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Spatio-temporal Diptera visitation to *Silene acaulis* flowers studied with time-lapse cameras in Svalbard and Greenland

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Cover photo: A muscid fly vising flowers of *Silene acaulis*, July 2022. Photo: Darwin Mayhew.

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Master of Science in Biology – Northern Populations and Ecosystems, August 2022

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Table of contents

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Foreword

This master thesis has two main aims. One is to investigate visitation of *S. acaulis* flowers and overall cushions, focusing on Diptera (true flies) in time and space in four Arctic sites. Second, to demonstrate how the implementation of time-lapse cameras can improve the study of the long-term monitoring of Arctic flower visitation. I present the first subset of results from a seasonal time series of image-annotated invertebrate visitors from Bjørndalen Integrated Gradients (UNIS, 2021) and the BitCue project, along with the first inverte trap samples from Bjørndalen Integrated Gradients. To my knowledge, this is the first investigation of both temporal and spatial time-lapse annotated flower visitors in the Arctic.

Line Klausen (LK) established the study and developed the hypotheses. Invertebrate samples and images from camera tending were collected by LK in Bjørndalen in 2021 in collaboration with UNIS employees connected to Bjørndalen Integrated Gradients. LK assembled camera clusters and tended cameras in Narsarsuaq 2019 in collaboration with other students. LK identified invertebrate trap material, facilitated by Stephen Coulson. Toke T. Høye (TH) retrieved and formatted the time-lapse images and provided scripts to help handle raw annotation data. LK annotated the images, and further annotation handling. The analysis was made by LK with inputs from Nigel Yoccoz.

The Svalbard fieldwork and site was supported by UNIS and financed by Bjørndalen Integrated Gradients program (BIG), funded by Olav Thon Foundation and the University Centre in Svalbard (UNIS, 2021). Greenlandic camera sites and the fieldwork in Narsarsuaq were funded by the BitCue project granted TH by INTERACT, Villum Foundation, and the Independent Research Fund Denmark.

1 Abstract

Flower visitation by flying arthropods has mainly been studied by direct human observation, which usually neglects seasonal development of flower abundance even though this is known to be important for visitor dynamics and match between trophic levels. In the present study, the arthropod visitor community focusing on Diptera was investigated on the cushion plant *Silene acaulis* (L.) Jacq. in relation to the available flower area. This was done using time-lapse cameras at one sub-Arctic, one low Arctic, and two high Arctic sites at Svalbard and Greenland. The *S. acaulis* flower visitor match at the Svalbard site was in addition characterized by using independent invertebrate traps located next to the camera site. Image annotation of cushion's visitors ensured a high temporal resolution of data throughout the flowering season and showed a highly increased visitation frequency when more flowers were open. Individuals from several trophic levels visited *S. acaulis*, supporting the claim of *S. acaulis* as nursing plant and community hotspot. True flies (Diptera) were by far the most abundant visitors of the visitors identified. The Diptera visitor abundance per unit flower area showed large variations and varied over seasonal development, years, and between sites. Image-annotated visitors were observed both on open flowers and the remaining image. In average 40 % of Diptera visitors were observed on flowers. This percentage followed the increase in image area with open flowers and peaked the same time as flowering peak, thought the number was also site and year specific. For the largest camera site in Svalbard, this percentage of visitors on flowers strongly decreased during the three-year study period. The decrease may have been enhanced by delays in flowering onset that led to increased competition with other flower species, making *S. acaulis* flowers less attractive to visitors.

2 Introduction

Arthropods (Arthropoda) have a very diverse fauna in the Arctic in terms of species richness and abundance. Furthermore, they serve as important connections between trophic levels, in addition several species act as important indicators of changing environments (Gillespie et al., 2020). The focus on arthropod declines has increased since Hallmann et al. (2017) found more than 75 % decline over 27 years in total flying insect biomass in protected areas (Loboda et al., 2018). A general arthropod abundance decline is seen in multiple biomes (Hallmann et al., 2017; Sànchez-Bayo & Wyckhuys, 2019; Loboda et al., 2018). Despite possible overestimation (Mupele et al., 2019) it has been suggested that up to 40 % of the world's insect species may be threatened with extinction (Sànchez-Bayo & Wyckhuys, 2019). For several decades, surface air temperatures in the Arctic region have warmed approximately twice the global rate, up to 5°C in the 20th century (Larsen et al., 2014). Arctic amplification is expected to continue during the remaining 21st century (IPCC, 2022), and ecological interactions and species dynamics may likewise be more affected here than in other regions (Koltz et al., 2018; Vincent, 2020).

The ecological importance of arthropods is well established (Gillespie et al., 2020), but the arthropod fauna in the Atlantic Arctic region is poorly studied compared to that of vascular plants and vertebrates (Gillespie et al., 2020; Høye, 2020). Arthropods are often highly habitat dependent, relying on characteristics such as temperature, moisture, and vegetation (Høye, 2020; Loboda et al., 2018; Høye et al., 2013; Dahl et al., 2018), which contribute to make herbivore-arthropods associations with the plants they feed on useful as indicators of Arctic environmental change (Gillespie et al., 2020; Loboda et al., 2018). Arthropod studies are in general geographically, spatially, temporarily, and taxonomically restricted, which makes generalizations unreliable as changes in population dynamics and responses are markedly higher in weather exposed areas (Høye et al., 2021; Miller-Rushing et al., 2010; Hegland et al., 2009). The considerable knowledge gaps concerning Arctic arthropods make it difficult to predict long-term responses to environmental alteration (Høye et al., 2021; Gillespie et al., 2020).

2.1 Flower visitation

Flower visitation, defined as visits by arthropods to plant reproductive organs, has traditionally been regarded as unimportant in Arctic regions due to the lack of traditional pollinators (as bees and butterflies) and enhanced self-fertilization (Tiusanen et al., 2016; Gillespie et al., 2020). This view has been challenged (Hoodkinson et al., 2004; Gillespie et al., 2020), as the richness of arthropod fauna becomes increasingly known, and awareness of the complex ecological system expands concerning pollination contribution to Arctic plant reproduction success. As traditional pollinator abundances are reduced with increasing latitude, the importance of true flies (Diptera) as pollinators increases, and so does their importance as study objects (Gillespie et al., 2020; Loboda et al., 2018; CAFF, 2013). Flower visitation can be used as an indicator of phenological features and may tell how the pollinator community responds to weather variability and climatic changes. Visitor abundance in relation to the available floral resources allows us to accurately investigate visitation frequency, while avoiding the bias that increased flower areas will attract more visitors. So far this angle has not been investigated because of inadequate approaches. Traditional methods to study flower visitation include collection with sweep nettings and direct observation next to flowers of interest (Berglund & Milberg, 2019; Klecka et al., 2018; Hoyle et al, 2018). This is both time demanding and biased since observations must be instantly written down and taxonomical identification is prioritized at the cost of registrations of visitor behavior. This also proves difficult for plants where flowers are small and numerous, such as *S. acaulis.* Cameras are becoming increasingly implemented in flower visitaiton research, and visitor abundance in relation to the available floral resources approach can be used to identify changes in visitation services.

As pollination services are a product of flower visitation, flower visitation largely also represents pollination services. Flowers provide both habitat and energy resources to invertebrates. Previous Arctic flower visitation studies have had the general assumption that flying visitors that land on flower plants aim for floral resources and may assist in pollination (Tiusanen et al., 2016; Tiusanen et al., 2020). The proportion of larger invertebrate visitors that visit sterile vs. plant reproductive organs during the season is yet to be investigated**.** Visitation frequency of flowers over time is typically used as proxy for the pollinator abundance without correcting for visitors' attraction to increased floral resources during flowering peak (Tiusanen et al., 2016; Tiusanen et al., 2020). Nectar sucking arthropods could be more detected on cushions when floral resources are high vs. when they are low, which does not indicate a change in local abundance. To my knowledge, no study has so far investigated the percentage cushion visitors on open flowers over time and the visitor abundance in relation to the available floral resources.

2.2 Arctic Diptera communities

The Arctic is characterized by a short, cold summer season resulting in a small ecological window of summer-based life cycle events such as flowering and insect activity. This short window makes environmental conditions such as phenological timing critical for survival (Semenchuk et al., 2016; Høye et al., 2007; Høye & Forchhammer, 2008). The increase in temperatures over the last decades has induced earlier spring phenology in Arctic flora and fauna (Cohen et al., 2018; Semenchuk et al., 2016). Insects show high sensitivity to temperature changes (Cohen et al., 2018; Loboda et al., 2018; Høye et al., 2013; Høye et al., 2007; Høye & Forchhammer, 2008) and exhibit greater phenological shifts than birds and mammals (Cohen et al., 2018), which makes trophic uncoupling likely to become more pronounced than today with predicted climate changes (Loboda et al., 2018). For Arctic plants, the flowering season has shortened due to spatial variation in phenological responses to anthropogenic warming (Høye et al., 2013). This has likely led to increased temporal uncoupling of trophic events with decreased resources for visiting species and reproductive success for the groups involved (Høye et al., 2013). For some arthropods, e.g., flies that facilitate in plant pollination, premature snow melt may facilitate earlier development and emergence, whereas a late snow melt and emergence may result in unfinished life cycles. Alternative replacements for these niches may be unable to respond due to specialized or inflexible life cycles (Høye et al., 2007; Høye, 2020; Gillespie et al., 2020), making the taxa vulnerable to projected climate changes.

Estimating precise Diptera population trends demand long-term monitoring, as communities are highly variable in both time and space (Høye et al., 2021). Consistent Arctic monitoring programs are logistically and financially challenging to set up, especially on large spatial scales (Høye, 2020). The most complete long-term study of Diptera trends in the North Atlantic Arctic region is done at Zackenberg Research Station in NE Greenland (Loboda et al., 2018; Gillespie et al., 2020). At this station Loboda et al. (2018) found that warmer temperatures were directly associated with a decline in Diptera, as well as indirectly through phenological changes with a shorter flight period and consequently a shortened reproductive period. Trap samples in the period 1996-2014 showed a decrease in the Muscidae family 80 %, parallel to a temporal mismatch between Diptera activity and flowering (Loboda et al., 2018). Some of the Diptera that experienced this temporal mismatch were found to be important pollinator species (Loboda et al., 2018). Also, in Zackenberg, Høye et al. (2007) found that the average muscid fly activity advanced 20 days per decade. *Silene acaulis* flowered in this study in average 11 days earlier per decade, despite a large variability (Høye et al., 2007). Large variability of *S. acaulis* flowering period highlights the importance of studying multiple habitats (Loboda et al., 2018). If an adult Diptera emerge earlier than the flowering of its preferred flowering plants, this may lead to mismatches in the species' activity season, and from the plants' perspective reduce plant seed production (Tiusanen et al., 2020; Alatalo & Molau, 2021). This may lead into an increasingly negative feed-back loop. Similar trends in pollinator abundances in other biomes are known to effect ecosystem functions negatively with reduction in pollination potential (Memmott et al., 2007).

2.3 Diptera ecology

Diptera are both the most abundant and the most diverse group of arthropods in Arctic regions (Coulson 2007). Among classic Arctic pollinator families are Syrphidae and Muscidae where Muscidae are considered key pollinators (Tiusanen et al., 2016; Gillespie et al., 2020; Loboda et al., 2018). Solid data regarding pollination by other insect families is largely anecdotal. Chironomidae are present on all continents, including the Antarctic, and are both species rich and abundant in Arctic areas (Stur & Ekrem, 2020). Previously, it was thought that adult Chironomidae did not feed, but the last two decades have showed that many adults feed on nectar and pollen resources (Burtt, 2006). Fungus gnats, the Sciaridae and Mycetophilidae families, feed on decaying material and fungi as larvae, and are occasionally characterized as pollinators (e.g., Mochizuki & Kawakita, 2017). Dung Diptera, Scathophagidae, predate other small invertebrates and are commonly seen hunting on flowers, with some species also known as pollinators (Lippok & Renner, 2022; Blanckenhorn et al., 2010). In Svalbard rather hairy species of Scathophagidae ssp. have been observed visiting *Silene acaulis* (Line Klausen & Geir E. Søli, pers. observations). In lack of better pollinators Scathophagidae may make a significant difference in the pollination. Nonbiting midges, Chironomidae, can be present in large blooms throughout the season, but has in not been found to have a significant effect on seed production (Tiusanen et al., 2016).

2.4 *Silene acaulis* as a community hotspot

Silene acaulis is a common nurse and pioneer plant with a circumpolar Alpine-Arctic distribution and has been increasingly used as a study plant in Arctic pollinator research (Alatalo & Molau, 2021; ITEX, 1993; UNIS, 2021; Høye et al., 2020; Oh & Lee, 2021). In Svalbard and Greenland, *S. acaulis* is gynodioecious, in which only female and hermaphroditic plant species exist within populations (Elven et al., 2020; Shykoff, 1988). Female plants have in several studies been classified as the most productive gender in terms of nectar resources and offspring, being vital for population expansion (Shykoff, 1992). However female plants are fully dependent on pollinator activity in contrast to their hermaphroditic counterpart.

Flowers increase fertilization with pollinator visits and compete both inter- and intraspecific with other flowers for visitors. This is most often done by offering nectar and pollen resources when fitting pollinators are available. Nectar resources are energetically expensive, and depending on strategy, nectar resources are not to be wasted when pollination is unnecessary or unlikely to happen. It is beneficial for both pollinators and flower plants that flowering and pollinator abundance are synchronized. *S. acaulis* as an early flowering plant (Alatalo & Totland, 1997) makes fruit set more limited by the availability of pollinators than by the length of the growing season (Molau, 1993; Alatalo & Totland, 1997). With too early flowering, pollinators may not have emerged while late flowering may increase competition with other plant species.

Flowers like *S. acaulis* may provide other services for arthropods aside from energy resources as they grow densely in cushions and retains heat which ameliorate stressful environmental conditions. This causes a warm microclimate with higher invertebrate richness, abundance and diversity compared to other vegetative non-cushion sites (Molenda et al., 2012). *S. acaulis* provides shelter through the microclimate along with nectar and pollen resources, and potentially mating ground, basking ground, and sites for ovipositioning in complex food web (Molenda et al., 2012). Loss of foundation plants negatively impacts ecosystem stability and invertebrate diversity. The decreased density of Arctic cushion plants due to anthropogenic climate changes may be a first step in assessing Diptera responses to habitat loss (Molenda et al., 2012; Ellison, 2005).

2.5 Time-lapse cameras' monitoring potential

Even though Diptera are recognized for their importance in ecosystem functioning, it is uncertain how climate changes will alter the strength of their interactions with plants and other insects (Gillespie et al., 2020; Taylor et al., 2020). Traditionally, flower visitations have been recorded by direct observations, but this is both time-consuming, financially, and logistically demanding to keep consistent (Steen, 2017). Field identification of species or catching these for later identification takes place at the same time as behavioral registration on the cushions. Observer's presence may disturb the visitors' frequency and behavior, and while writing notes, the observer cannot pay much attention to visiting animals (Rader et al., 2016; Steen, 2017). The quality of direct observations is further complicated when flower visitors are frequent, simultaneous, and/or very small in size. Arctic flower visitor communities consist mostly of very small Diptera (Høye 2013) thereby leading to a potentially large observer bias. Monitoring over a large spatiotemporal scale is usually impossible with traditional direct observations (Steen, 2017). With large variations in Diptera population dynamics in the Arctic, direct observations are thereby highly challenging as a primary monitoring tool.

These issues can be avoided by remote camera monitoring. Recent technological advances with increased image resolution in time-lapse cameras followed with affordable prices allow new approaches such as large-scale monitoring of flower visitation (Høye et al., 2021). Advances in computer vision and machine learning have also aided monitoring of species interactions and their response to environmental change (Høye et al., 2020).

In the last decade, video monitoring equipment has increasingly replaced on-site human observations in pollination monitoring (Steen, 2017, Bjerge et al., 2021). Video monitoring has the disadvantage that it either requires a large amount of power and storage space or highly efficient algorithms (e.g., machine learning) that can identify visitors in real time. Good identification by algorithms is challenging to make when visitors are slow-moving, dark-colored, and the body size is small, as is usually the case for Arctic pollinators (Mousseau, 1997).

The latter years, monitoring with time-lapse cameras that record with a regular frequency has been used as a new approach to study invertebrate visitors (Kromer et al., 2019; Høye et al., 2020; Ferkingstad, 2020; Rader et al., 2016). To my knowledge, no time-lapse camera studies have been published on Arctic invertebrates so far (Steen, 2017; Høye et al., 2020). Automatically triggered cameras are a time-efficient procedure and produce large quantities of cost-efficient data but with variable image quality resulting in taxonomical limitations in visitor identification (Ferkingstad, 2020). Most Diptera taxa cannot be identified to species level no matter the image quality. However, the accuracy of our ability to distinguish between different groups will increase with image quality. Invertebrate traps catch both visiting and non-visiting invertebrates as they are independent of flower monitoring. Trap material can be identified to high taxonomic accuracy, and to some extent compensate for images' taxonomic inaccuracy. As invertebrate traps are monitored during the whole summer, they may also show whether potential flower visitors are still present in the local area before and after the investigated flowers have withered. This helps to place the investigated flowers in a seasonal timeline which further aid in the identification of mismatches between trophic levels.

This master thesis aims to investigate arthropod visitation, with a focus on Diptera, of *Silene acaulis* cushions in Greenland and Svalbard in relation to the available floral resources. Alongside, I test whether the implementation of a new monitoring methods with time-lapse cameras may improve the study of the long-term effect of Arctic climate changes. Finally, by using cameras along with descriptive, independent invertebrate data, I aim to describe *S. acaulis* flower visitation in time and space. I hypothesize that (*i) Silene acaulis* have visitors belonging to several trophic levels; (ii) The Diptera flower attraction is a product of available flower resources; and (iii) The surrounding visitor community has a large effects on both the Diptera visitor abundance and proportion observed on flowers.

3 Material and method

3.1 Study sites

Time-lapse cameras were installed on *Silene acaulis* cushions at two high Arctic, one low Arctic, and one Subarctic study sites. The most extensively studied site was in the Bjørndalen valley in 2019-2021 (W Svalbard, 79.52°N, 19.01°E); together with three sites in Greenland 2019-2020: In the Narsarsuaq valley (S Greenland, 61.19°N, 45,37°E), by the fjord named Kobbefjord (SW Greenland, 64.15°N, 51.47°W), and on the island named Ella Ø (NE Greenland, 72,81°N, 24,92°W), respectively (Fig. 2, Table 1).

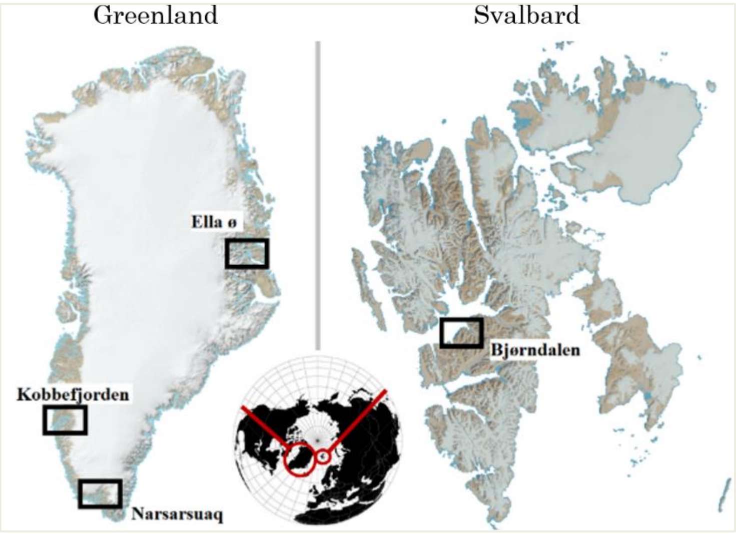


Figure 1. Study sites in Greenland and Svalbard. The locations of camera clusters are indicated by black squares. Sites are named after geographical places. The hemisphere projection was retrieved from Depositphotos and the topographical maps from NUNAgis ©Asiaq and TopoSvalbard ©Norwegian Polar Institute.

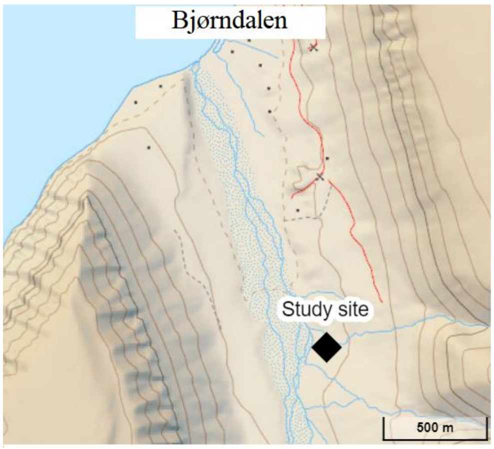


Figure 2. Location of the largest study site in terms of cameras in Bjørndalen, Svalbard. Bjørndalen had invertebrate traps as the only study site.

Study sites aimed to be representative of the broader area and with a high *S. acaulis* abundancy. The four sites were in three different bioclimatic zones, with the two Northernmost sites, Ella Ø and Bjørndalen, having characteristics of a high Arctic environment with more extreme climatic conditions. Kobbefjord has the characteristics of a Southern Arctic climate, and Narsarsuaq is in the sub-Arctic bioclimatic zone as described by CAVM Team (2003). The site in Bjørndalen valley was on the Eastern side of the valley, facing the Isfjord that connects to Atlantic waters towards the North. (Fig. 2). Narsarsuaq valley has the Kiattutt Semiat glacier in the NE end, and the Tunulliarfik fjord in the SW end. It was not possible to obtain specific coordinates for the study sites in Ella Ø and Kobbefjord, but Ella Ø lies in the inner part of Kong Oscar Fjord and is shielded by the

Trail islands from the open Atlantic waters. Kobbefjord is one of the outer fjords in a larger fjord system, and the site lies in the inner NE fjord area.

Table 1: Sampling overview and data amount for cameras and invertebrate traps (inv. traps) in the study sites. Bioclimatic zones are as described by the Circumpolar Arctic Vegetation Map (CAVM Team 2003). Years with camera data from each site is marked with green. A detailed table for camera IDs' used at each site is found in Appendix 1.

Site name	Location	Bioclimatic Zone (A-E)	Cameras installed	Inv. traps	Study years		
					2019	2020	2021
Bjørndalen	Svalbard	B	9	Yes	🟩	🟩	🟩
Ella Ø	Greenland	B	2	No	🟩		
Kobbefjorden	Greenland	D	2	No	🟩		
Narsarsuaq	Greenland	E	2	No		🟩	

3.2 Time-lapse cameras

3.2.1 Installation and dataset

15 waterproof time-lapse cameras (TimelapseCam Pr) were attached to open aluminum boxes that functioned as umbrellas (Fig. 3a). Five cameras were installed in Bjørndalen 2019-2021 and 4 more in 2020 only. Two cameras were installed in Narsarsuaq, Kobbefjord, and Ella Ø. Time-lapse cameras had a fixed 60 cm distance with adjusted zoom between the camera lens and ground at all sites. Cameras were powered with either disposable lithium batteries (Narsarsuaq and Bjørndalen) or solar panels (Narsarsuaq, Kobbefjord and Ella Ø). Images were stored on 128 GB SD cards in the field and later downloaded and uploaded to the National Infrastructure for Research Data (NIRD), project number: NS9320K, for Bjørndalen images, and hard disks made available by Toke T. Høye for Greenlandic sites. During annotation, images were made available from storage units by Toke T. Høye.

The cameras were a part of several larger projects with different scopes, and images were taken more often than this study had capacity to manually look through. No significant difference in flower visitor abundances over a 24 h timeframe has been found in Bjørndalen, Svalbard, but Subarctic latitudes are found to have higher activity at noon (Djuberg, 2021; Totland, 1994). For dataset to have sufficient quality within the time restrains, 60 images were retrieved each day from every 60 second between 13:00-13:59 from the first day of flowering to withering for each investigated cushion.

S. acaulis was chosen as the study plant due to its role as one of the BIG project's study plants and its role as the main species in the International Tundra Experiment (Molau & Mølgaard, 1996; BIG, 2021). All investigated *S. acaulis* cushions in Bjørndalen and Narsarsuaq were female (Ween, 2022). The sexes of cushion on the remaining sites were unknown.

3.2.2 Image annotation

Images were manually annotated using the Visual Geometry Group (VGG) Image Annotator tool 2.0.8 (Dutta & Zisserman, 2019). Annotation followed the procedures described by Ween (2022) with the following modifications: Invertebrate taxa and location were identified for each flower visitor instead of flowering state. Annotations were further made using a Samsung S22B300H 21,5" and a BenQ GL2260-T 21.5" LED Monitor screen, both with a resolution of 1920x1080 pixels. Due to low image resolution and relatively large distance to cushions (60 cm), the invertebrates were categorized by size for Diptera (<5 mm, 5-9 mm, >9 mm), and mostly order for other taxa. Invertebrate sizes were estimated relative to the surroundings, from the assumption that average sized flowers were 1.0 cm (Elven et al., 2020). Invertebrate location on cushion was either marked as "flower", "not flower" or "other". "Flower" were flower visits to either blooming or almost blooming/early withering stages of *S. acaulis*. "Other" were flower visits to other species than *S. acaulis*. "Not flower" was marked when visitors did not fall into the two first categories. Invertebrates were counted as on flowers when either a leg was placed on the flower, the head leaned over it, or the head was touching it. Cushion visits were defined as invertebrate visits to both fertile and sterile plant parts. All concepts and definitions can be found in Table 2. It was not possible to differentiate between cushion visitors that had been counted at previous images vs. new arrivals to cushion. Therefore, all visitors were counted during each sequence.

Table 2: Concepts and definitions used in this study.

Level	Concept	Definition
Flower	Flowering period	The time period a specified number of *S. acaulis* cushions/cushion has open flowers.
	Flower area	The area (pixels) covered with open *S. acaulis* flowers at images.
Visitors	Visitor	Any animal observed on camera images.
	Cushion visitors	Visitors observed on images. This includes floral parts.
	Flower visitors	Visitors observed on floral parts only.
	Visitation frequency	Number of visitors over time.
	Percentage flower visits	The percentage of visitors on images that was observed on open flowers.

Preliminary results from Ween (2022) showed that *S. acaulis* flowers have a longevity of 7.7 days in Narsarsuaq. Therefore, an image subset was made of one image every 24 hours for all invertebrate annotated time-lapse series to mark all open flowers. Floral resources were measured in the form of number of pixels with open flowers in VGG Image Annotator at each daily image. This is referred to as 'flower area'. Withered flowers and buds were not marked as flower area. Annotation files were exported to CSV format and processed in R version 4.1 (R core Team, 2022). Invertebrate annotations without location on cushion (N = 27,373) were omitted in the calculations for visitor location. The large number without annotations, were due to a data handling error.

3.3 Invertebrate traps

Ten 100 mL wet pitfall traps with 5.5 cm diameter were placed next to cameras at the camera cluster in Bjørndalen. One pitfall was placed next to one camera. As far as Diptera are concerned, pitfall traps operate as water traps. A 0.5 L bottle was strapped to an East facing malaise tent of the Townes model in the middle of the cluster (Fig. 3b). The cluster with pitfalls, malaise and cameras had a total diameter of 25 m. Traps were filled with an 80 % ethanol and 20 % distilled water solution and emptied once a week. Pitfall material was mixed into one bottle, so that one pitfall sample and one malaise trap sample were obtained each week (Fig. 3c). The same pitfall holes were reused every summer season. In 2020 a kitchen cloth was used to sieve and transfer invertebrates to smaller tubes in the laboratory for storage purposes. In 2019 and 2021 a sieve with 1 mm x 1 mm mesh size was used. Storage tubes were filled with a new 80 % ethanol solution.

Figure 3. The field site in Bjørndalen. (a) Three steel mounted time-lapse cameras on top of Silene acaulis cushions, (b) the malaise tent next to the camera cluster, and (c) a combined sample from five pit fall traps. Photos: Line Klausen, 2021.

Samples prior to week 29 in 2020 were not obtainable due to logistical challenges. Malaise tents were destroyed by reindeer during the study periods of 2019 and 2020 which led to sample gaps. Material from invertebrate traps was identified with a Stereo zoom microscope with 10-12x magnification (Leica S9 E, Leica Microsystems, Wetzlar, Germany). Due to time limitation, taxonomic skills, and image resolution, invertebrates from traps were identified to family level for Diptera and mainly order for other taxa.

3.4 **Weather data**

Weather data was obtained from the weather station administrated by Avinor at Svalbard Airport (SN99840), WGS84 78.2453º N, 15.5015º E from Norsk Klimaservicesenter at seklima.met.no. Due to logistical challenges, weather data was not available from the weather station in Bjørndalen, that was put up prior to the 2021 flower season by BIG (2021). Weather data from Narsarsuaq, Kobbefjord, and Ella Ø were not used in this study. The weather station at Svalbard Airport is in a topographical more exposed area with higher wind speeds, than is the case for Bjørndalen valley. Precipitation is assumed to be similar between the two areas. Wind speed was derived as one daily value in the study period, calculated as the average windspeed (m/s) detected 10 m above the ground from 11:50 to 12:00 by Norsk Klimaservicesenter. The total precipitation per hour was summed to precipitation per day. Temperatures in Svalbard Airport were measured 2 m above ground and derived at 12:00 each day. The time-lapse cameras installed at sites measured and logged surface air temperature during each recording. Camera temperatures at 12:00 were averaged per site per each day.

3.5 Data analysis

Statistical analyses for image annotations were made in R version 4.1.2 (R Core Team, 2022) and analyses for invertebrate trap material were made in Microsoft Excel (version 2019 (16.0)).

The joint area of all *S. acaulis* markings was calculated in an empty data frame to hold data from *S. acaulis* flowering and other open flower species separate. Pixels with several overlapping markings of flower area were only registered as flower area once.

In total, 51,609 arthropods were counted on 34,253 images during investigated tufts flowering period. 26,843 of these annotations had no location or taxa in the data output, possible due to an error in the coding interpretation, and were omitted from dataset along with orders containing less than 10 counts (N = 13). This left 24,753 arthropod annotations (Table 3, see examples at Fig. 6a-f). For the analysis, 50 Diptera were omitted due to no missing size category. In the analysis of the percentage of Diptera cushion visitors observed on open flowers (hereafter referred to as percentage flower visits), Diptera without cushion location were omitted (N = 508). Remaining data with visitor location were summed and made into a proportion table as fractions of the marginal sum. A subset of the original data frame is shown in Appendix 2.

The main drivers of the Dipteran visitor frequency were identified using Generalized Additive Mixed Models (GAMM) implemented with the gamm function from the mgcv package (Wood 2017).

Explanatory variables for Diptera visitors and Diptera visitors per unit flower area were defined using Camera ID as random effect, and day of year, site, camera temperature, flower area, year, and Diptera taxa as fixed effects.

A non-metric multidimensional scaling (NMDS) for taxa with more than 10 annotations was made based on Bray-Curtis dissimilarities to see the community position of 'unidentified invertebrates' and other taxa (Appendix 3). During annotation, this group was already suspected to be very small Diptera and was therefore included in figures, along with the three size groups.

To identify the effect of weather factors on Diptera visitor abundance per unit flower area, only image annotations from Bjørndalen were used, as wind and precipitation data were available from Svalbard Airport weather station only (4.7 km from the Bjørndalen study site). Camera ID was set as random effect, and day of year, camera temperature, flower area, year, avg. wind speed, daily precipitation, and Diptera taxa as fixed effects.

The main explanatory variables for the percentage flower visits and percentage flower visits per unit flower area were identified using day of year, Diptera visitor abundance, Diptera taxa, year, flower area, site and camera temperatures as fixed values and camera ID as random effect.

When fitting DOY as predictor for Arctic invertebrate abundances in linear models, the response difference is the largest when values are lowest (early season) and highest (late season) as invertebrate abundances usually are higher in Arctic systems during the middle of the growth season (DOY ≈195). In addition, visitor frequencies and flower area had a complex relationship (Appendix 5-8). To resolve this, both flower area and DOY were fitted using a spline-based smoother with the 's' function from the mgcv package when the splined based smoothed factor and the original factor had a complex, nonlinear relationship. Graphs showing the relationship between day of year, flower area and the spline functions can be found for each model in Appendix 5-9. Quasi-likelihood methods (using the argument family = quasipoisson) were used for all models due to overdispersion in count data. I used test statistics, P-values and 95 % confidence intervals of effect sizes to assess statistical significance of linear effects (as implemented by the summary function provided for the gamm function). Significance of nonlinear (i.e., spline) effects as well as the complexity of these nonlinear effects (measured by their degrees of freedom) was assessed using the same approach.

Pearson product-moment correlation coefficient was used to compare surface air temperatures between Svalbard Airport weather station and cameras, and between Chironomidae and Acari abundance from trap material.

4 Results

4.1 Image-annotated visitors

Site	Taxa	Counts
Bjørndalen	Acari	638
	Araneae	48
	Lepidoptera	8
	Coleoptera	74
	Diptera	11248
	Apocrita	13
	Symphyta	532
	unidentified inv.	5450
Ella Ø	Acari	1
	Araneae	8
	Coleoptera	1
	Diptera	231
	Lepidoptera	8
	Symphyta	6
	unidentified inv.	144
Kobbefjorden	Acari	11
	Araneae	113
	Coleoptera	90
	Diptera	351
	Lepidoptera	8
	Apocrita	6
	Symphyta	1
	unidentified inv.	32
	Acari	17
	Araneae	757
	Coleoptera	78
	Diptera	3923
	Lepidoptera	6
	Apocrita	7
	Symphyta	43
	unidentified inv.	887

Table 3. Observations of different taxa (mainly orders) at images 2019-2021 at the four study sites. If the same animal stayed at cushion for more than one minute, it was counted several times.

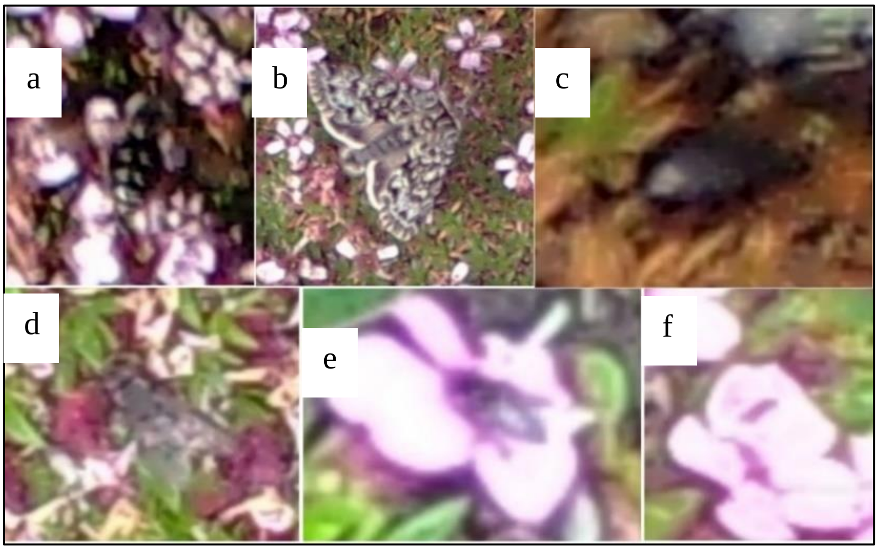


Figure 4. Subset of visitors found on images representing different taxa categories. Images were taken from the four study sites, Bjørndalen (N = 26,561), Narsarsuaq (N = 3360), Kobbefjord (N = 1464), Ella Ø (N = 2868). Syrphidae (a) from Kobbefjord, Lasionycta leucocycla (DET: Steffen Adler, 2022) (b) from Kobbefjord, Coleoptera (c) from Kobbefjord, Diptera >9mm (d) from Bjørndalen, Diptera 5-9 mm (e) from Narsarsuaq, Diptera <5mm (f) from Bjørndalen.

Of the visitors identified (Table 3, Fig. 6), Diptera were by far the taxonomic order with the highest visitor abundance at all sites. In total 63.6 % of observed visitors were Diptera (N = 15,753), which were observed in three size categories: <5 mm (N = 6106), 5-9mm (N = 6346), and >9 mm (N = 3251). 6513 counts (26.3 %) were not identified (unidentified invertebrates, Table 3) but had similar data patterns to Diptera (Appendix 3). At study sites, the proportion of unidentified visitors varied between 5 and 36 %, whereas Diptera varied between 57 and 68 %. Spiders were the most abundant predatory visitor taxa and visited cushions the most in the two Southernmost sites, Narsarsuaq (13.2 % of total visitation) and Kobbefjord (18.5 % of total visitation), and the least in the two high Arctic sites, Ella Ø (2.0 %) and Bjørndalen (0.2 %, Table 3). Spiders in Narsarsuaq were observed both as camouflaged sit-and-wait predators in flowers and as wolf spiders running in and out of the cushions. In Svalbard Bjørndalen were visited by mites (Acari) and Symphyta observations significantly more frequent than in Greenlandic sites (Table 3).

4.1.1 Image-annotated Diptera visitor community

Overall, the late and early part of the season had a smaller number of annotated visitors and showed larger variations than mid season (Fig. 5ab). The number of observations in the different Diptera size groups dependent largely on the specific site and season. For Bjørndalen only, large Diptera visitors were the most frequent size group per unit flower area (>9 mm, Appendix 5). In the model for all sites, medium-sized Diptera (5-9 mm) were the most visiting size group (Table 4). This was largely influenced by the southernmost site, Narsarsuaq. Narsarsuaq had fewer large Diptera visitors (>9 mm) than Bjørndalen throughout the season, but a larger proportion of medium-sized Diptera (5-9 mm, Fig. 5b). Both for Bjørndalen only and for all sites, the smallest size group (<5 mm) were the least visiting size group pr. unit flower area (Table 5, Appendix 5).

Both Ella Ø and Kobbefjord had overall low visitor abundances with the most visitors in the early half of the *S. acaulis* flowering period (Fig. 6de). Diptera visitors in Ella Ø were largely unidentified invertebrates, which changed towards Diptera <5 mm in the late season (Fig. 5b).

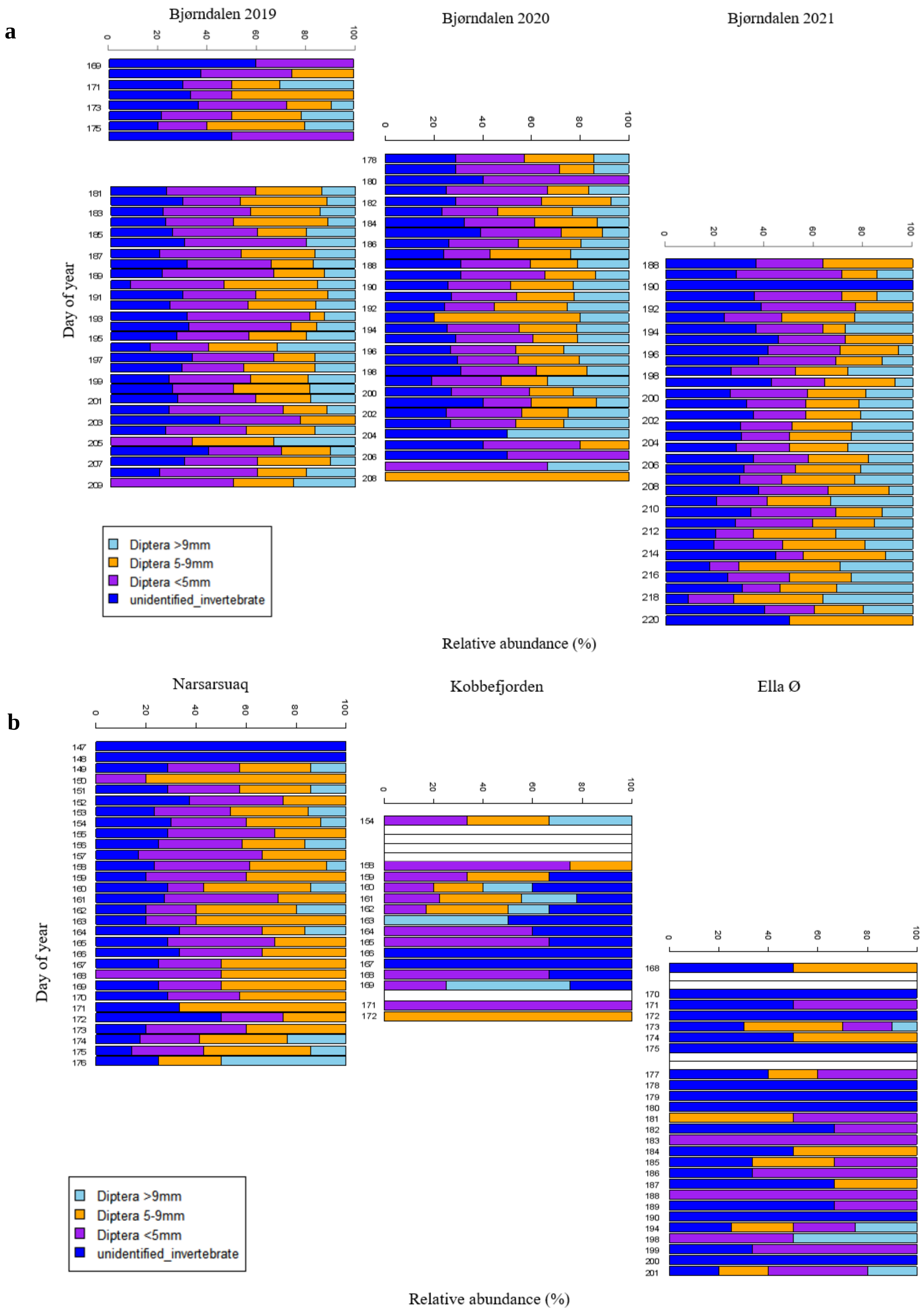
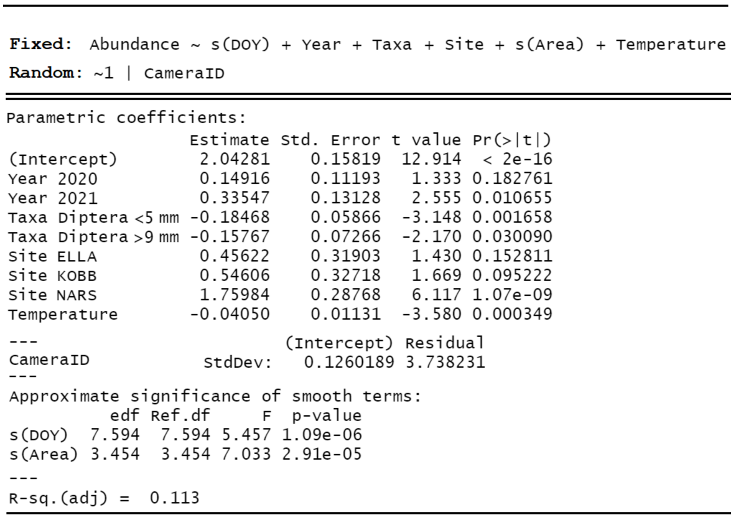


Figure 5. Bar plot of Diptera visitor community over time from camera-based images for Bjørndalen (a) and Greenlandic sites (b). Unidentified invertebrates were assumed to mostly consist of very small Diptera. Each bar represents visitors for one day (written left of each bar) with each color presenting one Diptera group. Flowering days without visitors as white bars. Flowering days without data due to power outage are left as holes in the data set.

Visitors showed large seasonal variation per investigated tuft, year, and site (Table 4), and visitor abundance per unit flower area changed likewise with seasonal progression (Table 5).

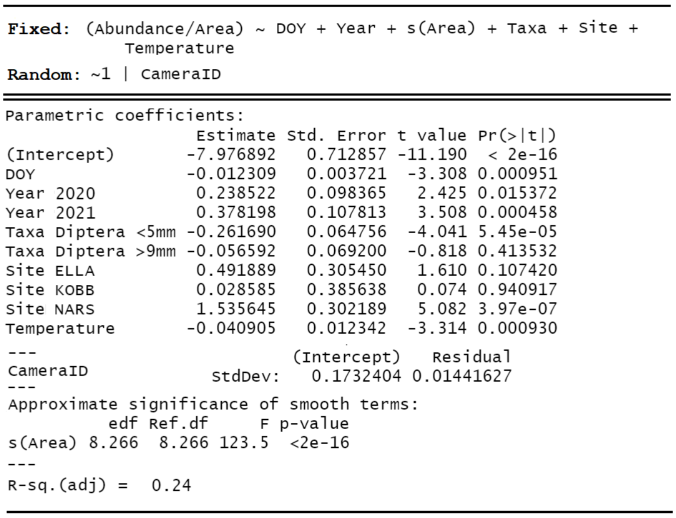
Table 4. Model output for Diptera visitor abundance for the study sites Ella Ø (ELLA), Kobbefjord (KOBB), Narsarsuaq (NARS) with Bjørndalen (BJOR) as reference. Area refers to unit area with open flowers within camera frame. Day of year and unit flower area were fitted using splines due the complex relationship shown in (Appendix 6).



```
Fixed:  Abundance ~ s(DOY) + Year + Taxa + Site + s(Area) + Temperature
Random: ~1 | CameraID

Parametric coefficients:
                   Estimate Std. Error t value Pr(>|t|)
(Intercept)         2.04281    0.15819  12.914  < 2e-16
Year 2020           0.14916    0.11193   1.333 0.182761
Year 2021           0.33547    0.13128   2.555 0.010655
Taxa Diptera <5 mm -0.18468    0.05866  -3.148 0.001658
Taxa Diptera >9 mm -0.15767    0.07266  -2.170 0.030090
Site ELLA           0.45622    0.31903   1.430 0.152811
Site KOBB           0.54606    0.32718   1.669 0.095222
Site NARS           1.75984    0.28768   6.117 1.07e-09
Temperature        -0.04050    0.01131  -3.580 0.000349
---                           (Intercept) Residual
CameraID             StdDev:    0.1260189 3.738231
---
Approximate significance of smooth terms:
          edf Ref.df     F  p-value
s(DOY)  7.594  7.594 5.457 1.09e-06
s(Area) 3.454  3.454 7.033 2.91e-05
---
R-sq.(adj) =  0.113
```

Table 5. Model output for Diptera visitor abundance (Abundance) per unit flower area (Area). The model output (a) represents estimate, standard error, t-value and p-value for each term in the model. Unit flower area was fitted using splines due the complex relationship (Appendix 7).



```
Fixed:  (Abundance/Area) ~ DOY + Year + s(Area) + Taxa + Site +
               Temperature
Random: ~1 | CameraID

Parametric coefficients:
                   Estimate Std. Error t value Pr(>|t|)
(Intercept)       -7.976892   0.712857 -11.190  < 2e-16
DOY               -0.012309   0.003721  -3.308 0.000951
Year 2020          0.238522   0.098365   2.425 0.015372
Year 2021          0.378198   0.107813   3.508 0.000458
Taxa Diptera <5mm -0.261690   0.064756  -4.041 5.45e-05
Taxa Diptera >9mm -0.056592   0.069200  -0.818 0.413532
Site ELLA          0.491889   0.305450   1.610 0.107420
Site KOBB          0.028585   0.385638   0.074 0.940917
Site NARS          1.535645   0.302189   5.082 3.97e-07
Temperature       -0.040905   0.012342  -3.314 0.000930
---                           (Intercept)   Residual
CameraID              StdDev:   0.1732404 0.01441627
---
Approximate significance of smooth terms:
          edf Ref.df     F p-value
s(Area) 8.266  8.266 123.5  <2e-16
---
R-sq.(adj) =  0.24
```

Flower area was highly significant for visitor abundances (Table 5) and visitator abundance per unit flower area increased with larger flower area (Table 5). Both cameras in Narsarsuaq featured large cushions, and one camera (NARS-20) was the only camera in this study with two individual cushions (Fig. 9). The investigated cushions in Narsarsuaq had the highest visitor abundance and Bjørndalen the lowest (Table 4), also after factoring for the larger flower area (Table 5). The temperature association to visitor patterns were not found to influence the number of cushion visitors positively in models (Table 4, 5, Appendix 5), and only few drops in temperature, in Bjørndalen 2019 and 2021 respectively, were followed by a likewise sharp decrease in visitation (Fig. 6).

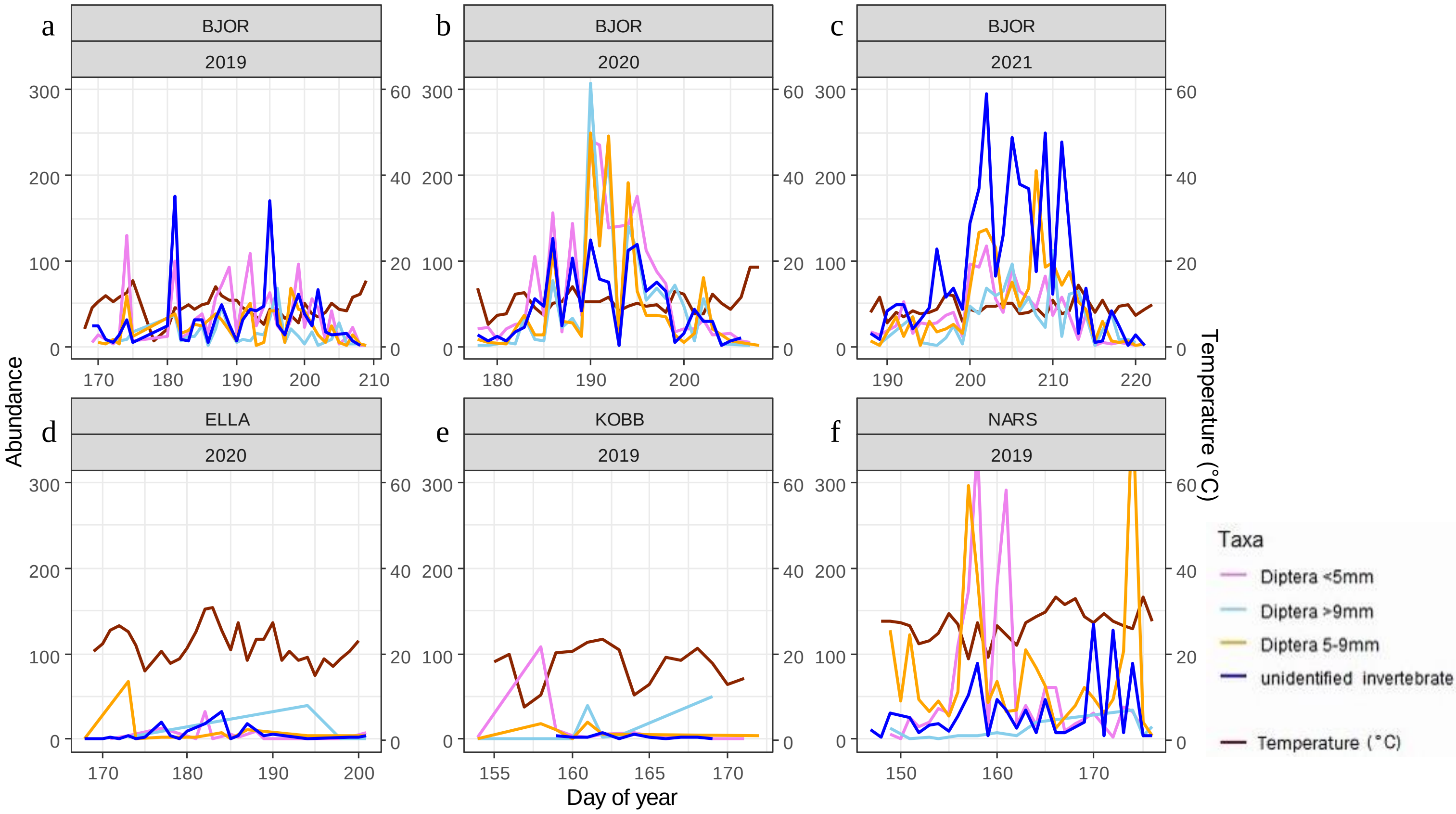


Figure 6. Image-annotated Diptera visitor community over time for all cameras in Bjørndalen 2019 (a), Bjørndalen 2020 (b), Bjørndalen 2021 (c), Ella Ø (d), Kobbefjord (e), and Narsarsuaq (f). Kobbefjord and Ella Ø have small sample sizes and large variation. Averaged camera-measured surface air temperature (C) is indicated by a brown line.

For the five continous camera ID series in Bjørndalen, almost twice the number of Dipteras visited the cushions in 2021, compared to earlier years (3673 in 2019, 3518 in 2020, 6796 in 2021). Peak time over the study period to later in the season. Between 2021 and 2020 this peak was approcimately two weeks (DOY ≈ 205-211 in 2021). However the highest visitator abundance per unit flower area in Bjørndalen was in 2020 (Appendix 5). Bjørndalen 2020 also differed from other years, with large (>9 mm) and medium-sized Diptera (5-9 mm) reaching large numbers in mid-July (DOY ≈ 190-195, Fig. 6b).

4.2 Invertebrate trap communities

13,202 invertebrates were counted in traps from Bjørndalen, Svalbard, 2019-2021. 8532 (Diptera: 7257) counts from malaise traps (MS) and 4850 (Diptera: 3225) from pitfall traps (PS) in 2019 (N = 4450, Diptera: 3556), 2020 (N = 2108, Diptera: 1129) and 2021 (N = 6644, Diptera: 5697) respectively. Trap material contained individuals from 10 Diptera families in Bjørndalen, with

Chironomidae (N = 7122) as the most abundant family, followed by the Diptera families Sciaridae (N = 1503) and Mycetophilidae (N = 1156).

Diptera communities in malaise material showed little variation, with Chironomidae dominating the material from 91.8-96.8 % of the annual Diptera caught (Fig. 7a). In addition, malaise traps showed high abundances of Acari, (15.6 % of all individuals). The Acari abundance increased from early summer to a peak in late July. Acari was associated to Chironomidae abundance (0.45, CI = 0.20–0.65), likely due to parasitism as many Acari were observed attached to Diptera individuals.

Pitfall traps caught a more diverse community with a high catch rate of Sciaridae (30.6 %) and Mycetophilidae (22.2 %). In total Acari constituted 6.3 %, spiders (Araneae) 8.3 %, Aphidae 6.3 %, Chironomidae 5.4 % and Apocrita 4.7 % of the material (Fig. 7b). One family, Empididae, was only present in 2019 in mid-June. Sciaridae were abundant in the mid-flowering season (late June-early July in 2019, July in 2021). Mycetophilidae had the highest relative abundance early and late season, outside the Sciaridae mid-summer bloom. In 2021 Mycetophilidae had an August bloom in both

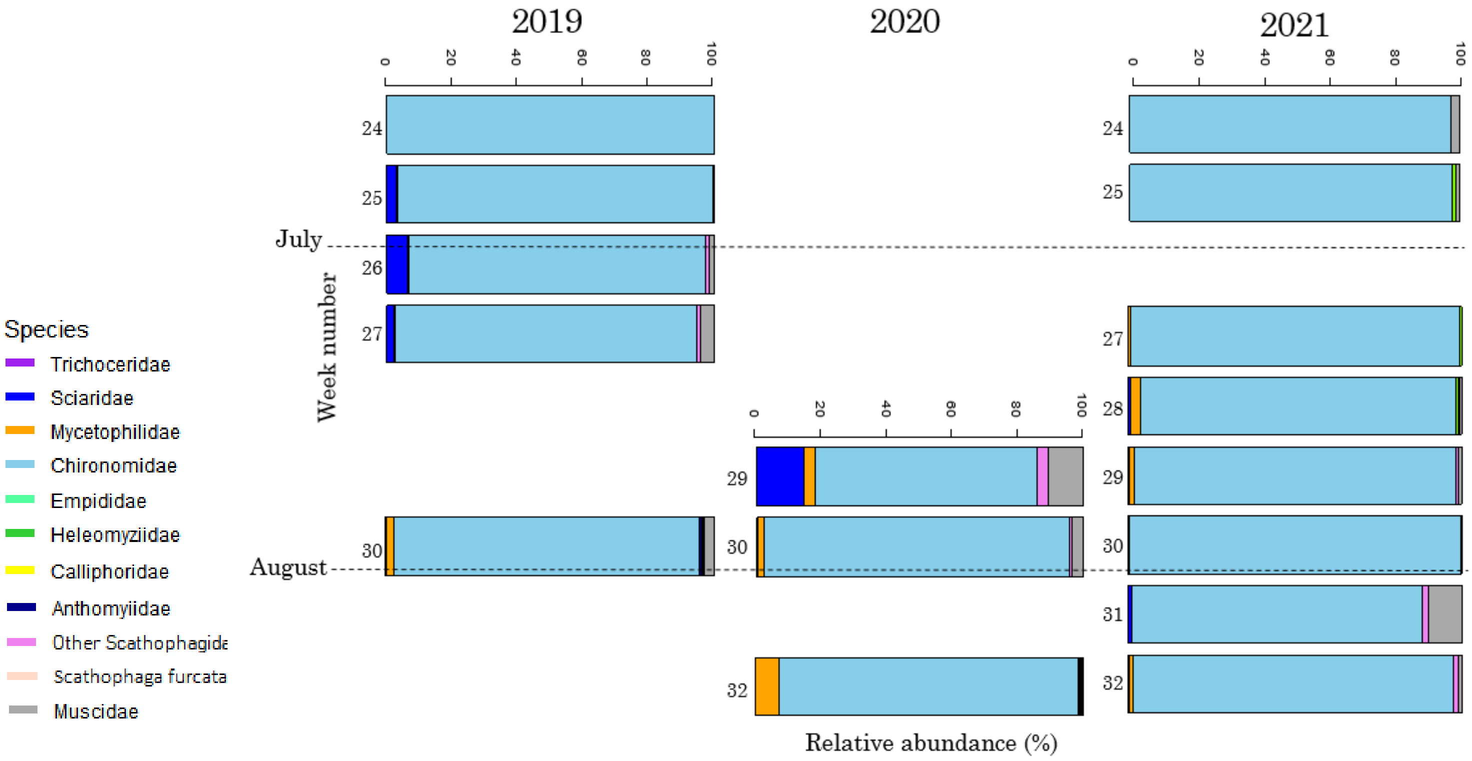


Figure 7. Bar plot the relative abundancy of Diptera families collected from malaise traps for the three study years in Bjørndalen, Svalbard. Each bar represents one sample, with each color presenting one Diptera family. Week numbers for data collection are written left of each sample.

pitfalls and malaise traps (Fig. 7b, Fig. 8). The only three families in the trap data that frequently contained individuals over >9 mm, were Muscidae, Scathophagidae and Calliophoridae. Trap material had a total of five Calliophoridae individuals 2019-2021, whereas Muscidae and Scathophagidae were abundant and showed similar abundance patterns (Fig. 9).

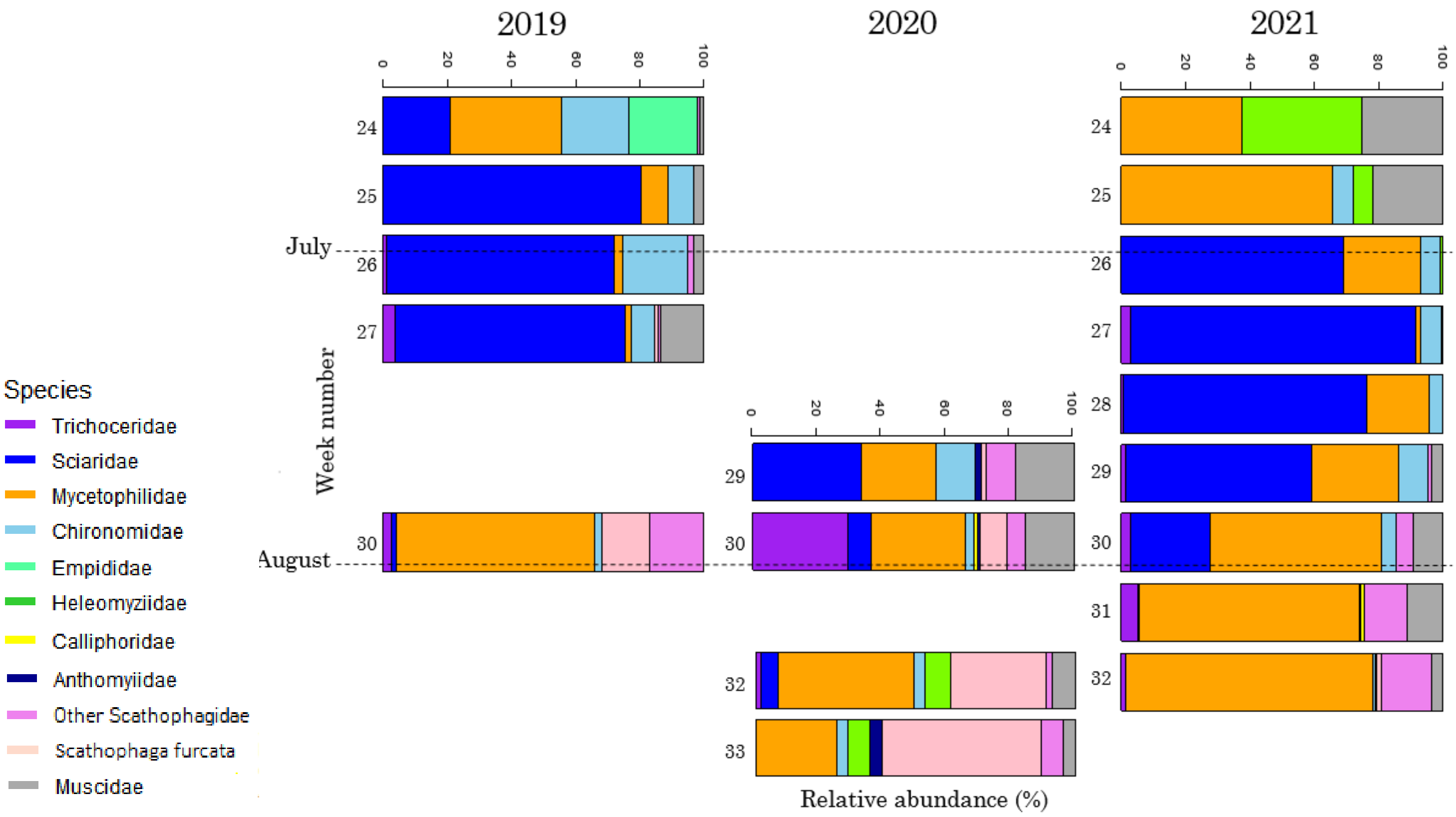


Figure 8. Bar plot of the relative abundancy of Diptera families collected from pit fall traps for the three study years in Bjørndalen, Svalbard. Each bar represents one sample, with each color presenting one Diptera family. Week numbers for data collection are written left of each sample.

2020 was only represented by material from the end of the season but differed in late season community by having low abundances of the Diptera families that were caught in high numbers 2019 and 2021, such as Mycetophilidae and Sciaridae (Fig. 8b, Fig. 9). For two late season families, Scathophagidae and Mycetophilidae, the sampling period did not capture the abundance peak either study year. Scathophagidae (N = 284) appeared in late July and had the highest abundance shortly after Muscidae at the end of each sampling period. The hairy species *Scathophaga furcate* accounted overall for 72.5 % of the Scathophagidae caught in traps (Fig. 10).

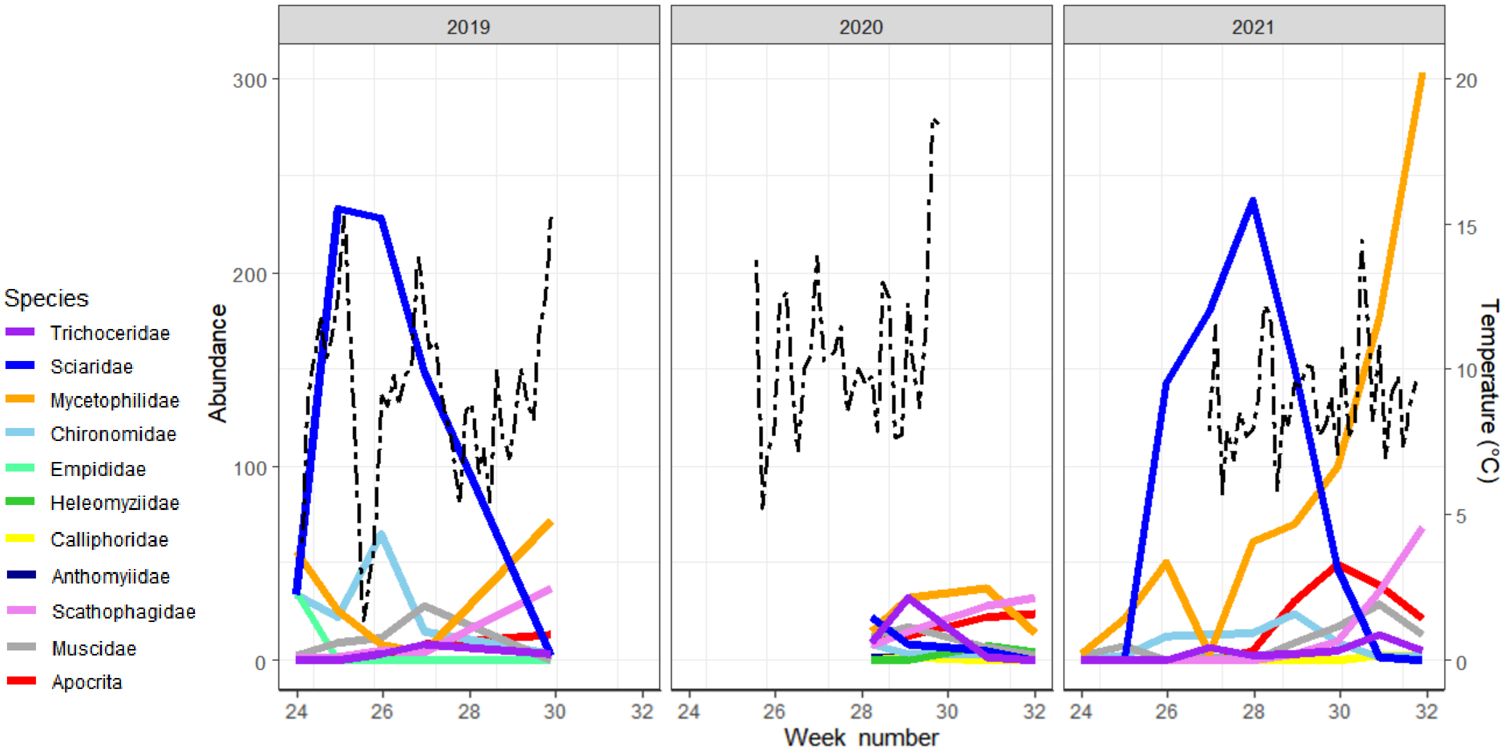


Figure 9. Abundance plot for Diptera trap data from pitfalls over time the three study years in Bjørndalen, 2019-2021. Camera-measured surface air temperature are shown with a dashed line.

For families that peaked in abundance within the study period in 2019, the peaks in 2021 were significantly delayed. The Arctic pollinator family Muscidae (N = 278) were present during the entire sample period with a relatively similar distribution and abundance all study years, but followed the general delay in timing on family level each study year (Fig. 9). Muscidae peaked in pitfall traps July 8th (week 27) in 2019, July 21st (week 29) in 2020, and as late as August 6th (week 31) in 2021, 30 days later than in 2019. Trichoceridae peaked likewise 30 days later, and the abundant families Sciaridae and Chironomidae both peaked three weeks later in 2021 than 2019 (22 and 24 days, respectively).

Figure 10. The predatory Scathophaga furcata seen through a stereo microscope with 10 times magnification.

4.3 Floral resources and cushion visitation

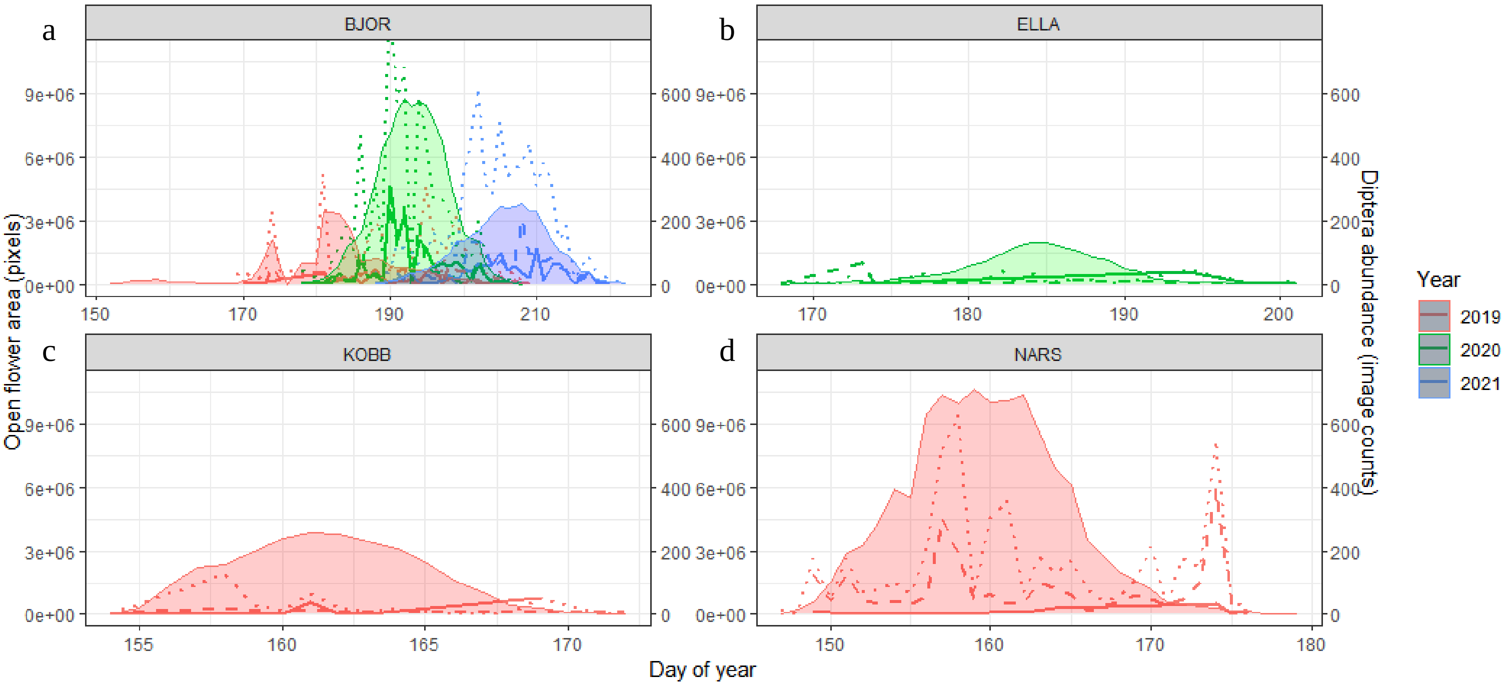


Figure 11. Seasonal flower area and Diptera annotations based on camera images. Total area of site-specific cameras per day of year is marked as filled areas. Lines represent the sum of Diptera and unidentified invertebrate counts (dotted lines), Diptera >9mm (solid line) and Diptera 5-9mm (dashed line), respectively.

Narsarsuaq covered the largest flower area per camera and the longest average flowering period of 27.5 days per camera, followed by Ella Ø with 25.4 days per camera. Kobbefjord had small cushions and the shortest flowering season (camera average of 21.6 days). Bjørndalen had a total average of 25 days per cushion but showed large variations between seasons. For the five continuous cameras in the Bjørndalen study period, the average flowering period varied from 29 days in 2019, to 21.4 days in 2020 (19.1 days with the extra 2020 cameras), and 24.6 days in 2021. The monitored cushions that continued in all seasons flowered in average 9 days later each year (Fig. 12).

Cushions in southern locations had earlier flowering onsets and withering (Fig. 11). The average cushions withered as early as June 24th (DOY 176) in Narsarsuaq, June 29th in Kobbefjord (DOY 180) and July 15th in Ella Ø (DOY 195). The flowering onset investigated in Bjørndalen 2019 started May 31st (DOY 151) but few flowers bloomed until June 21st (under 1,250,000 pixels, DOY 172, see Fig. 12).

In Bjørndalen 2019, the first visitor was registered June 17th (DOY 168), 17 days after the first flower appeared (Fig. 11a). In Greenland and the remaining study seasons in Bjørndalen, cushions were visited during the whole length of the flowering period (Fig. 11a-d). Bjørndalen 2021 had a short flowering season, but had despite this more floral resources available for visitors in the form of flower area and twice the numbers of visitors for the five continuous cameras as in 2019 and 2020. Ella Ø and Narsarsuaq both experienced a medium-sized Diptera visitation peak when there were barely any open flowers in cushions (Fig. 11bd). Greenlandic sites showed no clear patterns of visitor abundances corresponding with the increase in flowering area, as was the case for Bjørndalen and Narsarsuaq.

In Bjørndalen, Muscidae continued to increase in abundance after *S. acaulis* started to wither (Fig. 12). In 2021 Muscidae were present in pitfall and malaise samples early in the season but barely present (0-2 individuals per sample) until the abundance increased July 21st (DOY 202), 36 days after the first occurrence (June 16th, DOY 167).

From 2019-2021 the only peak in total trap caught Diptera abundance was found in 2019 (Fig. 12), thought several families had their peak before the end of the sample period in 2021. In 2019 Diptera in malaise and pit fall traps reached high numbers (<200 counts per weekly sample) as *S. acaulis* had flowering onset, but in 2021 Diptera became equally abundant three weeks before flowering onset and continued to increase in abundance after flower withering (Fig. 12).

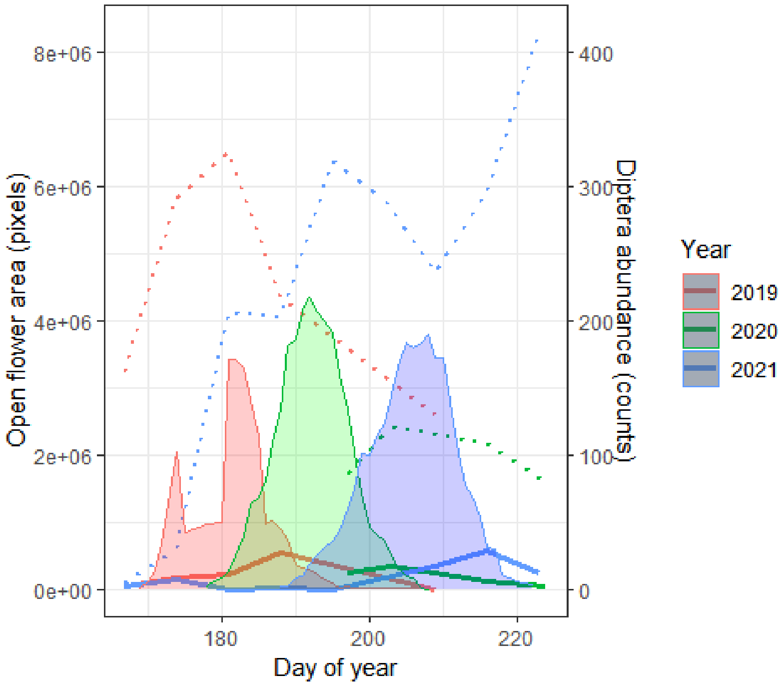


Figure 12. Total flower area and Diptera counts of the five continuous cameras in Bjørndalen 2019-2021. Lines represent counts for total Diptera counts (dotted lines) and Muscidae counts (solid lines). Flower area is marked as solid area.

4.4 Cushion visitors observed on flowers

Ten cameras had other flower species than *S. acaulis* within the camera frame (mainly *Cerastium ssp*. and *Bistorta vivipara*, Line Klausen pers. observation) (Table 6, Appendix 10), but visits to these flowers only took up a small fraction of the total visitation (*S. acaulis*: 6114, others: 149).

Table 6: Image-annotated taxa (mainly orders) and their location of observation. Locations are defined as on top S. acaulis flowers (flower), at other flowers than S. acaulis (other) or not at flowers (not flower).

Taxa	Position		
	Flower	Not flower	Other
Acari	26	632	0
Araneae	200	700	0
Apocrita	15	11	0
Coleoptera	60	179	1
Diptera	6114	9015	149
Lepidoptera	11	13	0
Symphyta	74	505	0
unidentified inv.	1769	4514	205

Symphyta were mostly counted in larvae stage on camera images and were together with low sample size (9 individuals in Bjørndalen traps 2019-2021, 579 at images, see Table 6) thought to be of less importance in the visitation of *S. acaulis* relative to Diptera. Apocrita had a total of 26 image observations (16 spotted on flowers, 10 of which were from Bjørndalen) and were likewise assumed to be of little visitation importance, despite being abundant in Bjørndalen surroundings (N = 337 for 2019-2021 trap material) and with a high percentage of flower visitation when present on cushion (59.26 % on average) (Table 6).

Of the cushion visitors were 31.4 % beetles observed on flowers (Coleoptera, N = 174), 22.2 % of spiders (Araneae, N = 900), and 36.1 % Diptera with the most flower targeted size category being >9 mm. Diptera were the most abundant flower visitors and showed a clear preference to *S. acaulis* cushions and flowers (Appendix 9) but were percentage wise not observed on flowers particular more often than other nectar sucking taxonomic groups. Camouflaged spiders, likely Thomosidae (Line Klausen, pers. observation), were observed hunting in *S. acaulis* flowers in investigated cushions in Narsarsuaq. Despite the association to nectar-sucking Chironomidae in malaise traps, Acari only showed a 4.0 % presence on flowers. Images and traps are believed to catch different Acari species, as image-annotated Acari were larger in size and a different color than trap-caught Acari, and trap-caught Acari mainly were Dipteran-born parasites (Line Klausen, personal observation).

Table 7: Model output for percentage Diptera visitors on flowers (Flower) per unit flower area (Area). The model output (a) represents estimate, standard error, t-value and p-value for each term in the model. Day of year and flower area were fitted using splines due the complex relationship shown (Appendix 8).

```
Fixed: Flower/Area ~ s(DOY) + Year + Abundance + s(Area) +
       Taxa + Site + Temperature
Random: ~1 | CameraID
```

```
Parametric coefficients:
                   Estimate Std. Error t value Pr(>|t|)
(Intercept)      -1.031e+01  1.956e-01 -52.701  < 2e-16
Year 2020         8.940e-01  8.610e-02  10.384  < 2e-16
Year 2021         6.738e-01  9.862e-02   6.832 1.01e-11
Abundance         1.325e-04  2.779e-03   0.048 0.961980
Taxa Diptera <5mm 1.817e-01  4.966e-02   3.659 0.000258
Taxa Diptera >9mm 3.773e-01  5.033e-02   7.497 8.53e-14
Site ELLA        -1.977e+00  4.653e-01  -4.248 2.22e-05
Site KOBB        -1.246e+00  7.111e-01  -1.752 0.079794
Site NARS        -1.305e+00  5.484e-01  -2.379 0.017435
Temperature       5.265e-02  1.173e-02   4.487 7.48e-06
---                         (Intercept)    Residual
CameraID             StdDev:   0.3039683 0.02357883
---
Approximate significance of smooth terms:
          edf Ref.df      F p-value
s(DOY)  8.626  8.626  45.12 <2e-16
s(Area) 8.108  8.108 214.00 <2e-16
---
R-sq.(adj) =  0.543
```

Percentage of Diptera visitors observed on flowers (percentage flower visits) followed a normal distribution with a minimum at flowering onset and withering (Fig. 13, 14). The larger the flower area and higher the air temperature, the larger the proportion of cushion visitors were present on flowers (Table 7). Dynamics varied between sites and years, with the lowest percentage flower visits in Narsarsuaq and Ella Ø (Table 7).

Bjørndalen showed an overall decrease in percentage flower visits each year during the study period (Fig. 13). 2019 had a long flowering season with a generally high percentage of flower visits (34.4 % of all cushion visits). 2020 had a shorter flowering period with 29.4 % flower visitation and 2021 had many flowers, but a low percentage flower visits at only 14.8 %.

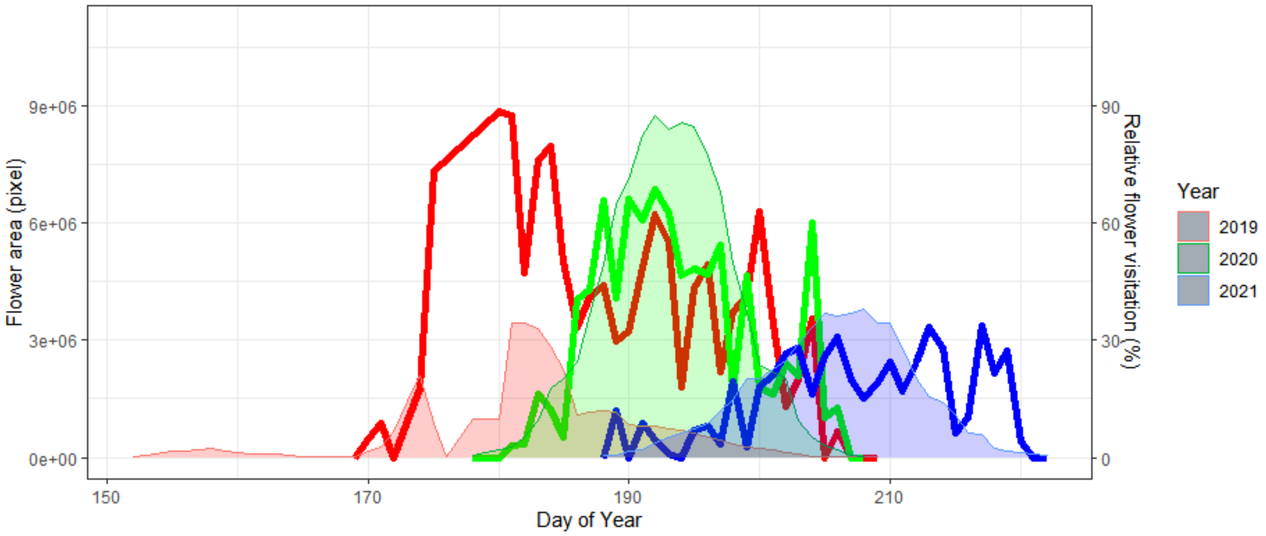


Figure 13: Bjørndalen flower area (filled areas) and the daily average of the percentage flower visitation (lines) based on the total Diptera image-observation 2019-2021. Area on camera images with open flowers are summed and with increased numbers in 2020 where four more cameras were installed.

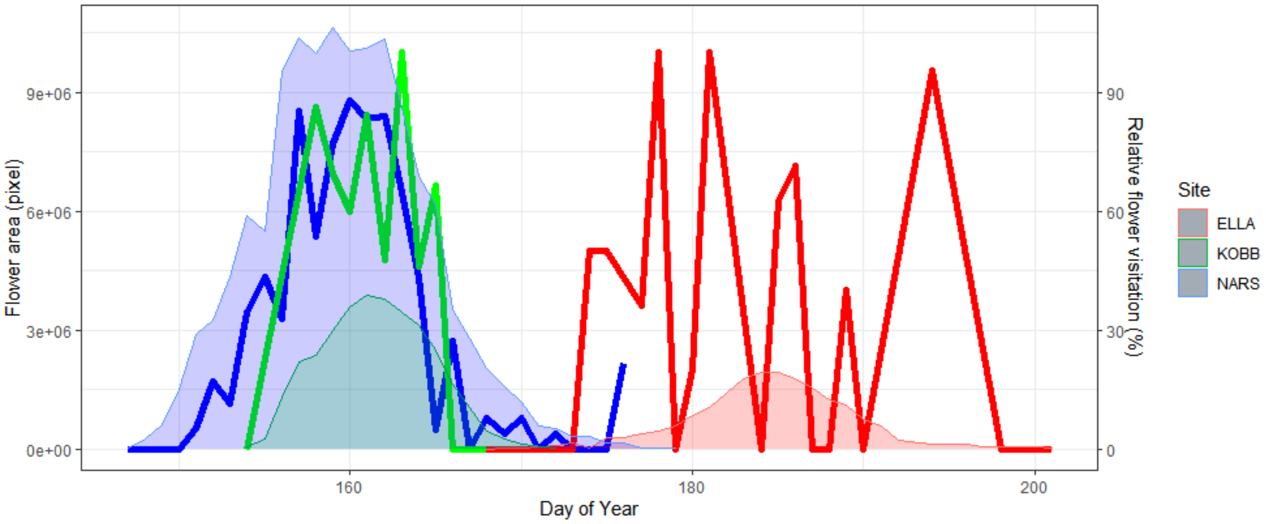


Figure 14: Summed image-annotated flower area (filled areas) and the daily average of the percentage flower visitation (lines) in Greenlandic study sites. All Greenlandic camera sites had two cameras installed.

Kobbefjord and Narsarsuaq had similar timed flowering events and showed similar trends in percentage flower visits with the highest relative flower visit June 8th (DOY ≈ 160). Ella Ø had several days without flower visitation and a low total visitor abundance. Following, Ella Ø got a ruptured pattern, which ranged from 0 to 100 % of cushion visitors observed on floweres several times during the study period (Fig. 14).

5 Discussion

This study revealed highly complex visitation patterns of *Silene acaulis* by arthropods belonging to several taxa and strong trends in the percentage of cushion visitors that were observed on flowers. At all sites Diptera were the most abundant cushion and flower visitor with medium-sized Diptera (5-9 mm) being the most abundant size category, but also the least observed category on top of flowers per unit flower area. Both Diptera visitator abundance and percentage of Diptera observed on flowers were strongly correlated with flower area, and this relationship with flower area changed with seasonal progress, study site and year. In Bjørndalen the percentage of Diptera observed on flowers per unit flower area significantly decreased over the study years 2019-2021, at the same time as the visitor abundance increased and the Diptera abundance from invertebrate traps became abundant later in relation to the flowering onset.

5.1 Trophic cushion systems

Diptera were in overall numbers the most abundant visitors on *S. acaulis* at Svalbard and Greenland. In Adventdalen valley, that neighbors the Bjørndalen valley, Gillespie & Cooper (2020) found 11 Diptera families by looking at 19 different plant species. The 10 Diptera families caught by traps in Bjørndalen are likely representative of the local Diptera community. Size class is a simplistic approach for classifying Diptera, as images without measurements bands or something relatable in size are highly subjective. Diptera also show large variety between as well as within families and species (Tiusanen et al., 2016; Meagan, 2013). Chironomidae and Sciaridae both showed both abundances and are rather small in size. Individuals have likely been categorized as unidentified invertebrates or Diptera <5 mm when visiting. The numbers of very small Diptera found on images in this study would have been close to impossible to spot and accurately count by traditional observations in field, and may be underrepresented by traditional observation methods. In Bjørndalen trap material only individuals from the Scathophagidae, Calliphoridae, and Muscidae families were large enough to contribute to the largest Diptera size group in images (>9 mm). Calliophoridae likely made an insignificant proportion of large Diptera visits due to very low abundances in trap material, whereas Scathophagidae and Muscidae had higher abundancies and likely made up most of the large visiting Diptera.

The lack of spiders present in Svalbard images compared to Greenlandic images may have been exaggerated by the fact that spider species in Svalbard tend to have smaller body sizes than Greenlandic species. For instance, there are no wolf spiders found in Svalbard which are the largest spider species in Greenland. This makes individuals less likely to be spotted during image review. Acari, (N = 658) had 95.9 % observations other places than at flowers. This indicates that Acari were on *S. acaulis* due to other resources than floral resources. Acari on Svalbard have been reported to have higher densities close to vegetation cover than on bare ground (Gwiazdowicz & Coulson, 2020; Molenda et al., 2012). The Acari observed may be using *S. acaulis* cushions as shelter and hunting grounds. Similarly, Molenda (2012) found *S. acaulis* cushions with a high visitor abundance of Diptera, spiders and Acari in Canada by vacuuming cushions, suggesting that this is a circumpolar trend. Symphyta in this study were mostly found in larvae state, supporting the use of *S. acaulis* as nursing ground. The many trophic functions of visitors found in this study, support a complex cushion-wise microsystem with several trophic levels as suggested in hypothesis (i).

5.2 Flower attracted taxa

Diptera visitor abundance and percentage observations on open flowers were proportional to the cushion area covered with floral resources. In addition the abundance and percentage flower visitors per unit flower area were impacted by both seasonal progress, year, and site. Nectar sucking taxa except Symphyta had a higher percentage flower visitation than non-nectar sucking taxa, likely due to flower attraction. However, Diptera was the only abundant nectar sucking taxa with a high percentage flower visitation (40 %), indicating that the visitation was majorly due to floral attraction as predicted in hypothesis (ii). This was however a lower percentage flower visits of the observed cushion visits than would be the case, if floral resources were the only attractant. As described in section 2.3, some Diptera families such as Scathophagidae, do not feed on floral resources but rather use flowering plants as hunting grounds. In Bjørndalen Scathophagidae has been observed as a common visitor to *S. acaulis* that often hang around flowers waiting to ambush prey (Geir E. E. Søli, personal obs.). Species with similar ecology as the Scathophagidae family may lower the percentage of cushion visitors observed on flowers. As the visitor abundance increased in 2020 and 2021, flowers may be nectar depleted during high visitation rates, leading to decreased flower attraction by visitors. This is thought unlikely to be the cause, as visitor abundance were not found to have a statistically significant effect on percentage flower visits per unit flower area. A potential bias to the percentage flower visitors, is that all arthropods on images were annotated instead of only those present on *S. acaulis* cushions. Some individuals may have been trespassing and been counted even they were not attracted to nor targeting the cushions. Most investigated cushions had barren surroundings on camera images and observations were clustered at *S. acaulis* cushions (Appendix 9), likely diminishing this impact on the results.

5.3 Changes in flower attraction with flowering delay

Høye et al. (2013) found that *S. acaulis* has shorter flowering period with increased mean summer temperatures. Bjørndalen had a decreased flowering period from 2019 to 2021 even though the temperatures did not increase**.** Despite the shorter flowering period in the investigated cushions, the floral resources available for visitors in the form of flower area increased. Likewise, visitors increased in abundance to twice the numbers in 2021 compared to 2019 and 2020, with 38 % (2021) and 24 % (2020) more visitors per unit flower area than in 2019, respectively. This suggests that the quantity of floral resources is more important in attracting Diptera to the cushion than the time of available resources.

Opposite to the increase in visitor abundance, the average percentage of visitors present on flowers in Bjørndalen decreased from 34.4 % in 2019, 29.4 % in 2020, to only 14.8 % in 2021. During the study period, the flowering season peaked ~15 days later and the general delay in Diptera families was 3-4 weeks. The delay in the flowering period could have caused a temporary offset between *S. acaulis* and surrounding flower visitors, which gave rise to a behavioral change on cushions. Normally with early flower plants, later flowerings increase the overlap with more competitive plants. In Bjørndalen, the study site was next to a study site of *Dryas octopetala* (UNIS, 2021). *S. acaulis* generally blooms before *D. octopetala* and receives a reduction in pollination services when *D. octopetala* blooms (Tiusanen et al., 2020).

Diptera are known to have large annual and spatial variation. Environmental changes such as warmer temperatures create an increasingly large possibility for temporal uncoupling between trophic links**.** A reduction in fruit set of *S. acaulis* reduces the recruitment and as a consequence reduce the nurse- and pioneer plants, which effects the diversity and abundance of organisms from the trophic levels related to *S. acaulis* services.

The accuracy of the yearly Diptera dynamics compared to *S. acaulis* flowering would have been more accurate if samples had been obtainable from the whole 2020 season and started earlier in 2019 to catch the beginning of the Diptera abundance increase. Also, 51% of image annotations missed visitor location due to an unknown error, which may have significantly altered the results**.** Variable and contradictory responses are common when time series are not available (Gillespie et al., 2020; Høye et al., 2021) and the margin for error given a short, inconsistent study window is large. Our results suggest that the surrounding Diptera community effects both the *S. acaulis* visitation abundance and the percentage flower visitors as predicted by hypothesis (iii), but more complete time series from 2020 and preferably other years in addition would be needed before trends could be concluded.

5.4 Challenges with the image accuracy

The number of visitors in Diptera communities at both Ella Ø and Kobbefjord widely fluctuated. These two sites had a low sample size and the lowest visitation frequency per unit flower area, which likely were a significant cause of the variance together with weather factors. Visitor bias from other flower species have had little effect in the study of *S. acaulis* in images (3.03 % of all visits, Appendix 9), although some cameras had other flower species in their recording. Instead, a part of the variance between sites may also have been affected by behavioral differences between and within species at sites, as it was not possible to track individual visitors through images. Some visitors were likely not detected, and some were detected several times. More frequent data recordings will significantly increase the data amount and detection of flies.

The number of pixels with open flowers is also not able to quantify the quality or precise quantity of nectar- and pollen resources, but higher image resolution may increase accuracy in quantification of floral resources by flower recognition. The image resolution allowed this study's most abundant visitors, Diptera, to be detected to size categories. Size categories were strongly biased by the annotator's perception of size and variances in the vegetation size and should therefore be seen as broad estimates. Furthermore, image quality was affected by light intensity and clouded days increased the difficulty of detecting small visitors by long shutter speed and motion blur. Light intensity was though not included in models due to a lack of available data. Dark coloration gives a high contrast when sitting on bright-colored flowers such as *S. acaulis* petals compared to dark colored vegetation and dirt. This is especially challenging with small visitors, in which abundance may have been underestimated outside of *S. acaulis* flower area. During annotations, small Diptera may further have been misidentified with Coleoptera that are known to visit *S. acaulis* flowers (Jones

& Richards, 1962; Lundbye et al., 2012). With higher image resolution it is unlikely that species identification of small black Diptera are allowed to species level, but resolution may allow identification to more accurate identification than in this study, potentially to low taxonomic levels.

5.5 Weather factors

Average wind speed at noon and daily precipitation in Bjørndalen were not found to have an effect on the visitor frequency and the visitor frequency per unit of floral resources. Most studies of visitor frequency have found the opposite, as pollinators tend to avoid bad weather and be more active with less wind and precipitation (Totland, 1994). The total precipiation measured in this study was very low, and may have been insufficient to uncover Diptera reactions. The lack of response to weather variables may also be due to Diptera having a quicker reaction time to localized weather than meassured in this study, where windspeed and precipitation were measured 5 km from study site.

Camera-measured surface air temperatures in Ella Ø had a daily average above 30°C three times during the 33 days study period in 2020 and a total average of 23.5°C. This seems unlikely since the average July surface air temperature the same year in Ittoqqortoormiit, 280 km SSE from study site, were 5.6°C (DMI, n.d.). Unfortunately, a polar bear destroyed the installed weather station making it impossible to validate the measured camera temperatures. Temperature differences between the camera measurements in Bjørndalen and Svalbard Airport Weather Station were the largest at warm days (Appendix 4. Fig. b), and we suggest that the camera cases may have had a slight greenhouse effect. However, this effect would not be strong enough to explain the differences in temperature measurements between cameras in Ella Ø and the weather station in Ittoqqortoormiit. Higher surface air temperatures are known to increase pollinator activity at *S. acaulis* (Bergman et al., 1996; Totland, 1994) even though the midnight sun lowers temperature association (Djuberg, 2021). In Svalbard, only Mycetophilidae seemed to be affected by surface air temperatures with two visible declines in 2019 and 2021 during periods of low temperatures (Fig. 5). The high temperatures measured in Ella Ø and Kobbefjord, together with low visitation frequency, may have been what caused model estimates of temperature in Table 4 and Table 5 to have a negative effect on visitation abundance. However, surface air temperature also showed to have a negative effect on visitation abundance in relation to the available floral resources for the cameras in Bjørndalen (Table a in Appendix 5). A lack of other environmental factors may have stressed the effect from temperature, although it does not explain negative correlations. Some environmental factors such as soil humidity and snow melt were not included despite previous findings showing significant influence on arthropod timing, development, and abundance (Gillespie et al., 2020). A lack of abiotic parameters may have caused the models to be inaccurate in regards of temperature.

5.6 Outlook

Deep neural network models for automatic species and flower detection may provide a breakthrough in monitoring extent and accuracy with decreased data cost in time and logistics. Cameras can observe visitors in space and time, and model training with manual image-annotations may facilitate algorithms to automatically differentiate between arthropod taxa and estimate floral resources in the form of open flowers over time. This can aide large-scale flower visitor monitoring, detect changes in visitation dynamics, and thereby increase the knowledge of climatic impacts on visitor patterns. In this analysis two out of three study sites in Greenland experienced large variation possibly due to limited image-based observations. This variation indicates that under Arctic conditions two cameras are often not enough to capture visitation trends of *S. acaulis* over time. Future studies are encouraged to use more than two cameras at study sites, and a large monitor with high image resolution during invertebrate identification and numbering.

Our use of time-lapse cameras and arthropod time series provided a new look at Arctic visitation dynamics of *S. acaulis* cushions. We found that the available floral resources measured as pixels with open flowers can explain a significant proportion of Diptera visitation dynamics, both in terms of taxa diversity and behavior while visiting. Furthermore, the percentage of *Diptera* visitors observed on flowers per unit flower area declined during the three-year study period, possibly affected by a simultaneous delay in the seasonal onset and increased competition between flowering species to attract visitors. Investigating visitation frequencies as a product of flower area and in relation to local fly abundances, can with long time series show accurate responses in visitation dynamics to changes in flowering periods. Future research is encouraged to focus on the development of appropriate algorithms to enable large-scale monitoring, and account for the increased attraction to growing floral resources when studying flower visitor dynamics.

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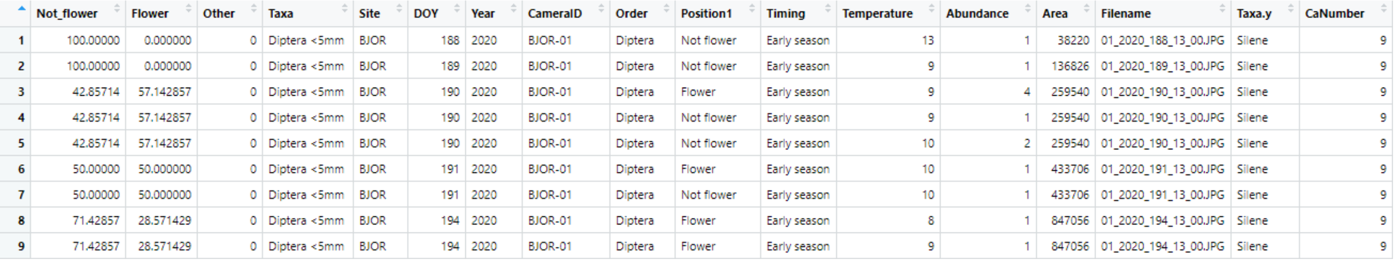
Appendix 1

Camera ID and usage at the four study sites. Year(s) of usage is marked by an X.

Site	Camera-ID	2019	2020	2021
Bjørndalen	BJOR-01	X	X	
	BJOR-03	X	X	
	BJOR-04		X	X
	BJOR-05			X
	BJOR-09	X	X	X
	BJOR-11	X	X	
	BJOR-13	X	X	X
	BJOR-16		X	
	BJOR-17		X	
	BJOR-18		X	
Ella Ø	ELLA-03		X	
	ELLA-08		X	
Kobbefjorden	KOBB-04	X		
	KOBB-12	X		
Narsarsuaq	NARS-14	X		
	NARS-20	X		

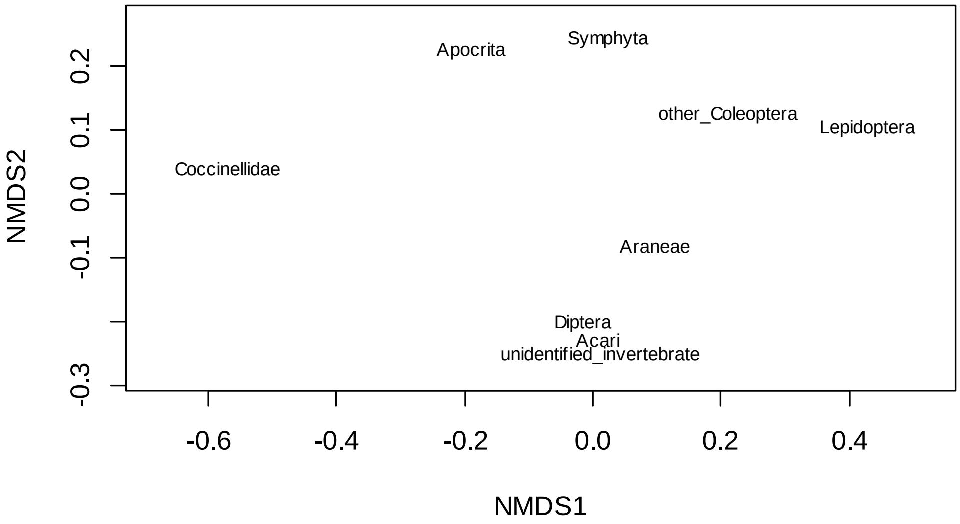
Appendix 2

The first rows of the data frame obtained from camera images, upon which the models were build.



	Not_flower	Flower	Other	Taxa	Site	DOY	Year	CameraID	Order	Position1	Timing	Temperature	Abundance	Area	Filename	Taxa.y	CaNumber
1	100.00000	0.000000	0	Diptera <5mm	BJOR	188	2020	BJOR-01	Diptera	Not flower	Early season	13	1	38220	01_2020_188_13_00.JPG	Silene	9
2	100.00000	0.000000	0	Diptera <5mm	BJOR	189	2020	BJOR-01	Diptera	Not flower	Early season	9	1	136826	01_2020_189_13_00.JPG	Silene	9
3	42.85714	57.142857	0	Diptera <5mm	BJOR	190	2020	BJOR-01	Diptera	Flower	Early season	9	4	259540	01_2020_190_13_00.JPG	Silene	9
4	42.85714	57.142857	0	Diptera <5mm	BJOR	190	2020	BJOR-01	Diptera	Not flower	Early season	9	1	259540	01_2020_190_13_00.JPG	Silene	9
5	42.85714	57.142857	0	Diptera <5mm	BJOR	190	2020	BJOR-01	Diptera	Not flower	Early season	10	2	259540	01_2020_190_13_00.JPG	Silene	9
6	50.00000	50.000000	0	Diptera <5mm	BJOR	191	2020	BJOR-01	Diptera	Flower	Early season	10	1	433706	01_2020_191_13_00.JPG	Silene	9
7	50.00000	50.000000	0	Diptera <5mm	BJOR	191	2020	BJOR-01	Diptera	Not flower	Early season	10	1	433706	01_2020_191_13_00.JPG	Silene	9
8	71.42857	28.571429	0	Diptera <5mm	BJOR	194	2020	BJOR-01	Diptera	Flower	Early season	8	1	847056	01_2020_194_13_00.JPG	Silene	9
9	71.42857	28.571429	0	Diptera <5mm	BJOR	194	2020	BJOR-01	Diptera	Flower	Early season	9	1	847056	01_2020_194_13_00.JPG	Silene	9

Appendix 3



NMDS plot of the visitor communities, (mostly orders, stress = 0.06) at the four sites. Orders with less than 10 counts are excluded.

Appendix 4

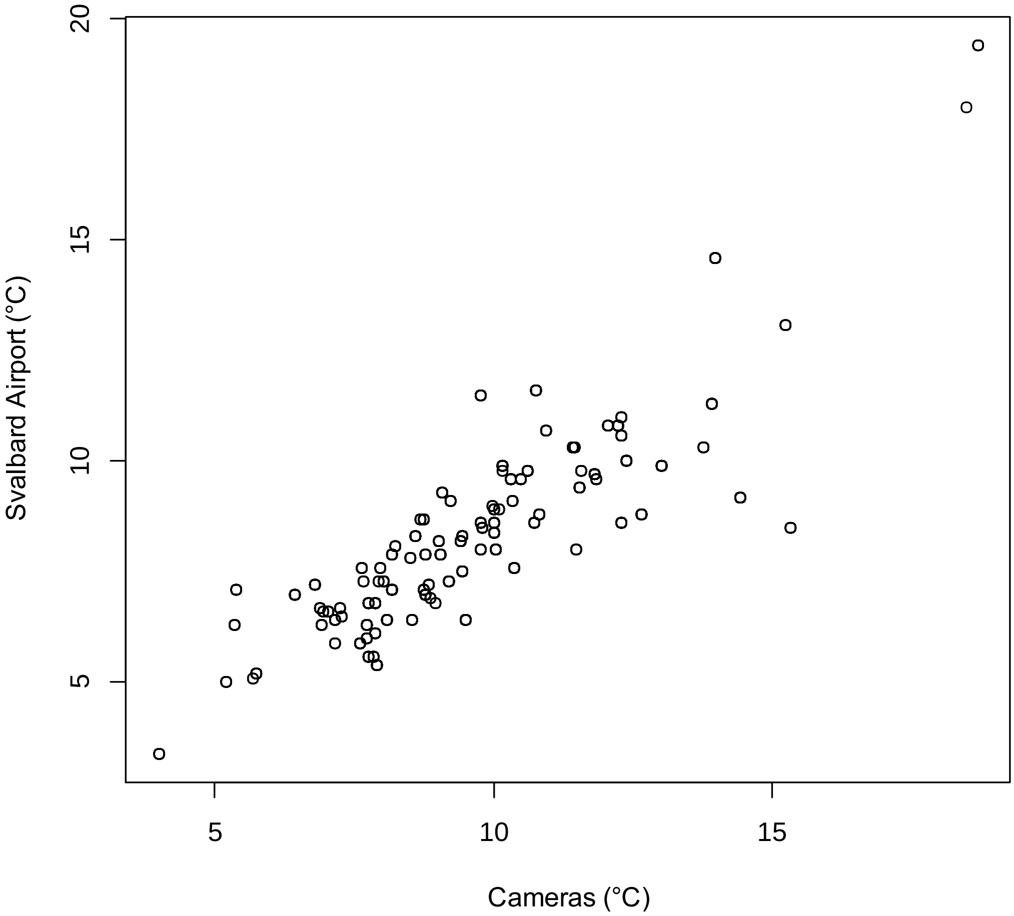


Figure a. Correlation between temperatures measured by cameras in Bjørndalen and Svalbard Airport weather station. Axis labels show temperature origin.

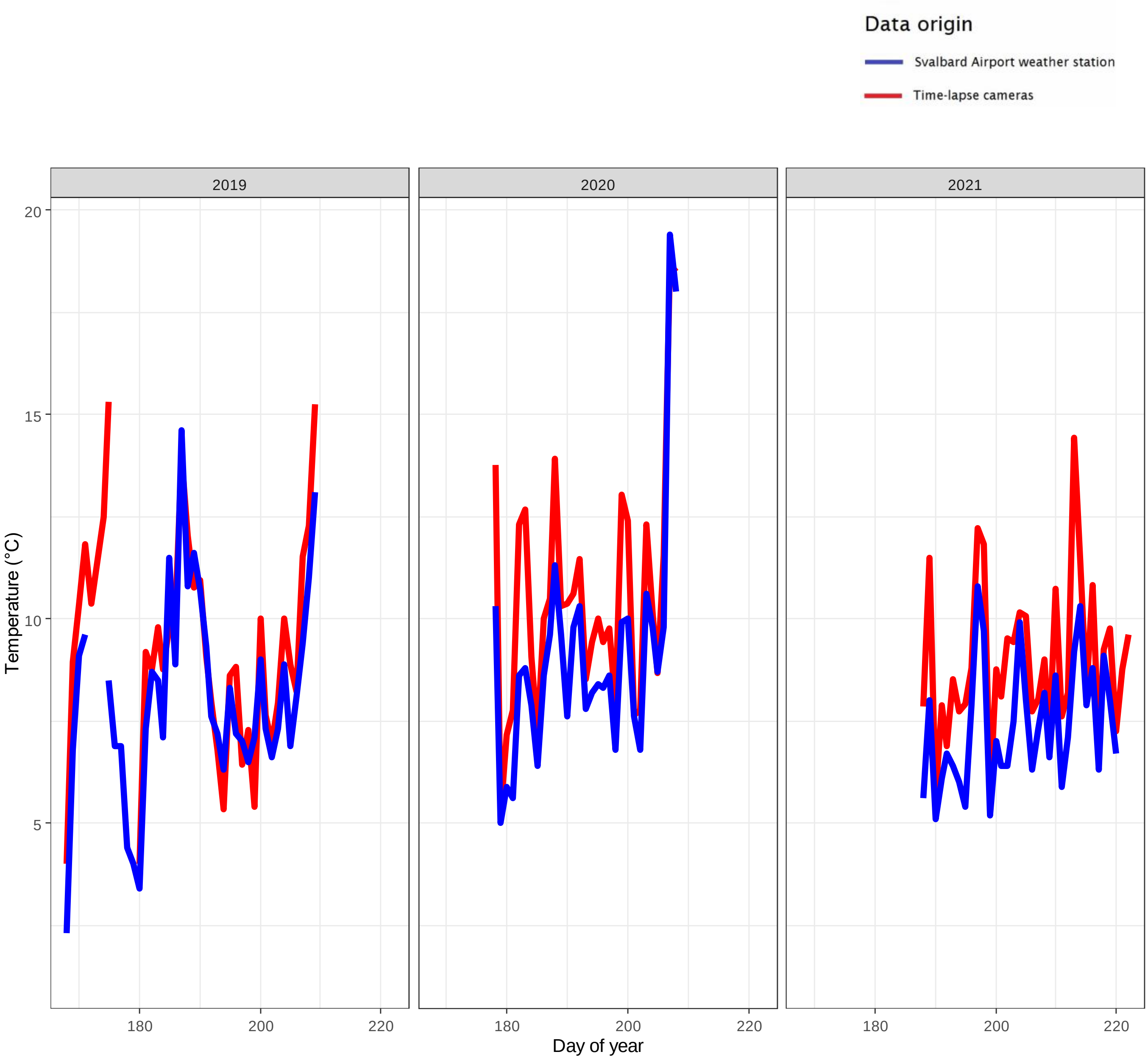


Figure b. Accuracy of camera-measured temperatures. The average of camera-measured temperatures during the study period 2019-2021 are indicated with red lines. Temperatures measured at Svalbard Airport weather station (red lines) are assumed to be accurate.

Appendix 5

Table a. Model outputs for Diptera visitor abundance per unit flower area in Bjørndalen. The table represents estimate, standard error, t-value and p-value for each term in the model. Day of year and unit flower area were fitted using splines due the complex relationship shown in Appendix 5 Fig. ab.

```
Fixed:  (Abundance/Area) ~ s(DOY) + Year + s(Area) + Taxa + Windspeed +
            Temperature + Precipitation
Random: ~1 | CameraID
```

```
Parametric coefficients:
                  Estimate Std. Error t value Pr(>|t|)
(Intercept)       -9.96827    0.16616 -59.993  < 2e-16
Year 2020          0.38442    0.08131   4.728 2.39e-06
Year 2021          0.37974    0.08618   4.406 1.09e-05
Taxa Diptera <5mm -0.11149    0.06129  -1.819    0.069
Taxa Diptera >9mm  0.08328    0.06314   1.319    0.187
Windspeed         -0.01829    0.01158  -1.579    0.114
Temperature       -0.06896    0.01286  -5.363 8.91e-08
Precipitation      0.01704    0.02784   0.612    0.541
---                          (Intercept)  Residual
CameraID                StdDev: 1.729979e-131 0.0118851
---
Approximate significance of smooth terms:
          edf  Ref.df       F p-value
s(DOY)   7.32    7.32   14.33  <2e-16
s(Area)  8.06    8.06  202.51  <2e-16
---
R-sq.(adj) =  0.289
```

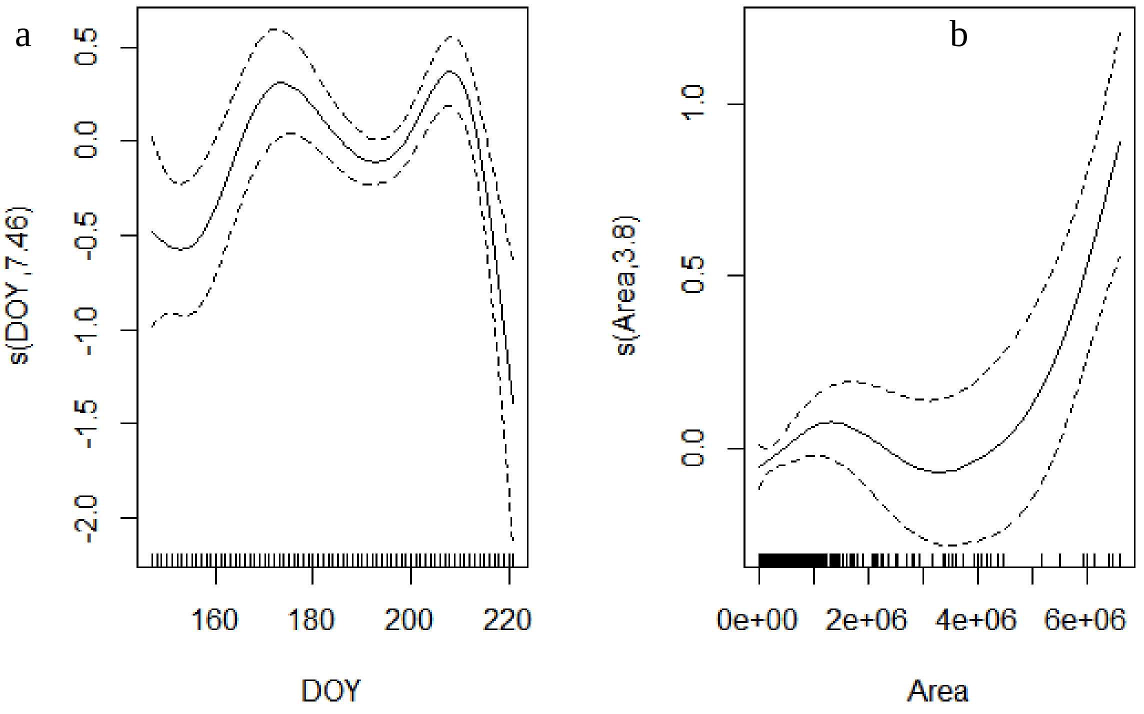
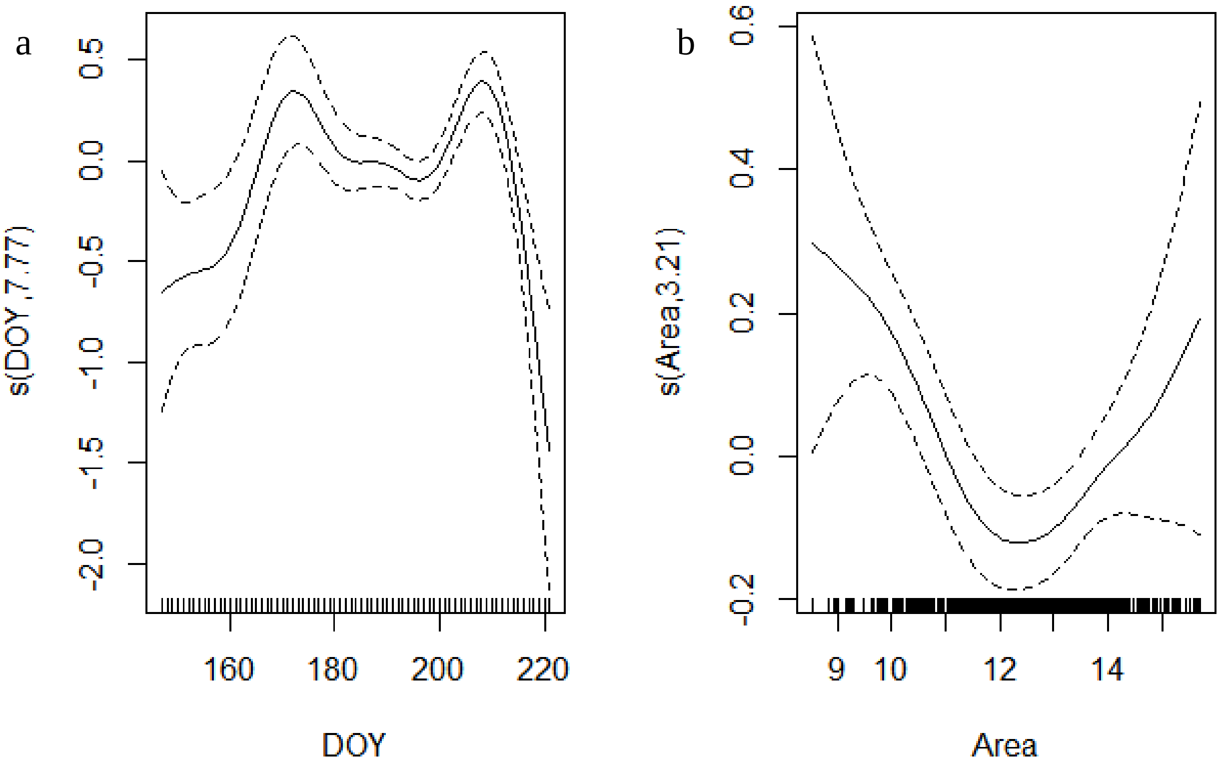


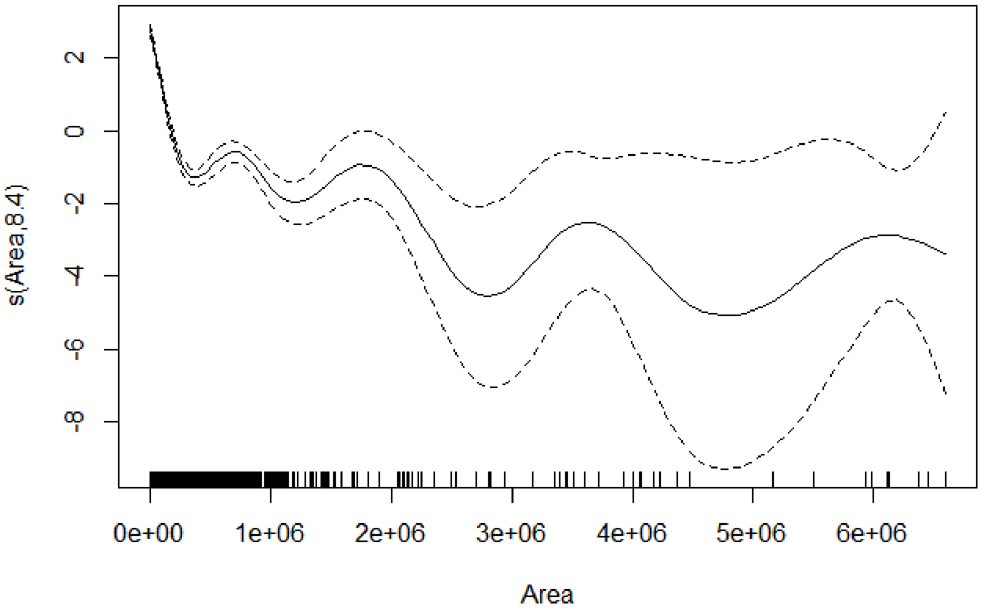
Figure ab. Plots for the relationship between explanatory variables and their splined function in Appendix 5 Table a, for Diptera visitor abundance per unit flower area in Bjørndalen. The spline based smoothed variables are plotted against the corresponding variables Day of year, DOY (a) and unit flower area, Area, (b) to check for complex associations.

Appendix 6



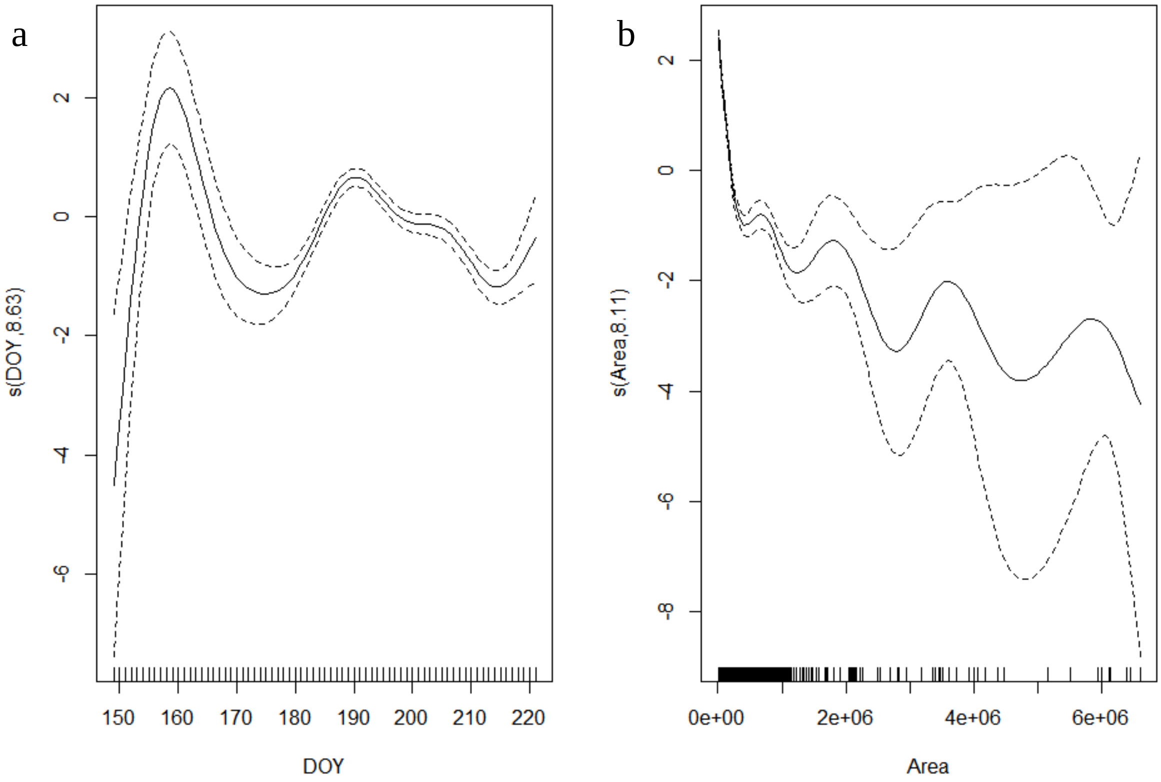
Plots for the relationship between explanatory variables and their splined function in Table 4 for Diptera visitor abundance from camera images. The spline based smoothed variables are plotted against the corresponding variables Day of year, DOY (a) and unit flower area, Area, (b) to check for complex associations.

Appendix 7



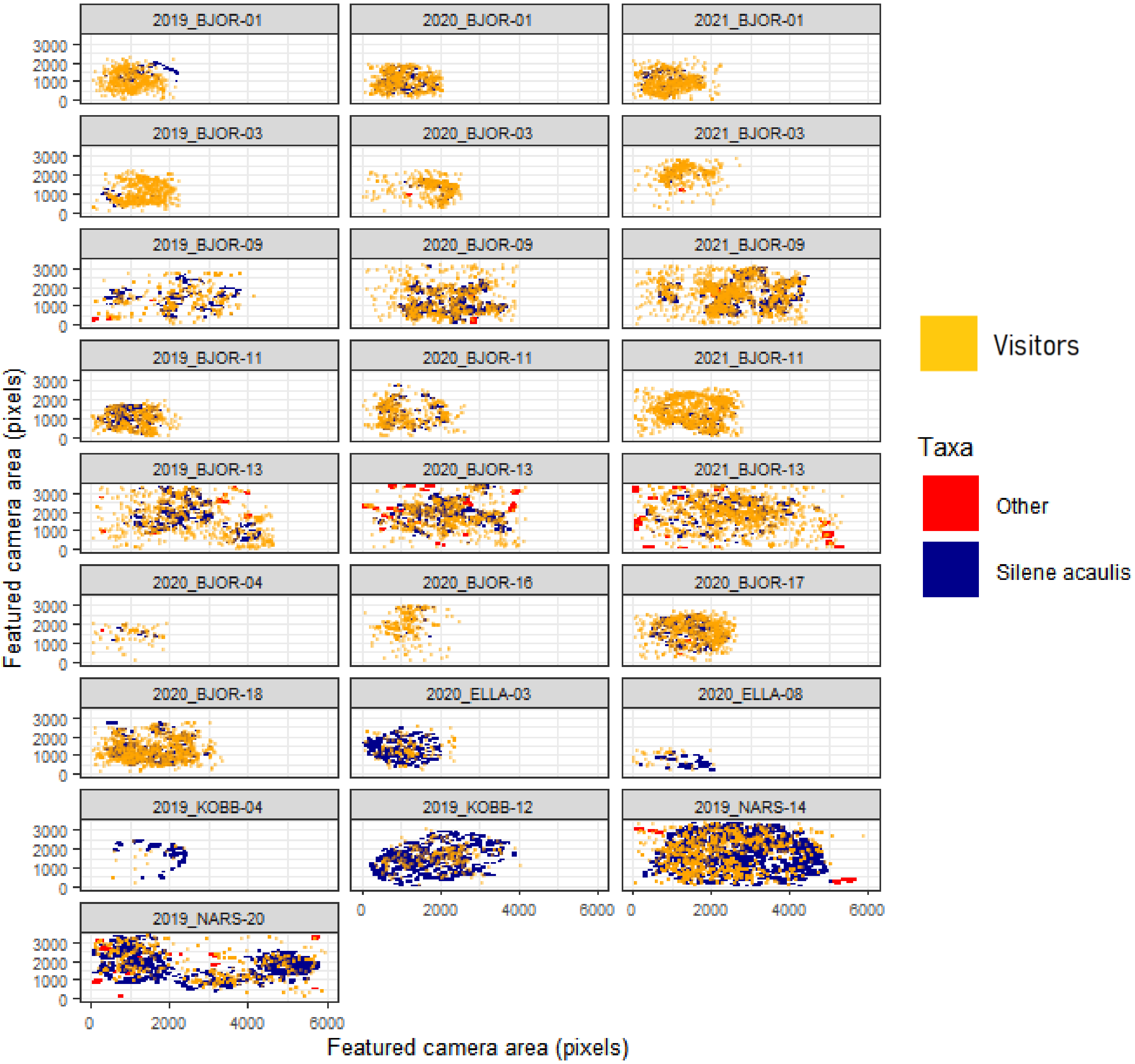
Plot for the relationship between the explanatory variable unit flower area (Area) and the splined function of this for the model of Diptera visitor abundance per unit flower area, Table 4.

Appendix 8



Plots for the relationship between explanatory variables and their splined function for the model for percentage visitors observed on flowers per unit flower area, Table 7. The spline based smoothed variables are plotted against the corresponding variables Day of year, DOY (a) and unit flower area, Area, (b) to check for complex associations.

Appendix 9



Accumulated spatial Diptera visitor and flower location on camera images for each individual camera at a given site and year. Annotations are shown in area (pixels) covering the images and is the accumulated area of flowers blooming at any time. Annotated areas show open S. acaulis flowers (blue area) and open flowers from other ssp. than S. acaulis (red area). Headlines over each accumulated image annotations, show year, site, and camera ID for the annotations. The abbreviations for the four sites are Narsarsuaq (NARS), Bjørndalen (BJOR), Ella Ø (ELLA), and Kobbefjord (KOBB).