Reproductive allocation and floral traits of insect-pollinated forbs along climatic gradients in semi-natural grasslands

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Front cover photos by Gunvor Skjelstad
The view from Høgsete, Aurland
Euphrasia sp. growing at Rambera, Vik i Sogn

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Abstract

Anthropogenic climate change is increasing both temperatures and precipitation in Western Norway, and these trends will be magnified in the future. This is expected to alter ecosystems, and to affect plants at different stages through their life cycle. Investigating variation in plants functional traits along spatial climatic gradients can be used to understand the effects of climate, and climate change, on different aspects of the plant life cycle. Many have used such space-for-time approaches to study vegetative traits, but reproductive- and floral traits have so far received less attention. Knowledge about these traits is important for understanding plant-pollinator interactions and how these interactions could be affected by future climate change. The aim of this study was to investigate how reproductive allocation and floral traits of insect-pollinated forbs in perennial grasslands vary with temperature and precipitation. I collected approximately 1300 individuals of 45 different species of forbs for measurements of plant vegetative and reproductive size, reproductive allocation and floral traits. To investigate intraspecific variation of reproductive allocation and floral traits, I also studied four species individually; *Campanula rotundifolia, Potentilla erecta, Ranunculus acris* and *Veronica officinalis*. The plants were collected in a climatic grid in western Norway consisting of 12 sites of semi-natural grasslands across three temperature levels and four precipitation levels.

My results showed that across the community, forbs allocated more biomass to reproductive organs when temperatures were lower, while size and colour of floral displays were similar along the temperature gradient. Precipitation did not affect reproductive allocation or floral traits of the community. *R. acris* showed the same trend as the community for reproductive allocation, while there was no intraspecific variation along the temperature gradient for the other species. Size of floral displays of the four species changed little with temperature, as for the community. Increasing precipitation affected the number and size of floral displays of *R. acris* and *P. erecta* negatively, while *C. rotundifolia* and *V. officinalis* showed no effects of precipitation. The different trends found for the four species along both the temperature- and the precipitation gradient imply that these species have different reproductive strategies. These results also indicate that some species are more vulnerable to climate change than others. However, the effects of climate change on the forb communities and the individual species will be highly dependent on how pollinators and plant-pollinator interactions are affected by increasing temperature and precipitation.

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Introduction

The climate is changing, and the ongoing anthropogenic climate change is expected to cause widespread alterations of ecosystems, communities and species. We know that global temperature is already approximately 1 °C higher today compared to pre-industrial temperature, and that it will continue to increase at even higher rates the next decades (IPCC, 2018). Even though the increasing temperatures are often the main focus, we also expect changes in precipitation levels. The predicted changes in precipitation vary considerably between different parts of the world. Some areas will have reduced precipitation and be vulnerable to desertification (IPCC, 2019), while others will experience an increase of heavy precipitation (IPCC, 2018). Climate changes are happening faster at high latitudes and elevations (IPCC, 2018), which means that Norway is definitely exposed to these changes, as the northern and mountainous region this country is. Regional climate projections show that both temperature and precipitation will increase in most parts of the country, but especially western Norway will experience more extreme levels of precipitation (Hanssen-Bauer et al., 2017). These changes will affect both ecosystem composition and function, for example by leading to higher plant productivity, species turnover (Komatsu et al., 2019; Parton et al., 1995; Rustad et al., 2001; Wu et al., 2011) or shifts in species ranges (Parolo and Rossi, 2008). Increased temperature and precipitation will also impact the plants' life cycles in many ways, for instance by prolonging the growing season (Menzel and Fabian, 1999), increase vegetative growth (Arft et al., 1999) and cause shifts in phenology (Fitter and Fitter, 2002; Scaven and Rafferty, 2013).

A plant's nutrient- and energy budget is limited, meaning that allocation of resources to different life functions, such as leaves, stems, roots and reproductive organs can reflect the climate and associated ecological and evolutionary pressures and drivers they are exposed to in the environment in which they grow (Poorter et al., 2012). Allocation is a trade-off where plants have to find the most optimal strategy in their habitat (Wenk and Falster, 2015). Clear patterns of plant size can be seen along temperature- and elevational gradients. Plants generally produce more biomass in warmer, lowland habitats (Halbritter et al., 2018), and the plants growing here are challenged by competition with other plants for light and resources (He et al., 2013; Olsen et al., 2016). With higher plant productivity, investing a relatively large part of the energy budget in vegetative growth could be a good strategy in order to grow fast and tall and compete for nutrients, light and water (Arft et al., 1999). Plant productivity is lower in alpine habitats, as shorter growing seasons, low temperatures, more wind and nutrient poor soils limit growth (Billings and Mooney, 1968), meaning that environmental stress is more limiting for growth than competition with other plants for light and resources (He et al., 2013). Environmental stress is also causing challenges for plant reproduction in the alpines, as pollinator abundance decreases at high elevations due to low temperatures and wind (Totland, 2001). Especially bees, which are important pollinators in the lowland, become less numerous in the alpines (Totland et al. 2013). The pollinator community is instead dominated by flies (Diptera) which are able to fly and forage at harsher climatic conditions than bees (Lázaro et al., 2008; Totland, 1993). The combination of lower abundance and diversity of pollinators and the short growing seasons in the alpines, makes insect-pollination less reliable (Totland et al. 2013). Alpine plants can cope with this challenge by allocating more of their biomass to reproductive organs at the cost of vegetative growth (Fabbro and Körner, 2004; Hemborg and Karlsson, 1998; Kawano and Masuda, 1980), which could be the best strategy in habitats where competition for the few available pollinators exceeds competition for other resources.

The pollinators with their behaviours, preferences and physical characteristics are drivers of selection and evolution in a range of floral characteristics, also known as floral traits (Campbell and Powers, 2015; Gervasi and Schiestl, 2017). The floral traits again affect pollinator communities, so that floral traits of the plant communities and the pollinator communities interactively affect one another (Biesmeijer et al., 2006; Gervasi and Schiestl, 2017). Floral traits are crucial for plants´ sexual reproduction and they play important roles in shaping plant-pollinator interactions, competition or facilitation of pollinators among the plants and the diversity of pollinating insects in a community (Carvalheiro et al., 2014; Junker et al., 2015). Competition both between plants for attention from pollinators and between the pollinators for access to the best food resources has given rise to numerous strategies within floral traits like shapes, sizes, scents and colours, and impacted how much resources the plants invest in their flowers (Nicolson and Wright, 2017). The quantity and quality of floral traits can to a high degree influence the behaviour of pollinators; for instance plants with larger floral display areas, numerous open flowers or more available nectar are more visited by pollinators than other species growing in the same environment (Cnaani et al., 2006; Conner and Rush, 1996; Hegland and Totland, 2005; Stang et al., 2006). Floral colour is also an important trait for attracting pollinators, and studies have shown that bees are usually associated with colours seen by the human eye as blue and violet, while flies prefer colours that humans perceive as white and yellow (Lázaro et al., 2008; McCall and Primack, 1992). Yellow has been associated with several different groups of insects and is assumed to be a common colour of plants with a generalistic pollination strategy (Kevan, 1972; McCall and Primack, 1992).

Plants growing under contrasting environmental conditions can potentially exhibit large variation in floral traits due to differences in selective pressure, even within the same species (Adier et al., 2014; Fabbro and Körner, 2004; Helsen et al., 2017; Maad et al., 2013). If the pollinator community changes in species composition or abundance, the selective pressure is also changing, and the plants will have to respond by adapting their floral traits in order to reproduce successfully. For instance, alpine plants need to adapt to the lower abundance and species richness of pollinators (Totland, 2001). They can respond to this challenge by being pollinator generalists (Totland, 1993) or extending their flower longevity (Fabbro and Körner, 2004; Stenstrom and Molau, 1992). Several studies have also found that flower size increases with elevation (Herrera, 2005; Kudo and Molau, 1999; Maad et al., 2013) as a strategy for attracting more pollinators. However, others have found flower size to be constant along an elevational gradient (Fabbro and Körner, 2004). It is also not clear if certain floral colours are more common in the alpines than others (Arnold et al., 2009), even though associations between particular pollinators and floral colours are found (Lázaro et al., 2008; McCall and Primack, 1992). In general, much is still unknown when it comes to how floral traits change along temperature gradients and there is a need of more research on this topic.

While most studies have focused on variation along elevational- and temperature gradients, precipitation could also affect reproductive allocation and floral traits. Water loss through inflorescences can be high in dry environments, especially when the flowers have large surface-to-volume ratios (Galen et al., 1999). Therefore, it could be beneficial for plants growing in arid ecosystems to reduce their flower numbers and size. There is also evidence that plants experiencing drought stress save resources by decreasing the proportion of sexual reproduction for the benefit of clonal propagation (Xie et al., 2016). In addition, soil moisture is important for carbon assimilation, meaning that plants in dry soils gain fewer resources to allocate to sexual reproduction (Lambrecht and Dawson, 2007). Many studies have investigated reproductive traits under drought stress, but the effects of high levels of precipitation on plant-pollinator interactions, reproductive allocation and floral traits have received less attention so far. More precipitation leads to increased plant productivity (Wu et al., 2011), which could enhance competition between plants and select for allocation to vegetative growth at the cost of reproduction. Heavy rain will also reduce the pollinators' flight activity and flower visitation rates (Poulsen, 2008; Totland, 1994), and leave flowers more vulnerable to physical damage (Pacini 1984, cited in Lawson and Rands, 2019). In addition, a thicker snow cover and a shorter growing season (Jonas et al., 2008) could possibly also have effects on reproductive allocation and floral traits. More research on flowering plants along gradients including sites with high precipitation levels is needed to understand the effects of this.

Trait-based approaches have become important in ecological research and are being used to study impacts of abiotic and biotic factors on plant communities (Diaz et al., 2004; McGill et al., 2006). Many studies exist on the vegetative functional traits of plants, but reproductive traits or floral traits have so far received less attention, despite their importance for plant reproduction, pollinator communities and various aspects of ecosystem functioning. Knowledge about several plant traits, reflecting several functions, both vegetative and reproductive, is important for understanding the complexity of ecosystem and community responses to climate change (Junker and Larue-Kontić, 2018). The aim of this study was to investigate how resource allocation to sexual reproduction and floral traits of plant communities and individual species vary with different levels of temperature and precipitation. To answer this, I collected flowering plants of a number of insect-pollinated forbs from several sites of semi-natural grasslands along climatic gradients in western Norway.

My questions are as follows:

- Is allocation to reproductive organs changing along temperature and/or precipitation gradients?
- How are floral traits affected by changes in temperature and/or precipitation?
- Are reproductive allocation and floral traits of individual species changing in accordance with the trends of the community, or do individual species follow different species-specific trends?

Based on the literature presented above, I expect that (1) plants in colder environments increase allocation to their reproductive organs in terms of biomass proportion and have more floral displays and a larger total display area in relation to total biomass; (2) plants' floral displays are larger in cold environments compared to in warmer environments; (3) there will be shift from the floral colours associated with bees to colours associated with flies with decreasing temperature; (4) reproductive allocation and the size and number of floral displays will increase with increasing precipitation; (5) individual species will follow similar trends by adapting genetically or through phenotypic plasticity.

Methods

Study sites

To study the effects of temperature and precipitation on reproductive allocation and floral traits of insect-pollinated forbs, I collected plants in a natural climate grid consisting of 12 sites. The sites are a part of the SeedClim grid and have been used for several studies over the last decade (Guittar et al., 2016; Klanderud et al., 2015). The grid has three temperature levels, where mean summer temperature is 6.5, 8.5 and 10.5 °C, and four precipitation levels, where mean annual precipitation is 650, 1300, 1950 and 2900 mm (See Table 1 for detailed information about each site; Climate data from Norwegian Meteorological Institute). The grid is set up so that temperature and precipitation vary independently from each other. In order to obtain this wide variety of temperature and precipitation, the sites are located from the boreal to the alpine zone and from the wet western to the drier eastern Norway (Figure 1). Distance between the sites ranges from 650 m to 175 km (Klanderud et al., 2015).

To minimize variability caused by other factors than climate, the sites are chosen so all these factors are as similar as possible. All sites are semi-natural grasslands, dominated by graminoids, moderately grazed, broadly south-facing and with calcareous bedrock (Klanderud et al., 2015). Prevalent and abundant forbs in the grid are *Achillea millefolium*, *Potentilla erecta*, *Bistorta vivipara*, *Veronica officinalis* and *Campanula rotundifolia* (Klanderud et al., 2015).

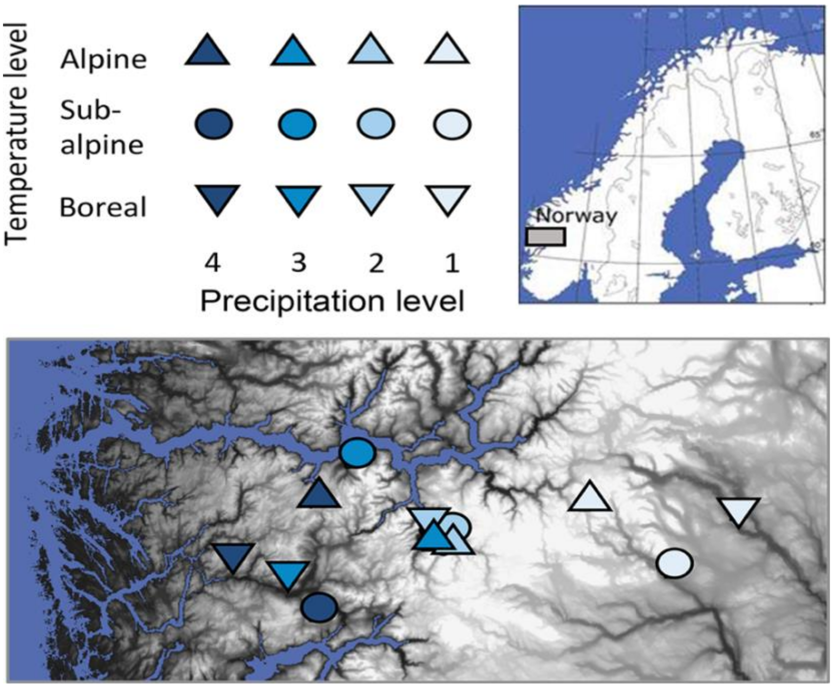

Figure 1*:* 12 sites and their locations in Western Norway. The sites make up a climate grid with three temperature levels (mean of four warmest months: 6.5, 8.5 and 10.5 °C) illustrated with shaped figures and four precipitation levels (650, 1300, 1950 and 2900 mean mm/year) illustrated with lighter and darker colour. Climate data from Norwegian Meteorological Institute (met.no). Figure originally from Klanderud et al. 2015.

Table 1*:* 12 sites with information about their GPS-coordinates, elevation, precipitation, temperature and bedrock. Interpolated climate data is from Norwegian Meteorological Institute. The sites make up a climate grid in Western Norway, where insect-pollinated plant species were collected to study how temperature and precipitation affects reproductive allocation and floral traits.

Site	**UTM zone 33** *Coordinate x*	**UTM zone 33** *Coordinate y*	**Elevation** *(m a.s.l.)*	**Precipitation** *(Mean annual, mm)*	**Temperature** *(Mean of four warmest months, °C)*	**Bedrock**
Alpine						
Ulvehaugen	128833.00	6785010.00	1208	596	6.17	Ryolite. Ryodacite. Dacite
Låvisdalen	80587.50	6767820.00	1097	1321	6.45	Phyllite. Mica schist
Gudmedalen	75285.30	6769540.00	1213	1925	5.87	Phyllite. Mica schist
Skjellingahaugen	35627.60	6785870.00	1088	2725	6.58	Marble
Subalpine						
Ålrust	157951.00	6759200.00	815	789	9.14	(Meta)sandstone. Shale
Høgsete	75917.50	6774330.00	700	1356	9.17	Phyllite. Mica schist
Rambera	49407.80	6801320.00	769	1848	8.77	Phyllite. Mica schist
Veskre	35390.20	6742090.00	797	3029	8.67	(Meta)sandstone. Shale
Lowland						
Fauske	180405.00	6781200.00	589	600	10.30	Phyllite. Mica schist
Vikesland	75604.70	6774850.00	474	1161	10.55	Phyllite. Mica schist
Arhelleren	27494.10	6756720.00	431	2044	10.60	Phyllite. Mica schist
Øvstedal	7643.94	6762220.00	346	2923	10.78	Ryolite. Ryodacite. Dacite

Data collection and trait measurements

Sampling of plants

The goal was to collect as many species from the community of insect-pollinated forbs as possible for each of the 12 sites. I also included three insect-pollinated woody species (*Dryas octopetala*, *Phyllodoce caerulea* and *Vaccinium vitis-idaea*) as these were prevalent components of the field layer vegetation at the sites. Despite these exceptions, I will still use the term “forbs” when referring to all collected plants in this thesis. The plant collection was done during the flowering season, between 13th of June and 2nd of August 2019 (Figure 2). Because different species flower at different times in the season, I visited all 12 sites twice with two-four weeks between each visit. Usually, I spent one day per visit at each site. The most abundant species were prioritized and collected first. I also prioritized species that grow at several of the 12 sites and hence could provide useful data for sites comparisons. Some species flowered too early or too late in the season to be available during the period of my fieldwork. It was therefore not feasible to collect all the prevalent forbs. I collected between 7 and 14 species at each site, with an average of 10.5 species per site and a total of 45 different species across the grid (See Appendix 1 for an overview of all collected species at each site).

Figure 2: Sampling of *Pinguicula vulgaris* at the subalpine site Veskre, summer 2019. Photo: Gunvor Skjelstad

At each site, I collected ten individuals of each species. They were mostly collected within a radius of approximately 30-50 meters from the center of the field site (i.e. the climate station). To achieve a representative selection, I chose individuals haphazardly by throwing an object, such as a pencil, and then collected the individual of the target species that the pencil pointed at. I only included mature individuals with a minimum of one open flower without any large damages or signs of developing seeds (i.e. entering post-flowering reproductive stages). This was done to make sure I measured all floral traits on flowers at the same stage; when they were open and available for pollinators. I did not follow this plant selection procedure strictly for less abundant species if there were few individuals to choose from. Instead, I then searched the area until I had ten individuals with minimum one open flower. All individuals of the same species were collected minimum 2 meters apart to make sure that they were different genetic individuals. When several shoots emerged from the same point in the ground, I assumed them to be of the same individual and therefore collected them as one. After measuring reproductive height (see below), all of each individuals' aboveground biomass was collected. Hereafter, aboveground biomass will always be referred to as biomass.

Measurements of plant size and floral traits

For each individual, I measured the reproductive height from the ground to the uppermost open flower and counted all the floral structures (Hereafter: floral displays). The species were separated into two groups based on their type of floral display: floral displays consisting of solitary flowers and floral displays consisting of inflorescences (several flowers in a cluster) (Table 2). For solitary species, one open flower per individual was randomly chosen for measurements of diameter, flower height and petal width and length (Figure 3, Figure 4 a-d). For species with inflorescences, the diameter(s) and height of the whole floral display was measured, while one individual flower was randomly chosen for measurements of petals (Figure 4 e-f). For species with round and radial symmetric floral displays, I measured only one diameter, while I measured two diameters for the species with floral displays of other shapes (Figure 4, Table 2). I used a digital caliper (Cocraft 0-150 mm, with 0.01 mm precision) for all measurements. No parts of the plants were stretched or unfolded during any of the measurements. I also registered floral colour in four colour categories: Pink, yellow, violet

Figure 3: Using a digital caliper to measure flower diameter of an individual of *Silene dioca* at the boreal site Øvstedal. Photo: Ragnhild Gya

and white. Most species had one colour per flower, while five species were multicoloured. In addition, four species included a minority of individuals with more than one colour (Table 2). Maximum three colours were registered per individual.

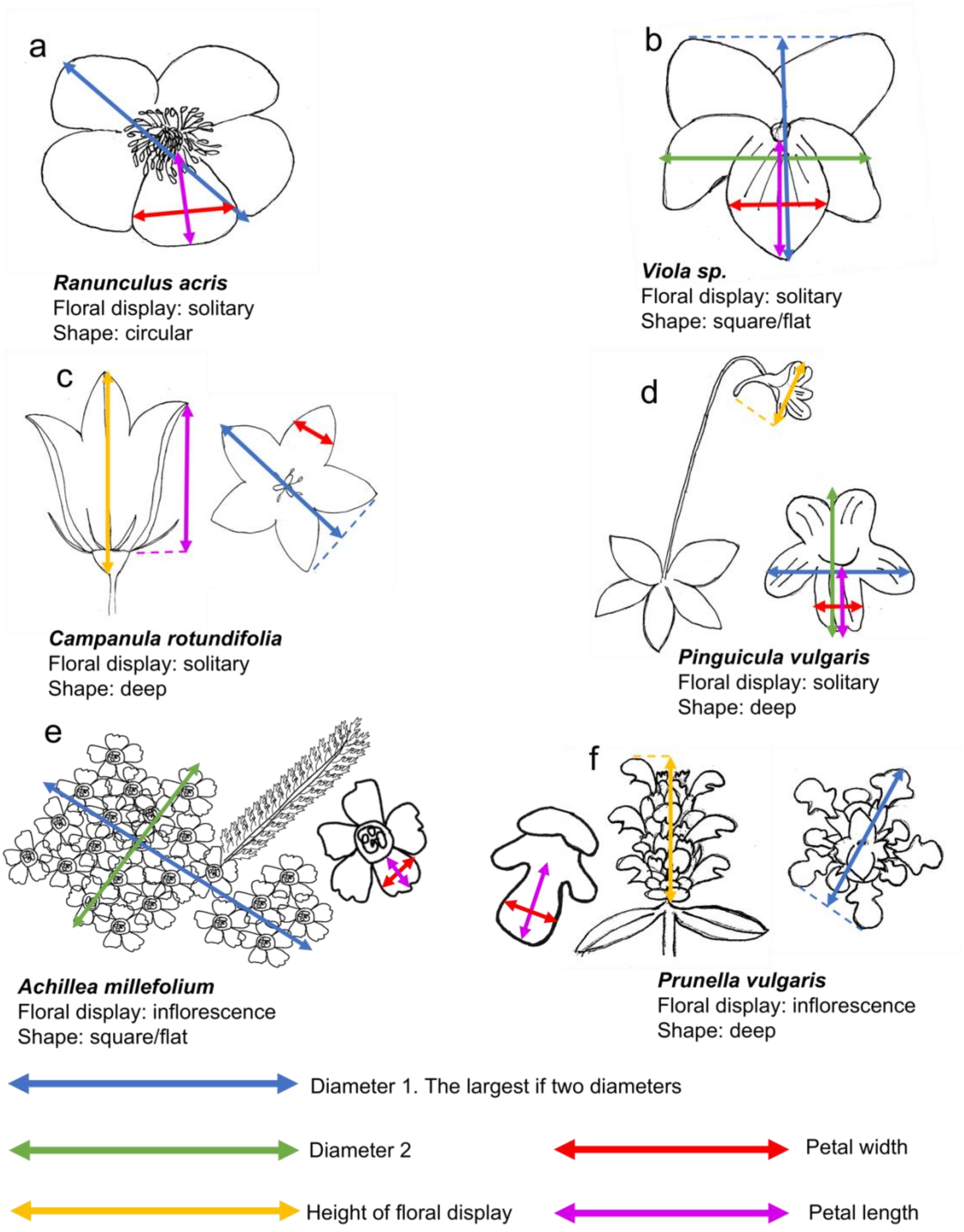

Figure 4**:** A selection of the collected species illustrating some of the different flower structures and shapes. The arrows show how diameters, height of floral display and petal width and length were measured in the field. This illustration only shows how height of floral displays were measured for the species were this measure was a part of the formula for calculating area of floral display, although it was measured for all collected species. Insect-pollinated forbs were collected during the flowering season of 2019 in a climatic grid consisting of semi-natural grasslands in Western Norway. Illustration: Gunvor Skjelstad

Each individual plant was put into a separate, marked paper bag and brought back to the lab. Immediately after return, the paper bags containing the plants were dried in a drying oven (Termaks TS 5410) on 65 °C for 72 hours. The dry plants were stored in plastic containers until all fieldwork was done and I could start the lab work.

To make sure that the samples were totally dry during weighing, they were redried for minimum one day before they were weighed. I kept 3-4 samples at a time in a desiccator with silica gel while weighing. All mentions of biomass in this thesis will refer to the dry mass.

For each plant individual, plant organs were sorted into reproductive parts and vegetative parts using tweezers. The main rule used in this study is that the reproductive part of a plant starts after the last foliage leaf before the flower(s). No foliage leaves were included in reproductive parts, but bracts were (Figure 5). Open flowers were weighed individually, maximum ten flowers per individual plant.

Exceptions were the species *Leucanthemum vulgare, Hieracium sp., Leontodon autumnalis, Solidago virgaurea* and *Knautia arvensis* where I weighed the whole floral display as one flower. In this study, these species are treated as they have solitary flowers, even though they in reality have inflorescences. This was because the individual flowers were too small to be counted, measured and weighed individually. For all species, the flowers, including buds, withered flowers and seeds, were weighed together with all flower stalks as a measure of the reproductive biomass.

Finally, I weighed vegetative biomass (i.e., remaining above-ground mass) and the total biomass. All weighing was done on the same scale (VWR SM425i, with a resolution of 0.01 mg) to avoid errors due to differences between scales.

Figure 5: Separation of plant organs, here illustrated with the species *Viola biflora.* Red lines show where reproductive parts were separated from vegetative parts. Bracts were included in reproductive mass, while foliage leaves were not. Illustration: Carl Lindman (Swedish botanist 1856-1928)

Table 2*:* All the species collected in the study and some of their basic flower characteristics used in the analyses. For floral displays, I=inflorescences and S=solitary flowers. For display area formulas, d1= diameter 1, d2=diameter 2, r=radius and h=height of floral display. For floral colour, P=pink, V=violet, W=white and Y=yellow. Insect-pollinated forbs were collected during the flowering season of 2019 in a climatic grid consisting of semi-natural grasslands in Western Norway.

Species	**Individuals collected**	**Floral display**	**Shape of floral display**	**Number of diameters measured**	**Display area formula**[a]	**Floral colour**	**Number of colours per individual**
Achillea millefolium	40	I	Square/flat	2	d1*d2	W/P	1
Antennaria dioica	20	I	Square/flat	2	d1*d2	W/P	1-2
Atocion rupestre	10	S	Circular	1	πr^2	W	1
Bistorta vivipara	40	I	Deep	1	$2\pi rh+\pi r^2$	W/P	1-2
Campanula rotundifolia	120	S	Deep	1	$2\pi rh+\pi r^2$	V	1
Cerastium alpinum	10	S	Deep	1	$2\pi rh+\pi r^2$	W	1
Cerastium cerastoides	10	S	Deep	1	$2\pi rh+\pi r^2$	W	1
Chamaepericlymenum suecicum	10	S	Circular	1	πr^2	W	1
Dianthus deltoides	10	S	Circular	1	πr^2	P	1
Dryas octopetala	10	S	Circular	1	πr^2	W/Y	2
Euphrasia stricta	20	I	Deep	2	$2\pi rh+\pi r^2$	W/V/Y	2-3
Euphrasia wettsteinii	20	I	Deep	2	$2\pi rh+\pi r^2$	W/Y/V	2-3
Geranium sylvaticum	40	S	Circular	1	πr^2	V	1
Hieracium pilosella[b]	36	I	Circular	1	πr^2	Y	1
Hypericum maculatum	20	I	-	2	-	Y	1
Knautia arvensis	20	I	Circular	1	πr^2	V	1
Leontodon autumnalis	20	I	Circular	1	πr^2	Y	1
Leucanthemum vulgare	10	I	Circular	1	πr^2	W/Y	2
Lotus corniculatus	20	I	Deep	2	$2\pi rh+\pi r^2$	Y	1
Melampyrum pratense	10	S	Depth	2	$2\pi rh+\pi r^2$	Y	1
Parnassia palustris	20	S	Circular	1	πr^2	W	1
Phyllodoce caerulea	10	S	Deep	1	$2\pi rh+\pi r^2$	P	1
Pinguicula vulgaris	40	S	Deep	2	$2\pi rh+\pi r^2$	V	1
Potentilla erecta	90	S	Circular	1	πr^2	Y	1
Prunella vulgaris	20	I	Deep	1	$2\pi rh+\pi r^2$	V/P	1
Ranunculus acris	110	S	Circular	1	πr^2	Y	1
Rhinanthus minor	20	I	-	2	-	Y	1
Saxifraga aizoides	20	S	Circular	1	πr^2	Y	1
Saxifraga stellaris	10	S	Circular	1	πr^2	W	1
Silene acaulis	10	S	Circular	1	πr^2	P	1
Silene dioica	10	S	Circular	1	πr^2	P	1
Solidago virgaurea	20	I	-	2	-	Y	1
Trientalis europaea	30	S	Circular	1	πr^2	W	1
Trifolium medium	10	I	Deep	1	$2\pi rh+\pi r^2$	P	1
Trifolium pratense	20	I	Deep	1	$2\pi rh+\pi r^2$	P	1
Trifolium repens	30	I	Deep	1	$2\pi rh+\pi r^2$	W	1
Vaccinium vitis-idaea	40	I	Deep	2	$2\pi rh+\pi r^2$	P/W	1-2
Veronica alpina	10	S	Deep	2	$2\pi rh+\pi r^2$	V	1
Veronica chamaedrys	40	S	Deep	2	$2\pi rh+\pi r^2$	V	1
Veronica officinalis	70	S	Deep	2	$2\pi rh+\pi r^2$	V	1
Viola biflora	20	S	Square/flat	2	d1*d2	Y	1
Viola canina	30	S	Square/flat	2	d1*d2	V	1
Viola palustris[b]	9	S	Square/flat	2	d1*d2	P	1
Viola tricolor	40	S	Square/flat	2	d1*d2	V/W/Y	3
Viscaria vulgaris	10	S	Circular	1	πr^2	P	1

[a] For species where two diameters were measured, diameter 1 (d1), the largest diameter, was used to find r used in calculations of display area, in addition to being used in statistical analyses of flower diameter.

[b] Some individuals were removed from the dataset as they turned out to be of a different species.

Data preparations and statistical analyses

Data preparations

For each individual, the mean mass of all the weighed open flowers were calculated to find mass per floral display (hereafter: flower mass). To calculate the area of floral displays, I used a method by Hegland and Totland (2005). Three different formulas are made for different shaped floral displays: Circular (e.g. *Ranunculus acris, Leontodon autumnalis*), flat (e.g. *Achillea millefolium, Viola sp.)* and floral displays with depth (e.g. *Campanula rotundifolia, Prunella vulgaris*) (Table 2). It is important to mention that these formulas only result in simplifications of the floral displays' area. Some areas may be overestimated, while others might be underestimated. For a few species this became a bigger problem. I decided to remove *Hypericum maculatum, Rhinanthus minor, Solidago virgaurea* from analyses including display areas, as it was very clear that the way I measured them in the field resulted in highly overestimated values. I also removed *Vaccinium vitis-idaea* collected at Høgsete and *Lotus corniculatus* collected at Fauske from the same analyses since measurements of the relevant traits were done differently here than for the same species at other sites.

Statistical models

First, I investigated how the overall plant size changes along the gradients including all species. The measures used in these models were reproductive height, total-, vegetative- and reproductive biomass (See all model specifications below). Having information about plant size is important when studying reproductive allocation for understanding how the relationship between plant size and reproductive organs changes. Second, I made a model with reproductive mass/total mass (reproductive to total mass ratio) as response variable to test the effects of temperature and precipitation on reproductive allocation of the plant communities. I also made models for number of floral displays per gram plant mass (floral displays/total biomass) and total display area per gram plant mass (number of floral displays*display area/total biomass). The two latter ratios were included because they could be an expression of the result or the output of the plants´ reproductive allocation. To answer how floral traits change with temperature and precipitation, I made models with number of floral displays, display area and flower mass as response variables. In the analysis of flower mass at community level I only included species with solitary floral displays (Table 2). This was because flowers from inflorescences were weighed individually. In order for the data to be comparable to solitary flowers, the inflorescences should instead have been weighed as one unit. I chose four species for further investigations of intraspecific variation of reproductive allocation and floral traits. *Campanula rotundifolia, Potentilla erecta* and *Ranunculus acris* were chosen for these analyses because they were the only species collected at all temperature- and precipitation levels, and at most of the sites. I also chose *Veronica officinalis* which was collected at all precipitation levels. Models were made for all the same measures on plant size, reproductive allocation and floral traits as already listed for the community of species. I also included a few additional floral traits at species level: petal length, petal width and flower diameter. The huge variation in floral shapes and sizes between species make these traits less applicable for analyses at community level. The largest diameter was used in the analysis of flower diameter of *V. officinalis*, which was one of the species with two diameters measured (Figure 4, Table 2).

All statistical analyses were done in R studio version 1.1.456 using the packages lme4 (Bates et al., 2015) and nlme (Pinheiro et al., 2019). Since the data is clustered, mixed effect models were used. I used linear mixed effect models (lme) for all analyses on continuous data, which were all measurement of plant size, reproductive allocation and floral traits, except from number of floral displays. Most of the data was non-normal distributed and needed to be log transformed before running the lme-models. Only data on floral traits at species level (display area, flower diameter and -mass, petal length and -width) did not need log transformation. For number of floral displays, which is count data, a generalized mixed effect model (glmm) with penalized quasilikelihood (PQL) was used. Both when using lme and glmm, temperature, precipitation and their interaction were used as fixed effects. Temperature and precipitation were scaled in order to be of similar magnitude in the models. Site was specified as random effect. In models including several of or all the collected species, species was also added as random effect. To determine if effects were significant, I used 95% confidence intervals. Effects with confidence intervals that did not include zero were considered significant.

Floral colour

I also investigated the distribution of floral colours in the communities of insect-pollinated forbs across the two gradients. To get a comprehensive overview of floral colours of the communities, I supplemented the data with species composition data from 2017 (Vandvik, unpublished data). This data includes cover estimates of all vascular plant species from 25x25 cm permanent experimental plots at each site from previous studies, from where I used the cover data from the control plots for two purposes: First, to supplement the list of insect-pollinated forb species at each site for colours. Species that I had not registered before were added with the help of this dataset. I used “Gyldendals Nordiske Feltflora” (Mossberg and Stenberg, 2006) to score floral colours. I only used the main colour of flowers, if the flower of a species had several colours. Together with the species I had collected, this was used to find the proportion of species of each colour at the sites. Second, to find community abundance-weighted proportion of each colour, which reflect relative abundances of the different colours in the communities, and thus the floral resources available to pollinators. Only the main colour of flowers was used here as well. I calculated the sum of cover of all forb species with the same colour across the control plots at each site. Then I divided this by the total cover of forbs in all control plots at each site, resulting in abundance weighted floral colour proportions at each site. The site Øvstedal was excluded from these calculations, as the species composition data only included one insect-pollinated forb species in the control plots at this site. I was not able to test how temperature and precipitation affects proportions of floral colours in the plant communities in a satisfactory way because I did not have enough replicate data for statistical analyses.

Data availability

Data on floral traits and biomass of insect-pollinated forbs collected by the author of this study during flowering season 2019 is documented with metadata and available in Appendix 2. This data and metadata include all measures of traits and biomass, also those that were not included in this thesis. The species composition data from 2017 used for investigations on floral colour are documented and available in the SeedClim dropbox (Vandvik, unpublished data). All climatic data used in this study are from met.no (Norwegian Meteorological Institute) and retrieved via SeedClim data. See Appendix 3 for Data Sharing Agreement. More information about the SeedClim sites and data documentation can be found here: https://docs.google.com/document/d/1RUOqkf8V_TqwZabu8LUjwQvephE5EClyYegV9wPAgfs/edit?usp=sharing

Results

Effects of temperature and precipitation on the community of forbs

Overall plant size and reproductive allocation

There was a huge variation in size between the species, but in general, forbs at boreal sites were larger than forbs at subalpine and alpine sites. Reproductive height, total biomass, vegetative biomass and reproductive biomass all significantly increased with temperature (Figure 6 a-c, Table 3). The mean total biomass of forbs collected at boreal sites was 0.57 g, while it was 0.25 g and 0.15 g for forbs from subalpine and alpine sites, respectively. With increased precipitation, all measures of plant sizes trended towards lower values, although not significantly. The interactive effects of temperature and precipitation on the plant size-traits were all weak and non-significant.

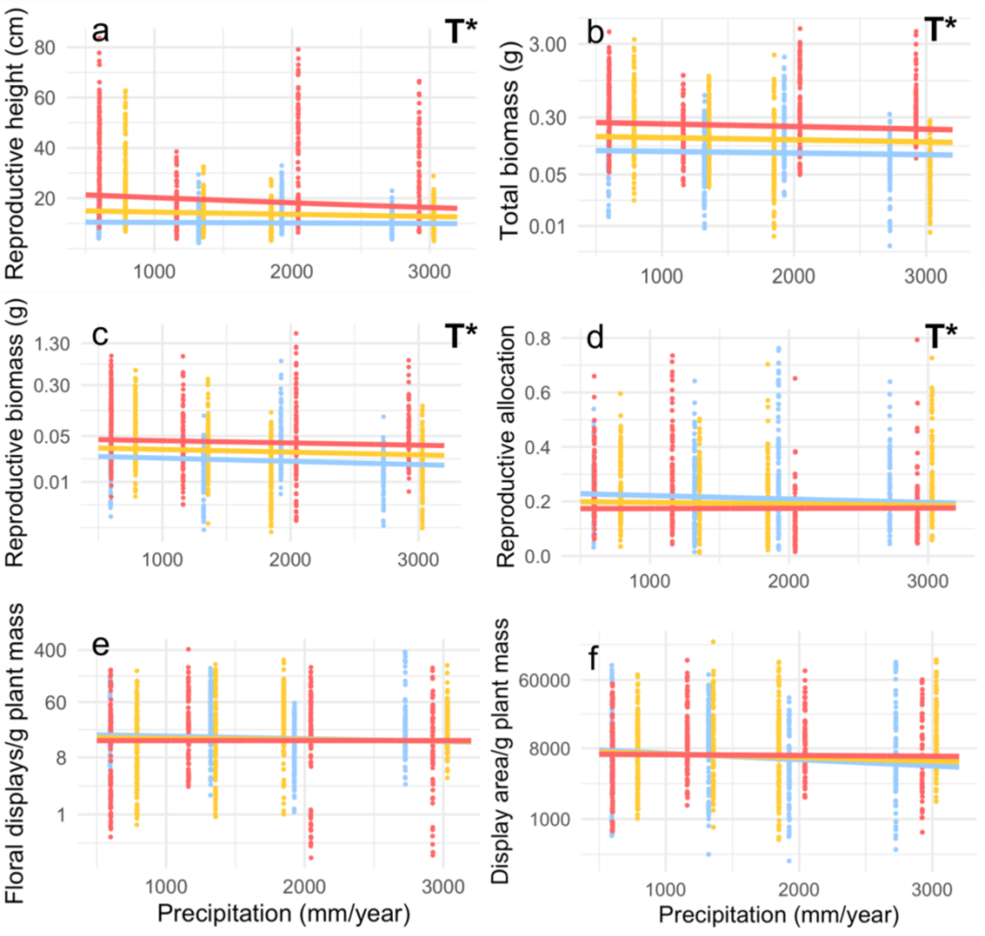

Figure 6: Figure caption on next page

Figure 6 (previous page): Changes in plant size (Reproductive height, total biomass and reproductive biomass), reproductive allocation (Reproductive biomass/Total biomass), number of floral displays per gram plant mass and total display area per gram plant mass with temperature (Mean of four warmest months: red = boreal sites (10.5 °C), yellow = subalpine sites (8.5 °C), blue = alpine sites (6.5 °C)) and precipitation (mean annual) of the community of insect-pollinated forbs. Note that the y-axes of plot b-c and e-f are log-scaled. The lines are predictions based on linear mixed models with temperature and precipitation as fixed effects and site and species as random effects. Significant trends were determined by confidence intervals not overlapping zero and are here indicated by T* (Temperature), P* (Precipitation) or T:P* (Interaction between temperature and precipitation). Insect-pollinated forbs were collected during the flowering season of 2019 in a climatic grid consisting of semi-natural grasslands in Western Norway.

Reproductive allocation varied between species, ranging from approximately 2% to 80%, and there was also a difference between different temperature levels. Mean reproductive allocation of alpine forbs were 25.1% compared to 23.6% and 21.7% for subalpine and boreal forbs, respectively. Reproductive allocation decreased significantly with increasing temperature (Figure 6d, Table 3), meaning that the fraction of the plants' total aboveground biomass dedicated to reproductive organs increased at lower temperatures. There was a trend towards higher reproductive allocation at dry alpine sites, but neither precipitation or the interaction between temperature and precipitation had a significant effect. Number of floral displays/g plant mass and display area/g plant mass (Figure 6 e-f, Table 3) showed no significant effects along any of the gradients.

Floral traits

The plants generally produced more floral displays at higher temperatures. Mean number of floral displays was 2.6 for forbs collected at alpine sites, 5.3 for forbs collected at subalpine sites and 10.0 for forbs collected at boreal sites. Number of floral displays increased significantly with increased temperature (Figure 7a, Table 3). Precipitation and the interaction between temperature and precipitation only showed weak and nonsignificant effects for this trait. For display area and flower mass, there was no significant effects of either temperature, precipitation or the interaction (Figure 7b-c, Table 3). There was a large variation between species, but size of floral displays seemed to be constant along the gradients.

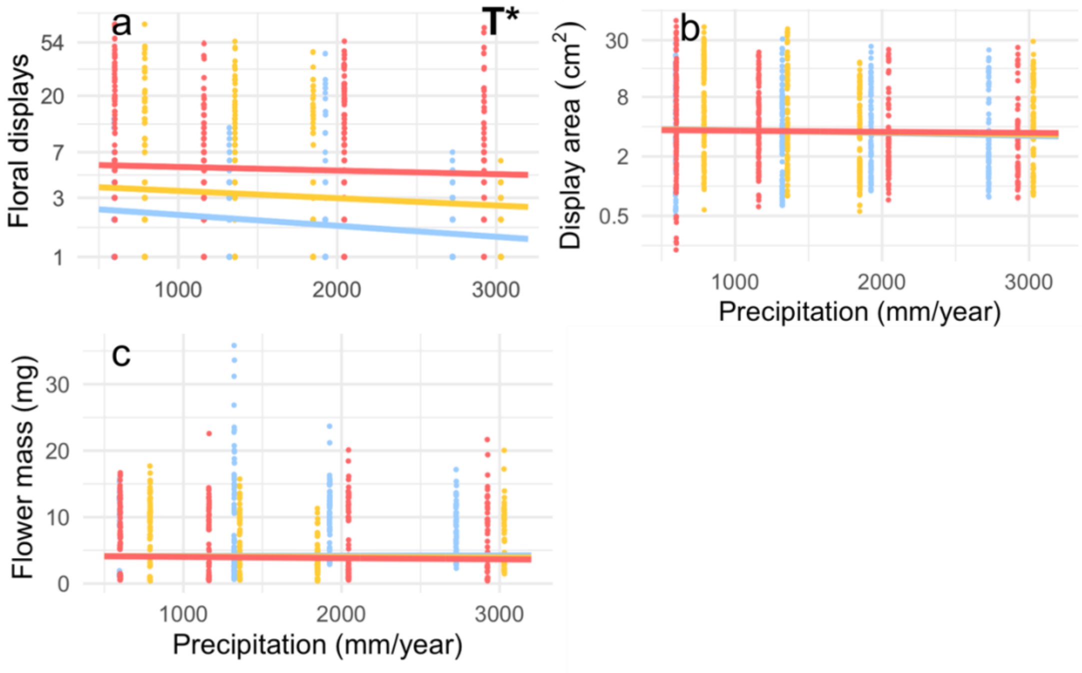

Figure 7: Changes in number of floral displays, display area and flower mass of flowers from solitary floral displays and with temperature (Mean of four warmest months: red = boreal sites (10.5 °C), yellow = subalpine sites (8.5 °C), blue = alpine sites (6.5 °C)) and precipitation (mean annual) of the community of insect-pollinated forbs. Note that the y-axes of plot a-b are log-scaled. The lines are predictions based on linear mixed models (exception: a generalized linear mixed model with penalized quasilikelihood was used for number of floral displays) with temperature and precipitation as fixed effects and site and species as random effects. Significant trends were determined by confidence intervals not overlapping zero and are here indicated by T* (Temperature), P* (Precipitation) or T:P*. Insect-pollinated forbs were collected during the flowering season of 2019 in a climatic grid consisting of semi-natural grasslands in Western Norway.

Table 3: The slopes of the changes in values of plant size, the relationship between plant size and reproductive organs (Reproductive allocation = Reproductive biomass/Total biomass) and floral traits per unit of increased, scaled temperature and precipitation with standard errors (± SE) for the community of insect-pollinated forbs, retrieved from linear mixed models (exception: a generalized linear mixed model with penalized quasilikelihood was used for number of floral displays) with temperature and precipitation as fixed effects and site and species as random effects. Significant trends (bold) were determined by confidence intervals not overlapping zero. Insect-pollinated forbs were collected during the flowering season of 2019 in a climatic grid consisting of grasslands in Western Norway.

Community of forbs	**Temperature**	**Precipitation**	**Interaction**
Plant size (log units, *10$_2$)			
Reproductive height	**26.1 (±7.1)**	-5.4 (±7.1)	-3.0 (±7.0)
Total biomass	**36.0 (±9.0)**	-5.5 (±9.0)	-1.1 (±8.8)
Vegetative biomass	**38.0 (±9.3)**	-5.0 (±9.3)	-2.0 (±9.2)
Reproductive biomass	**27.0 (±7.3)**	-7.6 (±7.3)	1.2 (±7.2)
Relationship – plant size and reproduction (log units, *10$_2$)			
Reproductive allocation	**-8.7 (±3.7)**	-2.1 (±3.6)	2.2 (±3.6)
Floral displays/g plant mass	-4.4 (±5.3)	-3.6 (±5.3)	3.3 (±5.2)
Display area/g plant mass	2.6 (±5.1)	-7.9 (±5.0)	5.5 (±4.9)
Floral traits			
Floral displays (n)	**0.4 (±0.1)**	-0.1 (±0.1)	0.1 (±0.1)
Display area (log units, *10$_2$)	0.6 (±2.2)	-3.5 (±2.0)	1.4 (±2.0)
Flower mass (Solitary flowers) (log units, *10$_2$)	-3.2 (±2.3)	-1.7 (±2.2)	-1.8 (±2.2)

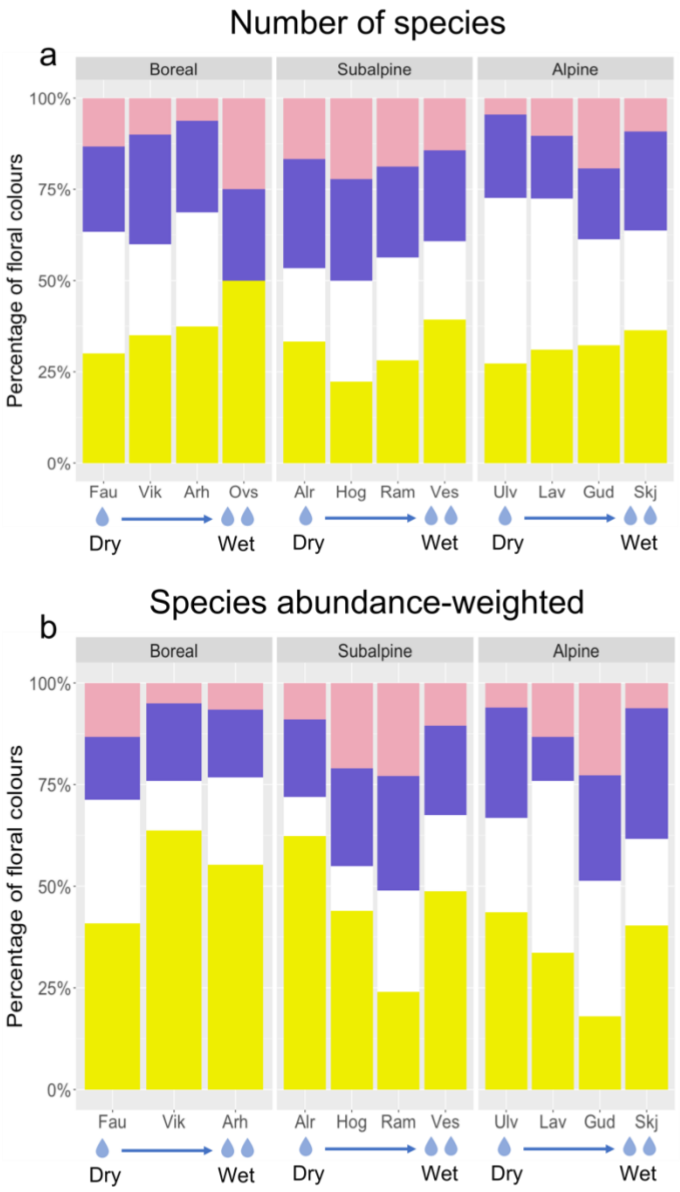

Figure 8: Percentage of floral colours at each site, sorted in temperature levels, where boreal = 10.5 °C, subalpine = 8.5 °C and alpine = 6.5 °C. Within temperature levels, sites are sorted from low to high precipitation levels. Fau=Fauske, Vik=Vikesland, Arh=Arhelleren, Ovs=Øvstedal, Alr=Ålrust, Hog=Høgsete, Ram=Rambera, Ves=Veskre, Ulv=Ulvehaugen, Lav=Låvisdalen, Gud=Gudmedalen, Skj=Skjellingahaugen. Colours of the plots represents a simplified version of the actual floral colours. **a)** Percentage of floral colours in terms of number of species **b)** Percentage of floral colours when species are weighted after relative abundance. Due to lack of registered insect-pollinated forbs in the species composition data used, the boreal and wet site Øvstedal is not included here.

Yellow was the most frequent floral colour overall followed by white, violet and pink in terms of number of species. White tended to become more common with increasing elevation and lower temperatures, while there was no clear difference for the other colours along the temperature gradient. Yellow tended to have a small increase with increased precipitation (Figure 8a, not tested).

Abundance-weighted colour proportions reflect relative abundances of the different colours in the communities, and thus the floral resources available to pollinators. When species were abundance weighted, the proportion of yellow became higher at most sites, especially at boreal sites and drier sites. There was still a trend of higher proportions of white at alpine sites, but the difference was smaller than it was when species were not abundance weighted. Yellow did no longer seem to increase with higher precipitation levels. There were no clear and observable trends for violet and pink along the gradients (Figure 8b, not tested).

Effects of temperature and precipitation on four focal species

Overall plant size and reproductive allocation

Individuals of *Campanula rotundifolia* were larger at boreal sites compared to subalpine and alpine sites. Mean total biomass for individuals collected at boreal, subalpine and alpine sites were 0.27 g, 0.1 g and 0.08 g, respectively. Reproductive height, total biomass, vegetative biomass and reproductive biomass all increased significantly with increasing temperature (Figure 9a, Table 4). Precipitation and the interaction between temperature and precipitation showed no significant effects for plant size of this species. For *P. erecta* there were no significant effects of temperature on overall plant size, but reproductive biomass decreased with increased precipitation (Table 5). *R. acris* showed significant positive trends with increased temperature for reproductive height, total biomass and vegetative biomass (Figure 9c, Table 6). Mean total biomass for individuals of this species collected at boreal sites were 0.37 g compared to 0.21 g and 0.14 g at subalpine- and alpine sites, respectively. There were no significant effects of precipitation or the interaction on plant size of *R. acris.* For *V. officinalis,* the only significant effect on plant size was an increase in total- and vegetative biomass with the interaction between temperature and precipitation (Figure 9d, Table 7) (See Appendix 4 for more plots on plant size of these four species).

Reproductive allocation of *R. acris* was higher at alpine sites compared to subalpine and boreal sites, with a mean of 25%, 21% and 19%, respectively. There was a significant negative effect on reproductive allocation with increasing temperatures (Figure 9g, Table 6). Although reproductive allocation trended towards lower values with increasing temperatures for *C. rotundifolia* and *P. erecta* as well (Figure 9e, f), these effects were not significant. Precipitation and the interaction between temperature and precipitation did not affect reproductive allocation significantly for any of the species. *C. rotundifolia* showed an increase in number of floral displays/g plant mass and display area/g plant mass with increasing temperature (Table 4), while *R. acris* showed a decrease in number of floral displays/g plant mass with increasing precipitation (Table 6). There were no significant trends of these ratios for the other species.

Floral traits

Both *C. rotundifolia* and *R. acris* produced significantly more floral displays as temperature increased (Figure 9i, k, Table 4, 6). *P. erecta* and *V. officinalis* also showed positive trends for this trait with increasing temperature, but they were not significant. Increased precipitation caused a significant decrease in number of floral displays for *P. erecta* and *R. acris* (Figure 9 j-k, Table 5-6), with negative, but not significant, trends also for *C. rotundifolia* and *V. officinalis.* The interaction had no significant effects on number of floral displays for any of the species. Display area was relatively constant along the gradients for most species. The only significant effect of this trait found was a decrease with increased precipitation for *P. erecta* (Figure 9n, Table 5). Petal length decreased with increased temperature for *C. rotundifolia* and *R. acris* (Figure 9q, s). Petal length of *R. acris* was also positively affected by the interaction. There was a trend towards lower values of display area and petal length at wet, alpine sites for all four species, although the effects were not significant. There were few significant effects of the other flower size traits: flower diameter, flower mass and petal width. Flower diameter decreased with increased precipitation for *P. erecta*, while flower mass decreased with increased temperature for the same species (Table 5). No significant effects on petal width were found for these species. None of the floral traits of *V. officinalis* were affected significantly by either temperature, precipitation or the interaction (See Appendix 4 for more plots on floral traits of these four species).

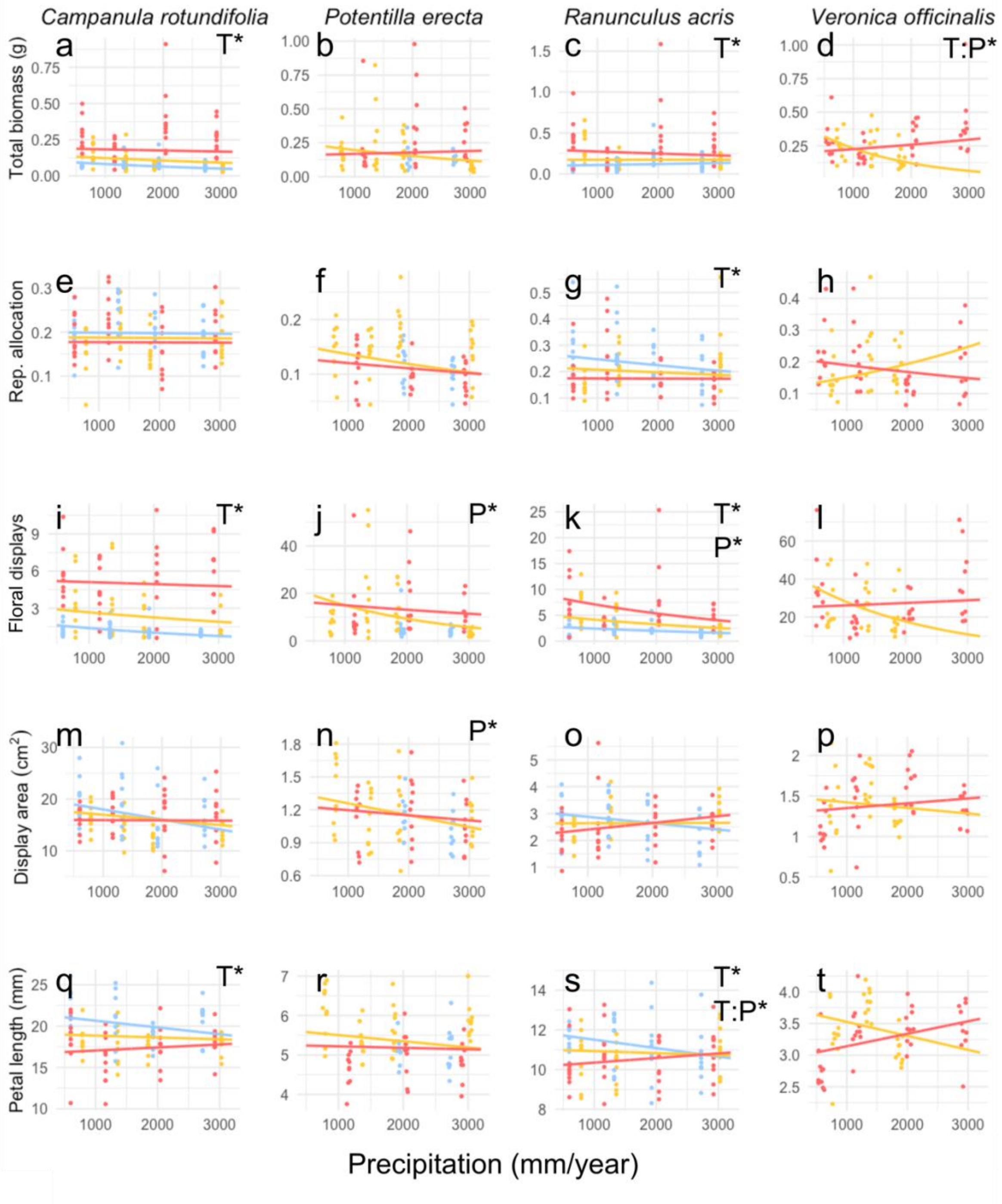

Figure 9: Changes in total biomass, reproductive allocation (Reproductive biomass/total biomass), number of floral displays, display area and petal length of four investigated species with temperature (Mean of four warmest months: red = boreal sites (10.5 °C), yellow = subalpine sites (8.5 °C), blue = alpine sites (6.5 °C)) and precipitation (mean annual). The lines are predictions based on linear mixed models (exception: a generalized linear mixed model with penalized quasilikelihood was used for number of floral displays) with temperature and precipitation as fixed effects and site as random effects. Significant trends were determined with confidence intervals not overlapping zero and are here indicated by T* (Temperature), P* (Precipitation) or T:P* (Interaction between temperature and precipitation). Individuals of these species were collected during the flowering season of 2019 in a climatic grid of consisting of semi-natural grasslands in Western Norway.

Table 4*:* The slopes of the changes in values of plant size, the relationship between plant size and reproductive organs (Reproductive allocation = Reproductive biomass/Total biomass) and floral traits per unit of increased, scaled temperature and precipitation with standard errors (± SE) for the species *C. rotundifolia*, retrieved from linear mixed models (exception: a generalized linear mixed model with penalized quasilikelihood was used for number of floral displays) with temperature and precipitation as fixed effects and site as random effects. Significant trends (bold) were determined by confidence intervals not overlapping zero. Individuals of the species were collected during the flowering season of 2019 in a climatic grid consisting of grasslands in Western Norway.

C. rotundifolia	**Temperature**	**Precipitation**	**Interaction**
Plant size (log units, *10$_2$)			
Reproductive height	**26.8 (±6.3)**	-3.3 (±6.3)	1.5 (±6.6)
Total biomass	**41.0 (±13.5)**	-11.6 (±13.6)	7.5 (±14.0)
Vegetative biomass	**43.0 (±13.5)**	-11.3 (±13.6)	7.4 (±14.0)
Reproductive biomass	**37.0 (±14.3)**	-12.0 (±14.3)	7.6 (±14.8)
Relationship – plant size and reproduction (log units, *10$_2$)			
Reproductive allocation	-5.0 (±5.1)	-0.4 (±5.1)	0.12 (±5.3)
Floral displays/g plant mass	**15.3 (±7.2)**	-0.2 (±7.2)	-2.3 (±7.5)
Display area/g plant mass	**13.6 (±6.9)**	-5.5 (±6.9)	1.1 (±7.1)
Floral traits			
Floral displays (n)	**0.7 (±0.1)**	-0.1 (±0.1)	0.1 (±0.1)
Display area (mm$_2$)	-33.2 (±53.5)	-79.7 (±53.7)	71.0 (±55.5)
Flower diameter (mm)	0.5 (±0.4)	-0.7 (±0.4)	0.4 (±0.4)
Flower mass (mg)	-0.7 (±0.8)	-0.3 (±0.8)	0.7 (±0.8)
Petal length (mm)	**-1.3 (±0.3)**	-0.2 (±0.3)	0.4 (±0.4)
Petal width (mm)	-0.1 (±0.2)	-0.2 (±0.2)	0.2 (±0.2)

Table 5: The slopes of the changes in values of plant size, the relationship between plant size and reproductive organs (Reproductive allocation = Reproductive biomass/Total biomass) and floral traits per unit of increased, scaled temperature and precipitation with standard errors (± SE) for the species *P. erecta*, retrieved from linear mixed models (exception: a generalized linear mixed model with penalized quasilikelihood was used for number of floral displays) with temperature and precipitation as fixed effects and site as random effects. Significant trends (bold) were determined by confidence intervals not overlapping zero. Individuals of the species were collected during the flowering season of 2019 in a climatic grid consisting of grasslands in Western Norway.

P. erecta	**Temperature**	**Precipitation**	**Interaction**
Plant size (log units, *10$_2$)			
Reproductive height	-4.8 (±11.3)	-10.0 (±10.0)	0.2 (±15.2)
Total biomass	12.2 (±15.1)	-14.4 (±14.7)	0.19 (±20.4)
Vegetative biomass	12.9 (±16.1)	-13.0 (±15.6)	0.19 (±21.6)
Reproductive biomass	6.4 (±12.1)	**-24.1 (±11.7)**	0.2 (±16.2)
Relationship – plant size and reproduction (log units, *10$_2$)			
Reproductive allocation	-5.8 (±9.8)	-9.7 (±9.5)	3.5 (±13.2)
Floral displays/g plant mass	11.5 (±10.9)	-10.2 (±10.6)	0.17 (±14.7)
Display area/g plant mass	10.9 (±11.1)	-15.6 (±10.8)	3.5 (±14.9)
Floral traits			
Floral displays (n)	0.3 (±0.2)	**-0.3 (±0.2)**	0.2 (±0.2)
Display area (mm$_2$)	-0.2 (±3.4)	**-7.2 (±3.3)**	3.8 (±4.6)
Flower diameter (mm)	-0.02 (±0.2)	**-0.4 (±0.2)**	0.2 (±0.2)
Flower mass (mg)	**-0.2 (±0.1)**	0.02 (±0.1)	-0.1 (±0.1)
Petal length (mm)	-0.1 (±0.2)	-0.1 (±0.2)	0.07 (±0.3)
Petal width (mm)	-0.07 (±0.1)	-0.03 (±0.1)	0.04 (±0.1)

Table 6: The slopes of the changes in values of plant size, the relationship between plant size and reproductive organs (Reproductive allocation = Reproductive biomass/Total biomass) and floral traits per unit of increased, scaled temperature and precipitation with standard errors (± SE) for the species *R. acris*, retrieved from linear mixed models (exception: a generalized linear mixed model with penalized quasilikelihood was used for number of floral displays) with temperature and precipitation as fixed effects and site as random effects. Significant trends (bold) were determined by confidence intervals not overlapping zero. Individuals of the species were collected during the flowering season of 2019 in a climatic grid consisting of grasslands in Western Norway.

R. acris	**Temperature**	**Precipitation**	**Interaction**
Plant size (log units, *10$_2$)			
Reproductive height	**28.6 (±13.1)**	-4.7 (±13.2)	2.2 (±14.2)
Total biomass	**36.9 (±16.8)**	-0.17 (±16.9)	-8.0 (±18.2)
Vegetative biomass	**40.8 (±18.3)**	1.1 (±18.4)	-9.3 (±19.8)
Reproductive biomass	23.6 (±13.1)	-4.36 (±13.2)	-4.2 (±14.1)
Relationship - plant size and reproduction (log units, *10$_2$)			
Reproductive allocation	**-13.4 (±6.0)**	-4.2 (±6.0)	3.8 (±6.5)
Floral displays/g plant mass	8.4 (±9.0)	**-19.1 (±9.0)**	2.3 (±9.7)
Display area/g plant mass	5.8 (±12.0)	-18.2 (±12.1)	11.3 (±13.0)
Floral traits			
Floral displays (n)	**0.5 (±0.1)**	**-0.2 (±0.1)**	-0.03 (±0.1)
Display area (mm$_2$)	-6.9 (±9.6)	1.27 (±9.7)	19.7 (±10.4)
Flower diameter (mm)	-0.2 (±0.3)	0.07 (±0.3)	**0.7 (±0.4)**
Flower mass (mg)	0.3 (±0.3)	-0.3 (±0.3)	-0.2 (±0.3)
Petal length (mm)	**-0.3 (±0.1)**	-0.08 (±0.1)	**0.3 (±0.1)**
Petal width (mm)	0.1 (±0.1)	-0.2 (±0.1)	0.09 (±0.1)

Table 7: The slopes of the changes in values of plant size, relationship between plant size and reproductive organs (Reproductive allocation = Reproductive biomass/Total biomass) and floral traits per unit of increased, scaled temperature and precipitation with standard errors (± SE) for the species *V. officinalis*, retrieved from linear mixed models (exception: a generalized linear mixed model with penalized quasilikelihood was used for number of floral displays) with temperature and precipitation as fixed effects and site as random effects. Significant trends (bold) were determined by confidence intervals not overlapping zero. Individuals of the species were collected during the flowering season of 2019 in a climatic grid consisting of grasslands in Western Norway.

V. officinalis	**Temperature**	**Precipitation**	**Interaction**
Plant size (log units, *10$_2$)			
Reproductive height	9.0 (±7.2)	-1.8 (±8.8)	-0.9 (±9.5)
Total biomass	15.3 (±8.2)	-7.3 (±10.0)	**23.0 (±10.8)**
Vegetative biomass	14.7 (±8.4)	-6.9 (±10.3)	**25.0 (±11.0)**
Reproductive biomass	16.5 (±14.6)	-8.2 (±17.8)	12.2 (±19.2)
Relationship – plant size and reproduction (log units, *10$_2$)			
Reproductive allocation	1.2 (±11.3)	-0.9 (±13.7)	-10.8 (±14.8)
Floral displays/g plant mass	-8.6 (±7.6)	-0.6 (±9.3)	-7.4 (±10.0)
Display area/g plant mass	-8.9 (±6.3)	2.3 (±7.7)	-5.5 (±8.3)
Floral traits			
Floral displays (n)	0.1 (±0.1)	-0.1 (±0.1)	0.16 (±0.1)
Display area (mm$_2$)	-0.13 (±10.6)	1.6 (±12.9)	3.8 (±13.9)
Flower diameter (mm)	0.04 (±0.3)	-0.03 (±0.3)	0.02 (±0.4)
Flower mass (mg)	0.03 (±0.04)	-0.04 (±0.05)	0.03 (±0.06)
Petal length (mm)	-0.06 (±0.2)	0.05 (±0.2)	0.1 (±0.2)
Petal width (mm)	0.01 (±0.1)	0.1 (±0.1)	-0.03 (±0.2)

Discussion

To investigate how reproductive allocation and floral traits change under different climatic conditions, I collected insect-pollinated forbs along a temperature- and precipitation gradient. The results show that the community of insect-pollinated forbs do allocate more of their total biomass to reproductive organs at alpine sites compared to boreal sites. At the community level, temperature was the most important factor for plant size, reproductive allocation and floral trait distributions. Even though the range of precipitation is large (nearly 2500 mm between the driest and wettest site), I found no effects of precipitation. Four of the species present in the climatic grid responded differently to changes in temperature and precipitation, and each seemed to have their own species-specific strategies. *C. rotundifolia* responded strongly to increased temperature in terms of plant size and floral traits but was not affected by precipitation at all. *P. erecta* showed the opposite pattern with almost no significant effects of temperature, but instead several floral traits were affected negatively by increased precipitation. *R. acris* responded to both increased temperature and precipitation and was the only species out of these four that followed the trend of the community with an increase in reproductive allocation at lower temperatures. *V. officinalis* changed minimally along the gradients. I will first discuss changes in plant size along the gradients, as this is important for understanding the relationship between plant productivity, competition for resources and allocation to reproduction. Furthermore, I will look into trends of reproductive allocation and floral traits and try to explain the different responses of the community and the species. Finally, I will discuss potential effects of climate change on the communities of insect-pollinated forbs and the four species.

Effects of temperature and precipitation on overall plant size

Plant sizes within these grassland communities increased towards higher temperatures, coinciding with a well-known pattern; the overall plant size decreases drastically with increasing elevation (Halbritter et al., 2018; Körner et al., 1989). This indicates that competition between plants for light are higher at warmer sites (Arft et al., 1999; He et al., 2013; Olsen et al., 2016). *C. rotundifolia* and *R. acris* followed the trend of the community and clearly increased in plant size with increasing temperature as well. For *R. acris,* these results are consistent with previous studies which have found variation in plant size of this species at different elevations (Totland, 2001) and that it showed plastic responses when moved to a warmer and wetter climate (Delnevo et al., 2018). *P. erecta* and *V. officinalis* did not follow the same trend, and the plant size of these two species remained constant along the temperature gradient. *V. officinalis* is the only out of the four species that does not occur at the alpine sites (‘Legeveronika’, n.d.), which suggests that it is not equipped, in terms of traits, to cope with the low temperatures and short seasons of these habitats. On the other hand, *V. officinalis* was the only species that showed an increase in growth with the interaction between temperature and precipitation. Although it cannot tolerate alpine conditions, it seems to be a strong competitor in habitats where plant productivity is high. This is emphasized by a study by Olsen et al. (2016), which found that *V. officinalis* reduced its vegetative growth when competitors were removed, indicating that vegetative growth is of higher priority when competition with other plants is high. Since plant productivity and competition generally increase with both warmer and wetter climate (Arft et al., 1999; Wu et al., 2011), I would have expected more species to show such interactive effects.

Considering that there is a difference of nearly 2500 mm in annual precipitation between the driest and the wettest site, it is surprising that precipitation seemed to have no effects on plant size. The community and all four species showed no change in reproductive height, total biomass or vegetative biomass along the precipitation gradient. My findings coincide well with earlier studies on vegetative traits conducted in the same grid, which also found mostly weak and non-significant effects of precipitation (Guittar et al., 2016; Gya, 2017). Although not significant, it is still noteworthy that all measures of plant size investigated showed a negative trend of increased precipitation, both at the community level and for the four species. While other studies have looked at overall plant productivity (Wu et al., 2011), I only included forbs in my study. There is evidence that graminoids benefit more from increased temperature and precipitation, and that forbs are negatively affected by the higher competition from graminoids (Klanderud et al., 2015). This could be related to the negative trends of precipitation and the lacking interactive effects of this study. An alternative explanation for the negative trends of precipitation could be that water is not a limiting resource in these communities, meaning that more precipitation is not leading to higher productivity. Instead, the precipitation levels of the wetter sites could be closer to the point where stress caused by too much precipitation is induced. For instance, stress related to water logging or a thick snow cover which shortens the growing season could lead to a decrease in plant productivity (Elzenga and Van Veen, 2010; Jonas et al., 2008).

Effects of temperature and precipitation on reproductive allocation

One of the questions asked in this study was if reproductive allocation changes with temperature and/or precipitation. With decreasing temperature, plants within these communities became smaller but at the same time they dedicated a larger fraction of their total biomass to flowers and flower stalks, which matches my prediction. This is also consistent with the findings of Fabbro and Körner (2004) in a similar community-level study. The change in reproductive allocation could be interpreted as a shift from high competition for light and/or other resources in the lowland to high competition for pollinators in the alpines. High competition for light and resources means that vegetative growth is a matter of high priority, thus allocation to sexual reproduction is reduced. In the alpines, plant productivity and competition for resources is lower (Arft et al., 1999; Halbritter et al., 2018; Körner et al., 1989), but competition for pollinators is increased due to lower pollinator abundance, which means that the plants need to invest more of their biomass in reproductive organs in order to get sufficiently pollinated (Fabbro and Körner, 2004; Hemborg and Karlsson, 1998; Kawano and Masuda, 1980). Even though reproductive allocation increased at lower temperatures, there were no change in the number of floral displays per gram plant mass or total display area relative to total plant mass at the community level. This implies that alpine plants need to invest more of their biomass to achieve the same output in pollinator attractiveness in relation to plant size compared to lowland plants. The four species showed different trends for reproductive allocation along the temperature gradient. *C. rotundifolia*, *P. erecta* and *V. officinalis* showed no change in reproductive allocation along the temperature gradient. *V. officinalis* is not experiencing the potentially low pollinator abundances at alpine sites since it is not growing in these habitats, which could explain the lacking response of this species. Only *R. acris* followed the trend of the community with increased reproductive allocation at lower temperatures. This suggests that the overall community response is rather caused by species turnover than by intraspecific changes along the temperature gradient.

The different strategies in reproductive allocation between the four species might be explained by their relationship with pollinators. *R. acris* is not able to self-pollinate and is fully dependent on insect pollinators (Totland, 1993). It is almost exclusively visited by flies, which are inefficient pollinators (Totland, 1994). Consequently, the flowers need to be visited several times in order to get sufficiently pollinated. To compare, other studies have found that only one visit by a bumblebee is enough (Molau et al., 1989; Stenstrom and Molau, 1992). If flowers of *R. acris* and other fly-pollinated species need several visits, this would increase the competition for pollinators, especially at high elevations where pollinator abundance is low (Totland, 2001). Investing more biomass in flower organs could therefore be a good strategy for species that do not have the benefit of getting pollinated by bumblebees. The fact that *R. acris* have green photosynthesizing achenes could help the plants keep the photosynthetic activity high enough and mitigate the cost of investing less in vegetative organs (Galen et al., 1993). On the other hand, *P. erecta* did not show the same increase in reproductive allocation despite that this species is also self-incompatible and mainly fly-pollinated (Hegland and Totland, 2005; Matfield et al., 1970). It has been suggested that this species has some of the characteristics that could make it work as a “magnet species” among fly-pollinated species, which is a particularly attractive species that facilitates pollinator visitation rates for other flowering species (Hegland and Totland, 2005). This is emphasized by another study where they found that pollination of *P. erecta* was high no matter if other flowering species were abundant or not (Goyder, 1983). The characteristics that are regarded highly attractive to flies are long flowering period and radial symmetric yellow flowers (Hegland and Totland, 2005; Lázaro et al., 2008). Despite that *R. acris* has similar characteristics, *P.* erecta are found to get substantially more pollinator visits, both by flies and other pollinator groups, than *R. acris* (Hegland and Totland, 2005). *P. erecta* could possibly be such a strong competitor for pollinators that it does not have to increase allocation to reproductive organs when pollinator abundance decreases.

For *C. rotundifolia*, no change in reproductive allocation with temperature could perhaps be explained by their tight relationship with bumblebees. In addition to flies (Lázaro et al., 2008), bumblebees are also important pollinators of alpine habitats (Bingham and Orthner, 1998; Yu et al., 2012) as they are more cold-tolerant than bees (Bishop and Armbruster, 1999). Bumblebees are efficient pollinators for *C. rotundifolia*, depositing more pollen per visit to their flowers than any other pollinator group (Bingham and Orthner, 1998). It has been suggested that the efficient pollination by bumblebees in addition to the increased flower longevity found for this species at higher elevations, compensates for the lower pollinator abundance and visitation rates in the alpines (Bingham and Orthner, 1998). If this is the case, it could mean that investing more biomass in reproductive organs is less necessary for this particular species. *C. rotundifolia* also has tubular-shaped and violet flowers, which are traits bumblebees prefer (Lázaro et al., 2008; Raine and Chittka, 2007). This is possibly making the species a strong competitor in attracting this group of pollinators.

Previous studies have found that low precipitation levels have the potential of reducing number of flowers and reproductive allocation (Galen et al., 1999; Lambrecht and Dawson, 2007; Xie et al., 2016). I found no significant effects of precipitation on reproductive allocation indicating such drought stress. What separates the other studies from mine, is that they were conducted in precipitation grids that included sites with lower precipitation levels. The driest sites of the studies by Lambrecht and Dawson (2007) and Xie et al. (2016) had a mean annual precipitation of 380 mm and 110 mm, respectively. Since I found no signs of the same trends, it suggests that the driest site of this study, with an annual precipitation of 596 mm, is not dry enough to cause any drought stress for the plants. It is possible that the precipitation range of the study only includes relatively favorable precipitation levels which are not inducing enough stress to cause any changes in either plant growth, as we saw earlier, or reproductive allocation. Although the precipitation gradient of this study covers a large range, it does not include extremely low or high precipitation levels, if compared to all biomes of the world (Mucina, 2019). A second explanation of the non-significant effects of precipitation is that mean annual precipitation could be an inadequate explanatory factor. It does not take into account underlying factors that are more important for the plants' water availability, for instance the distribution of precipitation between seasons, if precipitation falls as rain or snow, soil type or the soil's water-holding capacity (Moles et al., 2014). There was no effect of the interaction between temperature and precipitation either, although it seems that reproductive allocation is somewhat higher at dry alpine sites compared to dry boreal sites, while temperature matters less at wet sites.

Effects of temperature and precipitation on floral traits

To investigate how floral traits are affected by changes in temperature and precipitation, I looked at how many floral displays the plants produced in addition to several traits related to size of floral displays (i.e. display area, flower mass, flower diameter, petal length and width. I also investigated proportions of floral colours in the communities.

The results show that the forbs within these communities produced more floral displays at higher temperatures. *C. rotundifolia* and *R. acris* followed the same trend of increasing number of floral displays. Since I found the plants at the community level and these two species to also increase in overall plant size as it got warmer, it could indicate that production of flowers is at least partly dependent on plant size, in addition to climate, as suggested by Meineri et al. (2014). *V. officinalis* did not show an increase in floral displays along any of the gradients, despite that plant size increased as it got warmer and wetter, meaning that there must be other factors than plant size involved as well.

R. acris and *P. erecta* significantly reduced the number of floral displays with increasing precipitation, suggesting that high levels of precipitation have a stress-inducing effect. At the same time there was no effect of precipitation on number of floral displays at the community level or for the other species. Because *R. acris* and *P. erecta* are self-incompatible (Matfield et al., 1970; Totland, 1994), they are vulnerable to high levels of precipitation during flowering season as this reduces pollinator activity sharply and in worst case limits the reproductive output (Totland, 1994). If pollinator visitation rates are low due to rainfall, it could be a better strategy to not waste resources producing flowers that would not get sufficiently pollinated anyway. *C. rotundifolia* has down-facing flowers which protects the nectar and pollen grains when it rains (Aizen, 2003). Moreover, bumblebees remain more active than other pollinator groups during rainfall (Tuell and Isaacs, 2010). Even though outcrossing is the dominant type of fertilization, *C. rotundifolia* and *V. officinalis* are able to self-pollinate (Bielawska, 1973; Scalone et al., 2013). For these reasons, *C. rotundifolia* and *V. officinalis* could be less vulnerable to high levels of precipitation compared to *R. acris* and *P. erecta*. High precipitation levels will also increase the amount of snow and shorten the growing season in alpine and subalpine habitats. A previous study conducted in parts of the same climatic grid as in this study found that late snowmelt at the wet alpine site caused *R. acris* to drastically reduce flower production (Delnevo et al., 2018). Even though I only detected significant negative trends for *R. acris* and *P. erecta*, figure 9 shows that the combination of cold and wet conditions results in the lowest number of floral displays for all species. This could indicate that snow cover and shorter seasons limit flower production for both the community and all four species to various extent.

Despite an increase in reproductive allocation at lower temperatures, the floral displays had the same area and mass across the temperature gradient at the community level. I also only detected a few significant effects of temperature at species level; *C. rotundifolia* and *R. acris* showed an increase in petal length at lower temperatures, while *P. erecta* showed an increase in flower mass. In general, size of floral displays thus remained constant along the temperature gradient, in contrast to my prediction of larger floral displays. These findings coincide with the findings of Fabbro and Körner (2004), who also found flower sizes to be very similar along an elevational gradient. I did not see the same clear increase in flower size of *C. rotundifolia* at higher elevations as other studies have found, which is suggested to be an adaptation to larger bumblebees in the alpines (Maad et al., 2013). The contrasting findings could be a result of different methodology for measurements of flower size traits, as the traits measured in the study by Maad et al. (2013) are quite different compared to the traits of my own study. I also had a smaller sample size. Another explanation could be that body size of bumblebees are more constant along the temperature gradient of this study. However, this was not investigated in this study. Previous studies have found that flower longevity increases at higher elevations (Fabbro and Körner, 2004; Stenstrom and Molau, 1992). This adaptation is found for *R. acris* and *C. rotundifolia* as well (Maad et al., 2013; Totland, 1994). Increased flower longevity could be an important adaption to lower pollinator abundance, as it gives each flower more time to get sufficiently pollinated (Totland, 1994). It is possible that this adaptation leads to higher total visitation rates over the growing season and thus higher reproductive output per unit floral size at high elevations, and that increasing flower longevity is less resource demanding than producing larger flowers. If the forbs have increased flower longevity at the alpine sites of this study, it could perhaps explain why I did not find a clearer increase in size of floral displays with decreasing temperatures.

Increased precipitation had significant negative effects on display area and flower diameter for *P. erecta,* while there were no effects of precipitation alone at the community level or for the other three species. More interestingly, petal length and flower diameter of *R. acris* significantly increased with the interaction between temperature and precipitation. Such interactive effects could possibly exist for size of floral displays of all the four species, even though significant effects were not detected. Display area and petal length of all four species decreased with increased precipitation at cold sites but had a smaller decrease or even an increase at warm sites (Figure 9). This could mean that precipitation is a resource in combination with higher temperatures leading to an increase in plant productivity (Wu et al., 2011), possibly resulting in that plants have more resources to produce larger flowers. In combination with low temperatures, precipitation could have the opposite effect and be a stress-inducing factor, leading to thicker snow cover, shorter growing season and reduced plant productivity (Delnevo et al., 2018).

To investigate if there could be a relationship between floral colours and climatic conditions, as a result of differences in the species composition of the pollinator communities, I studied the proportions of floral colours at 12 sites, both in terms of number of species and species weighted after their abundance. Yellow seemed to be the most common floral colour overall, especially when species were abundance weighted. This colour is associated with a generalistic pollinator strategy and is visited by several different groups of pollinators (Kevan, 1972; McCall and Primack, 1992). Having yellow flowers could therefore be an efficient strategy under several different climatic conditions. The proportion of white seemed to be higher at alpine sites, both in terms of number of species and when species were abundance weighted. An increase of white along an elevation gradient was also found in the study by Arnold et al. (2009) conducted in alpine meadows, but the trend was not significant. Still, it could be related to the fact that flies dominate the pollinator communities of alpine habitats (Totland, 1993), since studies have shown that white flowers, together with yellow flowers, consistently attracted flies (Lázaro et al., 2008). The proportions of pink and violet did not seem to change noteworthy between the temperature levels. Since bees, which prefer violet/blue flowers (McCall and Primack, 1992), become less abundant in the alpines (Totland et al., 2013), I would have expected to see a clearer difference in the proportion of violet between boreal and alpine sites. In addition to flies, bumblebees are highly present in the alpines (Bingham and Orthner, 1998; Yu et al., 2012), and they also prefer violet and blue flowers (Raine and Chittka, 2007). This could explain why the proportion of this colour seemed to be relatively similar between temperature levels. To my knowledge there are no studies investigating how precipitation affects proportion of floral colours, but bees are found to dominate in dry habitats, while flies are more abundant in wetter habitats (Devoto et al., 2005). Despite this, I saw no clear differences in colour proportion between precipitation levels indicating a shift from a bee-dominant to a fly-dominant pollinator community, especially not when species were abundance weighted. Although some possible patterns could be seen between temperature levels, it is important to mention that the dataset was relatively small and that this was not statistically tested.

Possible effects of climate change

My results showed that plant size increased, while reproductive allocation decreased at warmer sites at the community level. This suggests that a warmer climate in the future will lead to an increase in vegetative growth and competition for light and resources (Arft et al., 1999; Wu et al., 2011), possibly leading to a decrease in reproductive allocation. *C. rotundifolia, R. acris* and *V. officinalis* are likely to handle the increased competition well, since they were found to be able to increase their total- and vegetative biomass as it got warmer or warmer *and* wetter. In general, I found few significant effects of precipitation on plant size of the investigate community and species of forbs, but many negative trends could indicate that we could start to see negative effects if precipitation increases substantially in the future, especially if abundance of graminoids increases (Klanderud et al., 2015). *R. acris* and *P. erecta* responded to increased precipitation by reducing number and/or size of floral displays, indicating that these two species are more vulnerable to higher precipitation levels, especially if rainfall strikes in the flowering season (Totland, 1994), as discussed earlier. At the same time, some of the negative effects and trends of increased precipitation on both plant size and floral traits of the community and individual species could be caused by snow cover and short growing seasons (Delnevo et al., 2018; Jonas et al., 2008), which means that these limitations might become smaller in the future when temperatures increase in the alpines.

We know that species richness and abundance of pollinators decreases in alpine environments due to harsh conditions (Totland, 1993, 2001; Totland et al., 2013). With higher temperatures in the alpines, it could seem logical that more insects will expand their range to higher elevations causing an increase in pollinator activity, however this seems not to be the case. Studies have shown that pollinators lag behind and are not expanding their range fast enough to keep pace with climate warming (Bedford et al., 2012; Kerr et al., 2015). Climate change is also regarded as one of the causes of the current global decline in pollinators (Potts et al., 2010). Even though my results did not show that the community or the four species are excessively and directly threatened by climate change in the nearest future, what happens to the pollinator communities and the plant-pollinator interactions will be crucial. For instance, my findings imply that *C. rotundifolia* is not particularly vulnerable to the direct effects of climate change, as this species showed positive effects of increased temperature and no effects of increased precipitation. At the same time, this species seems to be dependent on bumblebees (Bingham and Orthner, 1998). Studies have found that bumblebees have narrow climatic niches (Williams et al., 2007) and that their ranges are contracting with climate change worldwide (Kerr et al., 2015). This could potentially cause problems for pollination and thus reproduction of *C. rotundifolia* in the future. In addition, only *R. acris* showed an increase in reproductive allocation at higher elevations. If the other species are not able to increase their allocation to reproduction and thus adapt to the increased competition for pollinators, they could be vulnerable to pollinator declines.

Limitations of the study and future research

In general, I found few significant effects of the interaction between temperature and precipitation. There could exist trends at the community level that were not detected because of low statistical power, as I was only able to collect parts of the community of insect-pollinated forbs at the sites. Huge variation in plant size and floral traits between species could also have made such interactions difficult to detect. I suspect that there exist trends of the interaction at species level as well, as display area and petal length of all four species trended in the more or less opposite direction at warm and cold sites. In retrospect, I see that I should have made sure to collect these species at all sites where they occur. *P. erecta* was for instance not collected at the two driest alpine sites because it was less abundant there. It would of course have been preferable to have trait measures of these species at all possible sites, as this would have given the analyses more statistical power. Lack of statistical power also became a problem when investigating floral colour along the gradients. Although I was able to visualize the proportions of floral colours at each site, I did not have enough replicates in the dataset to conduct a proper statistical analysis. It is possible that this problem could have been solved somehow, for instance by using abundance data from earlier years, which includes more replicates than the dataset from 2017.

Community weighted means, where trait values are weighted after relative abundance of a species, is a common approach in trait-based ecology (Miller et al., 2018). This approach would have been useful in this study as well, as it could have provided a more realistic picture of the distribution of reproductive strategies and floral traits in these communities. It has been used in earlier studies on vegetative traits conducted at the same sites (Guittar et al., 2016; Gya, 2017), and the results have turned out to be somewhat different compared to results of analyses of non-weighted trait data (Gya, 2017). For this analysis, one should have collected traits for minimum 80% of the plant community (Pakeman and Quested, 2007). Collecting all the species needed at flowering stage was not logistically possible in this study but is something that should be of high priority for future investigations on reproductive allocation and floral traits at these study sites.

Increased flower longevity at higher elevations (Fabbro and Körner, 2004; Totland, 1994) could be an important adaptation to ensure sufficient pollination when pollinator abundance is low, as discussed earlier. Since this study, along with others (Fabbro and Körner, 2004; Stenstrom and Molau, 1992; Totland, 1994), showed no increase in size of floral displays with increasing elevation, it would be of interest to assess if increased flower longevity could be a lower-cost substitute for having larger and more attractive flowers in alpine habitats where plant-productivity is lower (Billings and Mooney, 1968). More knowledge about the pollinator communities at these sites is also needed, as this would make it possible to link the findings of this study to the pollinators in addition to the climatic factors. For the individual species, I detected some trends that could possibly be explained by their relationship with a particular pollinator group, but it remains unclear how strongly the pollinator communities are affecting reproductive allocation and floral traits of these species. No previous studies have looked at how species composition and abundance of the pollinator communities vary with temperature and precipitation in the climatic grid where this study was conducted. We know that reproductive allocation and floral traits are highly linked to the pollinator community and that the traits of insect-pollinated plants reflects which pollinators are present and vice versa (Hegland and Totland, 2005; Junker et al., 2015). To get a better understanding of the relationship between reproductive allocation, floral traits and pollinators, which is important for predicting effects of climate change on these communities, we need to know more about the pollinators in these ecosystems.

Conclusion

This study has shown that the community of insect-pollinated forbs responds to increased temperature by increasing their overall plant size and number of floral displays, while decreasing allocation to sexual reproduction. Despite this, size of floral displays remained constant along the temperature gradient. No trends were detected for increased precipitation or the interaction between temperature and precipitation at the community level. The focal species responded quite differently to changes in temperature and precipitation, and my results indicate that they have different reproductive strategies possibly caused by differences in the relationship with pollinators. More research on pollinator species composition, abundance and visitation rates in these communities is needed to gain a better insight into the relationship between plants' reproductive traits and pollinators. This will also be important for predicting effects of climate change on reproductive strategies and success of forbs.

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Appendix 1

Table A1: An overview of the species collected at each site. Ten individuals per species per site were collected for measurements of plant size and floral traits during the flowering season of 2019. Site abbreviations: Fau = Fauske, Vik = Vikesland, Arh = Arhelleren, Ovs = Øvstedal, Alr = Ålrust, Hog = Høgsete, Ram = Rambera, Ves = Veskre, Ulv = Ulvehaugen, Lav = Låvisdalen, Gud = Gudemedalen, Skj = Skjellingahaugen.

Species	**Fau**	**Vik**	**Arh**	**Ovs**	**Alr**	**Hog**	**Ram**	**Ves**	**Ulv**	**Lav**	**Gud**	**Skj**
Achillea millefolium	x	x			x	x						
Antennaria dioica									x			x
Atocion rupestre									x			
Bistorta vivipara							x	x		x		x
Campanula rotundifolia	x	x	x	x	x	x	x	x	x	x	x	x
Cerastium alpinum										x		
Cerastium cerastoides										x		
Chamaepericlymenum suecicum							x					
Dianthus deltoides	x											
Dryas octopetala										x		
Euphrasia stricta							x	x				
Euphrasia wettsteinii									x			x
Geranium sylvaticum	x		x		x						x	
Hieracium pilosella	x			x	x							
Hypericum maculatum			x	x								
Knautia arvensis	x				x							
Leontodon autumnalis		x						x				
Leucanthemum vulgare	x											
Lotus corniculatus	x				x							
Melampyrum pratense			x									
Parnassia palustris											x	x
Phyllodoce caerulea							x					
Pinguicula vulgaris							x	x		x		x
Potentilla erecta		x	x	x	x	x	x	x			x	x
Prunella vulgaris					x			x				
Ranunculus acris	x	x	x	x	x	x		x	x	x	x	x
Rhinanthus minor					x						x	
Saxifraga aizoides							x				x	x
Saxifraga stellaris										x		
Silene acaulis										x		
Silene dioica				x								
Solidago virgaurea			x								x	
Trientalis europaea			x				x	x				
Trifolium medium	x											
Trifolium pratense					x	x						
Trifolium repens		x				x			x			
Vaccinium vitis-idaea						x	x		x		x	
Veronica alpina										x		
Veronica chamaedrys	x	x	x			x						
Veronica officinalis	x	x	x	x	x	x	x					
Viola biflora							x			x		
Viola canina					x	x		x				
Viola palustris						x						
Viola tricolor	x	x			x	x						
Viscaria vulgaris	x											

Appendix 2

SeedClim / FunCaB / INCLINE Dataset Metadata

Dataset: Floral traits in the SeedClim Grid (SG.18)

1. Dataset metadata

1. ***What is the content of the dataset***

The dataset contains floral traits measures and weighed biomass from the SeedClim grid (SG.18).

The dataset contains floral traits measures and weighed biomass of 42 forb species and 3 woody species (all insect-pollinated), from all 12 SeedClim sites.

The plants were collected between June 13th and August 2nd, 2019. The plants were weighed September 2019 – January 2020.

2. ***Data collection methods***

- Only insect-pollinated species were collected. Mainly forbs, but three woody species were included as these were prevalent components of the field layer vegetation at the sites: (*Dryas octopetala, Phyllodoce caerulea* and *Vaccinium vitis-idaea*)
- The plants were mostly collected within a radius of approximately 30-50 meters from the center of the field site (i.e. the climate station) and outside the fenced area. Individuals of the same species were collected minimum 2 meters apart.
- Only plants with minimum one open flower without signs of large damages or developing seeds were collected
- A digital caliper was used for all trait measurements, except from reproductive height.
- All individuals were dried for 72 hours in a drying oven with 65 °C before weighing.

The following traits were registered/measured in the field:

Reproductive height (RepH)

Measured from the ground and up to the top of the highest open flower, without stretching, lifting or moving the plant. The goal was to find the flower´s natural position in the terrain and how the pollinators see it.

Number of flowers per floral display (NFFD)

This point separates the species into two groups.

Solitary flower species: Only one flower per floral display. NFFD is always 1 for these species.

Inflorescence species: Floral display consists of several flowers. Here, NFFD is the sum of NB, NOF, NWF and S (see below).

Number of floral displays (NFD)

The total number of floral displays.

For species with solitary flowers: the sum of number of open flowers, closed flowers, buds, withered flowers and deflowered flowers that has started to develop seeds.

For species with inflorescences: the number of inflorescences.

The following traits, NOFD, NCFD, NBFD, NWFD and NSFD are only relevant for species with solitary floral displays

Number of open floral displays (NOFD)

The number of open flowers of the plant. Sometimes, some of these were damaged, for instance with lacking petals, the flower was wet or somehow had an altered shape. These were still counted as open flowers as long as they still had the majority of their petals left, did not look withered or had started to develop seeds.

Number of closed floral displays (NCFD)

Number of closed flowers. It could be challenging to decide if it was a bud or a closed flower. A closed flower is when a flower closes due to rain or night-time, but I also included flowers that were in the phase between bud and open flower, where you can clearly see most of the petals – they are just not unfolded yet. Stamen and stigma not visible.

Number of budded floral displays (NBFD)

Number of buds per plant. Flower buds that have not opened or started to open yet.

Number of withered floral displays (NWFD)

Flowers or buds that are withered because they are aborted/failure in development or due to damage, for example by insects. Deflowered floral displays that have gone through normal and successful development were not included here. They are counted as NSFD.

Number of seeded floral displays (NSFD)

Number of withered floral displays that contains seeds OR withered floral displays that look like they will continue to develop seeds.

The following traits, NB, NOF, NWF and S, are only relevant for species with inflorescences

Number of flower buds per floral display (NB)

The number of flower buds in a randomly chosen floral display (if there was more than one)

Number of open flowers per floral display (NOF)

The number of open flowers in the same randomly chosen floral display.

Number of withered flowers per floral display (NWF)

The number of withered flowers in the same randomly chosen floral display.

Number of seeds per floral display (S)

The number of withered flowers that already had seeds or were about to develop seeds in the same chosen floral display.

Diameter of floral display (D1 and D2)

Solitary floral displays:
Diameter of a randomly chosen flower. Chosen flowers were always open and without any large damages or signs of seed development. Diameters were measured where the flower were at its widest – from petal tip to petal tip.
Two diameters were measured (D1 + D2) for species with non-radial symmetric flowers

Inflorescence floral displays:
Diameter of the same randomly chosen floral display. The diameter was measured of the whole chosen inflorescence, always measured at the widest part. For most species, two diameters were measured. The second diameter was measured in the opposite direction of the first. For a few species, only one diameter was measured, for example *Trifolium sp.* and *Bistorta vivipara*, which have round floral displays.

Height of flower/floral display (H)
Solitary floral displays:
Height of the chosen flower was measured from as of the receptacle and up to the highest point of the flower. Depending on the flower, this could be either a petal, the stigma or the stamens.

For inflorescences:
Height of the chosen inflorescence/floral display was measured from the lowest part of the lowest flower and up to the highest point of the highest flower. Here, everything was considered a flower, no matter if it was an open flower, a closed flower, a bud or a deflowered flower with or without seeds. The whole inflorescence was included, no matter which condition the different flowers were in.

Petal width and length
Same for procedure for both solitary floral displays and inflorescences. Petal width and length was measured on a randomly chosen petal within the chosen flower or inflorescence used for the other measures. Both measures were done on the same petal. For species with petals of different shapes/sizes (*Viola sp., Veronica sp. ++)*, the widest petal was always used for measures.

Corolla diameter

Corolla diameter was measured where the petals meet and connect. Only measured for species with tubular shaped flowers.

Colour

Colour of petals. Most species had petals with only one colour, but some had two or three different colours or shades. Colour was determined with a premade colour chart with 5-6 coded shades of pink, violet, yellow, red, orange, blue and white. Maximum 3 colours/shades per individual was registered. Colour chart can be found here: https://drive.google.com/file/d/1DtUd8BPkufiEmnDcdLPte7GT9vIKt1XE/view?usp=sharing

The following organs were weighed for all individuals:

Total biomass

All aboveground biomass

Vegetative biomass

Mass of all aboveground vegetative organs

Reproductive biomass

Mass of all aboveground reproductive organs (flowers+flower stalks). Main rule used: reproductive part stars after the last foliage leave before the flower(s).

Mass of open flowers

Mass of all open flowers of an individual

Mass of flower stalks of open flowers

Mass of all the flower stalks of the open flowers of an individual. Not weighed for species without or with very small flower stalks.

Total flower mass

Mass of all flowers, including buds, withered flowers and seeds of an individual

Total flower stalk mass

Mass of all flower stalks of an individual. Not weighed for species without or with very small flower stalks.

Mass of individual open flowers

Up to 10 flowers were measured per individual

Mass of individual flower stalks

Mass of the flower stalks of the weighed individual open flowers. Flower stalk 1 belongs to Flower 1, and so on.

3. Dataset authors

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Dataset author	***role***	***contact info***
Gunvor Skjelstad	*Study design, collected and managed data (MSc student)*	gunvorskj@gmail.com
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4. Others who contributed to create the data

Contributor name	***role***	***contact info***
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5. *Where was it collected*

The data collected at all 12 sites of the SeedClim project. More information to the sites can be found in the SeedClim and FunCaB data documentation: https://docs.google.com/document/d/1RUOqkf8V_TqwZabu8LUjwQvephE5EClyYegV9wPAgfs/edit?usp=sharing

6. *When was it collected*

The data was collected June-August 2019 (fieldwork) and September 2019-January 2020 (labwork, weighing)

7. *Experimental / study design (describe here if do not described in project readme)*

The goal was to collect as many species from the community of insect-pollinated forbs as possible for each of the 12sites. I also included three insect-pollinated woody species (*Dryas octopetala*, *Phyllodoce caerulea* and *Vaccinium vitis-idaea*) as these were prevalent components of the field layer vegetation at the sites. The plant collection was done during the flowering season, between 13th of June and 2nd of August 2019. Because different species flower at different times in the season, I visited all 12 sites twice with 2-4 weeks between each visit. Usually, I spent one day per visit at each site. The most abundant species were prioritized and collected first. I also prioritized species that grow at several of the 12 sites and hence could provide useful data for sites comparisons. Some species flowered too early or too late in the season to be available during the period of my fieldwork. It was therefore not feasible to collect all the prevalent forbs. I collected between 7 and 14 species at each site, with an average of 10.5 species per site and a total of 45 different species across the grid. A full overview of species collected at each site can be found here: https://drive.google.com/file/d/1aeUqWziSuf-8S_dj6izZlHSnKhYYqrOQ/view?usp=sharing

At each site, I collected ten individuals of each species. They were mostly collected within a radius of approximately 30-50 meters from the center of the field site (i.e. the climate station). To achieve a representative selection, I chose individuals haphazardly by throwing an object, such as a pencil, and then collected the individual of the target species that the pencil pointed at. I only included mature individuals with a minimum of one open flower, avoiding individuals with any large damages and individuals that showed signs of developing seeds (i.e. entering post-flowering reproductive stages). This was done to make sure I measured all floral traits on flowers at the same stage; when they were open and available for pollinators. I did not follow this plant selection procedure strictly for less abundant species if there were few individuals to choose from. Instead, I then searched the area until I had ten individuals with minimum one open flower. All individuals of the same species were collected minimum 2 meters apart to make sure that they were different genetic individuals. When several shoots emerged from the same point in the ground, I assumed them to be of the same individual and therefore collected them as one. After measuring reproductive height, all of each individuals' aboveground biomass was collected. See descriptions above for how floral traits were registered/measured.

Each individual plant was put into a separate, marked paper bag and brought back to the lab. Immediately after return, the paper bags containing the plants were dried in a drying oven (Termaks TS 5410) on 65 °C for 72 hours. The dry plants were stored in plastic containers until all fieldwork was done and I could start the lab work.

To make sure that the samples were totally dry during weighing, they were redried in for minimum one day before they were weighed. I kept 3-4 samples at a time in a desiccator with silica gel while weighing. For each plant individual, plant organs were sorted into reproductive parts and vegetative parts using tweezers. The main rule used was that the reproductive part of a plant starts after the last foliage leaf before the flower(s). No foliage leaves were included in reproductive parts, but bracts were. Open flowers were weighed individually, maximum ten flowers per individual plant. Exceptions were the species *Leucanthemum vulgare, Hieracium sp., Leontodon autumnalis, Solidago virgaurea* and *Knautia arvensis* where I weighed the whole floral display as one flower. These species were treated as they have solitary flowers, even though they in reality are inflorescences. This was because the individual flowers were too small to be counted, measured and weighed individually. For all species, the flowers, including buds, withered flowers and seeds, were weighed together to with all flower stalks as a measure of the reproductive biomass. Finally, I weighed vegetative biomass (i.e., remaining above-ground mass) and the total biomass. All weighing was done on the same scale (VWR SM425i, with a resolution of 0.01 mg) to avoid errors due to differences between scales

8. *How was the data collected and developed (curation, corrections, etc) and where is it stored*

- The information from the field data sheets was manually entered into digital worksheets, manually proof-read and stored in Excel files.
- Obvious errors were corrected in the Excel sheets before starting the data analysis.
- A few individuals were deleted from the dataset, because they turned out to be of a different species than originally assumed, leaving a total of 1255 individuals for the analyses.
- The data is stored in the SeedClim Dropbox and can also be found here: https://drive.google.com/file/d/1sUvIR41RUq79xwUpu0Chj_Lk0paZYD5x/view?usp=sharing

9. *Other datasets within the project of direct relevance (e.g. predictor data)*

- All site-level predictor variables, especially

SG.101	SG temperature;
SG.102	SG precipitation
SG.103	SG soil moisture
SG.104	SG UVB
SG.106	SG TT soil chemistry
SG.107	SG gridded climate data

10. *Data usage – Publications*

11. *Data usage – Theses*

Skjelstad, Gunvor. 2020. “*Reproductive allocation and floral traits of insect-pollinated forbs along climatic gradients in semi-natural grasslands”*. MSc-theses, Department of biological sciences, University of Bergen.

2. Data Dictionary

Variable name	Variable type	variable range or levels	variable or factor level definition	how measured	units / formats
Date		DDMMYYYY			Date

Site	Treatment/ covariable	12 levels	Geographic location		Three first letter of site name
Temperature	Treatment/ covariable	Alpine	Tetraterm temperature ca. 6.5 C	Met.no data	Level and actual temperature
		Subalpine	Tetraterm temperature ca. 8.5 C	Met.no data	Level and actual temperature
		Boreal	Tetraterm temperature ca. 10.5 C	Met.no data	Level and actual temperature
Precipitation	Treatment/ covariable	Level 1 (continental)	Annual precip ca. 600 mm	Met.no data	Level and actual prec in mm
		Level 2 (sub-continental)	Annual precip ca. 1300 mm	Met.no data	Level and actual prec in mm
		Level 3 (sub-oceanic)	Annual precip ca. 2000 mm	Met.no data	Level and actual prec in mm
		Level 4 (oceanic)	Annual precip ca. 2700 mm	Met.no data	Level and actual prec in mm
Weather	covariable	word			factor
Registrator	covariable	Name (initials)			factor
Species	covariable	Species identity	Species name	visually	Species name (first three letters of latin names)
Floral display	covariable	Word/letter	Groups: Solitary (S) Inflorescence (I)	visually	factor
Shape of floral display	covariable	Word	Groups: Circular Square/flat Deep/Depth	visually	factor

ID					
Reproductive height (RepH)	Response	0-n	mm	measure	mm
Nr. of floral displays (NFD)	Response	0-n	count	count	count
Nr. of open floral displays (NOFD)	Response	0-n	count	count	count
Nr. of closed floral displays (NCFD)	Response	0-n	count	count	count
Nr. of budded floral displays (NBFD)	Response	0-n	count	count	count
Nr. of withered floral displays (NWFD)	Response	0-n	count	count	count
Nr. of floral displays with seeds (NSFD)	Response	0-n	count	count	count
Nr. of flowers per floral display (NFFD)	Response	0-n	count	count	count
Nr. of buds per floral display (NB)	Response	0-n	count	count	count
Nr. of open flowers per floral display (NOF)	Response	0-n	count	count	count
Nr. of withered flowers per	Response	0-n	count	count	count

floral display (NWF)					
Nr. of flowers with seeds per floral display (S)	Response	0-n	count	count	count
Diameter of floral display (D1 and D2)	Response	0-n	mm	measure	mm
Height of floral display (H)	Response	0-n	mm	measure	mm
Petal width (PW)	Response	0-n	mm	measure	mm
Petal length (PL)	Response	0-n	mm	measure	mm
Corolla diameter (CD)	Response	0-n	mm	measure	mm
Colour 1-3	Response	colour	colour	visually	factor
Comment	Any comments of potential relevance (or not) for entry, cleaning, and usage of the data. Comments often related to condition of particular individuals or categorical traits that were difficult to determine (for instance colour)				
Total biomass (TotalMass)	Response	0-n	g	weight	g
Reproductive biomass (RepMass)	Response	0-n	g	weight	g
Vegetative biomass (VegMass)	Response	0-n	g	weight	g
Mass of open flowers (OFMass)	Response	0-n	g	weight	g
Mass of stalks of	Response	0-n	g	weight	g

open flowers (OFSMass)					
Total flower mass (TFMass)	Response	0-n	g	weight	g
Total flower stalk mass (TFSMass)	Response	0-n	g	weight	g
Open flower 1-10 (OF 1-10)	Response	0-n	g	weight	g
Flower stalk 1-10 (FS 1-10)	Response	0-n	g	weight	g

Appendix 3

Data Sharing and Management Agreement BetweenTheFjords

This Data Sharing and Management Agreement regulates data management, availability, usage and ownership of data within the BetweenTheFjords group, led by Prof Vigdis Vandvik at the University of Bergen. The BetweenTheFjords group and is responsible for running two main experimental field systems in western Norway: the SeedClim climate grid$_{S}$ and LandPress climate gradient$_{L}$. Within these field systems, there are a number of externally funded research projects* and educational projects**, each with a designated Principal Investigator (PI), a number of researchers and students, and various collaborators and smaller and larger sub-projects.

The aim of this data sharing and management agreement is to facilitate collection of high-quality research data, to optimize data use and reuse, and to pre-empt data and metadata quality problems and misunderstandings or disputes over data ownership and rights.

BetweenTheFjords adhere to FAIR Data and Open Science principles as part of a broader commitment to maximise the use, re-use and impact of our hard-earned and publicly-funded data. This means, firstly, that we strive to collect, manage, store and publish our data in ways that ensure they are Findable, Accessible, Interoperable, and Reusable (i.e, FAIR). Further, we will share our data openly with the scientific community and beyond, as part of a broader Open Science commitment. However, note that we expect proper attribution to the original source when our data are used in downstream analyses, following community standards, and that we expect that the downstream use of the data, in most cases, should also adhere to FAIR Data and Open Science principles. All researchers, technicians and students collecting or using BetweenTheFjords data must sign this agreement.

I. Data collection and management agreement

1. All staff and students involved in collecting data in BetweenTheFjords and associated projects agree to follow the data gathering protocols agreed for each (sub)project, and to collect, record and report high-quality research data.
2. To avoid loss of data all staff and students commit to comprehensive data and metadata documentation by following protocols, accurately filling in field sheets, collecting accurate and comprehensive field notes, taking pictures in the field and/or lab, digitalizing datasheets, etc. All this should be done as early in the process to minimize risk of data loss and errors.

3. High-quality and well documented research data is key to ensure scientific reproducibility. It requires all data to be correctly and fully recorded and documented; including full openness and transparency about any data errors, data loss, uncertainties, data cleaning procedures, outlier treatment, etc..

II. Data documentation, ownership, usage, and sharing agreement

1. Unless otherwise specified, the raw data and accompanying data documentation belongs to the individual research projects and the institution of the PI of each specific research project.
2. All subprojects, data collection, data storage and data usage should be described in the project ReadMe file for each main project, and in a Data Documentation file for each dataset.
3. The complete data, including data documentation and code from the (sub)projects will be delivered to the PI upon completion.
4. Project PIs are responsible for collecting and safely storing project data and metadata
5. All data and code from the collaborating projects will be shared with the BetweenTheFjords group, and will be made available to the group members as needed and agreed.

III. Authorship rights to reports and downstream publications

1. All research project participants' authorship rights to reports and downstream publications based fully or in part from the project data, are regulated by international research ethics standards (cf. the Vancouver Protocol, and the Norwegian National Research Ethics Committees).
2. Following these standards, authorship credit should be based on;

a. substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data;

b. drafting the article or revising it critically for important intellectual content; and

c. final approval of the version to be published.

3. Authors should meet conditions a, b, and c. In addition to being accountable for the parts of the work they have done, an author should be able to identify which co-authors are responsible for specific other parts of the work. In addition, authors should have confidence in the integrity of the contributions of their co-authors.
4. BetweenTheFjord practice an open and inclusive authorships policy, this means that potential co-authors (anyone that has contributed to a) above), should be offered the opportunity to earn co-authorship by contributing to b) and c) above.
5. These rules apply to all project participants, from students to PIs.

6. Master students hold the rights to be lead author on papers primarily based on their thesis work for 12 months after graduating, unless agreed otherwise beforehand. If the student has not taken any initiative and made no progress towards publishing their thesis within this period, the right to be main author can be transferred to another project participant with co-author rights. The student still holds the rights to earn co-authorship rights based on conditions a) – c) above.
7. The PI regulates the usage of data in downstream research publications for each project.

IV. Data sharing outside of the BetweenTheFjords group

1. Unpublished project data can be used, shared or presented outside the projects but this should be explicitly agreed (on a case-by case basis with the relevant project PI).
2. Published data are openly available, but we note that intellectual ownerships and authorship rights of the data and broader meta-data (including the study design, raw data, data documentation, etc.) follows the data when shared outside of the BetweenTheFjords group. Any potential issues should be discussed before data sharing (following best community standards, roughly as reflected by our full data including data documentation are published under CC-BY of CC-BY-SA license or similar).
3. Any publications using the BetweenTheFjords data must follow current international research ethics standards such as the Vancouver Protocol, and the Norwegian National Research Ethics Committees).
4. BetweenTheFjords have an Open Science policy, and we will share and make date and code publicly available, either as a standalone dataset or when appropriate in databases. We expect that the original publication is appropriately cited when data is used in downstream publications.

V. Reference to projects in acknowledgement

1. All papers based on or using BetweenTheFjords project sites, data, or metadata shall refer to the project short name and funding source and project code in the acknowledgements.

By signing this agreement, I agree to comply by the BetweenTheFjords data sharing and management regulations set out above, and I gain rights to access and use project data as needed and agreed with the PIs.

Printed name: Gunvor Skjelstad

Place, date: Suldal, 02.06.2020

Signature: Gunvor Skjelstad

Appendix: BetweenTheFjords project overview as of January 2019: *Research projects **Educational projects $_{S}$Seedclim climate grid $_{L}$LandPress climate gradient:

Three-D*$_{S}$: Integrated assessment to aid mitigation of negative impacts by THREE global change Drivers on alpine biodiversity and ecosystem function. NORWEGIAN RESEARCH COUNCIL MILJØFORSK project 287801. kNOK 6.220. 2019 – 2022. PI Halbritter, Vandvik

EMERALD*$_{SL}$: Terrestrial ecosystem-climate interactions of our EMERALD planet. NORWEGIAN RESEARCH COUNCIL KLIMAFORSK project 294948. kNOK 29.992. 2019 – 2022. PI Stordal/ WP lead Vandvik

Fra vugge til grad*$_{S}$: Student research – from cradle to grade. Olav Thon Stiftelsen student active research project grant XXX. kNOK 1.500. 2019 – 2021. PI Vandvik, Førland, Gya, Lygre.

ExperTS$_{SL}$**: Experiments, Traits, Synthesis: Using knowledge from global ecological experiments to validate, assess, and improve trait-based theory. NORWEGIAN RESEARCH COUNCIL INTPART project 287784. kNOK 5.960. 2019 – 2021. PI Vandvik, Enquist

INCLINE*$_{S}$: Indirect climate change impacts on alpine plant communities. NORWEGIAN RESEARCH COUNCIL FRIMEDBIO project 274712. kNOK 11.009 .2018 – 2021. PI Vandvik, Töpper

RECITE$_{SL}$:** Research and Education Partnership in Climate Change Impacts on Terrestrial Ecosystems. NORWEGIAN RESEARCH COUNCIL INTPART project 274831. kNOK 5.787. 2018 – 2021.PI Vandvik

HiddenCosts*$_{L}$: Hidden costs of implementing afforestation as a climate mitigation strategy: A comprehensive assessment of direct and indirect impacts. NORWEGIAN RESEARCH COUNCIL KLIMAFORSK project 268243. kNOK 10.936. 2017 – 2020. PI Lee

LandPress*$_{L}$: Land use management to ensure ecosystem service delivery under new societal and environmental pressures in heathlands. NORWEGIAN RESEARCH COUNCIL MILJØFORSK project 255090. kNOK 12.983. 2016 – 2019.PI Vandvik, Velle

TraitTrain$_{SL}$**: Comparing climate change impacts on High North vs. Alpine ecosystems through research and training in trait-based approaches. SIU project HNP-2015/10037. kNOK 1.500. 2016 – 2018. PI Vandvik

FunCaB*$_{S}$: The role of Functional group interactions in mediating climate change impacts on the Carbon dynamics and Biodiversity of alpine ecosystems. NORWEGIAN RESEARCH COUNCIL KLIMAFORSK project 244525. kNOK 7.900. 2015 – 2018. PI Vandvik

DRIVE*$_{S}$: The plant root microbiome diversity and resilience in a changing climate. NORWEGIAN RESEARCH COUNCIL FRIMEDBIO project 240897. 2014 – 2017. PI: Vik

TransPlant$_{S}$:** SIU project UTF-2013/10074. kNOK 1.109. 2014 – 2016. PI Vandvik

SEEDCLIM*$_{S}$: The role of seeds in a changing climate - linking germination ecophysiology to population and community ecology. NORWEGIAN RESEARCH COUNCIL NORKLIMA project 184912. kNOK 9.566. 2008 – 2015. PI Vandvik

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Appendix 4

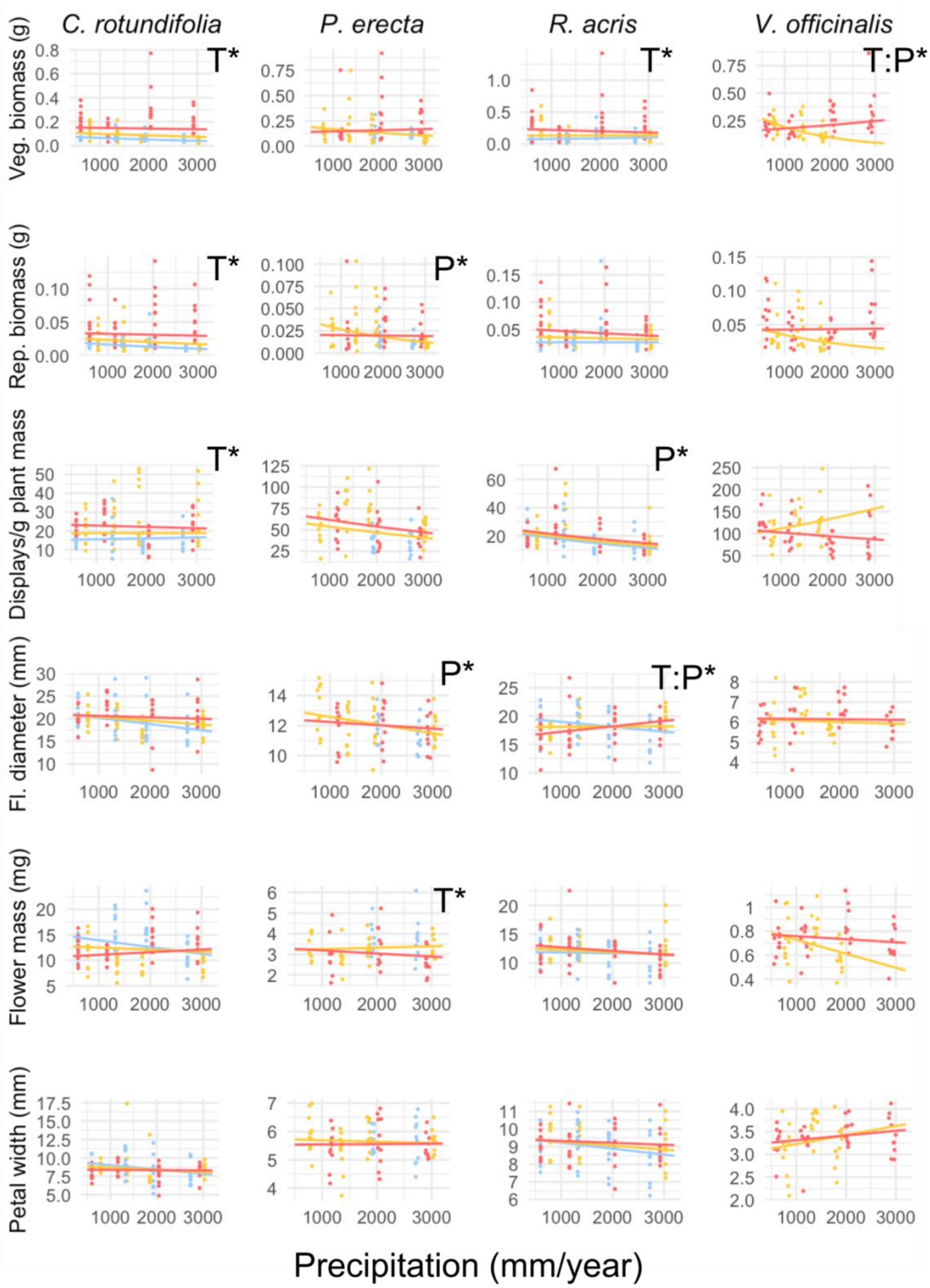

Figure A1: Figure caption on the next page

Figure A1 (previous page): Vegetative biomass, reproductive biomass, number of floral displays per gram plant mass, flower diameter and petal width of *Campanula rotundifolia*, *Potentilla erecta*, *Ranunculus acris* and *Veronica officinalis* and how these measures vary with changes in temperature (Mean of four warmest months: red = boreal sites (10.5 °C), yellow = subalpine sites (8.5 °C), blue = alpine sites (6.5 °C)) and precipitation (mean annual). The lines are predictions based on linear mixed with temperature and precipitation as fixed effects and site as random effects. Significant trends were determined with confidence intervals not overlapping zero and are here indicated by T* (Temperature), P* (Precipitation) or T:P* (Interaction between temperature and precipitation). Individuals of these species were collected during the flowering season of 2019 in a climatic grid of consisting of semi-natural grasslands in Western Norway.