

Trends in groundberry cover under climate change in the southern and central Yukon, 1997–2022

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Abstract

Groundberries are an important component of the flora of the boreal forest and provide seasonally important food for many birds and mammals, as well as local people in northern Canada. Here, we ask whether there has been a change in the cover of groundberries in the Yukon boreal forest over the last two decades. We monitored five common species at undisturbed forest sites spaced 300 km apart. At our Kluane site, we monitored 710 fixed quadrats per year for 26 years (1997–2022), and at Mayo 500 quadrats per year for 18 years (2005–2022). The cover of four species, *Arctostaphylos uva-ursi* (L.) Spreng. (bearberry), *Arctostaphylos rubra* (Rehder & E.H. Wilson) Fernald (red bearberry), *Empetrum nigrum* L. (crowberry), and *Geocaulon lividum* (Richardson) Fernald (toadflax), declined annually by 0.2%–0.8% at both sites. In contrast, *Vaccinium vitis-idaea* L. (lingonberry) increased annually by 0.5% and 0.8%. We tested whether increases in summer temperature and rainfall were correlated with the observed changes but found no significant relationships. These boreal plants are changing in abundance, but we have limited data on the extent and speed of these changes. We recommend experiments to understand the cause(s) of these changes in groundberry productivity. Our study is a start in monitoring important berry species in this critical ecosystem of northern Canada.

Key words: boreal forest, groundberries, climate change, Yukon, declining cover, long-term study

Introduction

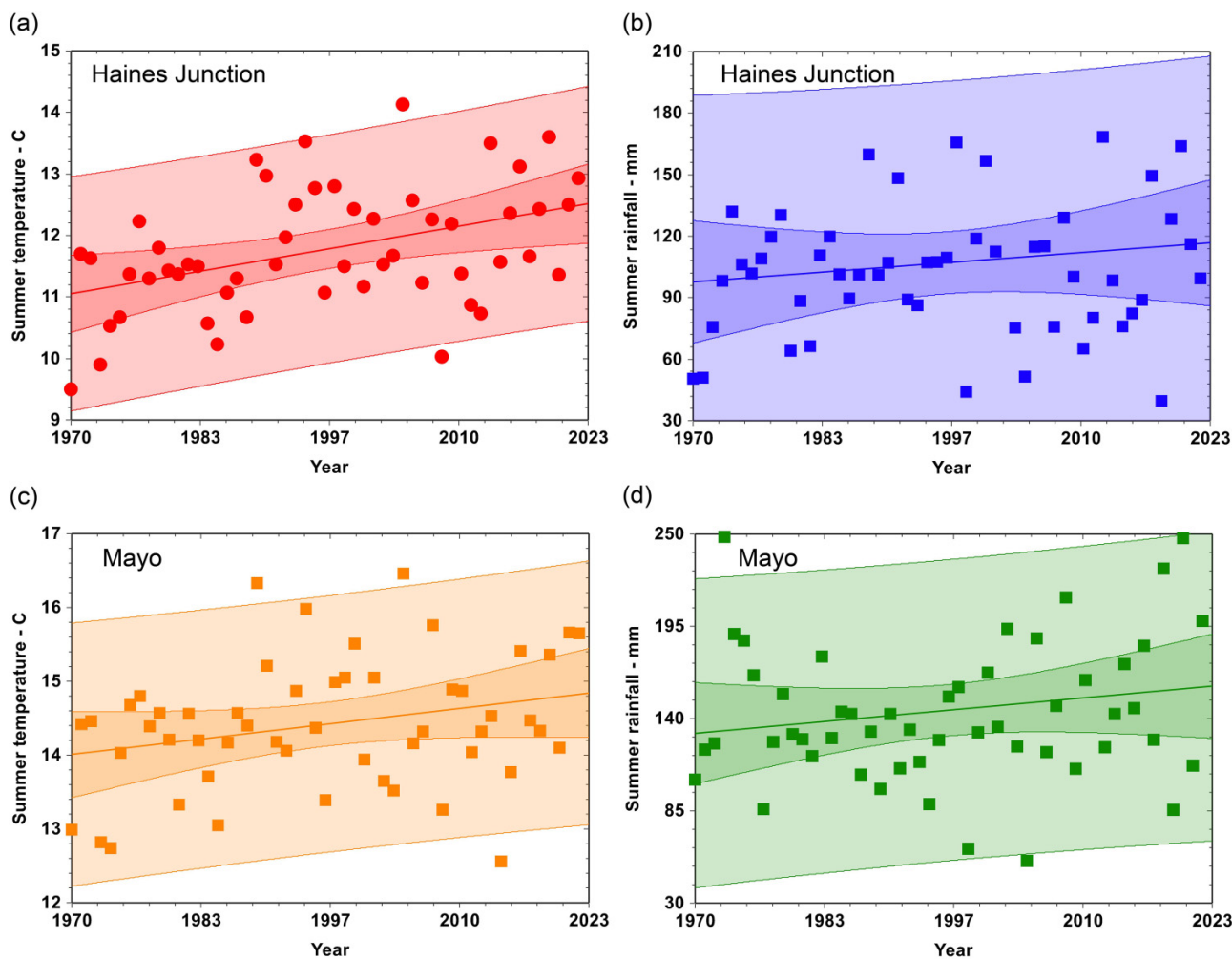
Groundberries form an important part of the understory flora of the boreal forest in the northern hemisphere and are dominant in the Yukon (Krebs et al. 2009; Boonstra et al. 2017). Despite their role in providing food for berry pickers as well as small mammals and birds across the entire boreal forest biome, they have been little studied in Canada. Research in North America has focussed heavily on consumption of groundberries by wild mammals and birds, and from this, we know that these berries are consumed seasonally by voles (West 1982), caribou (Miller 1976; Hall and Shay 1981), moose (Stevens 1970), grizzly and black bears (e.g., Raine and Kansas 1990; Munro et al. 2006), grouse (Ellison 1966), among others. In contrast European botanists have a long history of studies on their groundberries, given their importance for human food (Kuchko 1988; Ihalainen et al. 2003; Selås et al. 2021). Considerable research has been carried out in boreal areas that have been harvested for wood products because of the potential for harvesting to affect groundberry productivity (Granath et al. 2018). Little research has been carried out on the possible responses of groundberries to climate change in undisturbed boreal forest in Canada.

Although the boreal forests in northwestern Europe and Canada are similar at the tree level, they differ fundamentally at the understory level. In Fennoscandia, dwarf shrubs dominate, whereas in the North American boreal forest, tall shrubs dominate. The key driver of this continental difference is the more severe winter climate in the Canadian north than in the northwestern Eurasian boreal forests (Boonstra et al. 2016). Current climatic warming is causing the tall shrub component of Yukon forests to grow rapidly (Hedwall et al. 2021).

The realization of climate change and our early research at Lhù'ààn Mân' (Kluane Lake) (Krebs et al. 2001) made us realize that long-term monitoring was essential to following changes in the boreal forest. We recognize that groundberries were a particular set of plants that had not been sufficiently studied in the boreal forest, given their importance as food utilized by wildlife, First Nations, and many northern residents.

Two questions about groundberry ecology are of critical importance: (1) for each species do berry counts and plant cover vary from year to year, and (2) for each species what is the impact of climate change on berry counts and cover? We had the opportunity to sample five species of groundberries

Fig. 1. (a and b) Summer (1 June–31 August) average temperature and total rainfall (mm) at the major sampling sites of Kluane and (c and d) Mayo. The narrow-shaded area indicates confidence limits for the regression line prediction and the wider shaded area indicates confidence limits for individual year predictions. Data from Haines Junction and Mayo Environment Canada weather stations.



at Kluane Lake in the southwestern Yukon for 26 years since 1997 and in the central Yukon since 2005. Four of the species have a circumboreal or polar distribution, occurring in both Eurasia and North America (bearberry—*Arctostaphylos uva-ursi* (L.) Spreng. s.l., red bearberry—*Arctostaphylos rubra* Rehd. & Wils., crowberry—*Empetrum nigrum* L., and lingonberry *Vaccinium vitis-idaea* L.), and one occurs only in North America (toadflax—*Geocaulon lividum* (Richards.) Fern.). During that time, the Yukon temperature and rainfall have been increasing in the summer growing season (Fig. 1). In a previous study we have analyzed how groundberry counts adjusted in each quadrat to 50% cover for that species have changed over time and to identify the climatic variables that might be correlated with these changes (Krebs et al. 2009). We found no directional pattern in groundberry counts (adjusted to 50% cover) associated with climate change over this time. Here, we consider how groundberry cover has changed, asking the same questions as we did with groundberry counts.

Methods

We sampled small, fixed quadrats in the southwestern and central Yukon each year by counting berries and estimating cover for the five main species of groundberries in our area. Eight local sites were sampled near Lhù'ààn Mân' (Kluane Lake), and five local sites were sampled near Mayo. Quadrat size was 40 × 40 cm, and corners were permanently marked with long nails with flagging. We sampled the exact same quadrats each year. At Kluane, an average of 706 quadrats were counted each year from 1997 to 2022 on eight sites scattered along the Alaska Highway and Haines Highway from the Donjek River to St. Elias Lake (232 km). At Mayo, an average of 512 quadrats were counted each year from 2005 to 2022 on five sites (Table S1). Most sites were within 1 km of the highway. Between 75 and 100 quadrats were counted at each site in late July in mid-growing season and before the berries were ripe for eating. Not all five berry species were found on each plot. Plots were not placed randomly

but set at sites with at least 50% total groundberry cover (including all five of the species of concern). Plots that were destroyed by tree fall or had groundberry cover decline to less than 20% were removed from the study and not used in data analysis. Overall 3.5% of the original quadrats were removed from the study due to groundberry cover dropping below 20%.

Five species were abundant enough to be sampled: common bearberry, red bearberry, crowberry, lingonberry, and toadflax. Although we sampled groundberries intensively at two major sites (Kluane and Mayo), we also sampled three other sites less intensively in the southern Yukon (Faro 2007–2022, Watson Lake 2005–2022, and Whitehorse 2005–2022). We extended the analysis of berry plots to these three additional sites: Watson Lake, 540 km ESE of the Kluane sites, Whitehorse, 180 km east of Kluane, and Faro, 290 km northeast of Kluane. We had fewer permanent plots at these three sites: 161 per year on average at Watson Lake, 204 plots at Whitehorse, and 112 plots at Faro. We estimate that an average of 400–500 quadrats are needed to define precisely the small annual changes in groundberry cover. For these three sites, we examined the groundberry species that had a maximal amount of data.

Cover values were estimated by eye to the nearest 5% for each species. Details of the sampling methods are reported in the Supplementary material. Cover values were estimated by two observers in most plots, one observer with multiyear experience and one summer student with little or no experience. We evaluated the consistency of these cover estimates from year to year by calculating repeatability (Krebs 1999; p. 554), which measures the proportion of the variation that occurs between two adjacent years on the same plots. If measurements of cover are identical from one year to the next, there will be zero variance among years and repeatability will be 1. If measures of cover between 2 years for the same species vary greatly, repeatability will approach zero. In our study, the repeatability between cover estimates in adjacent years on the same plots averaged 0.64 for *A. uva-ursi* and 0.77–0.81 for the other four species sampled (Table S2). This added variance to our estimates of cover. There was little visible year-to-year growth in these groundberries, so we expected for repeatability that the percentage cover in year x would be very similar to that in year $x + 1$ for a particular species on a particular plot. The repeatability score thus measures both observer to observer variation in estimating cover as well as changes in year-to-year growth.

All quadrat samples within each of the study sites for each of the five species were averaged to provide a mean estimate of average percent cover for that site for that year. More information on the repeatability of cover is given in the Supplementary material (Table S2).

All statistical calculations were carried out in Number Crunching Statistical System (NCSS 2023, LLC, Kaysville, Utah, www.ncss.com). All field sites were treated as independent tests of observed trends, and all species were treated independently. Trends in cover from year to year were analyzed by simple linear regression. All results tested the null hypothesis of no trends in percentage of plant cover over time. Since sample sizes were largest at Kluane (710 quadrats per year)

and Mayo (499 per year), we analyzed these first and then compared their results to the other three sites (Whitehorse, 204; Watson Lake, 161; and Faro, 112) to detect whether the observed changes were consistent over this large geographical area.

To investigate the possibility that changes in cover might be caused by changes in temperature and rainfall during the summer growing season, we used stepwise regression to investigate for all species possible correlations between changes in cover and temperatures in early summer (May–July) and mid-summer (June–August) and rainfall for these same time periods of summer. We used current year climate variables and 1 year time-lagged climate variables to test for significant stepwise regressions.

Results

Yearly trends in almost all species on all sites rejected the simple hypothesis of no trend in percentage cover over the two decades of study. Most species declined in cover. There were no clear correlations between groundberry cover changes and climate variables.

The annual cover changes for common bearberry *A. uva-ursi* have been declining significantly at Mayo but only slightly at Kluane (Fig. 2). At Kluane, the decline in percentage cover has been about 0.07% per year on average, so that cover has fallen 2% in 26 years, a nonsignificant change (Table 1). At Mayo, common bearberry cover has declined at a faster annual rate than Kluane (Fig. 2). The annual decline at Mayo has been 0.8% on average, resulting in a decline of about 14% over 18 years (Table 1; Fig. 2). There was no evidence of browsing on bearberry shrubs and no evidence of bears digging on these plots.

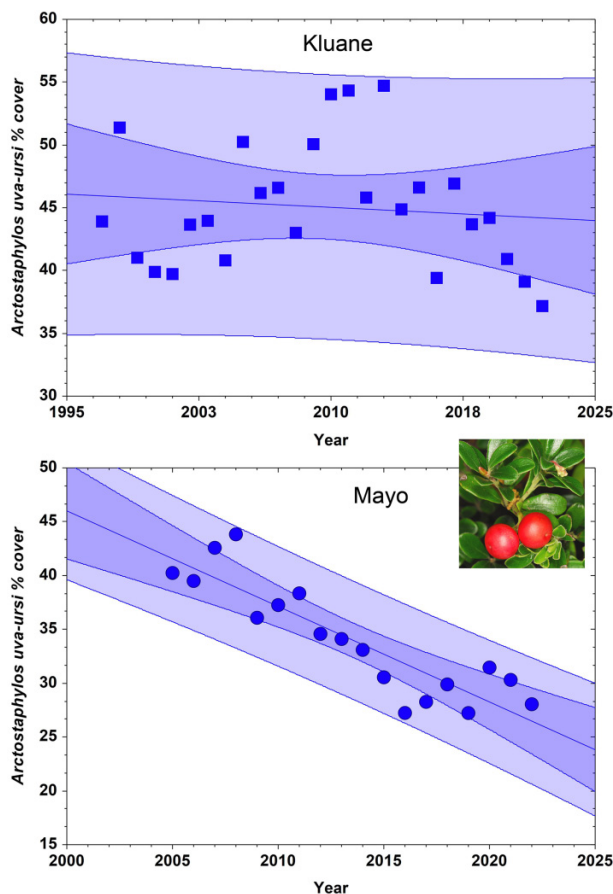
At Kluane, the percent cover of red bearberry *A. rubra* has declined significantly at a rate of about 0.7% per year on average, so that it has fallen 18% in 26 years (Table 1; Fig. 3). This trend was also observed at our Mayo site, where the average annual decline of red bearberry was 0.5% per year, resulting in an overall decline of about 9% over 18 years (Table 1; Fig. 3).

Similarly, the percentage cover of *G. lividum* has declined at both sites (Fig. 4). At Kluane, the decline was 0.3% per year on average (Table 1), with an overall decline of about 8% over 26 years. At Mayo, the annual rate of decline in cover of *G. lividum* was 0.4% per year (Table 1; Fig. 4), or nearly 7% over 18 years.

The percentage cover of crowberry *E. nigrum* has also been declining at our two main sites. At Kluane, the cover of *E. nigrum* has been declining by 0.25% per year (Table 1; Fig. 5), for an overall decline of about 7% over 26 years. At Mayo, crowberry declined in cover by 0.22% per year, for an overall decline of about 4% over 18 years (Fig. 5).

In contrast to the previous four berries at both our Kluane and Mayo sites, the percent cover of lingonberry *V. vitis-idaea* has significantly increased during our monitoring period (Table 1; Fig. 6). At Kluane, lingonberry cover increased 0.75% per year, resulting in a 20% increase over 26 years. At Mayo, cover of lingonberry showed a significant increase per year of 0.5% (Table 1; Fig. 6), with an increase of about 9% over the 18 years of monitoring.

Fig. 2. Percentage cover of *Arctostaphylos uva-ursi* in all sites at Kluane (1997–2022) and Mayo (2005–2022) sites in Yukon, Canada. Each data point is 1 year. The narrow-shaded area indicates confidence limits for the regression line prediction and the wider shaded area indicates 95% confidence limits for individual year predictions. Sample sizes and regression values are presented in [Table 1](#).



We viewed the groundberry cover counts at Mayo from 2005 to 2022 as a replicate study of the clear trends found at Kluane. The Mayo sites are 300 km NNE of Kluane Lake. The same methods of cover estimation used at Kluane were used at the five sites in the Mayo area. These four patterns of declining groundberry cover at Mayo mimic those at Kluane Lake. The result was that all the five species of groundberry showed similar directional trends in cover at Kluane and Mayo, four species declining and one species (*V. vitis-idaea*) increasing.

Total groundberry cover (of all five species) in aggregate was declining 0.6% per year at Kluane and 1.5% per year at Mayo over the study period ([Fig. 7](#)). [Table 2](#) summarizes the shape of the regressions over time for all five groundberry species. The absolute value of the effect sizes for these changes varied from 0.3% per year to 1.3% per year, and the overall average of the absolute value of the effect sizes is 0.64% per year.

Lingonberry at Watson Lake showed increasing cover from 2005 to 2022 ($p < 0.01$), the same pattern found at Kluane and

Mayo. *Geocaldon* declined at Whitehorse. For the overall data set, with Kluane set as the standard, there was no disagreement in trend out of five species for Mayo and Watson Lake, disagreement for one species for Whitehorse, and three for Faro. We place less reliance on the trends in the latter three areas because of smaller numbers of permanent quadrats (which averaged only 20%–30% of the sample size achieved at Mayo and Kluane). We are encouraged that the patterns of change in groundberry cover seem to apply broadly over this large area of boreal forest.

To summarize, at Kluane and Mayo, we have four major groundberry plants in fixed plots in the Yukon boreal forest declining in cover over the last 18–26 years, and significant changes in three other areas sampled less intensively ([Table 2](#)). One species—*V. vitis-idaea*—increased at three of the five sites.

The cause of these changes is not clear, and the one suggestion is that these changes in cover might be caused by changes in temperature and rainfall during the summer growing season. We used stepwise regression to investigate for all species possible correlations between changes in cover and temperatures in early summer (May–July) and mid-summer (June–August) and rainfall for these same time periods of summer. We used current year climate variables and time-lagged climate variables to test for significant stepwise regressions. We could find no significant stepwise regression for any of the five groundberry species. [Table 3](#) shows the results of this stepwise regression analysis and the failure to find any simple climatic correlations with these changes in cover for Kluane. Analysis of Mayo data provided the same results. Details are in [Table S4](#).

Discussion

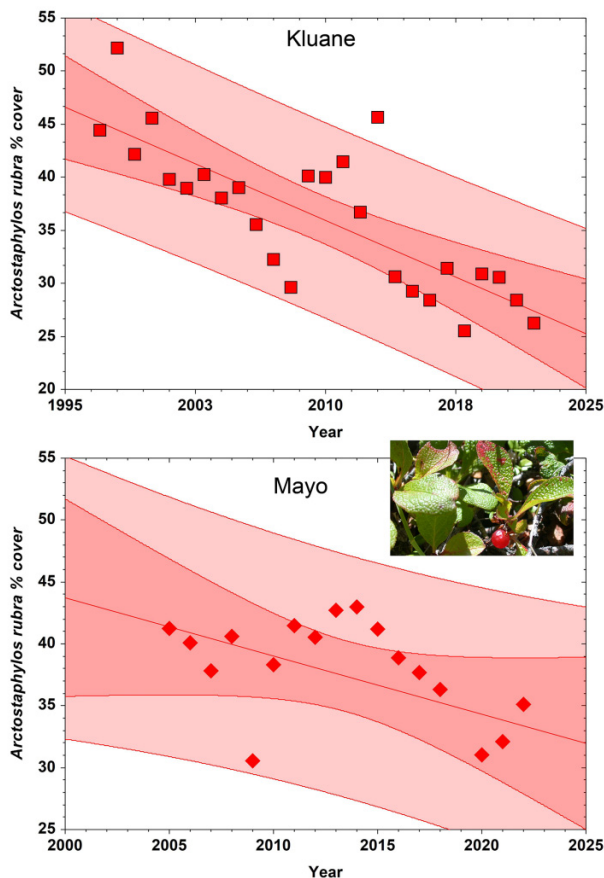
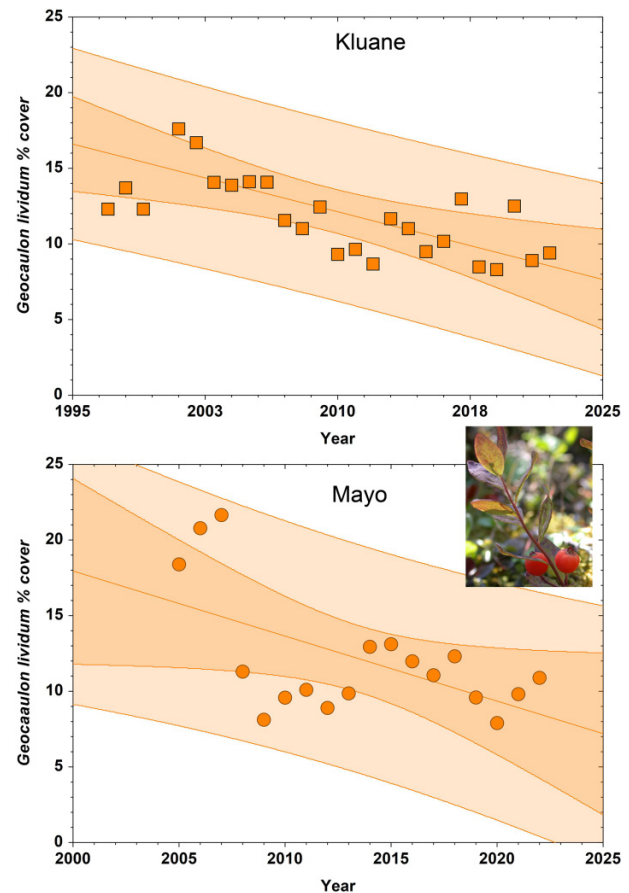
Groundberries are a major component of the forest floor plants in the Northern Hemisphere boreal forests, and thus their response to climate change may provide a useful indicator of the speed and the time scale of change, and how they are affecting humans. [Markkula et al. \(2019\)](#) reviewed how climate change may be affecting the indigenous people of northern Finland via ecosystem services. Finnish research on their northern ecosystems is much more advanced than it is in northern Canada. Berries are an integral dietary item for Alaska native people, and [Kellogg et al. \(2010\)](#) discuss the contributions berries can make to our diet. [Boulanger-Lapointe et al. \(2019\)](#) pointed out the importance of harvesting berries to the Inuit of northern Canada as a cultural activity, and the importance of berries as food to birds and mammals in tundra environments. The same is true for the First Nations peoples in the Yukon where we worked.

The five species investigated here have never been analyzed for long-term changes in cover anywhere in Canada. Data have been published for the adjusted annual production of berries in these species, and these show high variability from year to year over 26 years but no clear trends of increase or decline ([Krebs et al. 2009](#)). Berry production is partially controlled by rainfall and temperature during the growing season ([Ihalainen et al. 2003](#); [Krebs et al. 2009](#)), and the high variability in berry crops is well known to First Nations peo-

Table 1. Trends in groundberry cover regressions at the Kluane (1997–2022; 26 years) and Mayo (2005–2022; 18 years) sites, Yukon, Canada, and the average rate of change per year in cover for each species sampled.

Species	Kluane						Mayo					
	n	Trend	Slope	r	CV	p	n	Trend	Slope	r	CV	p
<i>Arctostaphylos uva-ursi</i> (bearberry)	3800	None	-0.07	-0.11	0.11	0.60	1173	Decline	-0.83	-0.75	0.13	<0.001
<i>Arctostaphylos rubra</i> (red bearberry)	5292	Decline	-0.71	-0.78	0.12	<0.001	1679	Decline	-0.52	-0.59	0.11	<0.01
<i>Geocaulon lividum</i> (toadflax)	1574	Decline	-0.30	-0.64	0.23	<0.001	1952	Decline	-0.40	-0.56	0.27	<0.02
<i>Empetrum nigrum</i> (crowberry)	2369	Decline	-0.25	-0.45	0.13	0.02	839	Decline	-0.22	-0.44	0.08	0.07
<i>Vaccinium vitis-idaea</i> (lingonberry)	3123	Increase	+0.75	+0.76	0.22	<0.001	4233	Increase	0.52	0.69	0.09	<0.002
Total all species	16 158	Decline	-0.63	-0.39	0.08	0.05	9876	Decline	-1.45	-.65	0.07	<0.004

Note: The slope is the rate of change of the regression lines illustrated in Figs. 2–7.

Fig. 3. Percentage cover of *Arctostaphylos rubra* in all sites at Kluane (1997–2022) and Mayo (2005–2022) sites in Yukon, Canada. Each data point is 1 year. The narrow-shaded area indicates 95% confidence limits for the regression line prediction and the wider shaded area indicates confidence limits for individual year predictions. Sample sizes and regression values are presented in Table 1.**Fig. 4.** Percentage cover of *Geocaulon lividum* in all sites at Kluane (1997–2022) and Mayo (2005–2022) sites in Yukon, Canada. Each data point is 1 year. The narrow-shaded area indicates confidence limits for the regression line prediction and the wider shaded area indicates 95% confidence limits for individual year predictions. Sample sizes and regression values are presented in Table 1.

ple and others who live in the boreal zone of the northern hemisphere (e.g., Selås et al. 2021).

We expected little change in percent cover of these slow-growing boreal forest understory plants. However, we found two clear patterns of change, with cover declining in five species and increasing in one species at Kluane and Mayo.

Our observed declining trends in plant cover do not fit the site-selection-bias mode of Fournier et al. (2019) because we established our initial sites with the only stipulation that each quadrat contained one or more of the five groundberry species of interest with a total cover greater than 50%—the possibility of site-selection bias is much reduced in multi-

Fig. 5. Percentage cover of *Empetrum nigrum* in all sites at Kluane (1997–2022) and Mayo (2005–2022) sites in Yukon, Canada. Each data point is 1 year. The narrow-shaded area indicates 95% confidence limits for the regression line prediction and the wider shaded area indicates confidence limits for individual year predictions. Sample sizes and regression values are presented in [Table 1](#).

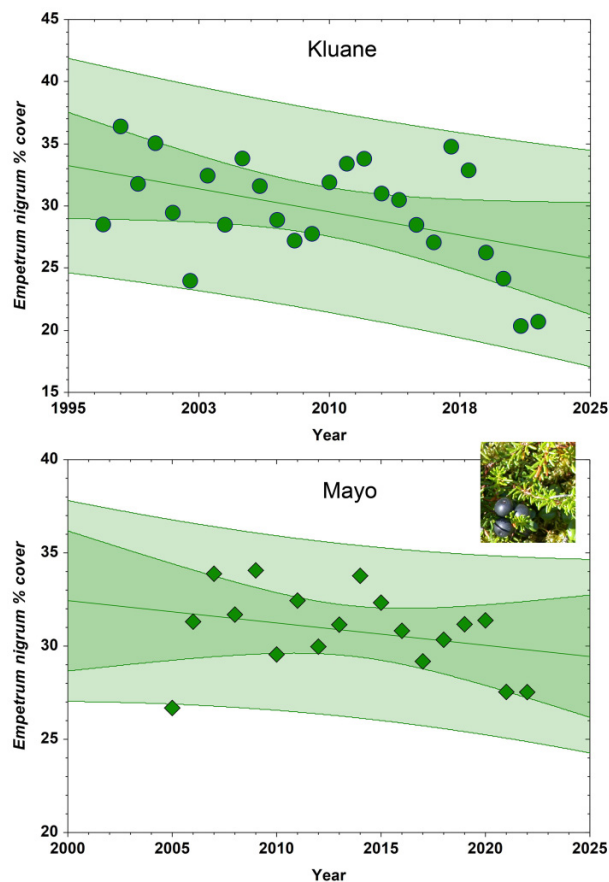
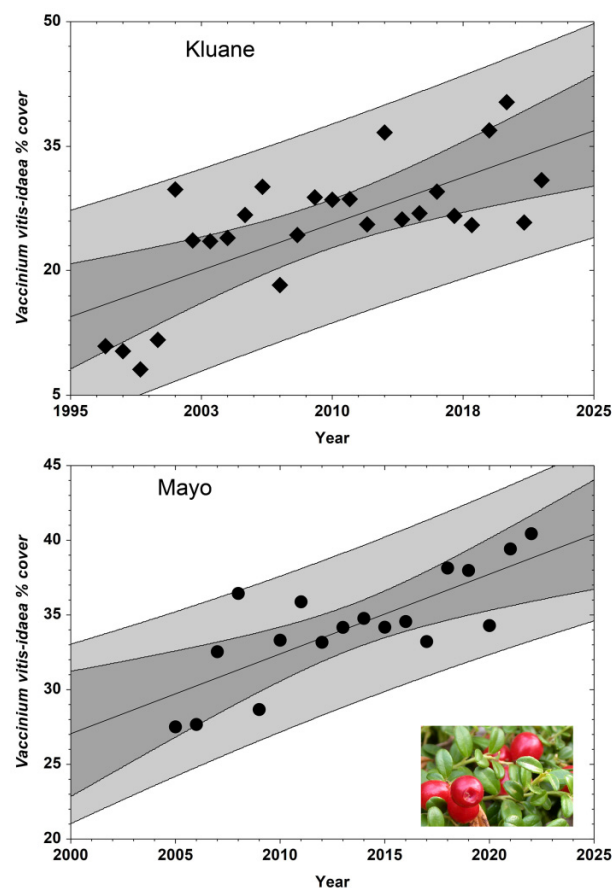


Fig. 6. Percentage cover of *Vaccinium vitis-idaea* in all sites at Kluane (1997–2022) and Mayo (2005–2022) sites in Yukon, Canada. Each data point is 1 year. The narrow-shaded area indicates 95% confidence limits for the regression line prediction and the wider shaded area indicates confidence limits for individual year predictions. Sample sizes and regression values are presented in [Table 1](#).

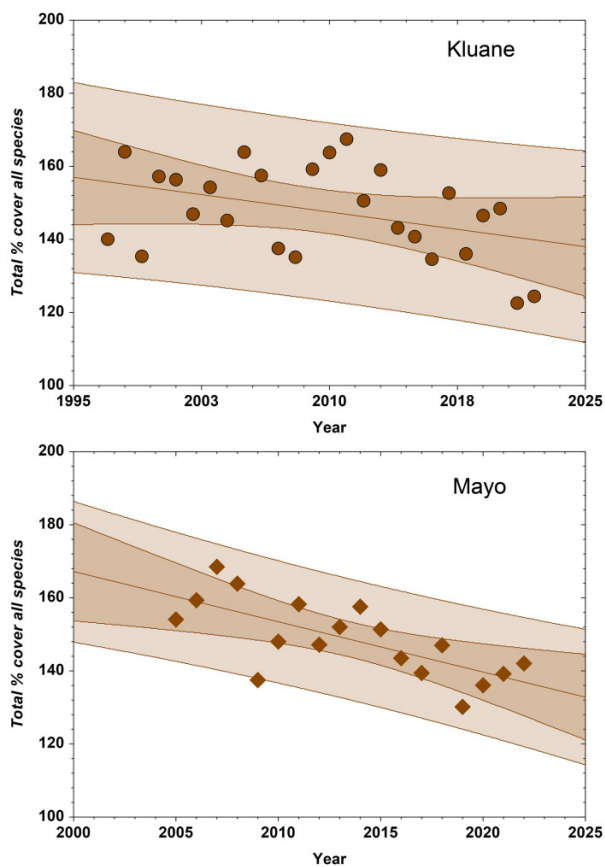


species studies. We had multiple sites of study, and there was no way to know the prior abundance of the five species at the start of our study. The site-selection-bias problem could not be applied to lingonberry that increased in cover over the two decades of study. We have only one study of total coverage of groundberries on random plots from the work of Stella Sotorra (pers. comm., 2018), who sampled ground berries at random in two 33 ha areas on our study site. She found an average cover of 5.6% for *A. uva-ursi*, 3.4% for *A. rubra*, and 1.6% for *E. nigrum*, in 147 random 1 m² plots. Groundberries are essentially uncommon species in the Yukon boreal forest and biased site selection was essential to gather any data on these questions.

There are six possible categories of variables that could affect changes in cover in these plants: temperature, rainfall, soil nutrients, light, herbivory, and competition with other plants. We have not tested for winter effects of snowfall or winter temperatures since we could not postulate any clear hypotheses for winter effects. We could find no significant correlations with summer temperature or rainfall. We have observed very few signs of herbivory on leaves or stems. We

do not see clear damage to the leaves of these five species from small mammals, insects, or snowshoe hares. We have observed some visible signs of disease in groundberries over these years, but the evidence is spotty over time with no temporal trends, so we do not think that species-specific diseases are a major cause of cover declines. If the cause of these changes lies in the physical environment, we remain puzzled. Much of the discussion about the dynamics of plants on the forest floor refer to changing light levels, and our early observations were during an outbreak of the spruce bark beetle from 2001 to 2007 in the Kluane region in which about 22% of large white spruce were killed in a patchwork of infections (Berg et al. 2006; Campbell et al. 2019; Krebs et al. 2023). This thinning of the forest should have increased light incidence on the forest floor, with the expectation that forest floor plants should increase their growth rates in the years after 2001 if light is limiting. We observe just the opposite in *A. rubra*, *Geocaulon*, and *Empetrum* (Figs. 3–5). Figure 6 for *Vaccinium* shows a strong increase in cover. There is some indication that the tall shrub layer—the willow and birch layer—has increased over this time period (Grabowski 2015), which

Fig. 7. Total cover estimates of all five species combined for Kluane (1997–2022) and Mayo (2005–22). The narrow-shaded area indicates 95% confidence limits for the regression line prediction and the wider shaded area indicates confidence limits for individual year predictions.



in turn may lower the amount of light reaching the groundberries. The point here is that we should in future use a standard procedure for measuring light levels at each plot, but this equipment was not available to us while the study was being done. Finally, summer rainfall and temperatures were increasing during our entire period of observation in general across the Yukon, but these climate changes were not predictive of the observed pattern of changes in groundberry cover over this time. Despite these failures of climatic prediction, we note that water availability may be limiting even with higher rainfall because of warmer temperatures. Hence, the need for the measurement of soil moisture in future work on groundberries.

We have limited evidence to explain the cause of these changes in cover for these five species of groundberries and can only speculate why these patterns have arisen. We suggest two possible explanations for some of the patterns observed, one based on available light as discussed above, and one based on competition between groundberry plants and other plants colonizing our permanent quadrats. We observed during these studies that plants like twinflower (*Linnaea borealis* L. 1753) were aggressively colonizing some quadrats, and in general, grasses were becoming more common. We

failed to record the cover value of these non-berry-producing plants, so we cannot test the competition hypothesis with our study data. The fact that total groundberry cover of all five species combined was declining at both Kluane and Mayo (Fig. 7) is consistent with the general hypothesis of competition for space.

Although soils in our study areas are very low in nitrogen, we do not think that nitrogen deposition in this region is significant, in contrast to the suggestion by Hedwall et al. (2021) in Sweden boreal forests. For 2 years, we carried out experimental nitrogen fertilizer additions to small plots at Kluane that included all these five groundberry species (Boonstra et al. 2017). We expected a strong response from nitrogen addition in all the species except toadflax (*Geocaulon*), which is hemi-parasitic and gathers nitrogen from trees, shrubs, and herbs growing nearby. In this 2-year experiment, both *Arctostaphylos* species declined in cover when even very low levels of nitrogen fertilizer were added. By contrast, *Empetrum* cover was not affected by nitrogen fertilization. Unfortunately, we do not have measurements of soil nitrogen in this study, so we cannot test the suggestion that the observed changes in these species were a product of soil nitrogen changes.

The climate is changing in the Yukon, as Fig. 1 illustrates. However, we have not been successful in using the observed year-to-year variation in summer temperatures and rainfall to predict the observed cover changes in any of our species (Table 2). Unfortunately, we are left without a suggestion for the general hypothesis that climate change is producing our observations. Two possible explanations are that some unmeasured component of increasing temperature and rainfall is involved.

From the animals' point of view, as berries are food, the key question is how many berries are available each year. Because berry counts fluctuate under the direct control of weather (Krebs et al. 2009), there is a high variance from year to year in the number of berries produced. If berry crops on plots adjusted to 50% cover and cover overall is declining, presumably overall abundance of berries on the landscape is also declining.

Our results are observation based, and what is now required is a more sophisticated observational and experimental approach to examine these trends in cover to both determine whether they continue and to explore alternative variables of potential interest. As observational variables, the measurement of soil moisture and pH, and incident radiation as trees recover and shrubs expand are needed. Experimental research on the tolerance levels of each species in greenhouse experiments should help us to understand these trends in cover. A field-based experiment would be to selectively remove or reduce the tall shrubs (birch and willow) over 5–10 years to increase light and possibly reduce below-ground competition. This could provide insights into the cover response of groundberries. Alternatively, a laboratory-based experiment in which one held light constant (to match that at ground level in the forest), but increased temperature, moisture, and both (in a 2 × 2 experiment) to match current conditions under the new climate, one could determine the physiological niche of these species and determine which

Table 2. Summary of groundberry cover changes in direction and magnitudes over all five areas sampled.

Species	Kluane	Mayo	Watson Lake	Whitehorse	Faro
<i>Arctostaphylos uva-ursi</i>	Decline	Decline	No data	Decline	No data
<i>Arctostaphylos rubra</i>	Decline	Decline	No data	No data	Decline
<i>Geocaulon lividum</i>	Decline	Decline	No data	Decline	Increase*
<i>Empetrum nigrum</i>	Decline	Decline	No data	Decline	No trend*
<i>Vaccinium vitis-idaea</i>	Increase	Increase	Increase	Decline	Decline

Note: Faro, Watson Lake, and Whitehorse had much smaller sample sizes than Kluane and Mayo, so the changes in cover are more difficult to pin down. Trends estimated with less than 400 total plots over 18 years are indicated by *.

Table 3. Stepwise multiple regression predictive power for groundberry cover in relation to summer temperature and rainfall (June–August) of the current year (t) and the previous year ($t - 1$), and a repeated analysis for early summer temperature and early summer rainfall (May–July) for (t) and ($t - 1$).

Kluane variables	<i>Arctostaphylos uva-ursi</i>	<i>Arctostaphylos rubra</i>	<i>Geocaulon</i>	<i>Empetrum</i>	<i>Vaccinium</i>	Total all
Summer temperature (t)	0.03	0.0	0.03	0.10	0.02	0.08
Summer temperature ($t - 1$)	0.01	0.05	0.02	0.01	0.02	0.01
Summer rainfall (t)	0.05	0.00	0.12	0.08	0.00	0.00
Summer rainfall ($t - 1$)	0.00	0.04	0.0	0.00	0.00	0.01
Early summer temperature (t)	0.00	0.01	0.05	0.07	0.06	0.02
Early summer temperature ($t - 1$)	0.03	0.11	0.00	0.00	0.01	0.01
Early summer rain (t)	0.02	0.00	0.12	0.00	0.01	0.00
Early summer rain ($t - 1$)	0.02	0.03	0.04	0.04	0.01	0.01
Mayo variables	<i>Arctostaphylos uva-ursi</i>	<i>Arctostaphylos rubra</i>	<i>Geocaulon</i>	<i>Empetrum</i>	<i>Vaccinium</i>	Total all
Summer temperature (t)	0.03	0.01	0.03	0.10	0.02	0.08
Summer temperature ($t - 1$)	0.01	0.05	0.02	0.01	0.02	0.01
Summer rainfall (t)	0.05	0.00	0.12	0.08	0.00	0.00
Summer rainfall ($t - 1$)	0.02	0.04	0.04	0.00	0.00	0.01
Early summer temperature (t)	0.02	0.01	0.05	0.07	0.06	0.02
Early summer temperature ($t - 1$)	0.07	0.11	0.00	0.02	0.01	0.01
Early summer rain (t)	0.07	0.09	0.03	0.02	0.00	0.01
Early summer rain ($t - 1$)	0.00	0.00	0.04	0.00	0.15	0.01

Note: Kluane and Mayo data. $N = 26$ years for Kluane and 18 years for Mayo. Table values are R^2 values from the multiple regressions.

environmental factor or their interaction might be driving the changes in cover in these species.

In addition, if our observations of a long-term decline in four of the berry-producing ground species are widespread throughout the boreal forest, this may have negative impacts on populations of small mammals, black and grizzly bears, caribou and moose, and grouse and ptarmigan that seasonally consume these berries in autumn, under the snow in winter and after snowmelt in spring. Thus, comparative studies on them are also necessary, but the only group for which we have long-term data are the small mammals (Krebs et al. 2019). Hence, it is important to monitor the densities of the other species that feed on these berries as well.

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Data availability

Data presented and analyzed for this study are available from the corresponding author upon request (krebs@zoology.ubc.ca).

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjb-2023-0068>.

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