Variations in reproductive output in alpine populations of Ranunculus acris

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Abstract

Plant reproduction is affected both directly by small-scale abiotic heterogeneity in the alpine topography (abiotic), and indirectly through flower density and plant-pollinator interactions (biotic). In this study we investigated how different abiotic and biotic factors influence reproductive output in alpine populations of *Ranunculus acris* over a two-year period. We used ten snowmelt gradients in an alpine area at Finse, southern Norway, where each gradient contained three stages representing three different times of snowmelt. Reproductive output, measured as both seed mass and number of seeds, in alpine *R. acris* was affected by different factors, varying between years and timing of snowmelt. Higher temperatures during seed maturation resulted in higher reproductive output in both years, with a lower output later in the growing season. We also found a negative correlation between seed mass and *R. acris* density in the surrounding vegetation in the second year, when flower density was substantially higher than in the first year. We found no signs of pollen limitation, suggesting that pollinators did not limit reproductive output. Our study shows that reproductive output in *R. acris* is affected by both abiotic and biotic factors, and since timing and length of the flowering period in alpine environments are expected to change due to climate change, this could have further implications for plants in this study system.

Introduction

Alpine habitats are characterized by low temperatures, strong winds, short growing seasons and heterogenous topography (Körner, 2003), which makes reproduction via seeds challenging. The heterogenous topography creates a mosaic of microhabitats with abiotic and biotic conditions changing within a few meters (Körner, 2003), such as a variation in snow cover, length of the growing season (Litaor et al., 2008) and start of the flowering season (Dunne et al., 2003). This creates a landscape with large spatial variation in the timing of pollinator emergence (Bale & Hayward, 2010), and seed maturation (Totland, 1993). Alpine plants are well adapted to reproduce under harsh conditions (Körner, 2003), however with ongoing and expected climate change (IPCC, 2023), abiotic and biotic conditions are changing and the challenges put on plants' sexual reproduction are increasing. An understanding of the most important factors influencing reproductive output in alpine plants are therefore essential (Roos et al., 2022).

Temperature before the growing season have a large impact on timing of snowmelt, determining when plants can start to flower, the length of the growing season, and ultimately time available for seed maturation (Rixen et al., 2022). Plants flowering early in the growing season will have more time for seed maturation (Huelber et al., 2006), however, flowering early can also be disadvantageous, as the beginning of the growing season often have more unstable temperatures (Wipf et al., 2006), and frost events are common (Inouye, 2008). For late emerging plants, the growing season is shorter (Huelber et al., 2006; Kudo & Suzuki, 1999), but temperatures are often higher when plants emerge, allowing for a shorter pre-flowering period (Delnevo et al., 2018) and higher reproductive success (Klady et al., 2011). In addition to temperature, attracting enough pollinators is important, species flowering at the same time tend to attract

the same pollinators (Totland, 1993), however this is scale specific (Hegland, 2014), and can also vary among microhabitats (Choler et al., 2001).

To understand how climate change affects alpine plant reproduction we need long term monitoring (CaraDonna et al., 2014), or experimental approaches (Wipf et al., 2006). Natural environmental gradients can be used as a space-for-time substitution (Pickett, 1989), to make predictions for long-term consequences of human induced climate change on plant populations and communities (Blois et al., 2013; Dunne et al., 2004; Fukami & Wardle, 2005). In alpine regions, a common approach is to use the heterogeneity of the landscape as natural gradients (Dunne et al., 2004), where plants are exposed to different timing of snowmelt, environmental and biotic conditions, reflecting the projected future of a changing climate (Stanton et al., 1994). The aim of this study is to identify what factors affect the reproductive output in *Ranunculus acris* L. in an alpine habitat in southern Norway. For this we used snowmelt gradients exposing plants to different abiotic and biotic factors. Along these gradients we registered timing of snowmelt and collected temperature recordings, in addition we registered phenology, and conducted a hand pollination study. Reproductive output per plant was measured as seed mass and number of seeds. We predict that (1) abiotic factors are important for *R. acris* reproductive output throughout the whole growing season, this because higher temperatures speed up seed maturation enabling the plant to produce more and larger seeds (Totland, 1999). And we (2) expect biotic factors to be more important for plants emerging later in the season, due to higher number of flowering *R. acris* individuals, increasing competition for pollinators (Totland, 1994).

Material and methods

Study area and study species

The study was conducted over two growing seasons (2016 and 2017) at Mount Sanddalsnuten (60.6136 °N, 7.5213 °E), near Finse in southwestern Norway (Fig. 1). The area has an alpine-oceanic climate (Moen, 1998), with an average annual temperature of − 2.2 °C, and an average summer temperature of 6.3 °C (June - August). Annual and summer (June – August) precipitation is 990 mm and 257 mm, respectively (www.seklima.met.no).

The study area is situated in the mid-alpine zone, between 1411 and 1489 m a.s.l., in a south-west facing slope. The growing season is short, and snowmelt normally starts in late May, with the whole mountain slope being free of snow by mid-July. As the bedrock is dominated by calcareous phyllite, it supports a species-rich heath community, where common species are *Dryas octopetala, Bartsia alpina, Bistorta vivipara, Thalictrum alpinum* and *Ranunculus acris.* In addition to being one of the most common species, *R. acris* is also very attractive to the local pollinator community (Totland, 1993, 1994), it spreads only by seeds and has been shown to be self-incompatible in alpine areas (Totland, 1994).

Study design

The heterogenous topography in the area causes the snow to melt at different times and exposes the plants naturally to different abiotic and biotic factors during the growing season. In spring 2016, we established ten study sites where *R. acris* was present and abundant. Each site was assigned one out of three snowmelt stages representing different timing of snowmelt. Due to very low seed set in the latest snowmelt stage in 2016 we discarded these sites and established eight new sites with snowmelt even earlier than the earliest sites from 2016. Our study system consequently consisted of eight sites in snowmelt stage 1, the earliest stage (sampled only in 2017), ten sites in snowmelt stage 2 (sampled approximately two weeks later and in both 2016 and 2017), ten sites in snowmelt stage 3 (sampled approximately two weeks later and in both 2016 and 2017), and ten sites in snowmelt stage 4, the latest stage (sampled approximately two weeks later in 2016; see Appendix A)

At each snowmelt stage we established five plots, resulting in 150 plots in 2016 and 140 plots in 2017. At each plot we established, and marked with metal tubes, two 0.5 x 0.5 m sub-plots, approximately 10 cm apart. The subplots were placed next to each other, where one subplot was used for a pollen supplementation experiment (see below) and the other subplot was left unmanipulated as a control.

Data collection

We obtained daily mean temperature data, from snowmelt to last seed collection in 2016 and 2017, from a local weather station (Finsevatn SN25830; 1210 m asl, 2 km south from study site) from the Norwegian Meteorological Institute (http://www.seklima.met.no/). Because the weather station was located 2-300 meters below our study sites, we adjusted the daily mean temperature at each site according to the global average adiabatic lapse rate, a 0.6 ℃ reduction in temperature per 100 meters elevation (Körner, 2003). We tested the lapse rate correction in 2016 by using temperature data from iButtons (DS1922L-F5) that were installed at each site in that year. The iButtons were placed inside a small, white, transparent fabric bag under two white plastic cones (Holden et al., 2013) and hung from a bamboo stick 0.5 m above ground, trying to prevent the logger from direct sunlight. The average temperature difference between the highest (1489 m a.s.l.) and lowest site (1411 m a.s.l.) measured by the iButtons was 0.86°C, justifying the laps rate correction. This is 0.26°C higher than expected from the global average adiabatic lapse rate and might be because the temperature from the weather station is recorded at 2 m above the ground, and thus expected to be lower compared to the iButtons closer to the ground (Graae et al., 2012).

To estimate the temperature the plants experienced during seed development, we calculated growing degree days as the sum of daily mean temperatures above 0 ℃ over the period starting when the individuals that underwent supplemental pollination had been pollinated (the average date between the first and last supplemental pollination per site) until the seeds were ripe and collected. We selected the threshold of 0 ℃ as it has been showed that most alpine plants need temperatures above 0°C to grow (Wipf et al., 2009).

To assess what effect the flowering density of *R. acris* have on reproduction, all flowering individuals within each plot were counted every other day, from 17 June to 18 August in 2016 and 11 June to 22

August in 2017. The mean number of flowering individuals per site throughout the whole flowering season was calculated and used as an estimate of flower abundance.

To test if *R. acris* was pollen limited, we marked four plants in each plot and randomly assigned a supplemental pollination treatment or left untouched for natural pollination ($n_{supplemental\ pollination}$ = 355 individuals, $n_{natural\ pollinationl}$ = 401 individuals). On one flower of the individuals receiving the supplemental pollination treatment we applied pollen from three anthers from five different individuals found in the surroundings of the plot. The treatment was applied on two different days. Most individuals only had one flower, however if two flowers were present only one of the flowers received supplemental pollination or got selected as control. In a few cases where too few *R. acris* individuals were found, individuals were selected < 0.5 m outside the plot. The first flowering individuals of *R. acris* in the plots were avoided because they are often sterile (Ø. Totland, *pers. com*). We ensured the individuals selected in each plot were in the same developmental stage, i.e., ready to receive pollen, and as a result, supplemental pollination was conducted over a longer period.

Seeds from the marked individual both years were collected and left to air dry in the lab for two to four weeks after field season had ended. In 2016 the number of seeds and ovules in each gynoecium were also counted. Reproductive output was estimated by a) the seed mass as the combined weight of all seeds and ovules from one flower (both years), and b) number of seeds and ovules produced (only in 2016).

Statistical analyses

To assess the effect different factors have on reproductive output in *R. acris* along the snowmelt gradients, we used generalized linear mixed effect models (GLMM) and linear mixed effect models (LMM) in the lme4 package (Bates et al., 2015) in R version 4.2.2 for Windows (R Core Team 2022). We fitted separate models with seed mass as response for 2016 and 2017, and one model with number of seeds as response from 2016. Timing of snowmelt (1–4), growing degree days (℃; hereinafter referred to as “temperature”), pollination treatment (supplemental pollination and control) and flower density (count) were used as fixed effects and site was included as random effect. For analyzing seed mass we used a LMM, with a normal error distribution, and homoscedasticity was achieved after log transforming the response variable. For the number of seeds we used a GLMM with a Poisson error distribution, and number of seeds plus number of ovules (total seed potential) was log transformed and added as an offset.

In all models the variable timing of snowmelt was converted to a numeric value between 1 (early) and 4 (late), because the difference in the timing of snowmelt between the stages is approximately 2 weeks. The timing of snowmelt ranges from 2–4 in 2016 and 1–3 in 2017.

Data are available on https://osf.io/gw39z/ and the code on GitHub: https://github.com/linnvassvik/Mismatch2022.

Results

Abiotic and biotic factors affect seed mass with variations between years.

The abiotic and biotic factors affecting seed mass differed between the two years of this study. Mean daily temperature was on average 1.5°C higher in 2016 than in 2017 ($P < 0.001$; Appendix B). In 2017 there were a total of 3.6 times more flowers during the whole growing season compared to 2016 ($P < 0.001$, $n_{2016} = 8451$, $n_{2017} = 30818$; Fig. 2). And seed mass was on average 1.6 times higher ($P < 0.001$) in 2016 (0.009 ± 0.006 g) compared to 2017 (0.006 ± 0.007 g) with the overall seed maturation being 32,8 days in 2016, compared to 29,1 days in 2017.

We tested whether abiotic factors are more important for seed mass during the whole growing season, compared to the biotic factors. In 2016, the timing of snowmelt had a negative impact on seed mass, meaning that seed mass decreased throughout the growing season. In 2017, seed mass increased with cumulate temperature but decreased with density of flowers (Table 1 and Fig. 3). Supplemental pollination did not affect seed mass in any of the years.

Table 1
Analysis of which abiotic (snowmelt stage and cumulative temperature) and biotic (flower density and pollination treatment) factors influence seed mass, using generalized linear mixed effect models, with the two years analyzed separately. Significant values ($P < 0.05$) are indicated in bold.

2016	**Estimate (± SE)**	**Degrees of freedom**	**t value**	***P* value**
Intercept	-4.17 ± 0.25	271	-17.02	< 0.001
Snowmelt stages	**-0.32 ± 0.08**	**24**	**-3.91**	**< 0.001**
Flower density	0.002 ± 0.09	24	0.02	0.984
Cumulative temperature	0.07 ± 0.05	271	1.42	0.157
Natural pollination	-0.08 ± 0.10	271	-0.80	0.422
2017				
Intercept	-5.09 ± 0.24	427	-21.23	< 0.001
Snowmelt stages	-0.15 ± 0.11	24	-1.27	0.216
Flower density	**-0.19 ± 0.08**	**24**	**-2.46**	**0.021**
Cumulative temperature	**0.38 ± 0.09**	**427**	**4.18**	**< 0.001**
Natural pollination	-0.02 ± 0.09	427	-0.32	0.749

We also tested whether the importance of the abiotic and biotic factors differed between the three different timing of snowmelt within the same year (Table 2). In 2016, increased cumulative temperature yielded a higher seed mass, but only for plants in the mid snowmelt stage (stage 3). Contrary, in 2017, the

cumulative temperature increased seed mass for plants with early and late timing of snowmelt (stage 1 and 3). Density of flowers had no effect on seed mass, when splitting the analysis by snowmelt stage. Supplemental pollination had no effect on seed mass in any of the snowmelt stages (Fig. 4).

Table 2
Analysis of which abiotic (snowmelt stage and cumulative temperature) and biotic (flower density and pollination treatment) factors influence seed mass, using generalized linear mixed effect models, with the different snowmelt stages and the two years analyzed separately. Significant values (P < 0.05) are indicated in bold.

2016	Estimate (± SE)	Degrees of freedom	t value	*P* value
Snowmelt stage 2				
Intercept	-4.62 ± 0.18	149	-25.43	< 0.001
Flower density	0.25 ± 0.33	8	0.76	0.472
Cumulative temperature	-0.02 ± 0.06	149	-0.25	0.799
Natural pollination	-0.15 ± 0.13	149	-1.21	0.229
Snowmelt stage 3				
Intercept	-5.16 ± 0.16	75	-32.47	< 0.001
Flower density	-0.17 ± 0.09	8	-1.91	0.092
Cumulative temperature	**0.23 ± 0.10**	**75**	**2.37**	**0.020**
Natural pollination	-0.06 ± 0.17	75	-0.33	0.739
Snowmelt stage 4				
Intercept	-5.25 ± 0.45	43	-11.69	< 0.001
Flower density	0.76 ± 0.38	5	2.03	0.098
Cumulative temperature	0.05 ± 0.36	43	0.14	0.893
Natural pollination	0.22 ± 0.27	43	0.84	0.407
2017				
Snowmelt stage 1				
Intercept	-6.06 ± 0.63	116	-9.58	< 0.001
Flower density	-1.69 ± 1.20	6	-1.41	0.209
Cumulative temperature	**0.35 ± 0.15**	**116**	**2.43**	**0.017**
Natural pollination	0.10 ± 0.20	116	0.50	0.621
Snowmelt stage 2				
Intercept	-5.44 ± 0.14	168	-38.13	< 0.001
Flower density	-0.62 ± 0.39	8	-1.60	0.149
Cumulative temperature	0.20 ± 0.20	168	0.97	0.332

2016	Estimate (± SE)	Degrees of freedom	t value	*P* value
Natural pollination	-0.03 ± 0.13	168	-0.26	0.792
Snowmelt stage 3				
Intercept	-5.47 ± 0.19	139	-28.90	< 0.001
Flower density	-0.17 ± 0.07	7	-2.27	0.058
Cumulative temperature	**0.49 ± 0.16**	**139**	**3.07**	**0.003**
Natural pollination	-0.11 ± 0.14	139	-0.78	0.434

Seed number is affected by both abiotic and biotic factors.

Testing our prediction that abiotic factors are more important also for seed number during the whole growing season was done only for 2016, as this is the only year with seed count data. Seed number was affected by both abiotic and biotic factors throughout the whole growing season. Timing of snowmelt had a negative effect on seed number, with less seeds being produced later in the growing season, while a higher cumulative temperature and a higher flower density resulted in higher seed production (Table 3 and Fig. 5). Supplemental pollination did not affect number of seeds produced. On average each individual *R. acris* flower produced 12.2 ± 8 seeds, and 10.6 ± 8 ovules, meaning a total of 55% of the gynoecium became a seed.

Table 3
Analysis of which abiotic (snowmelt stage and cumulative temperature) and biotic (flower density and pollination treatment) factors influence seed mass, with the two years analyzed separately. Significant values (P < 0.05) are indicated in bold.

2016	Estimate (± SE)	Z value	Pr(>|z|)
Intercept	-0.03 ± 0.15	-0.12	0.842
Snowmelt stages	**-0.22 ± 0.05**	**-4.12**	**< 0.001**
Flower density	**0.12 ± 0.06**	**2.02**	**0.043**
Cumulative temperature	**0.05 ± 0.02**	**2.67**	**0.008**
Natural pollination	-0.06 ± 0.03	-1.86	0.063

The factors affecting seed number changed with the different snowmelt stages. For plants in the early snowmelt stage (stage 2), higher flower density increased the number of seeds, while supplemental pollination surprisingly decreased the number of seeds (Fig. 6). Higher cumulative temperature resulted in more seeds produced in the latest snowmelt stage (stage 3). In the latest snowmelt stage (stage 4) none of the tested factors influenced seed number (Table 4).

Table 4
Analysis of which abiotic (snowmelt stage and cumulative temperature) and biotic (flower density and pollination treatment) factors influence seed number, using linear mixed effect models, with the different snowmelt stages and the two years analyzed separately. Significant values (P < 0.05) are indicated in bold.

2016	Estimate (± SE)	Z value	Pr(>|z|)
Snowmelt stage 2			
Intercept	-0.34 ± 0.08	-4.29	< 0.001
Flower density	**0.39 ± 0.16**	**2.43**	**0.015**
Cumulative temperature	0.03 ± 0.02	1.34	0.181
Natural pollination	**-0.11 ± 0.04**	**-2.59**	**0.010**
Snowmelt stage 3			
Intercept	-0.66 ± 0.07	-10.09	< 0.001
Flower density	0.04 ± 0.04	0.84	0.399
Cumulative temperature	0.07 ± 0.04	1.94	0.052
Natural pollination	0.03 ± 0.06	0.47	0.637
Snowmelt stage 4			
Intercept	-0.70 ± 0.29	-2.37	0.018
Flower density	0.49 ± 0.34	1.45	0.147
Cumulative temperature	0.16 ± 0.15	1.02	0.308
Natural pollination	-0.01 ± 0.10	-0.05	0.957

Discussion

The results from this study show that reproduction in alpine *R. acris* is affected by different abiotic and biotic factors throughout the growing season, and between years. This is partly in agreement with our predictions, however a higher temperature was also important for a higher seed mass later in the growing season, and a higher flower density increased seed number earlier in the growing season. In addition, we found no pollen limitation in any of the snowmelt stages, suggesting that pollinators were not restricting reproduction in our study system.

Temperature increased both seed mass and number, indicating that temperature is a limiting factor in this alpine system. This was also found by Totland (1999), where temperature was experimentally increased using open top chambers. A higher temperature can speed up the maturation process in plants (Totland & Birks, 1996), especially in plants like *R. acris* that have green photosynthetic achenes. In addition, we

found that temperatures effect on reproduction varied throughout the season, which could be related to the plants experiencing more benign temperatures at different periods during the growing season (Totland, 1993).

Our study site experienced frost in early august both years, damaging some of the seeds. This is contrary to what has been found in other systems, where frost events have been predicted to be more frequent early in the season (Inouye, 2008). Frost damage has also been detected previously by Totland (1997) on *R. acris* in our study area. A total of 33 individuals suffered from frost damage in our study, and individuals growing in the later snowmelt stages had the highest seed loss. This suggests that plants with seeds earlier in their developing phase are more sensitive to frost. Frost events later in the season was also found in Neuner et al. (2020), where undamaged *Leucanthemopsis alpina* individuals were only found in sheltered microhabitats.

Flowering later in the growing season also influenced seed mass and number of seeds produced. Later flowering individuals had a lower reproductive output, also found in Totland (1994), who suggested that individuals flowering later in the growing season had shorter longevity, meaning less time for pollinator visits and seed maturation. However, no pollen limitation was found throughout the whole flowering season our study, indicating that a lower seed mass and less seeds did not stem from a lack of flower visits. Previous research from the same area show contrasting results, were some find a pollen limitation on seed mass (Hegland & Totland, 2007; Totland, 1997), while others do not (Totland & Eide, 1999). However, when assessing number of seeds none of the studies found pollen limitation (Totland, 1997; Totland & Birks, 1996). This could indicate that the harsh alpine environment prevent the plant from utilizing all the supplemental pollen (Totland, 2004), and could also explain why only half of the gynoecium on *R. acris* developed into seeds in our study. We did however find a negative effect of supplemental pollination in the earliest stage. There could be several reasons for this, such as pollen crowding or stigma receptivity missed (Young & Young, 1992). Lundemo and Totland (2007) found the same in *Dryas octopetala* and suggested that due to the method being the same for all hand pollinating events, it is less likely that the hand pollination itself limited seed production, but support the fact that the species is not pollen limited.

A higher density of flowering *R. acris* in the surroundings resulted in a lower seed mass in general in 2017, this effect was not found in 2016. However, a higher density of surrounding *R. acris* individuals resulted in more seeds produced in 2016. There was almost four times as many flowering *R. acris* individuals in 2017 compared to 2016, potentially causing *R. acris* individuals in 2017 to experience a higher competition. As we found no pollen limitation for seed mass, a competition might be for resources, such as nutrients (Klanderud & Totland, 2005), rather than pollinators. *R. acris* is pollinated mainly by dipterans who tend to visit neighboring flowers (Totland, 1993, 1994), therefore a higher density could also be favorable, as we also found in 2016, when a higher density of flowers resulted in a higher seed production.

The drivers for plants reproductive output are closely linked to seasonal changes and variation in climate (Forrest & Miller-Rushing, 2010). We found both timing of snowmelt and temperature to be important factors for reproductive output in *R. acris* in our study, and even though we found no evidence for pollen limitation, it does not mean that this will continue to be the case. Increased temperatures with climate change are expected to result in changes in snow cover and spring snow melt date, where an earlier snowmelt due to warmer climate can cause a shift in species composition, favoring faster growing and taller plants (Jonas et al., 2008). Totland (1997) suggested that there is already an observable selection toward earlier emergence of *R. acris* at Finse due to a stronger increase in pollen limitation later in the season. An earlier snowmelt with no change in the frost dates can also be problematic for early flowering plants (Inouye, 2008), and this study have detected that *R. acris* reproductive output is sensitive to periods of frost.

Declarations

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The authors have no competing interests to declare.

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Figures

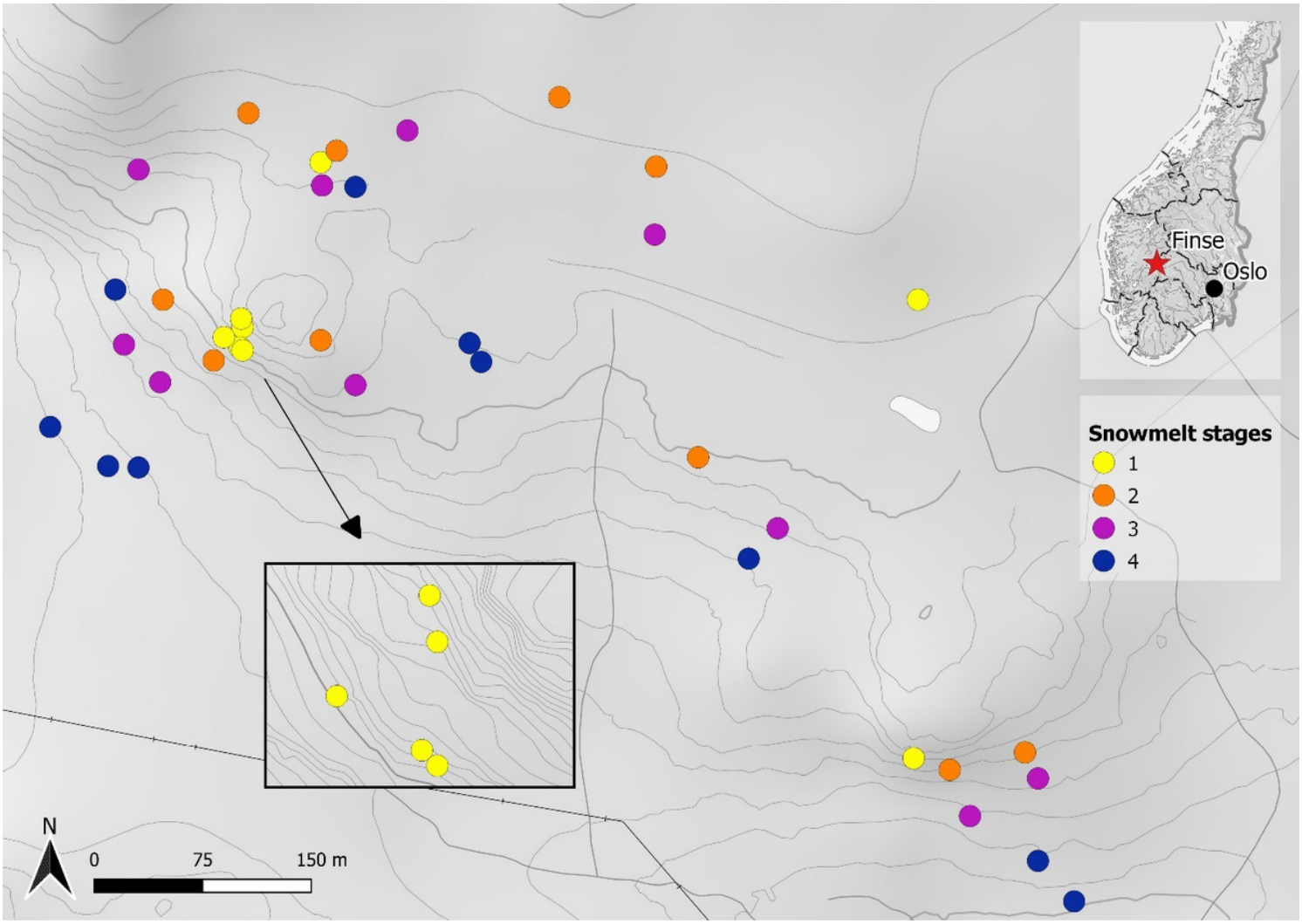

Figure 1

Map of the study area and all ten snowmelt gradients, each snowmelt gradient has four snowmelt stages, '1' being the earliest and '4' the latest snowmelt stages (referencing numerical values used in statistical analysis; see "Data Collection" for further explanation). The gradients are not located in a perfect line from lower to higher elevation due to the complex topography which defines the timing of snowmelt. Inset shows map of Southern Norway with Finse marked with a star.

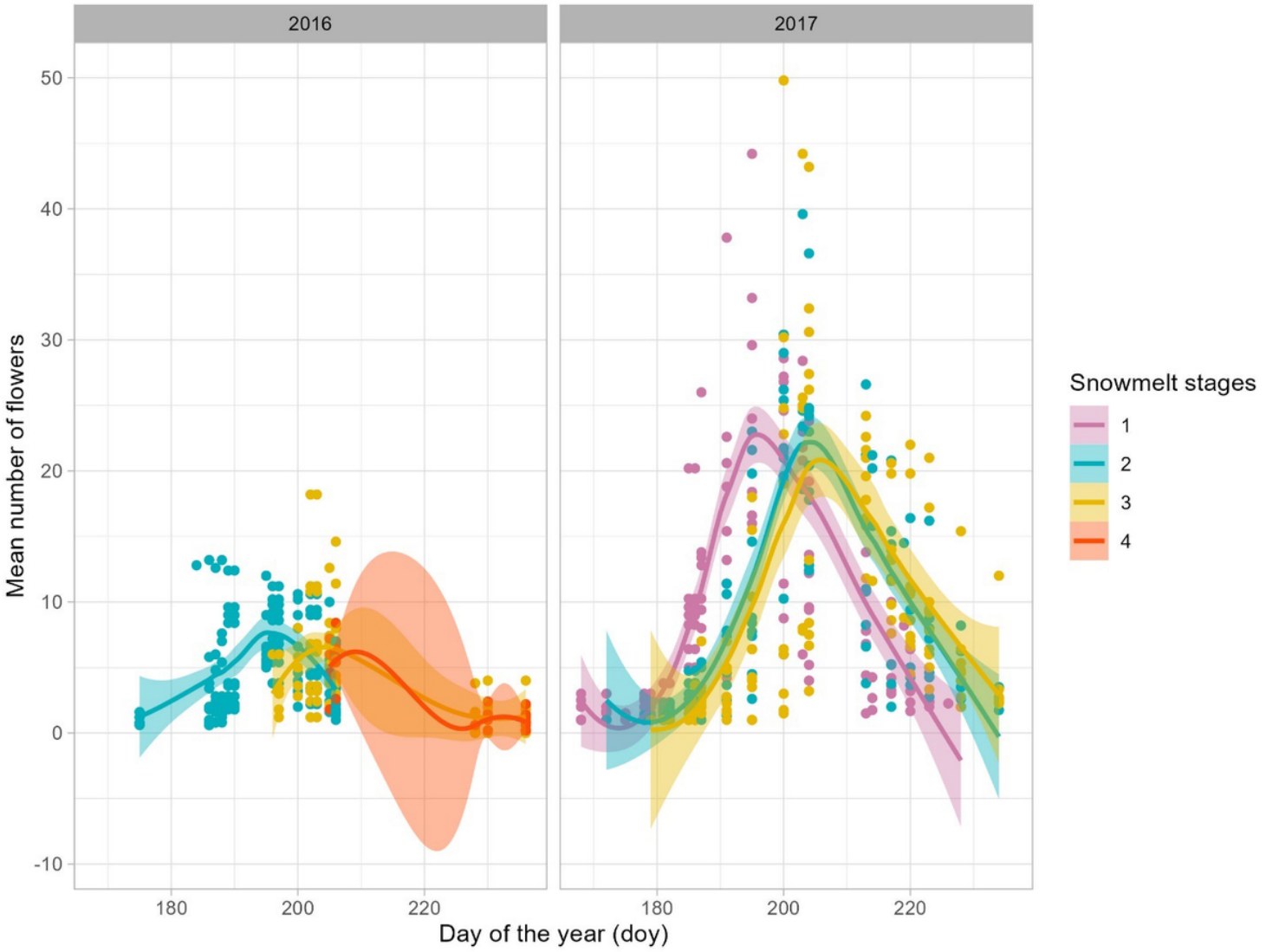

Figure 2

Number of flowers throughout the growing season at all three snowmelt stages split between the two years of the study, 2016 and 2017, at Fine, Norway. Colours represent the different snowmelt stages, with mean number of flowers per day marked with individual dots.

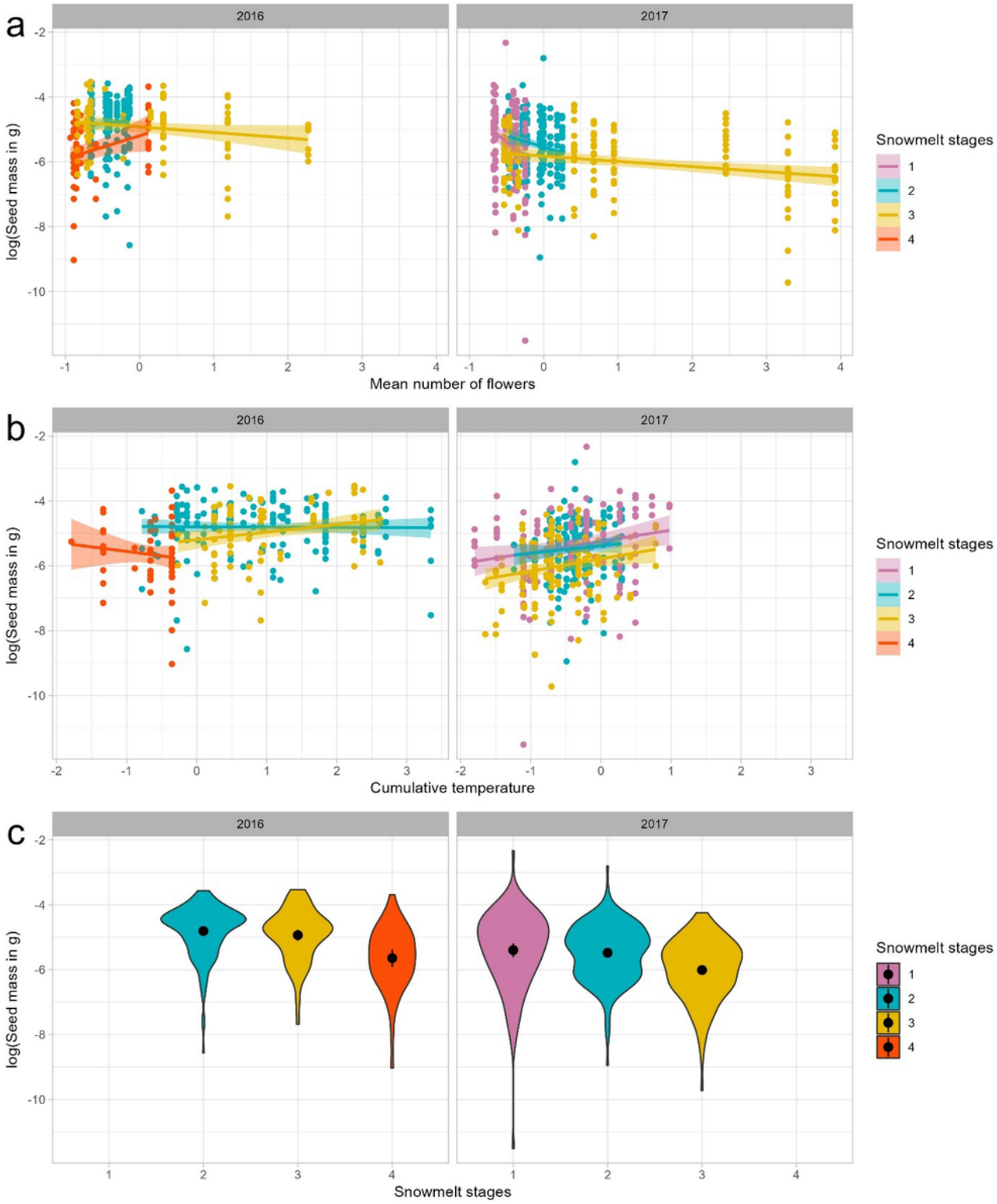

Figure 3

The relationship between seed mass (g) and **a)**mean number of flowers, **b)** cumulative temperature, and **c)** the three different snowmelt stages, split between the two years of the study, 2016 and 2017, at Finse, Norway. Colors represent the different snowmelt stages. In **a)** and **b)** the individual recordings are marked with dots, with lines fitted through linear regression. For the violin plot in **c)** the distribution is shown through the width of the violin, and standard error is added for each snowmelt stage.

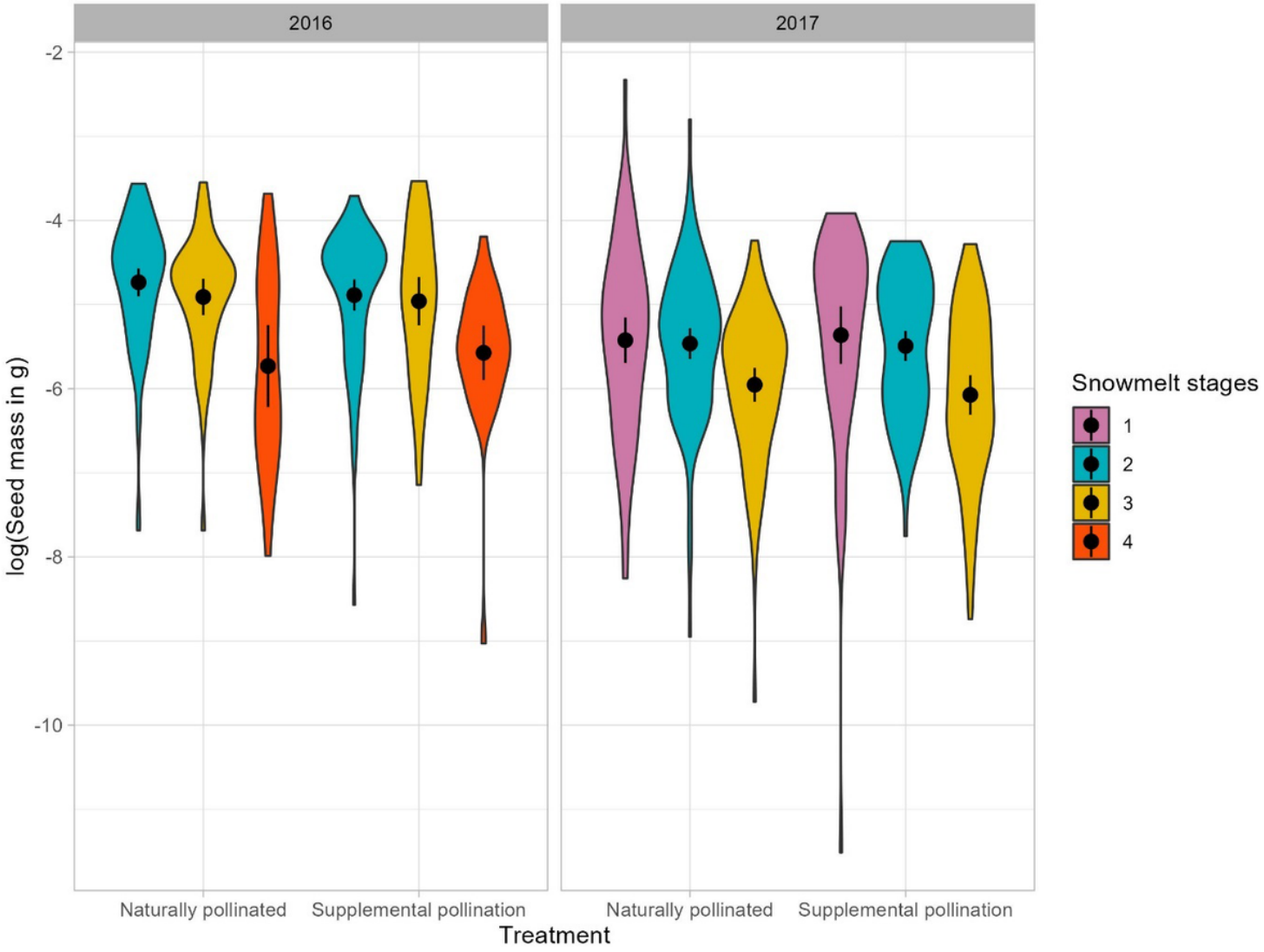

Figure 4

The relationship between seed mass (g) and the two pollination treatments, natural pollination and supplemental pollination, in three different stages of snowmelt, split between the two years of the study, 2016 and 2017, at Finse, Norway. The different colors represent the different snowmelt stages the distribution is shown through the width of the violin, and standard error is added for each snowmelt stage.

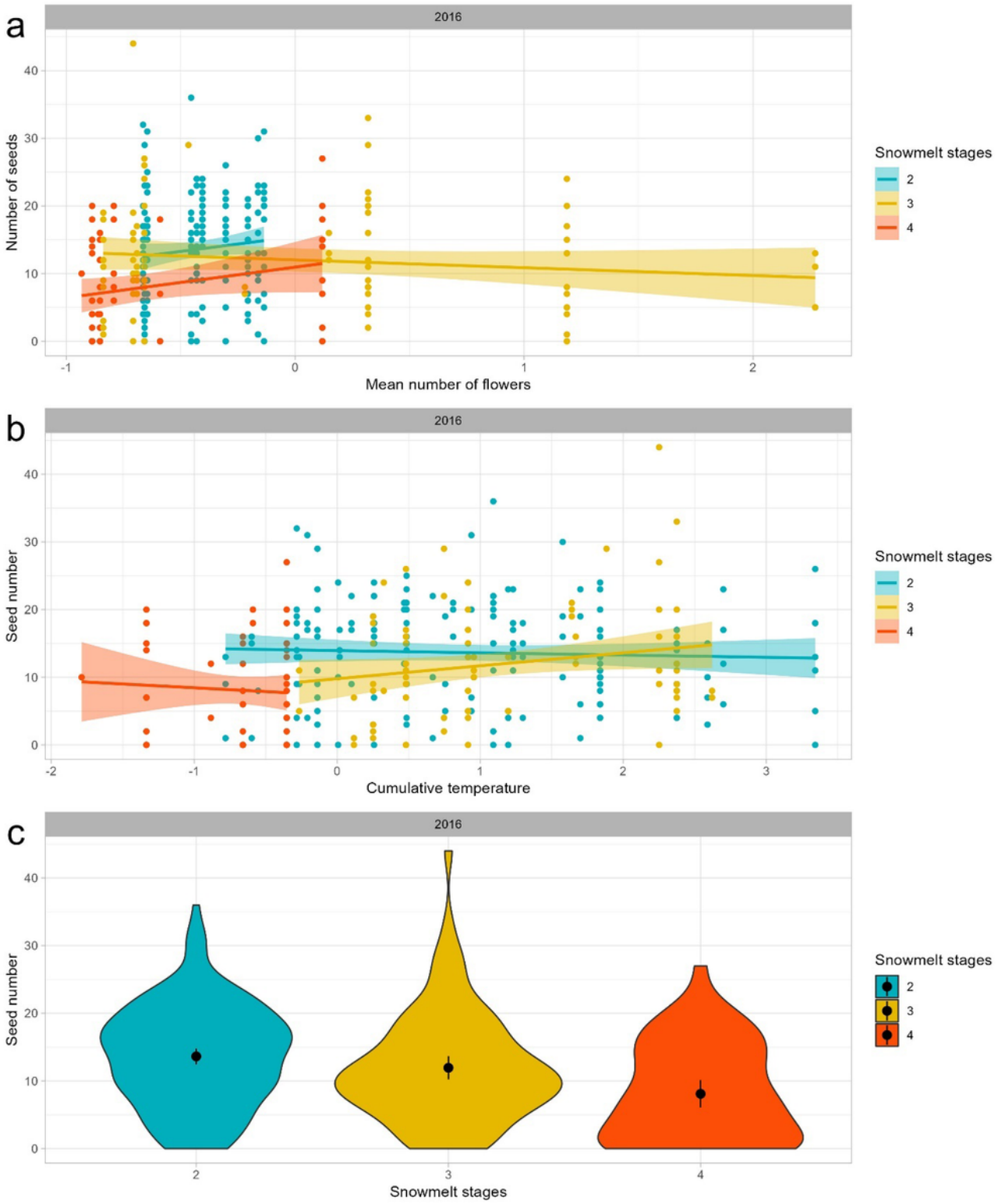

Figure 5

The relationship between seed number and **a)**mean number of flowers, **b)** cumulative temperature, and **c)** the three different snowmelt stages, from 2016, at Finse, Norway. Colors represent the different snowmelt stages. In **a)** and **b)** are the individual recordings are marked with dots, with lines fitted through linear regression. For the violin plot in **c)** the distribution is shown through the width of the violin, and standard error is added for each snowmelt stage.

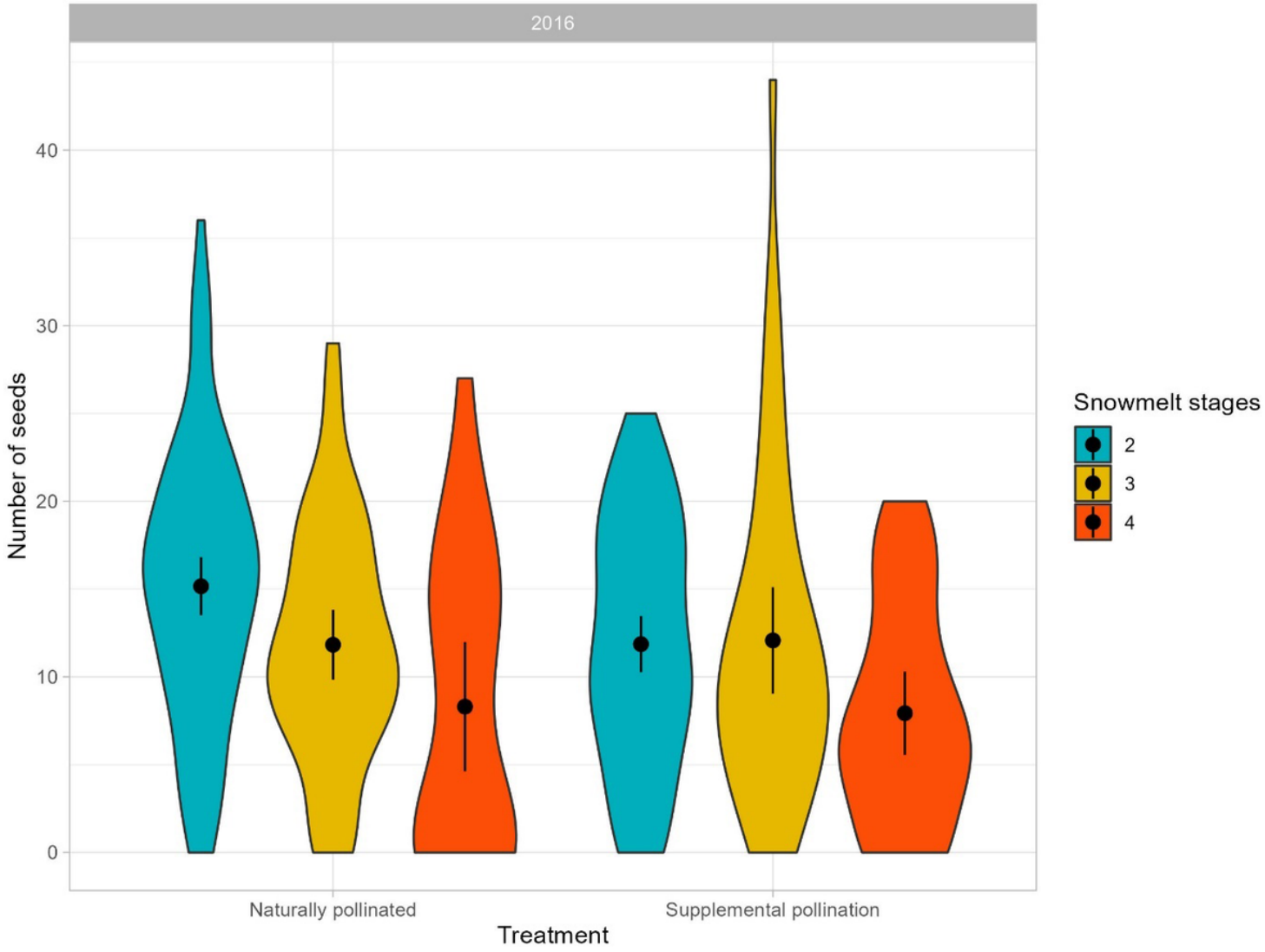

Figure 6

The relationship between number of seeds produced and the two pollination treatments, natural pollination and supplemental pollination, in three different stages of snowmelt, from 2016, at Finse, Norway. The different colors represent the different snowmelt stages. The distribution is shown through the width of the violin, and standard error is added for each snowmelt stage.

Supplementary Files

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- Appendices.docx