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Interspecific competition in Arctic plants for pollination services

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Photo: Diptera on a Dryas octopetala. (Malin Olsson, 2022)

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Abstract

The Arctic has a harsh environment that is challenging for the flora and fauna that inhabits the region. The ruling abiotic factors of the region results is a low species richness that creates a potential challenge for the region's plant species. Here, sexual reproduction becomes more difficult due to fewer accessible pollinators and a short period during the summer that I suitable for flowering. As a consequence of this, we can expect interspecific competition for pollination between plant species when the living conditions get more extreme. There is also the potential that plant species in the region are utilizing alternative strategies for reproduction, like autonomous selfing, to a higher degree when outcrossing is not as available. The aim of the study was to see if interspecific competition in Arctic plants changed between a southern and a northern Arctic site and to investigate if the plants had a dependency on pollinator services. Plant-pollinator networks from the High Arctic Svalbard and the subarctic eastern mountain of Tväråklumparna, Sweden, were described by catching pollinators that were interacting with flowers. By applying Müller's index, the interspecific competition was estimated at the sites. In addition, a pollination experiment was performed for the species mountain avens (*Dryas octopetala)* and moss campion (*Silene acaulis*), that are present at both sites. Three treatments were used, an open treatment, a hand-pollination and an exclusion treatment, to estimate pollinator dependency and pollen limitation. At the network level, the degree of interspecific competition was higher at Svalbard, compared to the site at Tväråklumparna ($p = 0.02$). While it couldn't be concluded that *S. acaulis* had a stronger impact on other plant species at any of the sites. However, *D. octopetala* appeared to be a strong competitor at Svalbard that attracted many of the local pollinators. Pollinator dependence seemed to be occurring in the species but while being able to reproduce by autonomous selfing, the selfing rates at Svalbard were low. This is raising the question of a relationship between a species' reproductive assurance and the selfing rate. Further research is needed to investigate if there is a connection between the two.

Keywords: *the Arctic, pollinator networks, competition, autonomous selfing*

Sammanfattning

Arktis har en sträng miljö som är utmanande för den flora och fauna som lever i regionen. De styrande abiotiska faktorerna i regionen har resultat i en låg artrikedom som skapar en potentiell utmaning för regionens växtarter. Här blir sexuell reproduktion blir svårare på grund av färre tillgängliga pollinatörer och en kort sommar som lämpar sig för blomning. Som en konsekvens av detta kan vi förvänta oss interspecifik konkurrens för pollinering mellan växtarter, när levnadsförhållandena blir mer extrema. Det är också möjligt att växtarter i regionen i högre grad använder alternativa strategier för reproduktion, så som autonom självpollinering, när utkorsning inte är lika tillgänglig. Syftet med studien var att se om interspecifik konkurrens i arktiska växter förändrades mellan en södra och en nordlig arktisk plats, och att undersöka om växterna var beroende av de tjänster som pollinatörer utför. Nätverket mellan växter och pollinatörer från det högarktiska Svalbard och det subarktiska östra berget Tväråklumparna, Sverige beskrevs genom att fånga pollinatörer som besökte blommor. Genom att tillämpa Müllers index uppskattades den interspecifika konkurrensen på platserna. Utöver detta, utfördes ett pollineringsexperiment för arterna fjällsippa (*Dryas octopetala)* och fjällglim (*Silene acaulis*), som finns på båda platserna. Tre behandlingar användes, en öppen behandling, en handpollinering och en uteslutningsbehandling, för att uppskatta behovet av pollinatörer och om de begränsas av tillgängligheten av pollen. På nätverksnivå var den interspecifika konkurren högre på Svalbard, jämfört med Tväråklumparna ($p = 0.02$). Även om det inte kunde dras slutsatsen att *S. acaulis* hade en starkare inverkan på andra växtarter på någon av platserna. *D. octopetala* verkade dock vara en stark konkurrent på Svalbard som lockade många av de lokala pollinatörerna. Ett beroende av pollinatörer verkade förekomma hos arten, trots att den har förmågan att föröka sig genom autonom självpollinering, var frekvensen av självpollinering på Svalbard låg. Detta väcker frågan om det finns ett samband mellan en arts garanti för reproduktion och hur mycket en växt självpollinerar. Ytterligare forskning behövs för att undersöka om det finns ett samband.

Nyckelord: *Arktis, pollinationsnätverk, konkurrens, autonom självpollinering*

Introduction

Animal mediated pollination is an essential ecosystem service. Animal pollinators are estimated to pollinate 87.5% of all angiosperms (Ollerton, et al., 2011). The interactions like these are part of a mutualistic network between plants and pollinators, which in turn are paramount for the function of ecosystems and to global biodiversity. That biotic pollinators act as a driver for biodiversity and evolution is an old idea that dates back to the 19th century when it was described by Darwin (Darwin, 1862). More recently, studies have shown that biotic pollination can increase species richness to a greater extent than abiotic pollination (i.e., pollination utilizing non-living vectors) (Dodd, et al., 1999). Plant specialization has the ability to change depending on the kind of biotic pollinator a plant interacts with (Gervasi & Schiestl, 2017).

Insects are widely regarded to be the most important group among animal pollinators. There is a high dependency in plants for insect pollination for seed set (80% of wild plants, 75% of cultivated plants) (Rodger, et al., 2021; Ollerton, et al., 2011). The reliance on insect pollinators for seed set exists globally, including regions with harsh climate such as the high Arctic (Kevan, 1972). Evidence from the last decades shows that there is a decline in pollinators on a global scale (Potts, et al., 2010). This effect of pollinators is also prominent in the Arctic, were the most abundant types of pollinators are in decline (Loboda, et al., 2018; Høye, et al., 2013) The underlying causes behind the decline are thought to be a combination of multiple drivers such as in land use, use of pesticides, invasion of alien species and climate change (Høye, et al., 2013).

Life in the Arctic

The number of species in most Arctic taxa is considered low and tends to decrease with increasing latitude (CAFF, 2013). This statement is also true when it comes to insects (CAFF, 2013). The low diversity of pollinators in the High Arctic is possibly explained by the environmental conditions, which can be variable and harsh. The High Arctic is characterized by an ecosystem that is constrained by low temperatures that are below freezing for large parts of the year (Billings, 1987; Bliss, 1971). In addition to the low air and soil temperatures, the plant communities need to live in an environment in which the soil cover is generally thin and low in nutrients (Billings, 1987). The environmental conditions allow for only a short growing season in which plants need to complete their reproductive cycle within a few weeks (Bliss, 1971; Tiusanen, et al., 2020). South of the Arctic (i.e., the High Arctic and the Low Arctic) we find the subarctic regions (Figure 1). In general terms, the constricting abiotic factors (e.g., air and soil temperature, nutrients, drought and growth period) become less extreme in the subarctic region, which allows for higher species richness (in plants and pollinators alike) (CAFF, 2013).

Figure 1. The boundaries of the Arctic and subarctic regions. Copyright: The Conservation of Flora and Fauna (CAFF).

Plant-pollinator interactions

When working with pollinators one aspect that can be of interest is how successful an insect is as a pollinator. There are two components when determining how successful a provided pollination service will be, which are visitation frequency and pollinator effectiveness (King, et al., 2013). The visitation frequency is describing how fast a pollinator is moving between flowers. Pollinator effectiveness is the measurement of the pollen transfer ability, which King et al. (2013) define as the number of conspecific pollen grains (i.e., pollen from the same species) that are transferred during a single visit. Flies (*Muscidae*) seem to have generally lower pollen effectiveness when comparing them to e.g., bumblebees (*Bombus spp.*) and the western honeybee (*Apis mellifera*) (Gervasi & Schiestl, 2017; King, et al., 2013). In some areas in the Arctic (e.g., Svalbard) there is a deficit or an absence of bumblebees and other pollinators from the family *Apidae* (Kevan, 1972), while instead houseflies (*Muscidae*) are the primary pollinator (Tiusanen, et al., 2016). Pollinators with low pollination effectiveness would possibly be able to move between individuals of the same

species of plant with a higher frequency and that way provide a satisfactory pollination service (King, et al., 2013). When the pollinators in a community for some reason can't transfer a sufficient amount of conspecific pollen, it can have effects on the plants. Often flowering plants are pollen limited (i.e., a shortage of pollen in quantity or quality), which leads to a reduced seed set (Ashman, et al., 2004; Knight, et al., 2005; Rodger, et al., 2021). A low quantity of pollen can be a result of fewer visits by pollinators, or a lower amount of pollen transferred per visit. The quality of pollen might be considered low if it's heterospecific (i.e., pollen from a different species), closely related, self-pollen or in other ways incompatible (Ashman & Arceo-Gómez, 2013; Ashman, et al., 2004; Husband & Schemske, 1996). Pollen limitation can be persistent, yet in most cases fluctuating temporally and spatially (Burd, 1994). Thus, a community can recover from a previous season of pollen limitation if the reasons behind the insufficient pollen transfer are mitigated. Yet, the cause for pollen limitation can be difficult to determine, although it can arise from disturbances in the ecosystem that shifts the equilibrium between plant and pollinators (Ashman, et al., 2004). Potential disturbances could be the introduction of alien species, loss of native pollinators, changes in plant abundance or co-flowering (Ashman, et al., 2004; Knight, et al., 2005)

A competitive coexistence

Over time, pollen limitation is thought to select for traits giving a stronger pollinator attraction. Possible responses could be a change or intensification in the color display of the petals or the scents that the flower produces to attract pollinators (Trunschke, et al., 2021). Ratnieks and Balfour (2021) hypothesize that in generalistic networks (i.e., networks where many species are inter-linked with each other) where plants are not receiving sufficient pollination, this can possibly cause the nectar production to increase at a community level. Nectar is the reward pollinators receive for visiting the flower and a higher amount of available nectar can have a higher attraction value. Even though this purpose of attracting pollinators is an important one, it is also a costly one that can affect future reproductive success (Ratnieks, et al., 2021; Pyke, 1991). To further increase the chances for successful pollination, it also might be possible that there is selective pressure for increased pollen production (Cunha, et al., 2022). The mentioned adaptations are all for raising the likelihood of outcrossing, but if pollination remains absent it could also lead to a selection pressure for alternative reproductive modes that limit the reliance on pollinators (e.g., autonomous selfing, i.e., the self-fertilization of a hermaphroditic flower) (Ashman, et al., 2004; Burd, 1994). Utilizing autonomous selfing as a strategy of reproducing comes with both its benefits and drawbacks. Husband and Schemske (1996) found that plant species that reproduce through autonomous selfing have a lower seed set than those that reproduce sexually. Note that many species are not restricted to a single reproduction mode but rather have a mixed mating system. There are however plant species that are obligately outcrossed due to being self-incompatible.

The reasons behind competition for pollinators can have a variety of causes. As stated, plants in the Arctic are given a short window of time to reproduce, which could imply that most of the plants are competing for a limited abundance of pollinators. It is noteworthy though that co-flowering can have the ability to facilitate pollinator sharing in plants (i.e., one species of pollinator is associated with multiple plant species) (Ashman & Arceo-Gómez, 2013). In a study by Bergamo, et al., (2022) co-flowering in a community with high biodiversity seemed to facilitate pollination from pollination-effective hummingbirds, instead of creating competition for pollinators.

However, it's still not well understood how the relationship between pollinators and plants function in a system with low diversity. In order to disentangle the relationship, we need a better understanding of factors that might affect potential pollinator dependence and interspecific competition in plants.

Aims of the study

The primary aim of the study was to explore how plants might be affecting each other though their shared pollinators in Arctic-alpine plant communities. Furthermore, I explored whether this effect varies depending on the biodiversity and structure of the networks they are part of. Finally, I investigated the differences in competition between species of flowering plants in two different Arctic environments (high Arctic and subarctic). Specifically, I asked:

i) What network structure and degree of interspecific competition for pollinators can be observed among plant species?
ii) Does the degree of competition among Arctic plant species differ between Arctic regions, and
iii) Does the degree of autonomous selfing and outcrossing differ between the regions?

I hypothesized that interspecific competition between plant species will be greater in the High Arctic than the subarctic due to a variety of causes. These include hasher living conditions, which makes pollination more difficult (Rodger, et al., 2021; Cunha, et al., 2022). This could in turn lead to a greater reliance on pollinators for outcrossing. Furthermore, I expected that the High Arctic will have a higher proportion of autonomous selfing. This is because of an assumed longer exposure to an environment deficient in pollinators and stronger interspecific competition.

Material and method

The study sites

Sampling was conducted in the vicinity of Longyearbyen, Svalbard (78°13′N 15°38′E) from late June to late July of 2022. The site is situated in the High Arctic and has a variable topography, in which the altitude ranges between 0 to approximately 1700 meters above sea level (Noël, et al., 2020). The mean air temperature in the period June to August 2022 was 7.4°C (measured at Svalbard Airport) (Mamen, et al., 2022). This was a record-high mean temperature for the period, which was 0,2°C warmer than the previous highest temperature that occurred in 2020 (Mamen, et al., 2022). The site that is representing the subarctic region in this project is the eastern mountain of Tväråklumparna in Jämtland county ("Tväråklumpen" hereafter), Sweden. Data was previously collected at the site between 22-06-2021 and 24-07-2021. Note that the same protocols for data collection were used at both sites.

While the two sites have different compositions of plants, there is an overlap between the two sites. Therefore, there are several species that occurred in both surveys (see Table A2.1 and Table A2.2). It should be noted that just because plants only occurred in one survey, it doesn't mean that certain plants don't have the potential to occur in both sites (e.g., *Harrimanella hypnoides* was only part of the recorded network at Tväråklumpen but is known to occur on Svalbard as well).

Data collection

Insect data

To assess the local pollinator-plant community structure, sampling and observation of visitation patterns of insects were done in seven transects along an elevation gradient that ranged from approximately 40 to 430 meters above sea level. The transects were walked at a slow to moderate pace by a minimum of two observers (between 10:00 and 19:00 in the day) during the period of 28-06-2022 and 20-07-2022. The sampling was restricted to suitable weather (i.e., calmer and dry weather) to avoid behavior in the pollinators where they seek shelter on the plants. Once an insect was observed to have contact with the reproductive organs (i.e., the pistil and/or the stamen) of a flower, the visitation pattern (i.e., the number of visits to multiple inflorescences) of the insect and

the species of plants visited were recorded in the field. If a visit lasted for 10 seconds, the insect was collected with a hand net. The collected insects were placed in Eppendorf tubes and stored at −16°C for later processing. All plant visitors meeting the above-stated criteria were considered pollinators upon collection.

The total survey time for the observers added up to 59 h 50 min in Svalbard. At Tväråklumpen the survey time was 83 h 14 min.

All collected insects were visually identified in a laboratory with the help of a variety of identification keys (Zimin & Elberg, 1989; Oosterbroek, 2006; Shamshev, et al., 2020; Stur & Ekrem, 2020; Bartsch, 2009). In addition, help from experienced entomologists was used to ensure correct identification. The goal was to achieve high taxonomic resolution and insects were identified to species level whenever possible. In cases where this wasn't conceivable, higher taxonomic levels were used.

Pollination experiment

To estimate the reproductive output and the pollinator contribution in local plants, a series of pollination experiments were performed during the visit to Svalbard. Here three treatments were used: i) including hand-pollination (outcrossing), ii) pollination exclusion and iii) open treatment. The plants that are part of the open treatment are marked up and left to be pollinated by the local insects. They are left without further interference until the seeds are collected at the end of the season. This treatment is used to evaluate seed production in natural conditions and acts as a basis to investigate pollen limitation and pollinator dependence. In order to evaluate the possible pollen limitation in a plant the hand-pollination treatment is used. Here a minimum of 3 pollen donor plants are used, all of which were located at least 5 meters away from any other plant used in that specific pollination occasion. The pollen is then manually put on the stigma of the treated plant. The stigma thus receives a large amount of pollen through outcrossing which is then thought to produce close to the highest possible seed set. The pollination exclusion treatment is used to evaluate the dependence on pollinators for seed production. If we hinder insect pollination for a plant, which is then only capable of producing a small number of seeds in comparison to the open treatment, we can then say that there is a reliance on insects for effective pollination (see Table 1 for a short summary of the treatments). When the exclusion treatment was performed, tightly closed buds were covered with a mesh cage to eliminate plant-insect interactions. Continuously as the seed pods matured, they were gathered and placed in paper bags. These were then stored in bigger plastic bags filled with silica until they could be counted.

Table 1. Summary and aim of the treatments that were done as part of the pollination experiment.

Treatment	Pollen source	Coverage	Aim
Hand-pollination	Intraspecific flowers	No cover	Evaluate the pollen limitation
Pollinator exclusion	Self	Covered	Evaluate the reliance on insect pollinators
Open	Natural pollination	No cover	Evaluate seed set under natural conditions

Statistical analysis

Analyses were done in R version 4.2.1, mainly with the package bipartite (Dormann, 2022) and the package vegan (Oksanen, et al., 2022). In order to determine the network structure and the degree of interspecific competition all interactions were summed up between the pollinators and the plants and compiled into interaction matrices, one for each plant-pollinator network. To adjust for the difference in abundance among plant species, data from vegetation surveys were used. These vegetation surveys were performed during the same periods as from when insects were collected at the two sites. From these surveys, the average plant cover for each species was calculated (Svalbard: 67 plots, Tväråklumpen: 36 plots). This was multiplied with the relative abundance of visited plants in the transects to create a proxy for abundance over the flowering season.

To investigate the network structure I used a variation of network metrics which include interaction strength (Bascompte, et al., 2006), nestedness (NODF), modularity (Q), species specialization degree (*d'*) (Blüthgen, et al., 2006), network specialization degree (H_2') (Blüthgen, et al., 2006). Nestedness describes a specific pattern of interactions between pollinators and plants, where the specialists (i.e., species that interact with one or a few other species) in the network are interacting with a subset of the species that the generalist are interacting with (Bascompte & Jordano, 2007). A sorted nestedness plot will therefore create a diagonal over the plot, which is a typical look for a network that is nested. When running an analysis for modularity, you are looking for modules (i.e., a set of species that are forming sub-communities) (Dormann & Strauss, 2014). This makes detection of species that are potentially dependent on each other easier, but the analysis can also help us identify species that are connecting these sub-communities. The metric species specialization degree (*d'*) can describe how specialized the interactions a species has within its network. Network specialization degree (H_2') helps us describe how specialized the network is and can be used to compare networks.

For evaluating if the structure given by the nestedness and modularity metrics were different from randomly assembled ones, both metrics were run against a set of null models. This was done by generating several new matrices by randomizing the observed data matrix. The value for the observed data, given by the chosen metric, is then compared to the distribution of all values given by the randomized matrices (Gotelli & Ulrich, 2012). For NODF there is a variety of pre-built algorithms that put different constraints on the null models that are generated. How these constraints are used can create a balancing issue. On one hand, if the algorithm is too unconstrained, it increases the risk of type I errors. On the other hand, too many constraints increase the risk of type II errors. Creating and running a benchmark test is a complex task and in the absence of better alternatives two different algorithms were used to test for nestedness (Gotelli & Ulrich, 2012). The first algorithm used was *quasiswap*, which keeps the margin sums fixed in rows and columns and is considered to be the more conservative algorithm of the two. The second algorithm that was used was *c0* where the margin sums of the columns are fixed, while the rows are allowed to randomize freely. For all null models, 10 000 permutations were used. For calculating modularity, the QuanBiMo algorithm was used (Dormann & Strauss, 2014). For the steps and tolerance, the settings of 10^8 and 1^{-10} were applied. The null model *vaznull* was used, which preserves the same level of connectance as in the observed data but doesn't fix margin sums. When reporting on the significance of the modularity, the p-value and a standardized z-score are used; the latter is recommended by Dormann and Strauss (2014). Z-scores over 2 are considered to be modular.

To estimate the interspecific competition, I have used Müller's index, which is a binomial variable that assesses the probability of an acting plant species (i.e., the plants species that is creating the effect) affecting a target plant species (i.e., the plants species that is being affected) through their shared pollinators. A Müller's index of 0 indicates that the acting plant has no influence on the target plant, due to no shared pollinators. Values > 0 indicate that there is influence on the target plant to various extents (Carvalheiro, et al., 2014). In the package bipartite, Müller's

index is referred to as PAC (Potential for Apparent Competition) and is calculated as seen below (equation 1.) (Carvalheiro, et al., 2014). When comparing the plant species at the two sites, each transect that had 5 or more observed individuals of the acting plant species was used as its own replicate. The data was non-normalized and had uneven sample sizes. Because of this, a non-parametric test was used. Note that overlapping species (e.g., *Saxifraga oppositifolia*) were excluded from the comparison due to the low number of interactions it had on both sites (< 10).

$$d_{ij} = \sum_{k} \left[\frac{\alpha_{ik}}{\sum_{l} \alpha_{il}} \times \frac{\alpha_{jk}}{\sum_{m} \alpha_{mk}} \right]$$

Equation 1. The calculation for Müller's index (d_{ij}). α_{ik} represents the total number of interactions between the target plant species (i) and the pollinator species (k). The sum of all interactions between all pollinators and the target plant species is represented by l. α_{jk} represents the total number of interactions between the acting plant species (j) and the pollinator species (k). The sum of all interactions between the pollinator species and all plant species that are visited by the pollinator (k) is represented by m.

To assess the seed set, potential pollen limitation and pollinator dependency for the plant species that were part of the pollination experiment, the Kruskal Wallis test was used. Due to unequal sample sizes and non-normal distributions in the data. For the post hoc test I used Dunn's multiple comparison test with Dunn-Sídák correction to adjust the p-values. To compare the treatments between the sites the relative median of the samples that were part of the hand-pollination treatment was used to estimate a maximum level of possible seed production.

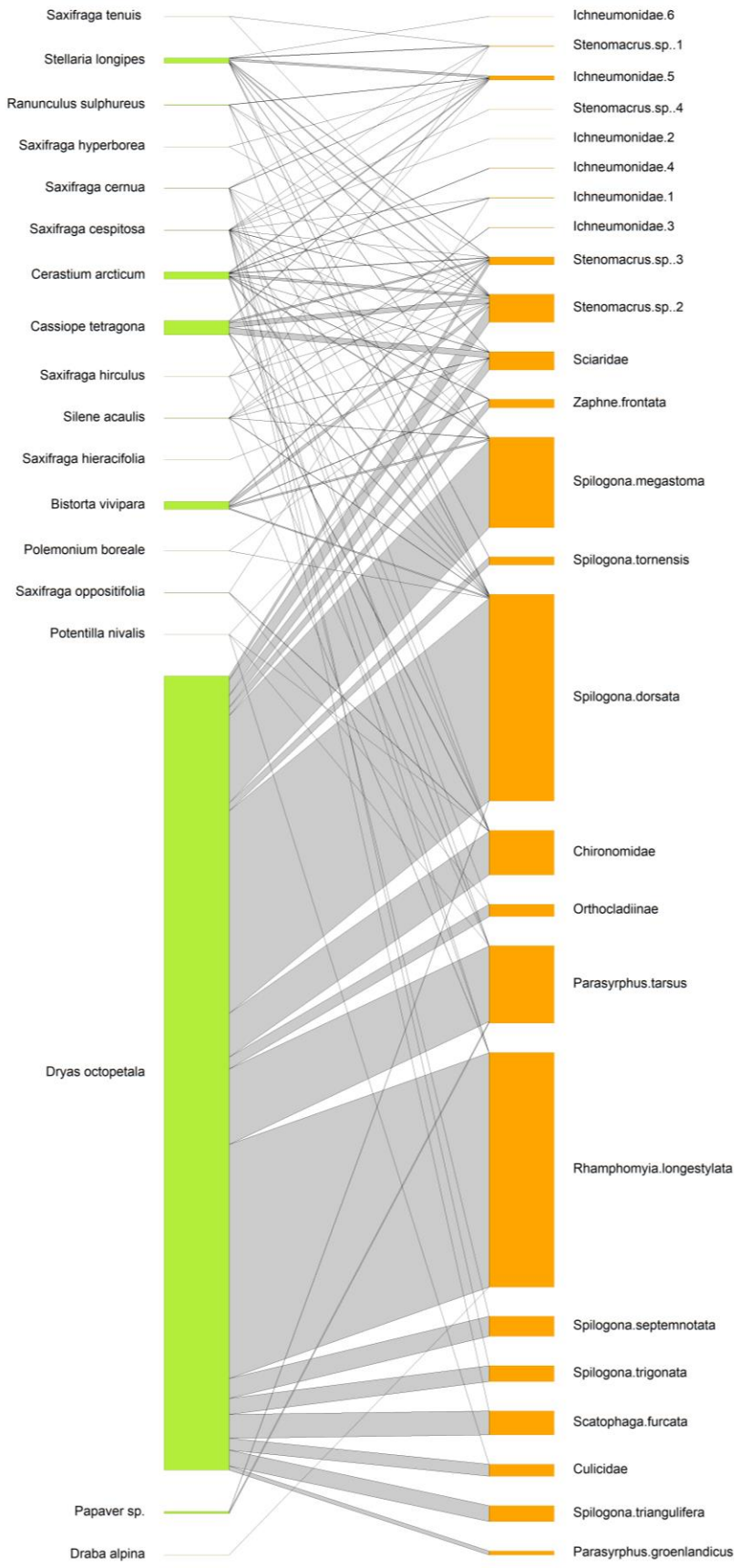
Results

The pollinator-plant network on Svalbard (SB) consisted of 25 insect species/morphospecies (belonging to 8 families) and 18 plant species (belonging to 9 families) (see Table A2.1 and Table A3.1). At Tväråklumpen (TK), the network consisted of 103 insect species/morphospecies (belonging to 33 families) and 57 plant species (belonging to 26 families) (see Table A2.2 and Table A3.2). In total 638 interactions were observed in Svalbard and 2000 interactions were observed at Tväråklumpen (Figure 2).

The connectance in the Svalbard network is 0.24 and at Tväråklumpen it is 0.06. The network specialization degree for the two communities was somewhat lower at Svalbard (SB: H_2'= 0.43; TK H_2'= 0.54). As for the species specialization degree for the pollinators (SB: *d'*= 0 – 0.72; TK *d'*= 0 - 1) it can be stated that on Svalbard higher levels of specialization degree are shown by species in the family *Ichneumonidae*, with the highest given by the morphospecies *Ichneumonidae 5*. This generalization is not true for Tväråklumpen, where the species with the highest specialization degree is more mixed between families, *Scaptomyza pallida* being the highest of the species (Table A3.1 and Table A3.2). Just as for the pollinators the specialization degree for the plants has a lower max value on Svalbard than on Tväråklumpen (SB: d'= 0 – 0.52; TK d'= 0 - 1) highest (Table A2.1 and Table A2.2).

In the case of nestedness, it is not clear from our statistical tests whether the networks are nested or not (SB: NODF = 57.44, p(*quasiswap*) = 0.4 and p(*c0*) = < 0.01; TK: NODF = 18.69, p(*quasiswap*) = 0.15 and p(*c0*) = < 0.01). Looking at the plots (see Figure A4.1 and Figure A4.2) there is a moderate diagonal separation that is typical for nested communities. At Svalbard, the network is not modular (Q = 0.6, p = 1, z-score = -7.73) (Figure A5.1). At Tväråklumpen no modularity was identified (Q = 0.27, p = 0.90, z-score = -2.90) (Figure A5.2). The interaction strength for the plant species varied between species in both networks (SB: 1.44E-06 – 15.56; TK: 9.38E-07 – 21.16) (Table A2.1 and Table A2.2).

A)


Saxifraga tenuis
Stellaria longipes
Ranunculus sulphureus
Saxifraga hyperborea
Saxifraga cernua
Saxifraga cespitosa
Cerastium arcticum
Cassiope tetragona
Saxifraga hirculus
Silene acaulis
Saxifraga hieracifolia
Bistorta vivipara
Polemonium boreale
Saxifraga oppositifolia
Potentilla nivalis
Dryas octopetala
Papaver sp.
Draba alpina
Ichneumonidae.6
Stenomacrus.sp..1
Ichneumonidae.5
Stenomacrus.sp..4
Ichneumonidae.2
Ichneumonidae.4
Ichneumonidae.1
Ichneumonidae.3
Stenomacrus.sp..3
Stenomacrus.sp..2
Sciaridae
Zaphne.frontata
Spilogona.megastoma
Spilogona.tornensis
Spilogona.dorsata
Chironomidae
Orthocladiinae
Parasyrphus.tarsus
Rhamphomyia.longestylata
Spilogona.septemnotata
Spilogona.trigonata
Scatophaga.furcata
Culicidae
Spilogona.triangulifera
Parasyrphus.groenlandicus

B)

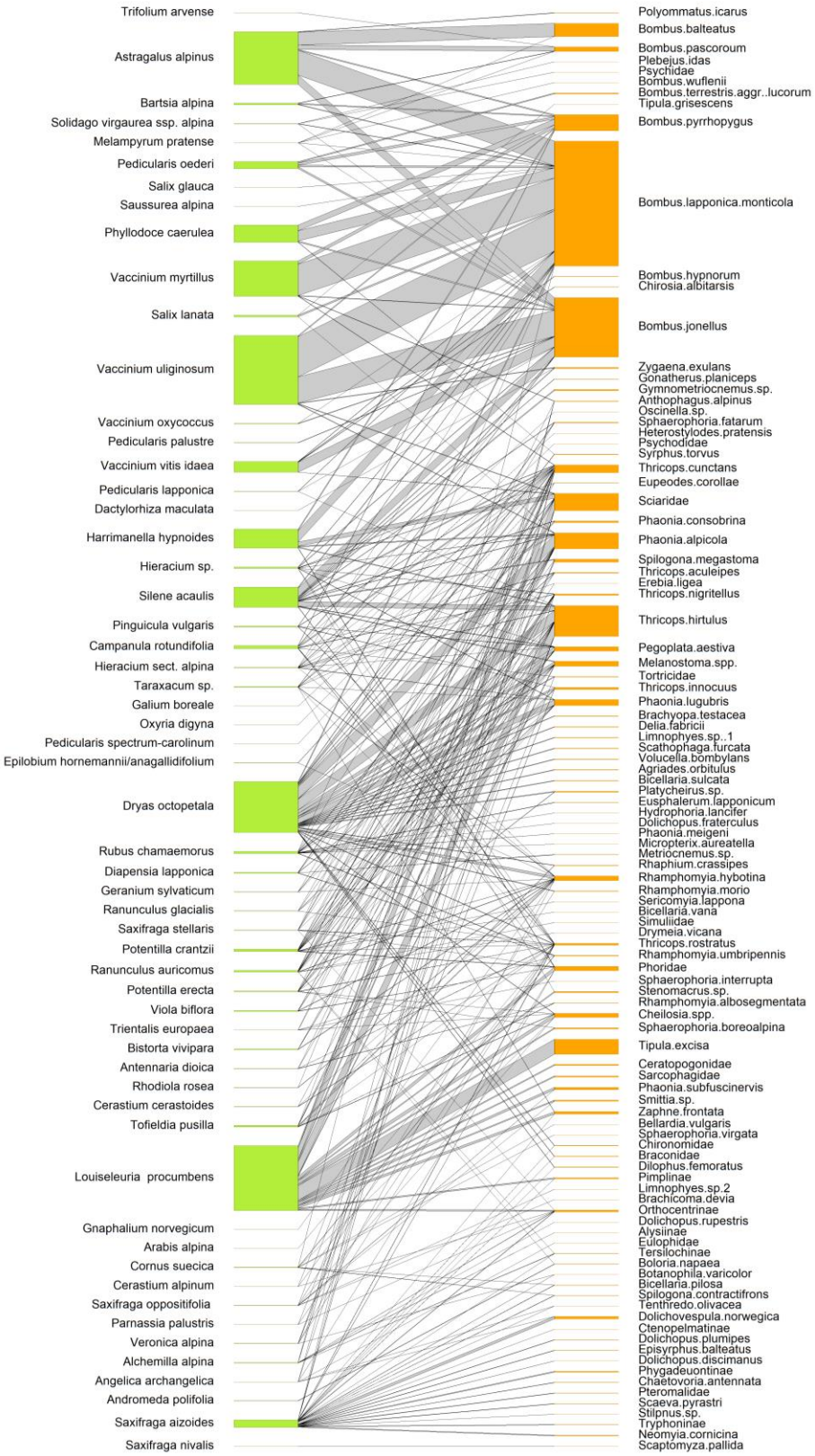


Figure 2. Two mode networks constructed based on the plant-pollinator interactions from A) Svalbard and B) Tväråklumpen. In both of the networks the green boxes represent the plants and the orange boxes represent the pollinators.

Interspecific competition on Svalbard

When looking at Müller's index for the network at Svalbard it becomes clear that *D.octopetala* has the highest value as an acting plant (see Table A6 for all values). *Dryas octopetala* is also the acting plant with the higher Müller's index on all target plants, except for *Saxifraga tenuis* where *Stellaria longipes* has a higher index as an acting plant (Figure 3)

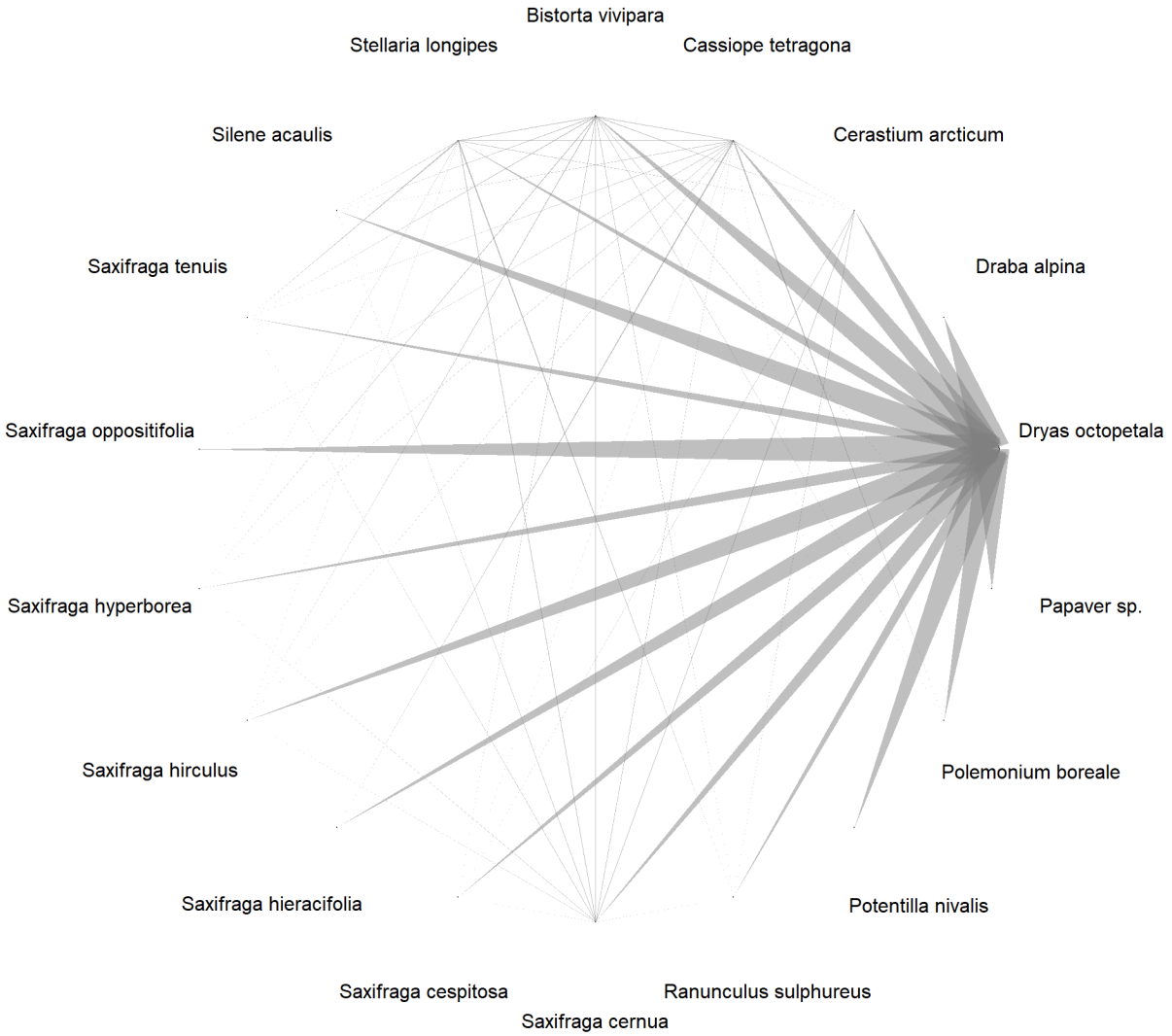


Figure 3. Plot visualizing the Müller's index given for Svalbard. Links between plant species indicate shared pollinators. The width of the link is influenced by the probability of an acting plant influencing a target plant trough their shared pollinators.

Interspecific competition in species present at both sites

At a network level, the median interspecific competition (Müller's Index) is different between the sites (SB: d_{ij}_median = 0.0007, TK: d_{ij}_median = 0; Mann Whitney U test, W = 698, p = 0.02), where the competition at Svalbard is higher than that at Tväråklumpen. When looking at the species that are overlapping for the sites, *Silene acaulis* and *D. octopetala*, *S. acaulis* has a similar level of interspecific competition at the two sites (Figure 4; Mann Whitney U test, W = 8, p = 0.055). *Dryas octopetala* has a stronger acting effect at Svalbard than at Tväråklumpen (Figure 4; Mann Whitney U test, W = 30, p = 0.008). To control for whether outliers present in the Svalbard data aren't driving the result, the analysis was repeated, which is showing that the difference is remaining significant ($p < 0.05$).

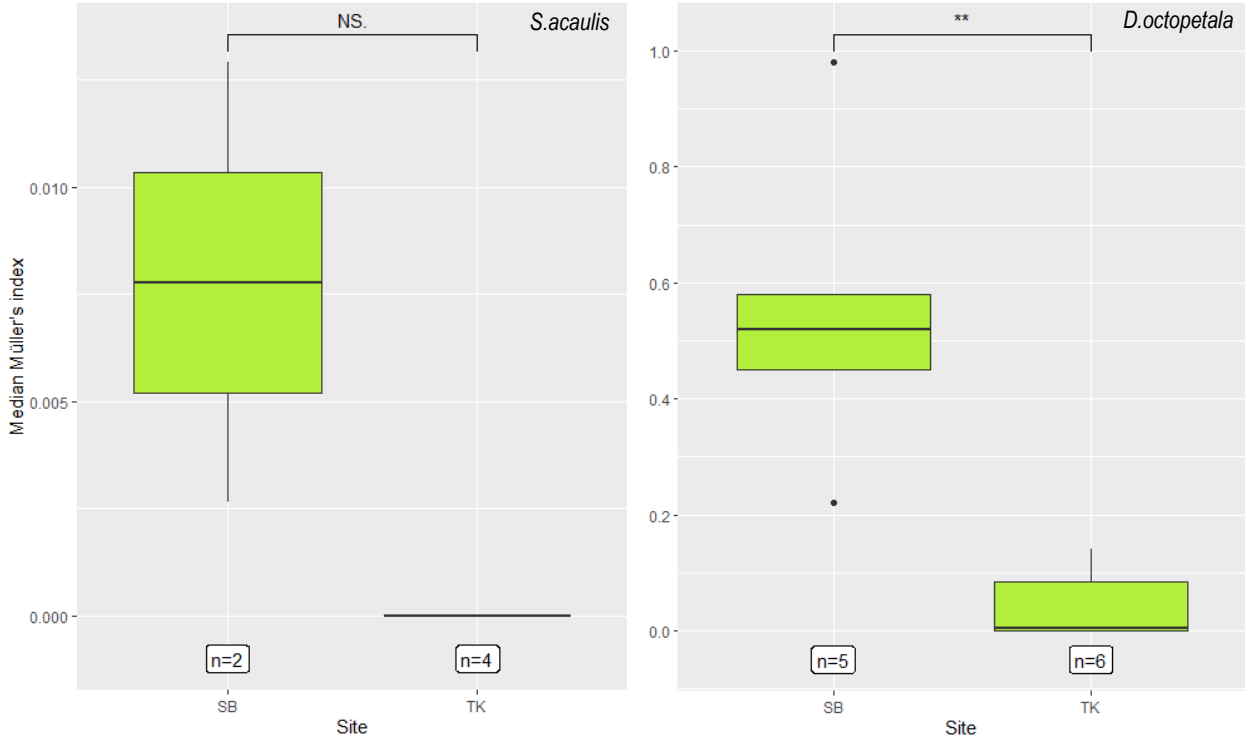


*Figure 4. The median Müller's index for S. acaulis (left) and D. octopetala (right) at Svalbard (SB) and Tväråklumpen (TK). The asterisks denote a statistically significant difference between the sites (NS. = $p > 0.05$, ** = $p \leq 0.01$).*

Reproductive output in species present at both sites

For *S.acaulis* there was a difference in seed yield between the treatments, for both of the sites (Figure 5; Kruskal Wallis test, SB: H = 17.14, df = 2, p = 0.0002; TK: H = 29.58, df = 2, p < 0.0001). The post hoc test shows that the exclusion treatment yielded fewer seeds than the open and hand-pollination treatments at Svalbard (p = 0.003 and p = 0.0001 respectively). There was no difference between the control and the hand-pollination treatment (p > 0.05). At Tväråklumpen the hand-pollination treatment produced more seeds than the open treatment and the open treatment yielded more seeds than the flowers that were part of the exclusion treatment (p = 0.006 and p = 0.014 respectively) (Table 2). Again, the outliers did not affect the significance of the result.

For *D. octopetala* I found a difference between the treatments at both sites (Figure 5; Kruskal Wallis test, SB: H = 13.22, df = 2, p = 0.001; TK: H = 10.79, df = 2, p = 0.005). The exclusion treatment at Svalbard yielded fewer seeds than when hand-pollinated (p = 0.0009). No difference could be found between the open treatment and the hand-pollination or between the exclusion and the open treatment (p > 0.05 for both). At Tväråklumpen the exclusion treatment yielded fewer seeds than the open and hand-pollination treatments (p = 0.009 and p = 0.016 respectively). There was no difference between the open and hand-pollination treatment (p > 0.05) (Table 2).

Table 2. The median seeds per flower for each treatment (E = exclusion, O = open, H = hand) at Svalbard (SB) and Tväråklumpen (TK). The p-values are adjusted with the Dunn-Sídák correction. The bold z-values with asterisks denote statistical significance between the treatments (= p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001, **** = p ≤ 0.0001.*

		Median per treatment (n)			z-val. & sig.		
Site	Species	Exclusion	Hand	Open	E - O	H - O	E - H
SB	*Dryas octopetala*	0 (20)	44 (18)	2.5 (30)	-2.13	1.89	**-3.63*** **
SB	*Silene acaulis*	0 (10)	4 (21)	3 (38)	**-3.28** **	1.53	**-4.12*** **
TK	*Dryas octopetala*	31 (15)	50 (18)	48 (18)	**-2.98** **	-0.19	**-2.79* **
TK	*Silene acaulis*	0 (14)	6.5 (14)	2 (20)	**-2.82* **	**3.08** **	**-5.44**** **

When comparing the treatments at the sites and comparing the relative median seeds produced for *S. acaulis* neither the open nor the hand-pollination treatment produced a different number of seeds at the two sites (Figure A7.1; Mann Whitney U test, W = 460, p = 0.08 for the open treatment and W = 151, p = 0.91 for the hand-pollination) (Table 3). After removing one outlier in the open treatment at Svalbard, the difference between the two sites became significant (Mann Whitney U test, W = 479, p = 0.042). Due to all relative medians for the exclusion treatments all consisting of zeros a Mann Whitney can't be performed. When all relative medians are the same, a statistical test is not needed to state that the treatments on the sites are the same.

For *D. octopetala* the relative median for seed production in the open treatment and exclusion were lower at Svalbard than at Tväråklumpen (Figure A7.2; Mann Whitney U test, W = 113, p = 0.0007 for the control and W = 75, p = 0.006 for the exclusion). The hand pollination treatments yielded the same number of seeds (p = 0.22) (Table 3).

Table 3. The relative median of seeds per flower for each treatment between the sites and the p-values from Mann Whitney U test. The bold p-values denote statistical significance between the sites (p ≤ 0.05)

		Relative median per treatment (n)			p-val.		
Site	Species	Exclusion	Hand	Open	Exclusion	Hand	Open
SB	*Dryas octopetala*	0 (20)	1 (18)	0.06 (30)	**0.006**	0.22	**0.0007**
TK		0.62 (15)	1 (18)	0.96 (18)			
SB	*Silene acaulis*	0 (10)	1 (21)	0.75 (38)	-	0.91	**0.08**
TK		0 (14)	1 (14)	0.31 (20)			

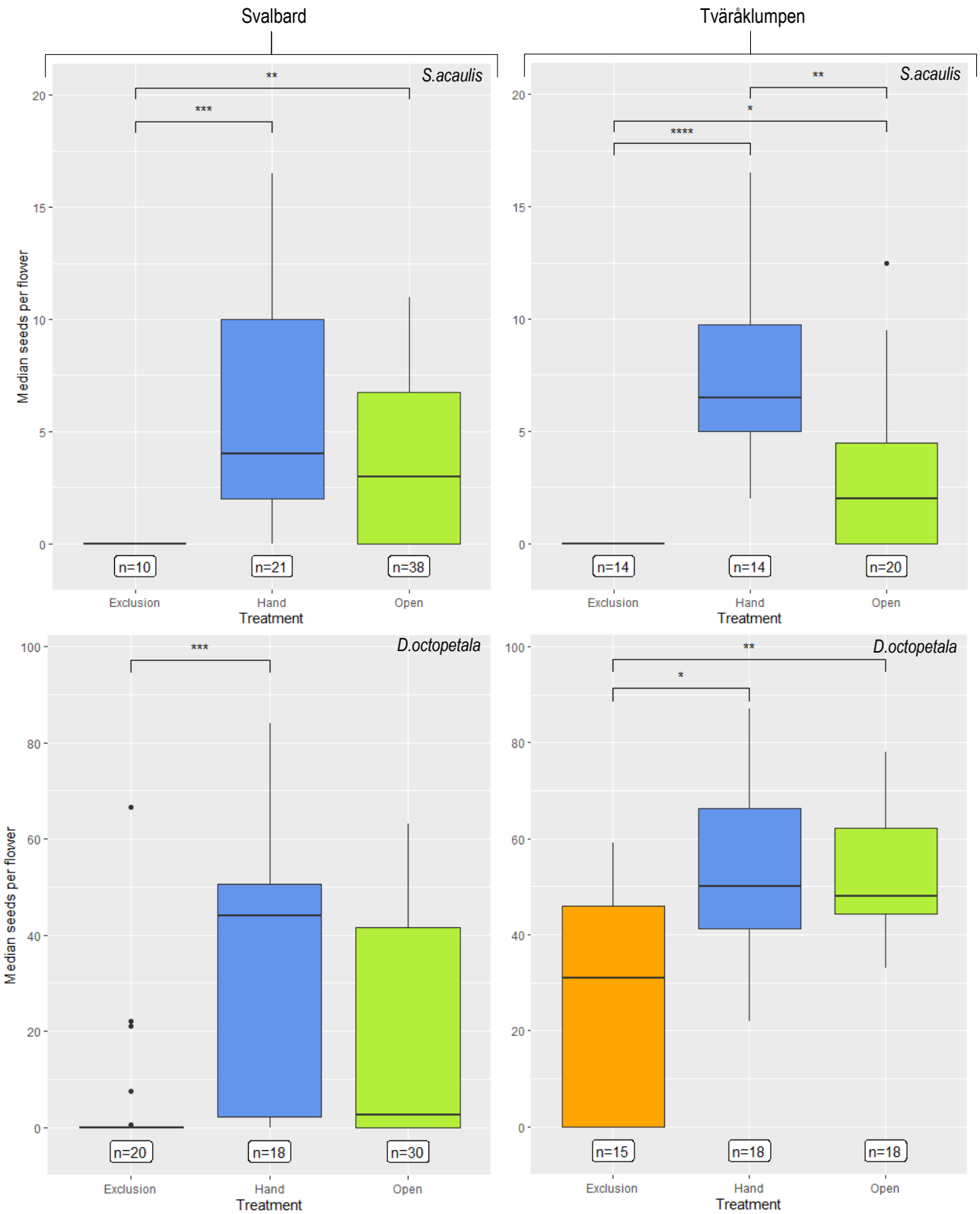


Figure 5. The median seed number per flower produced. The left column represents the plants from Svalbard and the right column represents the plants from Tväråklumpen. The asterisks denote statistical significance between the treatments (= $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$, **** = $p \leq 0.0001$).*

Discussion

The results indicate that the assumed interspecific competition is higher at Svalbard than at Tväråklumpen, both at a community level and in the two overlapping species that occur in both sites. This supports our hypothesis that the competition would be greater in the High Arctic than in the subarctic region. Naturally, data from multiple other Arctic sites are needed to be able to state in more general terms that the interspecific competition is greater in higher latitudes, but this could be an indication of a trend where competition could increase with higher latitudes.

In *S. acaulis*, pollen limitation could only be observed at Tväråklumpen. This could possibly mean that the pollinator community at Svalbard is able to supply pollination services more effectively for *S. acaulis* than at Tväråklumpen. If the pollen limitation observed was caused by pollen of insufficient quantity or quality is not investigated in thesis. With *S. acaulis* at Svalbard having a lower species specialization degree (*d'*), this would mean that they are at a higher risk of receiving heterospecific pollen. The receipt of heterospecific pollen is in generally accepted to have a negative impact on the fitness of the receiving plant. The negative impact is not restricted to closely related plant species but also applies to more distantly related ones (Ashman & Arceo-Gómez, 2013; Buide, et al., 2015). Ashman and Arceo-Gómez (2013) pruposes a variety of mechanisms in co-flowering communites that potentially decreases the negative effects that heterospecific pollen can have (e.g., physical and chemical incompatibility or rejection due to genetic markers). In these High Arctic sites with short flowering seasons the phenology is more or less synchronous, which makes the risk of heterospecific pollen deposition even higher. It is however difficult to predict how affected a plant will be by the presence of heterospecific pollen (Ashman & Arceo-Gómez, 2013). It could be possible that *S. acaulis* at Svalbard are not reciving heterospeciefic pollen that have the potential to create these negative effects, due to natrual incompatibilitrs with the pollen from surrouding species. It could also be that comunities with a more synchronous flowering season have had a stronger selection pressure for mechanisms that lessens the negative effects of heterospecific pollen. Thus, making some communites more tolerante to pollen from co-flowering plant species.

The pollination experiment also showed that *S. acaulis* is pollinator dependent, as expected since the species is gynodioecious (i.e., the population consists of individuals being either females or hermaphrodites) and the majority of individuals with an exclusion treatment were females. At first thought one could believe that maybe the human factor was at play here and that the hand-pollination treatment at Svalbard was not effectively performed. Indeed, it was sometimes difficult to find male flowers that had a satisfying amount of pollen. It could also be explained by the pollen already being released or that pollinators eat a noticeable proportion of available pollen in plant-scarce places. However, seed production in the hand-pollination treatment at the two sites is similar, which indicates that the absence of pollen limitation on Svalbard is not due to poorly performed hand-pollination. In the case of *D. octopetala* none of the sites indicate that they are pollen limited. As for pollinator dependence, it can only be observed at Tväråklumpen. However, the results from the exclusion treatment from Svalbard show a large proportion of the samples (14 out of 20) didn't produce any seeds even if the species is capable of autonomous selfing. Out of the 6 samples that produced seeds there was one sample that produced a noticeable number of seeds that skews the relationship between the exclusion and the control.

Based on the reported statistics I cannot state that there is a higher dependence on pollinators for the species on Svalbard than at Tväråklumpen. But it should raise the question if this is a good representation of pollinator dependence when comparing the two sites. As stated, *D.octopetala* is the strongest competitor at Svalbard and had low selfing rates in the exclusion treatment. Based on the limited data, I propose a hypothesis that strong competitors put less energy into autonomous selfing, because these competitors already have reproduction assurance and the chance of receiving conspecific pollen is high. Weaker competitors that don't attract as many pollinators are then selfing to be able to coexist with the stronger competitors. The topic of the possible relationship

between a species' competitive ability and how this affects reproductive strategies seems to be poorly examined at the species level. In one study by Bell et al. (2005) they found that competition can lower the seed production and outcrossing rates in *Mimulus ringens*, which has the ability to self, when grown in mixed-species formations with *Lobelia siphilitica*. However, the study doesn't look at selfing-rates nor the strength of the interspecific competition. In another study where they looked at two co-flowering species of the genus *Silene* the stronger competitor species of the two had a noticeably lower selfing rate than the other species (Buide, et al., 2015).

Mutualistic networks in a changing world

When looking at the network metrics, Svalbard seems to be more general than the network at Tväråklumpen. The connectance is lower, but this might be connected to the network being of a smaller size (Olesen & Jordano, 2002). Supporting to the Svalbard being more general is also a lower network specialization degree (H_2'), which is not sensitive to network size (Blüthgen, et al., 2006). Some studies suggest that a generalized network structure would be more resilient to changes in the environment, due to the inter-linkage of numerous species (Zoller, et al., 2023). Others propose that a favorable structure of a mutualistic network is one with high nestedness, which is thought to be more resilient to extinction events (Burgos, et al., 2007). This is also thought to provide a higher maximum biodiversity, without an increase of available resources or services (e.g., pollination) and to lower the interspecific competition in the system (Bastolla, et al., 2009).

In the Arctic, there is a rapid warming of the climate (Rantanen, et al., 2022) that has the potential to drive changes in the species that are present there today. Structurally, historical climate change is thought to have had a moderate to no effect on the nestedness in a network (Dalsgaard, et al., 2013). This only describes that there is no change in the structure of the plant-pollinator network have persisted in past plant-pollinator networks. It's also likely that the effects of ongoing and future climate change might be more extreme than historical ones (Potts, et al., 2010). Regarding the response in the communities, changes in air temperature or the onset of snowmelt can affect the phenology. (Collins, et al., 2021). Arthropods in the Arctic are similar in this way because air temperature and solar radiation are thought to be the most effective variable of activity (Høye, 2020). Due to the short period of time in which pollination takes place in Arctic environments, small changes in phenology have the potential to alter or completely remove interactions in a plant-pollinator network (Høye, et al., 2013; Tylianakis, et al., 2010). The effects these shifts in phenology might have on the plants, the pollinators and the network are not fully understood but are a crucial part of being able to evaluate the possible outcomes and prospects in a changing world. In Zackenberg, Greenland, one study by Cirtwill et al. (2018) found that there has been an increase in insect pollinator turnover when looking at the periods 1996-1997 and 2010-2011. Due to the lack of data, in this specific study, it couldn't be determined if the change is caused due to climate change or other events. Either way, other studies have shown that there is an ongoing decline of pollinators in the Arctic as an effect of climate change (Høye, et al., 2013; Loboda, et al., 2018). These factors are beyond the scope of this study but will play a role in how these networks and all interactions within change over time. This will in turn change the dynamic in the interspecific competition in directions that are difficult to predict at this time.

Possible improvements and implications for future studies

The data for this study was collected in transect. While providing observations over a large area in a time effective way, something that can be favorable in sites with somewhat fickle weather changes. But to be able to better describe the seasonal variation in both phenology and abundance of the local flora a plot set-up might be a better choice in those aspects. So, if similar studies were to be performed in the future, one might consider changing the method for data collection if phenology and more precise measurements of the abundance are needed.

It should be acknowledged that the sample sizes in this study are at times very small, which is not optimal for statistical testing. Larger sample sizes might have returned different or clearer results. Thus, the study would benefit from being followed up on in order to paint a clearer picture of the networks and the relationships within. This could also make it possible to observe interactions with overlapping plant species that were observed at the site but in low numbers (e.g., *S. oppositifolia*) or not seen to interact with pollinators at all during the data collection (e.g., various species of *Draba*).

When working with a network we only show a moment of how all species in a network interact. In order to create a better representation of the competition one would possibly need to test over multiple seasons since the network has the potential to change over time. In addition, it's necessary to remember when we look for competition with the methods that were applied in this study, I test for assumed competition and not realized competition. To test for true competition, a manipulation study would be needed. Furthermore, all insects that visited a flower were assumed to be pollinators. This is not necessarily true. Even though many of the collected insects can be seen carrying pollen grains on their bodies, this says little about their contribution to the pollination effort of an area. To bring further nuance to the data it would be interesting to investigate the pollinator efficiency of the pollinators that are prominent in the High Arctic. This could add further information on a quite overlooked group of pollinators.

Conclusion

In conclusion, this study shows that there is competition for pollination services between the plants on the Arctic tundra. This competition also seems to be greater at higher latitudes when comparing it to environments in the subarctic where the environmental conditions are less extreme and there is higher biodiversity. Pollen limitation doesn't seem to be an overhanging issue for the investigated species at either of the sites. There is a dependence on pollinators to ensure reproductive success. There might be an interesting relationship between a plant's competitive strength and the reproductive modes that are utilized. Further research would be needed to find out if this is the case. Not only is it important to understand how pollinators and plants interact with each other, but also how different plant species are interacting. This might be of even greater interest when faced with major shifts in the networks, which is expected with a changing climate. If these interactions differ over latitude, understanding these differences is important to make educated choices for future conservation efforts.

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References

Ashman, T.-L. & Arceo-Gómez, G., 2013. Toward a predictive understanding of the fitness costs of heterospecific pollen receipt and its importance in co-flowering communities. *American Journal of Botany,* 100(6), pp. 1061-1070.

Ashman, T.-L.et al., 2004. Pollen Limitation of Plant Reproduction: Ecological and Evolutionary Causes and Consequences. *Ecology,* 85(9), pp. 2408-2421.

Bartsch, H., 2009. *Tvåvingar : blomflugor. Diptera : Syrphidae: Syrphinae.* 1 ed. Uppsala: Artdatabanken, SLU.

Bascompte, J. & Jordano, P., 2007. Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics,* 38(1), pp. 567-593.

Bascompte, J., Jordano, P. & Olesen, J. M., 2006. Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance. *Science (American Association for the Advancement of Science),* 312(5772), pp. 431-433.

Bastolla, U. et al., 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature,* 458(7241), pp. 1018-1020.

Bell, J. M., Karron, J. D. & Mitchell, R. J., 2005. Interspecific Competition for Pollination Lowers Seed Production and Outcrossing in Mimulus ringens. *Ecology,* 86(3), pp. 762-771.

Bergamo, P. J., Freitas, L., Sazima, M. & Wolowski, M., 2022. Pollinator-mediated facilitation alleviates pollen limitation in a plant–hummingbird network. *Oecologia,* 198(1), pp. 205-217.

Billings, W., 1987. Constraints to Plant Growth, Reproduction, and Establishment in Arctic Environments. *Arctic and Alpine Research,* 19(4), pp. 357-365.

Bliss, L. C., 1971. Arctic and Alpine Plant Life Cycles. *Annual Review of Ecology and Systematics,* 2(1), pp. 405-438.

Blüthgen, N., Menzel, F. & Blüthgen, N., 2006. Measuring specialization in species interaction networks. *BMC Ecology,* 6(1), p. 9.

Buide, M. L., del Valle, J. C., Pissatto, M. & Narbona, E., 2015. Night life on the beach: selfing to avoid pollinator competition between two sympatric Silene species. *Annals of Botany,* 116(2), pp. 201-211.

Burd, M., 1994. Bateman's Principle and Plant Reproduction: The Role of Pollen Limitation in Fruit and Seed Set. *The Botanical Review,* 60(1), pp. 83-139.

Burgos, E. et al., 2007. Why nestedness in mutualistic networks?. *Journal of Theoretical Biology,* 249(2), pp. 307-313.

CAFF, 2013. *Arctic Biodiversity Assessment,* Akureyri: Conservation of Arctic Flora and Fauna.

Carvalheiro, L. G. et al., 2014. The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. *Ecology Letters,* 17(11), pp. 1389-1399.

Cirtwill, A. R. et al., 2018. Between-year changes in community composition shape species' roles in an Arctic plant–pollinator network. *Oikos,* 127(8), pp. 1163-1176.

Collins, C. G. et al., 2021. Experimental warming differentially affects vegetative and reproductive phenology of tundra plants. *Nature Communications,* 12(1), pp. 1-12.

Cunha, N. L. d. et al., 2022. Increasing pollen production at high latitudes across animal-pollinated flowering plants. *Global Ecology and Biogeography,* 31(5), pp. 940-953.

Dalsgaard, B. et al., 2013. Historical climate-change influences modularity and nestedness of pollination networks. *Ecography (Copenhagen),* 36(12), pp. 1331-1340.

Darwin, C., 1862. *On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing.* London: John Murray.

Dodd, M., Silvertown, J. & Chase, M., 1999. Phylogenetic analysis of trait evolution and species diversity variation among angiosperm families. *Evolution,* 53(3), pp. 732-744.

Dormann, C. F., 2022. *Visualising Bipartite Networks and Calculating Some (Ecological).* [Online] Available at: https://cran.r-project.org/

Dormann, C. F. & Strauss, R., 2014. Detecting modules in quantitative bipartite networks: the QuaBiMo algorithm. *Methods in Ecology and Evolution,* Issue 5, p. 90–98.

Gervasi, D. D. L. & Schiestl, F. P., 2017. Real-time divergent evolution in plants driven by pollinators. *Nature Communications,* 8(1), p. 14691.

Gotelli, N. J. & Ulrich, W., 2012. Statistical challenges in null model analysis. *Oikos,* 121(2), pp. 171-180.

Husband, B. C. & Schemske, D. W., 1996. Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution,* 50(1), pp. 54-70.

Høye, T. T., 2020. Arthropods and climate change – arctic challenges and opportunities. *Current Opinion in Insect Science,* Volume 41, pp. 40-45.

Høye, T. T. et al., 2013. Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Climate Change,* 3(8), pp. 759-763.

Kevan, P., 1972. Insect pollination of high arctic flowers. *The Journal of Ecology,* 60(3), pp. 831-847.

King, C., Ballantyne, G., Willmer, P. G. & Freckleton, R. F. R., 2013. Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods in Ecology and Evolution,* 4(9), pp. 811-818.

Knight, T. et al., 2005. Pollen Limitation of Plant Reproduction: Pattern and Process. *Annual Review of Ecology, Evolution, and Systematics,* 36(1), pp. 467-497.

Loboda, S. et al., 2018. Declining diversity and abundance of High Arctic fly assemblages over two decades of rapid climate warming. *Ecography,* 41(2), pp. 265-277.

Mamen, J., Tajet, H. T. & Tunheim, K., 2022. *Været i Norge: Klimatologisk månedsoversikt August 2022,* Oslo: Meteorologisk institutt.

Noël, B. et al., 2020. Low elevation of Svalbard glaciers drives high mass loss variability. *Nature communications,* 11(1), pp. 4597-4597.

Oksanen, J. et al., 2022. *Community Ecology Package.* [Online] Available at: https://cran.r-project.org/

Olesen, J. M. & Jordano, P., 2002. Geographic Patterns in Plant-Pollinator Mutualistic Networks. *Ecology,* 83(9), pp. 2416-2424.

Ollerton, J., Winfree, R. & Tarrant, S., 2011. How many flowering plants are pollinated by animals. *Oikos,* 120(3), pp. 321-326.

Oosterbroek, P., 2006. *The European Families of the Diptera: Identification, diagnosis, biology.* Utrecht: KNNV Publishing.

Potts, S. G. et al., 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution,* 25(6), pp. 345-353.

Pyke, G. H., 1991. What does it cost a plant to produce floral nectar?. *Nature,* 350(6313), pp. 58-59.

Rantanen, M. et al., 2022. The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment,* 3(1), pp. 1-10.

Ratnieks, F. L. W., Balfour, N. J. & Irwin, R. I. R., 2021. Plants and pollinators: Will natural selection cause an imbalance between nectar supply and demand?. *Ecology Letters,* 24(9), pp. 1741-1749.

Rodger, J. G. et al., 2021. Widespread vulnerability of flowering plant seed production to pollinator declines. *Science Advances,* 7(42), p. eabd3524.

Shamshev, I. V., Sinclair, B. J. & Khruleva, O. A., 2020. The empidoid flies (Diptera: Empidoidea, exclusive of Dolichopodidae) of the Russian Arctic islands and Svalbard Archipelago. *Zootaxa,* 4848(1), pp. 1-75.

Stur, E. & Ekrem, T., 2020. The Chironomidae (Diptera) of Svalbard and Jan Mayen. *Insects,* 11(3), p. 183.

Tiusanen, M., Hebert, P. D. N., Schmidt, N. M. & Roslin, T., 2016. One fly to rule them all—muscid flies are the key pollinators in the Arctic. *Proc. R. Soc. B,* 283(1839), p. 20161271.

Tiusanen, M., Kankaanpää, T., Schmidt, N. M. & Roslin, T., 2020. Heated rivalries: Phenological variation modifies competition for pollinators among arctic plants. *Global Change Biology,* 26(11), pp. 6313-6325.

Trunschke, J. et al., 2021. Flower Color Evolution and the Evidence of Pollinator-Mediated Selection. Volume 12, pp. 617851-617851.

Tylianakis, J. M., Laliberté, E., Nielsen, A. & Bascompte, J., 2010. Conservation of species interaction networks. *Biological Conservation,* 143(10), pp. 2270-2279.

Zimin, L. S. & Elberg, K. Y., 1989. Muscidae. In: G. Y. Bei-bienko & G. C. Steyskal, eds. *Keys to the Insects of the European Part of the USSR.* Washington, D.C.: Smithsonian Institution Libraries and the National Science Foundation, pp. 893-974.

Zoller, L., Bennett, J. & Knight, T. M., 2023. Plant-pollinator network change across a century in the subarctic. *Nature Ecology & Evolution,* 7(1), pp. 102-112.

Appendix 1. Popular science summary

Fighting for pollination in the Arctic

If I were to ask you to imagine an insect pollinator, which one would you think of?

The bee is probably the first one many people would have in mind. Another popular choice might be the bumblebee. As you probably know, plants are commonly pollinated by insects. This is part of a mutualistic relationship between the insect and the plant, where the insect receives payment in the form of nectar or pollen. If pollen is successfully moved from the anther of one flower to the stigma of another flower there is a good chance that the receiving plant will sexually reproduce. This seemly simple act is paramount to the function of ecosystems and global biodiversity. This is something Charles Darwin wrote about in his lesser-known work *Fertilisation of Orchids*, where he presents the idea that pollination drives the evolution of orchids by gene mixing. There are other strategies that plants can be capable of, which result in asexual reproduction.

Two flies visiting mountain avens

Just like people - insect pollinators are not all made the same. Both bees and bumblebees are considered to be effective pollinators, while species of flies are assumed to offer less effective pollination services. Generally, the Arctic has lower diversity, and the number of available pollinators is fewer and less active. In addition to this, the flowering period only stretches over a few weeks, which creates an intense period for reproduction. But are there enough pollinators for everyone? If not, do plants compete to ensure that they are the ones that get to sexually reproduce? And does the reproduction mode change depend on the available pollinators? This is what I want to find out.

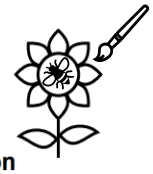
In the summer of 2022, I accompanied a research group to Svalbard to investigate if such effects can be observed. The data comes from observations and identification of interactions between pollinators and plants. All interactions are then put together into a network that shows how communities of plants and insects interact. Likewise, in how people might interact, some might have a lot of connections, while others might have fewer but more exclusive connections. In addition to mapping out the plant-pollinator network, a pollination experiment was performed.

What is a pollination experiment?

A pollination experiment consists of a series of treatments that can help us assess how effectively a plant is being pollinated. After the flowering period has passed, all fruits are collected for the seeds to be counted.

Possible treatments:

1. **Control**
Pollen source: Natural pollination
Aim: Evaluate seed set under natural conditions
Coverage: No cover



2. **Hand-pollination**
Pollen source: From plants of the same species
Aim: Evaluate the pollen limitation
Coverage: No cover

3. **Exclusion**
Pollen source: None
Aim: Evaluate the reliance on insect pollinators
Coverage: Covered with mesh to exclude interaction with pollinators

The questions are yet to be answered but they could bring further insight into the relationship between plants and insects in a system of low diversity. Today we are facing major changes to the climate and the Arctic is warming up at a rapid pace. To be able to evaluate the possible outcomes it might have for the species and ecosystems that are affected we need to acquire more knowledge in unexplored areas of research.

Appendix 2. Plant species at each site

Table A2.1. Plant species that were visited by pollinators at Svalbard.

Order	Family	Species	Sum of links	Interaction strength	d'
Caryophyllales	*Polygonaceae*	*Bistorta vivipara*	5	0,35	0,26
Ericales	*Ericaceae*	*Cassiope tetragona*	6	0,88	0,52
Caryophyllales	*Caryophyllaceae*	*Cerastium arcticum*	11	2,27	0,22
Brassicales	*Brassicaceae*	*Draba alpina*	1	1,44E-06	0
Rosales	*Rosaceae*	*Dryas octopetala*	17	15,56	0,23
Ranunculales	*Papaveraceae*	*Papaver sp.*	2	0,02	0,15
Ericales	*Polemoniaceae*	*Polemonium boreale*	2	4,03E-06	0,04
Rosales	*Rosaceae*	*Potentilla nivalis*	4	6,00E-05	0,05
Ranunculales	*Ranunculaceae*	*Ranunculus sulphureus*	5	0,05	0,23
Saxifragales	*Saxifragaceae*	*Saxifraga cernua*	8	0,03	0,10
Saxifragales	*Saxifragaceae*	*Saxifraga cespitosa*	16	2,12	0,10
Saxifragales	*Saxifragaceae*	*Saxifraga hiarcifolia*	1	3,70E-06	0,17
Saxifragales	*Saxifragaceae*	*Saxifraga hirculus*	5	4,02E-04	0,05
Saxifragales	*Saxifragaceae*	*Saxifraga hyperborea*	2	7,93E-04	0,21
Saxifragales	*Saxifragaceae*	*Saxifraga oppositifolia*	3	0,15	0,26
Saxifragales	*Saxifragaceae*	*Saxifraga tenuis*	2	1,39E-03	0,29
Caryophyllales	*Caryophyllaceae*	*Silene acaulis*	8	1,08	2,04E-03
Caryophyllales	*Caryophyllaceae*	*Stellaria longipes*	9	2,47	0,42

Table A2.2. Plant species that were visited by pollinators at Tväråklumpen

Order	Family	Species	Sum of links	Interaction strength	d'
Rosales	*Rosaceae*	*Alchemilla alpina*	6	2,72	0,69
Ericales	*Ericaceae*	*Andromeda polifolia*	1	0,77	0,96
Apiales	*Apiaceae*	*Angelica archangelica*	6	1,00	0,30
Asterales	*Asteraceae*	*Antennaria dioica*	4	0,36	0,34
Brassicales	*Brassicaceae*	*Arabis alpina*	1	1,38E-05	0,28
Fabales	*Fabaceae*	*Astragalus alpinus*	6	3,38	0,39
Lamiales	*Orobanchaceae*	*Bartsia alpina*	3	0,10	0,20
Caryophyllales	*Polygonaceae*	*Bistorta vivipara*	3	0,14	0,34
Asterales	*Campanulaceae*	*Campanula rotundifolia*	9	1,78	0,40
Caryophyllales	*Caryophyllaceae*	*Cerastium alpinum*	3	0,02	0,32
Caryophyllales	*Caryophyllaceae*	*Cerastium cerastoides*	3	0,02	0,25
Cornales	*Cornaceae*	*Cornus suecica*	7	2,71	0,64
Asparagales	*Orchidaceae*	*Dactylorhiza maculata*	1	1,94E-05	0,30
Ericales	*Diapensiaceae*	*Diapensia lapponica*	5	1,25	0,37
Rosales	*Rosaceae*	*Dryas octopetala*	30	21,16	0,66
Myrtales	*Onagraceae*	*Epilobium hornemanni/anagallidifolium*	2	0,29	0,77
Gentianales	*Rubiaceae*	*Galium boreale*	1	3,35E-03	0,33
Geraniales	*Geraniaceae*	*Geranium sylvaticum*	4	0,17	0,47
Asterales	*Asteraceae*	*Gnaphalium norvegicum*	1	5,04E-06	0,21
Ericales	*Ericaceae*	*Harrimanella hypnoides*	6	0,62	0,19
Asterales	*Asteraceae*	*Hieracium sect. alpina*	11	1,47	0,09

Asterales	*Asteraceae*	*Hieracium sp.*	10	0,38	0,03
Ericales	*Ericaceae*	*Louiseleuria procumbens*	17	13,46	0,79
Lamiales	*Orobanchaceae*	*Melampyrum pratense*	5	1,00	0,02
Caryophyllales	*Polygonaceae*	*Oxyria digyna*	1	2,44E-03	0,32
Celastrales	*Celastraceae*	*Parnassia palustris*	3	0,06	0,47
Lamiales	*Orobanchaceae*	*Pedicularis lapponica*	3	3,61E-03	0
Lamiales	*Orobanchaceae*	*Pedicularis oederi*	4	1,20	0,29
Lamiales	*Orobanchaceae*	*Pedicularis palustre*	1	1,58E-03	0,10
Lamiales	*Orobanchaceae*	*Pedicularis spectrum-carolinum*	1	3,05E-06	0,18
Ericales	*Ericaceae*	*Phyllodoce caerulea*	4	0,61	0,26
Lamiales	*Lentibulariaceae*	*Pinguicula vulgaris*	5	0,14	0,14
Rosales	*Rosaceae*	*Potentilla crantzii*	14	2,36	0,24
Rosales	*Rosaceae*	*Potentilla erecta*	10	0,92	0,42
Ranunculales	*Ranunculaceae*	*Ranunculus auricomus*	12	2,91	0,47
Ranunculales	*Ranunculaceae*	*Ranunculus glacialis*	6	0,02	0,18
Saxifragales	*Crassulaceae*	*Rhodiola rosea*	2	0,03	0,42
Rosales	*Rosaceae*	*Rubus chamaemorus*	13	5,74	0,45
Malpighiales	*Salicaceae*	*Salix glauca*	1	9,38E-07	0
Malpighiales	*Salicaceae*	*Salix lanata*	3	1,01	0,07
Asterales	*Asteraceae*	*Saussurea alpina*	1	6,00E-04	0
Saxifragales	*Saxifragaceae*	*Saxifraga aizoides*	28	16,80	0,85
Saxifragales	*Saxifragaceae*	*Saxifraga nivalis*	1	1	1
Saxifragales	*Saxifragaceae*	*Saxifraga oppositifolia*	7	2,17	0,51
Saxifragales	*Saxifragaceae*	*Saxifraga stellaris*	8	0,63	0,37
Caryophyllales	*Caryophyllaceae*	*Silene acaulis*	14	4,14	0,32
Asterales	*Asteraceae*	*Solidago virgaurea ssp. alpina*	4	2,00	0,21
Asterales	*Asteraceae*	*Taraxacum sp.*	9	1,16	0,21
Alismatales	*Tofieldiaceae*	*Tofieldia pusilla*	8	1,20	0,55
Ericales	*Myrsinaceae*	*Trientalis europaea*	5	1,04	0,36
Fabales	*Fabaceae*	*Trifolium arvense*	1	2,64E-05	0,24
Ericales	*Ericaceae*	*Vaccinium myrtillus*	5	1,10	0,35
Ericales	*Ericaceae*	*Vaccinium oxycoccus*	2	0,01	0,10
Ericales	*Ericaceae*	*Vaccinium uliginosum*	6	1,26	0,34
Ericales	*Ericaceae*	*Vaccinium vitis idaea*	5	2,18	0,44
Lamiales	*Plantaginaceae*	*Veronica alpina*	5	0,39	0,32
Malpighiales	*Violaceae*	*Viola biflora*	4	0,11	0,27

Appendix 3. Occurring insects on sites

Table A3.1. The final ID of the insects collected in Svalbard.

Order	Family	Final ID	Sum of links	Interaction strength	d'
Diptera	*Chironomidae*	*Chironomidae*	7	1,14	0
Diptera	*Culicidae*	*Culicidae*	2	0,05	0
Hymenoptera	*Ichneumonidae*	*Ichneumonidae 1*	3	0,21	0,59
Hymenoptera	*Ichneumonidae*	*Ichneumonidae 2*	1	0,01	0,63
Hymenoptera	*Ichneumonidae*	*Ichneumonidae 3*	1	0,03	0,68
Hymenoptera	*Ichneumonidae*	*Ichneumonidae 4*	1	0,02	0,53
Hymenoptera	*Ichneumonidae*	*Ichneumonidae 5*	8	2,13	0,72
Hymenoptera	*Ichneumonidae*	*Ichneumonidae 6*	1	0,02	0,56
Diptera	*Chironomidae*	*Orthocladiinae*	3	0,18	8,80E-04
Diptera	*Syrphidae*	*Parasyrphus groenlandicus*	1	0,01	0
Diptera	*Syrphidae*	*Parasyrphus tarsus*	6	2,35	0,01
Diptera	*Empididae*	*Rhamphomyia longestylata*	5	1,41	0,02
Diptera	*Scathophagidae*	*Scatophaga furcata*	2	0,04	0
Diptera	*Sciaridae*	*Sciaridae*	9	2,26	0,18
Diptera	*Muscidae*	*Spilogona dorsata*	12	2,13	9,218E-05
Diptera	*Muscidae*	*Spilogona megastoma*	7	0,96	0
Diptera	*Muscidae*	*Spilogona septemnotata*	2	0,05	0
Diptera	*Muscidae*	*Spilogona tornensis*	2	0,03	0
Diptera	*Muscidae*	*Spilogona triangulifera*	1	0,02	0
Diptera	*Muscidae*	*Spilogona trigonata*	2	0,04	0
Hymenoptera	*Ichneumonidae*	*Stenomacrus sp. 1*	5	0,78	0,65
Hymenoptera	*Ichneumonidae*	*Stenomacrus sp. 2*	12	3,39	0,20
Hymenoptera	*Ichneumonidae*	*Stenomacrus sp. 3*	9	0,66	0,19
Hymenoptera	*Ichneumonidae*	*Stenomacrus sp. 4*	1	0,01	0,63
Diptera	*Anthomyiidae*	*Zaphne frontata*	4	0,09	4,97E-03

Table A3.2. The final ID for the insects collected at Tväråklumpen.

Order	Family	Final ID	Sum of links	Interaction strength	d'
Lepidoptera	*Lycaenidae*	*Agriades orbitulus*	1	0,01	0,06
Hymenoptera	*Braconidae*	*Alysiinae*	1	0,14	0,71
Coleoptera	*Staphylinidae*	*Anthophagus alpinus*	4	0,21	0,16
Diptera	*Hybotidae*	*Bellardia vulgaris*	1	0,29	0,81
Diptera	*Hybotidae*	*Bicellaria pilosa*	2	0,07	0,36
Diptera	*Hybotidae*	*Bicellaria sulcata*	1	0,01	0,06
Diptera	*Hybotidae*	*Bicellaria vana*	1	0,03	0,48
Lepidoptera	*Nymphalidae*	*Boloria napaea*	2	1,02	0,85
Hymenoptera	*Apidae*	*Bombus balteatus*	2	0,58	0,57
Hymenoptera	*Apidae*	*Bombus hypnorum*	1	0,03	0,34
Hymenoptera	*Apidae*	*Bombus jonellus*	16	5,75	0,46
Hymenoptera	*Apidae*	*Bombus lapponica/monticola*	22	9,15	0,50
Hymenoptera	*Apidae*	*Bombus pascoroum*	4	1,24	0,39

Hymenoptera	*Apidae*	*Bombus pyrrhopygus*	8	1,57	0,40
Hymenoptera	*Apidae*	*Bombus terrestris aggr. lucorum*	1	0,15	0,55
Hymenoptera	*Apidae*	*Bombus wuflenii*	1	0,02	0,72
Diptera	*Anthomyiidae*	*Botanophila varicolor*	2	0,18	0,43
Diptera	*Sarcophagidae*	*Brachicoma devia*	1	0,14	0,74
Diptera	*Syrphidae*	*Brachyopa testacea*	1	0,01	0,06
Hymenoptera	*Braconidae*	*Braconidae*	2	0,02	0,03
Diptera	*Ceratopogonidae*	*Ceratopogonidae*	1	0,02	0,01
Diptera	*Tachinidae*	*Chaetovoria antennata*	1	0,01	0,32
Diptera	*Syrphidae*	*Cheilosia spp.*	7	0,54	0,26
Diptera	*Chironomidae*	*Chironomidae*	2	0,02	0,03
Diptera	*Anthomyiidae*	*Chirosia albitarsis*	1	0,01	0,31
Hymenoptera	*Ichneumonidae*	*Ctenopelmatinae*	1	0,01	0,32
Diptera	*Anthomyiidae*	*Delia fabricii*	1	0,01	0,06
Diptera	*Bibionidae*	*Dilophus femoratus*	2	0,02	0,03
Diptera	*Dolichopodidae*	*Dolichopus discimanus*	1	0,01	0,32
Diptera	*Dolichopodidae*	*Dolichopus fraterculus*	1	0,03	0,49
Diptera	*Dolichopodidae*	*Dolichopus plumipes*	1	0,02	0,36
Diptera	*Dolichopodidae*	*Dolichopus rupestris*	1	0,14	0,71
Hymenoptera	*Vespidae*	*Dolichovespula norwegica*	2	0,58	0,74
Diptera	*Muscidae*	*Drymeia vicana*	1	0,02	0,48
Diptera	*Syrphidae*	*Episyrphus balteatus*	1	0,05	0,42
Lepidoptera	*Nymphalidae*	*Erebia ligea*	2	0,08	0,57
Hymenoptera	*Eulophidae*	*Eulophidae*	1	0,13	0,86
Diptera	*Syrphidae*	*Eupeodes corollae*	3	1,10	0,73
Coleoptera	*Staphylinidae*	*Eusphalerum lapponicum*	1	0,05	0,54
Diptera	*Scathophagidae*	*Gonatherus planiceps*	1	0,01	0,22
Diptera	*Chironomidae*	*Gymnometriocnemus sp.*	1	0,06	0,31
Diptera	*Anthomyiidae*	*Heterostylodes pratensis*	1	0,05	0,63
Diptera	*Anthomyiidae*	*Hydrophoria lancifer*	1	0,05	0,54
Diptera	*Chironomidae*	*Limnophyes sp. 1*	1	0,01	0,06
Diptera	*Chironomidae*	*Limnophyes sp.2*	1	0,14	0,74
Diptera	*Syrphidae*	*Melanostoma spp.*	8	0,51	0,21
Diptera	*Chironomidae*	*Metriocnemus sp.*	1	0,14	0,70
Lepidoptera	*Micropterigidae*	*Micropterix aureatella*	1	0,03	0,49
Diptera	*Muscidae*	*Neomyia cornicina*	1	0,09	0,48
Hymenoptera	*Ichneumonidae*	*Orthocentrinae*	6	0,76	0,18
Diptera	*Chloropidae*	*Oscinella sp.*	1	0,02	0,45
Diptera	*Anthomyiidae*	*Pegoplata aestiva*	9	0,82	0,33
Diptera	*Muscidae*	*Phaonia alpicola*	16	2,39	0,46
Diptera	*Muscidae*	*Phaonia consobrina*	2	0,04	0,15
Diptera	*Muscidae*	*Phaonia lugubris*	9	0,59	0,41
Diptera	*Muscidae*	*Phaonia meigeni*	1	0,03	0,49
Diptera	*Muscidae*	*Phaonia subfuscinervis*	2	0,18	0,24
Diptera	*Phoridae*	*Phoridae*	8	0,59	0,26
Hymenoptera	*Ichneumonidae*	*Phygadeuontinae*	1	0,10	0,49

Hymenoptera	*Ichneumonidae*	*Pimplinae*	2	0,03	0,00
Diptera	*Syrphidae*	*Platycheirus sp.*	2	0,12	0,08
Lepidoptera	*Lycaenidae*	*Plebejus idas*	1	0,14	0,74
Lepidoptera	*Lycaenidae*	*Polyommatus icarus*	1	4,03E-03	0,05
Lepidoptera	*Psychidae*	*Psychidae*	1	0,14	0,74
Diptera	*Psychodidae*	*Psychodidae*	1	0,06	0,63
Hymenoptera	*Pteromalidae*	*Pteromalidae*	1	0,04	0,40
Diptera	*Empididae*	*Rhamphomyia albosegmentata*	2	0,29	0,61
Diptera	*Empididae*	*Rhamphomyia hybotina*	15	4,69	0,49
Diptera	*Empididae*	*Rhamphomyia morio*	2	0,15	0,10
Diptera	*Empididae*	*Rhamphomyia umbripennis*	4	0,85	0,63
Diptera	*Dolichopodidae*	*Rhaphium crassipes*	2	0,05	0,08
Diptera	*Sarcophagidae*	*Sarcophagidae*	1	0,02	0,01
Diptera	*Syrphidae*	*Scaeva pyrastri*	1	0,03	0,38
Diptera	*Drosophilidae*	*Scaptomyza pallida*	1	1	1,00
Diptera	*Scathophagidae*	*Scathophaga furcata*	1	0,01	0,06
Diptera	*Sciaridae*	*Sciaridae*	11	1,61	0,37
Diptera	*Syrphidae*	*Sericomyia lappona*	1	0,03	0,48
Diptera	*Simuliidae*	*Simuliidae*	1	0,02	0,48
Diptera	*Chironomidae*	*Smittia sp.*	2	0,16	0,02
Diptera	*Syrphidae*	*Sphaerophoria boreoalpina*	2	0,05	0,01
Diptera	*Syrphidae*	*Sphaerophoria fatarum*	3	0,05	0,00
Diptera	*Syrphidae*	*Sphaerophoria interrupta*	1	0,14	0,78
Diptera	*Syrphidae*	*Sphaerophoria virgata*	1	0,06	0,65
Diptera	*Muscidae*	*Spilogona contractifrons*	2	0,07	0,36
Diptera	*Muscidae*	*Spilogona megastoma*	3	0,12	0,23
Hymenoptera	*Ichneumonidae*	*Stenomacrus sp.*	2	0,04	0,01
Hymenoptera	*Ichneumonidae*	*Stilpnus sp.*	1	0,01	0,32
Diptera	*Syrphidae*	*Syrphus torvus*	2	0,01	0,01
Hymenoptera	*Tenthredinidae*	*Tenthredo olivacea*	2	0,13	0,32
Hymenoptera	*Ichneumonidae*	*Tersilochinae*	3	0,32	0,50
Diptera	*Muscidae*	*Thricops aculeipes*	5	0,73	0,19
Diptera	*Muscidae*	*Thricops cunctans*	21	5,55	0,29
Diptera	*Muscidae*	*Thricops hirtulus*	18	3,07	0,35
Diptera	*Muscidae*	*Thricops innocuus*	6	0,57	0,23
Diptera	*Muscidae*	*Thricops nigritellus*	9	1,43	0,61
Diptera	*Muscidae*	*Thricops rostratus*	17	3,39	0,22
Diptera	*Tipulidae*	*Tipula excisa*	1	0,23	0,53
Diptera	*Tipulidae*	*Tipula grisescens*	1	0,02	0,50
Lepidoptera	*Tryphoninae*	*Tortricidae*	3	0,28	0,07
Hymenoptera	*Ichneumonidae*	*Tryphoninae*	1	0,04	0,40
Diptera	*Syrphidae*	*Volucella bombylans*	1	0,01	0,06
Diptera	*Anthomyiidae*	*Zaphne frontata*	3	0,11	0,22
Lepidoptera	*Zygaenidae*	*Zygaena exulans*	3	1,04	0,03

Appendix 4. Binary nestedness plots

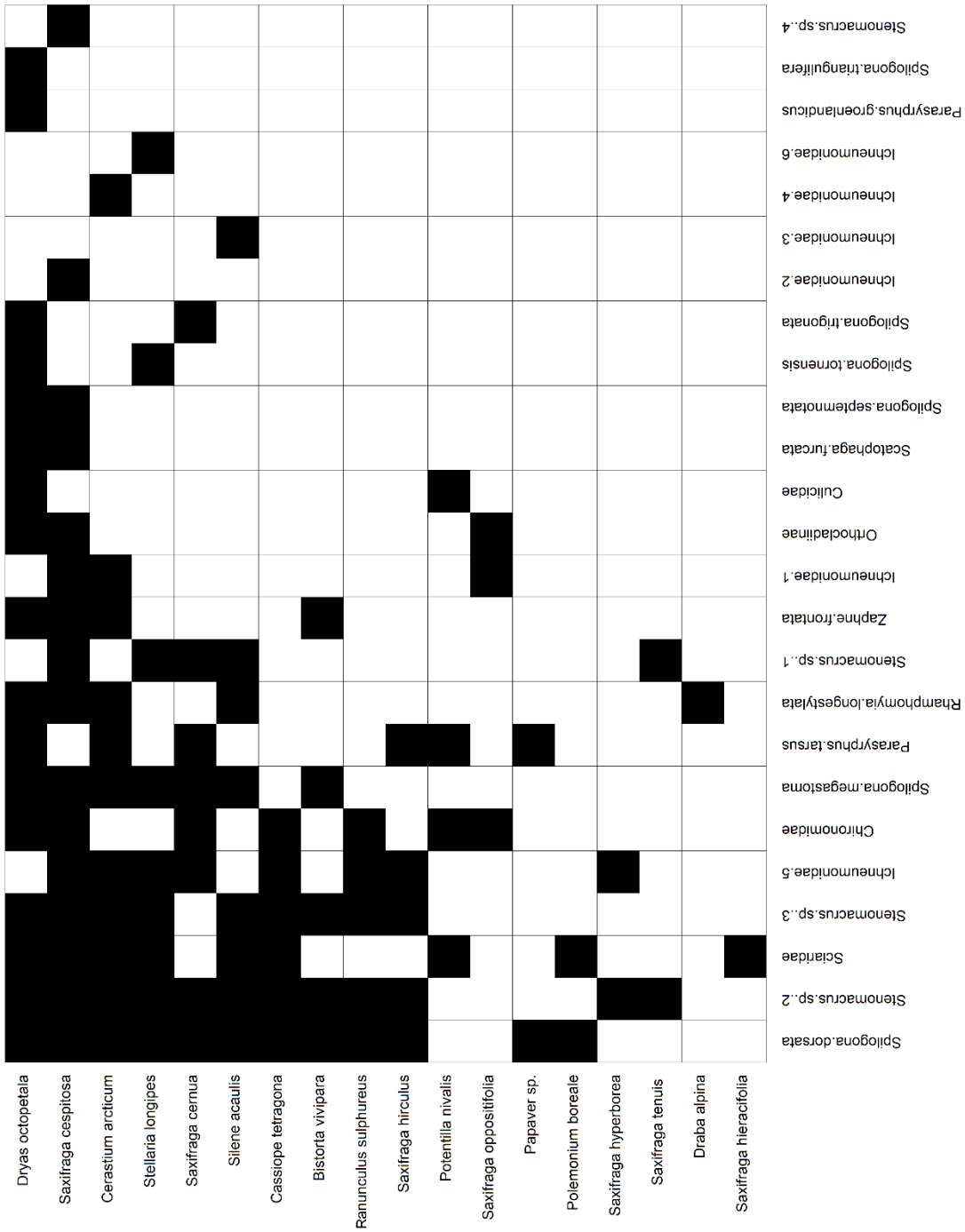


Figure A4.1. Nestedness plot for Svalbard. A black square shows a presence of an interaction between the species. An absence of interaction is shown with a white square.

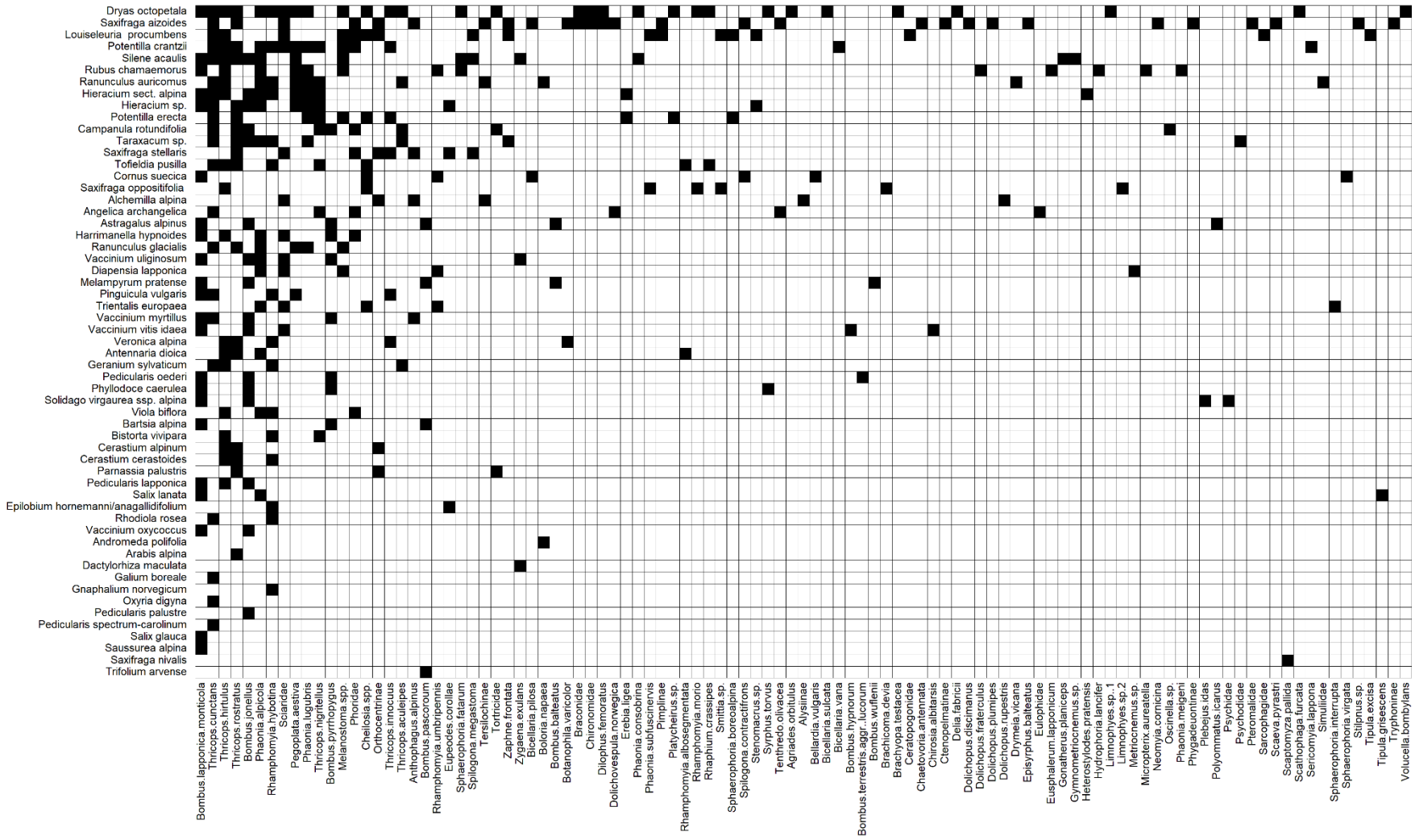


Figure A4.2. Nestedness plot for Tväråklumpen. A black square shows a presence of an interaction between the species. An absence of interaction is shown with a white square.

Appendix 5. Modularity plots

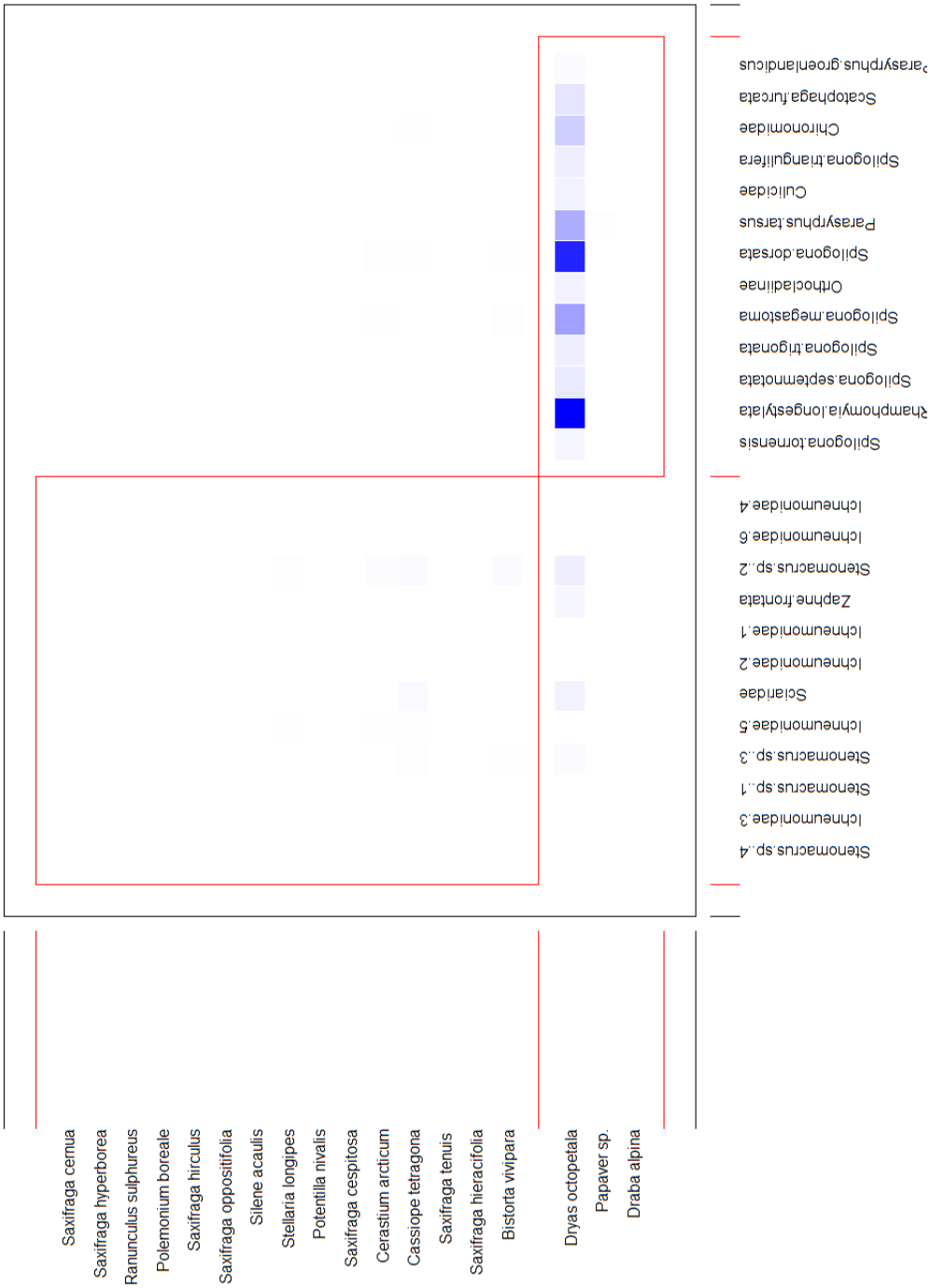


Figure A5.1. Modularity plot for Svalbard. Darker squares indicate more frequent interactions.

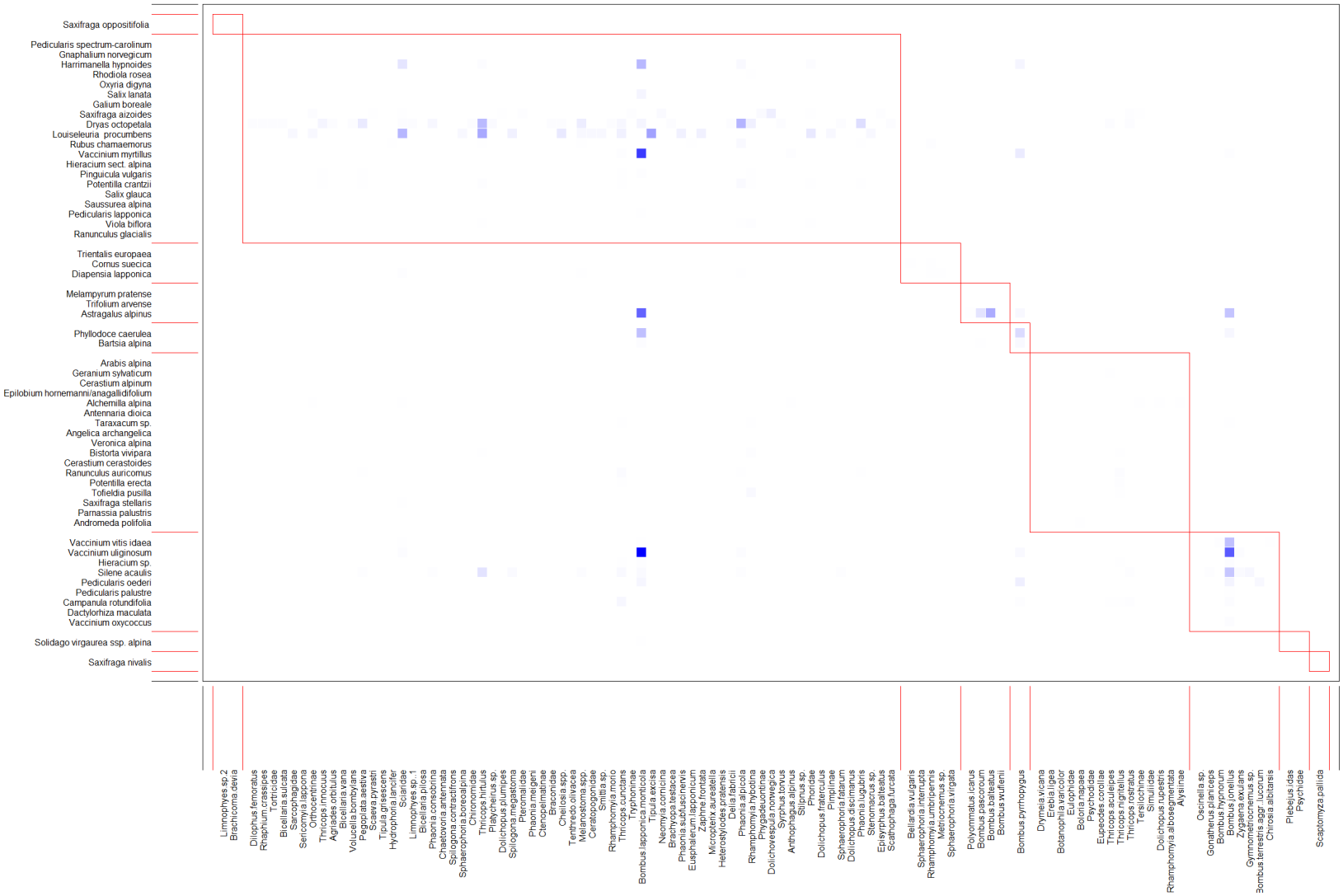


Figure A5.2. Modularity plot for Tväråklumpen. Darker squares indicate more frequent interactions.

Appendix 6. Müller's index for Svalbard

Target species \ Acting species	Bistorta vivipara	Cassiope tetragona	Cerastium arcticum	Draba alpina	Dryas octopetala	Papaver sp.	Polemonium boreale	Potentilla nivalis	Ranunculus sulphureus	Saxifraga cernua	Saxifraga cespitosa	Saxifraga hieracifolia	Saxifraga hirculus	Saxifraga hyperborea	Saxifraga oppositifolia	Saxifraga tenuis	Silene acaulis	Stellaria longipes
Bistorta vivipara	0,082	0,108	0,046	0	0,728	1,25E-04	5,16E-08	0	0,002	3,22E-04	0,002	0	2,25E-05	7,65E-05	0	9,18E-06	0,002	0,030
Cassiope tetragona	0,059	0,226	0,048	0	0,607	3,31E-05	1,55E-06	7,62E-06	0,003	0,001	0,003	1,54E-06	2,91E-05	8,60E-05	1,84E-04	7,27E-06	0,002	0,051
Cerastium arcticum	0,051	0,096	0,122	2,36E-08	0,606	0,001	1,30E-07	7,19E-07	0,008	0,002	0,005	6,06E-08	6,19E-05	1,60E-04	0,005	7,15E-06	0,001	0,102
Draba alpina	0	0	4,97E-04	1,44E-06	0,999	0	0	0	0	0	1,86E-05	0	0	0	0	0	1,42E-04	0
Dryas octopetala	0,007	0,011	0,005	4,25E-07	0,971	0,002	1,39E-07	3,29E-06	1,67E-04	1,02E-04	2,57E-04	5,54E-08	6,62E-06	3,63E-06	2,92E-04	4,36E-07	3,75E-04	0,002
Papaver sp.	0,001	2,48E-04	0,002	0	0,976	0,020	2,84E-08	2,40E-05	2,16E-05	8,27E-05	7,32E-06	0	4,64E-05	0	0	0	7,47E-05	1,20E-04
Polemonium boreale	0,003	0,163	0,007	0	0,816	3,97E-04	2,01E-06	8,78E-06	1,24E-04	3,17E-05	0,001	1,85E-06	1,67E-06	0	0	0	0,001	0,008
Potentilla nivalis	0	0,039	0,002	0	0,940	0,016	4,26E-07	2,24E-05	6,64E-05	7,03E-05	0,000	4,26E-07	3,69E-05	0	0,001	0	7,01E-05	0,002
Ranunculus sulphureus	0,037	0,125	0,163	0	0,369	1,13E-04	4,67E-08	5,15E-07	0,023	0,006	0,010	0	1,50E-04	3,44E-04	3,15E-04	4,67E-06	0,001	0,266
Saxifraga cernua	0,017	0,063	0,105	0	0,548	0,001	2,90E-08	1,33E-06	0,015	0,006	0,010	0	9,85E-05	2,20E-04	9,81E-05	9,31E-05	0,005	0,230
Saxifraga cespitosa	0,035	0,113	0,102	1,64E-08	0,534	3,61E-05	4,35E-07	2,90E-06	0,009	0,004	0,032	4,20E-07	6,29E-05	1,47E-04	0,005	0,000	0,005	0,160
Saxifraga hieracifolia	0	0,323	0,006	0	0,652	0	3,69E-06	1,76E-05	0	0	0,002	3,69E-06	0	0	0	0	0,001	0,016
Saxifraga hirculus	0,025	0,058	0,062	0	0,738	0,012	3,16E-08	1,44E-05	0,008	0,002	0,003	0	8,03E-05	1,28E-04	0	3,52E-06	0,001	0,091
Saxifraga hyperborea	0,079	0,160	0,149	0	0,380	0	0	0	0,016	0,004	0,007	0	1,20E-04	3,25E-04	0	1,45E-05	0,002	0,202
Saxifraga oppositifolia	0	0,009	0,117	0	0,843	0	0	5,15E-06	4,11E-04	5,24E-05	0,007	0	0	0,000	0,023	0	0	0
Saxifraga tenuis	0,059	0,085	0,042	0	0,285	0	0	0	0,001	0,011	0,026	0	2,06E-05	9,08E-05	0	0,001	0,039	0,452
Silene acaulis	0,039	0,060	0,025	1,20E-07	0,746	3,53E-04	2,48E-07	4,88E-07	0,001	0,002	0,005	1,03E-07	1,23E-05	4,04E-05	0	1,19E-04	0,035	0,086
Stellaria longipes	0,045	0,137	0,140	0	0,335	4,33E-05	2,19E-07	9,58E-07	0,018	0,006	0,012	2,02E-07	1,24E-04	2,94E-04	0	1,05E-04	0,007	0,300

Table A6. Müller's index for plants at Svalbard. The table is read as the acting species (columns) on target species (rows).

Appendix 7. Relative median of seeds produced at the sites

Silene acaulis

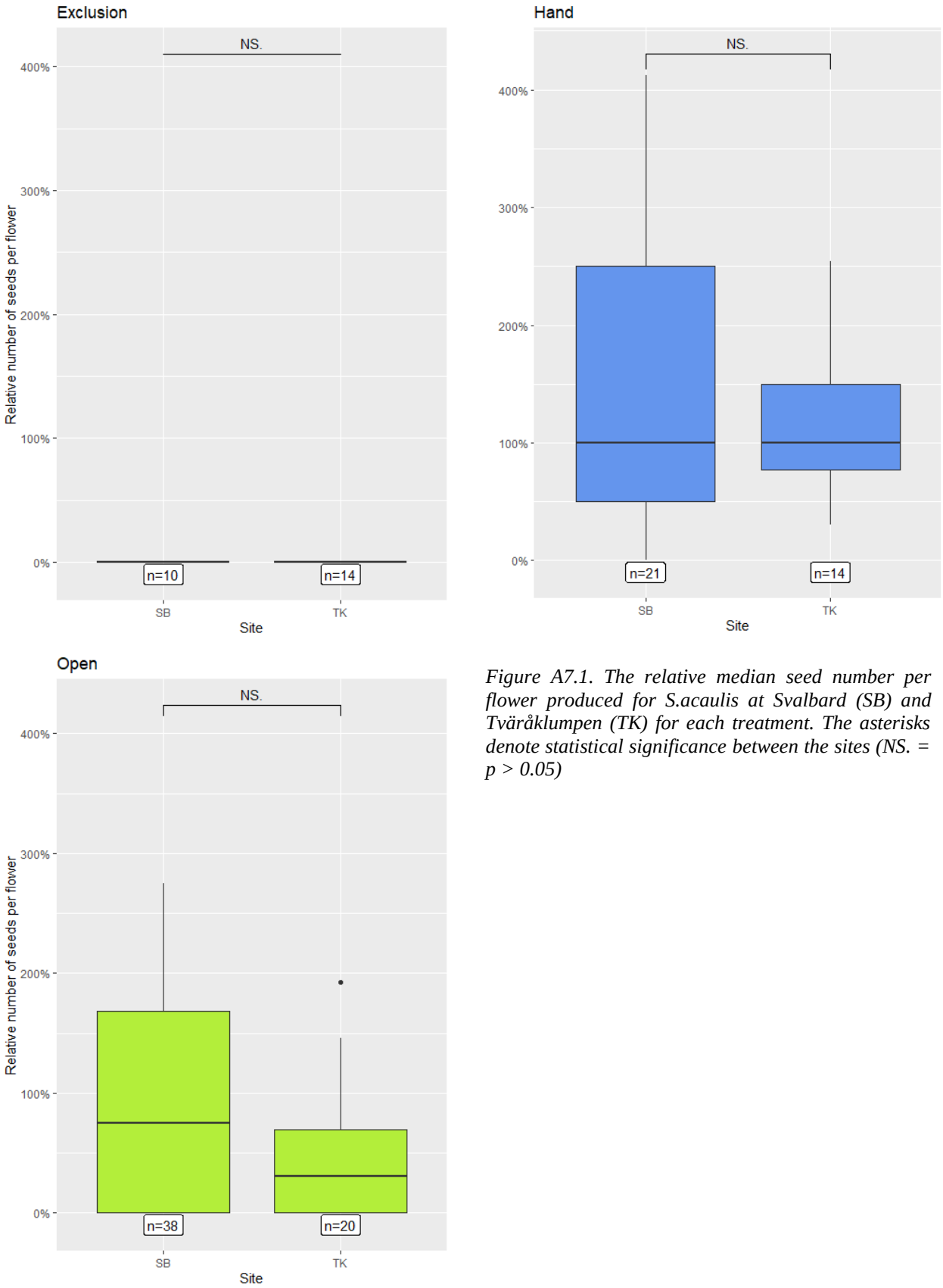
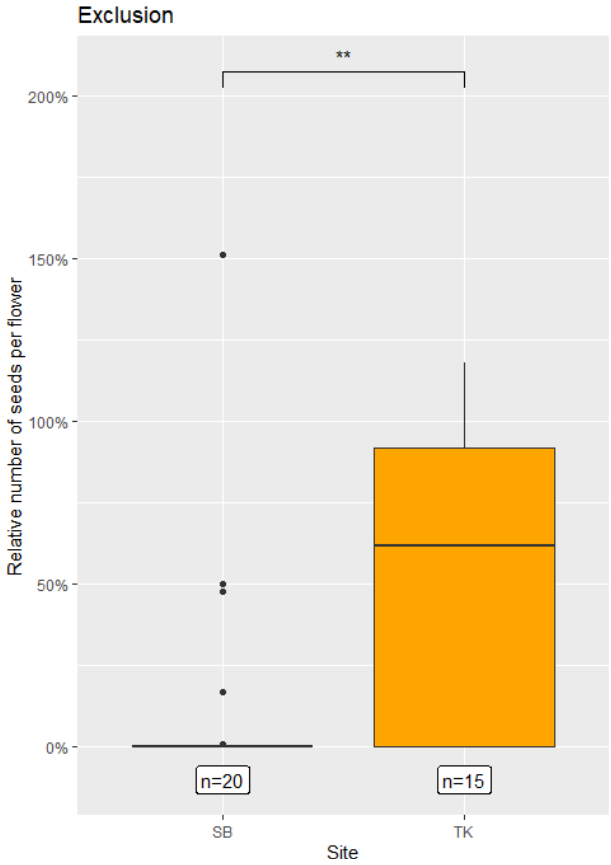
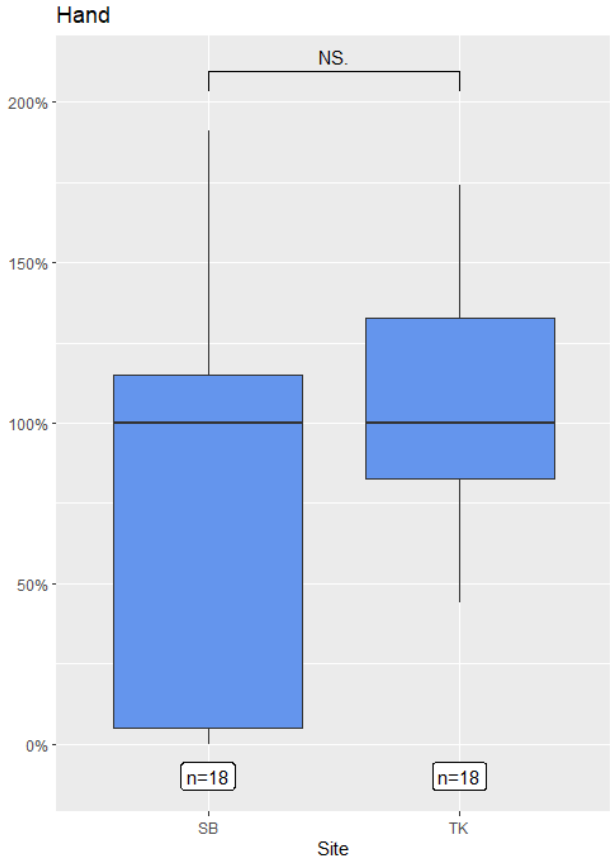


Figure A7.1. The relative median seed number per flower produced for S.acaulis at Svalbard (SB) and Tväråklumpen (TK) for each treatment. The asterisks denote statistical significance between the sites (NS. = p > 0.05)

Dryas octopetala





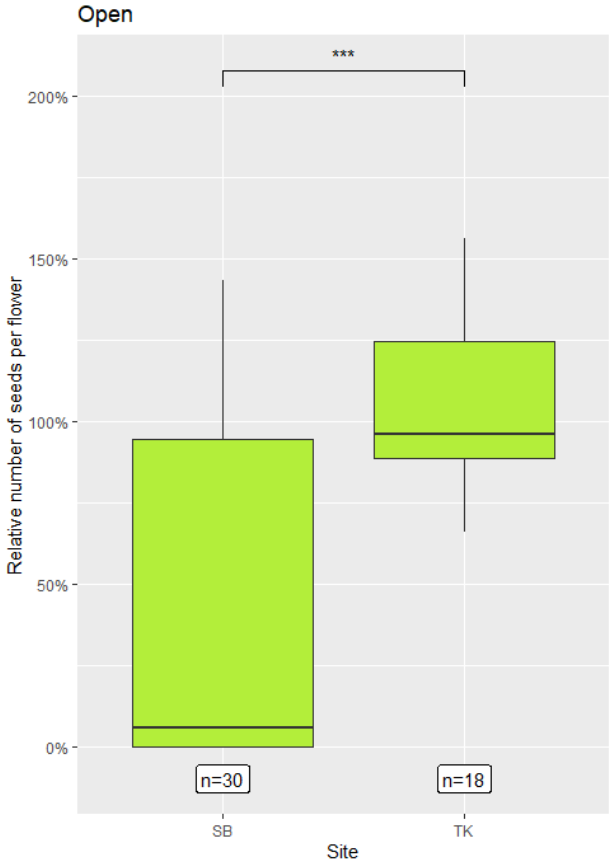


*Figure A7.2. The relative median seed number per flower produced for D.octopetala at Svalbard (SB) and Tväråklumpen (TK) for each treatment. The asterisks denote statistical significance between the sites (NS. = $p > 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$)*