

Plant-pollinator interactions in the alpine:
Landscape heterogeneity acts as a potential buffer
against climate-change induced mismatch in the
pollinator-generalist *Ranunculus acris*



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June 2018

Front page: *Ranunculus acris* with Dipteran pollinator (Finse, 01.08.17).
Photo: Silje Andrea Hjortland Östman

Acknowledgements

I would like to thank my supervisors *Dr. Aud H. Halbritter* and *Prof. Vigdis Vandvik* for the possibility to conduct this study and for all their help throughout the process. To *Aud* for always finding time for me, sharing her knowledge, and having a lot of patience. To *Vigdis* for bringing new ideas to the table. I would also like to thank *Prof. Ørjan Totland* for valuable input about the project and the study species.

A huge thanks to *Aud, Iselin*, and especially *Debbie* for coming to Finse and helping me with fieldwork. To *the Ecology and Environmental Change Research Group* for welcoming and including me into their great research environment. To *the Writing Group* for good, constructive feedback on my drafts and to *Cathy Jenks* for proofreading. To *the codeRClub* for help with R and statistical analyses.

To *friends and family* for support and encouragement.

Abstract

Phenology changes are a common response to global warming and the timing of phenological events is important for symbiotic interactions, such as pollination. If symbiotic species respond differently to global warming, this could lead to loss of facilitative interactions due to phenological mismatches between species. Global warming is faster and stronger in alpine regions, which could induce stronger asynchrony in plant-pollinator interactions in alpine habitats. However, most alpine plant species are pollinator-generalists and thus are expected to be less vulnerable to plant-pollinator mismatches. This study investigates plant-pollinator interactions in the pollinator-generalist plant species *Ranunculus acris* L. along a snowmelt gradient in the alpine area of Finse in western Norway over two growing seasons (2016 and 2017). The snowmelt gradient creates patches with different times of snowmelt, and thus onset of flowering. I use the spatial distribution of flowering and pollinator activity to investigate whether sub-populations with different times of flowering experience different synchrony with their pollinators, assessing the potential for temporal plant-pollinator mismatches. In addition, I conduct a hand-pollination experiment to investigate whether a sub-population's synchrony with its pollinators affects plant reproductive ability.

Plant-pollinator mismatch was not detected between *R. acris* and its pollinators in any of the snowmelt stages or years. Pollinator visitation rate was constant throughout the seasons of both years, but pollinator activity was lower for individuals flowering later in the season in 2017. Reproductive output was not found to be pollen limited, although lower achene mass correlates with lower pollinator visitation rates in late-flowering individuals in 2017. I conclude that this pollinator-generalist is well synchronised with its pollinators, and that early flowering might be related to higher reproductive success, meaning that earlier snowmelt and flowering should not be problematic for this species, but later snowmelt and flowering might. In addition, I suggest that the patchiness of this kind of heterogeneous alpine landscape contributes to flowers always being available to insects, and for pollinators to move between the patches of highest flower abundance, which lowers the risk of temporal plant-pollinator mismatch.

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Introduction

Phenology is an important part of a species' life history that influences individual fitness, especially in temperate regions where climate restricts the length of the growing season. The timing of phenological events is, in many species, controlled by abiotic factors, such as temperature (Schwartz, 2013). Climate change is currently affecting many ecosystems, with mean annual temperatures expected to increase by 0.3–1.7°C by the end of the century (IPCC, 2014). Increasing temperatures may lead to phenology changes by shifting phenological events.

Changes in the timing of phenological events could interfere with key ecological events, such as pollination, which may be threatened by phenological shifts in plants and pollinators (Forrest, 2015; Memmott *et al.*, 2007). Most flowering plants depend on interactions with animal pollinators for sexual reproduction, and pollinators rely on flowers to forage upon (Willmer, 2011). For these interactions to occur, flowering and pollinator activity must coincide (Forrest, 2015). Currently, the phenology of both spring flowering and insect emergence are advancing with increased temperatures (Bartomeus *et al.*, 2011; Fitter & Fitter, 2002; Miller-Rushing & Primack, 2008; Parmesan, 2007; Primack *et al.*, 2004; Sparks *et al.*, 2000), but not necessarily at the same pace (Willmer, 2012). This is because some species may be more strongly controlled by abiotic factors than others (Forrest & Thomson, 2011; Parmesan, 2007; Willmer, 2012) and pollinating insects might hibernate in substrates affected differently by abiotic factors than the soil in which plants grow (Forrest & Thomson, 2011; Hegland *et al.*, 2009). In such cases, phenology changes could disrupt the synchrony between flowering and pollinator activity, resulting in phenological mismatches (Stenseth & Mysterud, 2002; Visser & Both, 2005). Plant-pollinator mismatch may result in reduced food availability for pollinators (Forrest, 2015; Memmott *et al.*, 2007) and prevent plant reproduction (Kudo, *et al.*, 2004; Thomson, 2010; Kudo & Ida, 2013), which could lead to population declines for both groups (Forrest, 2015; Hegland *et al.*, 2009; Miller-Rushing *et al.*, 2010).

The literature is divided on the importance of mismatches in nature. Plant-pollinator mismatches have been found in several different environments (e.g. Gezon *et al.*, 2016; Høye, *et al.*, 2013; Kudo & Ida, 2013; Petanidou *et al.*, 2014), but some studies indicate that many species and communities do not experience mismatch and are not expected to do so in the future (Bartomeus *et al.*, 2011; Ovaskainen *et al.*, 2013; Rafferty & Ives, 2011). The threat of plant-pollinator mismatch has also been questioned by the suggestion that a mismatch is the normal state for interactions in nature (Bolmgren & Eriksson, 2015) and that pollination

interactions are protected by high levels of biodiversity (Bartomeus *et al.*, 2013). It is currently unclear how, where, under which conditions, and to what extent, continuing and increasing global warming will affect plant-pollinator interactions in the future (Burkle *et al.*, 2013).

Climate change is generally expected to have a larger impact in alpine regions than at lower elevations because temperatures are increasing at a faster pace here (IPCC, 2014). As biological processes in alpine ecosystems are generally temperature limited, one could expect more rapid phenological changes in response to climate change in the alpine, resulting in more prominent plant-pollinator mismatches. Only a few plant-pollinator mismatch studies have been conducted in alpine or subalpine environments, most of which show that early-flowering plants are less synchronous with their pollinators (Forrest & Thomson, 2011; Kudo, 2014; Thomson, 2010), which is in agreement with the expectation for a fast-warming environment.

In alpine areas, most insect-pollinated plant species have traits typical of pollinator-generalists (Willmer, 2011), and are thus adapted to being pollinated by many species. Generalist species have been hypothesised to be less vulnerable to mismatch (Biesmeijer *et al.*, 2006; Memmott *et al.*, 2007), which is supported by a study where experimentally advanced flowering in a generalist species did not show any sign of a plant-pollinator mismatch (Gezon *et al.*, 2016). Thus, for the alpine, the expectation of more disrupted plant-pollinator interactions in rapidly warming environments contradicts the expectation of less vulnerability to mismatch in systems dominated by generalist species, and it is unclear how rapid warming will affect plant-pollinator interactions in generalist species. In this thesis, I investigate this further by studying the plant-pollinator synchrony of a pollinator-generalist species in an alpine environment.

This study uses natural snowmelt gradients provided by different snow accumulation on ridges and in snowbeds, creating patches that differ in the onset of flowering (Kudo, 1993; Kudo & Hirao, 2006). By studying plant-pollinator interactions along a snowmelt gradient, one can use the spatial distribution of flowering and pollinator activity to investigate temporal mismatch: if interactions differ between early- and late-flowering sub-populations, I can evaluate if advanced or delayed flowering is likely to result in disrupted plant-pollinator interactions. I expect that a mismatch can occur for both early- and/or late-flowering sub-populations. Mismatch in early-flowering sub-populations can occur if pollinating insects

emerge significantly earlier or later than the flowers. Contrarily, late-flowering sub-populations can experience mismatch if the flowering season extends significantly beyond the pollinators' active season. In addition to plant-pollinator synchrony, the ratio between the number of flowers and insects present controls the frequency of pollinator visits. Pollinator visitation rate, i.e. number of pollinator visits per flower, will differ with this ratio, and different ratios will cause different degrees of intra- or interspecific competition over pollinators (Alarcón *et al.*, 2008). Thus the pollinator visitation rate also suggests at what times during the growing season flowering is most favourable, which can be further used to indicate how potential phenology changes will affect plant-pollinator interactions.

In this study, I investigate the pollinator visitation rate and the synchrony of flowering and pollinator activity by recording the flower phenology of the widespread pollinator-generalist *Ranunculus acris* and the visitation activity of its pollinators along a snowmelt gradient at Finse (Hordaland, Norway). Additionally, I measure reproductive output of naturally pollinated and hand-pollinated individuals of *R. acris* to investigate potential effects of a plant-pollinator mismatch on plant reproductive ability. The study stretches over two consecutive years, which allows me to account for inter-annual differences in plant-pollinator synchrony, pollinator visitation rates, and reproductive output. With this study, I aim to answer the following questions: 1) Is there a mismatch between the flowering time of *R. acris* and the activity of its pollinators, and do their interactions differ within and between years? 2) Does the pollinator visitation rate vary between different times of snowmelt and throughout the growing season, and do the patterns vary between years? 3) If there is a mismatch, does it affect the reproductive output of *R. acris*, and does reproductive output vary between different times of snowmelt?

Methods

Site description

This study was conducted at Finse, Hordaland (Norway), during the summer season (June–August) in 2016 and 2017. Study sites were situated on the southern slope of Mount Sanddalsnuten, between 1400 and 1500 m a.s.l. (N60°36.7', E7°31.7'; central site), along ridge–snowbed gradients (Figure 1). These gradients show a pronounced gradient in date of snowmelt, and thus onset of the growing season, as snow accumulates differently in slopes and ridges. The area belongs to the mid-alpine zone, and the vegetation consists mainly of alpine grassland (Totland, 1994a). The area has a weak, oceanic climate (Fremstad, 1997) with 990 mm annual precipitation, and an average summer temperature (June–August) of 6.3°C (climate data provided by The Norwegian Meteorological Institute, www.yr.no).

Study plant and pollinators

For this study I used a widespread, insect-pollinated, perennial herb: *Ranunculus acris*. This species is a characteristic pollinator-generalist with many interacting pollinators. It is an abundant plant in the alpine grasslands of Finse and individuals flower for approximately ten days (Totland, 1994b). Populations of *R. acris* in this area are incapable of either self-pollination or asexual seed production (Totland, 1994b) and vegetative reproduction rarely occurs (one plant will henceforth be referred to as one individual; Totland, 1997). This means that Finse-populations of *R. acris* heavily rely on pollinators for reproduction, making it an ideal study species for investigating reproductive outputs based on pollinator activity.

Ranunculus acris is a convenient species for pollinator observations as it has a yellow inflorescence, which is one of the most attractive colours to dipteran pollinators (Pickering & Stock, 2003; Reverté *et al.*, 2016). Dipterans are the dominant pollinator group in alpine environments (Inouye & Pyke, 1988; McCall & Primack, 1992; Primack, 1983) including the Finse area (Totland, 1993), and *R. acris* is mainly pollinated by species of the Muscidae and Anthomyiidae families (Totland, 1993).

Experimental design

This study has a nested block design and was performed across ten snowmelt gradients on the southern slope of Mount Sanddalsnuten. Every gradient has three sites that differ in time of

snowmelt (early, mid, late), and each site contains five blocks (Figure 1). The snowmelt stages were chosen with a two week difference in snowmelt, and all sites within the same snowmelt stage were snow-free at approximately the same time. Only two snowmelt stages were used in 2016 (mid and late) because fieldwork could not be started early enough to include sites of the early snowmelt stage. The early stage was added in 2017, but only eight suitable sites were found for this stage. For the mid and late snowmelt stages, sites and blocks were reused in 2017, but as snow melted somewhat differently in 2017 than 2016, the time of snowmelt and onset of flowering overlapped between some mid- and late-stage sites that year (see Table I in Appendix A for details). Within each site, five study blocks were subjectively placed in locations containing leaves of *R. acris*, to ensure its presence in the blocks. All sites were fenced during the season to prevent grazing from free-ranging domesticated sheep (*Ovis aries*), which are present in the area from late June until the end of the growing season.

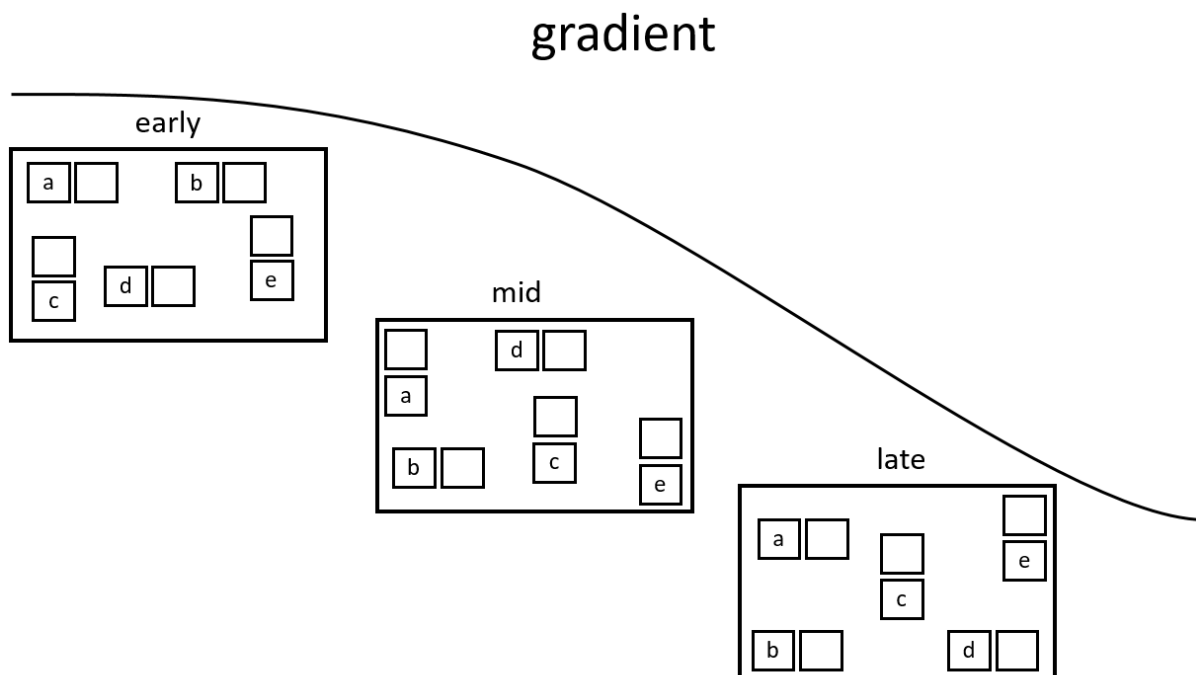


Figure 1. Example gradient with the three stages of snowmelt (early, mid, late), each represented by a site with five blocks (a-e) divided into two sub-blocks: one experimental and one undisturbed. Note that the size and shape of sites varied (see Table I in Appendix B), and distance between sites and blocks were not as uniform as illustrated in this figure.

The size of a site varied between ten and 70 m², depending on the placement of and distance between the blocks (see Table II in Appendix B for precise site measurements). Each block is

a 50x110 cm rectangle, divided into two 50x50 cm sub-blocks set apart by a 10 cm buffer zone, where one sub-block was used for manipulated sampling and the other one was left undisturbed. Neutrally coloured tubes were placed in each corner of the two squares to mark the blocks (Figure 2a).

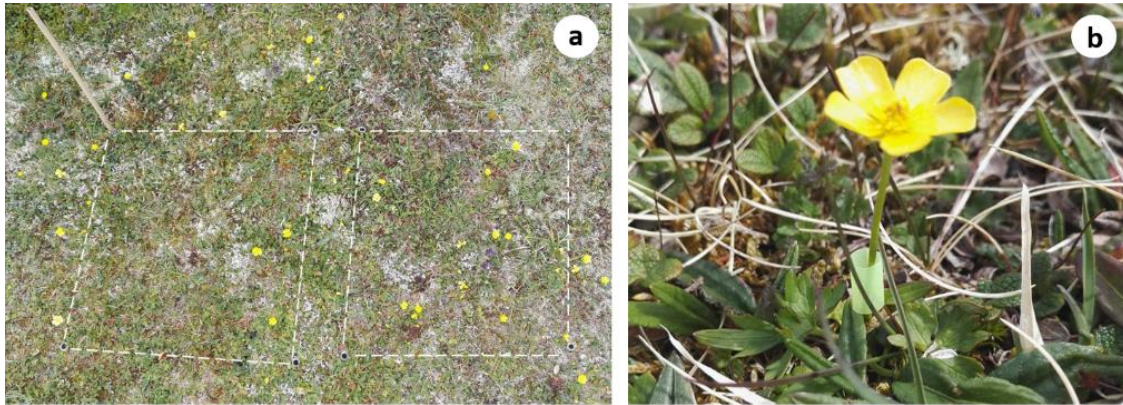


Figure 2. a) Example of a block, made up of two 50x50 cm sub-blocks with a 10 cm buffer zone between them. b) Individual of *R. acris* marked with a plastic straw around the stem.

Flowering phenology and pollinator activity

To investigate plant-pollinator interactions between *R. acris* and its pollinators, flowering phenology and pollinator activity were measured. Flowering was recorded by counting the number of open *R. acris* flowers (i.e. flowers responsive to pollinating insects) in all the blocks of a site. A flower was considered open when the petals were folded out completely. Observations were done every second day (with a few exceptions of a maximum of four days between observations), and were stopped when experimental plants were ripe (see *Hand-pollination and reproductive output*) even if some blocks still contained a few non-experimental flowering individuals.

Pollinator activity was measured as the number of pollinator visits to all *R. acris* flowers during five-minute observations. Pollinator observations were done by site, because blocks were too small to ensure that visits occurred during the five-minute periods. During each observation, the observer would count all pollinator visits to *R. acris* flowers within a site. These observations were primarily done between 0930 and 1700 hours on days with no precipitation, as precipitation limits pollinator activity (Kevan & Baker, 1983). The time of observation at the different sites varied, to ensure that observations were not always done at the same site early or late in the day. Observations were also avoided on days with very low

temperatures or when strong wind prohibited pollinators from moving within a flower. Pollinator activity was measured from the beginning to the end of the flowering period of each site. Mainly flies were observed as pollinators on *R. acris*, but butterflies were also observed on a few occasions in 2016.

Hand-pollination and reproductive output

To assess the effect of disrupted plant-pollinator interactions on plant reproduction, I investigated pollen limitation by measuring reproductive output in naturally pollinated and hand-pollinated individuals of *R. acris*. Four individuals were chosen from the experimental sub-block: two individuals were hand-pollinated and two were left as controls to be naturally pollinated by insects. I avoided the first two to three individuals that appeared in each block, as the earliest flowers tend to be sterile (Ø. Totland, personal communication). If the experimental sub-block did not contain enough flowers, individuals were chosen from the other sub-block or from close proximity of the block. Selected individuals were marked with pieces of plastic straw around the stems (Figure 2b), with different colours for controls and hand-pollinated individuals.

For hand-pollination I used pollen from individuals of *R. acris* collected from the close surroundings of the sites. The collected plants often contained little pollen and were therefore stored inside over night to increase pollen production, making fertilization more likely (Ø. Totland, personal communication). The hand-pollination was conducted by stroking five anthers from a donor individual on top of the mature stigmata of selected individuals. If an individual had more than one flower, the first maturing flower was chosen. Hand-pollination was usually performed two or three times for each individual (with a few exceptions of only one time per individuals), and was mainly conducted in dry weather to ensure that the pollen stuck to the stigmata. Notes were made about the weather if pollination was performed during less favourable conditions.

Reproductive output was measured as total mass, in grams, of the achenes (fruits of *R. acris*) for one flower head. As the achenes ripened, they were collected from each individual and stored in paper envelopes where they air-dried. If a control individual had more than one flower, achenes were selected from the first maturing flower. Achene mass was measured about two to four weeks after being collected.

Weather measurements

Abiotic factors such as precipitation, temperature and wind can potentially affect flowering (Fitter & Fitter, 2002; Hegland *et al.*, 2009), pollinator activity (Kevan & Baker, 1983), and reproductive output (Corbet, 1990). Therefore, weather conditions were registered during all pollinator observations, as one of four categories: sunny, sunny but partly cloudy, cloudy but partly sunny, and overcast. Wind and temperature data (hourly measurements from a weather station at Finse) were retrieved from The Norwegian Meteorological Institute (www.eklima.met.no). Wind strength was divided into four categories: 1–3 m/s = 1, 4–6 m/s = 2, 7–8 m/s = 3, and 9+ m/s = 4 (observations were rarely made during wind categories 3 and 4). However, the retrieved wind data only show the mean wind strength per hour, meaning that wind could have been stronger or weaker at the time of an observation.

Both temperature and precipitation varied very similarly through 2016 and 2017 (Figures I and II, Appendix C), although the summer (June–August) of 2016 was warmer and wetter than in 2017, by 1.4°C and 42.8 mm, respectively. Mean summer temperature was 7.7°C in 2016 and 6.3°C in 2017, while summer precipitation reached 336.7 mm in 2016 and 293.3 in 2017 (see Table III in Appendix C for more detailed weather data).

Data analyses

Dates of flowering and pollinator visits to *R. acris* were converted to Julian days for each site. Flowering and pollinator activity is expected to have bell-shaped distributions (Figure 3b-d), with a maximum number of flowering/pollinator activity (hereafter peak flowering/peak pollinator activity). Due to rainy periods, pollinator activity could not be observed as regularly as flowers, causing distributions to appear incomplete or not bell-shaped. This was solved by estimating peak flowering and peak pollinator activity for each site by fitting a generalised linear third order polynomial model with day of the year (hereafter DOY) as explanatory variable and number of flowers/pollinator visits as response variables for each site. Both second and third order polynomial models were tested, but as the third order model had the best fit for the majority of the sites, this was used for all sites to be consistent.

To test the relationship between flowering and pollinator activity, the day of peak pollinator activity was regressed against day of peak flowering. Further, to quantify any mismatch, I calculated the number of days between peak flowering and peak pollinator activity (Δ_{peak}), where $\Delta_{\text{peak}} = 0$ indicates perfect synchrony between peak flowering and peak pollinator

activity. A negative Δ_{peak} means that maximum flowering occurred before maximum pollinator activity, and a positive Δ_{peak} means that pollinator activity peaked first. To test if mismatches differed between the three snowmelt stages, a linear model with snowmelt stage as the explanatory variable and Δ_{peak} as the response variable was used.

Pollinator visitation rate was calculated as number of visits per flower and observation time (5-minute intervals) for each site. To test if the visitation rate varied throughout the growing season and with snowmelt stage, I used a linear model with DOY as the explanatory variable and pollinator visitation rate as the response variable. In the same way, I also tested if pollinator visitation rate varied by snowmelt stage, using snowmelt stage as the explanatory variable and pollinator visitation rate as the response variable.

Pollen limitation of reproductive output was tested by comparing achene mass of hand-pollinated and naturally pollinated individuals. For this, I used a separate linear model for each year, with pollination treatment as the explanatory variable and achene mass as the response. Further, to test the differences in reproductive output between the three snowmelt stages, a linear model with snowmelt stage as the explanatory variable and achene mass as response variable was used.

To investigate potential effects of weather, I summarised the daily mean temperature (cumulative precipitation) and the daily precipitation (cumulative precipitation) for the duration from first to peak flowering for each stage. To test if the cumulative temperature and precipitation varied between snowmelt stages, linear models were used, with snowmelt stage as the explanatory variable and cumulative temperature or precipitation as the response variable.

All statistical analyses were conducted separately for both 2016 and 2017 data, and were performed using the software program R 3.4.4 (R Core Team, 2018). All code used for the statistical analyses is available on github: <https://github.com/audhalbritter/Mismatch>

Results

Flowering phenology and pollinator activity

In the early sites (2017 only) *R. acris* flowered from 11 June to 22 August. In the mid sites, the flowering period lasted from 17 June to 11 August in 2016, and 24 June to 22 August in 2017. Flowering in the late sites lasted from 4 July to 18 August in 2016, and 3 July to 22 August in 2017. As observations were stopped when fruits had been collected, some sites flowered for a few more days than is registered. Note that onset of flowering overlapped for some sites of the mid- and late-stages in 2017 (Table I, Appendix A), as snow melted differently in 2017 than 2016. The first observed plant-pollinator interaction was 23 June in 2016 (for mid sites, as there were no early sites that year) and 27 June in 2017. Pollinators were observed on *R. acris* until the end of the growing season in both years. According to collected data, flowering and pollinator activity in the sites overlapped by a minimum of 10 days and maximum of 31 days in 2016 for all sites, but pollinator observations ended in the middle of the growing season due to unfavourable weather conditions, leaving the minimum and maximum days of overlap unrealistically low. In 2017, flowering and pollinator activity overlapped with a minimum of 33 days and a maximum of 60 days for all sites.

There is a clear correlation between peak flowering and peak pollinator visitation throughout the snowmelt gradient (2016: $F_{1, 27} = 56.62$, $P < 0.001$, 2017: $F_{26, 1} = 19.79$, $P < 0.001$; Figure 3a). Comparing peak flowering and peak pollinator activity shows three different plant-pollinator interaction patterns: flowering peaks before pollinator activity (Figure 3b; points above 1:1 line in Figure 3a), flowering and pollinator activity peak simultaneously (Figure 1c; points aligned with 1:1 line in Figure 3a), and pollinator activity peaks before flowering (Figure 3d; points below 1:1 line in Figure 3a). However, the synchrony between flowering and pollinator activity does not vary between sites of different snowmelt stages (2016: $F_{1, 18} = 1.352$, $P = 0.260$, 2017: $F_{2, 25} = 0.1374$, $P = 0.872$; Figure 4a).

Pollinator visitation rate, defined as number of pollinator visits per flower and observation time (5-minute intervals), did not vary significantly throughout the season or between snowmelt stages in 2016 ($F_{2, 205} = 0.84$, $P = 0.431$; Figure 4b). In 2017 the pollinator visitation rate did not vary over time either ($F_{3, 392} = 2.36$, $P = 0.070$), although it is worth noting that the rate dropped slightly at the time of peak flowering and peak pollinator activity in all three snowmelt stages, before slightly increasing again (Figure 4b). Additionally, the flowering

period of the late stage had a significantly lower pollinator visitation rate than the early- and mid-stages in 2017 ($P = 0.026$).

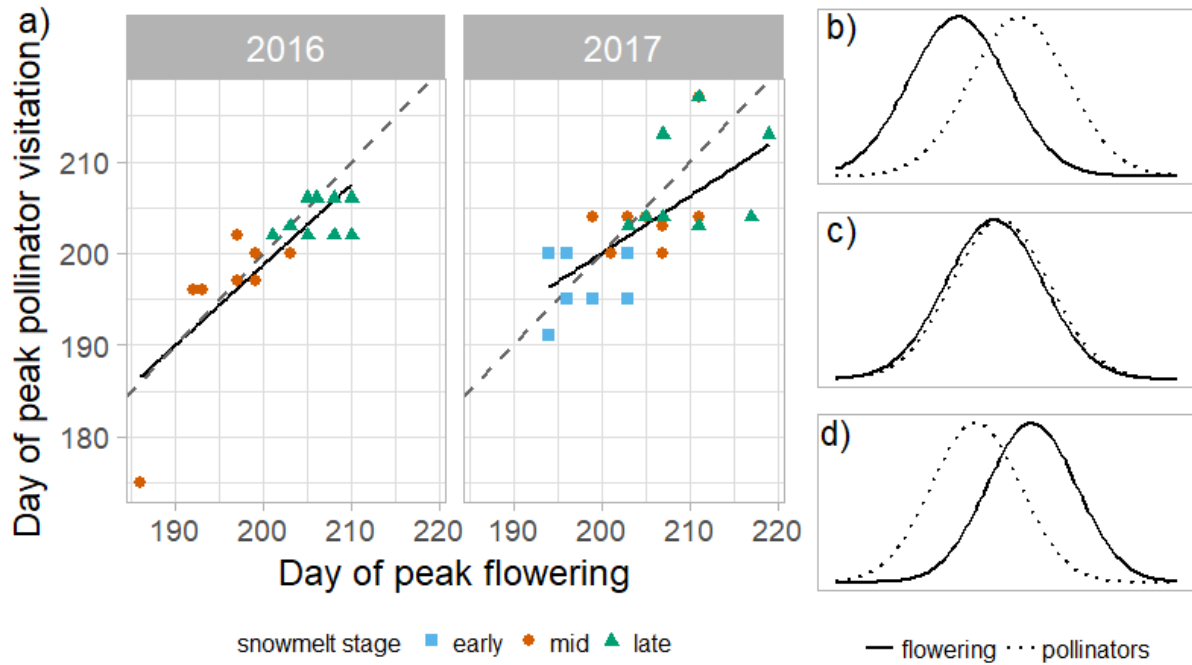


Figure 3. **a)** Day of peak flowering (y-axis) and day of peak pollinator visitation (x-axis) in the different sites. Shown are the 1:1 line (dashed line) and regression line (solid line). Symbols and colours illustrate the different stages: early (blue squares), mid (red circles), and late (green triangles), **b-d)** examples of plant-pollinator interaction patterns where **b)** flowering peaks before pollinator activity, **c)** flowering and pollinator activity peak simultaneously, and **d)** pollinator activity peaks before flowering.

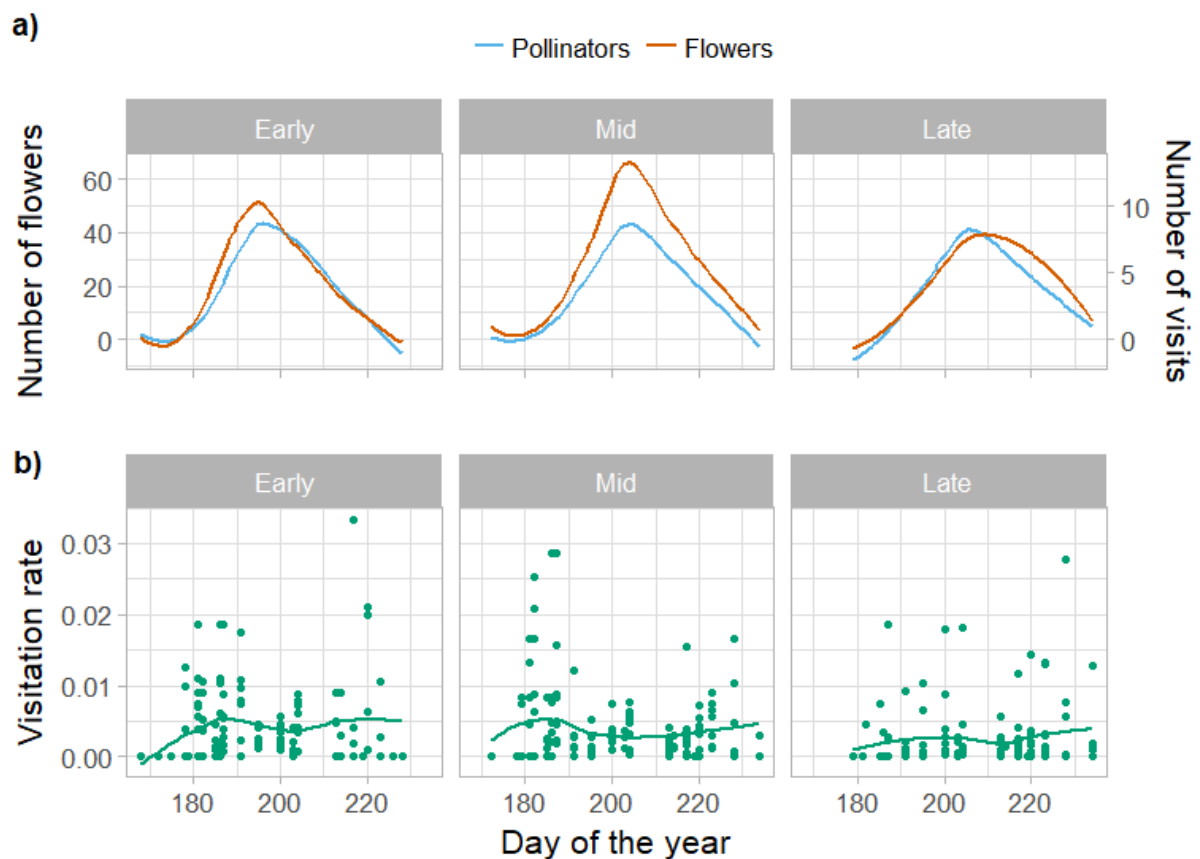


Figure 4. **a)** Estimated numbers of flowers (red) and pollinator visits (blue) per observation throughout the flowering period of each snowmelt stage in 2017, **b)** pollinator visitation rate (pollinator visits per flower per observation interval) for each snowmelt stage in 2017, the line is fitted with a LOESS function. (Figures only show 2017 data because of low pollinator activity in some of the sites in 2016.)

Reproductive output

Reproductive output (total mass of achenes per flower head) did not vary between hand-pollinated and naturally pollinated (control) individuals in 2016 or 2017 (2016: $F_{1,263} = 1.022$, $P = 0.313$, 2017: $F_{1,484} = 1.007$, $P = 0.316$; Figure 5). Further, the reproductive output of naturally pollinated individuals did not differ between the two snowmelt stages in 2016 ($F_{1,148} = 1.629$, $P = 0.204$), however individuals of the late stage in 2017 had lower reproductive output than the two other stages had that year ($P = 0.003$). There were no differences in reproductive output between different values of Δ_{peak} in any of the years (2016: $F_{1,148} = 0.0025$, $P = 0.960$, 2017: $F_{1,264} = 3.76$, $P = 0.054$).

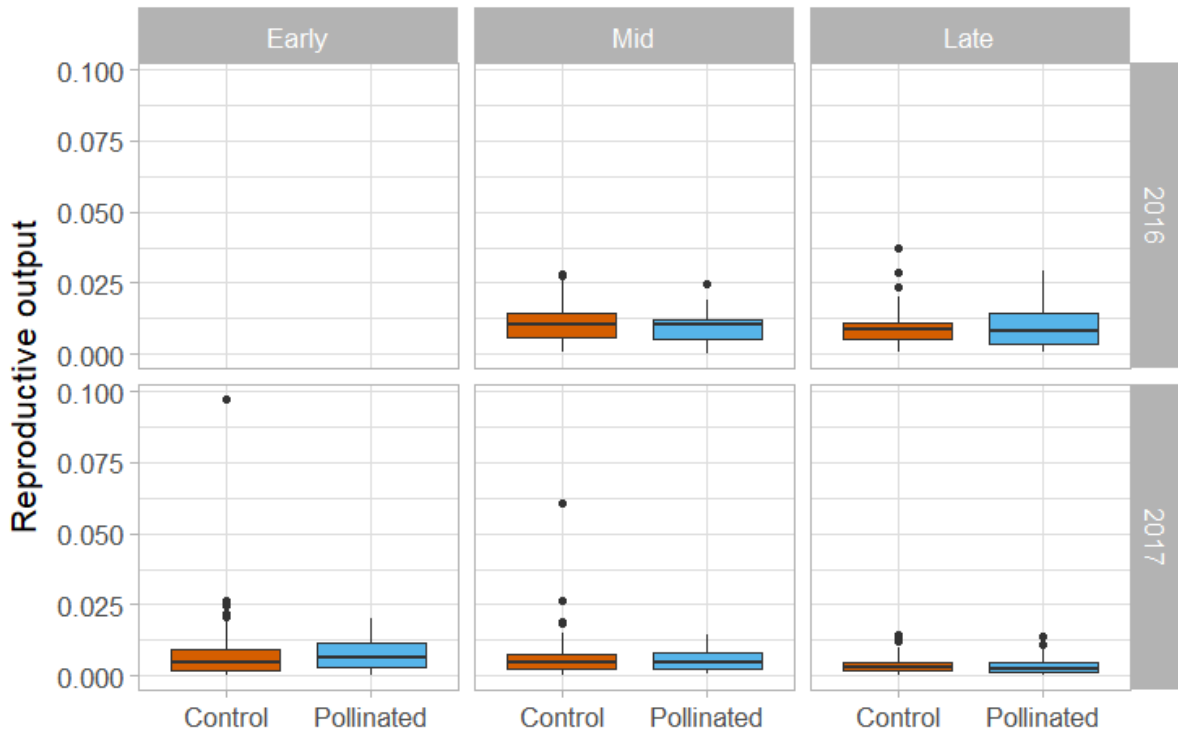


Figure 5. Reproductive output (total mass of achenes per flower head in grams; y-axis) by treatment (control = red, and hand-pollinated = blue; x-axis) for each snowmelt stage (vertical; early, mid, and late) and year (horizontal). (No data for early sites from 2016.)

Growing season temperature and precipitation

The only significant difference in reproductive output was in the late stage of 2017, thus comparisons of cumulative temperature and precipitation were done between snowmelt stages of this year. The daily mean cumulative temperature (summarised daily mean temperature above 0°C) for the duration of first flower to peak flowering of each snowmelt stage did not vary significantly between stages, but precipitation was significantly higher for the mid stage than for the early and late stages ($P = 0.009$; Figure 6).

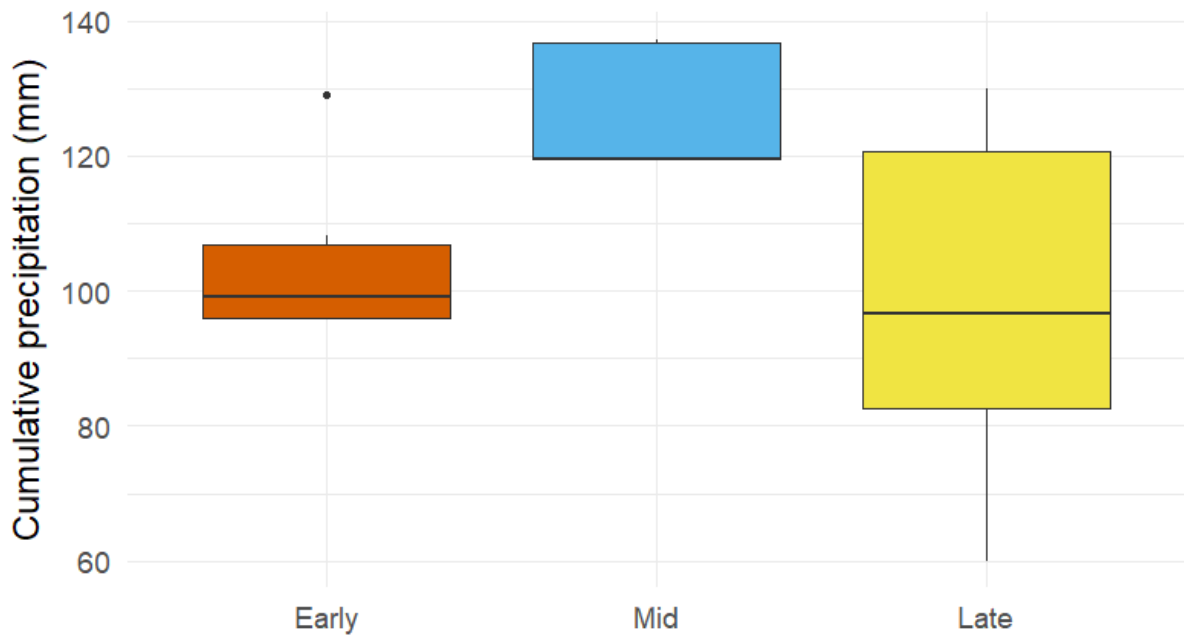


Figure 6. Cumulative precipitation for the duration from first flower to peak flowering for each snowmelt stage (early, mid, late), with the mid stage having significantly more precipitation.

Discussion

Plant-pollinator mismatch

In an alpine environment, I expected to see a mismatch in early and/or late flowering individuals of the pollinator-generalist *R. acris*. In this study, I found no mismatch and peak flowering and pollinator activity of *R. acris* did not differ significantly from each other at any of the sites (Figure 3). Although peak flowering and peak pollinator activity was not perfectly synchronised in most sites, the time of overlap between flowering and pollinator activity was long enough that it should ensure the occurrence of plant-pollinator interactions. When looking at flowering and pollinator activity by snowmelt stage, all three stages were well synchronised and there is no apparent difference between patches with early and late snowmelt (Figure 4a). This suggests that *R. acris* and its pollinators respond similarly to snowmelt. Although this was not what I initially expected, the results support previous predictions about mismatch being less of a threat to generalist species (Biesmeijer *et al.*, 2006; Hegland *et al.*, 2009; Memmott *et al.*, 2004; Miller-Rushing *et al.*, 2010) and with documented observations for a generalist species in a sub-alpine environment (Gezon *et al.*, 2016).

The first observed plant-pollinator interactions occurred six days after the first flower within the study sites in 2016 and 16 days after the first flower in 2017 (Table I, Appendix A). Although this could suggest that the first flowers appear before pollinators emerge, it is likely that some *R. acris*-pollinating insects were already active before the first *R. acris* flowers, as other plant species, mainly *Saxifraga oppositifolia* L. and a few *Silene acaulis* (L.) Jacq., started flowering before *R. acris* (personal observation). Although these species have pink/purple inflorescences, which are likely to attract other pollinating flies than the yellow inflorescence of *R. acris* (Willmer, 2011), previous studies on Mount Sanddalsnuten have showed that at least *S. acaulis* share several pollinator species with *R. acris* (Totland, 1993).

Pollinator visitation rate

The pollinator visitation rate did not change significantly throughout the season. Although not significant, all three snowmelt stages in 2017 had a trend of declining visitation rate around the time that flowering peaked, before increasing again (Figure 4). Previous pollinator studies on *R. acris* at Mount Sanddalsnuten also found that early-flowering individuals had a higher pollinator visitation rate than those at peak flowering (Totland, 1994b). Pollinator visitation

rate decreasing in parallel with increasing flower abundance could be explained by increased intra-specific competition for pollinators: higher abundance of *R. acris* flowers give pollinators a choice of which flowers to visit (Alarcón *et al.*, 2008) The trend of visitation rate increasing again after peak flowering (Figure 4) coincides with declining flower abundance, thereby decreasing the intra-specific competition.

Visitation rate was lower for sub-populations of the late stage of 2017 (i.e. less pollinator interactions per flower) than in the two earlier stages (Figure 4b), which can be explained by the emergence of the late-flowering species *Leontodon autumnalis* L. This species has previously been shown to start flowering towards the end of the growing season on Mount Sanddalsnuten (Totland, 1993), and started flowering at approximately the same time as individuals of *R. acris* in the late stages of 2017 (personal observation). Populations of *L. autumnalis* and *R. acris* on Mount Sanddalsnuten have been documented to share up to 14 pollinator species (Totland, 1993). Although intra-specific competition for pollinators might decrease late in the growing season, inter-specific competition may arise and decrease pollinator visits in late-flowering sub-populations of *R. acris*. The sites in this study were selected to have high abundance of *R. acris* individuals to ensure sufficient data on flowering and pollinator visits. Areas with high abundances of flowers will attract more insects than areas with lower abundances (Willmer, 2011), which would result in lower visitation rates and possibly other plant-pollinator interaction trends.

In 2016, the pollinator visitation rate did not decline for sub-populations of the late snowmelt stage. One explanation for this could be that the abundance of *R. acris* flowers was lower in 2016. Pollinator species may change their interaction patterns with plants from year to year, depending on flower abundance (Alarcón *et al.*, 2008), which could change competition patterns with *L. autumnalis*. In addition to competition, abiotic factors affect pollinator activity (Kevan & Baker, 1983). Low temperatures, high wind speed, and high amounts of precipitation will all cause a lower visitation activity to *R. acris* (Totland, 1994a). Climate data in this study does not provide a clear explanation for why there was a lower visitation rate for the late stage in 2017 and not in 2016, but it is worth noting that measurements were retrieved from a weather station a couple of kilometres south-west of the study location. More precise measurements from within the sites may have provided clearer differences, as microclimate is very important in this habitat.

Plant reproductive output

The hand-pollination treatment showed that achene mass of *R. acris* was not pollen limited in either of the years (Figure 5). This contradicts results of experimental hand-pollination on *R. acris* from previous studies, which has shown that supplementary pollen increases both seed mass (Totland, 1997) and achene mass (Hegland & Totland, 2007). However, Totland (1997) did show that reproduction in terms of seed to ovule ratio was not limited by pollen in alpine populations of *R. acris*. My results suggest that current plant-pollinator interactions are sufficient for pollinating *R. acris*, and support the absence of any plant-pollinator mismatch.

Late-stage individuals of 2017 had a significantly lower reproductive output than early- and mid-stage individuals, with achenes of many individuals failing to mature. This is in agreement with Totland's (1994b) observations of decreasing seed production in *R. acris* during a growing season and lack of seed production in late-flowering individuals. Similarly, studies on *Ranunculus adoneus* performed along a snowmelt gradient also show lower seed size in late-flowering individuals (Galen & Stanton, 1991). Both of these studies explain this with changes in abiotic factors, such as increasing number of days with precipitation throughout the season (Totland, 1994b). The late stage of 2017 did not receive higher amounts of precipitation during the period from first flower to peak flowering than previous stages (Figure 6), but the majority of days during the late stage flowering peak (peak \pm 10 days) had precipitation, some of them relatively heavy (up to 19.8 mm; Table III, Appendix C). Precipitation could potentially damage both pollen and anthers (Corbet, 1990), which could explain why seeds failed to mature. Galen and Stanton (1991) argues that the reduced seed size in late-flowering individuals is caused by the fact that they have less time available to grow big before they mature, which could also explain the lower reproductive output in late-stage individuals in 2017. Later-melting sites have also been noted to have less available resources (i.e. organic content, water content, nitrogen, phosphorus; Stanton *et al.*, 1994), which could also have reduced reproductive ability.

It is worth noting that both reproductive output and pollinator visitation rate were significantly different only in the late stage in 2017, both being lower than in earlier stages. Although results of reproductive output from hand-pollinated and control individuals indicate no pollen limitation, these results can be questioned for late-stage individuals of 2017. The majority of hand-pollination of late-stage individuals was performed on wet flowers, due to continuous days of unfavourable weather. This may have prevented the stigmata being receptive to the pollen (Corbet, 1990), resulting in similar reproductive outputs between hand

pollinated and naturally pollinated individuals. In which case, individuals of the late stage may have in fact been pollen limited, and the lower pollinator visitation rate caused a lower reproductive output. This resonates with previous findings of late-flowering individuals of *R. acris* being more pollen limited due to lower insect activity (Totland, 1997), and with the fact that mid and late stages of 2016 did not differ in pollinator visitation rates or in reproductive output.

Implications for future plant-pollinator interactions in a warming alpine environment

The lower pollinator visitation rate and plant reproductive output in late-flowering individuals in 2017 suggest that it is more beneficial to flower early in the season, as is also argued in previous studies of *R. acris* (Totland, 1997). Although early flowering might give higher reproductive output, there are risks of frost damage (Gezon *et al.*, 2016; Inouye, 2008; Thomson, 2010), but no signs of this was observed in 2016 or 2017. If earlier flowering is favoured, earlier snowmelt in the future should be of no consequence to *R. acris*. However, later snowmelt due to increased winter precipitation as snow in alpine regions can also lead to unchanged, or even delayed, phenology (Inouye & Wielgolaski, 2013). In western Norway, where Finse is located, more winter precipitation is expected (NCCS, 2015), which may be detrimental for *R. acris* if it leads to later flowering.

The higher potential for pollinator interactions in early-flowering species does not necessarily mean that late-flowering individuals are at risk of not being pollinated. The large variety of potential pollinators for a pollinator-generalist increases the likelihood for interactions to occur for individuals flowering at any time of the season (Miller-Rushing, *et al.*, 2010). In addition, the alpine environment which initially was suggested to be a threat to plant-pollinator interactions due to the stronger effects of climate change (IPCC, 2014), might actually increase populations' and/or communities' resistance and resilience to climate change because of its heterogeneous landscape (Graae *et al.*, 2017).

Graae *et al.* (2017) suggest that future species distribution and community responses to climate change depend on the topography of the landscape in which the communities exist, because populations in more patchy landscapes will have experienced selective pressures that have left them with increased resistance and resilience to climatic changes. In the same way, I suggest that an alpine heterogeneous landscape could confer resistance to plant-pollinator mismatches. The natural snowmelt gradients in alpine landscapes create patches with different

onsets and peaks of flowering (Kudo, 1993; Kudo & Hirao, 2006; Stanton *et al.*, 1994). These patches occur close together, which means that it is easy for insects to find patches with flowers, and such patches will be available for the insects during the entire growing season. In support of this hypothesis, the constancy of pollinator visitation rate seen in this study suggests that the pollinator activity in the landscape may be tracking microscale heterogeneity to focus on the patches of highest flower abundance at any particular time in the season. In this way, the heterogeneity of the landscape acts as an insurance to maximise pollination for the flowers and flower availability for the insects. This implies that a heterogeneous landscape secures plant-pollinator interactions, and that potential climate change-driven changes in snowmelt time may not have a great impact on plant-pollinator interactions.

To conclude, this study suggests that the chosen pollinator-generalist species, *Ranunculus acris*, is not threatened by a plant-pollinator mismatch despite alpine regions warming rapidly. This may be extended to the alpine flora in general, as most alpine plant species are pollinator-generalists that flower throughout most parts of the growing season. It also suggests that the patchy landscape acts as a buffer against any plant-pollinator mismatch. However, specialist and short-flowering plant species that are more dependent on specific pollinators or total plant-pollinator synchrony are not protected from mismatch by the landscape heterogeneity in the same way.

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Appendix A – Time of snowmelt, first flowers and pollinators

Table I. Time of snowmelt, first flower and first observed pollinator (given as day of the year) at each site for both years (2016 had no sites for the early stage).

| Site ID | Snow free | | First flower | | First pollinator | |
|---------|-----------|------|--------------|------|------------------|------|
| | 2016 | 2017 | 2016 | 2017 | 2016 | 2017 |
| E 01 | - | 140 | - | 162 | - | 168 |
| E 02 | - | 140 | - | 168 | - | 168 |
| E 03 | - | 150 | - | 164 | - | 168 |
| E 04 | - | 150 | - | 166 | - | 168 |
| E 05 | - | 150 | - | 162 | - | 168 |
| E 06 | - | 154 | - | 179 | - | 181 |
| E 07 | - | 140 | - | 164 | - | 168 |
| E 08 | - | 140 | - | 166 | - | 168 |
| M 01 | 169 | 161 | 179 | 179 | 186 | 178 |
| M 02 | 169 | 161 | 169 | 179 | 187 | 181 |
| M 03 | 169 | 161 | 169 | 179 | 175 | 179 |
| M 04 | 169 | 162 | 178 | 186 | 187 | 185 |
| M 05 | 169 | 161 | 179 | 175 | 186 | 172 |
| M 06 | 169 | 161 | 178 | 181 | 175 | 178 |
| M 07 | 169 | 161 | 181 | 184 | 186 | 179 |
| M 08 | 169 | 161 | 169 | 179 | 175 | 178 |
| M 09 | 169 | 171 | 173 | 188 | 175 | 191 |
| M 10 | 169 | 171 | 178 | 188 | 186 | 195 |
| L 01 | 186 | 162 | 197 | 184 | 202 | 185 |
| L 02 | 186 | 172 | 197 | 186 | 202 | 185 |
| L 03 | 186 | 167 | 192 | 186 | 197 | 186 |
| L 04 | 186 | 172 | 197 | 192 | 202 | 185 |
| L 05 | 186 | 162 | 192 | 184 | 202 | 186 |
| L 06 | 186 | 167 | 195 | 184 | 200 | 179 |
| L 07 | 186 | 172 | 201 | 188 | 202 | 191 |
| L 08 | 186 | 170 | 192 | 184 | 197 | 186 |
| L 09 | 186 | 175 | 186 | 188 | 196 | 195 |
| L 10 | 186 | 178 | 192 | 196 | 197 | 195 |

Appendix B – Additional site information

Table II. Site sizes, measured in square meters.

| Site ID | Size (m ²) |
|---------|------------------------|
| E 01 | 15.75 |
| E 02 | 10.0 |
| E 03 | 15.0 |
| E 04 | 10.0 |
| E 05 | 15.0 |
| E 06 | 13.5 |
| E 07 | 8.0 |
| E 08 | 18.0 |
| M 01 | 22.5 |
| M 02 | 29.75 |
| M 03 | 24.0 |
| M 04 | 17.5 |
| M 05 | 15.0 |
| M 06 | 30.0 |
| M 07 | 24.0 |
| M 08 | 22.5 |
| M 09 | 24.0 |
| M 10 | 21.0 |
| L 01 | 28.0 |
| L 02 | 73.5 |
| L 03 | 18.0 |
| L 04 | 18.0 |
| L 05 | 24.5 |
| L 06 | 110.5 |
| L 07 | 28.0 |
| L 08 | 28.0 |
| L 09 | 59.5 |
| L 10 | 88.0 |

Appendix C – Temperature and precipitation

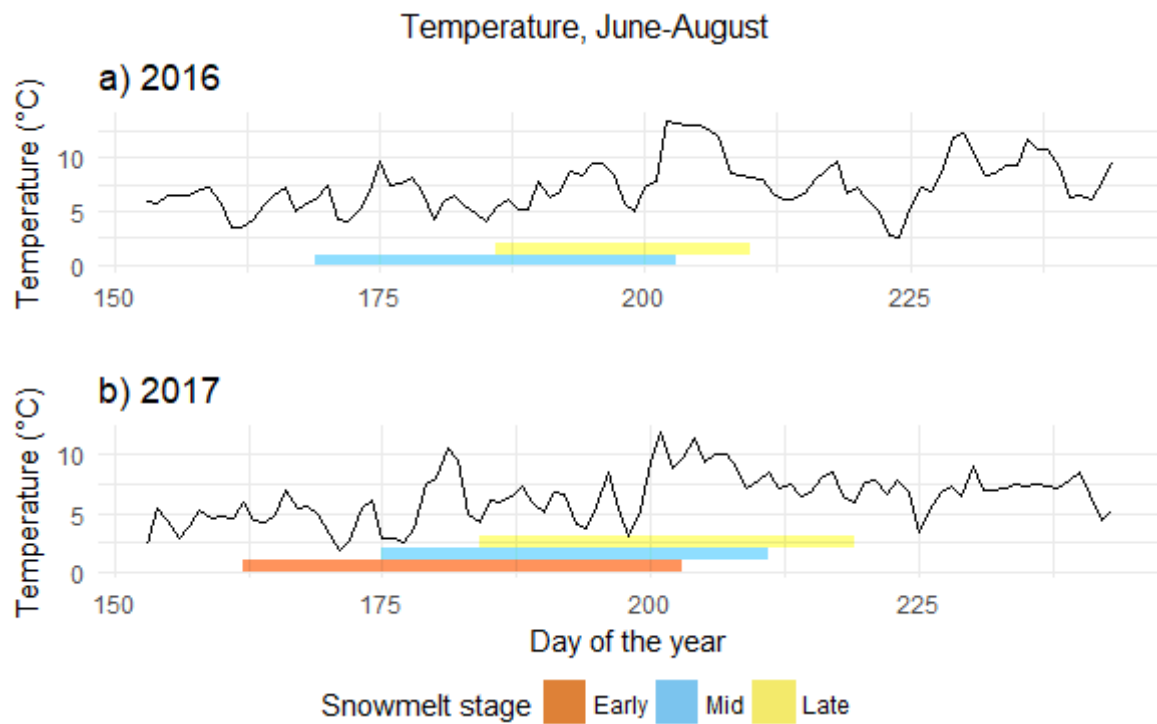


Figure I. Daily mean temperature (1 June–31 August), with the duration from first flower to peak flowering for each snowmelt stage marked (early = red, mid = yellow, late = blue) for **a)** 2016, and **b)** 2017.

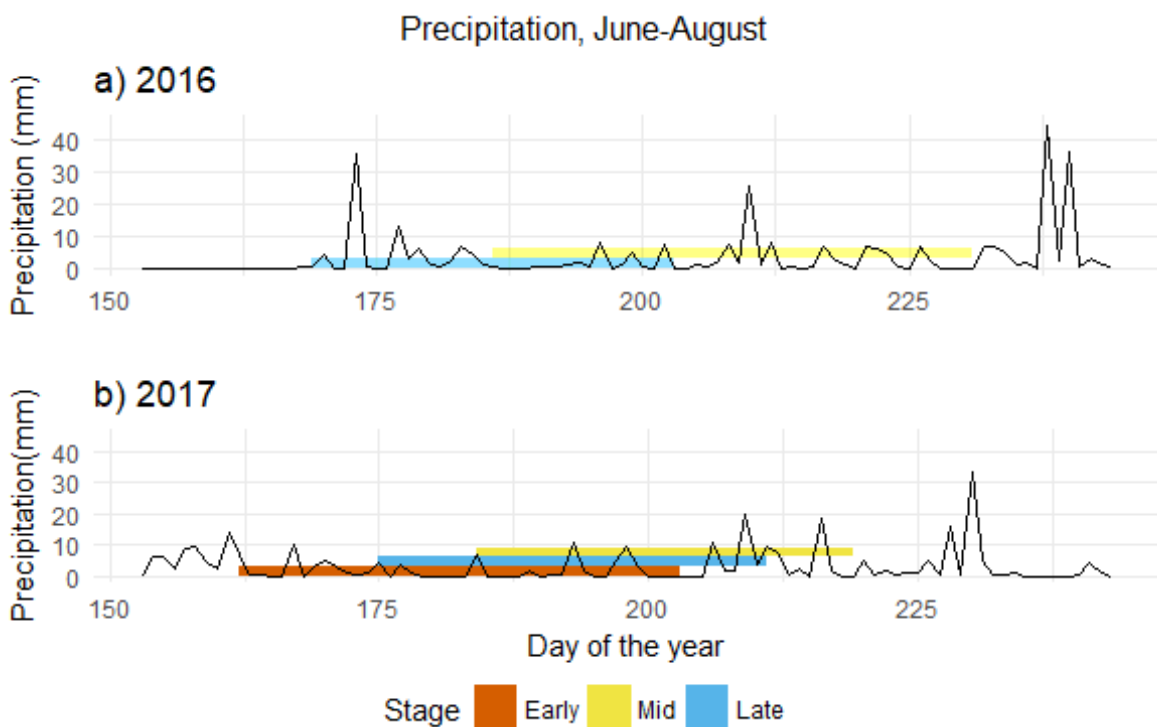


Figure II. Daily precipitation (1 June–31 August), with the duration from first flower to peak flowering for each snowmelt stage marked (early = red, mid = yellow, late = blue) for **a)** 2016, and **b)** 2017.

Table III. Daily mean temperatures and precipitation, June–August 2016 and 2017

| Date | Daily mean temperature (°C) | | Daily mean precipitation (mm) | |
|-------|-----------------------------|------|-------------------------------|------|
| | 2016 | 2017 | 2016 | 2017 |
| 01.06 | 5.9 | 1.1 | 0 | 0.8 |
| 02.06 | 5.7 | 2.3 | 0.1 | 0 |
| 03.06 | 6.4 | 5.4 | 0 | 6.2 |
| 04.06 | 6.5 | 4.4 | 0 | 6.4 |
| 05.06 | 6.4 | 2.8 | 0 | 2.3 |
| 06.06 | 7 | 3.9 | 0.1 | 9.2 |
| 07.06 | 7.2 | 5.2 | 0 | 9.8 |
| 08.06 | 5.7 | 4.5 | 0 | 4.1 |
| 09.06 | 3.5 | 4.8 | 0 | 2.6 |
| 10.06 | 3.6 | 4.6 | 0 | 14.3 |
| 11.06 | 4.3 | 5.9 | 0 | 7.1 |
| 12.06 | 5.6 | 4.4 | 0 | 0.4 |
| 13.06 | 6.5 | 4.2 | 0 | 0.5 |
| 14.06 | 7.2 | 5 | 0 | 0 |
| 15.06 | 5 | 6.9 | 0 | 0 |
| 16.06 | 5.7 | 5.4 | 0.7 | 10.3 |
| 17.06 | 6.1 | 5.6 | 0.7 | 0 |
| 18.06 | 7.5 | 5 | 4.2 | 3.3 |
| 19.06 | 4.2 | 3.2 | 0 | 4.9 |
| 20.06 | 4.1 | 1.8 | 0 | 3.3 |
| 21.06 | 5.1 | 2.7 | 35.2 | 1.2 |
| 22.06 | 6.9 | 5.4 | 0.5 | 0.2 |
| 23.06 | 9.7 | 6.2 | 0.1 | 1.2 |
| 24.06 | 7.5 | 2.9 | 0 | 4.2 |
| 25.06 | 7.6 | 2.8 | 12.9 | 0.1 |
| 26.06 | 8.2 | 2.5 | 3 | 3.8 |
| 27.06 | 6.8 | 3.8 | 6.3 | 1.3 |
| 28.06 | 4.3 | 7.5 | 0.9 | 0 |
| 29.06 | 6 | 8 | 0.3 | 0 |
| 30.06 | 6.4 | 10.5 | 2.6 | 0 |
| 01.07 | 5.5 | 9.5 | 6.7 | 0 |
| 02.07 | 4.9 | 5 | 4.2 | 0.1 |
| 03.07 | 4 | 4.2 | 1.2 | 6.8 |
| 04.07 | 5.3 | 6.1 | 0.4 | 0 |
| 05.07 | 6.1 | 6 | 0 | 0 |
| 06.07 | 5.1 | 6.5 | 0 | 0 |
| 07.07 | 5.1 | 7.3 | 0 | 0 |
| 08.07 | 7.7 | 6 | 0.5 | 1.8 |
| 09.07 | 6.3 | 5.1 | 0.3 | 0 |
| 10.07 | 6.9 | 6.8 | 0.8 | 0.5 |
| 11.07 | 8.7 | 6.7 | 1.4 | 0.5 |
| 12.07 | 8.4 | 4 | 2 | 10.8 |
| 13.07 | 9.5 | 3.8 | 0.5 | 1.5 |
| 14.07 | 9.4 | 5.6 | 8.2 | 0 |

| | | | | |
|-------|------|------|------|------|
| 15.07 | 8.3 | 8.6 | 0 | 0 |
| 16.07 | 5.8 | 5.5 | 1.1 | 5 |
| 17.07 | 5 | 3 | 4.8 | 9.6 |
| 18.07 | 7.3 | 5.3 | 0.7 | 3.2 |
| 19.07 | 7.7 | 9.3 | 0 | 0 |
| 20.07 | 13.4 | 11.9 | 7.4 | 0 |
| 21.07 | 13.1 | 8.8 | 0.2 | 0 |
| 22.07 | 13 | 9.7 | 0.1 | 0 |
| 23.07 | 12.9 | 11.5 | 1.2 | 0 |
| 24.07 | 12.6 | 9.4 | 0.3 | 0 |
| 25.07 | 11.9 | 10 | 1.9 | 10.8 |
| 26.07 | 8.6 | 10.1 | 7.3 | 1.5 |
| 27.07 | 8.3 | 8.9 | 1.9 | 1.9 |
| 28.07 | 8.2 | 7.1 | 25.8 | 19.8 |
| 29.07 | 8 | 7.8 | 0.9 | 3.8 |
| 30.07 | 6.7 | 8.5 | 7.8 | 9.6 |
| 31.07 | 6.2 | 7.1 | 0 | 7.8 |
| 01.08 | 6.2 | 7.5 | 0.8 | 0.2 |
| 02.08 | 6.7 | 6.5 | 0.1 | 2.4 |
| 03.08 | 8 | 6.8 | 0.8 | 0.1 |
| 04.08 | 8.7 | 8.2 | 7.1 | 18.7 |
| 05.08 | 9.6 | 8.6 | 2.3 | 1.5 |
| 06.08 | 6.6 | 6.4 | 0.9 | 0 |
| 07.08 | 7.3 | 5.9 | 0.1 | 0 |
| 08.08 | 6.2 | 7.7 | 6.9 | 5.3 |
| 09.08 | 5 | 7.9 | 6.3 | 0.4 |
| 10.08 | 2.7 | 6.7 | 4.1 | 1.6 |
| 11.08 | 2.5 | 7.8 | 0.5 | 0.2 |
| 12.08 | 5.5 | 6.8 | 0.1 | 1.2 |
| 13.08 | 7.2 | 3.4 | 7 | 0.9 |
| 14.08 | 6.8 | 5.3 | 2.2 | 4.7 |
| 15.08 | 8.6 | 6.8 | 0.2 | 0.5 |
| 16.08 | 11.9 | 7.3 | 0 | 16 |
| 17.08 | 12.3 | 6.4 | 0 | 0.3 |
| 18.08 | 10.6 | 9.1 | 0 | 33.8 |
| 19.08 | 8.4 | 6.9 | 6.8 | 5 |
| 20.08 | 8.6 | 7 | 6.7 | 0.7 |
| 21.08 | 9.3 | 7.1 | 4.9 | 0.2 |
| 22.08 | 9.3 | 7.5 | 1 | 1.2 |
| 23.08 | 11.6 | 7.3 | 1.7 | 0 |
| 24.08 | 10.8 | 7.5 | 0 | 0 |
| 25.08 | 10.8 | 7.4 | 44.2 | 0 |
| 26.08 | 9.1 | 7.2 | 2.4 | 0.1 |
| 27.08 | 6.3 | 7.9 | 36.3 | 0 |
| 28.08 | 6.5 | 8.6 | 0.7 | 0.3 |
| 29.08 | 6.1 | 6.6 | 2.9 | 4.1 |
| 30.08 | 7.6 | 4.4 | 0.9 | 1.3 |
| 31.08 | 9.5 | 5.3 | 0.8 | 0.1 |