ECOSPHERE

Climate and herbivore influence on *Vaccinium myrtillus* over the last 40 years in northwest Lapland, Finland

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Citation: Boulanger-Lapointe, N., A. Järvinen, R. Partanen, and T. M. Herrmann. 2017. Climate and herbivore influence on *Vaccinium myrtillus* over the last 40 years in northwest Lapland, Finland. Ecosphere 8(1):e01654. 10.1002/ecs2.1654

Abstract. Annual fluctuations in the abundance of wild berries have repercussions on animals and humans who depend on this important resource. Although studies have tried to disentangle the effect of climate and herbivores on inter-annual berry yield, there are still many uncertainties as to which factors are driving productivity. In this research, we evaluated the effect of climate and predation by rodents and moths on the abundance of bilberry (*Vaccinium myrtillus*) flowers and berries at the Kilpisjärvi Biological Station in northwest Finnish Lapland. The data were collected from 1973 to 2014 in a forest and an alpine site, both undisturbed by human activities. This dataset is unique due to the length of the sampling period, the availability of flower, berry, and rodent abundance data as well as the undisturbed nature of the habitat. Previous summer temperatures, the abundance of rodents, and the presence of a moth outbreak were complementary factors explaining the abundance of flowers. Herbivores had a larger impact on flower production than climate, but both variables were important to understand reproductive effort. Contrary to results from experimental studies, warmer winters did not significantly influence reproductive success. The abundance of fruits was strongly correlated with pollinator activity; the forest site, with a larger pollinator network, had a higher reproductive success and spring conditions were linked to inter-annual variability in fruit production. Our results illustrate the importance of the location of the population within the species distribution range to understand plant sensitivity to climatic fluctuations with fruit production only influenced by current year summer temperatures at the alpine site. Finally, we observed a general increase in flower and fruit production at the alpine site, which was driven by large yields since the early 1990s. Fruit production at the forest site was comparatively stable throughout the study period.

Key words: alpine; berry; climate; climate change; Finland; herbivore; Lapland; microtine; moth; pollination; shrub.

Received 19 October 2016; revised 23 November 2016; accepted 28 November 2016. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

Wild berries are key resources harvested by humans and animals in alpine and boreal ecosystems (Parlee and Berkes 2006, Turtiainen et al. 2011, Vaara et al. 2013, Cuerrier et al. 2015). In Finland, over half the population harvest berries and the activity is protected by the "everyman's right," the traditional right to access private and public forests (Pouta et al. 2006). Annual yield of bilberry (*Vaccinium myrtillus* L.) in Finland is estimated to vary between 92 and 312 million kg with about 5–6% of this production harvested for human consumption (Turtiainen et al. 2013). The species is widespread over Eurasia (Ritchie 1956) and is the most abundant forest floor shrub in Scandinavia (Nielsen et al. 2007). It is a major food source for small mammals (i.e., hare and vole; Andersson and Jonasson 1986, Hjalten et al. 2004), brown bears (Persson et al. 2001), moths, and a variety of birds (Atlegrim 1989, Honkavaara et al. 2007, Hofstetter et al. 2015).

Bilberry fruit production is expected to be sensitive to climate, herbivores, and forest management practices. Depending on the region and period studied, a number of climate factors have been found to explain bilberry yields. Those factors pertained to four stages of flower and fruit development: (1) temperature and precipitation in the year prior that influence flower primordia, (2) winter temperature and snow cover that may prevent or induce frost injuries and desiccation, (3) spring snow cover, temperature, and precipitation that may be favorable or not to flower bloom and pollinator activities, and (4) summer temperature and precipitation that determine the number of pollinated flowers producing viable fruits (Jacquemart 1997, Selas 2000, Krebs et al. 2009, Selas et al. 2015).

The main effects of climate change on *V. myrtillus* are expected to be winter (Taulavuori et al. 2013) and spring (Wipf et al. 2009) warming combined with a thinner layer of snow (Tahkokorpi et al. 2007). Warm conditions in the winter and spring are associated with early dehardening, exposure to drought (Rixen et al. 2010, Selas et al. 2015), and frost injuries (Tolvanen 1997). The fecundity (i.e., proportion of shoots with ripe fruits) has been found to be unrelated to snow cover and the species may recover vegetatively from frost injury through stimulated shoot elongation, although the number of flower buds aborted increases with the number of frost days after greening (Wipf et al. 2009).

Among animals relying on bilberry are exclusive frugivores, feeding on berries with little impact on the plant integrity, and opportunistic feeders eating both fruits and shoots. The berry eaters are mainly brown bears and birds. In northern Norway, bilberry was found to be an important part of the brown bear diet throughout the year and especially in the fall where it can make up to 9% of fecal volume (FV; all berries combined made 63% of FV; Persson et al. 2001). Frugivorous birds were associated with increased germinability of passed bilberry seeds (Honkavaara et al. 2007), and the abundance of some species has been correlated with bilberry cover (Hofstetter et al. 2015). While frugivorous species may eat a significant number of berries (Cadieux et al. 2005), they have little impact on plant integrity. On the other hand, moth outbreaks were found to reduce seed crop (Selas et al. 2013) and microtine grazing may remove up to 40% of bilberry phytomass during pre-peak winters (Andersson and Jonasson 1986). Semi-domesticated reindeer herds have significant impact on the vegetation in northern Fennoscandia; however, studies suggest that the cover of ericoid shrubs is not strongly affected by reindeer trampling and grazing (Bråthen et al. 2007, Kumpula et al. 2011).

Most forests in the Nordic countries and throughout Europe are affected by varying levels of management, and some practices are believed to be responsible for a recent decline in berry availability measured on average in Finnish forests (Reinikainen et al. 2000). Contrasting effects may at least partly be attributed to shading. Studies have shown that younger and denser forests have lower bilberry yield (Zmihorski 2011, Kilpeläinen et al. 2016), although a negative effect of forest age on reproductive success has been found in some regions (Nielsen et al. 2007). Kuusipalo (1988) determined that even if bilberry fertility is highest in open stands, the species also exhibits high fertility under heavy shading, which may be related to different allocation strategies under stressful conditions. Alternatively, Miina et al. (2009) suggested that bilberry yield increases with stand age up to a certain threshold, after which it gradually falls.

In this study, we evaluated the effect of climate and herbivore activity on the abundance of bilberry flowers and berries at the Kilpisjärvi Biological Station located in northwest Finnish Lapland. The data were collected from 1973 to 2014 in a forest and an alpine site, both undisturbed by human activities. This study complements a previous data synthesis performed at this site (Laine and Henttonen 1983). We hypothesize that, following results from experimental studies, bilberry flower and berry production should be sensitive to winter (Taulavuori et al. 2013) and spring (Wipf et al. 2009) conditions, notably snow cover (Tahkokorpi et al. 2007) and temperatures (Rixen et al. 2010). We expect bilberry plants located at the alpine site to be more sensitive to summer temperatures as this represents the edge of the range for *V. myrtillus* (Rixen et al. 2010). Following results from preliminary analyses (Laine and Henttonen 1983) and field observations, we also hypothesize that geometrid moth outbreaks and microtine grazing should have a significant impact on plant fitness although this impact might vary between sites.

Materials and Methods

Study species

Vaccinium myrtillus (bilberry) is a deciduous, clonal dwarf shrub, 10–60 cm tall with an extensive rhizome system (Jacquemart and Thompson 1996). The flowers are single or rarely in pairs in the leaf axils and present green to purple pendulous urceolate corollas (Ritchie 1956). The plants reproduce extensively through clonal growth and to a lesser extent from seeds (Ritchie 1956). Studies show different results regarding selfing rates (i.e., degree of self-pollination): While some identified an intermediate selfing rate (Jacquemart and Thompson 1996), others found that the species may require insect pollination (Nuortila et al. 2002). *Vaccinium myrtillus* is found throughout Eurasia and reaches its climatic optimum in northern Europe (Coudun and Gegout 2007). It is most commonly found on poorly drained and slightly moist to fairly wet acidic soils (Jacquemart and Thompson 1996). The species is moderately resistant to frost damage (Palacio et al. 2015).

Study sites

The Kilpisjärvi region (69°03′ N 20°48′ E) is located in northwest Finnish Lapland and is the only part of Finland extending into the Scandinavian mountain range (Fig. 1a). Long-term follow-up studies form the core of the research activities, and the station is part of the Long-Term Ecological and Socio-Ecological Research networks. There is a substantial snow cover from October to May–June, and snow melts from the mountain birch forest zone (tree line at 600 a.s.l.) in early June. The growing season is one of the shortest in continental Europe (about 100 d when mean daily temperature is ≥5°C; University of Helsinki 2015).

The study plots were located in two vegetation types: (1) the alpine heath (680 m a.s.l., 69°04.080′ N, 20°49.422′ E) dominated by *V. myrtillus* and *Phyllodoce caerulea* (Fig. 1b, c), and (2) the mountain birch forest (500 m a.s.l., 69°02.649′ N, 20°48.829′ E) dominated by *V. myrtillus* and *Cornus suecica* (see University of Helsinki 2015 for complete species list; Fig. 1d). At the study sites, the rodent community consists mainly of the gray-sided vole (*Clethrionomys rufocanus*) and to a lesser extent the field vole (*Microtus agrestis*), the red vole (*Clethrionomys rutilus*), and the Norwegian lemming (*Lemmus lemmus*; Hansen et al. 1999). Voles eat berries as well as current year twigs with leaves, while the Norwegian lemming feeds exclusively on mosses. A detailed description of rodent research at Kilpisjärvi can be found in Kalela (1957), Henttonen et al. (1977), Laine and Henttonen (1983), Henttonen et al. (1987) as well as in Järvinen (1987). Semi-domesticated reindeer are present in the region, although their impact on the study plots has not been measured. No traces of bear were ever observed in the vicinity of the study plots.

Field sampling

Daily meteorological data were retrieved from the Kilpisjärvi Biological Station records. The semi-automatized meteorological tower is located close to the research station at 480 m a.s.l. and records data every 10 min. Data quality control is performed for every observation by the Finnish Meteorological Institute. Available data include temperature, total precipitation, and snow cover for the period 1961–2015. The study area consisted of one 2 × 5 m plots in the alpine and forest sites. The abundance of flowers and berries was monitored within 40 permanent quadrats of 0.25 m^2 in each plot. The number of flowers was counted when most were in bloom although all flowers including flower buds were counted in the last week of June or at the beginning of July. The total number of berries was recorded when most were ripped during the second or third week of September. The alpine site was systematically monitored 1 week after the forest site.

The trapping method for rodents consisted of pairs of snap traps (the Finnish model) placed in lines at 7-m intervals and located 1–2 m from a signpost noting their location. Trap lines were 300–500 m long and located through a mosaic of moist and dry habitats, starting at low altitude in the birch forest and up to the tree line. The location of the lines has remained consistent since 1950. Traps were baited with bread, set on day 1,

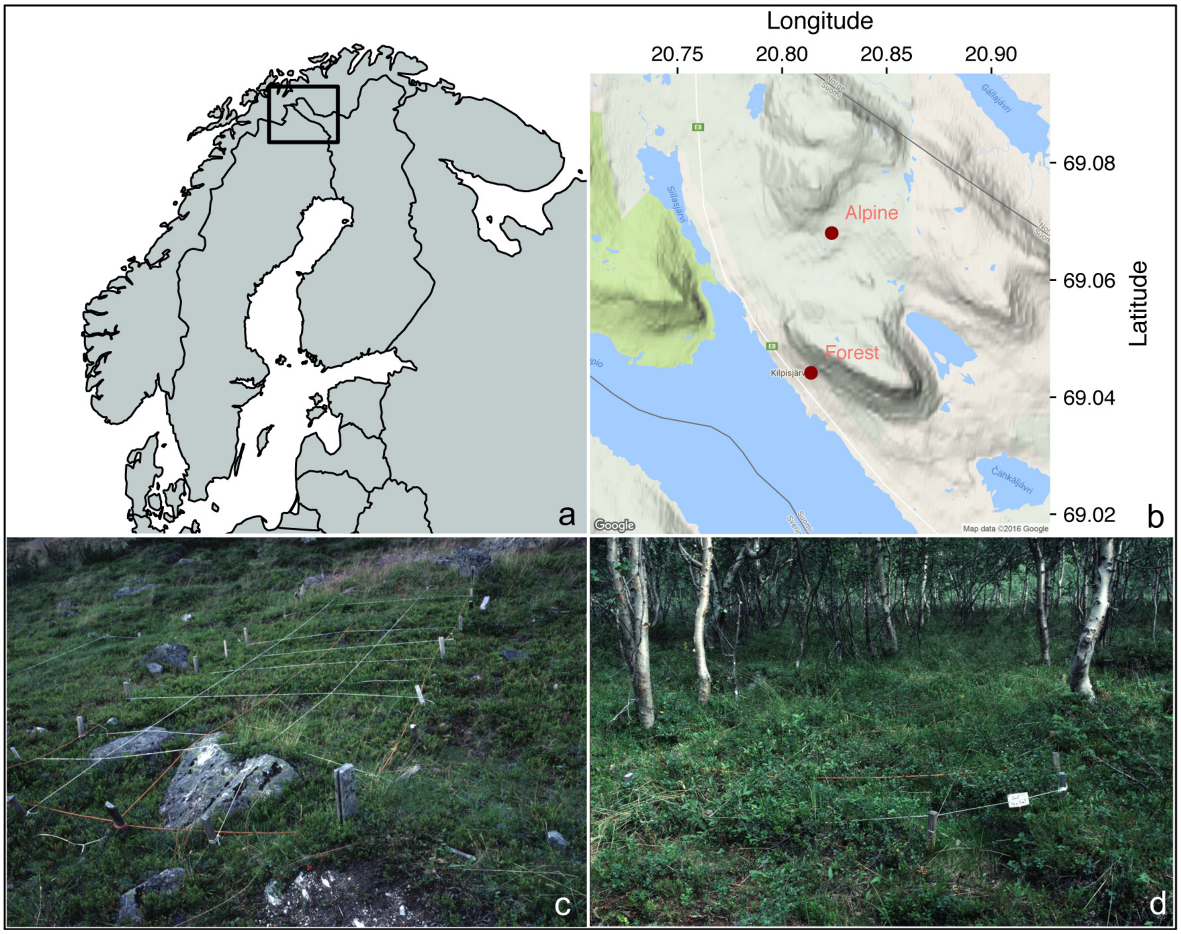

Fig. 1. Study sites in the vicinity of Kilpisjärvi Biological Station, NW Lapland: (a) location of the Kilpisjärvi region (map generated with GADM 2016), (b) location of the study sites (map generated with ggmap; Kahle and Wickham 2013), (c) photographs of the alpine, and (d) forest permanent plots (photographs from Kari Laine).

checked on day 2, and rechecked and removed on day 3. From 1950 to 1979, the number of trap nights per trapping period varied, with a minimum of 500 and usually many more. Since 1980, there has been a fixed trapping scheme with about 1000 trap nights per period. For the present analysis, we used an index of the abundance of rodents per 100 trap nights to account for the varying sampling effort. The spring trapping was done immediately after snow melted, in early to mid-June, and the fall trapping was done in mid-September. The gray-sided vole breeding occurs almost exclusively during the summer between the spring and fall samplings (Kalela 1957, Kaikusalo and Tast 1984). The spring sampling represents animals that have survived the winter and have established breeding home ranges (males) and territories (females; Hansen et al. 1999). The abundance of rodents at the alpine site is lower than at the forest site; however, populations vary in synchrony (Järvinen 1987); thus, results from the trap line were used for the analyses at both sites. The occurrence of geometrid moth (*Epirrita autumnata*) outbreaks was qualitatively assessed during flower count in the spring. Geometrid moth outbreaks are striking in the field. The insect eats birch leaves until the resource is exhausted, after which they start eating current year shoots and buds of shrubs, including bilberry.

Statistical analyses

Monthly averages of temperature, snow cover, and total precipitation were calculated from the daily meteorological data collected at the Kilpisjärvi Biological Station. We tested the variables used in the model for linear trends using the *F*-statistic. The flower counts and berry productivity data were available at the plot level for the period 1985–2014. Unfortunately, due to the loss of the original dataset, we only had access to the average per site for the period 1973–1984. Since we were not interested in the variance structure of the nested design, the mean berry production for each year was used in the statistical analyses. Statistical analyses were performed using R software (R Core Team 2016).

We tested the flower and berry time series for linear trend using the *F*-statistic for the entire monitoring period as well as separately for the periods 1973–1990 and 1991–2014. We evaluated the difference in the abundance of flowers and berries with a paired *t* test. The reproductive success was calculated as the ratio of the total number of fruits to the number of flowers for each site. We tested the berry and flower time series for autocorrelation at each site using an autoregressive moving average (ARMA) model with a lag of 1 and 2 (corARMA function in mgcv and nlme R libraries). This allowed us to measure the influence of year-to-year productivity, that is, whether a productive year might negatively affect the productivity in the subsequent year by depleting plant resources. We tested the correlation between the rodent abundance index in June and September using the Pearson coefficient.

We used four generalized linear models (GLMs) to evaluate the influence of standardized environmental variables ((variable − mean of variable)/standard deviation of variable), the standardized rodent abundance index (number of rodent trapped/100 trap nights) as well as the presence/absence of a geometrid moth outbreak on berry and flower productivity at the forest and alpine sites. We constructed four Poisson GLMs, one for each combination of production (berry and flower) and site (forest and alpine). Since we detected overdispersion, we corrected the standard errors using a quasi-GLM where the variance is given by $\Phi \sim \mu$, where μ is the mean and Φ the dispersion parameter (Zuur et al. 2009). This transformation provides the same coefficient estimates, residual deviance, and degrees of freedom as the Poisson distribution, but adjusts the inference parameters (i.e., CI, *P*-values) to address overdispersion. Based on ecological assumptions as well as the literature, the explanatory variables selected for the abundance of flowers were (1) mean total precipitation from July to September of the previous year, (2) mean temperature from July to September of the previous year, (3) number of days with temperature above 0°C from November to April of the current year, (4) mean snow cover from November to April of the current year, (5) mean snow thickness in May of the current year, (6) mean temperature in May of the current year, (7) mean total precipitation in June of the current year, (8) mean temperature in June of the current year, (9) the abundance of rodents in June of the previous year, (10) the abundance of rodents in June of the current year, and (11) presence/absence of a geometrid moth outbreak during the previous year (only at the forest site because moths were never observed at the alpine site). The variables selected for berry productivity were (1) mean total precipitation from July to September of the current year, (2) mean temperature from July to September of the current year, (3) mean snow thickness in May of the current year, (4) mean temperature in May of the current year, (5) mean total precipitation in June of the current year, (6) mean temperature in June of the current year, (7) the abundance of rodents in September of the current year, and (8) the flower index of the current year (standardized number of flowers). In both cases, the final models were chosen following a backward selection method; that is, the variables with the lowest fit were successively dropped. We validated our final models by visual evaluation of the plotted response and by Pearson's scaled and deviance residuals (Zuur et al. 2009).

RESULTS

There was a high degree of variability in the climate variables tested for the period 1973–2014 (Fig. 2). Mean annual temperature was −2 ± 0.16 (SE)°C and mean temperature from July to September was 8 ± 0.14 (SE)°C. The number of days with temperature above 0°C from November to April was 13 ± 1 (SE) day. Mean snow cover from November to April was 650 ± 28 (SE) mm, and mean total precipitation from July to September was 510 ± 26 (SE) mm. We detected significant positive trends ($P < 0.05$) in the mean summer temperature from July to September and

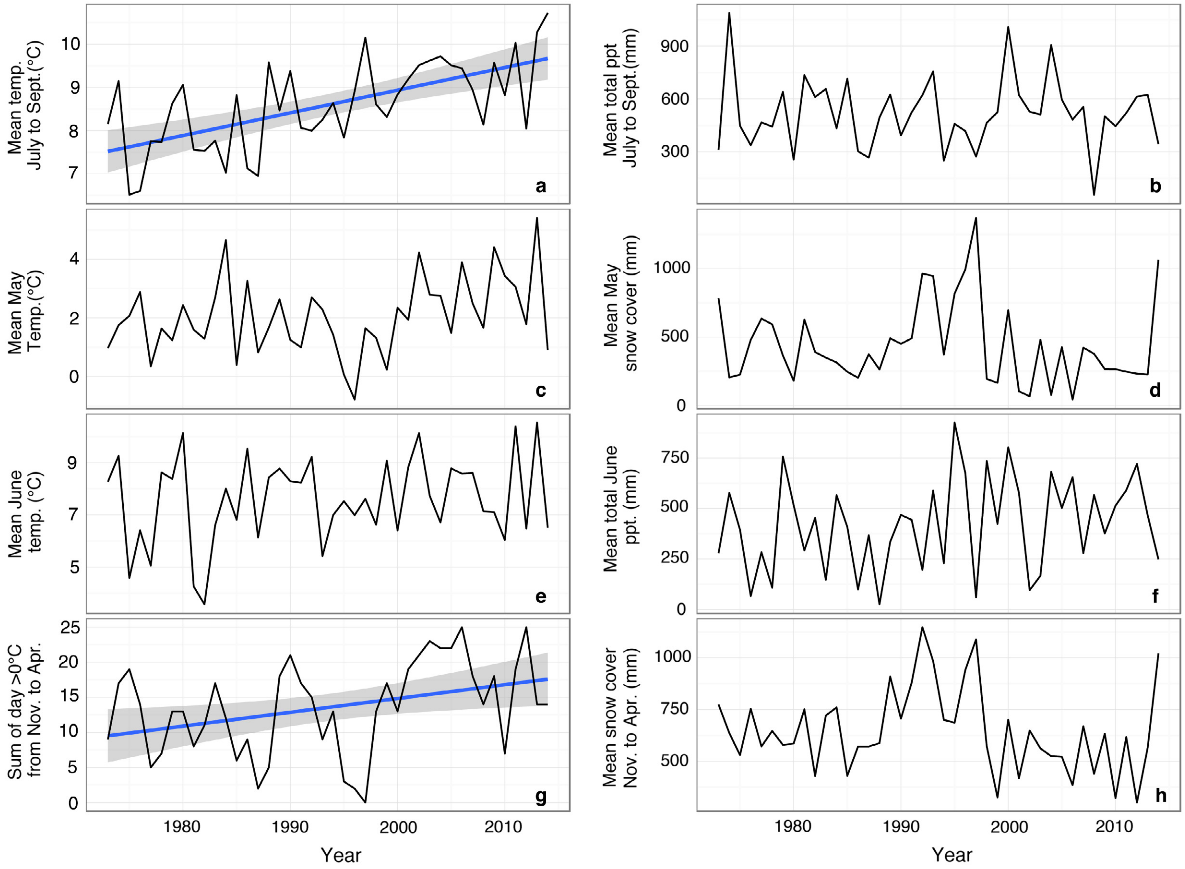

Fig. 2. Climate variables used for modeling flower and berry abundance for the period 1972–2015 at the Kilpisjärvi Biological Station: (a) mean monthly temperature from July to September (°C), (b) mean total monthly precipitation from July to September (°C), (c) mean May temperature (°C), (d) May snow cover (mm), (e) mean June temperature (°C), (f) mean total June precipitation (mm), (g) sum of days >0°C from November to April, and (h) mean snow cover from November to April (mm). Blue lines present significant linear trends ($P < 0.05$).

the sum of days above 0°C from November to April.

The abundance of flowers fluctuated from 0 to 867 flowers/m^2 with significantly more flowers produced at the alpine than at the forest site ($P < 0.01$; average of 281 ± 38 [SE] and 70 ± 8 [SE] flowers/m^2 for the alpine and forest site, respectively; Fig. 3a). We observed a positive trend for the abundance of flowers at the alpine site for the period 1973–2014 ($P < 0.01$), which was driven by a large increase after 1990 (estimate of the slope for 1973–1990: 1.33 [$P > 0.05$]; estimate of the slope for 1991–2014: 16.03 [$P < 0.05$]). No such trend was observed for the abundance of flowers at the forest site. The abundance of berries ranged from 0 to 113 berries/m^2 and there was a similar number produced at each site ($P > 0.05$; 36 ± 5 [SE] and 28 ± 5 [SE] berries/m^2 for the alpine and forest site, respectively; Fig. 3b). There was a positive trend for the abundance of berries at the alpine site for the period 1973–2014 ($P < 0.01$), which was once again driven by a large increase after 1990 (estimate of the slope for 1973–1990: −1.05 [$P > 0.05$]; estimate of the slope for 1991–2014: 2.52 [$P < 0.01$]). Although we observed more berries at the forest site after 1990, there was no significant trend for the period studied. The reproductive success at the forest site was twice that of the alpine site (average of 0.18 ± 0.005 [SE] and 0.44 ± 0.011 [SE] for the alpine and forest site, respectively; Fig. 3c). No autocorrelation of first or second order was detected in the flower and berry

Fig. 3. Abundance of (a) flowers and (b) berries (nb/m^2) as well as (c) reproductive success (number of berries/ number of flowers) at the alpine and forest sites along with (d) rodent abundance index (number of rodent trapped/100 trap nights) in June and September. Geometrid moth outbreaks at the forest site are marked with an asterisk (*).

time series. The rodent time series had cyclic abundance with peaks at a similar level for the period 1973–2014, except for the last two peaks (2010 and 2014) during which the population was exceptionally large (Fig. 3d). There was a significant correlation between rodent abundance in June and September (0.59 [$P < 0.001$]).

Despite the large number of variables tested, we obtained succinct models that explained a large proportion of the variance in the abundance of flowers and berries (Table 1). Unless otherwise mentioned, all variables included in the models were significant at $P < 0.05$. The best model for the abundance of flowers at the forest site included a positive effect of the mean temperature from July to September of the previous year as well as a negative effect of geometrid moth outbreaks and the abundance of rodents in June of the previous year (49% of the variance explained by the model). However, the variable "abundance of rodents in June of the previous year" in this model was only marginally significant ($P = 0.10$). The best model for the abundance of flowers at the alpine site included a positive effect of the mean temperature from July to September of the previous year and a negative effect of the abundance of rodents in June of the previous year (26% of the variance explained by the model). The best model for the abundance of berries at the forest site included a positive effect of the mean snow thickness and the flower index in the current year as well as a negative effect of the mean temperature in May of the current year (47% of the variance explained by the model). Finally, the best model for the abundance of berries at the alpine site included a positive effect of the mean total precipitation in June, the mean temperature from July to September, and the flower index of the current year (63% of the variance explained by the model).

Table 1. Variables and percentage of variance explained for the four time series tested as well as the slope (standard error) of the variables included in the models.

Time series	Percentage of variance explained	Variables	Slopes (SE)
Flower			
Forest	49	Mean temp. July–Sept ($t - 1$)	0.401 (0.107)**
		Abun. rodent June ($t - 1$)	−0.188 (0.110)*
		Moth outbreak (t)	−2.911 (0.867)**
Alpine	26	Mean temp. July–Sept ($t - 1$)	0.262 (0.125)**
		Abun. rodent June ($t - 1$)	−0.432 (0.177)**
Berry			
Forest	47	Mean May temp. (t)	−0.309 (0.132)**
		Mean May snow thickness (t)	0.256 (0.108)**
		Flower index	0.535 (0.132)**
Alpine	63	Mean total June. ppt. (t)	0.357 (0.098)**
		Mean temp. July–Sept (t)	0.316 (0.108)**
		Flower index	0.356 (0.090)**

Note: Asterisks indicate degree of significance of the variables selected in models ($^{**}P < 0.05$, $^{*}P = 0.1$).

DISCUSSION

This study is based on the longest known record of *Vaccinium myrtillus* reproduction and links the influence of climate and herbivores to the abundance of flowers and berries. Following most recent berry yield analyses (Krebs et al. 2009, Selas et al. 2015), we found no autocorrelation in the time series indicating the absence of an inherent annual rhythm in flower and berry production. Instead, we observed the complex response of reproductive success to environmental stressors, climate, pollinator activity, and predation.

The number of flowers recorded at the alpine site was greater than in the forest site, which is in accordance with results from other studies in open and forested sites (Elisabetta et al. 2013) and may be related to higher radiation and decreasing apical dominance (Tolvanen 1995). The similar number of berries between sites indicates that the reproductive success (number of fruits/number of flowers) was much higher at the forest site. Reproductive success is expected to be influenced by pollinator activity and environmental conditions. More complex ecosystems, such as the forest site, can sustain larger pollinator networks (Vaupel and Matthies 2012). Moreover, pollinator specialization and diversity decrease rapidly with increasing elevation, resulting in higher-altitude sites having few generalist species (Hoiss et al. 2015). Moreover, environmental stressors can cause flowers to be less receptive to pollen. Jacquemart and Thompson (1996) demonstrated that fruit set was lowest on days preceded or followed by very cold nights, suggesting that pollen function, stigma receptivity, or other physiological aspects of fertilization were adversely affected by cold temperatures. Frost influences flower opening, damages newly opened flowers and flowers opened a few days before (Jacquemart and Thompson 1996). The importance of pollinator activity and environmental stressors on reproductive success in this study is also shown by the influence of spring conditions on berry abundance at both sites. However, the response observed was complex with temperatures in May having a negative effect on the abundance of berries in the forest, but the temperatures in June having a positive effect at the alpine site. Finally, in accordance with results from snow manipulation experiments (Wipf et al. 2009), we observed that May snow cover had a positive impact on reproductive success in the forest, meaning that a later snow cover is actually beneficial to plant fitness.

Rixen et al. (2010) found that annual growth of *V. myrtillus* was better at lower elevations than at higher ones, but only in years with relatively cold summers. Climate may then affect plant species differently depending on the location of the population within the species distribution range. Similarly, we observed a positive influence of the mean temperature from July to September on the alpine, but not the forest berry yield. Summer temperature must be a limiting factor at the alpine site where it improved annual bilberry performance throughout the study period. Contrary to results from snow removal and warming experiments (Rixen et al. 2010, Taulavuori et al. 2013), we did not observe a significant impact of warm winter temperatures. Although there has been a significant increase in winter temperatures since 1973, current changes in winter conditions must not yet be large enough to affect bilberry plants at this site (Ogren 1996, Wipf et al. 2009).

As was obvious in the field, the analyses indicated a significant effect of geometrid moth outbreaks on flower production. In the 5 yr where moth outbreaks were recorded, flower production was low. Although outbreaks are common in the region, we may expect them to be more frequent with predicted increase in winter temperatures (IPCC 2013, Young et al. 2014). In accordance with Laine (1978) and Laine and Henttonen (1983), we observed a synchrony between the abundance of flowers in the current year and the abundance of rodents in the previous year. The abundance of rodents only affected the number of flowers and not berry yield, which suggests that rodent species mainly eat plant vegetative structures and flower buds rather than berries, at least during the summer. The strength of the relationship between the abundance of rodents and flowers was more than twice as much in the alpine than in the forest site. These results may be linked to higher grazing pressure during the winter at the alpine site (Virtanen et al. 2002, Korslund and Steen 2006). Other herbivores such as hares, birds, and reindeer could have had an effect on the abundance of flowers and berries over the study period; however, we do not have the data to explain their influence on bilberry. Finally, even if herbivores have a larger impact on flower production than climate variables, the influence of previous summer temperatures is significant and important to understand reproductive effort.

The unique study design and length of observations of this research allowed us to obtain a relatively clear signal of the effects of climate and herbivores on *V. myrtillus*. Contrary to results from experimental studies, warmer winter temperatures did not significantly influence reproductive success. Instead, previous summer temperatures, the abundance of rodents, and moth outbreaks were found to determine the abundance of flowers. We also observed that conditions affecting pollinator activity were key to understand the abundance of berries. These were twofold, namely that spring conditions influence fruit set and that larger pollinator networks increase reproductive success. In contrast to some results from managed forests sites in southern locations (Reinikainen et al. 2000), we did not find a decline in the abundance of berries at the forest site. On the contrary, yields have generally been higher since the early 1990s than for period from 1973 to 1990, which suggests that forest management practices may have a negative impact on productivity. However, the different responses to summer temperature observed between sites in this study also suggest that climate affects populations differently depending on their location within the species distribution range. As such, populations located on the warmer end of the distribution range may be negatively affected by warming temperatures.

ACKNOWLEDGMENTS

Special thanks to the Kilpisjärvi Biological Station who bravely kept the bilberry monitoring program alive during the past 30 yr and to Greg Henry for comments on the manuscript. This work was made possible by the financial support of the Natural Sciences and Engineering Research Council of Canada, ArcticNet, and the W. Garfield Weston Foundation.

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