

# TRENDS IN MOUNTAIN BIRCH SEED ABUNDANCE AND ITS RELATION TO TEMPERATURE AND MOTH ABUNDANCE

A ten-year study from Swedish Lapland



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# TABLE OF CONTENTS

<b>ABSTRACT .....</b>	<b>2</b>
<b>SAMMANFATTNING .....</b>	<b>2</b>
<b>INTRODUCTION.....</b>	<b>3</b>
AIM AND HYPOTHESES .....	4
<b>METHOD.....</b>	<b>5</b>
STUDY SITE: ABISKO (68.328400, 18.835600).....	5
HOW THE SEEDS WERE COLLECTED.....	5
SORTING.....	5
ADDITIONAL DATA AND DATA PREPARATION.....	6
STATISTICAL ANALYSIS AND VISUAL PRESENTATION.....	6
<b>RESULTS.....</b>	<b>6</b>
SEED AND LARVAL ABUNDANCE OVER THE YEARS .....	6
THE EFFECTS OF TEMPERATURE AND LARVAL ABUNDANCE ON SEED PRODUCTION .....	7
THE RELATIONSHIP BETWEEN LARVAL ABUNDANCE AND TEMPERATURE .....	7
<b>DISCUSSION .....</b>	<b>8</b>
SEED AND LARVAL ABUNDANCE OVER THE YEARS .....	8
THE EFFECTS OF TEMPERATURE AND LARVAL ABUNDANCE ON SEED PRODUCTION .....	9
THE RELATIONSHIP BETWEEN LARVAL ABUNDANCE AND TEMPERATURE .....	10
<b>CONCLUSION.....</b>	<b>10</b>
<b>ACKNOWLEDGEMENTS.....</b>	<b>10</b>
<b>REFERENCES.....</b>	<b>11</b>

## Abstract

Boreal forest is the world's largest terrestrial biome. Being one of the most ubiquitous and cold-tolerant tree species in Sweden, the mountain birch forms a unique deciduous treeline and marks the forest-tundra ecotone. Its reproduction and ability to spread is therefore important from both a societal and ecological perspective, locally as well as globally. Folivorous larvae of the species autumnal moth and winter moth reach outbreak levels in arctic and alpine areas approximately every 9-10 years and can severely defoliate birch trees. Cold winters kill the eggs of the folivorous insects. Global warming and changed interspecific interactions possibly present new challenges for mountain birch growth and reproductive success. The aim of this study was to investigate trends in mountain birch seed abundance and how seed abundance is related to temperature and abundance of folivorous larvae. Further the aim was to investigate the effects of winter temperature on larval abundance. Seed rain was collected over a time period of ten years in Abisko, northern Sweden, by using seed traps set out from August to June. The seeds were manually sorted, and mountain birch seeds were counted. Larval abundance was counted as average number of larvae per hundred birch shoots. The results showed that seed abundance is neither increasing nor decreasing and that temperature and larval abundance do not significantly affect seed abundance. Larval abundance decreased over time but increased with increasing winter temperature, possibly indicating that larval abundance and distribution will increase with the increasingly warmer climate. Larval abundance and growing season temperature appear to not influence seed abundance and possible future changes in birch seed abundance might then be caused by other factors, such as precipitation, but for now appears to be rather stable.

## Keywords

*Betula pubescens*, climate change, seed production, *Epirrita autumnata*, *Operophtera brumata*, subarctic ecology, folivory, larval abundance

## Sammanfattning

Taigan är världens största landbiom. En av de mest köldtoleranta och vanligt förekommande träarterna i Sverige är fjällbjörken, och den bildar en unik trädgräns av lövträd samt markerar skog-tundra-ekotonen. Fjällbjörkens reproduktion och spridningsförmåga är därför viktiga både från ett socialt såväl som ekologiskt perspektiv, lokalt såväl som globalt. I arktiska och alpina miljöer når lövätande larver av arterna fjällbjörkmätare och mindre frostfjäril utbrottsnivåer cirka vart nionde-tionde år, och larverna kan orsaka allvarlig avlövning av björkarna. De lövätande insekternas ägg överlever inte alltför kalla vintrar. Möjligen utgör global uppvärmning och ändrade mellanartsinteraktioner nya utmaningar för fjällbjörkens tillväxt och reproduktiva framgång. Syftet med den här studien var att undersöka trender i björkfrö mängd och se hur björkfrö mängden påverkas av temperatur och antalet lövätande larver. Vidare var syftet att undersöka effekterna av vintertemperatur på larvmängd. Fröregn samlades in under en tioårsperiod i Abisko, i norra Sverige, genom att använda fröfällor som låg ute från augusti till juni. Fröna sorterades för hand och fjällbjörkfröna räknades. Larvmängd räknades genom att göra ett medelvärde av antalet larver per hundra björkskott. Resultaten visade att frö mängden varken ökar eller minskar och att temperatur och larvmängd inte har en signifikant effekt på frö mängden. Däremot minskade larvmängden över tid men ökade med högre vintertemperaturer, vilket kan indikera att larvmängd och larvutbredning kommer att öka med det allt varmare klimatet. Larvmängd och tillväxttemperatur verkar inte ha en effekt på frö mängd och möjliga framtida ändringar i frö mängd kan i så fall orsakas av andra faktorer, så som nederbörd, men verkar i nuläget stabilt.

## Nyckelord

*Betula pubescens*, klimatförändring, fröproduktion, *Epirrita autumnata*, *Operophtera brumata*, subarktisk ekologi, folivori, larvabundans

## Introduction

Being the most common broadleaf trees in the north, and also forming a unique northern hemisphere deciduous treeline, the reproduction and distribution of *Betula*, *i.e.*, birches, are of huge societal and ecological importance (Holm, 1994; Wielgolaski et al., 2005, and references therein; Ashburner & McAllister, 2016). Around the northern distribution limit, the species mountain birch (*Betula pubescens*) dominates. Environmental conditions are harsh and no other plants their size can manage to survive nor reproduce there, mainly because of low temperatures and dry winds (Anderson et al., 1966; Holm, 1994; Sveinbjörnsson et al., 1996). The sparse yearly resource uptake must therefore be distributed wisely, between vegetative growth, chemical defence and reproduction (U. Molau, personal communication). Propagation can occur either via the form of basal sprouts or via seeds, where monocormic (single-stemmed) growth forms mainly produce the latter (Wielgolaski et al., 2005).

Birches are known to be prolific pollen and seed producers (Hjelmroos, 1991; Sofiev et al., 2006; Rousi et al., 2019). Mountain birch seed production starts with the monoecious formation of flower buds in late summer. The buds overwinter and mature into unisexual catkins (flowers) which open at spring after a thermal sum of 35°C has been accumulated (Hicks et al., 1994). Pollen can spread very long distances (Hjelmroos, 1991; Sofiev et al., 2006; Rousi et al., 2019), but is usually found within a few tree crown diameters of the origin tree (Andersen, 1970, as cited in Holm 1994). Winged nutlets (seeds/fruits) are produced during the summer months, and are then dispersed, starting in August and continuing well into winter, where wind disperses the seeds on top of the snow. Seed dispersal is normally around 65 metres away from the origin tree (Liu & Evans, 2021).

With a changing climate, where high-latitude environments are especially affected, new challenges are facing the birches. The arctic is warming nearly four times as fast as the rest of the globe (Rantanen et al., 2022), and this has been shown to affect species distributions (Kullman, 2002), species interactions (Tenow et al., 1999) and productivity, for example in the form of increased seed yield (Wookey et al., 1994; Molau & Shaver, 1997; Welker et al., 1997; Caignard et al., 2017). However, these changes do not necessarily favour birches. The main disturbance factor in the birch forest ecosystems consists of the defoliating moths autumnal moth (*Epirrita autumnata*) and winter moth (*Operophtera brumata*). These moths are folivorous in their one month long larval stage and can cause severe damage to their hosts; occasionally even mortality (Tenow, 1972). Large areas of birch forests have died because of these larvae, leaving behind treeless "tundra", since the forests are not always able to recover (Kallio & Lehtonen, 1975). Outbreak years occur rather regularly in arctic and alpine areas. For autumnal moths these levels are reached approximately every 9-10 years and last for one to several years (Tenow, 1972). The moth population fluctuations have been claimed to depend on masting in birches (masting is the highly variable annual seed production, where large amounts of seeds are produced intermittently and in synchrony with other members of the same species) (Selås et al., 2001), birch defence chemicals (Haukioja, 1980) and temperature. Temperatures below -36°C kill the eggs of the moths, and with rising temperatures the moth distribution can therefore advance to places previously being too cold (Tenow & Nilssen, 1990; Virtanen et al., 1996). Temperature also affects pupal development and growth rate, but too high temperatures are harmful (Topp & Kirsten, 1991). Rising temperatures can also result in increases in the natural enemies of the moths, increases in pathogens (Bylund, 1999), and introduction of new species (Tenow et al., 1999), which affects the interspecific interactions within the ecosystem, and which makes predicting the effects of warming very complex.

Because birches form the forest-tundra ecotone (the border between tundra and forest), the reaction of birches to these different environmental and biotic drivers is important at a global level. Boreal forest is the world's largest terrestrial biome (Callaghan et al., 2002), and changes in these vast areas, such as advancements in the treeline, therefore have huge effects. Warming induces a positive feedback loop in tundra environments, causing increases in shrub density and growth (arctic greening), which in turn increases snow depth, which increases soil temperature, which increases microbial activity, which increases nutrient availability, which in turn increases shrub density again, closing the loop (see *e.g.*, Chapin et al., 2005; Bjorkman et al., 2018). Losing tundra to boreal forest therefore not only affects local climate, but also affects global climate and hydrology feedbacks, with for example losses in albedo and permafrost as consequences (Harding et al., 2002).

There is relatively little focus on birch seed production in the literature, as opposed to *e.g.*, birch pollen production, pollen dispersal and moth ecology. It has been shown however that seed production decreases after moth outbreaks and that birches, at the cost of reproduction, maintain leaf biomass. This effect was only seen during high (75%) degree of defoliation and not during low (25%) degree of defoliation (Kaitaniemi et al., 1999). Another study introduces the hangover effect (Molau & Larsson, 2000): after producing a lot of seeds during a mast year, birches produce far fewer seeds the next year. Reproduction is resource-demanding, so mast years likely explain some of the patterns in birch reproduction. Birch masting appears to depend on weather conditions and previous year's resource allocations (Ranta et al., 2005). Lastly, temperature plays a role in birch reproduction. Warming in previously cold areas can extend the growing season and therefore increase nutrient accumulation (Menzel & Fabian, 1999; Beaubien & Hamann, 2011). In climatically challenging environments, having more resources can make a crucial difference, and can be what enables the birches to spare resources into producing seeds. There are several studies claiming that increased temperature therefore can cause increased seed production (Wookey et al., 1994; Molau & Shaver, 1997; Welker et al., 1997; Caignard et al., 2017).

## **Aim and hypotheses**

The rapid temperature increases seen today in high-latitude environments stress the importance of understanding the effects of warming on seed production and thereby changes in vegetation cover and/or community composition, in a sensitive environment. Additionally, since different species react differently to warming, which results in changes in interspecific interactions, it is important to investigate how the relationship between mountain birches, autumnal moths and winter moths change over time and depending on temperature.

The aim of this study was to examine trends in seed abundance and larval abundance over the past decade, as well as determine how temperature and larval abundance relate with seed abundance. Further the aim was to investigate the effects of winter temperature on larval abundance. It is hypothesised that a) seed abundance will increase with increasing growing season temperatures, b) larval abundance will increase with increasing winter temperatures, c) seed abundance will decrease with high larval abundance, and d) seed abundance will decrease with the combination of higher temperature and higher larval abundance

## Method

### Study site: Abisko (68.328400, 18.835600)

Situated in the northernmost Swedish Lapland, this subarctic location has a relatively mild climate, with an average yearly temperature of  $-1.7^{\circ}\text{C}$  (Scharn et al., 2021). Summers are cool and winters are long and snow rich. July is the warmest month. The vegetation in the area consists of characteristic mountain birch forest, located at 400 m.a.s.l. and 200 metres below the treeline in a flat landscape. The growing season begins in May and ends in August. The study site was located approximately 100 metres west from the D-house at Abisko Scientific Research Station (ANS), where there is also a scientific reserve.

### How the seeds were collected

Between 2010 and 2019 seed rain from Abisko was collected by using seed traps. The seed traps were set up according to the ITEX manual standard for seed rain monitoring (Molau & Mölgaard, 1996). That is: four square plastic turf-resembling door mats,  $0.25\text{ m}^2$  in size, were used as traps. These were placed in the corners of a  $4\text{ m}^2$  square, i.e., one metre apart from each other, and secured with nails (Figure 1). The traps were put out in August and collected in June the following year. This is done in order to catch both seed rain and the winter wind dispersal that occurs on top of the snow. That means the seed rain collected in 2010 consists of seeds produced in 2009. The contents of the seed traps were then dried indoors and stored in paper envelopes until this analysis.

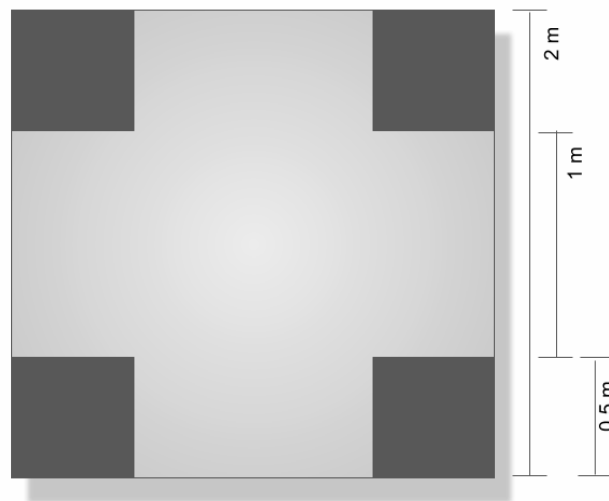


Figure 1: ITEX seed rain monitoring trap setup. The dark grey squares represent seed traps and the light grey background represents the ground.

### Sorting

The contents of the resulting forty paper envelopes were sorted by hand to lay aside and count the mountain birch seeds only. This was facilitated by using a sieve (grid size  $0.4\text{ cm} \times 0.4\text{ cm}$ ) to separate smaller debris from bigger. The only seed mountain birch might be mistaken for is dwarf birch (*Betula nana*), but dwarf birch seeds are generally smaller and have almost non-existent “wings” compared to mountain birch.

## Additional data and data preparation

Daily mean air temperature (°C) from 2008 to 2019, was retrieved from ANS. Since seed abundance data is yearly, these daily data were transformed into yearly means. Relevant temperatures for larval abundance are winter temperatures (21/12-19/3), while seed abundance is related to budding temperature (August to October the previous year, *i.e.* when flower production starts) and fruiting temperature (May to August the current year, *i.e.* when the seeds are produced). Budding and fruiting temperatures were combined and called fruit production temperature (as in Alatalo et al., 2021), and this was the mean used in the analyses.

Larval abundance data (unpublished, Helena Bylund at SLU) from 2009 to 2019, with missing data for 2016-2017, was collected at lake Vuolep Njakajaure (68.34120, 18.78056), in the form of yearly number of larvae per hundred shoots. To put this unit into perspective: during low moth abundance years there can be zero larvae per hundred shoots, while extremely severe outbreak years can have 160 larvae per hundred shoots (Tenow et al., 2001).

## Statistical analysis and visual presentation

All statistical analyses and graphs were made in R version 4.2.2 (R Core Team, 2022) with the packages *tidyverse* (Wickham et al., 2019) and *lme4* (Bates et al., 2015). All graphs were made using the *ggplot2* (Wickham, 2016) package (installed with *tidyverse*).

In order to answer the research questions, different types of generalized linear models were made. Since the response variables, seed abundance and moth abundance, are counts and cannot assume values below zero, all analyses used a Poisson error distribution. For abundance trends over time (*i.e.*, with year as predictor variable), I used generalized linear mixed models with a Poisson error distribution. Random intercepts for year were included to account for the non-independence of the four replicates (traps) collected in the same year. The effects of temperature and moth abundance on seed abundance was examined by creating a hierarchical model with seed abundance as response variable and temperature and moth abundance as predictor variables, with random intercepts for year, as described above. This model was repeated in different forms several times, first dropping the interaction between temperature and moth abundance, later dropping temperature and lastly dropping moth abundance, to see whether the changes made the model significantly worse, which was determined by a Chi-squared likelihood ratio test, using the *anova* function. The removed factor was not considered significant if the *anova* returned a p-value greater than 0.05. A separate model was made for temperature and seed abundance only, since the earlier models did not account for all temperature data when there was missing moth data for two of the years

## Results

### Seed and larval abundance over the years

There is no significant relationship between seed abundance and year ( $p = 0.58$ ), meaning that seed production was neither increasing nor decreasing over the ten-year time period (Figure 3 a). Larval abundance peaked in 2012 (27 larvae/100 shoots), with a significant decrease over the 10 years ( $p = 0.00231$ ) (Figure 3 b). The 2012 peak occurred one year after one of the seed abundance peaks. The next seed abundance peak was in 2016, but since there is no larval abundance data from 2017, it is not known whether the larvae peaked again.



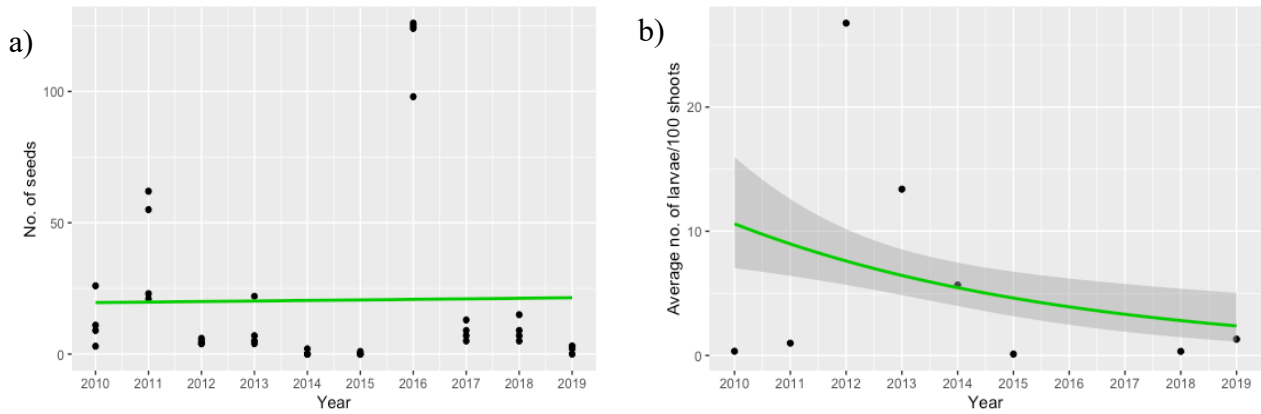


Figure 3: a) The relationship between birch seed abundance and year. The regression was not significant ( $p = 0.58$ ). The black dots represent counts of birch seeds of different traps. b) The relationship between larval abundance and year. The Poisson regression was significant ( $p = 0.00231$ ), and larval abundance decreased over time. The shading represents standard error ribbons.

### The effects of temperature and larval abundance on seed production

Neither temperature models ( $p = 0.72$ ) (Figure 4 a) nor larval abundance models ( $p = 0.91$ ) (Figure 4 b) could explain the variation in birch seed abundance. There was also no interaction between temperature and larval abundance ( $p = 0.82$ ). The yearly temperature means were very close to each other, ranging from 7.0 to 8.4°C. The Chi-squared likelihood ratio tests showed that none of the parameters investigated had a significant effect on seed abundance.

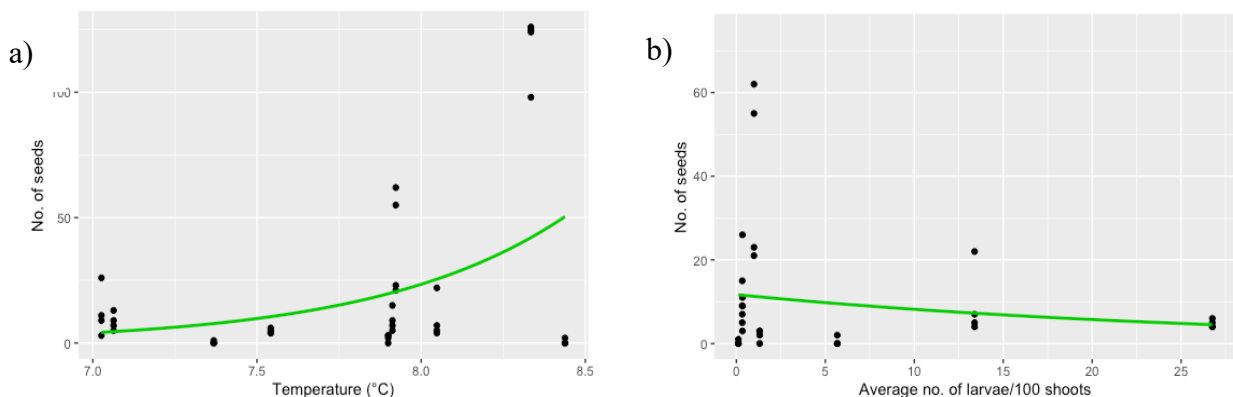


Figure 4: a) The relationship between seed abundance and growing season temperature. The Poisson regression was not significant ( $p = 0.72$ ). The black dots represent counts of birch seeds of different traps. b) The relationship between seed abundance and larval abundance. The Poisson regression was not significant ( $p = 0.91$ ). The black dots represent counts of birch seeds of different traps.

### The relationship between larval abundance and temperature

There was a significant positive trend between larval abundance and winter temperature ( $p < 0.001$ ), where there were more larvae after warmer winters. However, the warmest winter coincided with the smallest number of larvae (Figure 5).

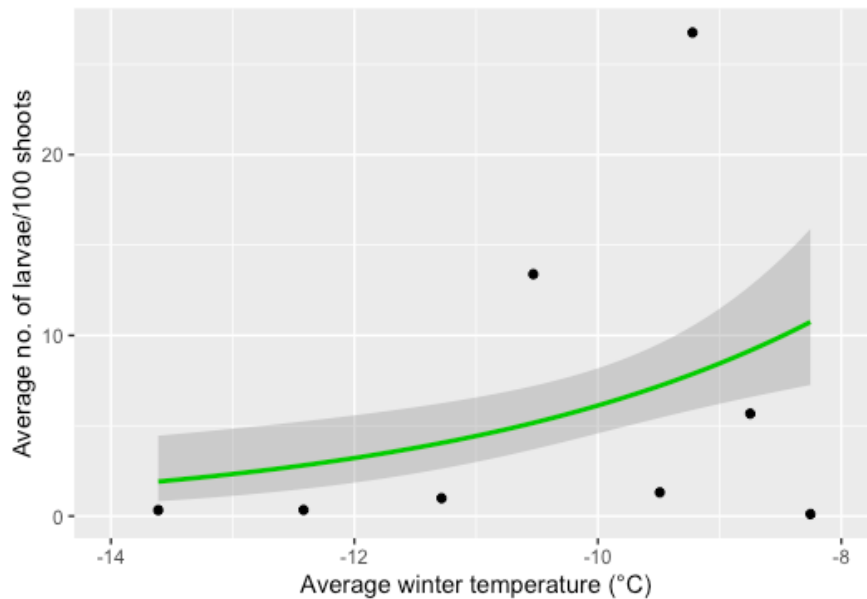


Figure 5: The relationship between larval abundance and winter temperature. The Poisson regression was significant ( $p < 0.001$ ), and there are more larvae when there are warmer winters. The shading represents standard error ribbons.

## Discussion

The absence of a significant relationship between seed abundance and temperature or larval abundance suggests that factors other than temperature and larval abundance are the main drivers controlling birch seed abundance. These results are in contrast to my hypotheses and the results of previous studies (*e.g.*, Welker et al., 1997; Karlsson & Weih, 2003, respectively). The hypothesis for larval abundance was however supported; there are more larvae when there are milder winters.

## Seed and larval abundance over the years

During this ten-year time period, there were two mast years, 2011 and 2016, one of which was followed by a peak in larval abundance and the other lacked data for larvae in 2017. Seed abundance was otherwise overall constant with no increases or decreases, which was quickly investigated by omitting the mast years. A stable level of seeds indicates that there were no major disturbances or changes in the environment, positive or negative, and no inferences about possible distribution or population changes can be made. But processes like reproduction and growth are costly in harsh environments and are therefore slow. Many studies express the need for even longer data-collection (see *e.g.*, Inouye & Tilman, 1995); so possible changes in seed production might not be detectable until *after* ten years; *if* there are changes. This is further aggravated by the fact that generative reproduction is not always the main mode of reproduction in colder high-altitude areas since it is so costly (Crawford, 1982); seed abundance might be a quite complex factor to investigate trends in. Different growth forms (*i.e.*, monocormic and polycormic) rely on different reproductive strategies, and changes in the proportions of the different growth forms can therefore be reflected in seed abundance (Wielgolaski et al., 2005). Seed abundance also changes with the age of the stand, where old trees produce fewer seeds (Bylund, 1997). Knowledge about the birches in the area is necessary to further interpret seed abundance trends.

Larval abundance significantly decreased during the duration of the study. Although this trend is significant, the cyclicity of the moth populations must be taken into account; it is possible that the downgoing trend is just the result of a pattern in the moth population size cycle. Autumnal moths

reach outbreak levels approximately every 9-10 years, and this study, lasting for ten years, is too short to truly investigate this, again calling for longer data-collection. Furthermore, there was only larval abundance data for eight of the ten years in this analysis, which is very little. The timing of the missing data is especially unfortunate, because it is the two years after the highest seed abundance year, which likely could have had an effect on larval abundance and the larval abundance trend over time, although the former was not one of the research questions and was not statistically investigated. But it is of course still a possibility that the trend is an actual decrease in larvae in this area, and this could be due to *e.g.*, foliage quality and birch defence chemicals, where the latter inhibits digestibility (Haukioja, 1980).

### **The effects of temperature and larval abundance on seed production**

Although the results of this study suggest that drivers other than temperature and larval abundance are more important for mountain birch seed production, temperature and larval abundance should perhaps not be completely dismissed as possible explanatory factors. Most likely no factor alone can explain birch reproduction. *E.g.*, the fact that birch mast seeding occurs not only at high latitude/altitude areas, but also at lower latitudes and altitudes, where moth outbreaks are very uncommon (Perela & Alm, 1990), supports the idea that larval abundance alone does not control seed abundance. Still, outbreaks are likely influencing birch reproduction, at the very least depending on the degree of defoliation (Kaitaniemi et al., 1999); severe defoliation can result in mortality, and no seeds, at worst. During this study, the highest density of larvae was 27 larvae per hundred shoots. Compared to the massive defoliation in 1955, with up to 160 larvae per hundred shoots (Tenow et al., 2001), this is very little. Birch reproduction is perhaps only affected by larval abundance when their populations reach high enough levels. But the relationship between birch reproduction and larval abundance is still not fully clear. Does birch success result in moth success, or does moth success result in birch failure? In this study, the mast year in 2011 was followed by a larval abundance peak in 2012. Did larval abundance peak because there had been some good condition years with much food, leading up to a birch mast year, or did larval abundance peak because birches had used up their resources on reproduction and not on chemical defence? The first alternative suggests that larval abundance depends on birch success and not the other way around; the opposite to what was investigated in this study. It seems like birch success influences moth success and moth success influences birch success at the same time. Alternatively, there is another factor at play, influencing both of them, such as temperature.

Temperature is chiefly what limits mountain birch distribution. It is therefore surprising that temperature did not have any effect on seed production. Were these trees, 200 metres below the treeline, not temperature-limited? More information about the age and growth forms of the stand could help partially explain this. One explanation of the results is that the calculated mean temperature used in this analysis, the so-called fruit production temperature, was too general. The chosen monthly range was possibly too broad, and the resulting means too similar. Furthermore, the chosen month ranges could be irrelevant for the processes investigated, and it is also possible that there is a lag effect. Other months and years should therefore be investigated, for example starting with the two components of fruit production temperature: fruiting temperature (May to August the current year) and budding temperature (August to October the previous year). It would also be interesting to explore how winter temperature affects seed abundance, since winter temperature has a significant effect on larval abundance. Another addition could be to investigate the relationship between precipitation and seed abundance, since new patterns in precipitation are expected with global warming. One study suggests that fruit production decreases with increased precipitation (Alatalo et al., 2021). Another study claims that precipitation is as important as temperature for seed production and suggests that it might be because the study site was

precipitation-limited (Brown et al., 2018). Maybe this study site was also either too wet or precipitation-limited, which could explain why temperature did not have any effect on seed production. Lastly, the complicating factor masting must be mentioned. Birch masting depends on weather conditions and previous year's resource allocations (Ranta et al., 2005), so temperature likely influences it. Regardless of that, in this study, perhaps mast years should have been removed and treated as outliers. The relationship between normal seed production years and growing season temperature could have been investigated instead, but after a quick additional analysis where mast years were removed, the results were still not significant.

### **The relationship between larval abundance and temperature**

The significant positive relationship between winter temperature and larval abundance supports the idea that higher temperatures lead to increased larval abundance; that larval distribution and abundance is temperature limited. This is likely because egg mortality decreases. Temperature also influences pupal development and growth rate, but too high temperatures can be harmful and retard adult emergence (Topp & Kirsten, 1991). A surprising detail in the data is that the warmest winter had the fewest larvae. This outlier could point to several explanations: it is possible that the relationship between temperature and larval abundance is unimodal, but it could also be because there is another factor than winter temperature influencing larval abundance. This other factor could be, as was implied earlier, birch success, or possibly birch defence failure. Some studies support this idea (*e.g.*, Selås et al., 2001). A way to test this could be to measure *e.g.*, larval weight during mast years to see whether those conditions are beneficial.

### **Conclusion**

Although warming and herbivory have been shown to affect seed production in other studies, neither appeared to influence mountain birch seed abundance over the ten years of this study, and the central hypothesis of this study was therefore not supported. The positive trend between winter temperature and moth abundance however supports the idea that warmer winters increase the number of moths, since it decreases moth egg mortality. Moth abundance also appeared to decrease over this ten-year time period, but whether this is an actual downgoing trend or if it is caused by the moth population cyclicity is unclear. Birch seed abundance is neither increasing nor decreasing. What this could point to long term is that moth abundance and distribution will increase with the warming climate, and that it might not have any significant effect on birch reproductive success, with the exception of moth outbreak years.

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