Four Decades of Plant Community Change in the Alpine Tundra of Southwest Yukon, Canada

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Abstract Repeat measurements from long-term plots provide precise data for studying plant community change. In 2010, we visited a remote location in Yukon, Canada, where a detailed survey of alpine tundra communities was conducted in 1968. Plant community composition was resurveyed on the same four slopes using the same methods as the original study. Species richness and diversity increased significantly over the 42 years and non-metric multidimensional scaling indicated that community composition had also changed significantly. However, the direction and magnitude of change varied with aspect. Dominant species were not replaced or eliminated but, instead, declined in relative importance. Fine-scale changes in vegetation were evident from repeat photography and dendro-ecological analysis of erect shrubs, supporting the community-level analysis. The period of study corresponds to a mean annual temperature increase of 2°C, suggesting that climate warming has influenced these changes.

Keywords Tundra · Yukon · Climate change · Arctic–alpine · Community ecology

INTRODUCTION

Observed changes in plant communities in both Arctic and alpine environments have been associated with recent climate warming (e.g., Post et al. 2009; Grabherr et al. 2010). These shifts in species abundance and diversity may lead to changes in surface energy budgets, primary productivity, nutrient cycling, and trophic interactions. In the absence of long-term monitoring, revisiting sites surveyed several decades earlier represents an important opportunity for detecting patterns of change. In the Arctic, these efforts have been led by the Back to the Future IPY Project (see

Callaghan et al. 2011 [this issue]), while alpine efforts have more recently been coordinated by the Global Observation Research Initiative in Alpine Environments, or GLORIA (e.g., Grabherr et al. 2010). These repeated observations allow more reliable assessment of the patterns and causes of change, and provide an essential temporal record for validating and scaling predictions of future changes.

Significant changes in both diversity and above-ground biomass have been associated with recent warming of both high Arctic (e.g., Hudson et al. 2010) and low Arctic (e.g., Euskirchen et al. 2009) sites. Floristic changes at alpine sites are similarly believed to be the result of ongoing climatic warming (Frei et al. 2010). For example, in the Swiss Alps, the observed increase in species richness over the past century averaged 86% (Vittoz et al. 2009); over the past 50 years, the observed increase in plant species richness on mountains in central Sweden was 58–67% (Kullman 2007); and in southern Norway, the increase in richness over the past 40 years averaged 90% (Odland et al. 2010).

Unfortunately, there are few observations or records from sites in the remote high latitude mountains of western North America, even though the *Arctic Climate Impact Assessment* (ACIA 2005) concluded that Alaska and the Canadian Yukon experienced the most dramatic recent warming in the Arctic, resulting in major ecological impacts at lower elevations including northward expansion of boreal forest in some areas, significant increases in fire frequency and intensity, and unprecedented insect outbreaks. Signs of warming are also increasingly apparent in these northern alpine ecosystems. For example, in southwest Yukon, where temperatures have increased significantly over the last 40 years, there is compelling evidence linking variation in climate and weather to changes in alpine treeline and the survival, reproductive success and

growth of several species of mammalian herbivores (Danby and Hik 2007; Morrison and Hik 2007). Observed changes in tundra plant communities have been related to herbivory (McIntire and Hik 2005) and interactions between plant species and the local environment (e.g., Mitchell et al. 2009), but long-term changes associated with warming are difficult to infer from short-term studies.

Fortunately, research conducted in 1967 and 1968 by Price (1970, 1971) provides a wealth of systematic work on alpine plant community composition in the Ruby Range, southwest Yukon, Canada. Although there are a few other contemporary observations from this region (for example, Douglas (1974) also conducted several surveys in alpine areas of the Kluane National Park and Reserve), the exact locations were not well documented and observations were often only descriptive. Motivated by the Back to the Future IPY project, and recognizing the significance of the transects established by Price in the late 1960's, we re-examined the alpine communities on these same slopes in 2010 to determine how alpine plant communities have changed over the last 42 years, and the potential for detecting a signal of climate warming that could be compared to other alpine and Arctic sites (Pauli et al. 2007; Holzinger et al. 2008; Post et al. 2009; Grabherr et al. 2010; Odland et al. 2010; Rammig et al. 2010).

MATERIALS AND METHODS

Study Area

The Ruby Range Mountains of southwest Yukon (Fig. 1a) are a broad, undulating upland ranging from 800 to 2300 m elevation (Smith et al. 2004). Valley forests of white spruce *Picea glauca* occupy elevations below 1200 m. Subalpine areas are locally variable, generally occurring between 1200 and 1500 m and are comprised of scattered spruce among thickets of tall shrubs (*Salix* spp. and *Betula glandulosa*). The alpine zone comprises various tundra plant communities that vary with topography and is the subject of this study. Our study site was located near the head of a tributary of the Gladstone Lakes complex (61.38°N, 138.20°W) where four slopes result from the confluence of two ridges (Fig. 1b). The slopes each have a distinct aspect (southeast, east, north and southwest) but similar underlying geology and slope gradients, and span the same elevation (Price 1970).

Southwest Yukon has experienced a significant climate warming since the mid-1960s (Prowse et al. 2009). Average annual temperature has increased approximately 0.5°C per decade at Burwash Landing (the nearest meteorological station to our site) since meteorological records began there in 1967, but there has been no statistically significant trend

in total annual precipitation (Fig. 2). Models predict temperature increases to continue (Laprise et al. 2003), making southwest Yukon a particularly useful locale for examining recent plant community dynamics in response to climate change.

Original Data Collection

The study site was the location of fieldwork for Price's doctoral research on the development and movement of solifluction lobes during 1967 and 1968 (see Price 1970). A component of this research involved the detailed description of vegetation on each of the four slopes as related to solifluction lobe development (Price 1971). A single transect was established along each of the four slopes in order to include representative areas of the major tundra plant communities. Transects varied in length depending on relative homogeneity of each slope (Fig. 1c). A 20 × 50 cm quadrat was used to collect data at 1.5 or 3.0 m intervals. Abundance, cover, and frequency of all vascular plant species, pooled mosses, pooled lichens, and bare ground were quantified according to the categories in Table 1. Definitions of each measure are also provided in Table 1. Data were converted to relative values, which were then summed and divided by three to yield a relative importance value out of 100 for each species (Curtis and McIntosh 1951; see Price 1971 for complete details).

Price analyzed the 1968 data to identify differences in composition related to variation in aspect, soil moisture, temperature, and microtopography. Community types were identified a priori based partly on aspect and microtopographic position. Richness was calculated and compared for each community type, but multivariate techniques were not used. Several distinct communities were found to occur in predictable patterns on the southeast and east aspects where solifluction terracing was highly pronounced. A hummocky *Carex*-moss community (called the "tussock community") was identified on the surface of solifluction lobes. Lobe fronts were vegetated with a comparatively rich herbaceous layer and much less graminoid and moss cover (the "front community"). Moist areas of high species richness, interspersed with small patches of exposed soil and rock, occurred in the lee of solifluction lobes (the "late snow melt community"). Within-slope differences were nearly absent on the north and southwest-facing aspects where solifluction lobes were less developed (Fig. 1c).

Contemporary Data Collection

We visited the general area of the site in July 2008, as part of a vegetation survey conducted during the International Polar Year. We were able to identify the four aspects central to the original study and repeat many of the

Fig. 1 Maps and schematic of the Ruby Range study site at three different scales. **a** Map of the study site within the regional context of southwest Yukon. **b** Map of the study site noting the location of the transects on the four slopes (1 = southeast aspect, 2 = east aspect,

3 = north aspect, 4 = southwest aspect). **c** Slope profiles along the length of each of the four transects illustrating the approximate boundaries of the different community types as originally defined by Price (1971)

coarse-scale and fine-scale photographs Price originally published in 1974. We returned to the site in July 2010 with the specific intent of resurveying the original transects. Quadrat size and sampling interval were identical to that used in the original study, and species cover and abundance were also recorded in the same manner. However, the original transects were not permanently marked, and evidence of their specific location had dissipated in the

intervening 42 years so we were unable to repeat the new transects on exactly the same lines. We used the distances between solifluction lobe fronts and the relative positions and distances between exposed rocky areas that were published in the original study to identify the most probable locations for each of the four original transects. We established two new transects on each slope to account for uncertainty in the exact location of the original transects

Fig. 2 Climate trends from the former Aishihik (1944–1965; shown in *blue*) and current Burwash Landing (1967–2007; shown in *red*) meteorological stations operated by Environment Canada illustrating **a** trends in mean annual temperature and **b** total annual precipitation. Linear trends based on least squares regression are presented for each data set. Data from the two stations were treated separately due to the distance between them (90 km; see Fig. 1)

and to test for within-slope variability (Rogers et al. 2008). Beginning and end points of each transect were determined using measured distances upslope and downslope of the solifluction fronts as well as the size of rocky areas that were published in the original study. In total, 363 quadrats from eight different transects were sampled.

In addition to the repeat photography and plant community data collection, we collected cross sections from the stems of 10 *Salix pulchra* shrub patches found growing near the transects on the southeast-facing slope. Price (1970, 1971) does not mention shrubs of any species when describing the vegetation so we wanted to identify the age of these individuals. Most shrubs were found growing on solifluction lobes in close proximity to the fronts. Shrubs were sampled along the crests of two fronts that generally followed the 1862 and 1835 m contour. Sampled shrubs were a minimum of 10 m apart. Two stems were sampled from each shrub. The first was the predominant ramet growing near the center of the shrub. The second was the

largest ramet growing near its perimeter. Two sections were obtained from each sampled ramet, for a total of 40 sections (i.e., 10 shrubs $\times$ 2 stems $\times$ 2 sections). The first was obtained at the true root collar, located by excavating the stem and sampling below soil surface. The age of this sample should correspond to year of establishment of the shrub patch (i.e., the genet; Bégin and Payette 1991). The second section was obtained at the root crown just above soil surface. This age should correspond to the age of the ramet itself. All sections were sanded to a fine polish and annual rings were counted under a stereo microscope. Cross-dating was conducted using iteratively identified marker years (Danby and Hik 2007).

Data Handling and Standardization

Taxonomic standardization was important to ensure comparability between years. We compiled a complete species list from the original study prior to fieldwork in 2010.

Table 1 Ordinal classes assigned to measures of abundance, cover and frequency

Class	Abundance (1), %	Percent cover (2), %	Frequency (3), %
1	1	<5	<10
2	2	5–24	10–24
3	3–5	25–49	25–49
4	6–9	50–74	50–74
5	10 or more	75–100	75–100

Break points between classes were used by Price (1971) in the 1968 survey and were therefore used for the repeat sampling conducted in 2010

(1) Abundance was determined by counting the number of individuals in the quadrat. When apparent, multiple stems from the same individual were counted as one individual (e.g., *Cassiope tetragona*). Clumps of cushion plants (e.g., *Silene acaulis*) were also counted as one individual

(2) Percent cover was estimated visually as the areal extent of each species in each quadrat

(3) Frequency was calculated as the number of quadrats of a specific community type that a particular species occurred in

Nomenclature was converted to be consistent with Cody (2000). Vouchers and photographs were collected of any species not positively identified in the field. These were later identified with the assistance of B. Bennett, Territorial botanist with the Yukon Government.

Price reported the relative importance values derived for each species in each of the original quadrats (Price 1970, 1971), but the raw data recorded from each quadrat (abundance and cover) was discarded in the years following the original research. Frequency is a transect-level derivative, and the raw frequency data were calculable from the published data by knowing the number of quadrats each species was present in. We were therefore able to remove the frequency component from the original data, yielding relative importance values based only on cover and abundance. We then calculated equivalent importance values for the 2010 data. Thus, the equations for the original and revised importance values are:

$$rI_{\text{original}} = (rC + rA + rF)/3,$$

$$rI_{\text{revised}} = (rC + rA)/2,$$

where rI is relative importance, rC is relative cover, rA is relative abundance, and rF is relative frequency. We decided to take this approach rather than applying the original formula to the 2010 data because we were unable to resurvey the precise locations of the original plots and the inclusion of the transect-level frequency metric might have inflated potential differences between 1968 and 2010 related to variation in transect placement.

We examined the entire 2010 data set and compared our two transects on each slope with each other to evaluate the

degree of within-slope variation in community composition. The analysis was conducted using multiple response permutation procedure (MRPP), a non-parametric test that does not rely on assumptions such as distributional normality and equal variance, using PCOrd 5.0 (McCune and Mefford 2006). Results (not shown) indicated that there was no significant difference in species composition between the two transects on any of the four slopes. This confirmed that the full range of variability for each community type on each aspect was captured within a single transect. We then removed one transect on each slope from the 2010 database, which was necessary to achieve balance with the 1968 data set. A decision was also made to include only the major community types on each slope in the analysis. Only a few quadrats fell in the solifluction front and dry community types on the southeast and east slopes and these were removed. The final data set used for analysis was divided into data from 1968 and 2010 collected in quadrats from the four different aspects.

Data Analysis

Species richness and diversity (based on the Shannon–Weiner index; MacArthur and MacArthur 1961) were calculated for each of the quadrats surveyed in 1968 and 2010. We used generalized linear mixed models in R v2.12 (R development Core Team 2010) to separately test whether richness or diversity varied with time or aspect. We tested the significance of the main effects with Markov Chain Monte Carlo (MCMC). Data were resampled using MCMC to create the distributions of each of the parameter estimates. From these estimates, both confidence intervals and p values were generated.

Non-metric multidimensional scaling (NMS) (McCune and Mefford 2006) was used to analyze variation in community composition between the two different years (1968 and 2010) on the four different aspects. Analysis was conducted using PCOrd 5.0 (McCune and Mefford 2006). The response matrix comprised importance values for the 63 species that occurred in 255 plots. We used Sorensen distance measures with random starting coordinates for 50 runs of real data each with 200 iterations and a stability criterion set at 1×10^{-5} . The dimensionality of the final solution was selected when additional dimensions provided less than 5% reduction in stress, which measures the fit between the observed data and distances among plots in the ordination (McCune and Grace 2002). Multiple-response permutation procedure (MRPP) was used to test for significant differences in species composition among aspects and between years (Mielke and Berry 2001; McCune and Grace 2002).

RESULTS

We were able to relocate several of Price's original photographic vantage points (Fig. 3). Comparison of the photographs with the originals indicates that the coarse-scale structure and pattern of tundra vegetation (generally above 1700 m) did not change (Fig. 3a). Photographs taken at a closer distance suggest some change in tundra plant cover and extent at a fine scale. In particular, graminoid cover appears to have increased (Fig. 3b) and areas of bare rock and soil in the late snowmelt areas located in the lee of solifluction lobes appear to have experienced some enlargement of vegetated patches (Fig. 3c).

The 10 *Salix pulchra* shrubs averaged 21.5 cm (SD $\pm$ 7.5) tall with a mean areal coverage of 1.04 m² ($\pm$ 0.55). Mean shrub age measured at root collar was 33.9 years ($\pm$ 13.1) and 27.1 years ($\pm$ 12.9) at the center and perimeter, respectively, of the shrub patches. Our qualitative observations through field and subsequent photographic analysis indicated that the two oldest shrubs (each 56 years) had a substantially higher number of dead ramets than the younger shrubs. Shrub density was not systematically measured, but based on the parameters of our sampling, we estimate areal coverage to be in the range of 1–3% at the crest of solifluction fronts on the southeast slope.

Total species richness increased on all four aspects between 1968 and 2010 (Table 2). The greatest proportional increase occurred on the east aspect (+118%), followed by the southeast (+48%), north (+40%), and southwest (+24%). Species diversity, measured for each quadrat using the Shannon–Weiner index, increased significantly from 1968 to 2010 ($pMCMC = 0.0001$, $p < 0.0001$). Diversity differed significantly between aspects ($pMCMC = 0.03$, $p = 0.0337$). Increases were greater on the Southeast and Southwest aspects compared to the North and East aspects (Fig. 4).

The multivariate community analysis indicated a significant difference in the overall community composition on each slope between 1968 and 2010. However, the differences were not equal among aspects. NMS indicated a greater amount of overlap between 1968 and 2010 for plots on the North, East, and Southeast aspects than for plots on the Southwest aspect (Fig. 5). This is confirmed in the MRPP separation statistics which indicate a much greater difference between the 2 years on the southwest aspect ($T = -23.933$, $A = 0.312$, $p < 0.0001$) relative to the north, east, and southeast aspects ($T = -17.314$, $A = 0.118$, $p < 0.0001$; $T = -21.098$, $A = 0.081$, $p < 0.0001$; $T = -20.618$, $A = 0.0798$, $p < 0.0001$, respectively).

The establishment of new species from a variety of functional groups was partly responsible for driving the compositional changes observed between 1968 and 2010 (Table 2a–d). Relatively few species were lost in the

42 years, though importance values did decline for many of the highest ranked species. On the southeast aspect, 19 new species were observed in 2010 and 6 were not detected. On the southwest, east, and north aspects, the number of species gained and lost totaled 23 & 4, 16 & 9, and 9 & 3, respectively.

New species of graminoids established themselves on each of the four aspects, notably *Poa arctica* and *Hierochloa alpina*, although species from all functional groups appeared. There was little pattern in the functional traits associated with the species that were lost. Although relative importance values changed significantly, the rank order of the most important species tended to remain consistent on the southeast and east aspects over the 42 years (Table 2a, b). In contrast, there was a much greater shift in species rankings on the southwest and north aspects (Table 2c, d).

DISCUSSION

Our results indicate that alpine plant communities at this study site in the Ruby Range Mountains of southwest Yukon have changed over the last four decades, but that the magnitude of change varied across the site.

Repeat Photography

Repeat photography did not indicate substantial changes in the structure of vegetation. Spruce has not advanced to this elevation and erect shrubs have not come to dominate. At a coarse-scale, the similarity between photographs is more compelling than the differences. This is not unexpected given that the site was squarely within the alpine life zone and several hundred meters above treeline in 1968. At a fine scale, there are differences evident in the photographs that suggest changes in community composition and/or increased biomass of communities. In particular, discrete patches of plants in sparsely vegetated areas—especially in

Fig. 3 Repeat photographic pairs from the study site. **a** The southeast facing slope (July 4, 1967 and July 8, 2008). Solifluction lobes are clearly evident as wave-like features in each photograph. Coarse-scale vegetation structure and pattern has not changed. **b** A stone stripe extending diagonally across the southeast-facing slope (July, 1968 and July 15, 2008). Some differences in the size and extent of grass and sedge tussocks are evident between the photos. **c** Late snow melt area on the southeast-facing slope (July, 1968 and July 15, 2008). Price painted a red line across the area to ascertain erosion extent and solifluction movement. The line is visible in the early photo, starting in the circle on the large rock in the foreground. Some differences in vegetation cover are evident between the photos, particularly enlarged patches of moss and herbaceous cover. Early photos originally published in Price (1974). Reprinted by permission of the publisher (Taylor & Francis Group, <http://www.informaworld.com>). (Figure displayed on next page)

Table 2 Relative importance values (mean and standard deviation) of species on each of the four aspects at the Ruby Range study site. The top 15 species or cover classes (moss, lichen, bare ground) in 2010 are presented alongside their respective rank in 1968. Bold typeface indicates species not observed in 1968

Species	Rank 2010	Rank 1968	Mean (SD) 2010	Mean (SD) 1968
(a) Southeast aspect				
Mosses	1	1	18.9 (6.3)	26.1 (10.7)
<i>Carex consimilis</i>	2	2	14.3 (3.9)	24.3 (8.9)
<i>Salix polaris</i>	3	3	13.1 (3.3)	12.6 (8.3)
Lichens	4	4	9.6 (4.9)	10.3 (8.1)
<i>Salix reticulata</i>	5	5	7.7 (8.4)	7.9 (11.4)
<i>Poa arctica</i>	6	–	6.9 (4.2)	0 (0)
<i>Polygonum viviparum</i>	7	–	4.0 (4.3)	0 (0)
Bare area	8	18	3.7 (4.6)	0.5 (2.2)
<i>Artemesia norvegica</i>	9	6	3.1 (4.7)	4.1 (6.2)
<i>Montia</i> spp.	10	8	2.1 (3.1)	1.4 (3.7)
<i>Antennaria monocephala</i>	11	9	1.9 (3.3)	1.3 (2.6)
<i>Petasites frigidus</i>	12	7	1.8 (3.8)	1.8 (4.6)
<i>Anenome parviflora</i>	13	11	1.2 (3.4)	1.1 (3.7)
<i>Stellaria longipes</i>	14	23	1.2 (2.5)	0.3 (1.4)
<i>Astragalus umbellata</i>	15	12	1.0 (3.2)	1.0 (3.8)
Total species	40	27		
(b) East aspect				
<i>Carex consimilis</i>	1	1	11.8 (6.7)	20.8 (8.7)
Mosses	2	3	11.5 (4.9)	17.1 (6.2)
<i>Salix polaris</i>	3	2	11.1 (3.3)	17.2 (7.9)
Lichens	4	4	11.1 (3.0)	11.6 (5)
<i>Dryas octopetala</i>	5	5	6.2 (7.5)	4.6 (7.6)
<i>Luzula arctica</i>	6	–	5.6 (4.2)	0 (0)
<i>Polygonum viviparum</i>	7	8	4.6 (4.0)	3.0 (3.6)
<i>Saussurea angustifolia</i>	8	6	4.6 (4.8)	4.4 (5.5)
<i>Minuartia biflora</i>	9	10	3.7 (4.7)	2.6 (3.5)
<i>Poa arctica</i>	10	–	3.0 (3.7)	0 (0)
<i>Saxifraga razshivinii</i>	11	15	3.0 (3.9)	1.2 (2.9)
Bare area	12	28	2.5 (2.9)	0.1 (0.7)
<i>Hierochloe alpina</i>	13	–	2.4 (3.6)	0 (0)
<i>Montia</i> spp.	14	12	2.2 (3.5)	1.4 (3.9)
<i>Oxytropis scammaniana</i>	15	7	1.9 (3.4)	3.4 (5.0)
Total species	36	29		
(c) Southwest aspect				
Lichens	1	1	12.1 (3.4)	31.2 (6.8)
Mosses	2	10	7.9 (2.4)	1.3 (3.5)
<i>Dryas octopetala</i>	3	2	7.8 (4.4)	29.6 (9.7)
<i>Salix reticulata</i>	4	3	7.5 (3.2)	10.9 (7.6)
<i>Salix polaris</i>	5	6	6.9 (2.4)	4.4 (6.3)
<i>Poa arctica</i>	6	–	6.8 (3.2)	0 (0)
<i>Antennaria monocephala</i>	7	5	6.3 (2.5)	4.7 (5.3)
<i>Hierochloe alpina</i>	8	–	5.4 (3.1)	0 (0)
<i>Carex consimilis</i>	9	7	5.2 (2.8)	4.0 (5.8)
<i>Campanula lasiocarpa</i>	10	–	4.6 (2.6)	0 (0)
<i>Artemesia norvegica</i>	11	–	4.2 (3.0)	0 (0)
<i>Saussurea angustifolia</i>	12	8	4.1 (3.3)	3.2 (5.4)
<i>Polygonum viviparum</i>	13	12	3.5 (2.8)	0.5 (2.1)
Bare area	14	–	3.4 (1.9)	0 (0)

Table 2 continued

Species	Rank 2010	Rank 1968	Mean (SD) 2010	Mean (SD) 1968
<i>Castilleja hyperborea</i>	15	–	1.7 (3.1)	0 (0)
Total species	35	16		
(d) North aspect				
Mosses	1	2	18.7 (7.4)	20.6 (4.9)
<i>Salix polaris</i>	2	4	13.7 (4.5)	13.8 (7.6)
Lichens	3	5	12.9 (4.2)	13.0 (5.2)
Bare area	4	3	10.3 (6.0)	14.1 (9.3)
<i>Carex consimilis</i>	5	1	9.3 (5.4)	20.7 (4.6)
<i>Luzula arctica</i>	6	–	8.1 (5.3)	0 (0)
<i>Poa arctica</i>	7	–	4.7 (4.9)	0 (0)
<i>Antennaria monocephala</i>	8	11	4.3 (4.1)	1.2 (2.8)
<i>Dryas octopetala</i>	9	12	4.2 (6.3)	0.8 (4.0)
<i>Ranunculus nivalis</i>	10	–	3.0 (3.7)	0 (0)
<i>Montia</i> spp.	11	6	2.7 (3.9)	5.0 (5.1)
<i>Taraxacum alaskanum</i>	12	8	2.1 (3.0)	2.3 (3.5)
<i>Lycopodium selago</i>	13	13	1.4 (2.7)	0.6 (2.3)
<i>Cassiope tetragona</i>	14	–	1.3 (5.4)	0 (0)
<i>Saxifraga razshivinii</i>	15	7	1.1 (2.4)	4.0 (5.2)
Total species	21	15		

Fig. 4 Mean values of Shannon–Weiner diversity index for quadrats on four aspects in 1968 and 2010. Error bars represent standard error. A statistically significant increase from 1968 to 2010 was detected for each aspect except north

the late snow melt areas—expanded in size between 1968 and 2008.

The repeat photography analysis is qualitative in nature, but increased plant growth and biomass of tundra vegetation at other long-term alpine and Arctic tundra sites supports our interpretation. Long-term sampling at Alexandria Fiord in Canada's high Arctic indicates a directional increase in the biomass of tundra communities since 1987 (Hudson and Henry 2009) that is in agreement with

satellite-based monitoring of indicators of primary productivity at northern latitudes over the same period (e.g., Jia et al. 2009). Temperature warming commensurate with these periods of analysis suggests a climatic connection that is supported by field experiments. For instance, tundra plants subjected to experimental warming at Alexandria Fiord over a period of 16 years exhibited significantly taller shoots and larger leaves than unwarmed individuals. Similar results have been observed at other Arctic and alpine sites worldwide (Walker et al. 2006; Rammig et al. 2010).

Shrubs

Age distribution of shrubs is consistent with the results of Myers-Smith (2011) who sampled 11 sites in southwest Yukon and found evidence that establishment of *Salix* spp. at the upper limit of their distribution has occurred just since 1970. Nevertheless, 2 of the 10 sampled shrubs predated Price's original survey and one dated to the same year. Because we only sampled live ramets, the high number of dead stems on these older individuals suggests that we may not have sampled the progenerate ramet and ages for these shrubs are therefore minima. Conversely, the lack or absence of dead ramets on the younger shrubs suggests that we obtained accurate year-of-establishment for these shrubs. We conclude that shrubs on the southeast aspect are not a recent phenomenon, but that their density has increased over the last four decades.

Fig. 5 Ordination based on non-metric multidimensional scaling of relative importance values for plant species on four different aspects collected in 1968 and 2010. Each point represents one quadrat

Community-Level Changes

The community-level analyses show that species richness increased on all slopes, diversity increased on three of the four slopes, and community composition changed significantly on each of the four slopes, with the most significant change occurring on the southwest aspect. These changes were the result of two factors: (1) the addition of many new, less abundant, species and (2) the reduction in relative importance values of many of the most dominant species. In fact, because species importance values were calculated relative to each other, the second factor is partly a function of the first.

The increase in species richness and diversity we observed is consistent with the results of repeat surveys from several other alpine and subarctic sites (e.g., Holzinger et al. 2007; Kullman 2007; Vittoz et al. 2009; Odland et al. 2010). No single functional group or species trait was predominantly associated with the addition or loss of species. However, we did detect several new graminoid species on each of the four slopes. This has been observed at other Arctic and alpine sites and at sites where experimental warming has been used (Walker et al. 2006). The trend toward increased richness of graminoids was observed despite a decline in the relative importance of *Carex consimilis*, the most abundant graminoid at the site.

However, because our values were calculated relative to all other species, this does not necessarily mean there was a widespread decline in *C. consimilis*; only that it is less important in overall community composition.

Dominant species were not entirely replaced or eliminated over the 42 years. For instance, tundra on the extensive solifluction treads (terraces) of the southeast aspect was still best described as a moss/*Carex consimilis*/*Salix polaris* community in 2010; just as it was in 1968. The greatest observed change was on the southwest aspect where moss increased and lichens and *Dryas octopetala* declined significantly in relative importance. This pattern was consistent with observations reported by Hudson and Henry (2009) who reported a shift toward increasing bryophyte dominance and a decrease in lichens at Alexandria Fiord, Nunavut, and those of Cornelissen et al. (2001) who documented a decline in lichen abundance at several Arctic and alpine sites. In the latter case, this change was hypothesized to be a response to increases in the abundance of vascular plants.

Engler et al. (2011) conducted a meta-analysis of the impact of recent climate change on mountain biodiversity and concluded that impacts on floras depend on the relative changes in both temperature and precipitation, with drought having a larger effect than regions where rainfall has been increasing. However, changes in community

composition and species diversity also vary with site and microsite characteristics. We similarly conclude that responses at our site are variable, as species that increased on one slope remained the same or even decreased on others. At the level of analysis conducted in our study, the differences are related to aspect. However, further analysis of differences within-slopes may reveal variation that is equally dependent on this finer-scale topography.

Climate change may be an important driver of the changes observed at this southwest Yukon site, but the specific mechanism(s) of change remain unclear. Price's original study (1970) identified several significant micro-climatic differences between the four aspects, notably soil temperature and soil moisture. These variables also differed within each aspect, particularly in relation to solifluction topography. The climate warming experienced over the last four decades could have influenced these variables differently on the four different aspects, and even at finer scales therein. Similarly, while trends in total annual precipitation were not statistically significant over the same period, seasonal variation must also be considered, especially in Arctic and alpine areas where snow is a significant constituent. These variables are likely to vary at a finer scale than annual means and are therefore critical to consider in light of the aspect-related change we observed.

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