UNIVERSITY OF GOTHENBURG

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DECADAL TRENDS IN ARCTIC BUMBLEBEE FLORAL PREFERENCES

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Abstract

Arctic warming is occurring at a rate two to three times faster than the global average, causing potential ecological consequences such as changes in community composition and shift in plant phenology. Both plants and pollinators are affected by phenological changes which may create a phenological mismatch between the pollinators and the plants they visit. However, it is unclear how bumblebees, being key pollinators of most Arctic plant species, are responding to these changes. To evaluate shifts in floral preferences over the three decades, a comparative study design which included field observation and microscopy analysis of samples collected in the field was used. Data on bumblebee foraging collected from Latnjajaure in the 1990s was compared with data collected during summer 2025. Pollen was collected from 65 queen bumblebees of six different species across the entire Latnjajaure valley. The phenology and abundance of the flowering species were estimated in three plots overlapping the area in which the historical floral data was recorded. The results show a change in the bumblebee foraging niche as *Saxifraga oppositifolia* a dominant early-season resource in the 1990s was absent from 2025 pollen loads. In contrast, *Salix*, a deciduous shrub emerged the early-season resource in 2025. This transition was accompanied by a significant contraction of the foraging niche as the median Shannon diversity Index (H') dropped from 0.596 to 0.068. This narrowing shows high foraging constancy towards high-rewarding species such as *Astragalus alpinus*. While early flowering may affect the reproductive success of forbs like *Saxifraga opp.*, the increase of shrubs such as *Salix* may provide the structural resilience necessary to maintain the plant pollinator network in the Arctic.

Keywords: Arctic, Bumblebees, Floral Preferences, Climate Warming, Phenological Mismatch, Foraging Niche

Introduction

The Arctic is warming at a rate two to three times faster than the global average (Rantanen et al., 2022) and this is leading to noticeable ecological consequences such as changes in vegetation, flowering time and shifts in plant phenology (Albertsson, 2024; Bjorkman et al., 2020; Collins et al., 2025). Early snowmelts and warmer summers have influenced flowering times (Cirtwill et al., 2023; Collins et al., 2025; Post et al., 2009), which can in turn affect pollinator activity and potentially create phenological mismatches between the plants and the pollinators. As pollinators play a vital role in facilitating reproduction in many flowering plants (Ollerton et al., 2011), these disruptions can lead to a reduction in the pollinator community, decrease in plant reproductive success (Andresen, 2019; Pyke et al., 2016) affecting food cycles and ecosystem resilience.

Bumblebees are key pollinators for many arctic and alpine plants (Cirtwill et al., 2023; Stenström & Bergman, 1998) and in the northern hemisphere are considered as the most important pollinators (Kudo et al., 2025). Their thick fur and long tongue give them the ability to forage in cold environments and visit deep flowers, making them key contributors to reproductive success in many Arctic plants. Given their crucial role in Arctic pollination, understanding how bumblebees are responding to the current changes in climate and phenology is essential for predicting ecosystem stability. Despite evidence that species composition and flowering phenology are changing in the Arctic, currently, it is unclear how the bumblebees are responding to the altered flowering conditions regarding their floral preferences. Understanding these responses is crucial because bumblebees are essential for ensuring seed set thus reproduction in most arctic plants (Cirtwill et al., 2023; Stenström & Bergman, 1998). Decrease in pollination success can alter plant community composition and resource availability eventually affecting ecosystem stability. Investigating these responses not only informs pollinator resilience but also supports future pollination and climate models. Understanding how these pollinators change or adjust their foraging behaviour can refine existing prediction models of pollinator success, plant reproduction and ecosystem resilience under subsequent warming events. Sustaining healthy pollination interactions is therefore important for maintaining biodiversity. Insights from this study will contribute to ecological and conservation strategies for Arctic species under the threat of global warming.

Insights on which climate conditions bumblebees are sensitive to will inform predictions on how environmental conditions affect their foraging behaviour. Karbassioon et al. (2023) found that temperature, humidity, light availability and wind speed significantly affect bee foraging behaviour with honeybees showing greater sensitivity to variable weather conditions than bumblebees. Under cooler, windier and more humid conditions, bumblebees were active, implying high resilience to environmental fluctuations. Although this study was conducted in the temperate apple orchards, it emphasises a key trait of bumblebees, that is their ability to sustain pollination services under changing climatic conditions. This resilience is particularly important in the alpine and Arctic ecosystems which are experiencing rapid warming where sustaining pollination service is important. However, all bumblebees in Latnjajaure are currently included on both the European and national Red Lists (Eide, 2020; Nieto et al., 2014). The main factors driving these declines appear to be increasingly hot summers and more frequent heatwaves, which negatively affect colony survival and reproduction in these cold-adapted species.

Although bumblebees exhibit great resilience in cooler environments, climate changes may create phenological mismatch between their active periods and floral availability. Long-term monitoring at Zackenberg, Greenland revealed a phenological mismatch between peak flowering times and the regular peak activities of worker bees due to earlier snowmelts (Høye et al., 2007). Other research on alpine plants and bumblebees further indicated that phenological mismatch increased variability and unpredictability in terms of resource availability, potentially limiting the ability of insects to

adapt (Redr et al., 2025). Similarly, Pyke et al. (2016) reported upward shifts in elevation in both plants and bumblebees and as a result of warming with early flowering accompanied with earlier bumblebee activity, but discovered a reduction in synchrony between flowering and bumblebee activity together with decreased bumblebee abundance. These findings show that plant-pollinator interactions are becoming less stable as the climate changes. However, the ecological consequences of these shifting interactions remain uncertain, particularly how specific groups of pollinators such as bumblebees respond to the altered floral availability.

Response pathways of bumblebees

Given the increasing variability in Arctic resource supply, bumblebees could respond to climate-driven shifts in flowering time through three distinct behavioural pathways:

Switch to available flowers

Bumblebees may exhibit high plasticity by shifting their preferences toward plant species that flower most abundantly during their active periods. Supporting this alternative, (Huang et al., 2024) found that some bumblebee populations do not maintain constant preferences but instead tracked and visited the most abundant floral resources available each year.

Expand range to include new species

Alternatively, pollinators may respond to environmental instability by broadening their floral range to include new or secondary species. This expansion of the foraging niche often occurs along altitudinal or environmental gradients as bees seek to supplement their diet in resource-poor windows (Miller-Struttmann & Galen, 2014). If bumblebees at Latnjajaure have expanded their floral range to include a wider variety of species than they did 30 years ago, then it would imply a move toward a more generalist foraging strategy.

Exhibit foraging constancy

Finally, bees may persist in visiting the same plant species they have historically preferred, despite shifts in phenology that make those plants less synchronized with bee activity. According to Huang et al. (2024) and Lattorff et al. (2025), bumblebees often maintain a high level of floral constancy, remaining persistent with specific targets even as abundance fluctuates or resources become limited toward the end of the season. While constancy can improve foraging efficiency in stable environments, this may lead to a phenological mismatch, where bees fail to adapt to earlier snowmelts which could have implications on survival in the Arctic.

This study explores these potential responses in the subarctic-alpine ecosystem of Latnjajaure in the north of Sweden, a climate-sensitive region ideal for long term study and where long-term data on bumblebee-plant interactions are available.

Aim

This study aims to determine whether and how bumblebees have shifted their foraging behaviour and floral preferences over the last three decades by comparing current bumblebee floral preferences with a historical dataset from the early 1990s. Specifically, the study aims to explore the following questions:

a) Which floral species are currently and historically most visited by bumblebees at Latnjajaure?
b) Have bumblebees expanded or narrowed their floral range over the past 30 years?
c) Have the bumblebees' choice of plants shifted following the changes in plant phenology?

To address these questions, the study combines field observation and pollen sampling in 2025 with historical data from the same site collected in the early 1990s to evaluate changes in bumblebee-plant interactions. By directly comparing the composition and abundance of bee-collected pollen in the past and present, this study provides a rare long-term perspective on pollinator foraging patterns in a subarctic- alpine ecosystem.

Material and methods

Study site and plot selection

The Latnjajaure Field Station (LFS) is a subarctic-alpine ecosystem located in northern Swedish Lapland, 15 km west of Abisko (68°21′ N, 18°29′ E). The ecosystem experiences short cool summers and long cold winters with mean annual temperatures between -2.2°C to -2.7°C, from 1993 to 1996. Due to the sensitivity of its climate system, it serves as an excellent location for long-term ecological research. The station has an extended history of data collection with a heightened interest considering the rate of warming and changes being observed in the arctic. There are detailed studies on the diverse plant communities and functional groups as well as limited human disturbance to the community making it an ideal site for plant-pollinator research. This site was specifically chosen to allow a direct comparison with historic data collected by Stenström and Bergman (1998). It was confined to a 2-km radius of the field station at an altitude of approximately 1,000 m above sea level.

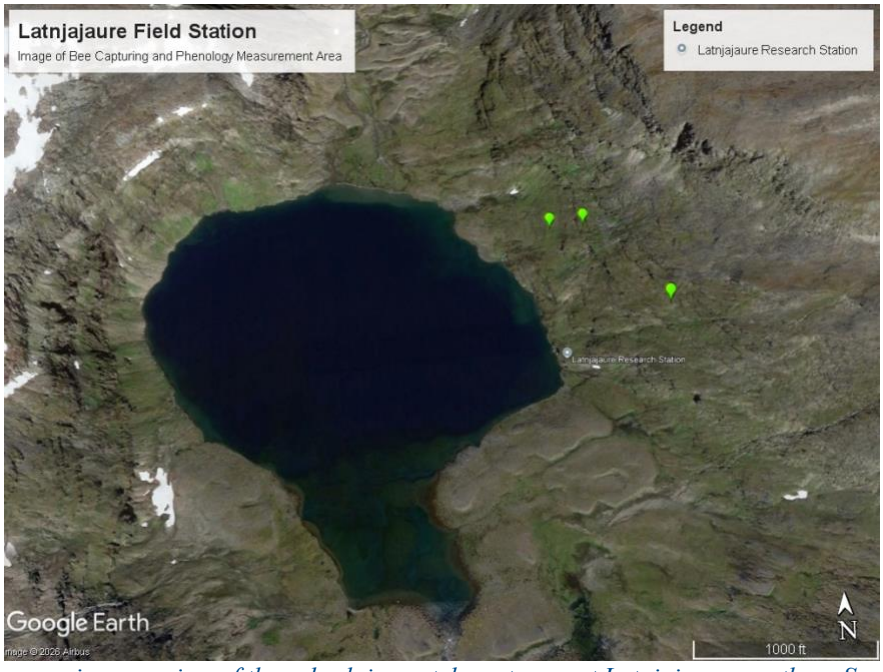

Figure 1. Satellite mapping overview of the sub-alpine catchment area at Latnjajaure, northern Sweden, highlighting the primary field monitoring plots utilized during the 2025 data collection seasons these plots overlap areas sampled in 1995. Geolocation pins mark the distinct vegetative micro-habitats designated for phenological tracking and bumblebee foraging observations. Map tiles generated via Google Earth.

Study species

The study focused on Arctic bumblebee species at Latnjajaure field station. A total of 65 queen bumblebees were captured from June to August of the growing season. These consisted of 6 different bumblebee species namely, *Bombus polaris, Bombus alpinus, Bombus monticola, Bombus hyperboreus, Bombus lapponicus and Bombus lucorum*.

Experimental Design

To evaluate shifts in floral preferences over 30 years, a longitudinal comparative design was adopted. This comparative design serves as the main driver of the study by using the historic dataset from 1995 as the basis to measure current interactions in 2025. We chose this comparative approach because it allows for a systematic analysis of how foraging niches have changed (Question A), narrowed or expanded (Question B) in response to documented shifts in plant phenology (Question C). To ensure consistency with the historical baseline, three plots were selected within the area surveyed by Stenström and Bergman (1998). GPS coordinates were recorded for each plot. This targeted selection was made to ensure that the plots provided phenology representative of the 1995 phenology. The 2025 sampling window was defined to capture the peak and late-season foraging of the bumblebee community. While the 1995 study captured the full growing season from May 31 to August 15 (Day 151-277), the 2025 phenology was conducted every fourth day from June 16 to July 28 (Day 167-209) to capture peak flowering. The bumblebees were caught on most days as they are mostly active in good weather.

Pollinator sampling

Pollinators were sampled by walking at a slow pace in each plot to record pollinator activity. Pollinator visits were recorded when a bee was spotted on a flowering plant. The genus and species of the flowering plant were recorded. Bumblebees were caught and identified, detailed images were taken of the bees that were not identified for later identification with help from experts. The bumblebees were captured on the plants using an insect net and then carefully transferred into a plastic tube. To ensure a non-lethal collection, the bumblebee was gently pushed to the top of the tube to get access to the corbicula. A toothpick was used to gently remove the corbicular pollen. This pollen was collected in a paper envelope and labelled with the bee species, the plant species the bee was captured on and the date the sample was taken. The paper envelopes were stored in a plastic bag containing silica gel to keep the pollen samples dry.

Floral Sampling and phenology

To establish the floral resource available to the bumblebee, we estimated flowering abundance every fourth day throughout the 2025 growing season consisting of all open and fresh flowers within the 3 study plots. This frequent monitoring allowed the determination of the peak flowering stages for the flowering species.

Pollen identification and counting

A staining medium was needed to improve visibility of the pollen under the microscope. To prepare the staining gel, 1 g of safranin (Sigma Aldrich) was dissolved in 1 ml of 70% ethanol (Honeywell) and then added to 100 g of glycerol gelatine (Sigma Aldrich).

To ensure accurate laboratory pollen identification, a floral reference library was collected by collecting representative samples of the flowering species from the sampling area. To prepare the reference slides, floral samples were collected from the study sites. Each slide was labelled with the corresponding plant species and the floral parts were examined under a dissecting microscope. A single flower was placed on a microscope slide, the stamen was carefully extracted using forceps and a drop of water was added to disperse the pollen and improve visibility. The stamen and remaining floral tissue were removed from the slide. The staining gel was spread evenly on a

coverslip, which was gently placed on the pollen smear. Slides were left to dry at room temperature before being examined under an Olympus BX60 microscope.

To prepare the bumblebee pollen slides, corbicular pollen loads collected from the bumblebees were transferred from labelled envelopes into Eppendorf tubes with matching labels. Next, 2 ml of 70% ethanol was added to each tube. Samples were then centrifuged at 1,000 rpm for 5 minutes. After discarding the supernatant, the pellet was smeared onto microscope slides using a disposable Pasteur pipette, stained and examined under the microscope.

Pollen identification and counting was performed at 200x magnification. The slide was gently placed on the stage, coordinate noted, and pollen grains counted in a parallel line to the end of the field of view. For each coordinate, both the pollen species and the number of grains were recorded. The stage was moved one to two units in a perpendicular direction, and counting continued until the proportion of species remained stable. For samples with multiple plant species, counting continued until 1,200 pollen grains were recorded (Å. Dahl, personal communication, 10 November 2025). For samples with a single plant species, counting ended after 600 grains.

Statistical analysis

All data processing and statistical analyses were done in R (version 2026.01.1+403). The following packages were used: *tidyverse* for data manipulation and visualization, the *glmmTMB* package for running a Multivariate Generalized Linear Mixed Model (MvGLMM). The *emmeans* package was used for interpreting model results and the vegan package was used for diversity analyses.

MvGLMM was used to test the interaction between 1995 and 2025 and plant species on corbicular pollen counts. This helped in identifying shifts in floral utilization over the 30-year interval. A Negative Binomial (*nbinom2*) error distribution was used to account for the non-negative type of the count data.

To standardize reproductive foraging effort and ensure consistency among samples, the total pollen grains per slide were added as a log-offset, to model the relative proportion of each plant species in the pollen load. Moreover, the *slide ID* (nested within *period*) was included as a random effect to account for the hierarchical structure of the data. Finally, a zero-inflation component was included in the model (*ziformula = ~1*) to address sparsity in the matrix, as many plant species were absent from specific bumblebee samples. Estimated Marginal Means were calculated from model interactions to help interpret the results. It allowed back-transformation of predicted values from the log-link scale to the original response scale of standardized pollen counts.

To evaluate the shift in foraging breadth, a Shannon Diversity Index (H ′) was calculated for each pollen sample. The diversity function was used to measure both richness and evenness of the floral species used by the bumblebees. To check the statistical significance of changes in diversity and richness, a nonparametric test, the Wilcoxon rank-sum test, was used. This was appropriate because H ′ values are often skewed, and this test handled outliers and sparsity in the dataset.

Results

Analysis of floral visitation and species composition

Seasonal patterns of floral utilisation shifted between the two sampling periods (Fig. 2b), *Saxifraga oppositifolia* was the dominant resource for bumblebees in the early season of 1995. This was followed by a mid-season shift to *Astragalus alpinus* and a transition to Ericaceae towards the end of the season (Fig. 2b). However, in 2025, *Salix* became the dominant species at the start of the sampling period. Ericaceae became the primary resource mid-season (See Appendix 2), followed by *A. alpinus* which maintained dominance through to the end of the season in both sampling periods, but it was utilized more in 2025 (Fig. 2a).

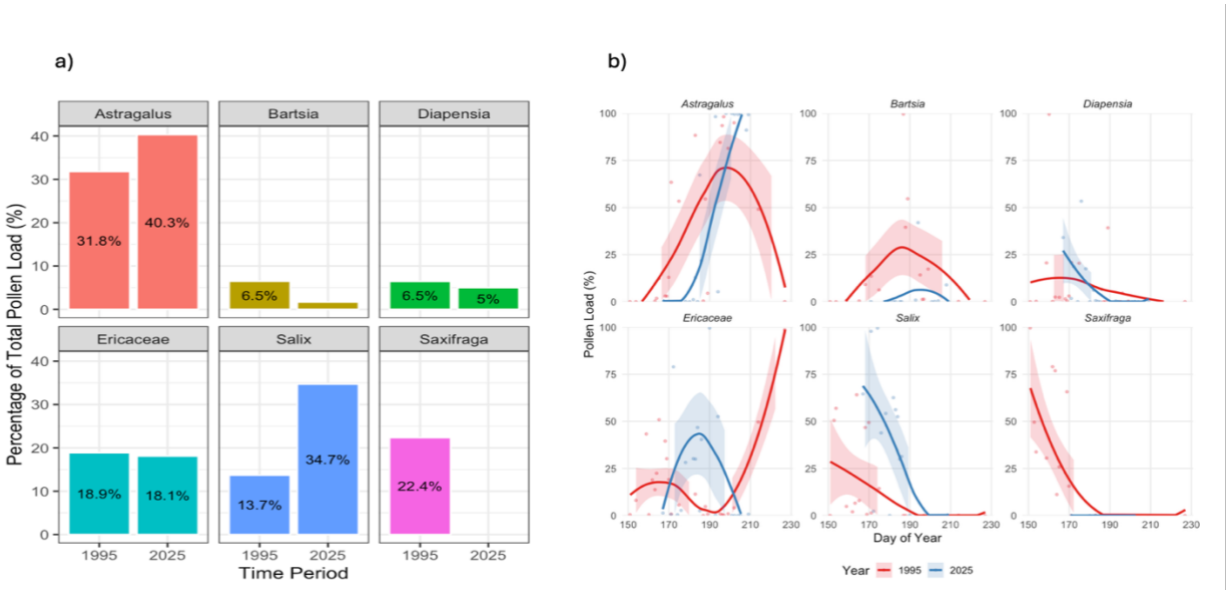

Figure 2: a) Comparison of relative abundance in pollen loads for major species in 1995 and 2025. b) Seasonal tracking of pollen load composition (%) in bumblebees across the day of the year at Latnjajaure, comparing the historical baseline from 1995 (red curves and shade) with the 2025 monitoring period (blue curves and shade). Individual points plot the pollen percentage. Continuous lines represent locally weighted scatterplot smoothing trends, and the error bars represent the 95% confidence interval.

The most significant shift in bumblebee floral utilization was a substantial reduction in the visitation to *S. oppositifolia*. The results of the pairwise contrast (Table 1) from the model indicated that the corbicular pollen load from *S. oppositifolia* decreased by an estimate of -232.95 in 2025 compared to 1995 (p= 0.0031). *S. oppositifolia* which was the dominant early-season resource in 1995 exhibited the largest reduction in corbicular pollen load and a statistically proven decline of all the species studied as seen in Table 1.

Bumblebees also exhibited an increased trend in the utilization of *A. alpinus* and *Salix* although these shifts were not statistically significant. *Salix* had a high increase in corbicular pollen load approximately by 194 (p= 0.10). Fig. 2b shows it as a dominant early resource in 2025, moving from around 20% of the early-season daily pollen load in 1995 to around 70% in 2025. Similarly, *A. alpinus* increased by an estimate of approximately +96 though this increase was not significant (p= 0.53).

Foraging on the other key species remained stable with marginal changes across the two study periods. *Diapensia lapponica* and Ericaceae remained effectively unchanged with negligible non-significant estimates (p>0.70). *Bartsia alpina* visitation showed a downward trend with an estimate of -52 but was not significant (p= 0.06).

Table 1. MvGLMM regression outputs evaluating shifts in bumblebee pollen load representation at Latnjajaure. Pairwise contrasts of estimated marginal means for corbicular pollen loads between 1995 and 2025 across six target plant taxa. SE = Standard Error, Significance is evaluated at α = 0.05 (indicated in bold).

Plant species	Estimate	SE	*z*-ratio	*p*-value
Astragalus	+95.92	154.0	0.62	0.5339
Bartsia	-52.13	27.8	-1.88	0.0605
Diapensia	-0.20	32.2	-0.01	0.9950
Ericaceae	+20.68	72.6	0.29	0.7759
Salix	+193.79	118.0	1.64	0.1015
Saxifraga	**-231.95**	**78.3**	**-2.962**	**0.0031**

Changes in foraging breadth

Corbicular pollen load showed lower floral diversity in 2025 than in 1995 (Fig. 3a). The Shannon Diversity Index (*H'*), which measures both species richness and evenness, showed a substantial decline from a median of 0.596 (*n*=67) in 1995 to a median of 0.068 (*n*=64) in 2025 (Fig. 3b). Weekly analysis further showed that pollen loads in 1995 had consistently higher floral diversity throughout most of the season (Fig. 3c). In 2025, the floral diversity was relatively lower overall, with a sharp decline after week six (W=3308, $p<0.001$). The Interquartile Range (IQR) dropped from 0.701 in 1995 to 0.338 in 2025 (See Appendix 2). While the maximum diversity in 1995 reached *H'*= 1.32, the 2025 maximum peaked at *H'*= 1.09.

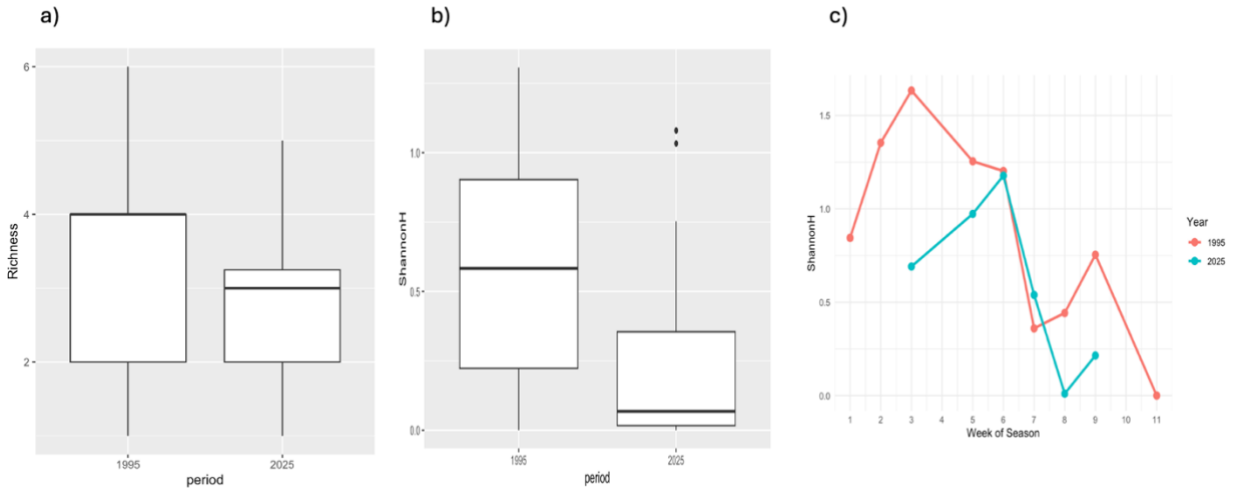

Figure 3: a) Narrowing foraging breadth expressed as species richness at Latnjajaure in 2025 compared with the historical baseline (1995). b) Narrowing bumblebee foraging breadth expressed as a function of the Shannon Diversity Index (H') calculated from unique plant taxa identified in individual corbicular pollen loads. c) Weekly details of narrowing foraging breadth. ShannonH represents the Shannon Diversity Index (H'). Week numbers start from May 31 onwards till the end of the season.

Phenological synchrony and tracking of available floral resources

Bumblebee foraging exhibited shifts in tracking resource availability between the 1995 and 2025 sampling periods (Fig. 4). The earliest flowering species was Saxifraga in 1995. It showed strong early-season utilisation by the bumblebees. The foraging broadened when other species started to

flower. Bee foraging on *S. oppositifolia* collapsed entirely in the 2025 window although part of the flowering was captured at the onset of the flowering period *Salix* emerged as the primary early-season resource for the bumblebees in 2025, with an increase in foraging activity of about 75% relative intensity. In the mid to late-season interactions, *Bartsia alpina*, which was utilised more in 1995 in synchrony with its flowering peak around day 190, exhibited foraging which nearly collapsed in 2025, even as the flowering phenology remained relatively stable. *A. alpinus* became dominant towards the end of the season in both years, particularly in 2025, where the pollen load exhibited dominance during peak flowering.

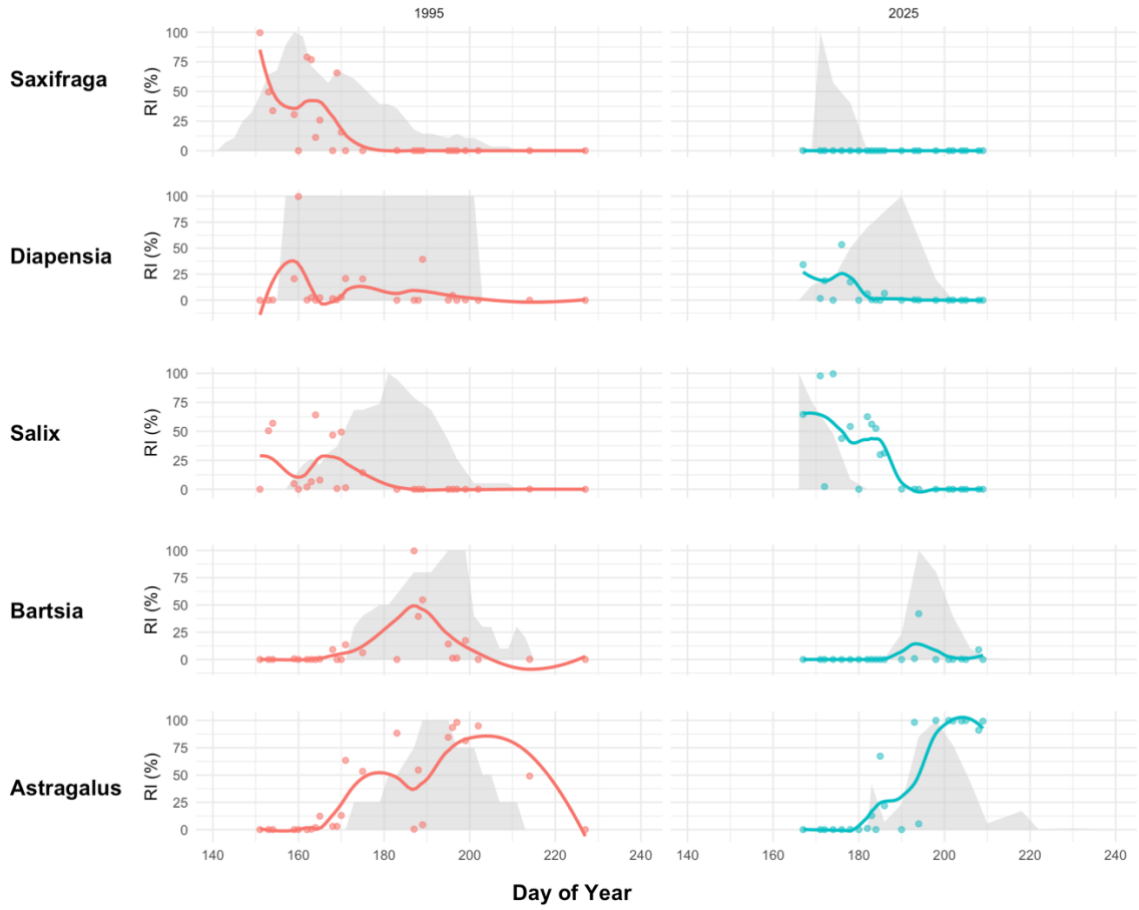

Figure 4. Comparison of flowering intensities (RI in %) and daily pollen load (RI in %) in bumblebees across the day of the year at Latnjajaure five primary plant taxa in 1995 and 2025, showed differences in floral availability. Solid lines indicate trend lines fitted to pollen load from bumblebees, grey shaded area represents flowering trends across the season.

Discussion

Overall, the results of this study demonstrate that species preferences did not shift intensely over time, but minor shifts did occur. Astragalus alpinus was the dominant pollen source in both years, but its dominance increased between 1995 (31.8% abundance) and 2025 (40.3% abundance) as seen in Fig. 2a. At peak season bumblebees preferred foraging on *A. alpinus* and was the most visited species in both years. In 1995 *A. alpinus* was the most visited species with an abundance of 31.8% of the total pollen load across the sampling period (Fig. 2a). *A. alpinus* maintained its dominance as the most visited species in 2025 with an even higher abundance (40.3%). The maintained dominance of *A. alpinus* supports previous findings that it is a high-rewarding species (Kudo & Molau, 1999) with fragrant pollen that is unusually attractive to bees (Swales, 1979). Stenström (1998) noted that analyses of the 1995 pollen loads showed that some were made up of about 91-100% *A. alpinus* pollen alone, highlighting this special attraction of bumblebees to this

plant when it is in flower. In the historical study by (Stenström & Bergman, 1998), in the early-season bumblebees visited *S. oppositifolia, Diapensia lapponica, Rhododendron lapponicum* and *Salix* species. *S. oppositifolia* recorded the highest abundance among the early-season species (22.4%). Data from Fig. 4 shows that bumblebees shift focus from these species to *A. alpinus* as soon as it starts to flower even when they have a good proportion of flowers available.

Results from this study indicate that plants utilised by the bumblebees in the early-season have changed between the two sampling periods. The early-season resource used by the bumblebees shifted from *S. oppositifolia* to *Salix*. *S. oppositifolia* pollen was absent in the corbicular pollen load collected in 2025, but instead *Salix* emerged as the dominant early-season resource (75%). This result also informs question c as there was an observed change in early-season preference. While it might seem apparent that *S. oppositifolia* has been replaced by *Salix*, it is difficult to arrive at this conclusion especially when the onset of flowering was not recorded and peak flowering of both taxa was recorded in the beginning of the sampling period (Fig. 4). *S. oppositifolia*, being an evergreen outcrosser is known to start flowering very early after snowmelt, usually being the first species to flower in Arctic habitats (Stenström & Molau, 1992). However, Stenström and Bergman (1998) also states that flowering does not end until the beginning of August, but flowering ended earlier in our plots. *Salix* is one of two particularly important plants that flower early in the season (Cirtwill et al., 2023). Their flowering onset usually occurs between late May and early June (Khorsand et al., 2024) which aligns with our phenology results shown in Fig. 4 where the peak was reached on the first sampling day similar to *S. oppositifolia*. *Salix* pollen, however, contains a suitable lipid and protein diet that is critical for founding queens as they emerge from hibernation (Martinet et al., 2022). Since our data focused only on queen bumblebees, this explains the possible bias in the early-season sampling such that queen bumblebees disproportionately visited Salix as they came out of hibernation. With 2025 having unusually late snowmelt compared to a few years prior (personal observation, Anne Bjorkman) bumblebees may have delayed a little in returning from hibernation thus explaining the spike in *Salix* visits early in the season instead of *S. oppositifolia*.

Alternatively, Stenström (1998) concluded that reproductive effort of *S. oppositifolia* was driven mainly by solar radiation accumulated during the previous season instead of current conditions. They noticed that flower production was directly affected by the irradiance from the previous mid to late-season, ultimately determining the quantity of flowers the following season. The flower buds form during this time and are kept through the winter. The shift in early-season preferences was seen at the beginning of the 2025 sampling season (Day 167, Fig. 4) and did not capture the whole flowering period of the two species. In 1995 pollen collected from *S. oppositifolia* started to decline around Day 170 despite its high abundance, but sampling in 2025 started on Day 167 where historically visits had dropped significantly. Additionally, the end of the growing season for *S. oppositifolia* was around Day 200 in 1995 and Day 180 in 2025. This could indicate a possible phenological shift where flowering started earlier in the growing season of 2025 and may have led to a phenological mismatch between the bumblebees and the flowers. This theory cannot be expanded upon due to the different sampling windows. Salix's emergence as the new dominant early-season resource also highlights a significant limitation in evaluating this shift which is the lack of historical phenology data for *Salix lanata.* In 1995, the species recorded in the monitoring squares was *Salix reticulata* but no bumblebee visits were recorded on that species. Although *Salix* pollen present in the corbicular loads were likely to be from *S. hastata* or *S. lanata* as they were present in the sampling area. Consequently, it is not possible to determine if the blooming window of *Salix* has also shifted to compete with *S. oppositifolia* or if its current increase is also because of increased abundance relative to forbs. Studies have shown that localized Arctic warming has facilitated shrub dominance at the expense of unspecialised forbs (Albertsson, 2024). This is a trend consistent with broader Arctic vegetation shifts (Scharn et al., 2022). A study by Stenström et al. (1997) indicated that there was a decrease in floral density of *S. oppositifolia* plants in

experimentally warmed plots. Therefore, the abundance of *S. oppositifolia* may decrease with the increasing Arctic temperatures.

Additionally, efforts were made to know if the bumblebee foraging has narrowed or expanded over the decades. From the results, a statistically significant contraction of the bumblebee community foraging niche was observed. The median Shannon Diversity Index(H') dropped from 0.596 in 1995 to 0.068 in 2025 (Fig. 3a). The bumblebees moved from the relatively broad diet observed in the 1990s (Stenström & Bergman, 1998) to a more specialised foraging strategy in 2025. This agrees to Stenström's claim that Arctic bumblebees were not generalists in comparison to their temperate counterparts as previously believed (Husband & Brown, 1976). Constancy is seen as a convenience for bumblebees since it is easier to keep visiting same flower than to learn to manipulate the specific structural complexity of a new flower type (Lattorff et al., 2025). As a result, bumblebees in Latnjajaure have maintained similar constancy as they did in 1995 with not much difference in floral preferences over the 30-year period. In 2025, bumblebees visited *A. alpinus* with even higher intensity. This trend became more pronounced as the season progressed. The sharp decline in floral diversity observed after week six (Fig. 3b), which corresponds to the transition from early-season resources like *Salix* to the peak flowering of *A. alpina* (Fig. 4). Consequently, the narrowing of the foraging niche reflects a behavioural pivot toward specialised constancy even as the Arctic landscape changes.

Methodological considerations and limitations

Temporal difference in sampling duration signifies a limitation of this longitudinal comparison. The 1995 historical baseline includes the full growing season from May 31 to August 15 (Day 151–277), whereas the 2025 sampling window was from June 16 to July 28 (Day 167–209). Consequently, the recent dataset does not include observations from the early emergence period in late May or the late-season foraging shifts occurring in August which were captured in the 1990s. This temporal difference was a major sampling deviation which must be considered together with interpretation of results. The study compared only two years so we do not know if these changes represent long-term trends or just interannual variation, additional data will be collected in the future to address what the changes observed represent.

Implications

Although results regarding changes in phenology are inconclusive, it points in the direction that warming may affect the abundance and phenology of *S. oppositifolia*. Additionally, because *S. oppositifolia* relies on insect pollination for reproductive success (Molau, 1993), the loss of bumblebee visits may reduce the reproductive success of the population following a phenological mismatch. While early flowering and reduced visitation may threaten the population viability of unspecialised forbs like *S. oppositifolia*, the compensatory rise of shrubs like *Salix* provides the structural resilience necessary to maintain the stability of the plant-pollinator network under climate stress. The dominance of *A. alpina* pollen suggests that it may outcompete co-flowering species for bumblebee visits. Bumblebees adapt their foraging behaviour to maintain important pollination services, providing the structural resilience necessary to withstand the reorganising Arctic landscape. Lastly this study highlights that the behavioural plasticity of bumblebees may serve as a buffer for the plant pollinator network and biodiversity, as important ecosystem functions will persist despite the changing climate. By documenting these changes and adaptations, this study serves as a vital road mark for future studies and conservation efforts. Reminding us about the importance of knowing how bumblebees, key pollinators for most Arctic plants are adjusting to an environment heating up faster than the rest of the world.

Conclusion

In this work, we evaluated decadal shifts in bumblebee foraging preferences at Latnjajaure over a 30-year interval. The results demonstrate that the bumblebee community has reorganised its

foraging niche, shifting from the broad seasonal menu documented in the 1990s to a highly specialised strategy. This contraction is evidenced by a statistically significant drop in the median Shannon Diversity Index. In 1995 the unspecialised forb *S. oppositifolia* served as the primary early-season resource, yet it was absent from all 2025 pollen samples. In its place, deciduous shrubs in the genus *Salix* have emerged as the dominant early resource. High-rewarding species like *A. alpinus* have become the focal point of peak foraging constancy. These findings confirm that while the localised Arctic warming of 0.3°C per decade may have driven these shifts, bumblebees adjust their foraging to maintain efficiency.

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Appendix 1: Popular science summary

Can Arctic bumblebees keep up with climate change?

The Arctic is warming four times faster than the rest of the planet, and nature's clock is spinning out of sync. Climate change the main driver of this warming is leading to earlier snowmelt and flowers are blooming before their pollinators are even active. But are the bumblebees which are seen as the most important pollinators in the Arctic adapting to this new reality? By comparing today's bees with records from thirty years ago at the remote Latnjajaure field station, my research reveals whether and how these vital insects are adjusting to survive in an environment heating up faster than the rest of the world.

By analysing the pollen collected from today's bees and comparing it to records from the early 1990s, I discovered some interesting findings from the mountains of Latnjajaure. Picture this, in the early 1990s, a queen bumblebee at the Latnjajaure field station would likely have spent her summer days visiting reliable staples like the bright purple Saxifrage (*Saxifraga oppositifolia*) or the Alpine Milk-vetch (*Astragalus alpinus*). However, a different story unfolded in 2025. Even though the queen still visits the Alpine Milk-vetch, visits to the purple mountain saxifrage may have been replaced by woolly willow (*Salix lanata*) even with available saxifrage flowers. This suggests that the warming climate maybe throwing nature's timing out of sync and the bees are probably missing the early-season resource observed in the 1990s. Unfortunately, the number of popular species visited reduced from 6 to 5 with intense visits to some species. This suggests that bumblebees are now relying on a narrower range of flowering plants than they did three decades ago, shifting from a broad seasonal menu to a more specialised foraging strategy. While this may reduce pollination opportunities for plants such as velvet bells (*Bartsia alpina*) and purple mountain saxifrage, it also highlights how bumblebees are adapting their behaviour to cope with a rapidly changing Arctic environment.

But why does a shift in a bumblebee's floral menu matter to those of us who do not live in the Arctic mountains? These insects are the essential couriers of the North, perfectly adapted with thick fur and long tongues to keep pollen moving in the Arctic landscape. Because of this, any disruption in their relationship threatens life in the Arctic. If the bees and plants fall out of sync, the results could be a silent catastrophe. Fewer seeds will lead to fewer plants, which will eventually disrupt the food supply for other animals and weaken the region's resilience. By mapping these 30-year shifts, my research provides a vital roadmap for conservationists working to protect Arctic biodiversity before these fragile connections are lost.

To uncover these hidden shifts, I had to get up close and personal with the bumblebees themselves. During the short Arctic summer, I carefully tracked sixty-five queen bees across the tundra at the Latnjajaure station. Using a gentle, harmless technique, I used a simple toothpick to collect the tiny loads of pollen they carried before releasing them back to their flowers. Using a microscope in the lab, I was able to identify exactly which flowers each bee had visited, allowing me to build a bridge between the foraging habits of the 1990s and the reality of the Arctic today.

While the Arctic's warming clock may be spinning faster than ever, my research shows that its most important pollinators are not simply standing still. By understanding how bumblebees have spent the last thirty years adapting their diets, we are better equipped to protect them and the fragile floral landscapes that depend on them.

Appendix 2: Supplementary figures and tables

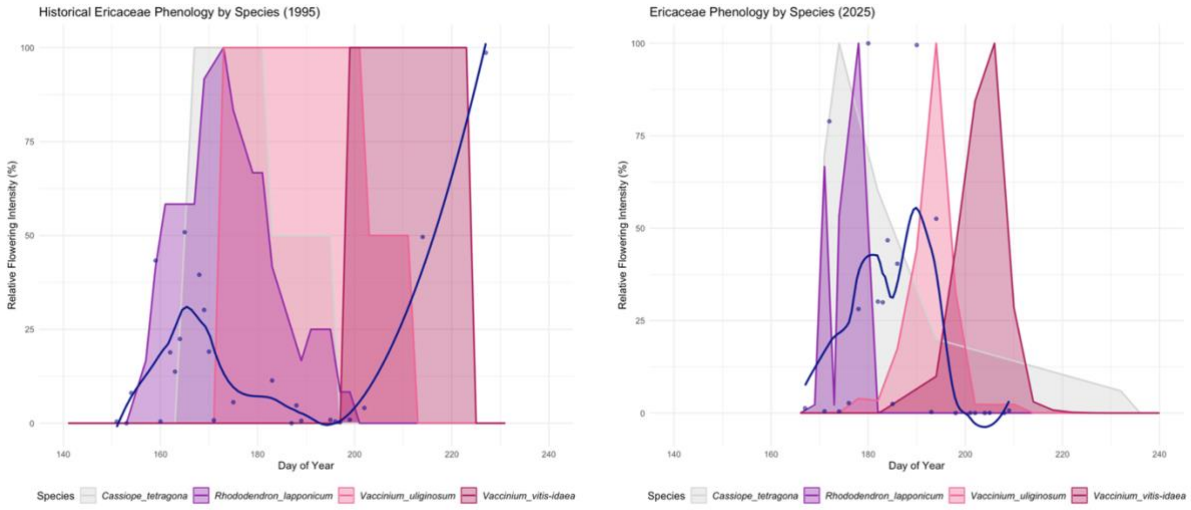

Figure A 1: Flowering intensities (RI in %) and daily pollen load (RI in %) in bumblebees across the day of the year of different Ericaceae species at Latnjajaure in 1995 and 2025.

Table A 1: Shannon Diversity Index summary

Period	n	Mean	Median	SD	IQR	Min	Max
1995	67	0.566	0.596	0.395	0.701	0	1.32
2025	64	0.217	0.0682	0.274	0.338	0	1.09

Table A 2: Information on model syntax, R package used and model output

Model syntax	glmmTMB(pollen_count~period*plant_species+offset(log(Total))+(1|Slide:period), data=filtered_long,ziformula = ~1, family = nbinom2)
R package	glmmTMB
Model output	

```
                                Estimate Std. Error z value Pr(>|z|)
(Intercept)                      -0.9267     0.3233  -2.866  0.00416 **
period2025                        0.2874     0.4519   0.636  0.52485
plant_speciesBartsia             -1.3617     0.4753  -2.865  0.00417 **
plant_speciesDiapensia           -1.4220     0.4485  -3.171  0.00152 **
plant_speciesEricaceae           -0.5541     0.4263  -1.300  0.19368
plant_speciesPedicularis         -5.3335     0.5014 -10.638  < 2e-16 ***
plant_speciesSalix               -0.7406     0.4478  -1.654  0.09819 .
plant_speciesSaxifraga           -0.2169     0.4532  -0.479  0.63222
period2025:plant_speciesBartsia  -1.5118     0.6945  -2.177  0.02951 *
period2025:plant_speciesDiapensia -0.2903    0.6474  -0.448  0.65389
period2025:plant_speciesEricaceae -0.1697    0.6107  -0.278  0.78115
period2025:plant_speciesPedicularis -0.4702  0.6969  -0.675  0.49984
period2025:plant_speciesSalix     0.5924     0.6430   0.921  0.35683
period2025:plant_speciesSaxifraga -10.0641   1.1988  -8.395  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Zero-inflation model:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -0.9275     0.3203  -2.896  0.00379 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Table A 3: Information on emmeans syntax, R package used and output

Emmeans syntax	EMM_at_mean <- emmeans(mod, ~ period | plant_species, offset = mean(log(filtered_long$Total)), regrid = "response") summary(contrast(EMM_at_mean, method = "revpairwise"), infer =TRUE)
R package	Emmeans
Output	plant_species = Astragalus: contrast estimate SE df asymp.LCL asymp.UCL z.ratio p.value period2025 - period1995 95.923 154.000 Inf -206.28 398.12 0.622 0.5339 plant_species = Bartsia: contrast estimate SE df asymp.LCL asymp.UCL z.ratio p.value period2025 - period1995 -52.129 27.800 Inf -106.57 2.31 -1.877 0.0605 plant_species = Diapensia: contrast estimate SE df asymp.LCL asymp.UCL z.ratio p.value period2025 - period1995 -0.203 32.200 Inf -63.27 62.86 -0.006 0.9950 plant_species = Ericaceae: contrast estimate SE df asymp.LCL asymp.UCL z.ratio p.value period2025 - period1995 20.677 72.600 Inf -121.68 163.03 0.285 0.7759 plant_species = Pedicularis: contrast estimate SE df asymp.LCL asymp.UCL z.ratio p.value period2025 - period1995 -0.232 0.683 Inf -1.57 1.11 -0.340 0.7337 plant_species = Salix: contrast estimate SE df asymp.LCL asymp.UCL z.ratio p.value period2025 - period1995 193.790 118.000 Inf -38.13 425.71 1.638 0.1015 plant_species = Saxifraga: contrast estimate SE df asymp.LCL asymp.UCL z.ratio p.value period2025 - period1995 -231.945 78.300 Inf -385.42 -78.47 -2.962 0.0031