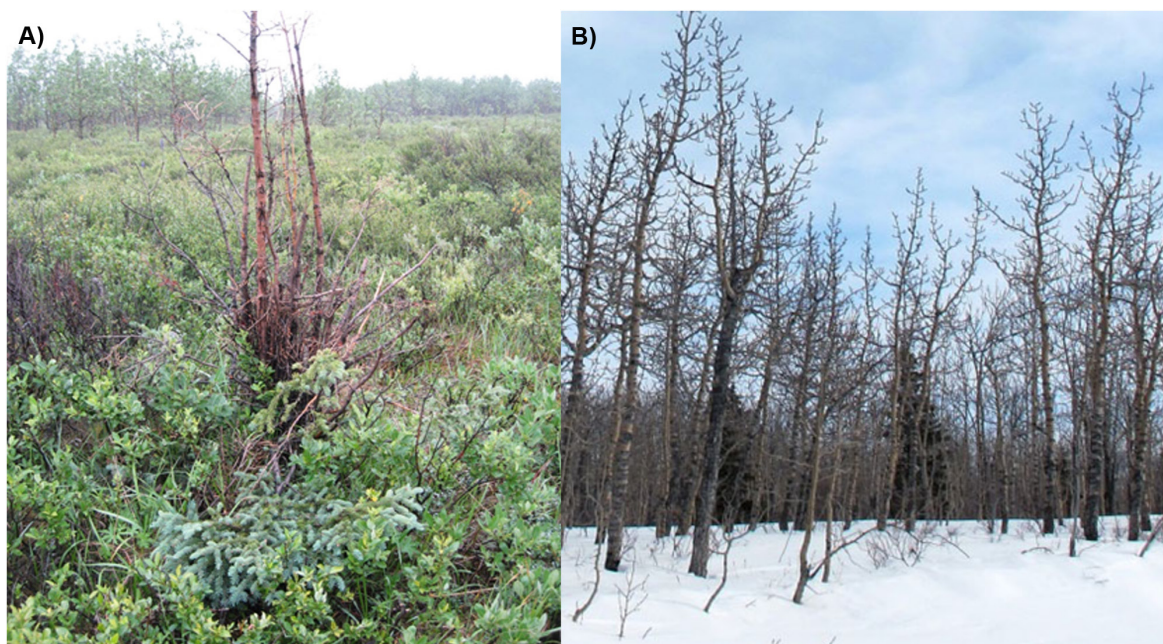


Fig. 17. (A) *Picea glauca* sapling with dead, krumholz top but live (and relatively lush) needles and branches below the shrub canopy and presumably the snow line; (B) a photograph taken in March 2014 showing several young spruce trees with a normal growth form in the understory of a *Populus balsamifera* woodland within the study area.

reflect divergent responses to recent climate warming among species groups (e.g., herbaceous forbs and graminoids vs. poplar and *Dryas integrifolia*), altered competitive interactions among species, or that some other stand attributes are less conducive to the establishment of a meadow mosaic. Given the major expansion of poplar and shrubs in stand 1, future formation of a meadow stage there is unlikely.

Our measurements in stand 2 revealed a widespread conversion of Viereck's "meadow stage" to the "early shrub" stage as expected in his model. However, a major exception was the unpredicted expansion of poplar frequency, cover, and stature there. Such a conversion was unlikely given the prevailing climate norms in 1958. Interestingly, both the predicted transition from herbaceous meadow into mossy scrub tundra and the unexpected conspicuous expansion and growth of poplar in the study area were captured in our remeasurement and repeat photography in the vicinity of PQ1 (see Fig. 5).

In stand 3, the significant differences in overall growth-form cover values over the sample interval were a modest decrease in forb cover

and increases in moss, lichen, and tree cover. As predicted by Viereck (1966), decreases in cover of early successional dwarf shrubs were balanced by increases in the late-successional dwarf shrubs at the species level. Among low shrubs, a similar pattern was observed, with sharp decrease in the meadow-dominant shrub *Salix barratiana* occurring in conjunction with a sharp increase in the late-successional *Vaccinium uliginosum* which occurs widely in cold, moist soils of shrub tundra across Denali. Among the feather-mosses, a decrease in *Hylocomium splendens* over the sample interval coincided with increases in *Pleurozium schreberi*, and to a lesser extent *Ptilium crista-castrensis*. These patterns all follow Viereck's expected trends in abundance of these species relative to stand development over time.

Similarly, in stand 4, the only substantial cover changes over the interval were a modest increase in moss cover concomitant with increasing cover of *Ptilium crista-castrensis*, and modest increases in the cover of late-successional dwarf shrubs within the cold, mossy vegetation mosaic that occupies much of this stand (especially in the central and eastern portions away from the moraines).



Fig. 18. Photographs showing the altered trajectory of vegetation development found in 2012 in poplar stands that have developed in three different terrace ages in the Muldrow Glacier study area, Denali National Park and Preserve, Alaska. In early stages, poplar trees are small and graminoid cover dominates, with scattered shrubs. In later stages, poplar have grown large and formed a complete canopy substantially altering light, temperature, and competitive dynamics at the ground level.

Both of these developments are also consistent with Viereck's successional model. An unanticipated floristic change, however, was an influx of boreal taxa into stand 4, particularly a suite of common mesophytic species including *Calamagrostis canadensis*, *Cornus canadensis*, *Polemonium acutiflorum*, and *Valeriana capitata*. The occurrence of these meadow species may reflect an increase in moisture availability in this area with the development of a deeper organic layer over time, or else reflect a larger-scale dynamic of lowland taxa infiltrating into this subalpine area and becoming more common as temperatures ameliorate.

The expansion of poplar across the study area

Both qualitative (i.e., repeated photographs) and quantitative lines of evidence reveal that poplar distribution, abundance, and stature have expanded substantially in the study area in recent decades, representing a significant departure from the successional dynamics extant at the time of the original study. Viereck's (1966) only mention of poplar was in his discussion of stand 2: "Along terrace edges and where there are remnants of older channels, there are occasional clonal clumps of balsam poplar." Furthermore, Viereck's field notes indicated that these occasional clumps occurred mostly in the western part of the study area, where "a few *P. balsamifera* reaching heights of 1.5 m" could be found growing in depressed areas (L. Viereck, *personal communication*). However, balsam poplar increased more than any other plant species in size, frequency, density, and distribution over the sample interval. In marked contrast to other taxa, poplar reached high cover and stature (in patches) across all stands 1–4. While the study area was generally alpine in appearance in 1958, much of it now supports a much taller, albeit patchy poplar woodland mosaic.

Recent summer warming that has occurred since the 1970s was perhaps the primary catalyst for the expansion of poplar. Paleoecological work has correlated expansions in *P. balsamifera* in Alaska with intervals with warmer summers in the past (Nelson and Carter 1987, Mann et al. 2010), and several experimental and observational studies show that balsam poplar requires warm soil temperatures to establish and persist in a site (Lawrence and Oechel 1983, Landhäusser et al. 1996, 2003, Hobbie and Chapin 1998,

Kalischuk et al. 2001, Roland et al. 2013). Mean soil temperatures observed in stands 3–5 in 2012 were below 5°C, a temperature thought to restrict the growth of *P. balsamifera* seedlings (Landhäusser et al. 2003). However, in the more open environment of the earlier successional stands 1 and 2, the recent warm summer air temperatures would have translated into warmer soil conditions favorable for *P. balsamifera* seedling germination and growth (approximately 6° to 12°C). Furthermore, a study of annual growth of poplar trees conducted adjacent to our study area found strong positive correlations between annual growth and increasing summer temperatures (Lev 1987).

Several additional attributes of *P. balsamifera* have likely allowed this species to take advantage of the increasing summer warmth to rapidly become a dominant element of the vegetation mosaic over a very short time span. In an arctic treeline, *P. balsamifera* was effective in invading formerly treeless areas due to its ability to resprout vegetatively, produce copious seeds at an early age, and effectively disperse its windborne seeds over long distances (Landhäusser and Wein 1993). These attributes likely facilitated balsam poplar's expansion into the Muldrow Glacier area as well, and in conjunction with poplar's ability to colonize freshly exposed mineral soils (Zasada and Phipps 1990), allowed establishment very early in succession, providing a crucial "head start" against late-successional competitors such as *Betula nana* and feathermosses. In this context, allelopathic balsam poplar litter could further add a competitive advantage (e.g., Jobidon and Thibout 1982).

Our occurrence model results indicate a directional cline of higher poplar probability of occurrence moving from the west to the east toward the glacier front. This pattern may reflect the consequences of a "wave" of poplar establishment from lower elevations into formerly more alpine conditions up the valley through time. Large stands of poplars are a conspicuous element of the alluvial terrace habitats in adjacent boreal areas of the park (Viereck et al. 1993, Roland et al. 2013).

Spatial patterns in poplar distribution

The expansion of poplar across the study area over the period 1958–2012, although dramatic,

was also a spatially patchy phenomenon likely controlled by a suite of interacting climate and site factors. Foremost, sporadic and discontinuous opportunities for seedling establishment for poplar are controlled by seedbed conditions that can be highly variable in time and space. Poplar requires availability of moist, fine-grained, and warm mineral soils in open sites during specific time periods coinciding with seed dispersal events to ensure germination and establishment of seedlings (Zasada and Phipps 1990). These conditions were generally more prevalent in stands 1 and 2 of the study area in recent decades due to the younger age of the surfaces and lower vegetation density.

Upon establishment of seedlings, the clonal habit of *P. balsamifera* may exaggerate the patchiness inherent in uneven seedling establishment through the clonal expansion of individuals through suckering (Comtois et al. 1986). Furthermore, areas that contain deep, fine-textured soils with higher moisture-holding capacity, such as those created by small-scale geomorphic disturbance along terrace edges, are likely to support more dense and vigorous poplar establishment and growth (Zasada and Phipps 1990, Kalischuk et al. 2001). However, in the absence of ground disturbance, competition with established vegetation, particularly long-lived woody species in areas with a deep insulating surface moss mat and cold soils, would diminish the growth and expansion of poplar clone on older surfaces.

We found that large stands of poplar trees developed in stand 4 along the northern and eastern margins of the study area. These colonization events were likely due to (1) local geomorphic disturbances caused by material slumping and flowing from steep, unconsolidated morainal deposits and terrace edges with subsequent alluvial redistribution of these materials, and (2) increased protection from wind adjacent to high moraine bluffs likely decreased injury to trees and increased growth in these protected areas. We observed a sizeable debris flow emanating from the unconsolidated morainal deposits debauching onto the surface of stand 4, creating freshly exposed sites with abundant, moist fines, and producing conditions for poplar establishment similar to those in the earlier successional stands. Rood (2006) reported a similar dynamic in western Canada when a large debris flow

obliterated pre-existing vegetation, thereby creating edaphic conditions resembling floodplain deposits that were subsequently colonized by *Populus trichocarpa* (a close relative of *P. balsamifera*) instead of the dominant species that formerly occupied the area prior to the disturbance.

Resistance of the late-successional vegetation mosaic to change

Although the footprint of dense poplar woodlands is spatially discontinuous, their rapid expansion over the sample interval suggests that these stands could coalesce to create continuous poplar woodland across the study area over time. An impediment to this process is competition with established late-succession shrub vegetation. For example, Brodie et al. (1995) found that a large poplar clone north of treeline in Quebec that was otherwise capable of expanding and producing new suckers had little recruitment in areas where *Betula glandulosa* was dense (presumably due to edaphic conditions and competition). Our data indicate that, in the absence of disturbance, late-successional areas supporting mossy *Betula nana* and sedge-scrub tussock tundra mosaics (large areas of stands 3–5) have changed very little over the sample interval. Experimental and observational work has shown that the thickness of the moss mat plays a crucial role in regulating soil temperature in high-latitude ecosystems (e.g., Gornall et al. 2007, Blok et al. 2011). Unsuitable seedbed conditions due to a lack of exposed mineral soil and cold soil temperatures in the feathermoss-dominated understory are impediments to poplar establishment in late-succession scrub tundra.

Consequence of observed changes in early succession and *P. balsamifera* expansion

In the altered successional context instigated by warming, newly deposited surfaces undergoing primary succession in our study area will likely follow a different trajectory from the one that resulted in the establishment of the mossy, shrub-dominated vegetation mosaic that currently dominates older flat and gently sloping surfaces in this region. Instead, newly deposited surfaces are likely to be colonized by woody species (especially poplar) much earlier, and undergo transition to a larger-statured woodland

mosaic similar to what occurs in adjacent boreal lowland river terraces in the region (see [Viereck et al. 1993](#)). In fact, our data indicate that taxa common and widespread in the boreal zone have already spread within this area, while some taxa that occur primarily in alpine areas in Alaska have become rarer over the past five decades.

Our analyses clearly indicate that the plant communities that occur with the development of poplar stands are distinctly different from the communities that developed in the dominant successional sequence described by Viereck (1966). Specifically, these woodland communities have a taller canopy, reduced cover and depth of the moss mat, warmer soil temperatures, altered species composition with more forbs, higher species richness of vascular plants, and deeper snow depths. Mean soil temperatures in our poplar plots were considerably warmer than the stand mean temperatures, a difference that was exaggerated with increasing stand age. Deciduous litter has been shown to reduce the growth and survival of feathermosses through both physical shading and chemical inhibition from phenolic compounds in the leaf tissue ([Startsev et al. 2008](#)). The negative effect of leaf litter in the poplar stands may be intensified by the wind-break effect that taller-statured poplar woodland vegetation creates, thereby increasing litter and its decomposition in situ relative to adjacent areas with low-statured scrub tundra vegetation. In the current warmer summer environment, understory conditions are unlikely to lead to the establishment of a deep and insulating moss mat, paludification, and cooling soils, as was formerly the case in this region ([Viereck 1966](#)). Thus, development of poplar communities across the study area represents a sharp departure from the original successional trajectory described by [Viereck \(1966\)](#). This alteration presages fundamental changes for the future landscape mosaic.

Another potentially important consequence of the increase in poplar is changing patterns of snowpack redistribution by wind where trees become established. We found that snow was deeper, on average, in poplar plots as compared to the full plots in the same stand. [Viereck \(1966\)](#) emphasized the importance of wind and its effect on snow accumulation, and how this dynamic interacts with vegetation development

in the study area. He described the evidence of injuries to plant tissues from “snow or sand blasting” from high-velocity winter winds, and the importance of larger-statured vegetation for trapping snow and ameliorating winter conditions at ground level during the course of succession. Indeed, the importance of interactions between snow distribution and depth and vegetation development in treeline environments has been recognized in a variety of ecosystems (e.g., [Hiemstra et al. 2006](#), [Zald et al. 2012](#)). Additionally, the deepening of the snowpack may translate into warmer soil profiles because the depth and character of the snowpack strongly controls heat exchange between the atmosphere and the soil profile ([Jafarov et al. 2014](#), [Park et al. 2015](#)). Experimental studies in northern Alaska have shown significant influences of variation in winter snow depth on summer soil temperature profiles with measureable ecophysiological responses by tundra plant species ([Pattison and Welker 2014](#)).

Importantly, the expansion of poplar woodlands in the study area seems likely to facilitate the recruitment of *Picea glauca* seedlings under the protection of a tree canopy ([Viereck et al. 1993](#)). We observed healthy *P. glauca* saplings growing in several parts of the study area in 2012, but only where they appeared to be protected by either sheltering topography or a dense poplar canopy. The protection from high-velocity winds and insulation provided by deeper snowpack may ultimately expedite the conversion of these areas from the low-statured scrub vegetation mosaic described by Viereck (1966) to a boreal conifer forest mosaic through the intermediate stage of poplar woodlands. Furthermore, we would expect that a large increase in *P. glauca* trees in this area would facilitate the direct colonization of dwarf birch scrub tundra there, because this species is capable of establishing within this type ([Stueve et al. 2011](#), [Roland et al. 2013](#)). This conversion would have profound implications for both ecosystem structure and function in this landscape.

Conclusions

We report the results of a resurvey 54 yr later of a chronosequence of primary succession on outflow terraces of the Muldrow Glacier. The original stand ages were reported as

25–30 yr (stand 1), 100 yr (stand 2), 150–200 yr (stand 3), and 250–300 yr (stand 4) in 1958 by Viereck (1966). The sampling interval was long enough for vegetation in plots to become more similar to 1958 plots in the next older stand age, although plots in stand 1 did not follow the expected trajectory of increasing herbaceous cover toward the establishment of the meadow stage (stand 2), but instead primarily experienced increases in woody taxa.

Our work reveals a rapid increase in the distribution, stature, and abundance of balsam poplar trees that strongly contrasts with the successional dynamic described in Viereck's original study (Viereck 1966) and appears to represent a directional change for this region. One likely reason for this unexpected change is the recent warming in summer temperatures that were unforeseen in 1966. We suspect that if this area is subject to continued warming, patches of poplar forest will continue to expand stimulating even more change. Our data suggest that the expansion will occur unevenly, proceeding rapidly in newly disturbed areas, much more slowly in areas with established late-successional vegetation, and not at all in areas that remain underlain by shallow permafrost.

Expansion of poplar forest would likely facilitate the expansion of white spruce underway in the subalpine zone of Denali (Stueve et al. 2011, Roland and Stehn 2013), by providing a protected environment for seedling establishment and reduced winter injuries to conifer saplings. White spruce is better able to colonize established *Betula nana* scrub tundra vegetation than poplar, likely because of its larger seed mass and ability to tolerate cooler, more organic-rich soil conditions (Hobbie and Chapin 1998, Roland et al. 2013). As more white spruce become established in the area and produce seeds, recruitment of this species is likely in areas of established vegetation where poplar recruitment rarely occurs.

Our results highlight the capacity of a single species to potentially catalyze the changes that may lead to the altering of the landscape mosaic. In our study area, the dispersal and colonization traits of balsam poplar allowed it to establish early in primary succession in subalpine sites distant from continuous boreal forest and thus capitalize on warming conditions to increase in abundance and distribution as it has elsewhere

in Alaska in the past (Mann et al. 2010). Another set of traits possessed by the species, including its tree growth form, clonality, and a deciduous habit, may in turn allow poplar to supersede the existing successional dynamic. Poplar may capture the successional dynamic by outcompeting smaller-statured shrub species, and then alter the understory dynamics by precluding the establishment of a deep, insulating moss mat. It appears that poplar may thus act as the “leading edge” of landscape change in this region, colonizing barren silt in the subalpine zone and, over time, leaving a substantially altered, boreal landscape in its wake. Furthermore, the effect of balsam poplar in facilitating recruitment of the more-shade and cool-soil tolerant white spruce may further catalyze the long-term conversion of subalpine areas of Denali into boreal forest in coming decades.

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LITERATURE CITED

- Barrett, K., A. D. McGuire, E. E. Hoy, and E. S. Kasischke. 2011. Potential shifts in dominant forest cover in interior Alaska driven by variations in fire severity. *Ecological Applications* 21:2380–2396.
- Beck, P. S., G. P. Juday, C. Alix, V. A. Barber, S. E. Winslow, E. E. Sousa, P. Heiser, J. D. Herriges, and S. J. Goetz. 2011. Changes in forest productivity across Alaska consistent with biome shift. *Ecology Letters* 14:373–379.
- Bellingham, P. J., D. A. Peltzer, and L. R. Lawrence. 2005. Contrasting impacts of a native and an invasive exotic shrub on flood-plain succession. *Journal of Vegetation Science* 16:135–142.

- Bliss, L. C., and J. E. Cantlon. 1957. Succession on river alluvium in northern Alaska. *American Midland Naturalist* 58:452–469.
- Blok, D., M. M. P. D. Heimans, G. Schaepman-Strub, J. van Ruiven, F. J. W. Parmentier, T. C. Maximov, and F. Berendse. 2011. The cooling capacity of mosses: controls on water and energy fluxes in a Siberian tundra site. *Ecosystems* 14:1055–1065.
- Brodie, C., G. Houle, and M.-J. Fortin. 1995. Development of a *Populus balsamifera* clone in subarctic Quebec reconstructed from spatial analyses. *Journal of Ecology* 83:309–320.
- Calcagno, V. 2012. glmulti: model selection and multimodel inference made easy. R package version 1.0.6. <http://CRAN.R-project.org/package=glmulti>
- Chapin III, F. S., et al. 2010. Resilience to climate change in Alaska's boreal forest. *Canadian Journal of Forest Research* 40:1360–1370.
- Cody, W. J. 1996. *Flora of the Yukon Territory*. National Research Council Press, Ottawa, Ontario, Canada.
- Comtois, P., J. P. Simon, and S. Payette. 1986. Clonal constitution and sex ratio in northern populations of balsam poplar (*Populus balsamifera*). *Holarctic Ecology* 9:251–260.
- Danby, R. K., S. Koh, D. S. Hik, and L. W. Price. 2011. Four decades of plant community change in the alpine tundra of southwest Yukon, Canada. *Ambio* 40:660–671.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invisibility. *Journal of Ecology* 88:528–534.
- Dortch, J. M., L. A. Owen, M. W. Caffee, and P. Brease. 2010. Late Quaternary glaciation and equilibrium line altitude variations of the McKinley River region, central Alaska Range. *Boreas* 39:233–246.
- ESRI. 2001. ArcGIS geostatistical analyst: statistical tools for data exploration, modeling, and advanced surface generation. ESRI, Redlands, California, USA.
- Esslinger, T. L. 2015. A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. North Dakota State University. <http://www.ndsu.edu/pubweb/~esslinge/chcklst/chcklst7.htm>
- Flora of North America Editorial Committee, editors. 1993+. *Flora of North America north of Mexico*. 18+ volumes. Oxford University Press, New York, New York, USA.
- Gornall, J. L., I. S. Jonsdottir, S. J. Woodin, and R. Van der Wal. 2007. Arctic mosses govern below-ground environment and ecosystem processes. *Oecologia* 153:931–941.
- Hiemstra, C. A., G. E. Liston, and W. A. Reiners. 2006. Observing, modelling, and validating snow redistribution by wind in a Wyoming upper treeline landscape. *Ecological Modelling* 197:35–51.
- Hobbie, S. E., and F. S. Chapin III. 1998. The response of tundra plant biomass, above-ground production, nitrogen, and CO₂ flux to experimental warming. *Ecology* 79:1526–1544.
- Hultén, E. 1968. *Flora of Alaska and neighboring territories: a manual of the vascular plants*. Stanford University Press, Stanford, California, USA.
- Jafarov, E. E., D. J. Nicolsky, V. E. Romanovsky, J. E. Walsh, S. K. Panda, and M. C. Serreze. 2014. The effect of snow: how to better model ground surface temperatures. *Cold Regions Science and Technology* 102:63–77.
- Jobidon, R., and J. R. Thibout. 1982. Allelopathic growth inhibition of nodulated and unnodulated *Alnus crispa* seedlings by *Populus balsamifera*. *American Journal of Botany* 69:1213–1223.
- Johnstone, J. F., and F. S. Chapin III. 2006a. Effects of soil burn severity on post-fire tree recruitment in boreal forest. *Ecosystems* 9:14–31.
- Johnstone, J. F., and F. S. Chapin III. 2006b. Fire interval effects on successional trajectory in boreal forests of Northwest Canada. *Ecosystems* 9:268–277.
- Johnstone, J. F., F. S. Chapin III, T. N. Hollingsworth, M. C. Mack, V. Romanovsky, and M. Turetsky. 2010a. Fire, climate change, and forest resilience in interior Alaska. *Canadian Journal of Forest Research* 40:1302–1312.
- Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin III, and M. C. Mack. 2010b. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology* 16:1281–1295.
- Kalischuk, A. R., S. R. Rood, and J. M. Mahoney. 2001. Environmental influences on seedling growth of cottonwood species following a major flood. *Forest Ecology and Management*. 2001:75–89.
- Kasischke, E. S., et al. 2010. Alaska's changing fire regime: implications for the vulnerability of its boreal forests. *Canadian Journal of Forest Research* 40:1313–1324.
- Landhäusser, S. M., and R. W. Wein. 1993. Postfire vegetation recovery and tree establishment at the arctic treeline: climate-change-vegetation-response hypotheses. *Journal of Ecology* 81:665–672.
- Landhäusser, S. M., R. W. Wein, and P. Lange. 1996. Gas exchange of three arctic tree-line tree species under different soil temperature and drought preconditioning regimes. *Canadian Journal of Botany* 74:686–693.
- Landhäusser, S. M., U. Silins, V. J. Lieffers, and W. Liu. 2003. Response of *Populus tremuloides*, *Populus balsamifera*, *Betula papyrifera* and *Picea glauca* seedlings to low soil temperature and water-logged soil conditions. *Scandinavian Journal of Forest Research* 18:391–400.

- Lantz, T. C., S. V. Kokelj, S. E. Gergel, and G. H. R. Henry. 2009. Relative impacts of disturbance and temperature: persistent changes in microenvironment and vegetation in retrogressive thaw slumps. *Global Change Biology* 15:1664–1675.
- Lawrence, W. T., and W. C. Oechel. 1983. Effects of soil temperature on the carbon exchange of tundra seedlings. II. Photosynthesis, respiration, and conductance. *Canadian Journal of Forest Research* 13:850–859.
- Lev, D. J. 1987. Balsam poplar (*Populus balsamifera*) in Alaska: ecology and growth response to climate. Thesis. University of Washington, Seattle, Washington, USA.
- Mann, D. H., P. Groves, R. E. Reanier, and M. L. Kunz. 2010. Floodplains, permafrost, cottonwood trees, and peat: What happened the last time climate warmed suddenly in arctic Alaska? *Quaternary Science Reviews* 29:3812–3830.
- McCune, B., and M. L. Mefford. 2006. PC-ORD: multivariate analysis of ecological data. Version 5.33. MjM Software, Gleneden Beach, Oregon, USA.
- McDonald, J. H. 2014. Handbook of biological statistics. Third edition. Sparky House, Baltimore, Maryland, USA.
- Mitchell, T. D., and P. D. Jones. 2005. An improved method of constructing a database of monthly climate observations and associated grids. *International Journal of Climatology* 25:693–712.
- Munier, A., L. Hermanutz, J. D. Jacobs, and K. Lewis. 2010. The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: implications for treeline advance with climate warming. *Plant Ecology* 210:19–30.
- Nelson, R. E., and L. D. Carter. 1987. Paleoenvironmental analysis of insects and extralimital *Populus* from an Early Holocene site on the Arctic Slope of Alaska, U.S.A. *Arctic and Alpine Research* 19:230–241.
- Ohmann, L. F., and R. R. Ream. 1971. Wilderness ecology: a method for sampling and summarizing data for plant community classification. USDA Forest Service Research Paper NC 49. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, USA.
- Park, H., A. N. Fedorov, M. N. Zheleznyak, P. Y. Konstantinov, and J. E. Walsh. 2015. Effect of snow cover on pan-Arctic permafrost thermal regimes. *Climate Dynamics* 44:2873–2895.
- Pattison, R. R., and J. M. Welker. 2014. Differential ecophysiological response of deciduous shrubs and a graminoid to long-term experimental snow reductions and additions in moist acidic tundra, Northern Alaska. *Oecologia* 174:339–350.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Roland, C. A., and J. H. Schmidt. 2015. A diverse alpine species pool drives a 'reversed' plant species richness-elevation relationship in interior Alaska. *Journal of Biogeography* 42:738–750.
- Roland, C. A., and S. E. Stehn. 2013. Denali repeat photography project reveals dramatic changes: a drier, woodier, and more densely vegetated park. *Alaska Park Science* 12:64–65.
- Roland, C. A., K. Oakley, E. M. Debevec, and T. Loomis. 2004. Monitoring vegetation structure and composition at multiple scales in the Central Alaska Network. NPS Technical Report CAKN-001. National Park Service, Fairbanks, Alaska, USA. <https://irma.nps.gov/App/Reference/Profile?code1/>
- Roland, C. A., J. H. Schmidt, and E. Fleur Nicklen. 2013. Landscape-scale patterns in tree occupancy and abundance in subarctic Alaska. *Ecological Monographs* 83:19–48.
- Rood, S. B. 2006. Unusual disturbance: forest change following a catastrophic debris flow in the Canadian Rocky Mountains. *Canadian Journal of Forest Research* 36:2204–2215.
- Shulski, M., and G. Wendler. 2007. The climate of Alaska. University of Alaska Press, Fairbanks, Alaska, USA.
- Simpson, J. J., G. L. Hufford, C. Daly, J. S. Berg, and M. D. Fleming. 2005. Comparing maps of mean monthly surface temperature and precipitation for Alaska and adjacent areas of Canada produced by two different methods. *Arctic* 58:137–161.
- St. John, M. G., P. J. Bellingham, L. R. Walker, H. H. Orwin, K. I. Bonner, I. A. Dickie, C. W. Morse, G. W. Yeates, and D. W. Wardle. 2012. Loss of a dominant nitrogen-fixing shrub in primary succession: consequences for plant and below-ground communities. *Journal of Ecology* 100:1074–1084.
- Startsev, N., V. J. Lieffers, and S. M. Landhäusser. 2008. Effects of leaf litter on the growth of boreal feather mosses: implication for forest floor development. *Journal of Vegetation Science* 19:253–260.
- Stueve, K. M., R. E. Isaacs, L. E. Tyrrell, and R. V. Densmore. 2011. Spatial variability of biotic and abiotic tree establishment constraints across a treeline ecotone in the Alaska Range. *Ecology* 92:496–506.
- Viereck, L. A. 1966. Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. *Ecological Monographs* 36:181–199.
- Viereck, L. A., C. T. Dyrness, and M. J. Foote. 1993. An overview of the vegetation and soils of the floodplain ecosystems of the Tanana River, interior Alaska. *Canadian Journal of Forest Research* 23:889–898.

Zald, H. S. J., T. A. Spies, M. Huso, and D. Gatzolis. 2012. Climatic, landform, microtopographic, and overstory canopy controls of tree invasion in a sub-alpine meadow landscape, Oregon Cascades, USA. Landscape Ecology 27:1197–1212.

Zasada, J. C., and H. M. Phipps. 1990. Balsam poplar (*Populus balsamifera* L.). Pages 518–529 in M. R. Burns and B. H. Honkala, editors. Silvics of North America. Volume 2: hardwoods. Agricultural handbook 654. USDA, Forest Service, Washington, DC, USA.

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