

MASTER'S THESIS

Course code: BIO5010

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Flowering and seed production of
Cypripedium calceolus in two different
habitats in boreal coniferous forests

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Preface

I have always found nature to astonish me because of the grand diversities of all beings. I am grateful my children will have the same opportunity to be both puzzled and amazed through own experiences, and I hope this to be true for children belonging to the future.

The journey towards this thesis has been demanding, but through the challenges I have earned higher understanding and new perspectives. In search for knowledge more questions will be raised, thankfully.

I am sincerely grateful for all the help, support and time given to me by Kristian Hassel and Håkon Holien, and I want to thank Amy Eycott for statistical support (and the best cup of tea). My family also deserves praises, as much time has been given to work instead of them.

Steinkjer, May 28th 2020

Silje Stavdal

Abstract

Background: *Cypripedium calceolus* is a red-listed deceptive orchid with wide geographical distribution but is restricted by specific ecological demands. Habitat loss due to forestry is the main threat of the species in Norway. The species is protected in Norway and internationally and is considered a flag-ship species for conservation of biologic diversity. Sexual reproduction of the species requires pollinator presence, which is negatively affected by human destruction and fragmentation of natural habitats. Cessation of traditional agricultural practice negatively influences both pollinator presence and habitat quality for *C. calceolus*. We wanted to explore if we could find differences in life history strategy between orchid populations growing in spruce *Picea abies* and pine *Pinus sylvestris* dominated forest stands at Snåsa in the region of Trøndelag, central Norway.

Results: As expected, we found significant differences in environmental factors between spruce and pine forest related to terrain features, soil chemical parameters and light conditions. These differences translated into clear distinctions in the vegetation composition with higher occurrence of woody species in pine forest and a more herbaceous dominated vegetation in the spruce forest. Despite differences in environment both regarding abiotic and biotic factors, this was not reflected in differences in life history traits for *C. calceolus*. The only environmental factors influencing orchid traits were related to light availability. One possible tradeoff on ramet level was observed between ramet flower number and capsule size.

Conclusions: Despite differences in environmental factors and vegetation composition, the plant traits of *C. calceolus* measured did not differ between forest stands. One explanation could be that traits were not highly responsive to the environmental variables. Another possibility is that the populations we investigated have low genetical variance and/or low phenotypic plasticity. Both possibilities raise new questions related to the ecology and biology of *C. calceolus*. More research regarding local populations vitality should be initiated to gain more knowledge for future management and conservation to be based upon. Light availability has proved to be an important factor influencing *C. calceolus* in other studies, this was also experienced by us. Large and old clones have probably higher fitness due to enlarged nutrient availability and resource allocation.

Keywords: *Cypripedium calceolus*, deceptive orchid, boreal coniferous forest, canopy cover, terrain feature, soil chemical parameters, habitat differences, plant reproductive traits, tradeoffs.

Introduction

The life histories of species are the composition of the different major features of their life cycles related to birth, maturation, reproduction, and death. Life history traits directly affects these major features through different ways of combining traits to adjust fitness. Some major life history traits are for example age and size at maturity, number and size of offspring, age- and size-specific reproductive investments and length of life (Stearns 1992). Life history traits are results of natural selection (Darwin 1859). Natural selection is dependent on the variation in traits and fitness among individuals. Observed phenotypic differences in life history traits are in addition to their genetic background, formed by plastic responses to environmental factors such as nutrient availability, light conditions, temperature and water movement (Smith & Smith 2009).

Organisms have limited resources and must allocate available resources between survival, growth and reproduction, known as tradeoffs. A tradeoff is an advantage gained through the development of one trait at the cost of another trait (Stearns 1992). An example of tradeoff between survival and reproduction can be seen in semelparous and iteroparous plants (Cole 1954). An semelparous plant has only one chance to produce offspring and must go all in to achieve offspring production, whereas an iteroparous plant would still need resources for survival through to next growing season, and would therefore depend on resources contributing to survival rather than seed production (Charnov & Schaffer 1973, Cole 1954, Partridge et al. 1988, Young 1981). An example of tradeoff between number of offspring and size of offspring can be observed between two species within the angiosperms. The seeds from the coco de mer palm, *Lodoicea maldivica* (J. F. Gmel.) Pers., can weigh up to 18 kg and are few in numbers (Edwards et al. 2015), whereas seeds from the orchid *Cynoches ventricosum* var. *chlorochilon* (Klotzsch) P. H. Allen only weigh 3.6 µg and one capsule can contain 4 000 000 seeds (Arditti & Ghani 2000).

Resource availability of plants are affected by different environmental factors. These factors can alone or in combination with other factors put constraints on the resource allocation in the plant. Nutrients are important for plant growth and function, especially macronutrients such as phosphorus (P) and nitrogen (N), among others. Phosphorus is a component of nucleic acids, phospholipids, ATP and coenzymes, and nitrogen is a component of nucleic acids, proteins, hormones, chlorophyll and coenzymes (Campbell et al. 2008). Elser et al. (2007) investigated growth responses on autotrophs of added phosphorus and nitrogen, separately and

simultaneously, for both terrestrial, freshwater and marine aquatic ecosystems. They found positive effects of singular additions of the macronutrients across all ecosystems and even stronger responses when the nutrients were added together, witnessing limiting effects of phosphorus and nitrogen on photosynthetic organisms (Elser et al. 2007).

Soil moisture is dependent on several factors such as precipitation, temperature, terrain features, soil texture, and soil organic content. Depending on available resources, plants will have to adapt to limitations. Allocation of carbon to above- or belowground growth will be at the expense of the other, imposing a tradeoff effect. High root production will ensure higher access to soil nutrients and water, whereas longer stem and bigger leaves will give the plant better access to light and carbon dioxide (Smith & Smith 2009).

Light is essential for plant growth and respiration. Plants growing in shade can increase height or leaf area to obtain sufficient light levels, in cold habitats plants can increase their temperature by following the sun, such as *Papaver dahlianum* Nordh., or store heat such as the cushion formed *Silene acaulis* (L.) Jacq. (Sandbakk et al. 2020a, 2020b). Light can also influence pollinator presence. In a study involving the bellflower *Campanulastrum americanum* Kilkenny and Galloway (2008) found that plants exposed to high light intensity had larger floral displays and attracted seven fold more pollinator visits than plants in the shade. Interestingly, when they separated the effects of irradiation from floral display size, they found no correlation with display size and frequency of pollinator visits, indicating that pollinator behavior was directly influenced by light availability (Kilkenny & Galloway 2008). *Cypripedium calceolus* L. our study species, seems to be both benefitted and limited by light conditions. Nilsson (1979) observed a higher frequency of pollinator visits for *C. calceolus* in sunlight, due to attraction by flower illumination. High light levels can on the other hand can increase presence of competitive species (Kull 1999).

The plant family of *Orchidaceae* relies on pollinator attraction. The species within this family are found on every continent in the world, except Antarctica, and thus great variation in floral traits are observed due to evolution in different environments (Cozzolino & Widmer 2005, Darwin 1877, Dressler 1981, Pijl & Dodson 1966). Orchid diversity is considered a result of pollinator diversity, not as a co-evolutionary relationship, but rather an asymmetric one, where the pollinator dependency of orchids have forced them to evolve in order to achieve sexual reproduction (Dressler 1981, Nilsson 1992, Pijl & Dodson 1966). Most orchids produce nectar that attract pollinators, but nearly one third of the estimated 20 000 to 25 000 species is known

to be deceptive (Ackerman 1986, Dressler 1981). Deception can have different forms of mimicry of rewarding species, such as floral color, odor, structures or even pheromones of insects (Ackerman 1986, Jersáková et al. 2006, Pijl & Dodson 1966). If nectar production is no longer available and resources are limited, other floral traits that contribute to increase fitness are more likely to evolve (Ackerman 1986, Nilsson 1992). Another strategy to improve fitness could be clonal growth, allowing plants to reproduce without pollinator interaction. However, clonal growth will not drive adaptation through natural selection, thus clonal plants are vulnerable to changing environments or events such as new diseases (Campbell et al. 2008, Graham et al. 2006). Some plants may have the ability to aggregate root structures in areas of augmented soil nutrition, enhancing plant nutrient uptake (Hutchings & de Kroon 1994). Ramets of clonal plants are often connected and may transfer nutrients within the plant (Herben et al. 2015, Stuefer 1998).

Habitat disturbance is one of the main threats to biologic diversity worldwide. Fragmentation of habitats, urban development, forestry, invasive species and changes in species composition, among others, may affect environmental variables, such as availability of light, moisture and nutrients. Plant fitness can be directly affected by variation in environment, since the environment supplies necessary resources to plants (Smith & Smith 2009). Climate change forces species to either adapt or move to survive. The ongoing fragmentation of habitats may leave the narrowly specialized *C. calceolus*, with few, if none, escape routes available. The widely distributed orchid is threatened by habitat loss and habitat change due to human exploitation (IUCN 2020). Today the species is protected internationally through the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), European Union Directive CE/92/43 on the Conservation of Natural Habitats and of Wild Fauna and Flora, and the Convention on International Trade in Endangered Species (Washington Convention, Devillers-Terschuren 1999, cited in Kull 1999).

In Norway *C. calceolus* is categorized as near threatened on the Red list of species due to continuous decrease and fragmentation of habitats. Typical threats to the species in Norway are reduction of habitats caused by modern forestry with dense forest plantations and downsizing of natural forest habitats. Cessation of traditional use of pastures with cattle and sheep result in succession of semi-natural forest towards denser forests. Previously was rhizome harvesting contributing to reduction of populations (Solstad et al. 2015). The calcareous forests in Snåsa

are under pressure from both forestry and developmental projects, such as construction of cottages (Hassel et al. 2009).

Locally there has been found several localities of *C. calceolus* in the areas around Lake Snåsa (Artsdatabanken 2020a, Brandrud et al. 2018, Hassel & Holien 2010, Hassel et al. 2009, Holien 2008, Holien et al. 2018, Holien et al. 2011). Finsåsmarka nature reserve contains Norway's largest population of the orchid, including 29 occurrences of approximately 3400 ramets counted in 2017 (Brandrud et al. 2018). Several of the populations of *C. calceolus* in Finsåsmarka, including both *Picea abies* (L.) H. Karst and *Pinus sylvestris* L. dominated forest stands are probably declining (Hassel & Holien 2010). Also at Bergsåsen, the population of *C. calceolus* seems to be decreasing (Holien & Hassel 2017). This study tries to get a better understanding of the performance of the local populations of *C. calceolus* and how this affect the reproduction. Future plans for conservation and management have never been more important in order to preserve biological diversity.

Aims

The aims of this study are to examine if there are differences in life history strategy between *C. calceolus* growing in forest stands dominated by *P. abies* and *P. sylvestris*, respectively. First, we investigate if the environmental conditions of the study sites in spruce and pine forest really are different. Secondly, we investigate if this translate into differences in 1) number of flowers, 2) frequency of capsules and 3) number of seeds per capsule. The results are explored in relation to soil chemistry and organic content, composition of surrounding vegetation, light condition and terrain features. The species is threatened due to loss of available habitats, and it is important to understand how *C. calceolus* perform in different habitats and how this affect the reproduction.

Methods

Study species

The research object in this study, *Cypripedium calceolus* (Figure 1), is a deceptive orchid with 1-2 (-3) flowers per stem. The plant is characterized by its bright yellow bowl-shaped labellum, 5 purple-brown petals and 3-5 large green leaves, with a stem height of 20-60 cm (Lid et al. 2005). The elongate capsule is 3-4 cm long with 6 longitudinal slits (Mossberg et al. 2007). Especially young plants benefit from symbiotic relationship with mycorrhizal fungi (Kull

1999).

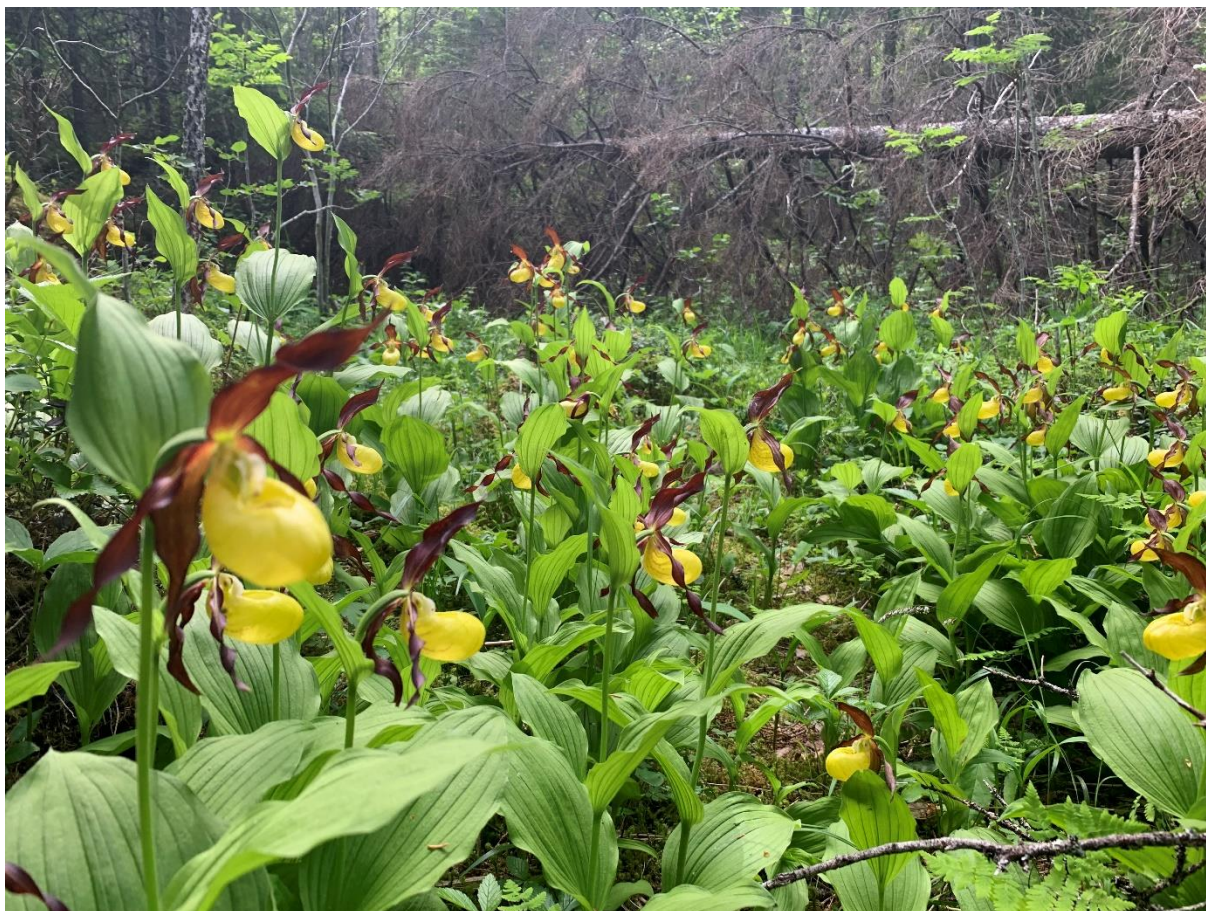


Figure 1 Abundance of *Cypripedium calceolus* in Finsåsmarka.

Flowering occurs in May-July, depending on altitude and latitude and lasts up to 3 weeks (Kull 1999). Pollination is achieved by attracting insects with floral scent (Bergstrom et al. 1992). Once trapped inside (Figure 2), the insects are forced to escape the labellum through one of the two narrow openings situated close to the anthers (Darwin 1877, Proctor & Harder 1994). In September, the capsule ripens (Figure 2) and opens during September-October. One capsule can contain up to nearly 17 000 minuscule seeds, primarily dispersed by wind (Kull 1999). Deceptive orchid species have been found to produce more seeds than nectar rewarding orchids, as a compensation for the lower fruit set (Sonkoly et al. 2016).

Cypripedium calceolus is a rhizomatous plant, with a ratio of sexual reproduction to vegetative reproduction of 1:200 for some populations (Kull 1999). Seedling establishment is only achieved by less than 0.06 % of all seeds (Kull & Arditti 2002, cited in Shefferson et al. 2005). The rhizomes, up to 0.9 cm in diameter, can be found ca. 10 cm below the vegetation cover. The growth of the rhizome takes place at the apical part, where two buds develop each year. One of the buds continues the rhizomatous growth, the other bud may stay dormant or start to

develop into a shoot in following years (Kull 1999). This vegetative growth can lead to groups of plants being a part of the same clone. Commonly smaller clones are up to 70 cm in diameter consisting of few plants, but larger clones are not rare (Kull 1999).

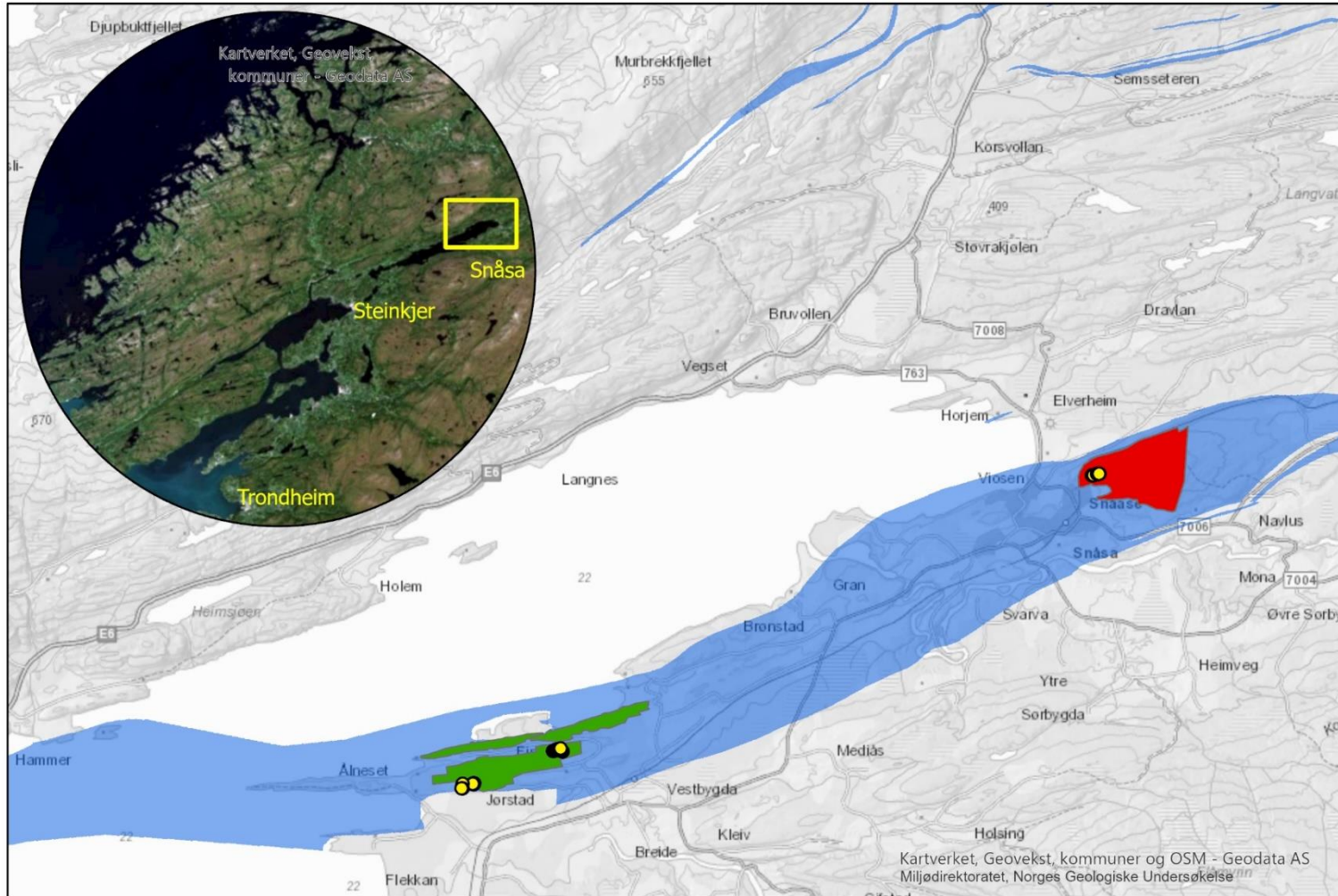
Darwin (1877) explains the pollination of *Cypripedium*, were it is necessary with mechanical aid to transport the pollen grains from the anthers to the stigma. Because of the complex sexual reproduction strategy of *C. calceolus*, it has been argued that pollinators once trapped inside the labellum, are discouraged from revisiting the same flower (Jersáková et al. 2006, Webster 1886), and absence of reward is assumed a reason for avoidance learning in pollinators (Juillet et al. 2011). However, Nilsson (1979) found that floral scent of *C. calceolus* interfere with the pheromone attraction of some of its common pollinators, creating confusion, whereby revisits may be plausible even after the negative experience made by pollinators.

The distribution of *C. calceolus* ranges from Great Britain through central parts of Europe, southern parts of Siberia and to the coast of Japan, with a height gradient variation from sea level up to 2700 meters in Switzerland. The orchid is found in a variety of habitats, but mainly in woodland. The light conditions influence the growth, the orchid seems to prefer partly-shading (Kull 1999). The Norwegian distribution is scattered from the southeast through the middle parts and north to the eastern parts of Finnmark in boreonemoral to northern boreal zones, rarely in low alpine zone. In Norway it is found from sea level to 1150 meters above sea



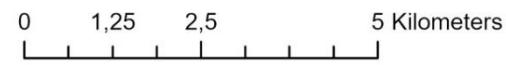
Figure 2 Insect trapped in the labellum, and capsules developed on twin flower

Study area



- Cypripedium calceolus
- Bergsåsen nature reserve
- Finsåsmarka nature reserve
- Calcareous bedrock

Geographical location for study area including Bergsåsen and Finsåsmarka nature reserves. Occurrences of calcareous bedrock and locations of registered study plots of *C. calceolus* are also included.



Spatial Reference
 Name: ETRS 1989 UTM Zone 33N
 PCS: ETRS 1989 UTM Zone 33N
 GCS: GCS ETRS 1989
 Datum: ETRS 1989
 Projection: Transverse Mercator

Figure 3

level (Lid et al. 2005). *Cypripedium calceolus* is restricted to calcareous soils and the main occurrence can be found in deciduous- and coniferous forests, but also stone strewn slopes and rarely in rich fens (Lid et al. 2005, Mossberg et al. 2007, Solstad et al. 2015).

Study area

The study was performed in the municipality of Snåsa, in the county of Trøndelag, Norway. Two main sites for the study were chosen based on the occurrence of *C. calceolus* (Hassel & Holien 2010, Holien 2008, Holien & Hassel 2017). Bergsåsen, situated north-east of Lake Snåsa and Finsåsmarka, situated 10 km to the west-south on the eastern side of Lake Snåsa. Lake Snåsa is a 122 km² large freshwater lake that previously was an elongation of Trondheim Fjord (Norges Geologiske Undersøkelse 2017b). Today the lake is separated from the fjord and is situated 23 meters above sea level (Figure 3, Rosvold 2018).

The study area is situated in southern boreal to middle boreal vegetation zone and on the border between weak to clearly oceanic vegetation section (Moen 1998). The mean annual temperature between 1961-1990 was 4.2 °C, with the lowest and highest temperatures registered in January (- 4.9 °C) and July (13.6 °C). The mean annual precipitation registered for the same period was 1040 mm. All registrations were recorded at Berg weather station nmb. 7091 (127 a.s.l., Aune 1993, Førland 1993).

The underlying bedrock for both Bergsåsen and Finsåsmarka is known as Snåsa limestone, a sedimentary rock consisting of blue-grey recrystallized limestone (Norges Geologiske Undersøkelse 2016, Roberts 1967) The limestone area runs in a northeast- southwest direction and covers both sides of Lake Snåsa (Norges Geologiske Undersøkelse 2016). Along this calcareous strip the main occurrences of *C. calceolus* in Snåsa and Steinkjer municipalities are found (Hassel & Holien 2010, Hassel et al. 2009, Holien 2008, Holien & Hassel 2017, Holien et al. 2011). In both Bergsåsen and Finsåsmarka the bedrock is to a large extent covered by peat and/or a thin humus layer (Norges Geologiske Undersøkelse 2017a).

Bergsåsen was established as a nature reserve in 1977 and covers an area of 1,4 km² (Forskrift om Bergsåsen naturreservat 1977). The altitude in the area ranges from 80 to 273 meters a.s.l. The forest is mainly a calcareous coniferous forest, with both *P. sylvestris* and *P. abies* and scattered deciduous trees. Calcareous low herb woodland vegetation is dominating. The area also contain rich fens and marshes (Holien & Hassel 2017). The dominating forest stand at the

study site in Bergsåsen is *P. sylvestris*. The species of *P. sylvestris* is favored by high light exposure and thrives in a wide range of nature types and moisture gradients (Artsdatabanken 2020b, Mossberg et al. 2007).

The terrain in Bergsåsen is coarse and consists of hollows and ridges of varying height that follows the south-west direction of the hillside. The chutes are moister than the ridges, often with a thicker soil layer. The ridges are dry, often covered in thin peat, with emerging bare calcareous rock (Figure 4), often porous and cracked with cavities (Holien & Hassel 2017). At Bergsåsen the study plots are found between 170 and 190 m a.s.l.

Finsåsmarka was protected as a nature reserve in 2016 with a total area of 1.36 km² (Forskrift om vern av Finnsåsmarka naturreservat 2018). The nature reserve is situated on a parallel ridge to the shores of Lake Snåsa. The highest point on the ridge is 115 m a.s.l. Both *P. sylvestris*, - and *P. abies*- dominated forest stands can be found in Finsåsmarka, but the occurrence of *P. abies* is much more common with a coverage of 85%, whereas *P. sylvestris* make up 10-12%.



Figure 4 *Cypripedium calceolus* on thin soil layer with calcareous rock emerging at Bergsåsen.



Figure 5 A small clone situated in *Picea abies* forest stand in Finsåsmarka.

The rest of the forest stands consists of *Betula* spp., *Alnus incana* (L.) Moench, *Alnus glutinosa* (L.) Gaertn., *Populus tremula* L., *Salix caprea* L. and *Juniperus communis* L. (Bøe et al. 2001).

In Finsåsmarka, one *P. sylvestris* dominated and one *P. abies* dominated area with *C. calceolus* were included in this study. The first area is a calcareous ridge situated west in Finsåsmarka, which shares many of the same terrain features present at Bergsåsen; both terrain, vegetation composition and canopy structure is similar. Patches of *J. communis* is quite common in this area. The forest stand is dominated by *P. sylvestris*, with scattered trees of *P. abies* (Hassel & Holien 2010). The study plots in this area are situated between 40- 80 meters a.s.l.

The second area of Finsåsmarka is a *P. abies* dominated forest stand (Figure 5). *P. abies* is a shade tolerant species, has higher need of moisture as the roots do not penetrate deep into the ground and can be found in a variety of nature types (Artsdatabanken 2020c, Institutt for biovitenskap 2020, Mossberg et al. 2007). Other tree species occurring here are *Betula pubescens* Ehrh., *Sorbus aucuparia* L. and *A. incana*. The height range of the registration plots in this area is 90- 100 meters a.s.l

Field registrations

42 plots of 2 × 2 meters were registered in this study, including both *P. abies*- and *P. sylvestris*-dominated forest stands. The center of the clone/ cluster of plants was considered the center of the registration plot. Within the registration plots every shoot of *C. calceolus* was registered and categorized as fertile or sterile. Fertile shoots were registered as single- or twin-flowered. Number of leaves per fertile plant was also recorded.

The vegetation was registered within the plot. Percentage of cover was ranked in three classes based on occurrence: rare 0-5 %, common 5-50 % and dominant 50+ %.

Light transparency was obtained through wide angle photographs taken in the center of each registration quadrat (with a GoPro HERO4 camera). The camera was placed at the same height as the topmost flowers of the clone, ensuring plant structures of *C. calceolus* were not covering the lens. The angle of the camera followed the slope of the terrain, as if the camera had been laid upon the ground. The reason for choosing a wide-angle camera instead of a fisheye camera was equipment availability. The reason for paralleling the camera with the slope was to focus on the light transparency qualities to the actual positions of the orchid. The light transparency was obtained by analyzing the digital photographs with the software ForestCrowns (Winn et al. 2016).

From each registration plot, soil samples were taken from the immediate proximity of the orchid's rhizomes. Before extracting the sample, the top peat cover was temporarily removed. Then a small shovel of 15 cm was inserted in the soil, to its full depth where possible. Typically, in the *P. sylvestris* forest stands, the soil layer was thin, due to more occurrence of bare ridges of calcareous rock and lower accumulation of organic material than in e.g. *P. abies* habitats. Chemical parameters investigated was nitrate (NO₃-), ammonium (NH₄+), total phosphorus (P), pH and loss on ignition (LOI).

Coordinates from the center of each registration plot were recorded (with a Garmin GPSMAP 64s). The level of accuracy desired for the position of the orchids was high, especially to implement the recorded positions in further analysis in a GIS. The handheld GPS- device used in this study operates with both GPS and GLONASS (Garmin® 2019a) which increases the accuracy of the recorded position. The producer of the device states that in 95% of the time, the accuracy for the Garmin GPS receivers is 15 meters, but that users can experience accuracy down to 5-10 meters (Garmin® 2019b).

The aspect and slope was found using a digital terrain model from Kartverket DTM 10 (Kartverket 2018a). From a raster dataset, aspect and slope was calculated for each of the locations of the plots.

LIDAR las-files created from data collected in July 2018 (Kartverket 2018b) was used to perform a canopy density analysis in ArcGIS. The result is an index from 0-1 which increases with augmented canopy density. The data can be used to compare the results of light transparency from the digital images.

In September, all the capsules were collected from the registration plots during two following days, the 26th and the 27th. In total 74 capsules were collected, 36 and 37 capsules from respectively *P. sylvestris*- and *P. abies*- dominated forest stands. Six of the capsules from each forest stand was collected from outside of registration plots. The capsules from *P. sylvestris* forest stand had developed faster than the capsules in the *P. abies* forest stand, therefore several of the capsules in the *P. sylvestris* habitat had started cracking before they were collected. In the *P. abies* habitat the capsules were whole, all but two capsules.

Capsule ratio, size and seed estimation

The capsules were measured in weight, length, width and volume if the capsule had not yet cracked. Volume was measured by lowering the capsule into a known volume of water. To extract the seeds, the capsules were humified to decrease their friability before a scalpel was used along the furrow of the capsules. By the aid of forceps, a metal needle and a small brush, the seeds were transferred from capsules to glass jars. A known volume of glycerin (80%



Figure 6 Capsule opening, seed extraction and seed counting.

solution with water) was added to the glass jars. Due to the structure of the orchid seeds, it was not possible to obtain a homogenous solution by water. The seeds immediately floated up because of the air-filled volume of the outer cell coat (Barsberg et al. 2013, Proctor & Harder 1994). On the other hand, a 99.5% glycerin solution with seeds proved to be unsatisfactory due to the high viscosity, which made extraction by automatic pipette difficult (the pipette was not able to extract the solution in proper amount). The jars were shaken by hand to ensure a homogenous distribution of the seeds. The use of an automatic mixer was not sufficient to this purpose, also experienced by Sonkoly et al. (2016). An automatic pipette was used to extract 50 μ l x 3 from the solution. A pipette tip cut to 45 degrees to get an opening large enough for seeds to enter. Extractions were transferred to objective glasses and seeds counted. The mean from the three droplets was used to get the total seed estimate of each sample (Figure 6).

Statistical analyses

Statistical analyses were carried out in R (R Core Team 2020).

A principal component analysis has been included to visualize differences of species occurrence in plots between forest stands (Vu 2011).

We used unpaired Welch two sample t-tests to test for differences in plant trait- and environmental related variables at plot level between the two forest stands. When data did not meet parametric assumptions, we performed ln- transformation. If assumptions were not met after transformation, we used non-parametric unpaired Wilcoxon ranked sums tests. To test for allometric relationship between seed numbers and capsule width, we used a simple linear regression. Differences between forest stands for variables at plant or capsule level were tested by using linear mixed effects models following Gaussian distributions (Kuznetsova et al. 2017) or generalized linear mixed effects models following Poisson distribution (Bates & Maechler 2015), depending on the distribution family of response variable. Forest stand was included as fixed effects factor and plot as random effects factor. Number of leaves and number of flowers were not amenable to mixed modelling due to a restricted range of potential response values, the statistical results from these analyses risk pseudoreplication and should be interpreted with caution.

To investigate the effects of environmental variables on our three main response variables we used generalized linear models following Poisson distribution for flower numbers and capsule numbers, and a linear mixed effects model with Gaussian distribution and maximum likelihood

deviance for capsule width, where environmental variables were included as fixed effects factors and plot included as random effects factor. For the GLM models we formulated full models including all environmental variables and performed automatic model selection with AICc (Venables & Ripley 2002). Model formulation for linear mixed models were performed by evaluating collinearity between environmental variables by correlogram (Peterson & Carl 2020) where we discarded variables that showed strong collinearity ($\rho > 0.50$ and $p > 0.05$) and prioritized variables of strong correlation with response variable. To evaluate importance of fixed effects we used model selection by AICc (Barton 2019).

To test for relationships between different aspects of plant traits we used simple linear regression, generalized linear models, and linear mixed effects models, depending on the distribution of the response variable and registration level of other included variables. If models could not be fitted to the data, we used Spearman rank correlation to test for association between the variables, or Kruskal- Wallis rank sum test to test for variance between groups. We also fitted full (generalized) linear mixed model for each of the main response variables, where we included plant size related variables as fixed effects factors and plots as random effects factor. A negative relation between variables of different plant traits should indicate a physiological trade-off. We used model selection by AICc (Barton 2019) to test if null model were better suited than full model for linear mixed models, and model selection with AICc (Venables & Ripley 2002) for generalized linear models.

Figures, tables and map, along with model validations for all significant (general) linear (mixed) models are found in the appendix (named with “A”).

Results

Species occurrence

The study plots in Bergsåsen and the *P. sylvestris* dominated part of Finsåsmarka have an open canopy structure, and the most common species of the bottom layer are *Hylocomium splendens* (Hedw.) Schimp., *Rhytidiadelphus triquetrus* (Lindb.) T. J. Kop., *Pleurozium schreberi* (Willd. Ex Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not. and *Cladonia rangiferina* (L.) F. H. Wigg, the latter indicating longer dry periods (Hassel 2020). The most common species of the field layer are *Convallaria majalis* L., *Empetrum nigrum* L., *Vaccinium vitis-idaea* L., *Vaccinium myrtillus* L., *Potentilla erecta* (L.) Raeusch., *Rubus saxatilis* L., *Carex digitata* L., *Carex* sp., *Hieracium* spp. and *Solidago virgaurea* L. An often-occurring species in the shrub

Table 1. Species presence/ absence in forest stands

Species	Pinus	Picea	Functional group	Species	Pinus	Picea	Functional group
<i>Cladonia arbuscula</i>	x	-	L	<i>Gymnocarpium dryopteris</i>	-	x	F
<i>Cladonia rangiferina</i>	x	-	L	<i>Gymnocarpium robertianum</i>	x	-	F
<i>Ctenidium molluscum</i>	x	x	B	<i>Hepatica nobilis</i>	x	x	H
<i>Dicranum sp</i>	x	x	B	<i>Hieracium sp</i>	x	x	H
<i>Hylocomium splendens</i>	x	x	B	<i>Lathyrus vernus</i>	-	x	H
<i>Peltigera britannica</i>	x	-	L	<i>Linnea borealis</i>	x	x	H
<i>Plagiochila asplenioides</i>	-	x	B	<i>Listeria ovata</i>	x	x	H
<i>Plagiomnium affine</i>	-	x	B	<i>Maianthemum bifolium</i>	-	x	H
<i>Pleurozium schreberi</i>	x	x	B	<i>Melica nutans</i>	-	x	G
<i>Ptilium- crista- castrensis</i>	x	x	B	<i>Ophrys insectifera</i>	x	-	H
<i>Racomitrium ericoides</i>	x	-	B	<i>Oxilidaceae acetosella</i>	-	x	H
<i>Rhytidiadelphus triquetrus</i>	x	x	B	<i>Paris quadrifolia</i>	-	x	H
<i>Rhytidiadelphus loreus</i>	-	x	B	<i>Poaceae sp</i>	-	x	G
<i>Sanionia uncinata</i>	-	x	B	<i>Potentilla erecta</i>	x	x	H
<i>Scapania aspera</i>	x	-	B	<i>Rubus saxatilis</i>	x	x	H
<i>Schistidium trichodon</i>	x	-	B	<i>Saxifraga cotyledon</i>	x	-	H
<i>Tortella tortuosa</i>	x	-	B	<i>Solidago virgaurea</i>	x	x	H
<i>Tritomaria quinquedentata</i>	-	x	B	<i>Taraxacum sp</i>	-	x	H
<i>Anemone nemorosa</i>	-	x	H	<i>Tussilago farfara</i>	-	x	H
<i>Calluna vulgaris</i>	x	-	W	<i>Vaccinium myrtillus</i>	x	x	W
<i>Carex sp</i>	x	x	G	<i>Vaccinium uliginosum</i>	x	-	W
<i>Cirsium sp</i>	-	x	H	<i>Vaccinium vitis- idaea</i>	x	x	W
<i>Convallaria majalis</i>	x	x	H	<i>Viola riviniana</i>	x	x	H
<i>Crepis paludosa</i>	-	x	H	<i>Alnus incana</i>	-	x	T
<i>Dactylorhiza sp</i>	-	x	H	<i>Betula pubescens</i>	x	x	T
<i>Dryas octopetala</i>	x	-	W	<i>Cotoneaster integerrimus</i>	x	-	T
<i>Empetrum nigrum</i>	x	-	W	<i>Frangula alnus</i>	x	x	T
<i>Epipactis atrorubens</i>	x	x	H	<i>Juniperus communis</i>	x	-	T
<i>Equisetum pratense</i>	-	x	F	<i>Picea abies</i>	x	x	T
<i>Filipendula ulmaria</i>	x	x	H	<i>Pinus sylvestris</i>	x	-	T
<i>Fragaria vesca</i>	x	x	H	<i>Salix caprea</i>	x	x	T
<i>Geranium sylvaticum</i>	x	x	H	<i>Sorbus acuparia</i>	x	x	T

x = presence, L= lichens, B= bryophytes, H= herbaceous vascular plants, W= woody vascular plants, G= graminoids, F= ferns, T= trees

layer is *Juniperus communis* L. The woody species are represented with higher occurrence in this forest stand. (Table 1, Table A.1.a-d).

The bottom layer of the study plots of the *P. abies* dominated forest stand in Finsåsmarka are dominated by *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Rhytidiadelphus triquetrus*, and in addition, quite commonly found *Plagiochila asplenioides* (Torr. Ex Nees) Lindenb., indicating only short periods of drought with otherwise stable moist-

conditions (Hassel 2020). The most common species of the field layer are *Anemone nemorosa* L., *Convallaria majalis*, *Carex* spp, *Crepis paludosa* (L.) Moench., *Filipendula ulmaria* (L.) Maxim., *Gymnocarpium dryopteris* (L.) Newman, *Hieracium* sp, *Rubus saxatilis*, *Vaccinium vitis-idaea* and *Vaccinium myrtillus* L. The species diversity of vascular plants is generally higher compared to the *P. sylvestris* dominated forest stands in Finsåsmarka and Bergsåsen. Other species occurring sporadically are *Dactylorhiza* sp., *Equisetum pratense* Ehrh., *Fragaria vesca* L., *Hepatica nobilis* Schreb., *Linnea borealis* L., *Listera ovata* (L.) R. Br., *Maianthemum bifolium* (L.) F. W. Schmidt, *Oxalis acetosella* L. and *Potentilla erecta*. Common species in the shrub layer are *Alnus incana* and *Sorbus aucuparia*. There is a higher presence of herbaceous plant species within *P. abies* forest stand compared with *P. sylvestris* forest stands (Table A.1.a-d).

Lichens only found in *P. sylvestris* forest stands are *Cladonia arbuscula* (Wallr.) Flot., *Cladonia rangiferina* and *Peltigera britannica* (Gyelnik) Holt-Hartw. *Cladonia arbuscula* and *Cladonia rangiferina* are both common in all areas in Norway and *Peltigera britannica* is commonly found in coastal areas with either high air- or soil humidity (Naturhistorisk Museum 2020). Bryophytes only found in *P. sylvestris* forest stands are *Racomitrium ericoides* (Brid.) Brid., *Scapania aspera* Bernet & M.Bernet, *Schistidium trichodon* (Brid.) Poelt and *Tortella tortuosa* (Hedw.) Limpr. *Racomitrium ericoides* is often found on open soil with drainage. *Scapania aspera* is found in calcareous turf or on calcareous rock, and prefers humid habitat, but not wet sites. *Schistidium trichodon* is associated with calcareous habitats, the same is true for *Tortella tortuosa* (British Bryological Society 2020). Vascular plants only found in *Pinus sylvestris* forest stands are *Calluna vulgaris* (L.) Hull, *Dryas octopetala* L., *Empetrum nigrum*, *Gymnocarpium robertianum* (Hoffm.) Newman, *Ophrys insectifera* L., *Saxifraga cotyledon* L., *Vaccinium uliginosum* (Brid) Bruch & Schimp., *Cotoneaster integerrimus* Medik., *Juniperus communis* and *Pinus sylvestris*. *Calluna vulgaris* is a woody plant, common on dry to moist, open habitats. *Dryas octopetala* thrives in dry, calcareous and exposed habitats, *Empetrum nigrum* is a woody species, commonly found on dry to moist soil. *Gymnocarpium robertianum* is rarely found in open habitats of moist calcareous soil, the same is true for *Ophrys insectifera*, which also is associated with *Pinus sylvestris*. *Saxifraga cotyledon* prefers moist rocky substrates, *Vaccinium uliginosum* is woody, common on moist poor soils. *Cotoneaster integerrimus* is rarely found in open, sun exposed habitats, *Juniperus communis* is common in open, dry to moist habitats and *Pinus sylvestris* is found on dry to moist soils (Mossberg et al. 2007).

Lichens are not registered in *Picea abies* forest stand. Bryophytes only found in *Picea abies* forest stand are *Plagiochila asplenoides*, *Plagiomnium affine* (Blandow ex Funck) T. J. Kop., *Rhytidiadelphus loreus* (Hedw.) Warnst., *Sanionia uncinata* (Hedw.) Loeske and *Tritomaria quinquedentata* (Huds.) H. Buch. *Plagiochila asplenoides* and *Plagiomnium affine* is favored by damp calcareous to acidic soils, *Rhytidiadelphus loreus* also occurs on moist soils, *Sanionia uncinata* thrives in a variety of habitats and *Tritomaria quinquedentata* prefers base-rich and humid habitats (British Bryological Society 2020, Hassel 2016). Vascular plants only found in *Picea abies* forest stand are *Anemone nemorosa*, *Cirsium* sp., *Crepis paludosa*, *Dactylorhiza* sp., *Equisetum pratense* Ehrh., *Gymnocarpium dryopteris*, *Lathyrus vernus* (L.) Bernh., *Maianthemum bifolium* (L.) F. W. Schmidt, *Melica nutans* (Hedw.) Lindb., *Oxalis acetosella* (L.), *Paris quadrifolia* L., *Poaceae* sp., *Taraxacum* sp., *Tussilago farfara* L. and *Alnus incana*. *Anemone nemorosa* is favored by damp habitats, *Cirsium* sp. was difficult to determine to species, hence we cannot distinguish habitat preferences. *Crepis paludosa* thrives in moist habitats, *Dactylorhiza* sp. was difficult to determine due missing inflorescence, but most likely it is *D. maculata* or *D. fuchsii*, both of which prefer damp to moist habitat, the latter only rarely on calcareous soil. *Equisetum pratense* thrives on damp to moist soils, *Gymnocarpium dryopteris* is common on moist soils and *Lathyrus vernus* is commonly found in moist calcareous habitats. *Maianthemum bifolium* is common in shady, damp to moist habitats, *Melica nutans* is found on moist soils and *Oxalis acetosella* on damp to moist soil. *Paris quadrifolia* is found in shady, damp to moist habitats. *Poaceae* sp. had not flowers and was not determined, and because of extended distribution not possible to associate with habitat preferences, the same is true for *Taraxacum* sp. *Tussilago farfara* is commonly found on damp to moist soils and *Alnus incana* also found on damp to moist soils (Mossberg et al. 2007).

Principal component analysis of species in plots

Principal component analysis is based on a 66 species dataset of 42 plots. Principal component 1 (PC1) explains 20.2 % of the variance and principal component 2 (PC2) explains 8.8 % of the variance. In total, the first two components explain 30 % of the variance of species registered in plots (Figure 7). The first axis, PC1, represents an increasing moisture gradient, whereas the second axis PC2 represents an increasing nutrient richness gradient. Even with relatively low variance included by the first two components, we observe cluster in the data, indicating that species composition differs between the forest stands but also between plots.

We need 20 principal components to include all components with eigenvalues over 1, in which case we obtain almost 90 % of the variance. (Table A.2, Figure A.1.a and Figure A.1.b).

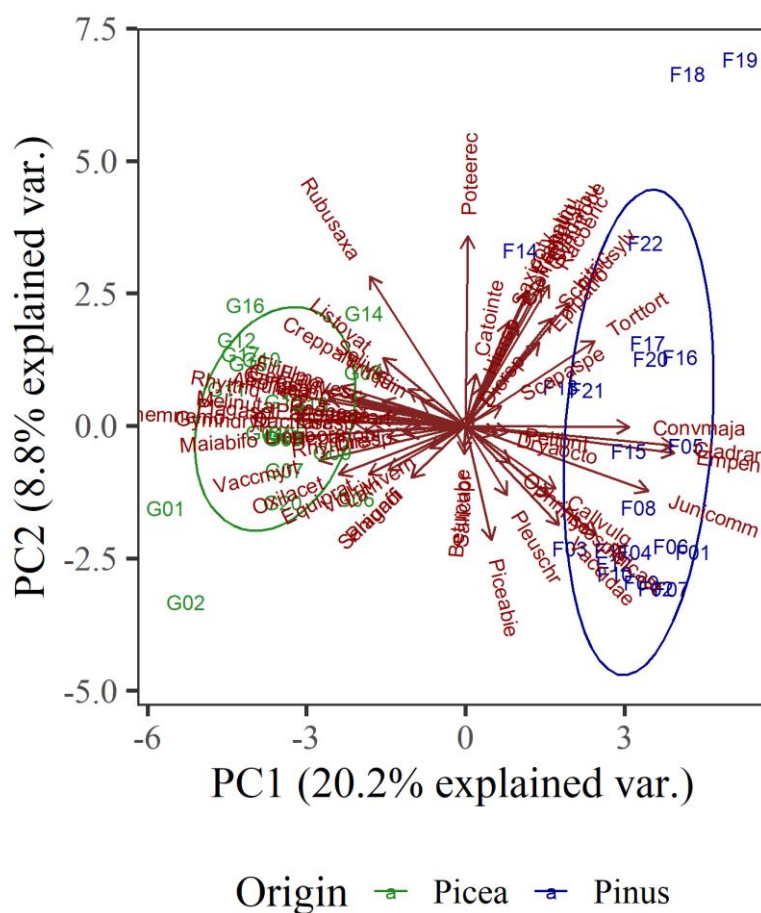


Figure 7. PCA of species in forest stands
66 species, 42 plots

Differences in environmental variables between forest stands

Almost all environmental variables are found to be significantly different between the forest stands (Table 2). Transparency and canopy cover, both of which are approximations of light availability, inversely confirm each other, saying plots in *P. sylvestris* forest stand are more exposed to light than plots in *P. abies* forest stand. Plots in *P. sylvestris* stands are situated in steeper terrain, and 20 of 22 plots face south, 2 face north (Figur A.2). Plots in *P. abies* forest stands are found in flatter terrain, all facing north. Nitrate amount in soil is not different between

Table 2 Differences in environmental variables between forest stands

Continuous Variables	\bar{x} Picea	<i>SD</i> Picea	\bar{x} Pinus	<i>SD</i> Pinus	<i>Statistic (t or W)</i>	<i>p-value</i>	Method
Transparency	18.9%	3.51	37.6%	10.49	-9.47	< 0.001	Welch Two Sample t-test
Canopy cover	80.6 %	5.53	65.8 %	9.19	419	< 0.001	Wilcoxon rank sum test with continuity correction
Slope ⁽¹⁾	4.1°	1.8	9.2 °	4.1	52	< 0.001	Wilcoxon rank sum test with continuity correction
Nitrate	6.3 mg/l	3.27	8.1 mg/l	4.65	36	0.305	Wilcoxon rank sum test with continuity correction
Ammonium	4.9 mg/l	6.97	11 mg/l	10.55	22	0.035	Wilcoxon rank sum test with continuity correction
Total phosphorus	3.2 mg/l	2.1	1.6 mg/l	1.07	77	0.034	Wilcoxon rank sum test with continuity correction
Loss on ignition	34.27 %	15.84%	42.12%	9.04%	-1.36	0.194	Welch Two Sample t-test
pH	7.8	0.15	7.6	0.12	2.6	0.021	Welch Two Sample t-test
Categorical Variable	<i>Df</i>	<i>Sample size</i>	χ^2			<i>p-value</i>	Method
Aspect ⁽²⁾	1	42	31.16			< 0.001	Pearson's Chi-squared test

(1) = 0-90° angle of terrain slope, (2) = Aspect classes in study 1: N (315-45°), 2: E (45-135°), 3: S (135-225°), 4: W (225-315°). All datapoints in study within class 1 or 3

Table 3 Differences in plant traits between forest stands

Continuous variables	\bar{x} Picea	<i>SD</i> Picea	\bar{x} Pinus	<i>SD</i> Pinus	<i>Statistic (t or W)</i>	<i>p-value</i>	Method
Flower number	7.2	19.14	6.85	7.2	0.38	0.69	Welch Two Sample t-test
Capsule number	1.5	2.3	1.36	1.26	198	0.57	Wilcoxon rank sum test with continuity correction
Capsules to flower ratio	0.2	0.15	0.12	0.22	279.5	0.13	Wilcoxon rank sum test with continuity correction
Leaves on fertile ramets	4.46	0.5	4.61	0.61	-1.38	0.18	Welch Two Sample t-test
Fertile ramets	13.45	16.86	7.36	5.47	0.73	0.47	Welch Two Sample t-test
Sterile ramets	13.75	15.22	6.5	6.29	256.5	0.36	Wilcoxon rank sum test with continuity correction
Total ramets	27.2	31.08	13.86	9.5	0.28	0.78	Welch Two Sample t-test
Fertile to total ramets ratio	0.59	0.23	0.58	0.22	0.23	0.82	Welch Two Sample t-test
Categorical variables	<i>Df</i>	<i>Sample size</i>			χ^2	<i>p-value</i>	Method
Occurrence of single and twin flowers	1	58			1.84	0.18	Pearson's Chi-squared test with Yates' continuity correction
Occurance of 4, 5 and 6 leaves	2	58			2.25	0.32	Pearson's Chi-squared test

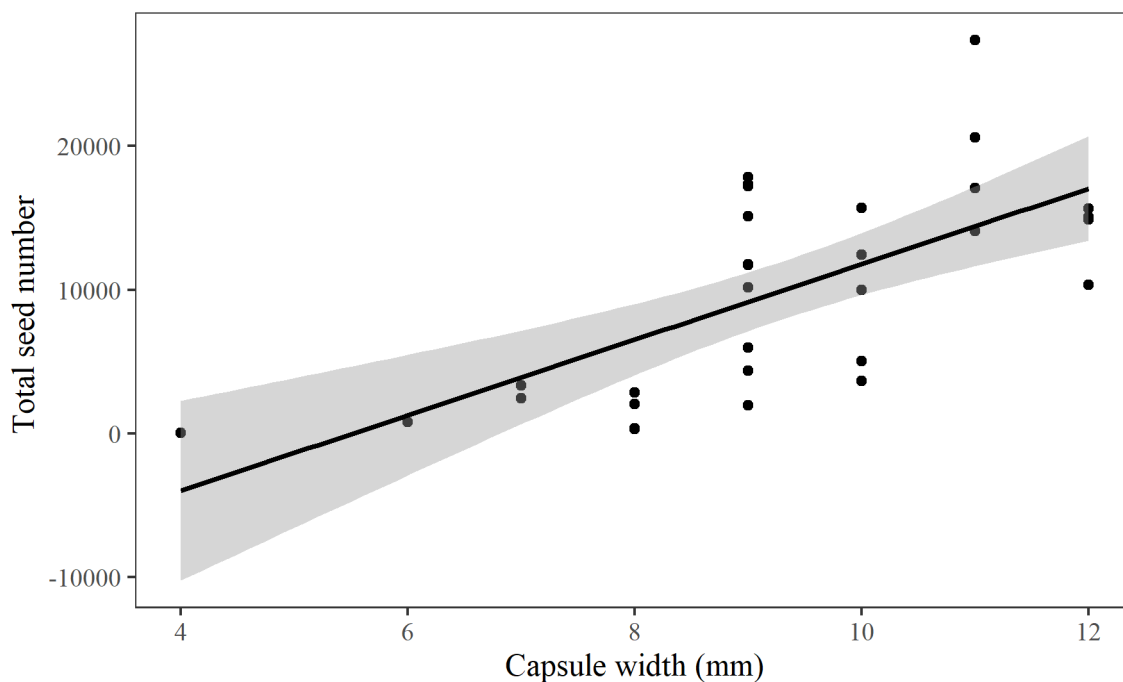


Figure 8. Relationship between capsule width and seed number.
Linear regression: $r^2 = 0.42$, $F = 23.05$, $df = 1,29$, $p\text{-value} < 0.001$

the forest stands, but amount of ammonium is significantly higher in *P. sylvestris* stands. Amount of total phosphorus in soil and pH value is significantly higher in *P. abies* stands, while loss on ignition is not significantly different between forest stands.

Differences in plant traits of *C. calceolus* between forest stands

There is a significant allometric relationship between seed number and capsule width, which allows us to use capsule width as representative for seed number in all following analyses. (Figure 8, Figure A.3). When we investigate differences in plant sizes between forest stands, we find no significant difference for flower numbers, capsule numbers, capsule to flower ratio, leaves on fertile ramets, fertile ramets, sterile ramets, total ramets or fertile to total ramets ratio. (Table 3 and Figure 9, Figure A.4.a-c).

Effect of environmental variables on plant traits

For the effects of environmental variables on flower number, we only find significant results for canopy cover, which has a positive effect on flower numbers ($\beta = 0.033$, $SE = 0.009$, $p = 0.005$, $AIC = 81.08$. Figure A.5). The only environmental variable showing a significant influence on capsule number is aspect, with more capsules likely to occur in the southern aspect than the northern ($\beta = 1.90970$, $SE = 0.77052$, $p = 0.013$, $AIC = 50.65$. Figure A.6). There is no significant effect of any of the environmental variables on capsule width.

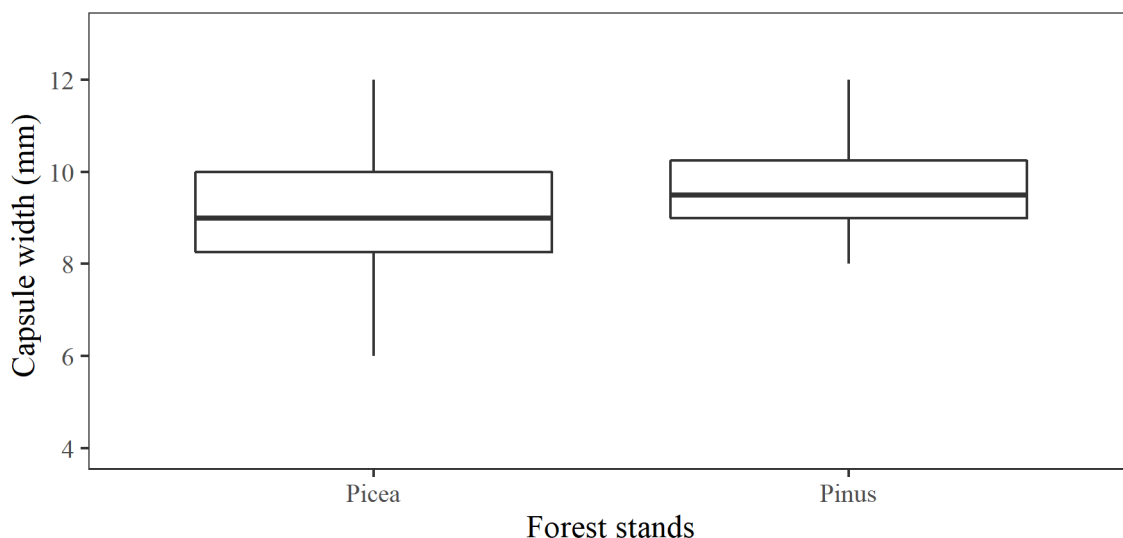


Figure 9. Capsule width between forest stands

Linear mixed effects model:

There were some variance within effects of forest stand on capsule width, but little of this variation is due to variation between plots.

Picea ($\beta=9.149$, $SE=0.339$, $p<0.001$, $AIC=241.7$)

Pinus ($\beta=0.5282$, $SE=0.486$, $p=0.29$, $AIC=241.7$) The standard errors of the means overlap, hence we cannot say if the effect of forest stand on capsule width is weaker than it is stronger.

Effects of plant traits on other plant traits

We test several plant part measurements against each other but do not find any effects or correlations between the following variables: capsule width and total ramets ($\beta=0.005$, $SE=0.005$, $df=0.85$, $p=0.39$, $AIC=244.69$), flower numbers and number of leaves ($\chi^2=1.84$, $df=1$, $p=0.18$). We cannot fit a model of capsule number and total ramets due to overdispersion. However, we find a significant negative effect of capsule width on capsules developed from twin flowers. They are likely to have smaller capsule width than capsules developed by a single flower and there is no or very little effect of the random effects of plots on capsule width (Figure 10, Figure A.7.a-c). There is also a positive relationship between flower numbers in plots and total ramets in plots (Linear regression: $r^2 = 0.40$, $F= 23.72$, $df= 1.33$, $p\text{-value} < 0.001$, Figure A.8.a, Figure A.8.b), and positive associations between capsule number and fertile ramets (Spearman's rank correlation rho: $S= 7613$, $p\text{-value}= 0.012$, $\rho= 0.38$, Figure A.9), flower numbers and capsule numbers (Spearman's rank correlation rho: $S= 7736$, $p\text{-value}= 0.014$, $\rho= 0.37$, Figure A.10) and a positive relationship between capsule width and leaf number of 4 ($\beta= 8.9565$, $SE= 0.372$, $df=54.9$, $p < 0.001$, $AIC= 238.49$, Figure A.11.a-d, should be interpreted with care, residuals are not normally distributed).

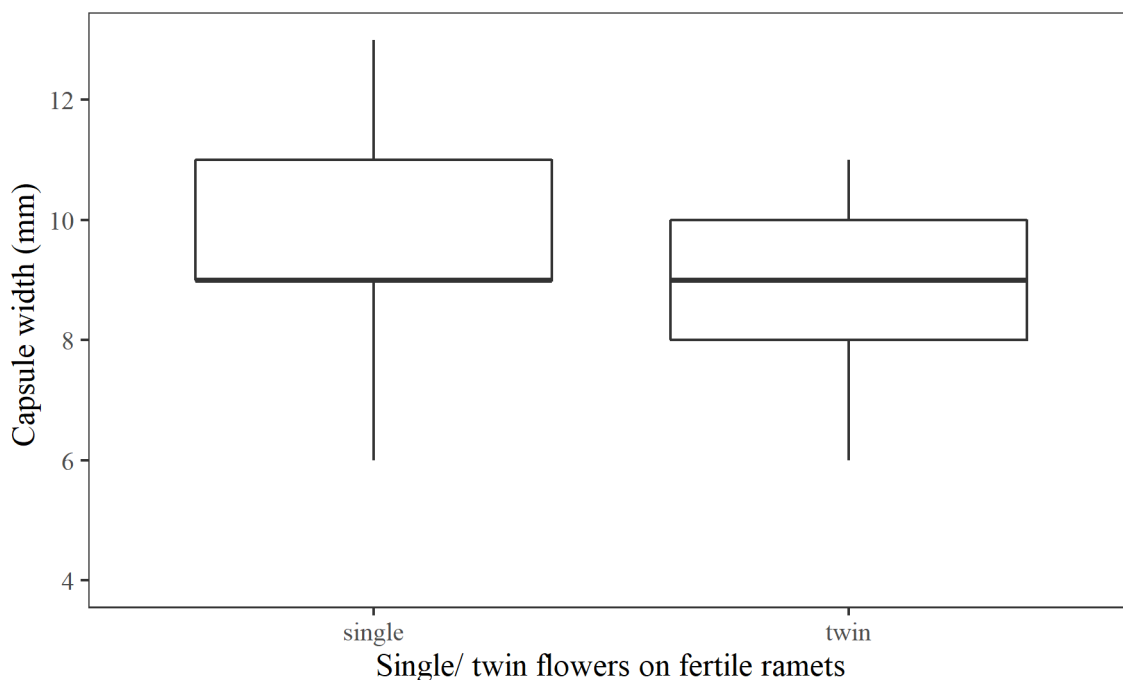


Figure 10. Capsule width between single- and twin flowers
 Linear mixed effects model: $\beta = -1.0977$, $SE = 0.5326$, $p = 0.044$, $AIC = 238.49$

Discussion

The aims of this study were to examine if there were differences in life history strategy between *C. calceolus* in *P. abies* and *P. sylvestris* forest stands, focusing mainly on reproductive traits. We expected to find differences in plant traits due to the different environments the plants experience in each forest stand. Species composition differed between forest stands, indicating differences in moisture and nutrient availability. However, contrary to our expectations, we found few differences in traits. We explored relationships between several environmental variables and reproductive traits, yet only light conditions showed some importance to *C. calceolus*. We found indication of trade-offs between ramet flower number and capsule width, where twin flowers developed smaller capsules than single flowers. Capsule width was used as estimator of seed number per capsule by using the allometric relationship between capsule width and capsule seed number.

Environmental differences

We registered occurrences of *C. calceolus* in both northern and southern aspects implying aspect direction alone does not restrict occurrence of the orchid. The terrain in *P. sylvestris* forest stand, southerly facing and with obvious slope, allows for high sun exposure. Even if

the terrain in *P. abies* forest stand faces north, the terrain was perceived as flat, hence not restricting sun exposure. Differences in aspect directions between forest stands can reflect the habitat preferences of *P. abies* and *P. sylvestris*.

Light transparency and canopy cover were measured using two different methods, by wide angle digital photo and LiDAR data. The year and month of registration of LiDAR data is important when assessing canopy structures. The LiDAR data used in this study was registered in July 2018. Even though the main constituents of the forest stands are coniferous trees, there is also presence of deciduous trees. The digital photos were taken in the month of June one year after LiDAR registrations, hence we can assume that canopy structure has not changed much by growth. As both light transparency and canopy cover show very good correlation, LiDAR proves an accurate and efficient method for light estimation on forest floor.

Based on the present factors in *P. sylvestris* forest stands, we can expect an earlier and prolonged growth season, with increased air and soil temperatures. This is supported by earlier maturation of flowers and capsules of *C. calceolus* in *P. sylvestris* forest stands. The slope and shallow soil on partly open bedrock allows for higher water runoff compared to *P. abies* with thicker humus and soil layer and probably higher water holding capacity (Bleam 2017). A thick humus layer suggests accumulation of organic material over time and higher recycling of phosphorus (Campbell et al. 2008). This could explain why we found higher amount of phosphorus in *P. abies* forest stands. We found no significant difference in nitrate, but higher ammonium concentration was registered in *P. sylvestris* forest stand. McFee and Stone (1968) found that ammonium was preferred over nitrate as nitrogen source for *Picea gleuca* (Moench) Voss and *Pinus radiata* D. Don., perhaps a preference shared by the closely related species of *P. abies* and *P. sylvestris*.

A significant difference in pH was observed between the forest stands, with pH 1.6 times more basic in *P. sylvestris* forest stands. A possible explanation for higher pH in *P. abies* forest stand could be deeper soil and flatter terrain, inhibiting washout of minerals. There was no difference in loss on ignition between the forest stands, but this can be owed to sampling at different soil depths (Skjellberg 1996).

The environmental variables measured are important for plant growth and function. Because we found significant differences in environmental variables between forest stands, one could

expect to find variability of species composition and variability within plant traits of species present in each forest stand.

Species

As can be seen in both Table 1 and in Figure 1 (Table A.2.a-d) the species composition varied between the two habitats. Species uniquely found in each forest stand indicated that the *P. sylvestris* dominated forest stands were periodically dry with more woody species and several lichens. There were also specialist saxicolous mosses on bedrock and specialist pioneer species on open soil. The *P. abies* dominated forest stand were dominated by more herbaceous species, almost lacking open soil and rocks. Comparison of unique species each forest stand reveals differences in habitat preference, observed for lichens, bryophytes and vascular plants. Some of the woody plants were only found in *P. sylvestris* forest stands, e.g. *C. vulgaris*, *E. nigrum*, *D. octopetala* and *J. communis*. There was a higher occurrence of moisture and nutrient demanding species, often thriving in more shady habitats in the *P. abies* forest stand, e.g. *A. nemorosa*, *Dactylorhiza* sp., *G. dryopteris*, *L. vernus*, *M. bifolium*, *O. acetosella* and *P. quadrifolia*. Even though many species are common in both habitats, the more demanding species indicate differences in moisture and nutrient availability between the forest stands.

Differences in plant traits of *C. calceolus* between forest stands

The difference in moisture and nutrient availability is not expressed in the plant traits measured in *C. calceolus*, which is surprising. It is possible that the traits measured in our study were not highly affected by the environmental variables. *Cypripedium calceolus* has been found to have relatively low nutrient demands (Kull 1999). A study of *C. calceolus* in Latvia found high variation in soil chemical composition, without finding strong correlation in leaf nutrient content, suggesting other factors were important for nutrient uptake (Klavina & Osvalde 2017).

One reason for not observing differences in traits between the forest stands might be low genetic variation and/or low phenotypic plasticity. The populations within the study area might be remains of the same population or a result of seed dispersal, but dispersal over longer distances is debatable. Brzosko et al. (2017) investigated dispersal distances of *C. calceolus* in an open habitat and a forested habitat. In both habitats, over 90 % of the seeds was found within a few meters. Based on these findings it is not very likely that seeds of *C. calceolus* could have been dispersed over many kilometers. However, Arditti and Ghani (2000) reports seed dispersal over hundreds of kilometers for several orchid species. They also investigated wind conditions and

found that seed morphology is of importance. As the seeds of *C. calceolus* are suited for wind dispersal, it is not impossible that they could spread over longer distances, given appropriate wind conditions.

As Norway was almost completely covered by ice during the last ice age, present populations of *C. calceolus* must have immigrated after the ice retreated. If orchid seeds have not travelled great distances, an eastern and/or southern immigration route is most probable. Fay et al. (2009) investigated genetic diversity in north-western Europe by mapping 23 different haplotypes. One of the populations investigated was situated in Jämtland, the eastern adjacent Swedish county of Snåsa. This population had only one out of 23 haplotypes present, and no genetic variation within the three samples. Because of the low genetic variance of *C. calceolus* in Jämtland, the neighboring populations in Snåsa might share the same genetical attributes. On the other hand, a low sample size and absence of samples from polymorphic sites limits the full picture of the genetic variance within Jämtland. In Dalarna, further south in Sweden, Fay et al. (2009) found 8 different haplotypes. A study from Estonia (Gargiulo et al. 2018) found high genetic diversity of *C. calceolus* in all 11 populations distributed from nemoral to boreal region, proving that high genetic variance occurs for the species.

Several factors could lead to low genetic variance over longer time within *C. calceolus*, such as founder effect and/or genetic drift, bottleneck events and low or no immigration constricting introduced gene material (Campbell et al. 2008). In addition, the very long lifespan of up to 100 years with high vegetative reproduction (Kull 1999), sparse distribution of the orchid, pollinator limitation and short distance foraging of the pollinators of *C. calceolus* (Antonelli et al. 2009, Linkowski et al. 2004, Neff & Simpson 1997, Nilsson 1979) along with low seedling establishment (Kull & Arditti 2002, cited in Shefferson et al. 2005) could inhibit rapid change in gene material. The small scattered populations of *C. calceolus* could be important for genetic diversity. Decrease in pollination frequency may lead to a shift towards a predominantly vegetative reproduction, which could negatively affect the possibilities of dispersal and the ability to adapt to habitat- and climatic change (Minasiewicz et al. 2018).

Phenotypic plasticity is suggested to be important for deceptive flowers in order to avoid pollinator learning (Heinrich 1975). Blinova (2012) investigated variations in morphological characters of *C. calceolus* along a latitudinal gradient across Europe and found low variance in traits, but this study was restricted by small sampling size. Zheng et al. (2017) found differences

of plant traits of *Cypripedium tibeticum* King ex Rolfe. within different light regimes, similar to a study by Li et al. (2008) involving *Cypripedium flavum* P.F. Hunt & Summerh.

Because other studies have found genetic variance within and among populations of *C. calceolus* (Fay et al. 2009, Gargiulo et al. 2018) and phenotypic variance within *C. calceolus* and other *Cypripedium* species (Blinova 2012, Li et al. 2008, Zheng et al. 2017), it is surprising that we are not able to detect more differences in plant traits. Genetic variance should be investigated for the populations of *C. calceolus* in Snåsa, ensuring conservation of genetically important populations, as the populations in Snåsa are among the most abundant populations in Norway (Brandrud et al. 2018).

Effect of environmental variables on plant traits

We found that canopy cover had a significant positive effect on flower numbers of *C. calceolus*. This result was not expected because thinning of forest structures in Finsåsmarka have resulted in population growth (Hassel & Holien 2010). Zheng et al. (2017) found increasing flower abundance with increased light intensities and Hurskainen et al. (2017) found that canopy thinning in boreal spruce forests increased probabilities of flowering and fruiting of *C. calceolus*. One explanation for our unexpected results could be interactions with other environmental variables, allowing for suitable conditions for flower abundance even with denser canopy structure. Another explanation might be that *C. calceolus* is already well established in the *P. abies* forest stand. The forest has likely been more open in the past, but due to a large population, probably consisting of old clones, the plants can have developed extended rhizomes enhancing resource uptake and allocation, thus allowing for higher abundance of flowers. Even though denser canopy (as found in *P. abies* forest stand) is related to flower numbers, capsule numbers were positively related to southern aspect (only registered in *P. sylvestris* forest stand). This might imply that pollinators are more attracted to flowers in sun rather than sheer flower abundance, as suggested by Nilsson (1979) and Kilkenny and Galloway (2008).

Trade-offs

We found that twin flowers were more likely to develop smaller capsules than capsules developed from single flowers, indicating a trade-off in ramet resource allocation. The presence of twin flowers proposes that the efforts of producing two flowers and eventually two capsules is worthwhile. The presence of two flowers increases chances of sexual reproduction, thus

production of double flowers could be a preferred strategy. Shefferson et al. (2003) investigated costs of flowering in *Cypripedium calceolus* var. *parviflorum* (Salisb.) Fernald. They did not find evidence for costs of reproduction and suggests that fitness of this species is not sensitive to sexual reproduction. Flowering clones had actually higher survival and dormancy occurred less frequently among clones producing flowers than vegetative clones. The results from the study of Shefferson et al. (2003) can explain our results of a positive relationship between numbers of ramets and numbers of flowers. If flowering clones have higher survival, clonal expansion is likely as the rhizomatic growth of *C. calceolus* continue each year (Kull 1999), increasing both rhizome length and possibly ramet numbers. We also found a positive association between fertile ramets and capsule numbers, and flower numbers and capsule numbers, which is reasonable given that the more fertile ramets and flowers produced, the higher chance of sexual reproductive success. More flowers can attract more pollinators, forward increasing chances of achieving pollination.

A positive significant relationship between four leaves and wider capsules can imply a tradeoff in resource allocation between ramet vegetative structure and ramet reproductive structure. This result should however be interpreted with caution, as residuals were not normally distributed in the statistical analysis.

Conclusion

Despite differences in environmental factors and vegetation composition, which witness differences in nutrient and moisture availability, the plant traits of *C. calceolus* measured did not differ between forest stands. One explanation could be that traits were not highly responsive to the environmental variables. Another possibility is that the populations we investigated have low genetical variance and/or low phenotypic plasticity. Both possibilities arise new questions related to the ecology and biology of *C. calceolus*. Light availability has proved to be an important factor influencing *C. calceolus* in other studies, this was also experienced by us. Large and old clones have probably higher fitness due to enlarged nutrient availability and resource allocation. More research regarding local populations should be initiated to gain more knowledge on which future management and conservation could be based upon. Other plant traits could be measured like ramet height and flower size, also interaction of pollinators and local pollinator availability should be explored. In addition, genetical studies could contribute to important knowledge regarding local genetical variance.

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Appendix

Table A.1.a		Species composition of plots. Lichens and bryophytes																	
PlotID	Forest.type	<i>Cladonia arbuscula</i>	<i>Cladonia rangiferina</i>	<i>Ctenidium molluscum</i>	<i>Dicranum sp.</i>	<i>Hylocomium splendens</i>	<i>Peltigera britannica</i>	<i>Plagiochila asplenoides</i>	<i>Plagiommium affine</i>	<i>Pleurozium schreberi</i>	<i>Ptilium-crista-castrensis</i>	<i>Racomitrium ericoideum</i>	<i>Rhytidadelphus triquetrus</i>	<i>Rhytidadelphus loreus</i>	<i>Sanionia uncinata</i>	<i>Scapania aspera</i>	<i>Schistidium trichodon</i>	<i>Torrella tortuosa</i>	<i>Tritomaria quinqueidentata</i>
F01	Pinus	0	1	0	0	3	0	0	0	2	3	0	0	0	0	0	0	1	0
F02	Pinus	0	2	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0
F03	Pinus	0	1	0	0	3	0	0	0	0	2	0	0	0	0	0	0	0	0
F04	Pinus	0	2	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0
F05	Pinus	0	3	0	0	0	1	0	0	2	3	0	2	0	0	0	0	1	0
F06	Pinus	0	2	0	2	3	0	0	0	2	2	0	0	0	0	0	0	1	0
F07	Pinus	0	2	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0
F08	Pinus	0	2	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0
F09	Pinus	0	2	0	0	3	0	0	0	2	3	0	1	0	0	0	0	0	0
F10	Pinus	0	1	0	0	2	0	0	0	3	2	0	3	0	0	0	0	0	0
F11	Pinus	0	1	0	0	3	0	0	0	2	3	0	0	0	0	0	0	0	0
F12	Pinus	0	1	0	0	3	0	0	0	2	2	0	0	0	0	0	0	0	0
F13	Pinus	0	1	0	0	3	0	0	0	2	0	2	1	0	0	0	0	0	0
F14	Pinus	0	0	1	0	3	0	0	0	0	1	0	3	0	0	0	0	0	0
F15	Pinus	0	1	0	0	3	0	0	0	1	3	0	1	0	0	0	0	0	0
F16	Pinus	0	2	2	0	3	0	0	0	0	1	1	2	0	0	0	1	1	0
F17	Pinus	0	2	1	0	3	0	0	0	1	1	0	1	0	0	0	1	1	0
F18	Pinus	2	1	1	0	2	0	0	0	0	1	3	0	0	0	0	0	0	0
F19	Pinus	1	2	0	0	2	0	0	0	0	2	2	0	0	0	0	1	2	0
F20	Pinus	0	2	0	0	3	0	0	0	0	0	1	1	0	0	1	0	1	0
F21	Pinus	1	1	0	0	3	0	0	0	2	2	0	2	0	0	0	0	1	0
F22	Pinus	1	2	1	1	3	0	0	0	1	2	0	2	0	0	0	1	1	0
Species mean		0,23	1,55	0,27	0,14	2,73	0,05	0	0	1	2,05	0,41	0,86	0	0	0,05	0,18	0,45	0
G01	Picea	0	0	0	0	3	0	2	0	2	2	0	3	2	0	0	0	0	0
G02	Picea	0	0	0	0	3	0	1	1	0	2	0	3	0	1	0	0	0	0
G03	Picea	0	0	0	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0
G04	Picea	0	0	0	0	2	0	0	0	0	1	0	3	0	0	0	0	0	0
G05	Picea	0	0	0	0	2	0	1	0	1	1	0	3	2	0	0	0	0	0
G06	Picea	0	0	0	0	2	0	1	0	0	1	0	3	0	0	0	0	0	0
G07	Picea	0	0	0	0	2	0	1	0	1	0	0	3	1	0	0	0	0	0
G08	Picea	0	0	0	0	2	0	0	0	0	2	0	3	0	0	0	0	0	0
G09	Picea	0	0	0	0	2	0	1	0	2	3	0	3	0	0	0	0	0	0
G10	Picea	0	0	0	0	2	0	1	0	0	0	0	3	0	0	0	0	0	0
G11	Picea	0	0	0	0	2	0	2	0	0	0	0	3	0	0	0	0	0	0
G12	Picea	0	0	0	2	2	0	3	0	1	1	0	3	0	0	0	0	0	1
G13	Picea	0	0	0	0	2	0	1	0	0	0	0	3	0	0	0	0	0	0
G14	Picea	0	0	2	0	2	0	1	0	0	0	0	2	1	0	0	0	0	0
G15	Picea	0	0	0	0	1	0	1	0	1	1	0	3	0	0	0	0	0	0
G16	Picea	0	0	0	0	2	0	0	0	0	0	0	3	0	0	0	0	0	0
G17	Picea	0	0	0	0	1	0	2	0	1	0	0	3	0	0	0	0	0	0
G18	Picea	0	0	0	0	2	0	2	0	1	0	0	3	0	0	0	0	0	0
G19	Picea	0	0	0	0	2	0	0	0	2	0	0	3	0	0	0	0	0	0
G20	Picea	0	0	0	0	3	0	1	0	0	2	0	3	0	0	0	0	0	0
Species mean		0	0	0,1	0,1	2,1	0	1,05	0,05	0,6	0,8	0	2,85	0,3	0,05	0	0	0	0,05

Class of coverage 1: < 5 %, 2: 5- 50%, 3: >50 %

Table A.1.b Species composition of plots. Vascular plants 1/3

PlotID	Forest.type	<i>Anemone nemorosa</i>	<i>Calluna vulgaris</i>	<i>Carex</i> sp.	<i>Cirsium</i> sp.	<i>Convallaria majalis</i>	<i>Crepis paludosa</i>	<i>Dactylorhiza</i> sp.	<i>Dryas octopetala</i>	<i>Empetrum nigrum</i>	<i>Epipactis atrorubens</i>	<i>Equisetum pratense</i>	<i>Filipendula ulmaria</i>	<i>Fragaria vesca</i>	<i>Geranium sylvaticum</i>	<i>Gymnocarpium dryopteris</i>
F01	Pinus	0	0	0	0	3	0	0	0	2	1	0	0	0	0	0
F02	Pinus	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0
F03	Pinus	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0
F04	Pinus	0	2	0	0	2	0	0	0	2	1	0	0	0	0	0
F05	Pinus	0	2	0	0	3	0	0	0	2	1	0	0	0	0	0
F06	Pinus	0	2	0	0	3	0	0	0	2	1	0	0	0	0	0
F07	Pinus	0	2	0	0	3	0	0	0	3	0	0	0	0	0	0
F08	Pinus	0	0	0	0	3	0	0	0	2	1	0	0	0	0	0
F09	Pinus	0	0	0	0	3	0	0	0	2	0	0	0	0	0	0
F10	Pinus	0	0	0	0	3	0	0	0	2	0	0	0	0	0	0
F11	Pinus	0	0	0	0	2	0	0	0	3	1	0	0	0	0	0
F12	Pinus	0	0	0	0	2	0	0	0	3	0	0	0	0	0	0
F13	Pinus	0	0	2	0	2	0	0	0	2	1	0	0	0	0	0
F14	Pinus	0	0	0	0	2	0	0	0	2	1	0	1	0	0	0
F15	Pinus	0	0	0	0	2	0	0	2	3	1	0	0	0	0	0
F16	Pinus	0	0	0	0	2	0	0	0	2	1	0	0	0	0	0
F17	Pinus	0	0	0	0	2	0	0	0	2	0	0	0	1	0	0
F18	Pinus	0	0	0	0	2	0	0	0	2	1	0	0	0	0	0
F19	Pinus	0	0	0	0	2	0	0	0	2	1	0	0	0	1	0
F20	Pinus	0	0	0	0	2	0	0	0	2	1	0	0	0	0	0
F21	Pinus	0	0	1	0	2	0	0	0	2	0	0	0	0	0	0
F22	Pinus	0	1	0	0	2	0	0	0	1	1	0	0	0	1	0
Species mean		0	0,5	0,14	0	2,32	0	0	0,09	2,05	0,64	0	0,05	0,05	0,09	0
G01	Picea	2	0	1	0	0	0	0	0	0	0	2	1	0	1	2
G02	Picea	2	0	0	0	0	0	1	0	0	0	2	2	0	2	2
G03	Picea	3	0	1	2	0	0	0	0	0	0	0	0	0	0	1
G04	Picea	3	0	1	2	0	0	0	0	0	0	0	0	0	0	1
G05	Picea	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
G06	Picea	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G07	Picea	2	0	0	0	0	0	1	0	0	1	0	0	0	0	1
G08	Picea	2	0	1	0	2	0	0	0	0	1	0	1	0	0	0
G09	Picea	0	0	2	2	1	0	1	0	0	1	1	0	2	0	0
G10	Picea	2	0	2	0	0	0	0	0	0	1	0	1	2	0	2
G11	Picea	2	0	1	0	0	2	0	0	0	0	1	2	0	1	2
G12	Picea	2	0	1	0	3	2	0	0	0	0	0	2	0	1	2
G13	Picea	2	0	1	0	2	1	0	0	0	0	0	0	1	0	2
G14	Picea	1	0	0	0	2	3	0	0	0	0	0	2	0	0	0
G15	Picea	2	0	1	0	0	2	0	0	0	0	0	1	0	1	2
G16	Picea	2	0	1	0	2	2	1	0	0	1	0	2	0	1	2
G17	Picea	2	0	1	0	2	0	1	0	0	1	0	0	2	1	0
G18	Picea	2	0	1	0	2	0	1	0	0	1	0	0	2	1	0
G19	Picea	2	0	2	0	1	0	1	0	0	0	0	0	0	1	2
G20	Picea	2	0	1	0	0	0	0	0	0	0	0	0	1	2	0
Species mean		1,95	0	0,9	0,3	0,85	0,6	0,35	0	0	0,35	0,3	0,7	0,5	0,6	1,15

Class of coverage 1: < 5 %, 2: 5- 50%, 3: >50 %

Table A.1.c Species composition of plots. Vascular plants 2/3

PlotID	Forest type	<i>Gymnocarpium obovatum</i>	<i>Hepatica nobilis</i>	<i>Hieracium</i> sp.	<i>Lathyrus vernus</i>	<i>Linnaea borealis</i>	<i>Listeria ovata</i>	<i>Maianthemum bifolium</i>	<i>Melica nutans</i>	<i>Ophrys insectifera</i>	<i>Oxalis acetosella</i>	<i>Paris quadrifolia</i>	<i>Poaceae</i> sp.	<i>Potentilla erecta</i>	<i>Rubus saxatilis</i>	<i>Saxifraga coryleodon</i>	<i>Solidago virgaurea</i>
F01	Pinus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
F02	Pinus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F03	Pinus	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	2
F04	Pinus	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0
F05	Pinus	0	2	2	0	0	0	0	0	0	0	0	0	0	1	0	2
F06	Pinus	0	2	2	0	1	0	0	0	0	0	0	0	0	0	0	1
F07	Pinus	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0
F08	Pinus	0	1	2	0	0	0	0	0	0	0	0	0	0	1	0	0
F09	Pinus	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0
F10	Pinus	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0
F11	Pinus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
F12	Pinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F13	Pinus	0	2	2	0	0	0	0	0	0	0	0	0	1	2	0	0
F14	Pinus	2	1	0	0	1	2	0	0	0	0	0	0	2	2	0	0
F15	Pinus	1	0	2	0	1	0	0	0	0	0	0	0	1	2	0	0
F16	Pinus	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0
F17	Pinus	0	0	2	0	1	0	0	0	0	0	0	0	0	1	0	2
F18	Pinus	1	1	1	0	0	0	0	0	0	0	0	0	2	2	1	1
F19	Pinus	2	1	2	0	0	0	0	0	0	0	0	0	2	2	0	2
F20	Pinus	1	1	2	0	0	0	0	0	0	0	0	0	1	2	0	0
F21	Pinus	0	0	2	0	1	0	0	0	0	0	0	0	2	2	0	1
F22	Pinus	0	1	1	0	0	0	0	0	0	0	0	0	2	2	0	1
Species mean		0,32	0,95	1,32	0	0,27	0,09	0	0	0,05	0	0	0	0,64	1	0,05	0,55
G01	Picea	0	2	2	0	1	0	2	0	0	2	1	0	0	2	0	2
G02	Picea	0	0	0	0	1	0	2	1	0	2	0	0	0	0	0	2
G03	Picea	0	2	0	0	0	0	2	1	0	0	0	1	0	2	0	1
G04	Picea	0	2	0	0	0	0	2	1	0	0	0	1	0	2	0	1
G05	Picea	0	0	1	0	1	0	1	1	0	0	0	2	0	2	0	0
G06	Picea	0	1	2	0	1	0	2	0	0	1	0	0	0	2	0	1
G07	Picea	0	2	2	0	0	0	2	0	0	1	0	0	0	0	0	1
G08	Picea	0	1	2	0	0	1	1	0	0	0	0	1	1	2	0	1
G09	Picea	0	2	2	0	0	1	0	1	0	0	0	0	0	2	0	2
G10	Picea	0	1	1	0	1	0	1	0	0	1	0	1	2	2	0	0
G11	Picea	0	1	2	0	1	0	2	1	0	0	0	0	1	2	0	0
G12	Picea	0	0	2	0	1	1	0	1	0	1	0	0	2	2	0	1
G13	Picea	0	1	1	0	1	0	1	1	0	1	1	0	0	2	0	2
G14	Picea	0	2	2	0	0	0	0	1	0	0	0	0	1	2	0	0
G15	Picea	0	2	0	0	0	0	1	1	0	0	0	0	1	0	0	0
G16	Picea	0	2	1	0	0	1	2	1	0	0	1	0	1	3	0	0
G17	Picea	0	2	2	0	1	2	2	1	0	0	0	0	1	2	0	2
G18	Picea	0	2	2	0	1	2	2	1	0	0	0	0	1	2	0	2
G19	Picea	0	2	2	0	1	1	0	0	0	0	1	0	1	2	0	0
G20	Picea	0	2	0	1	1	0	2	1	0	1	0	0	0	2	0	1
Species mean		0	1,45	1,3	0,05	0,6	0,45	1,35	0,7	0	0,5	0,2	0,3	0,6	1,75	0	0,95

Class of coverage 1: < 5 %, 2: 5- 50%, 3: >50 %

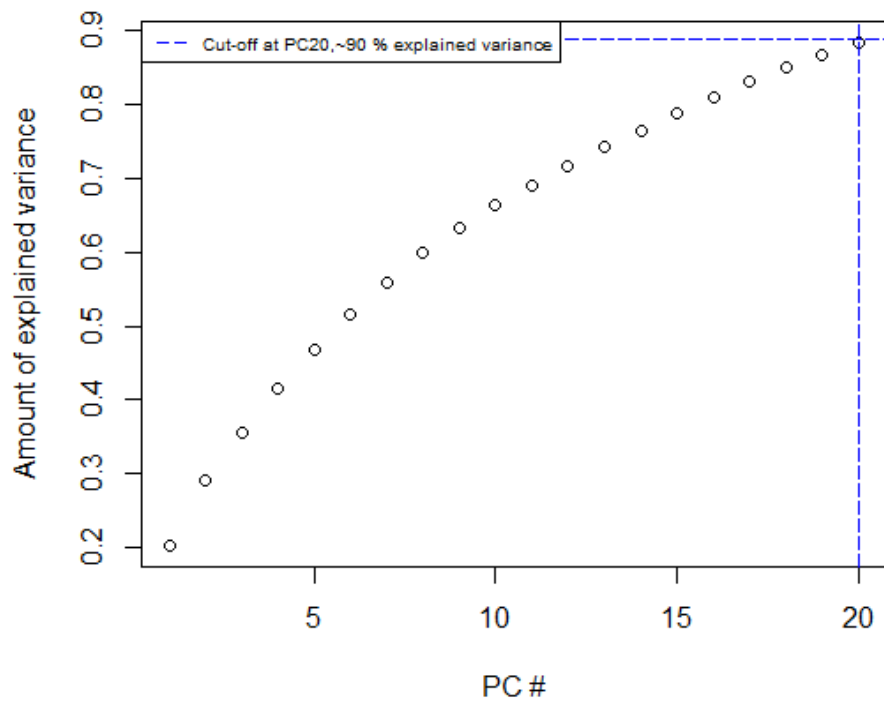
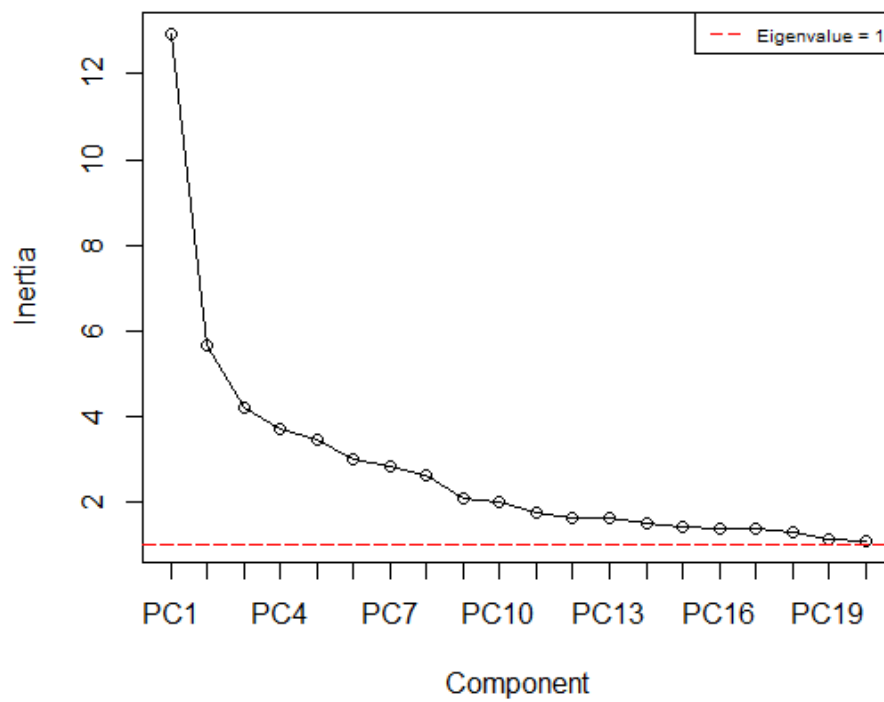
Table A.1.d Species composition of plots. Vascular plants 3/3

PlotID	Forest-type	<i>Taraxacum</i> sp.	<i>Tussilago</i> sp.	<i>Vaccinium myrtillus</i>	<i>Vaccinium uliginosum</i>	<i>Vaccinium vitis-idaea</i>	<i>Viola riviniana</i>	<i>Alnus incana</i>	<i>Betula pubescens</i>	<i>Cotoneaster integerrimus</i>	<i>Frangula alnus</i>	<i>Juniperus communis</i>	<i>Picea abies</i>	<i>Pinus sylvestris</i>	<i>Salix caprea</i>	<i>Sorbus aucuparia</i>
F01	Pinus	0	0	0	0	2	0	0	0	0	0	3	0	0	0	0
F02	Pinus	0	0	0	0	3	0	0	0	0	0	3	2	0	0	0
F03	Pinus	0	0	0	0	2	2	0	0	0	0	2	1	0	0	0
F04	Pinus	0	0	0	0	2	0	0	1	0	0	1	1	0	1	1
F05	Pinus	0	0	0	0	2	0	0	0	0	0	2	0	2	0	0
F06	Pinus	0	0	0	0	2	0	0	0	0	0	3	2	0	0	1
F07	Pinus	0	0	0	0	3	1	0	0	0	0	2	1	0	0	0
F08	Pinus	0	0	1	0	2	0	0	0	0	0	2	0	0	0	0
F09	Pinus	0	0	1	0	2	0	0	0	0	0	3	2	0	0	0
F10	Pinus	0	0	0	0	3	0	0	0	0	0	3	2	0	0	0
F11	Pinus	0	0	1	0	2	1	0	0	0	0	0	1	0	0	0
F12	Pinus	0	0	2	0	3	0	0	0	0	0	1	0	0	0	0
F13	Pinus	0	0	1	0	1	0	0	0	0	0	2	0	0	0	0
F14	Pinus	0	0	2	1	2	0	0	0	1	0	0	0	0	0	0
F15	Pinus	0	0	1	0	2	0	0	0	0	0	2	0	0	0	0
F16	Pinus	0	0	0	0	2	0	0	0	0	0	2	2	1	0	0
F17	Pinus	0	0	0	0	2	0	0	0	0	1	2	0	2	0	1
F18	Pinus	0	0	0	0	1	0	0	0	0	1	2	0	2	0	1
F19	Pinus	0	0	0	2	2	0	0	0	0	1	1	0	2	0	0
F20	Pinus	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0
F21	Pinus	0	0	0	0	2	0	0	0	0	0	0	2	1	0	0
F22	Pinus	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0
Species mean		0	0	0,41	0,18	2,09	0,18	0	0,05	0,05	0,18	1,73	0,73	0,45	0,05	0,18
G01	Picea	1	2	2	0	2	2	1	0	0	0	0	0	0	0	0
G02	Picea	0	0	2	0	2	0	0	0	0	0	0	2	0	0	1
G03	Picea	0	0	3	0	1	0	1	0	0	0	0	0	0	0	2
G04	Picea	0	0	3	0	1	0	1	0	0	0	0	0	0	0	2
G05	Picea	0	0	2	0	2	0	2	0	0	1	0	1	0	1	2
G06	Picea	0	0	2	0	2	2	0	0	0	0	0	2	0	0	0
G07	Picea	2	0	2	0	2	1	2	0	0	0	0	0	0	0	1
G08	Picea	0	0	2	0	1	0	3	0	0	0	0	0	0	0	1
G09	Picea	0	0	1	0	1	1	2	0	0	0	0	2	0	0	0
G10	Picea	1	0	0	0	2	1	2	0	0	0	0	0	0	0	1
G11	Picea	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0
G12	Picea	0	0	1	0	2	0	2	0	0	0	0	1	0	0	2
G13	Picea	0	0	2	0	2	0	0	0	0	0	0	1	0	0	1
G14	Picea	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0
G15	Picea	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1
G16	Picea	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
G17	Picea	1	0	2	0	2	1	0	0	0	0	0	0	0	0	1
G18	Picea	1	0	2	0	2	1	0	0	0	0	0	0	0	0	1
G19	Picea	0	0	2	0	2	0	0	0	0	0	0	0	0	0	1
G20	Picea	0	0	2	0	2	0	1	0	0	0	0	2	0	0	0
Species mean		0,3	0,2	1,55	0	1,45	0,55	1,1	0,05	0	0,05	0	0,55	0	0,05	0,85

Class of coverage 1: < 5 %, 2: 5- 50%, 3: >50 %

Table A.2 PCA of 66 species in 42 plots

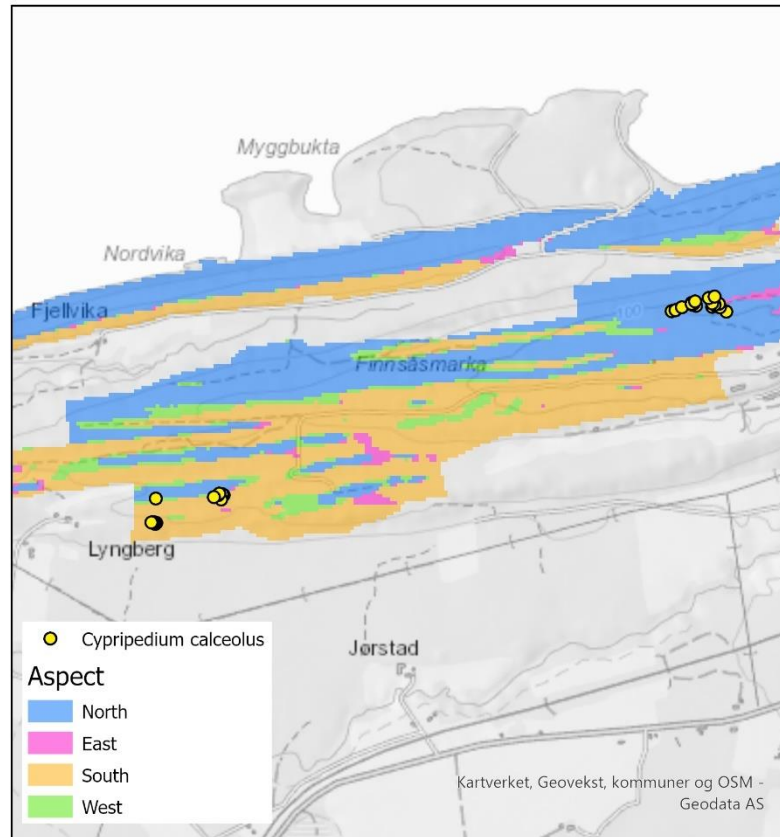
	Eigenvalue	Variance %	Cumulative variance %
Dim.1	12.9464849483292	20.2288827317643	20.2288827317643
Dim.2	5.64579266399059	8.8215510374853	29.0504337692496
Dim.3	4.21798980188573	6.59060906544645	35.6410428346961
Dim.4	3.70614726892051	5.7908551076883	41.4318979423844
Dim.5	3.43130316466865	5.36141119479477	46.7933091371791
Dim.6	3.0045044616183	4.69453822127859	51.4878473584577
Dim.7	2.83833193661339	4.43489365095843	55.9227410094162
Dim.8	2.62526714523021	4.1019799144222	60.0247209238384
Dim.9	2.05921319748898	3.21752062107653	63.2422415449149
Dim.10	2.01492256092861	3.14831650145096	66.3905580463659
Dim.11	1.74967975971901	2.73387462456095	69.1244326709268
Dim.12	1.63845067012056	2.56007917206338	71.6845118429902
Dim.13	1.61546980482253	2.52417157003521	74.2086834130254
Dim.14	1.49701055473263	2.33907899176974	76.5477624047951
Dim.15	1.41416913014839	2.20963926585687	78.757401670652
Dim.16	1.38665608506832	2.16665013291925	80.9240518035712
Dim.17	1.35497853204571	2.11715395632142	83.0412057598927
Dim.18	1.26974039630139	1.98396936922092	85.0251751291136
Dim.19	1.13173866294862	1.76834166085722	86.7935167899708
Dim.20	1.07511533523021	1.67986771129721	88.473384501268
Dim.21	0.986946871180426	1.54210448621942	90.0154889874874
Dim.22	0.843943092153941	1.31866108149053	91.3341500689779
Dim.23	0.731325575002251	1.14269621094102	92.476846279919
Dim.24	0.639367783937567	0.999012162402449	93.4758584423214
Dim.25	0.598900934186749	0.935782709666796	94.4116411519882
Dim.26	0.539275955873757	0.842618681052745	95.254259833041
Dim.27	0.501213669601955	0.783146358753055	96.037406191794
Dim.28	0.444723674954712	0.694880742116737	96.7322869339108
Dim.29	0.377657032621582	0.590089113471222	97.322376047382
Dim.30	0.342959805078188	0.53587469543467	97.8582507428167
Dim.31	0.334603583965013	0.522818099945333	98.381068842762
Dim.32	0.269615032640655	0.421273488501024	98.802342331263
Dim.33	0.205693483026587	0.321396067229042	99.1237383984921
Dim.34	0.146298329439017	0.228591139748464	99.3523295382405
Dim.35	0.137545682978791	0.214915129654361	99.5672446678949
Dim.36	0.0999996733257908	0.156249489571548	99.7234941574664
Dim.37	0.0739886069379693	0.115607198340577	99.839101355807
Dim.38	0.0458919269903044	0.0717061359223507	99.9108074917293
Dim.39	0.029413464268786	0.0459585379199782	99.9567660296493
Dim.40	0.0201740015156527	0.0315218773682073	99.9882879070175
Dim.41	0.00749573950878045	0.0117120929824695	100
Dim.42	2.55324395894229e-30	3.98944368584732e-30	100

Figure A.1.a. Cumulative variance plot**Figure A.1.b. Screeplot of the first 20 PCs**

Figur A.2

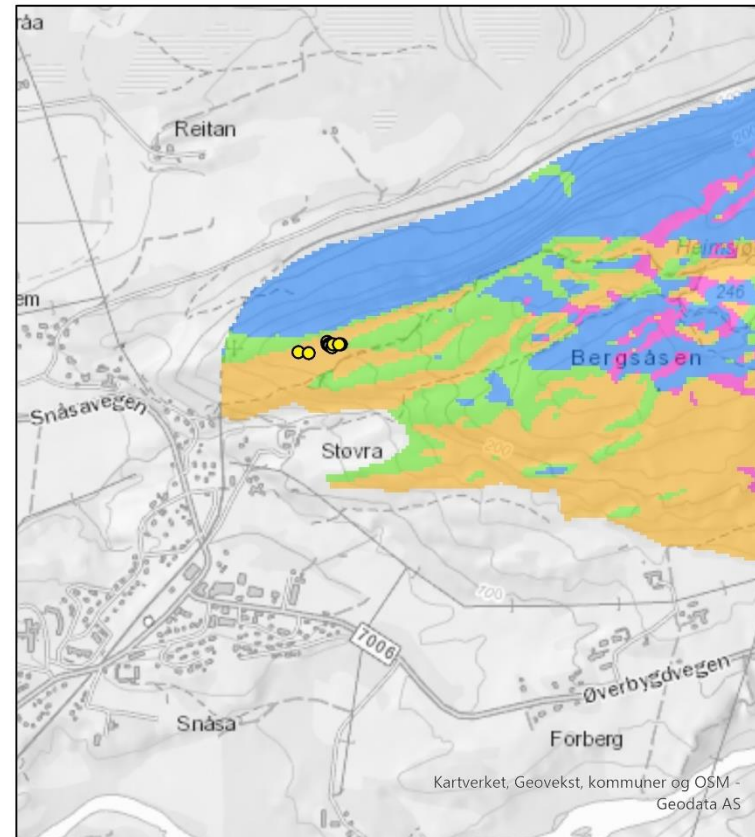
Aspect directions

Finsåsmarka



Aspect directions within the nature reserves of Finsåsmarka and Bergsåsen. Locations of plots with *C. calceolus* included.

Bergsåsen



0 0,25 0,5 1 Kilometer

Figure A.3

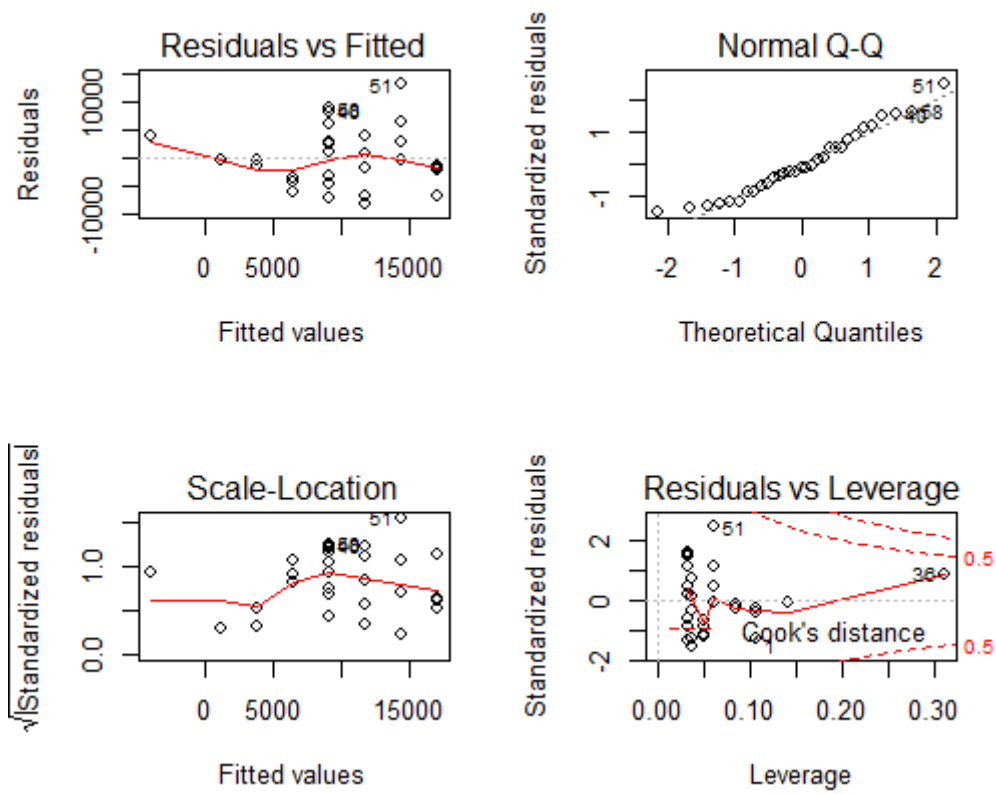


Figure A.4.a
Variance between groups

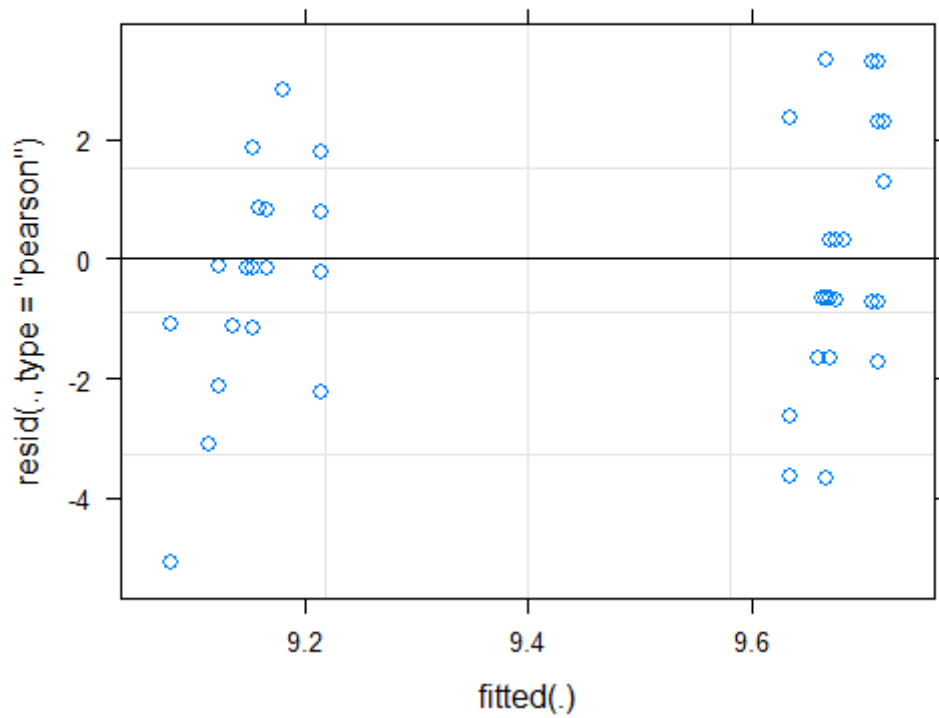


Figure A.4.b
QQ plot model residuals

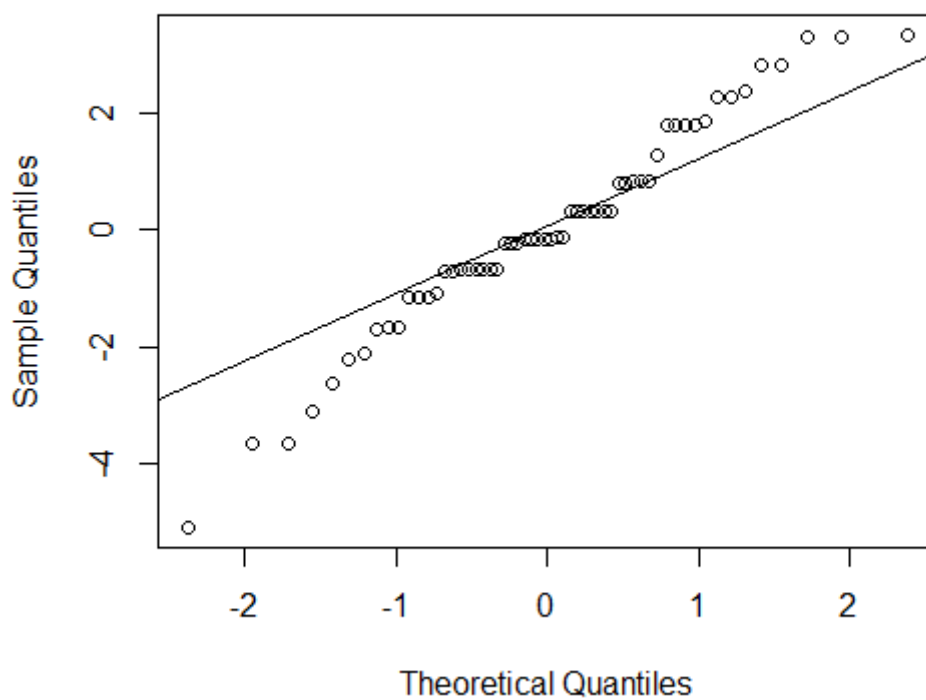


Figure A.4.c
Histogram of residual distribution

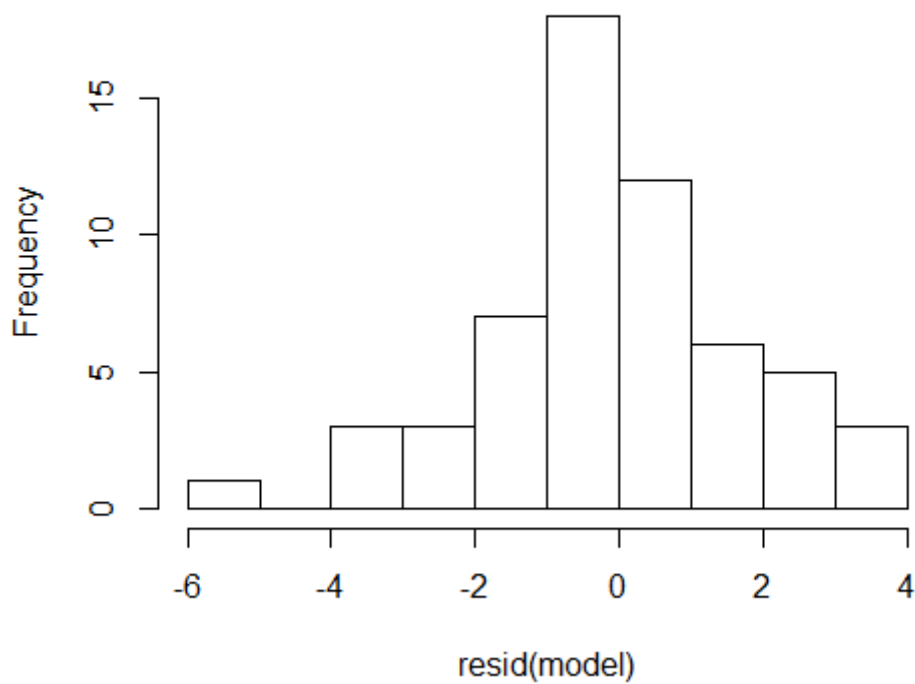


Figure A.5

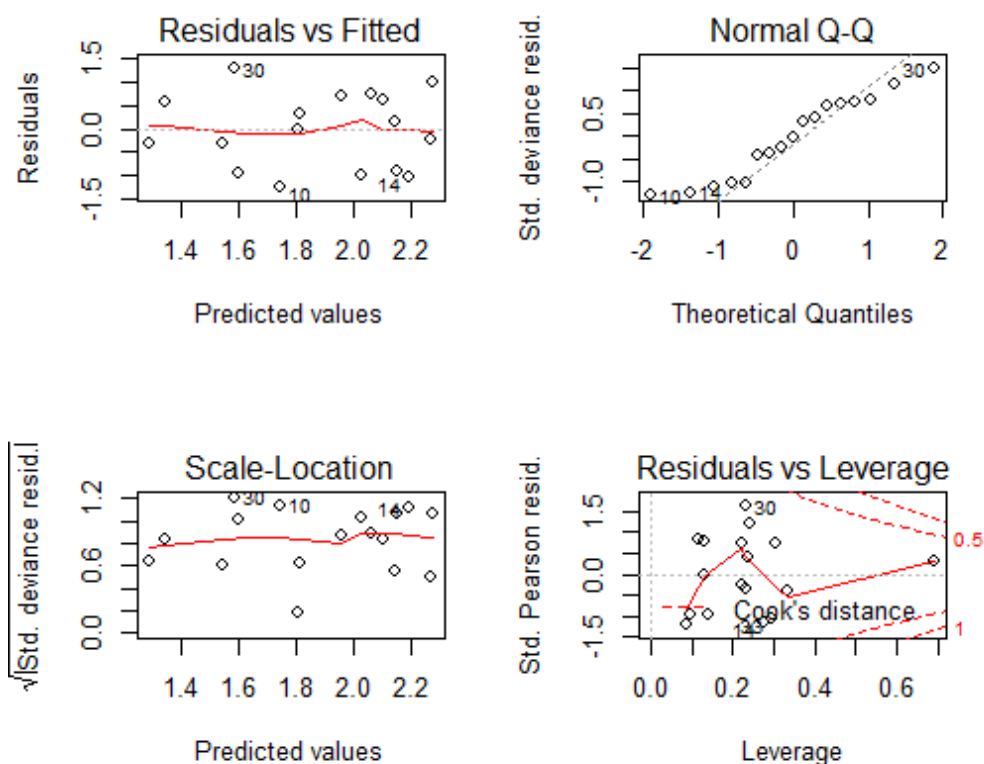


Figure A.6

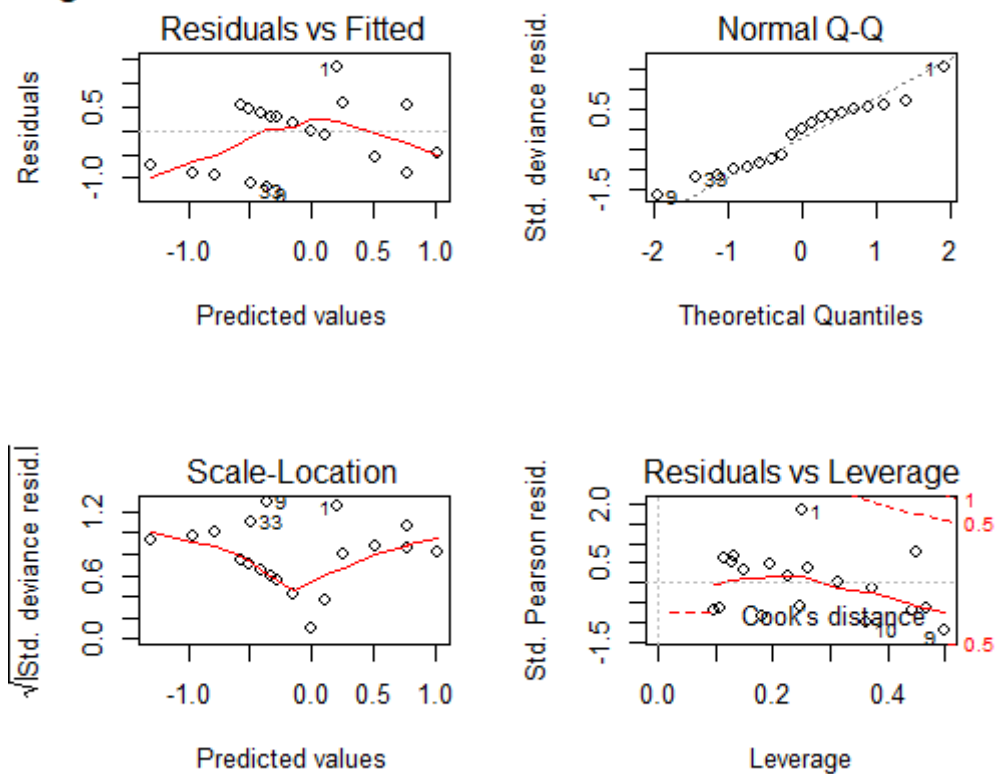


Figure A.7.a
Variance among groups

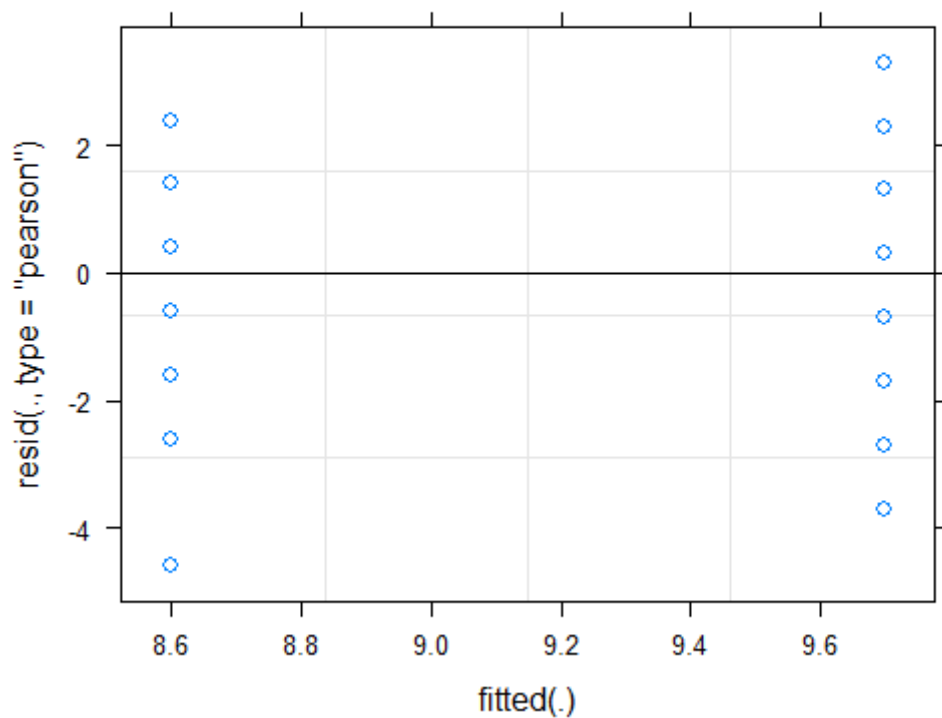


Figure A.7.b
QQ plot model residuals

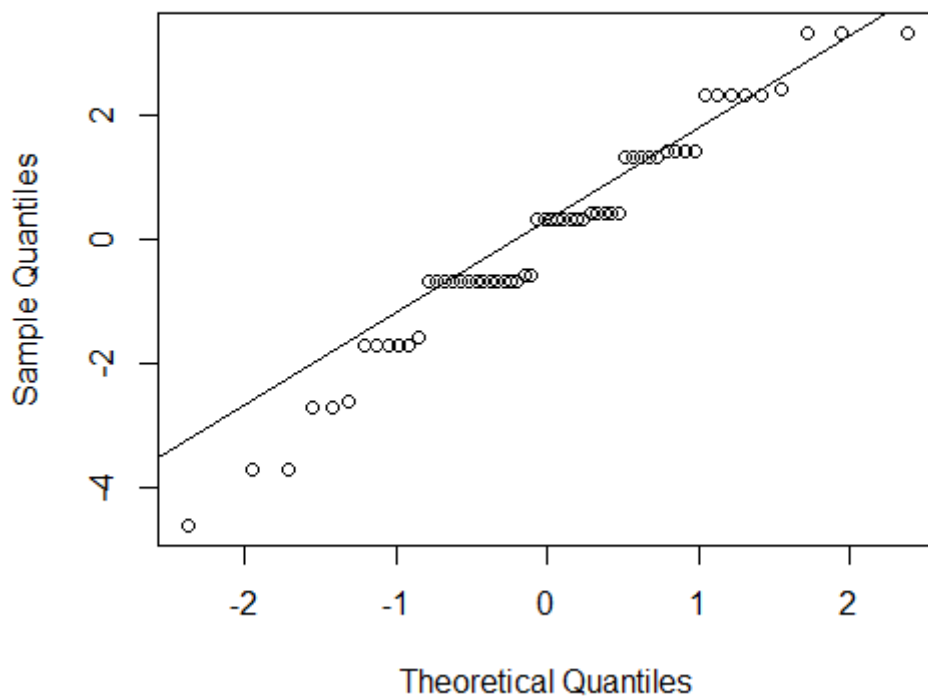


Figure A.7.c
Histogram of residual distribution

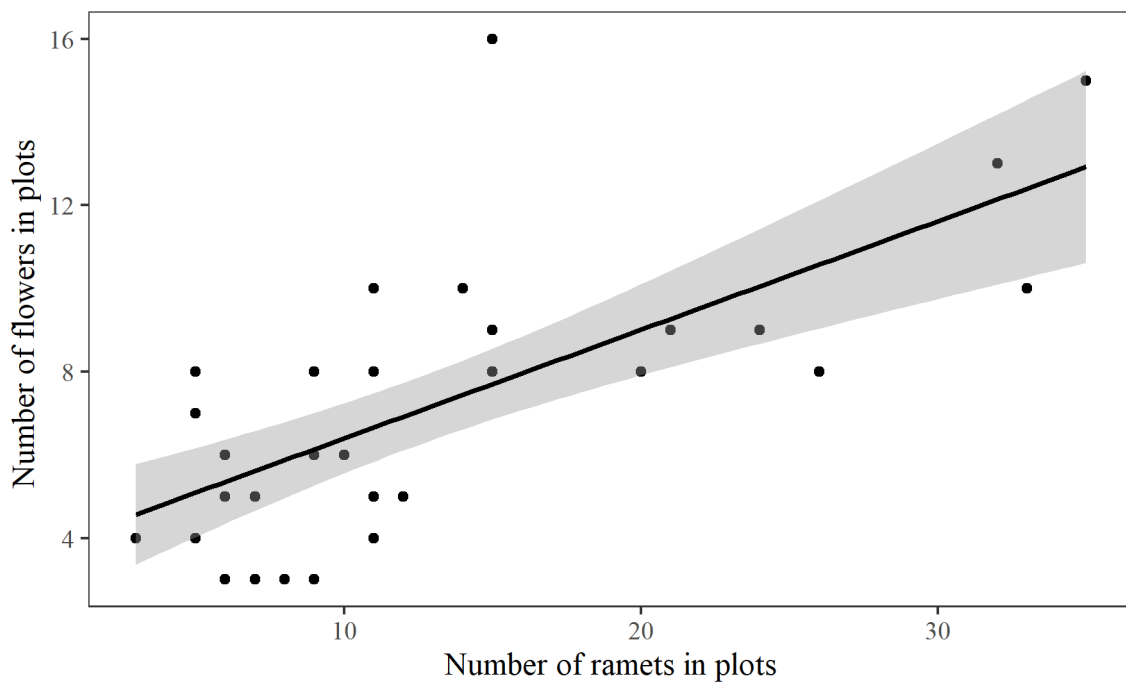
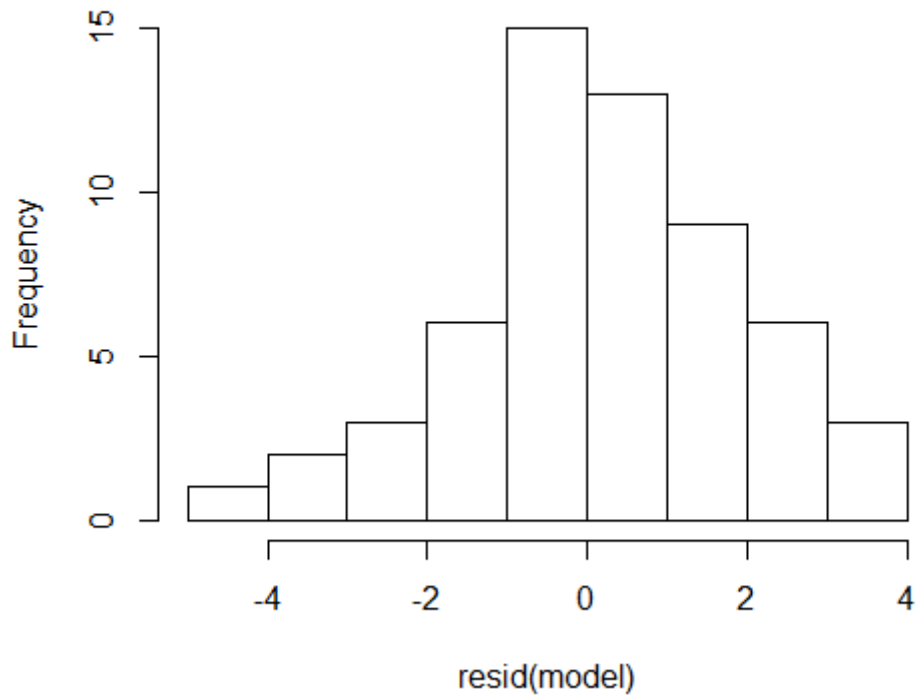


Figure A.8.a. Relationship between number of ramets and number of flowers in plots
 Linear regression: $r^2 = 0.40$, $F = 23.72$, $df = 1,33$, $p\text{-value} < 0.001$

Figure A.8.b

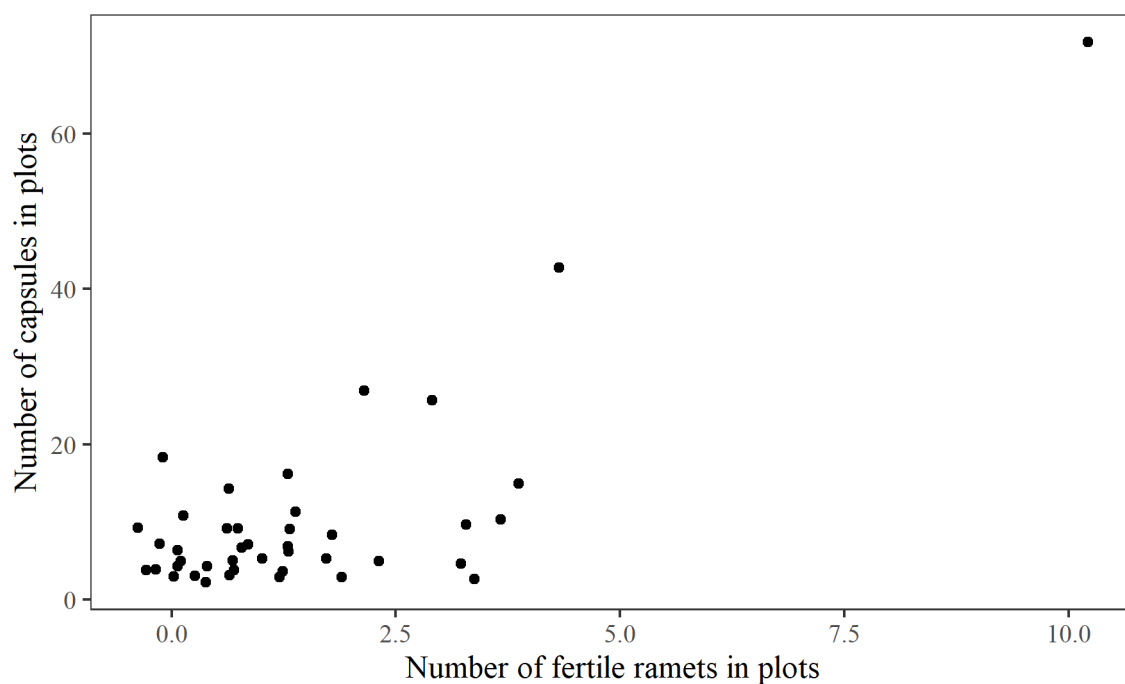
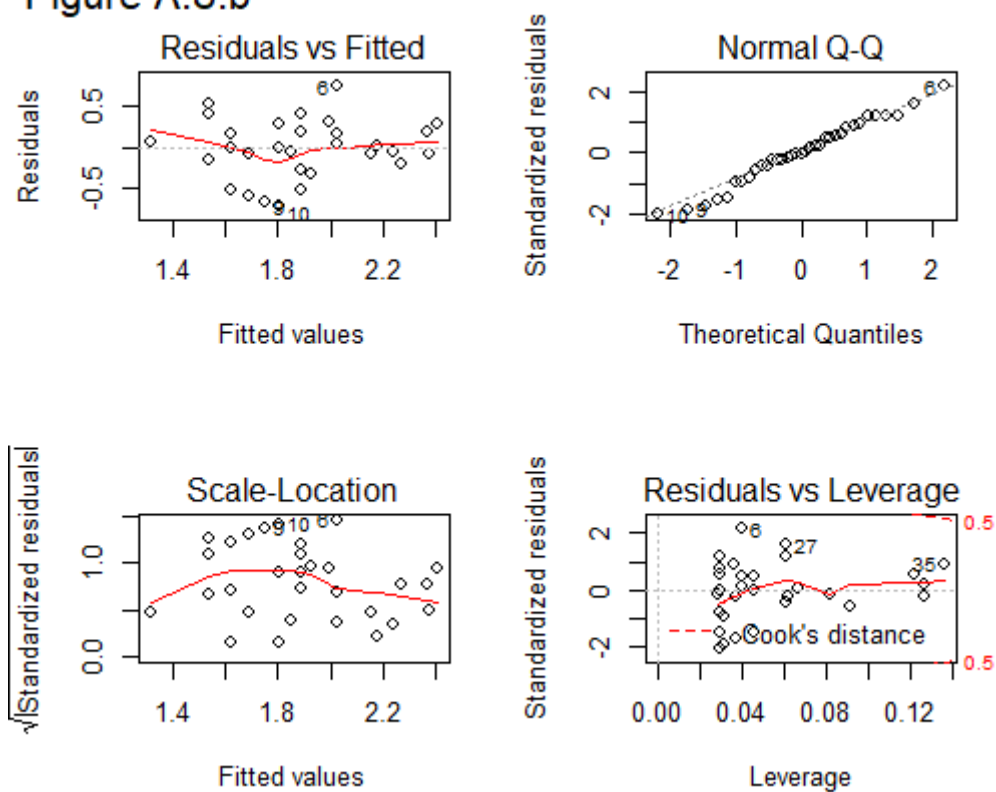


Figure A.9. Correlation between number of fertile ramets and capsules in plots
Spearman's rank correlation ρ : $S = 7613$, $p = 0.012$, $\rho = 0.38$

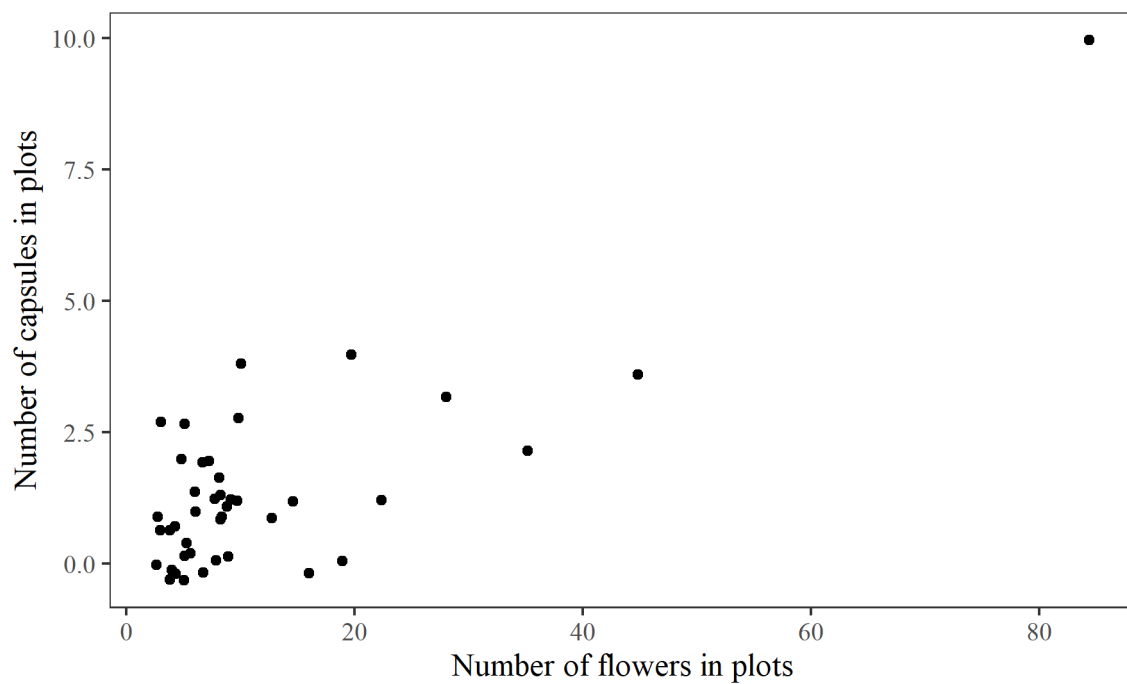


Figure A.10 Correlation between number of flowers and number of capsules in plots
Spearman's rank correlation rho: $S = 7736$, $p = 0.014$, $\rho = 0.37$

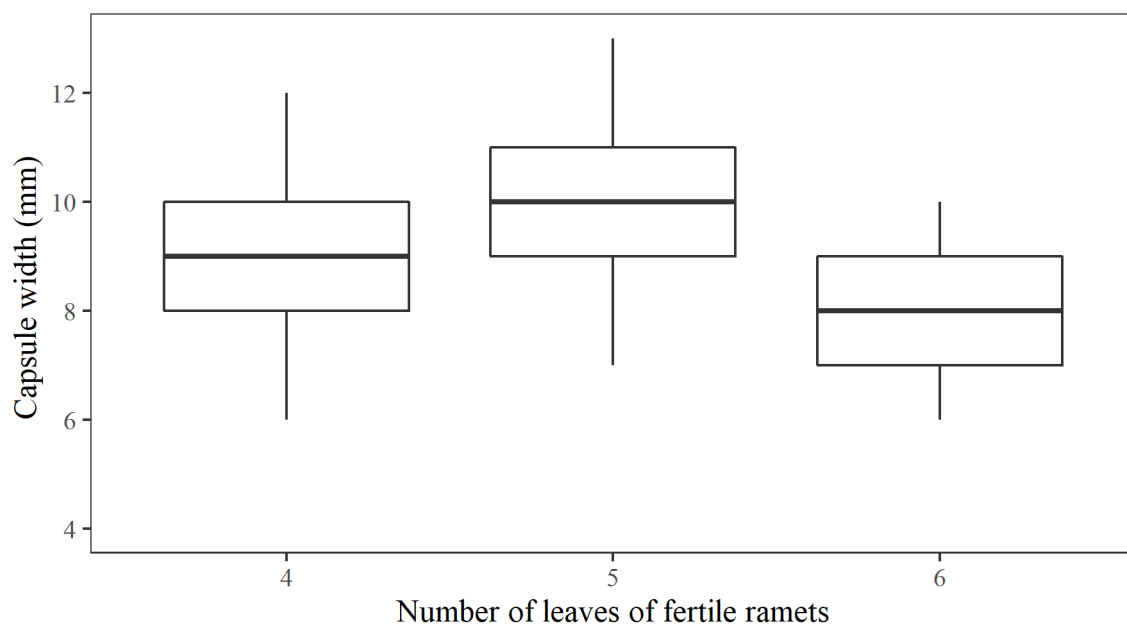


Figure A.11.a Capsule width between ramets of different leaf number
4 leaves: $\beta = 8.9565$, $SE = 0.372$, $df = 54.9$, $p < 0.001$
5 leaves: $\beta = 0.8617$, $SE = 0.4857$, $df = 54.9$, $p = 0.08$
6 leaves: $\beta = -0.9565$, $SE = 1.3183$, $df = 55$, $p = 0.47$. $AIC = 238.49$

Figure A.11.b
Variance among groups

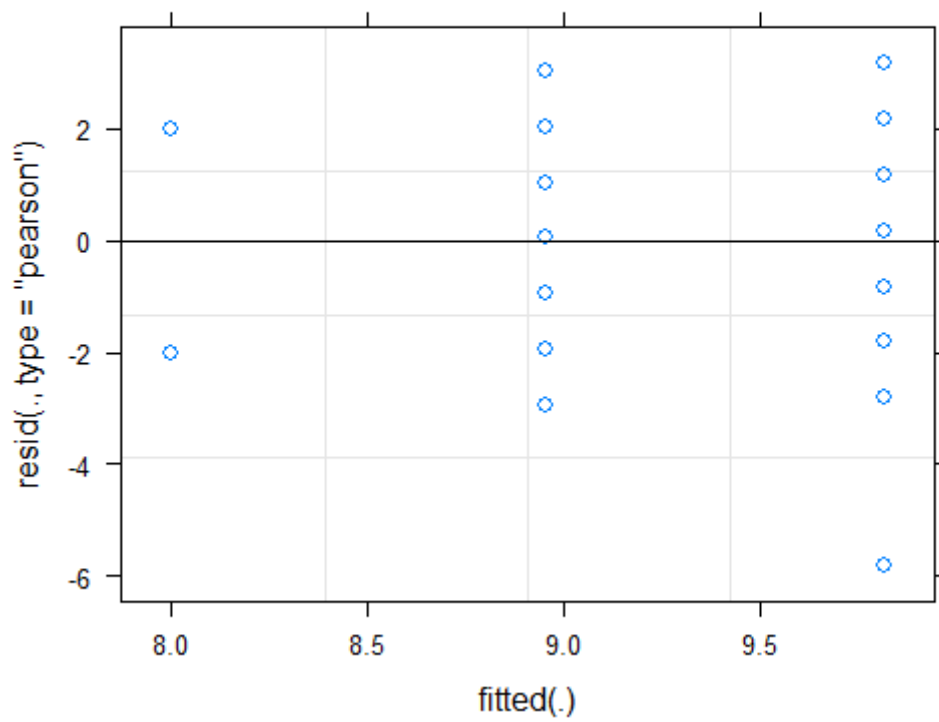


Figure A.11.c
QQ plot model residuals

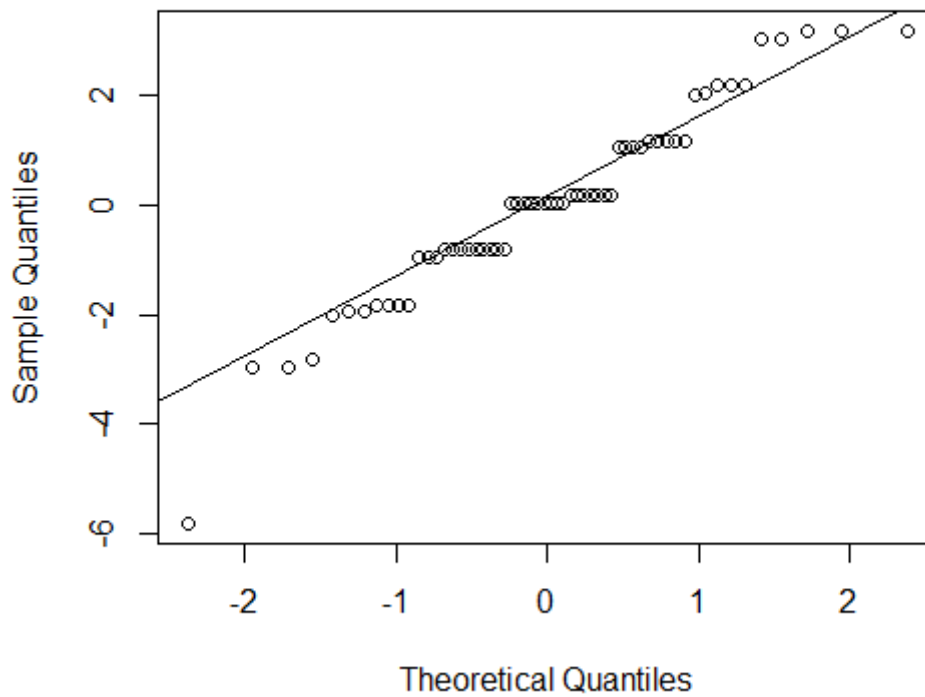


Figure A.11.d
Histogram of residual distribution

