

Research Article

Shifts in phenology influence synchrony of flowering plants and their pollinators along an elevation gradient

Mikko Tiusanen^{1,2}, Anna Norberg^{1,3} and Anna-Liisa Laine^{1,4}¹Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zürich, Switzerland²Institute of Integrative Biology, ETH Zurich, Zurich, Switzerland³Potsdam Institute for Climate Impact Research, Potsdam, Germany⁴Research Centre for Ecological Change, Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, FinlandCorrespondence: Mikko Tiusanen (mikko.tiusanen@usys.ethz.ch)

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Climatic conditions alter the phenology of species, which may threaten the synchrony of biotic interactions. However, how phenological synchrony across entire communities of plants and their pollinators responds to varying environmental conditions remains poorly understood. We recorded the communities and phenology of flowering plants and pollinators in herb-rich meadows at 22 sites between 600 and 1800 m a.s.l. on Calanda massif, Switzerland. During weekly visits, we counted 1 177 396 flowers belonging to 163 taxa and captured a total of 9707 insect pollinators across the study sites. We observed a decline in the flower abundance, numbers of flowering species, and insect abundance with increasing elevation. Additionally, we found strong and slightly differing seasonality in flower and pollinator abundance, resulting in increasing pollinator availability toward the end of the growing season. On average, flowering phenology was delayed by 1.4 days per 100 m of elevation gain, although species-specific responses varied substantially. We also detected a shift in the most contested flowering phenology along the gradient: late-flowering species showed higher overlap in flowering times at low elevations, whereas early-flowering species experienced greater niche overlap at high elevations. Meanwhile, overall synchrony between flowering plants and pollinators increased at higher elevations with shorter growing seasons, as pollinators showed greater temporal overlap with flowering species. At lower elevations, species with the highest flowering-time overlap coincided with periods of high pollinator availability in the late season. In contrast, at higher elevations, contested flowering phenology did not track pollinator availability. This suggests that flowering time is potentially more constrained by biotic factors (pollinator availability) at lower elevations, and by abiotic factors (season length) at higher elevations. These shifting biotic versus abiotic controls of plant–pollinator interactions may change substantially under future climate scenarios.

Keywords: plant–pollinator interactions, flowering phenology, phenology shift, niche overlap, elevation gradient


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Introduction

One of the most recognized effects of climate change is shifts in species phenology, i.e. the timing of life-history events (Diez et al. 2012, Duchenne et al. 2020). Phenological events are known to change along environmental gradients, and it has been widely observed that species phenology advances with a warming climate (Roy and Sparks 2000, Ovaskainen et al. 2013, Inouye 2022). However, interacting species may differ in how their phenology responds to changing conditions (Roslin et al. 2021, Fisogni et al. 2022, Prather et al. 2023). For example, a phenological mismatch can occur when plant flowering phenology adjusts to climate change while pollinator phenology does not (Hegland et al. 2009). Such mismatches can alter the synchrony of coevolved interactions within ecological networks (Schmidt et al. 2016, Kudo and Cooper 2019), with potentially far-reaching consequences for population dynamics and species persistence under global change. Hence, understanding the impacts of varying environmental conditions on species interactions at the community level is urgently needed (Visser and Gienapp 2019).

In addition to environmental conditions, the optimal timing of flowering and pollinator activity depends on one another, and it has long been recognized that plant species have evolved distinct flowering times (Clarke 1893, Kochmer and Handel 1986, Munguía-Rosas et al. 2011). It has been proposed that synchrony with and competition for pollinators is a driving force behind the differing flowering times among entomophilous plant species (Robertson 1895, Levin and Anderson 1970, Mosquin 1971). For successful pollination, flowering should coincide with suitable environmental conditions, the flowering of conspecific individuals, and the activity of pollinators. Successful pollination may thus be especially sensitive to changes in flowering phenology relative to pollinator activity, as well as to the flowering phenology of other species that share the same pollinator pool – typically leading to competition for pollinators (Mitchell et al. 2009, Tiisanen et al. 2020, Waters et al. 2020, Arroyo-Correa et al. 2024). Consequently, the timing of flowering is a critical component of both plant and pollinator fitness (Austen et al. 2017, Faust and Iler 2022). The magnitude of phenological overlap describes the potential for species to interact (e.g. plants and pollinators to have mutualistic interactions, or plant species to compete for pollinators) within a community (Thomson 1982). Yet, flowering phenology at the community level has only rarely been studied simultaneously with insect communities (Thomson 1982, Benadi et al. 2014). In particular, we often lack information on how the availability of insect pollinators matches the flowering schedule of entire plant communities (Iler et al. 2013b).

In seasonal systems, both abiotic (e.g. temperature, season length, resource availability) and biotic (e.g. pollinators, seed predators, competing plant species) factors influence optimal flowering phenology (Elzinga et al. 2007, Ehrlén and Münzbergová 2009, Weis et al. 2014, Austen et al. 2017). In general, earlier flowering is considered advantageous within

a species, as individuals gain a competitive edge over conspecifics (Munguía-Rosas et al. 2011). However, both early and late flowering can be risky due to environmental hazards, especially in cold and seasonal environments (Kudo and Suzuki 2002, Iler et al. 2019), while the optimal conditions are found between the extremes. Consequently, the abundance and diversity of both flowers and pollinators peak typically in the middle of the growing season (Elzinga et al. 2007, Fernandez-Conradi et al. 2020). Also, shifting pollinator availability within a season (Rafferty et al. 2016, Mizunaga and Kudo 2017, Lefebvre et al. 2018, Kehrberger and Holzschuh 2019) has direct effects on the optimal timing of flowering. In addition to pollinator availability, co-flowering species can reduce available pollination services through competition (Campbell and Motten 1985, Tiisanen et al. 2020, Waters et al. 2020), although facilitation is also possible (Ghazoul 2006). However, the relative importance of changing abiotic conditions versus pollinator availability for flowering phenology is still poorly understood at the community level (Paquette and Hargreaves 2021, for general patterns). Changes in season length are also expected to strongly influence optimal flowering (Ehrlén and Münzbergová 2009, Austen et al. 2017).

Elevation gradients in montane ecosystems provide unique opportunities to explore how steep variation in environmental conditions affects species phenology and interactions within defined geographical ranges (Benadi et al. 2014, Hoiss et al. 2015). Specifically, they provide shifts in climate (i.e. decreasing temperature with increasing elevation) and species phenology, while minimizing confounding factors such as day length (Dietrich and Körner 2014, Elmendorf et al. 2015). In mountains, increasing elevation and decreasing temperature reduce species richness of both plants and pollinators (Lara-Romero et al. 2019), lower pollinator visitation rates (Bingham and Orthner 1998), and promote more generalized visitation patterns (Hoiss et al. 2015, Lara-Romero et al. 2019). With decreasing temperature, species phenology is typically delayed at higher elevations, though recent climate warming has weakened this effect (Benadi et al. 2014, Vitasse et al. 2018). Nevertheless, phenology shifts observed along elevation gradients broadly mirror those caused by climate warming (Fisogni et al. 2022).

To examine the effects of climate on seasonal variation in flowering plants and their pollinators, we conducted a study along an elevation gradient in a subalpine ecosystem. Using herb-rich meadows on Calanda massif, south-eastern Switzerland, we monitored the abundance and phenology of both flowering plants and their pollinators to assess how varying climatic conditions and climate-induced phenological shifts influence community-level plant–plant and plant–pollinator interactions. Specifically, we ask:

- 1) How do elevation and seasonality affect communities of entomophilous plants and their pollinators? We expect flower abundance, the number of flowering species, and pollinator density to decrease with temperature along the elevation gradient. In addition, we expect flower

abundance, flowering species richness, and pollinator density to peak in the middle of the growing season, during the warmest and most favorable conditions.

- 2) How does elevation affect flowering phenology? We expect an overall delay in flowering phenology with increasing elevation. Additionally, we expect phenological shifts of different flowering species to be similar along the elevation gradient.
- 3) How does elevation affect phenological synchrony among flowering plants? We expect increased temporal synchrony (niche overlap) in flowering phenology at higher elevations, as shorter growing seasons compress flowering. We also expect early- and late-flowering species to show contrasting responses in within-guild niche overlaps, depending on season length (abiotic limitation) and pollinator availability (biotic limitation).
- 4) How does elevation affect phenological synchrony between plants and their pollinators? For the same reason as above, we expect increased niche overlap between flowering plants and pollinators at higher elevations, due to the compressed growing season.

Material and methods

We studied how flower abundance, flowering phenology, and phenological synchrony among different plant species, as well as pollinator density and availability (insect-to-flower ratio), vary along an elevation gradient, and how these changes influence plant–plant and plant–pollinator synchrony and interactions.

Study system

To investigate the structure of local communities of flowering plants and their pollinators, as well as their phenological variation and synchrony along an elevation gradient, we surveyed 22 study sites (50 × 50 m each, Supporting information) at the Calanda Biodiversity Observatory (CBO; Halliday et al. 2021). To capture variation in biotic and abiotic drivers of community structure, the sites were established along an elevation gradient (648–1749 m above sea level) below the tree line on the south-facing slope of Calanda massif (46°53'N, 09°28'E) in the canton of Graubünden, Switzerland.

In the study area, temperature decreases with increasing elevation (typically 0.54–0.58°C per 100 m, Rolland 2003), making elevation a reliable proxy for local temperature on the meadows studied ($R^2=0.89$, Halliday et al. 2021). The study sites are located on five community-owned meadows separated by forested areas and differences in elevation. The soil is calcareous, and meadow vegetation is diverse (Halliday et al. 2021). The CBO meadows are grazed by cattle twice per year (spring and autumn), with animals moved between low and high altitudes over two–three-week periods. Sampling was conducted between grazing events, from early June to late August 2019. Some early-flowering species occurring in spring were missed due to grazing, while by late August

flower numbers had already declined, marking the end of our sampling period (Fig. 1A).

Quantification of the floral community

To detect seasonal patterns in the abundance and species richness of the flowering community, we recorded the number of flowers (or inflorescences) for all the entomophilous species once a week for the flowering season resulting in 8–10 surveys per site through the growing season. The flower densities were monitored at the level of the study sites (50 × 50 m). If a species was abundant, first, a group of flowers was counted, and then this count was multiplied by the number of such groups found on the site (e.g. first, we counted a group 50 flowers, and then we approximated how many such groups of 50 flowers were found on the study site). Most of the plant species were identified to species level (following the Swiss national flora, www.infoflora.ch), and whenever this was not feasible, the lowest possible taxonomic level was used (treated as species in the analyses). To characterize the flowering phenology of each plant species and phenology shifts along the elevation gradient, we calculated the mean flowering date (mean occurrence of open flowers, indicated as DOY, day of year, Julian date) at the level of study site for each plant species. This was calculated as flower abundance-weighted average, by weighting each observation date by the number

$$\text{of flowers recorded: } \frac{\sum_{k=1}^n \text{DOY}_k \times \text{Number of flowers}_k}{\sum_{k=1}^n \text{Number of flowers}_k}.$$

k is an index for a single observation. In addition, to examine the phenology-driven competition potential for pollinators between the plant species in more detail, we quantified the site-specific temporal niche overlap between pairs of flowering species.

Quantification of the pollinator community

We monitored the pollinator community on a weekly basis to obtain a reliable estimate of local insect densities, independent of flower density and weather conditions, which naturally vary throughout the season. To achieve this, insects were captured by sweep-netting vegetation rather than focusing solely on those observed on flowers. Three parallel transects of 50 m each (150 m total per site) were established within each of the 22 study sites. During the survey, an observer walked along the transects and swept the vegetation using an insect net (Ø 40 cm). Captured insects were transferred individually into Eppendorf tubes containing 70% ethanol after every 16 m of transect (one-third of a 50 m transect length). Sweep-netting continued until either 50 insects were captured or 450 m of transect had been walked. If the first round did not yield 50 insects, the transects were repeated. Insect density was estimated by dividing the number of collected insects by the length of the transect walked to capture them. We use insect density (insect m⁻¹) to describe local insect abundance.

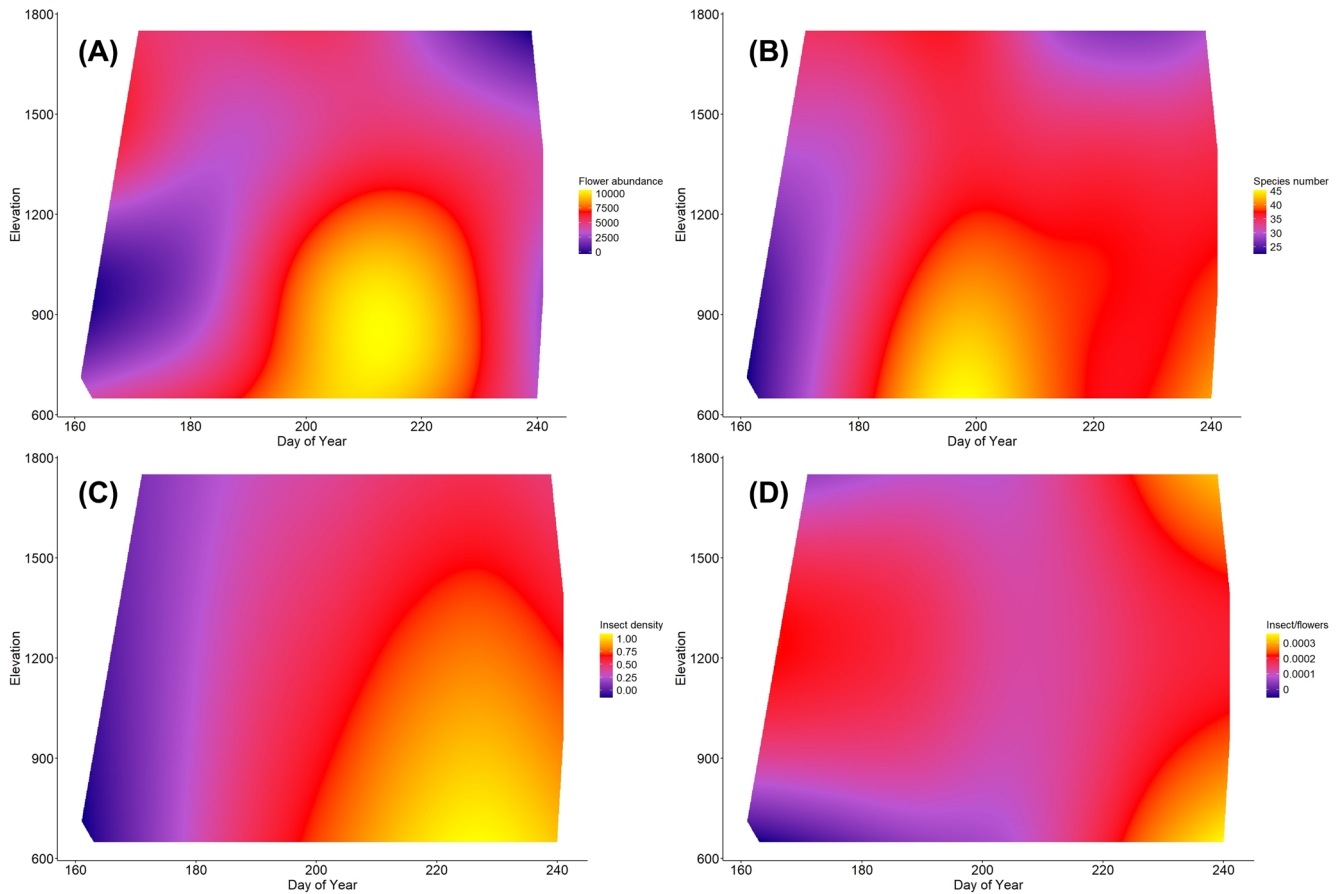


Figure 1. Predicted changes in flower abundance (A), number of flowering species (B), insect density (C; insects per 1 m of transect walk), and pollinator availability (D; insect-to-flower ratio) as functions of elevation and day of the year. The y-axes show elevation (m a.s.l.), and the x-axes show day of the year (Julian date) along the elevation gradient. Yellow and red indicate high values, while purple and blue indicate low values. Heatmaps are based on GAMM predictions. The outlined area represents the spatial and temporal limits of sampling. Details of the models are provided in the Supporting information.

Only insect groups known to actively visit flowers (Diptera, Coleoptera and Hymenoptera) and with a body size larger than 5 mm were collected, as larger insects have a higher potential for pollen transport. Lepidoptera were excluded for practical reasons (low abundance and large body size). Pollinator surveys were conducted on the same dates as flower counts, except during the first flower survey, when pollinators were not sampled due to low densities. This resulted in 6–9 pollinator surveys throughout the growing season.

Because weather and temperature strongly influence pollinator activity (Goodwin et al. 2021), insects were captured between 10:00 and 4:00 h, excluding periods of poor weather (e.g. rain or high winds). We acknowledge that this method does not specifically target pollinators or particular plant–pollinator interactions, and not all captured insects can be confirmed as pollinators. Nevertheless, we use the term ‘pollinator’ throughout the text, as the vast majority of captured insects belonged to groups observed visiting flowers during fieldwork. When tracking phenological patterns over the growing season, this method proved robust to variation in insect activity caused by seasonal weather conditions.

To allow direct comparison of flowering plant and pollinator communities, surveys for both groups were always conducted on the same day at each site. To maintain consistent sampling intervals, sites were always surveyed in the same order each week. Pollinators were identified to morphological groups according to the Swiss national fauna (www.infofauna.ch), with family-level identification used in the analyses. As with the flowering plants, we quantified the site-specific temporal niche overlap between flowering species and their pollinators.

Statistical analyses

All statistical analyses were conducted in the R ver. 4.0.3 (www.r-project.org). We examined the effects of time of season and elevation on flower abundance, number of flowering species, pollinator density (measured as pollinators caught per meter of transect), and pollinator availability (the ratio of pollinators to flowers, calculated as daily pollinator abundance divided by flower abundance). Because the response variables were expected to show non-linear patterns over the course of the season (e.g. flower abundance typically peaks in

mid-season), we fitted four generalized additive mixed-effect models (GAMMs). The response variables were flower abundance (model A), number of flowering species (model B), pollinator density (model C), and pollinator availability (model D, summary of the models in the Supporting information).

In all four models, day of year was included as a smooth term, elevation as a linear covariate (we first tried fitting models with elevation as a smooth term, but they resulted in linear fits), and an interaction between day of year and elevation was added (a tensor product interaction, ti). The random-effect structure accounted for study site nested within meadow. The models were fitted using a Gaussian error distribution. The number of daily samples was 210 for models A and B, and 186 for models C and D (Supporting information). The models were fitted using the R package 'mgcv' (Wood 2017).

We estimated phenological shifts of flowering species along the elevation gradient by modeling the mean date of flowering as a function of elevation separately for each species using the glm function and Gaussian error distribution. Flowering species recorded at three or fewer study sites were excluded from the analysis (summary in the Supporting information).

To examine the potential for competition for pollinators among plant species, we first characterized site-specific temporal niche overlap between flowering species, as well as between flowering species and their pollinators, using Schoener's index (SI; Schoener 1970). SI measures pairwise niche overlap of two entities based on discrete observations. Formally, SI is calculated as

$$SI = 1 - \frac{1}{2} \sum_i |p_{ji} - p_{ki}|$$

where p_{ji} and p_{ki} are the normalized flower abundances of species j and k on day i (weekly count divided by the season total at the site). SI ranges from 0 to 1, with higher values indicating greater overlap.

Next, we analyzed changes in SI values at the community level along the elevation gradient using SI values of all species pairs at each study site. For this, we fitted generalized linear mixed-effect models (GLMMs) using the 'brms' package (Bürkner 2017), with SI as the response variable, elevation as a fixed effect, and study sites nested within meadows as a random effect. To distinguish the effects of species' flowering phenology on temporal niche overlap along the elevation gradient, we fitted a separate GLMM including elevation, species' flowering phenology (averaged across all study sites), and their interaction as fixed effects, with SI as the response variable.

To analyze temporal matching between flowering species and pollinators along the elevation gradient, we calculated SI between flowering species and different pollinator groups. We then fitted GLMMs with elevation as a fixed effect and SI as the response, separately for all pollinators and for the groups Coleoptera, Diptera, Hymenoptera, Muscidae, Syrphidae and Anthophila. Depending on the SI values used in a given analysis, we applied beta, zero-inflated beta,

or zero-and-one-inflated beta distributions for the response variable. Otherwise, default package settings were used. We ran two Markov chain Monte Carlo (MCMC) chains for 1000 iterations with a 500-iteration warm-up, resulting in 500 posterior samples. Chain mixing and posterior distributions were visually inspected. All code and data to replicate the analyses are available at <https://github.com/MikkoTiusanen/Calandal>.

Results

Effects of elevation and seasonality on flowering and pollinator abundance

To quantify the spatial and seasonal patterns in local communities of flowering plants and their pollinators, we counted 1 177 396 flowers belonging to 163 taxa (Supporting information) and captured a total of 9707 insect individuals (hereafter 'pollinators', Supporting information) during 210 visits to the 22 study sites. Of the pollinators, 17.9%, 50.9% and 31.2% belonged to the orders Coleoptera, Diptera and Hymenoptera, respectively. Sixteen flowering species were found on all study sites, and 39 species were present on all meadows. On average, these species accounted for 46.4% (range: 27.3–69.2%) and 73.0% (range: 39.5–90.1%) of the local flowering community at the site and meadow level, respectively. In contrast, 24 species were found on only a single study site, and 40 species occurred on only one meadow.

The elevation gradient influenced both flowering plant and pollinator communities (Fig. 1, Supporting information). Overall flower abundance (model A: slope = -3.16 flowers/m, $t_{210} = -2.02$, $p = 0.045$, Fig. 1A, Supporting information), number of flowering species (model B: slope = -0.0064 species/m, $t_{210} = -2.89$, $p = 0.0043$, Fig. 1B), and pollinator density (model C: slope = -3.69×10^{-4} insects per meter of transect per meter of elevation, $t_{186} = -3.98$, $p = 1.00 \times 10^{-4}$, Fig. 1C) all declined significantly with increasing elevation. In contrast, elevation did not significantly influence pollinator availability (model D: slope = 4.43×10^{-9} insects per flower per meter, $t_{186} = 0.09$, $p = 0.93$, Fig. 1D).

All non-linear temporal patterns were significant for flower abundance, number of flowering species, pollinator density and pollinator availability (Fig. 1, Supporting information). Elevation and day of the year also showed significant interactions affecting flower abundance, species number, and pollinator availability. Peak flower abundance, species number, and pollinator density occurred mid-season and at lower elevations. The number of flowering species peaked first, followed by flower abundance and pollinator density, with the peak pollinator density occurring approximately two weeks after the flowering peak. Both flowering species number and pollinator density declined less sharply toward the end of the season compared to flower abundance. Because flowers and insects showed different phenological responses, pollinator availability was relatively low early in the season and during the flowering peak, reaching its highest values toward the end of the flowering season.

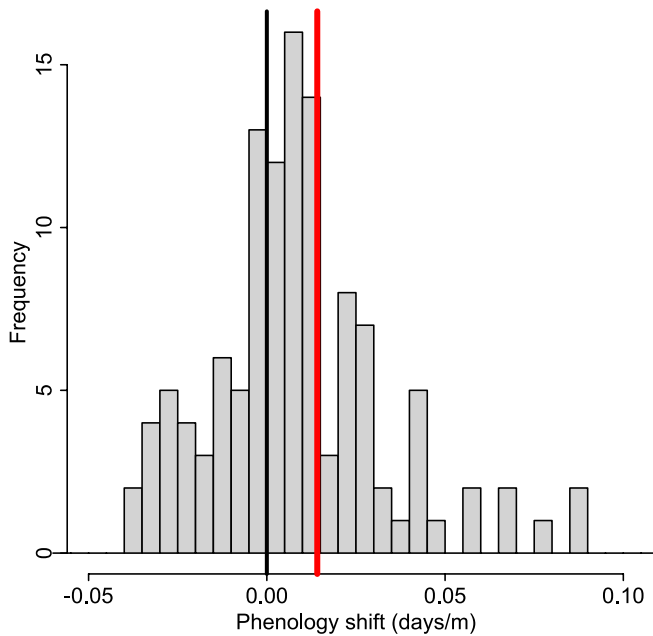


Figure 2. Distribution of shifts in flowering phenology along the elevation gradient. The grey histogram shows phenological responses to elevation across 123 flowering plant taxa, based on linear models where mean flowering date is explained by study-site elevation. The black vertical line indicates no phenological shift with elevation. On average, flowering is delayed by 1.41 days per 100 m increase in elevation, shown by the red vertical line (the scale on the axis is days per meter).

Effects of elevation on flowering species phenology

On average, the flowering of the observed plant species was delayed by 1.4 days per 100 meters of elevation gain (Fig. 2). However, species-specific responses varied, ranging from substantial delays to considerable advancements in flowering times.

Effects of elevation on phenological synchrony within flowering community and between flowering community and pollinators

At the community level, the average phenological overlap among flowering species did not differ along the elevation gradient when measured as the mean estimated effect on Schoener's index (odds ratio, $OR=1.05$, 95% credibility interval [95%-CI]=0.92–1.18, Supporting information). When the statistical interaction between elevation and the mean flowering date of the species was included as a fixed effect to explain niche overlap, early-flowering species showed increasing phenological overlap with increasing elevation, whereas late-flowering species exhibited the opposite pattern (Fig. 3A, interaction of elevation and phenology: $OR=0.061$, 95%-CI=0.047–0.080, Supporting information).

Phenological overlap between flowering species and pollinators increased with elevation ($OR=1.0003$, 95%-CI=1.00–1.0007, Fig. 3B, Supporting information). This pattern of increasing synchrony with elevation was consistent for Coleoptera and Diptera ($OR=1.0004$,

95%-CI=1.00–1.0009, and $OR=1.0003$, 95%-CI=1.00–1.0009, respectively, Fig. 3C, Supporting information), whereas the qualitatively similar trend for Hymenoptera was not significant ($OR=1.00$, 95%-CI=0.999–1.001, Fig. 3B, Supporting information). Although all pollinator subgroups analyzed showed a tendency toward increased niche overlap with flowering plants at higher elevations, none of these trends were statistically significant (Supporting information).

Discussion

To examine the effects of climate on complex communities, we measured spatial and temporal shifts in communities of flowering plants and their pollinators, as well as the synchrony between these two guilds, along an elevation gradient. Although our study is limited to a single growing season and the phenological patterns should be interpreted with caution, as they may vary between years, we next discuss the conclusions that can be drawn from our observations. We found that the number of flowering species, as well as flower and pollinator abundance, decreased with increasing elevation, while pollinator availability remained constant (Fig. 1). Additionally, strong seasonal variation was observed in the number of flowering species and the abundance of flowers and pollinators, with pollinator availability increasing toward the end of the growing season (Fig. 1). We also detected an overall delay in the phenology of flowering species along the elevation gradient, although individual species showed substantial variation in their responses (Fig. 2). Our results suggest that flowering phenology and niche overlaps with other flowering species respond to abiotic factors (e.g. temperature, season length) along the studied elevation gradient, and the variation in these responses can potentially be mediated by biotic factors (e.g. competition with co-flowering species, pollinator availability). Based on our analyses, the relative importance of the abiotic and biotic factors might be shifting within the studied gradient. Specifically, early-flowering species showed a shift from smaller to larger phenological overlaps along the elevation gradient, whereas late-flowering species exhibited the opposite pattern, shifting from larger to smaller overlaps (Fig. 3A), potentially indicating a shift from more biotic to abiotic determination of flowering phenology when moving up in elevation. Finally, we observed an overall increase in phenological overlap between flowering plants and their pollinators along the elevation gradient (Fig. 3B–C). Below, we discuss these results in more detail.

Effects of elevation and seasonality on flowering and pollinator abundance

Following our expectations and general biogeographical patterns (Grytnes and McCain 2007, McCain and Grytnes 2010, Lara-Romero et al. 2019), the studied communities showed a decrease in flower diversity and abundance, as well as in insect abundance, toward higher elevations (Fig. 1A–C). The constant pollinator availability along the elevation gradient (Fig. 1D) may reflect a causal relationship between

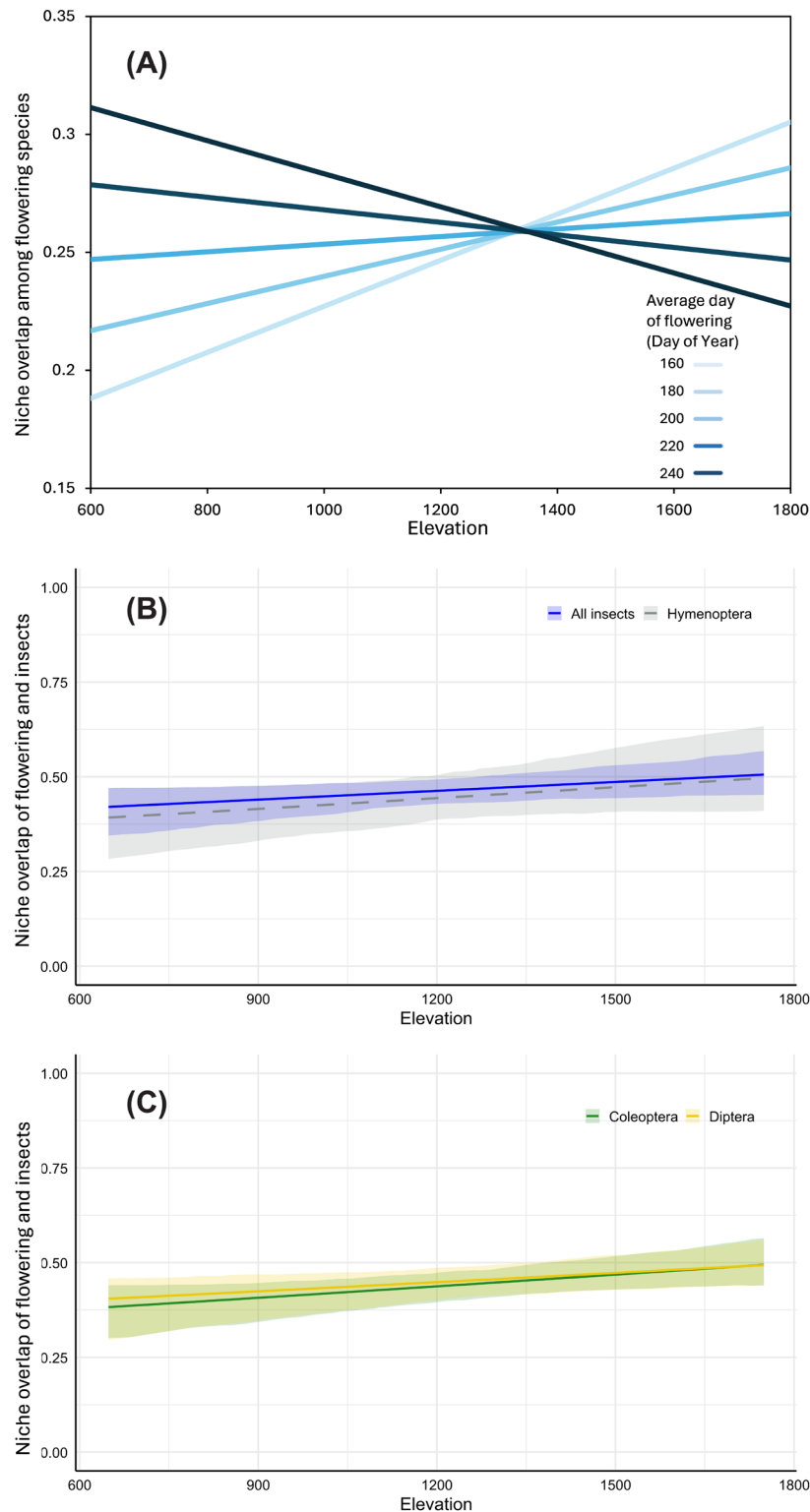


Figure 3. Phenological overlap among plant species (A) and between plants and pollinators (B, C) as a function of elevation. The y-axes show niche overlap using Schoener's index values, and the x-axes show elevation (m a.s.l.). (A) illustrates how average flowering phenology modifies the effect of increasing elevation on SI. Shades of blue, from light to dark, represent early- to late-flowering species. In (B), blue and grey lines represent the predicted mean SI of plants with all pollinators (blue, front) and with Hymenoptera (grey, background). In (C), green and yellow lines represent the predicted mean SI of plants with Coleoptera (green, front) and Diptera (yellow, background). Shaded areas in (B) and (C) indicate the 95% credibility intervals of the predicted means, and solid lines denote significant relationships. A summary of the models is provided in the Supporting information.

flowering plant and pollinator abundances: available pollination services may limit the populations of some flowering species (Biesmeijer et al. 2006), or floral resources may constrain the maximum number of pollinators (Westphal et al. 2003, Steffan-Dewenter and Schiele 2008). It is also possible that these two trophic layers respond independently but similarly to environmental variation. Taken together the lower pollinator density but constant pollinator availability towards higher elevations, our results might indicate that the general pattern of decreased visitation rates towards colder environments (Olesen and Jordano 2002) would be caused by decreased activity of individual pollinators, e.g. through lower activity levels in lower temperatures or changes in pollinator species pool (McCabe and Cobb 2021).

We observed the expected mid-season peak in flower and pollinator abundance and in the number of flowering species, typical of seasonal systems (Fig. 1A–C, Elzinga et al. 2007, Fernandez-Conradi et al. 2020). However, elevation significantly modified these shape and magnitude of seasonal patterns and caused the seasonal variation to be stronger at lower elevations. In our study, pollinator abundance and the number of flowering species did not decline sharply after the peak. Meanwhile, pollinator availability increased toward the end of the season (Fig. 1D). This creates a potential resource–fitness tradeoff for plants (MacTavish and Anderson 2020): fewer pollinators are available early in the season, making successful pollination more difficult, whereas later flowering increases the likelihood of encountering pollinators. However, early in the season, more resources (e.g. nutrients, water and time for seed production) are typically available, making late flowering risky as it limits opportunities to produce viable seeds before the end of the growing season (Kudo and Hirao 2006, Kehrberger and Holzschuh 2019).

Because higher elevations shorten the growing season, one might expect an earlier flowering phenology, which could increase pollinator sharing between early-season plants resulting in increased competition for pollinators. Indeed, our results on the magnitude of niche overlap among flowering species might suggest that early-flowering species face greater niche overlap at higher elevations compared to late-flowering species (Fig. 3A). Additionally, the higher availability of pollinators later in the season may partially support later flowering phenology in some species, even though this is generally considered an evolutionarily inferior strategy compared to early flowering (Austen et al. 2017).

Effects of elevation on species phenology

The delayed overall phenology of flowering species with increasing elevation (Fig. 2) is consistent with general patterns in which phenological events are postponed by later snowmelt and lower temperatures (Iler et al. 2013a). Although a warming climate generally advances flowering phenology, individual species may respond differently. For example, a long-term study of flowering phenology across 39 years found an overall advancement, but species-specific responses ranged from substantial advancements to slight delays (CaraDonna et al. 2014). Our results along the elevation gradient mirror this

pattern: despite an overall advancement of phenology at lower, warmer elevations, we observed species-specific shifts ranging from advancements to delays (Fig. 2). This suggests that climatic responses are not always linear, and that other factors (e.g. biotic interactions) may also influence the local phenology of species along the gradient (Rathcke and Lacey 1985, Ehrlén 2015, Elzinga et al. 2007). Such uneven phenological shifts have the potential to alter species interactions within the community.

Because grazing at our study sites proceeds from low to high elevation over a few weeks, roughly tracking meadow phenology, it is possible that grazing contributed to some of the observed flowering patterns. However, since species-specific responses ranged from advancements to delays (Fig. 2), and because phenological position did not determine response (i.e. early-flowering species were not consistently delayed while late-flowering species were unaffected), we consider it unlikely that grazing explains the overall patterns observed.

Effects of elevation on phenological overlap within flowering community and between flowering community and pollinators

We did not observe shifts in community-level phenological overlap in flowering along the elevation gradient (Supporting information), which contradicts our expectation of stronger overlap in the shorter growing season at higher elevations. However, species' flowering phenology modified niche overlaps along the gradient: the highest overlaps shifted from late-flowering species at low elevations to early-flowering species at high elevations (Fig. 3A). This pattern may indicate a shift in the main driver of flowering phenology – from competition for pollination at low elevations to limiting environmental conditions at high elevations.

In the shorter flowering season of high elevations, the costs of late flowering increase, as the risk of failing to produce viable seeds before snowfall is greater (Kudo and Hirao 2006). This may result in greater niche overlap among early-flowering species at high elevations. Moreover, in these harsher environments, the effects of aggregated flowering phenology – and the resulting potential for competition for pollinators – may be less important when plant populations and reproduction are more strongly limited by abiotic conditions than by pollination competition (Callaway et al. 2002).

As expected, plant–pollinator phenological overlap increased with elevation (overall, and within Coleoptera and Diptera, but not significantly within Hymenoptera or the tested pollinator sub-groups, Fig. 3B–C, Supporting information). These results suggest that pollinator activity periods align more closely with flowering seasons in the colder, shorter growing seasons at high altitudes. However, we did not observe a significant increase in synchrony between Hymenoptera and flowering along the elevation gradient. This may be partly explained by a community shift from bee-dominated, flower-resource-dependent Hymenoptera at low elevations to more wasp-dominated communities at higher elevations. Hymenoptera at high elevations tend to visit flowers primarily for their own nutrition rather than to provision

offspring, and thus require fewer floral resources throughout their life cycle. Consequently, temporal alignment with floral resources is likely less critical.

It is well established that pollinators in arctic and alpine regions are more generalized than those at lower latitudes and elevations (Elberling and Olesen 1999, Olesen and Jordano 2002). Based on our observations, this increased generalism may be driven by the greater temporal niche overlap between flowering plants and pollinator communities in the shorter growing season.

The potential effects of climate change on flowering plants

The differing shifts in niche overlap between early- and late-flowering species along the elevation gradient provide a potentially important mechanism for explaining patterns in flowering phenology and species distributions, particularly in the context of climate change. In high-elevation communities, where growing seasons are shorter, many plants flower early despite reduced pollinator availability – and therefore greater potential for pollinator sharing and competition – because delaying flowering greatly increases the risk of failing to set seed (abiotic control; Kudo and Hirao 2006). In contrast, at low elevations the environmental risks of late flowering are reduced, and later flowering becomes favored as it coincides with higher pollinator availability (biotic control). This is consistent with the general reduction in the relative importance of biotic interactions in colder climates reported in a recent systematic review (Paquette and Hargreaves 2021).

These results provide a valuable basis for understanding how plant–pollinator communities may change under a warming climate and an extended growing season. At high elevations, maximizing the time available for seed production will likely become less critical. Our findings suggest that late-flowering species may gain an advantage in colonizing high-elevation systems as their reproductive strategy becomes more favorable under relaxed competition for late-season pollinators. Indeed, invasive plants often display later flowering phenology (Lázaro-Lobo et al. 2025). Thus, as the climate warms and the growing season lengthens, late-flowering species at low elevations and latitudes may gain a competitive advantage over earlier-flowering species at higher altitudes and latitudes, further promoting their dispersal into new areas.

As expected, we also found delayed flowering in the colder climates of higher elevations, although species-specific responses varied. These changes in the relative timing of flowering alter the identity of competitors for pollination services. Because climate change drives heterogeneous shifts in phenology among species, future scenarios raise concerns about novel biotic interactions. Combined with changing abiotic conditions, these shifts could undermine the functioning of current plant–pollinator networks (Rafferty et al. 2016). While Fisogni et al. (2022) reported decreasing flowering synchrony with climate change, we found no consistent community-level pattern in synchrony along the elevation gradient. However, as noted above, the phenological position of species (early versus late flowering) strongly influenced their

shifts in synchrony and thus may determine the magnitude of their responses to climate warming.

Conclusions

In line with our expectations and previous findings, the communities of flowering plants and their pollinators changed considerably along the studied elevation gradient (Hoiss et al. 2015, Lara-Romero et al. 2019, Fernandez-Conradi et al. 2020) and elevation also modified the seasonal patterns of these communities. At higher elevations, we observed fewer flowers, fewer flowering species, and a later onset of flowering. Although elevation did not influence overall pollinator availability (insect-to-flower ratio) across the season, within the growing season we detected a marked temporal mismatch: pollinator abundance peaked later than the flowering peak, resulting in higher pollinator availability toward the end of the season. This seasonal disproportion in flowering and pollinator activity may explain why many species followed a later flowering schedule, contrary to expectations that earlier flowering would be favored (Austen et al. 2017). Moreover, the elevation gradient revealed contrasting shifts in flowering niche overlap between early- and late-flowering species, potentially suggesting a shift in the primary driver of phenology – from competition for the shared pollination at low elevations to abiotic constraints at high elevations.

Currently, the growing season in the European Alps is already lengthening (Vitasse et al. 2018), and plant species are migrating upward toward colder environments (Parolo and Rossi 2008, Rumpf et al. 2018). Our findings imply that under continued warming and longer growing seasons, typical early-flowering species at high elevations and latitudes may be disadvantaged compared to late-flowering species from lower elevations and latitudes. The latter, adapted to longer seasons, are likely to gain an advantage as their reproductive strategies become more favorable in novel conditions. Such shifts in phenological niches and synchrony have the potential to strongly influence the fitness of interacting species and reshape community composition. Therefore, phenological dynamics should be more explicitly integrated into considerations of species niches, distributions, ecological networks and conservation strategies – particularly in the context of ongoing climate change.

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Author contributions

Mikko Tiusanen: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal);

Methodology (lead); Project administration (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Anna Norberg:** Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Software (supporting); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Anna-Liisa Laine:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (lead); Validation (supporting); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (equal);

Data availability statement

Data are available from Github: <https://github.com/MikkoTiusanen/Calanda1>.

Supporting information

The Supporting information associated with this article is available with the online version.

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